Australian Echinoderms

BIOLOGY, ECOLOGY AND EVOLUTION

Editors: Maria Byrne
and Timothy D. O'Hara



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Plate 1 ***Linckia laevigata*** (Ophidiasteridae), the blue seastar, grazing biofilm and algae on the shallow reefs surrounding Lord Howe Island, Australia.

[J.Gilligan]



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Foreword

As one of the major phyla in the world's oceans, echinoderms are of considerable interest. Although systematic study of echinoderms in Australian waters did not begin until the first half of the twentieth century, studies since then have contributed greatly to understanding their importance. The geographic scope of this book is enormous. It considers echinoderms from around continental Australia including Tasmania, offshore islands including Macquarie Island, Lord Howe Island, Cocos (Keeling) Island, Australian External Territories including Christmas Island, Heard Island, Norfolk Island and the Australian Antarctic Territories, and the Australian Marine Exclusive Economic Zone. Consequently, the chapters on biology and ecology consider Australian echinoderms in a range of environments from the intertidal and shallow water to the deep sea, from the tropics to Antarctica. The book has splendid well-illustrated accounts of species of the families found in Australian waters. Here, the basic features, distribution, biology and ecology of each species are considered. Evolutionary relations within the phylum and the classes show complex relations. The scope and in-depth treatment of the species make this book important. The contents will be of interest in considering other species in the families in other geographical areas. This is a comprehensive book that compiles and synthesizes an immense amount of literature that makes it an authoritative account of Australian echinoderms in particular and echinoderms in general.

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Plate 2 Using long oral primary spines with a distal hoof, the bright and colourful fire urchin, ***Asthenosoma varium*** (Echinothuriidae), moves swiftly over tropical substrates. The shorter secondary spines on the aboral surface are often clustered together, bordered by venomous spines.

[C.Bryce]



Plate 3 The colobometrid ***Cenometra bella***, often seen clinging to sea whips, is found in the tropical waters of the east Indo-west-central Pacific including northern Australia. The crinoid's arms are not arrayed in the radial pattern typical of ***C. bella***, but that may be a function of weak current. The smaller feather stars partly obscured in the lower part of the image are likely to be ***Oligometra serripinna***, which also clings to sea whips and sea fans.

[F.Bavendam]

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Part 1:
Introduction to Echinoderms

1: Introduction

Maria Byrne

Echinoderms, what are they?

Seastars, sea urchins, brittle stars, feather stars and sea cucumbers are familiar animals commonly used to symbolise the marine environment (**Figs 1.1, 1.2**). With their distinct five-rayed profile and often brilliant colours, echinoderms form a conspicuous component of the invertebrate fauna of the ocean. Echinoderms are numerically dominant in many marine communities where they fulfil many ecologically important roles.

Five extant classes are recognised in the phylum Echinodermata: the Asteroidea (seastars and sea daisies), Ophiuroidea (brittle stars, basket stars and snake stars), Echinoidea (sea urchins, heart urchins and sand dollars), Holothuroidea (sea cucumbers) and Crinoidea (feather stars and sea lilies). Approximately 7,000 species of living echinoderms are described from across the world's oceans, of which some 1,400 are known from Australian waters. Echinoderms have a rich fossil record extending back to at least the Cambrian. Some 13,000 fossil species have been recorded with the richest diversity known from the Palaeozoic; many classes of extinct echinoderms are known only from the Palaeozoic era. The name Echinodermata is derived from the Greek for spiny, *ekhinos*, and skin, *derma*.

Several features define the Echinodermata, including the five-rayed (pentamerous) symmetry of adults, the distinctive water vascular system, a dermal skeleton which contains unique calcareous ossicles, mutable connective tissue and a bilateral larva (Byrne 2001). The five-rayed body organisation is seen most clearly in seastars and the test of regular sea urchins (**Figs 1.1C, 1.2D, 1.4**). The water vascular system is a complex hydraulic system of fluid-filled tubes or canals that includes the (locomotory) tube feet. It has a variety of functions including locomotion, respiration and excretion, and is considered to be a major evolutionary



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innovation of the Echinodermata. One of the most distinctive features of echinoderms is the presence of mutable connective tissue in the body wall where it connects parts of the skeleton and also serves as tendons connecting muscle and skeleton (**Box 1.1**). Mutable connective tissue, under neuronal control, can alter its physical state within a timescale of a second to a few minutes. These tissues may undergo reversible stiffening-softening changes when used for posture control or irreversible changes in which the connective tissue disintegrates resulting in autotomy, the detachment of body parts, such as when a seastar discards an arm in response to predatory attack (see **Chapter 2**). The calcareous skeleton lies beneath the surface tissue layer (**Fig. 1.5**), a feature that separates echinoderms from other invertebrate groups. The external surface of the skeleton also can have spines, tubercles and pedicellariae. Finally, they have a ciliated bilaterally symmetrical larva (see **Chapter 3**), an attribute that is important for understanding the relationships between echinoderms and other animals.

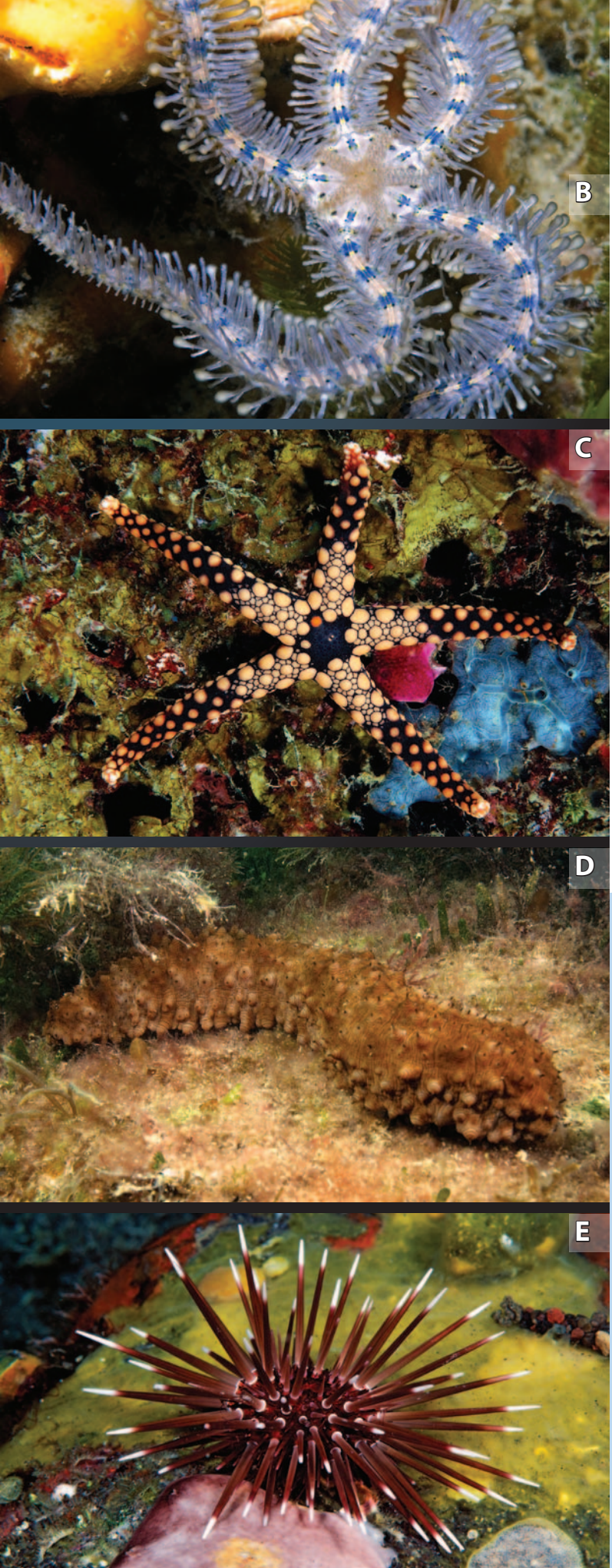


Figure 1.1 A group of striking animals some 7,000 species strong worldwide, living echinoderms are arranged into five distinct classes:

A, **Crinoidea** (feather stars), ***Himerometra robustipinna*** (Himerometridae).

B, **Ophiuroidea** (brittle stars), ***Macrophiothrix spongicola*** (Ophiotrichidae).

C, **Asteroidea** (seastars), ***Celerina heffernani***, (Ophidiasteridae).

D, **Holothuroidea** (sea cucumbers), ***Australostichopus mollis*** (Stichopodidae).

E, **Echinoidea** (sea urchins), ***Parasalenia gratiosa*** (Echinometridae).

[A,E, G.Bell; B,D, J.Finn; C, D.Harasti]

How to recognise the five classes

The five classes of extant echinoderms can be readily distinguished by their body shapes:

Ophiuroidea — brittle stars, basket stars and snake stars. Brittle stars have a distinctive simple star shape where the arms are usually clearly demarcated from a central disc. The arms move with a distinguishing whip-like action. Basket stars usually have more complex arms that repeatedly branch. Snake stars have long arms that coil around the substrate. Ophiuroids are mostly five-armed, but a few species are known to have six or more arms. **Figure 1.2A–C** and see **Chapter 9.**

Asteroidea — seastars, starfish and sea daisies. Seastars range from cushion- to star-shaped, with typically five or more radiating arms. Sea daisies are small disc-shaped animals with a ring of marginal spines; they have no radiating arms. **Figure 1.2D–F** and see **Chapter 8.**

Holothuroidea — sea cucumbers. Sea cucumbers have a fleshy, elongate, mostly sausage-shaped body. They are distinguished by their apparent secondarily evolved bilateral symmetry with three rows of tube feet (where present) on the 'ventral' surface and two on the 'dorsal' surface. **Figure 1.2G–I and see Chapter 11.**

Echinoidea — sea urchins, heart urchins and sand dollars. Typically, sea urchins are globular, but slightly depressed, with the surface of the body covered in spines. Heart urchins are somewhat more flattened and sand dollars are flattened to a disc. In general, sea urchins are either called regular echinoids or irregular echinoids. Regular echinoids have a globular test that is nearly perfectly pentaradiate; in irregular echinoids (sand dollars and heart urchins) the test is more elongate and flattened with an altered symmetry. **Figure 1.2J–L** and see **Chapter 10.**

Crinoidea — feather stars and sea lilies. Feather stars are distinguished by their feather-like profile; they have a central disc from which arise five or more flexible arms. Sea lilies are stalked crinoids. **Figure 1.2M–O** and see **Chapter 7.**

In spite of their diverse form, the bodies of all echinoderms typically are organised into five radii (ambulacrae) with intervening interradial regions (interambulacrae) (**Fig. 1.4**). Each radius has a nerve cord and a branch of the water vascular system from which arises the tube feet. The five-rayed pattern is clearly seen around the mouth of seastars, where the five radial canals diverge from the central mouth and are separated by interradial areas (**Fig. 1.4A**). Similarly, the sea urchin test is constructed of ten double rows of alternating ambulacral and interambulacral plates (**Fig. 1.4B**).

Among the characters that distinguish the classes of echinoderms there are differences in the water vascular system and the orientation of the mouth (**Fig. 6.2**). The oral or actinal and aboral or abactinal surfaces bear the mouth and anus, respectively. In seastars the radial water canal is external to the skeleton, running along grooves in each arm, the ambulacral grooves, on the aboral suface. This is called an open ambulacral system. In all other echinoderms the radial water canal is internal and so called a closed ambulacral system. Seastars, brittle stars and sea urchins have the oral surface closest (facing down) to the substratum, whereas feather stars have it directed upwards. Sea cucumbers can have an oral (actinal) surface that faces up or down.

Figure 1.2 The body forms of echinoderms.

A–C, Ophiuroidea – basket stars and brittle stars.
A, ***Gorgonocephalus chilensis***, basket star (Gorgonocephalidae).
B, ***Ophiopsammus assimilis***, brittle star (Ophiodermatidae).
C, ***Ophiomisidium flabellum*** (Ophiuridae).

D–F, Asteroidea – seastars and sea daisies.
D, ***Pentagonaster duebeni*** (Goniasteridae).
E, ***Crossaster multispinus*** (Solasteridae).
F, ***Xyloplax janetae*** (Xyloplacidae).

G–I, Holothuroidea – sea cucumbers.
G, ***Pseudocolochirus violaceus*** (Cucumariidae).
H, ***Chiridota gigas*** (Chiridotidae).
I, ***Molpadia bathycola*** (Molpadiidae).

J–L, Echinoidea – sea urchins and sand dollars.
J, ***Laganum depressum***, sand dollar (Laganidae).
K, ***Protenaster australis,*** heart urchin (Schizasteridae).
L, ***Salmacis sphaeroides***, regular urchin (Temnopleuridae).

M–O, Crinoidea – feather stars and sea lilies.
M, ***Neogymnocrinus richeri***, sea lily (Sclerocrinidae).
N, ***Saracrinus nobilis***, sea lily (Isselicrinidae).
O, ***Ptilometra macronema***, feather star (Ptilometridae).

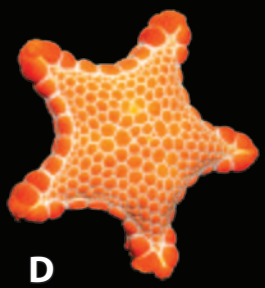
[A, B.Patullo; B,E,I,O, CSIRO; C, C.Harding; D, W.Boyle; F, C.Mah; G, A.Flowers & L.Newman; H, L.Altoff; J–L, A.D.Miskelly; M, N.Améziane; N, K.Gowlett-Holmes/CSIRO]

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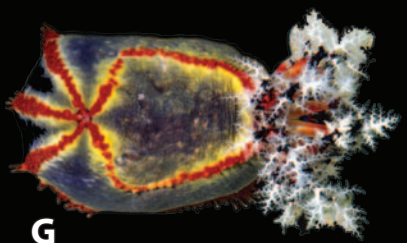

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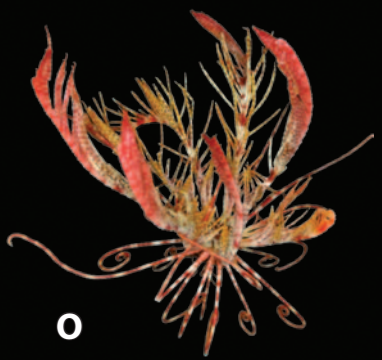

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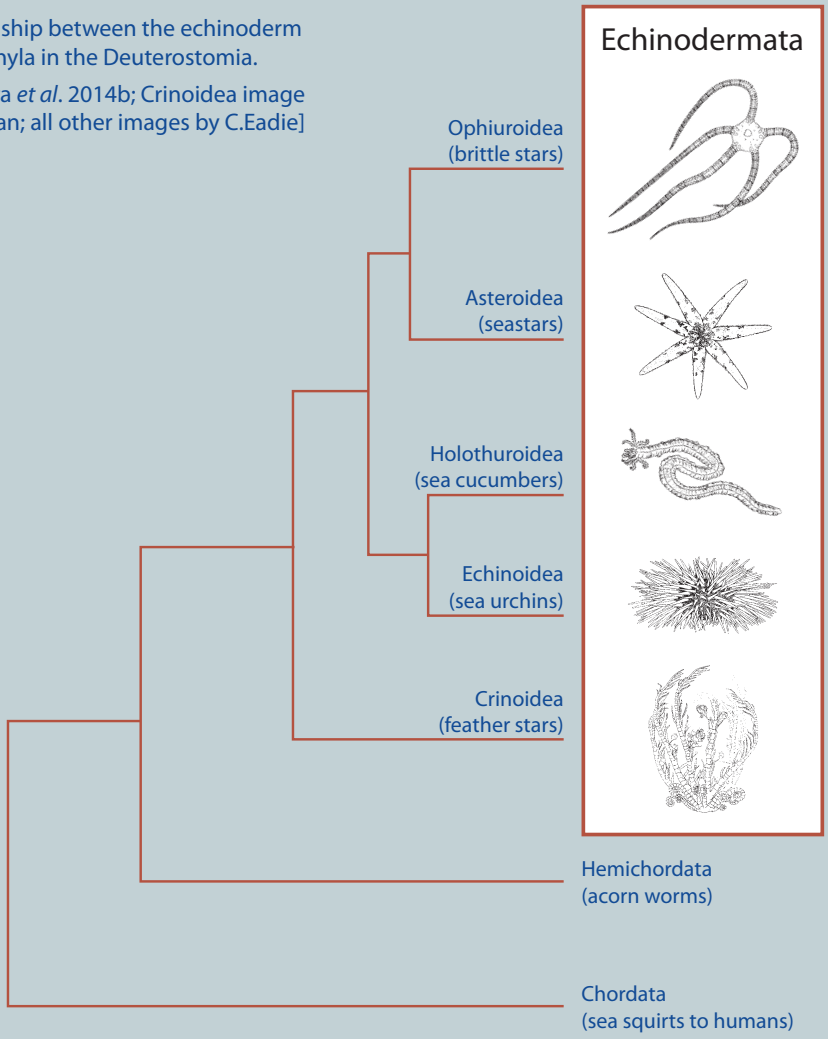


Figure 1.3 Relationship between the echinoderm classes and other phyla in the Deuterostomia.

[after O'Hara *et al*. 2014b; Crinoidea image by K.Nolan; all other images by C.Eadie]

Their place in the scheme of things

The Echinodermata, along with the Chordata (vertebrates) and the Hemichordata (acorn worms), are members of the Deuterostomia, a monophyletic group of multicellular organisms (Swalla 2006; Swalla & Smith 2008; Zamora *et al*. 2012; Byrne *et al*. 2016a; see also **Chapter 6**). Recent phylogenetic research has clarified the relationship between echinoderms and other deuterostomes and the class relationships within the Echinodermata (see Cannon *et al*. 2014; O'Hara *et al*. 2014b; Telford *et al*. 2014).

Although echinoderms have a unique adult pentameral morphology (**Fig. 1.4**), their deuterostome relationships are evident from their mode of development and the form of their bilaterally symmetrical larvae (see **Chapter 3**). Echinodermata and Hemichordata comprise the Ambulacraria, united by several features, including similar larval feeding methods (Byrne *et al*. 2006, 2007; Swalla 2006). These phyla form the sister group to the Chordata (**Fig. 1.3**). Bilateral symmetry, which includes a distinct anterior-posterior body axis,

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is the ancestral deuterostome body plan. Evolution of radial symmetry dramatically transformed echinoderms into what appear to be headless animals. Understanding the links between the radial echinoderms and other Bilateria is a challenge (Swalla & Smith 2008; Arnone *et al.* 2015; Byrne *et al.* 2016a). Fossils from the Cambrian indicate that the earliest echinoderms had bilateral symmetry, thus providing evidence of echinoderms evolving from a bilateral ancestor (Zamora *et al.* 2012).

Anatomy

With the exception of the digestive tract, the organisation of most anatomical structures of echinoderms reflects the five-rayed body plan. Reproductive anatomy is described in **Chapter 3**.

Body wall and skeleton

The body wall of echinoderms consists of a cuticle, epidermis and dermis that together form the integument, a muscle layer and the coelom lining. The integument is supported by a complex skeleton of plates or small elements known as ossicles, and connective tissue. The calcareous endoskeleton comprises mostly calcite with a high concentration of magnesium. The echinoderm endoskeleton has an unusual three-dimensional porous structure (**Fig. 1.5B**), of which the internal meshwork of interconnected spaces is known as a stereom. The stereom mesh (or spaces) is filled by cells and connective tissue. Adjacent skeletal plates typically are bound to and articulate with each other by collagenous ligaments. The structure of the endoskeleton is unique to echinoderms and differences in its morphology are important in echinoderm taxonomy.

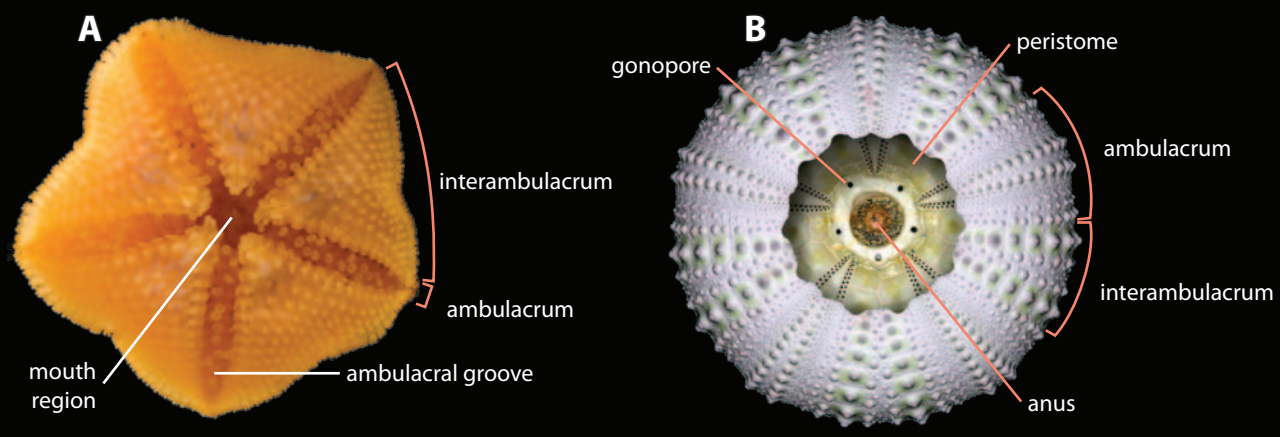


Figure 1.4 Pentamerous radial symmetry (a five-fold circular pattern) so characteristic of mature echinoderms is readily observed in the external features of seastars (Asteroidea) and the tests of sea urchins (Echinoidea).

A, oral (actinal) view of a seastar, ***Parvulastra vivipara*** (Asterinidae), showing the five ambulacral grooves and their associated tube feet. The tube feet lie along radii called ambulacra. The triangular regions between the ambulacral grooves are called interambulacra.

B, oral (actinal) view of a sea urchin test, ***Centrostephanus rodgersii*** (Diadematidae), showing the five ambulcra and five interambulacra all converging at the peristome; each ambulcrum and interambulcrum consists of a double column of plates. The ambulcra are perforated by pore-pairs for the tube feet.

[A, M.Byrne; B, A.D.Miskelly]

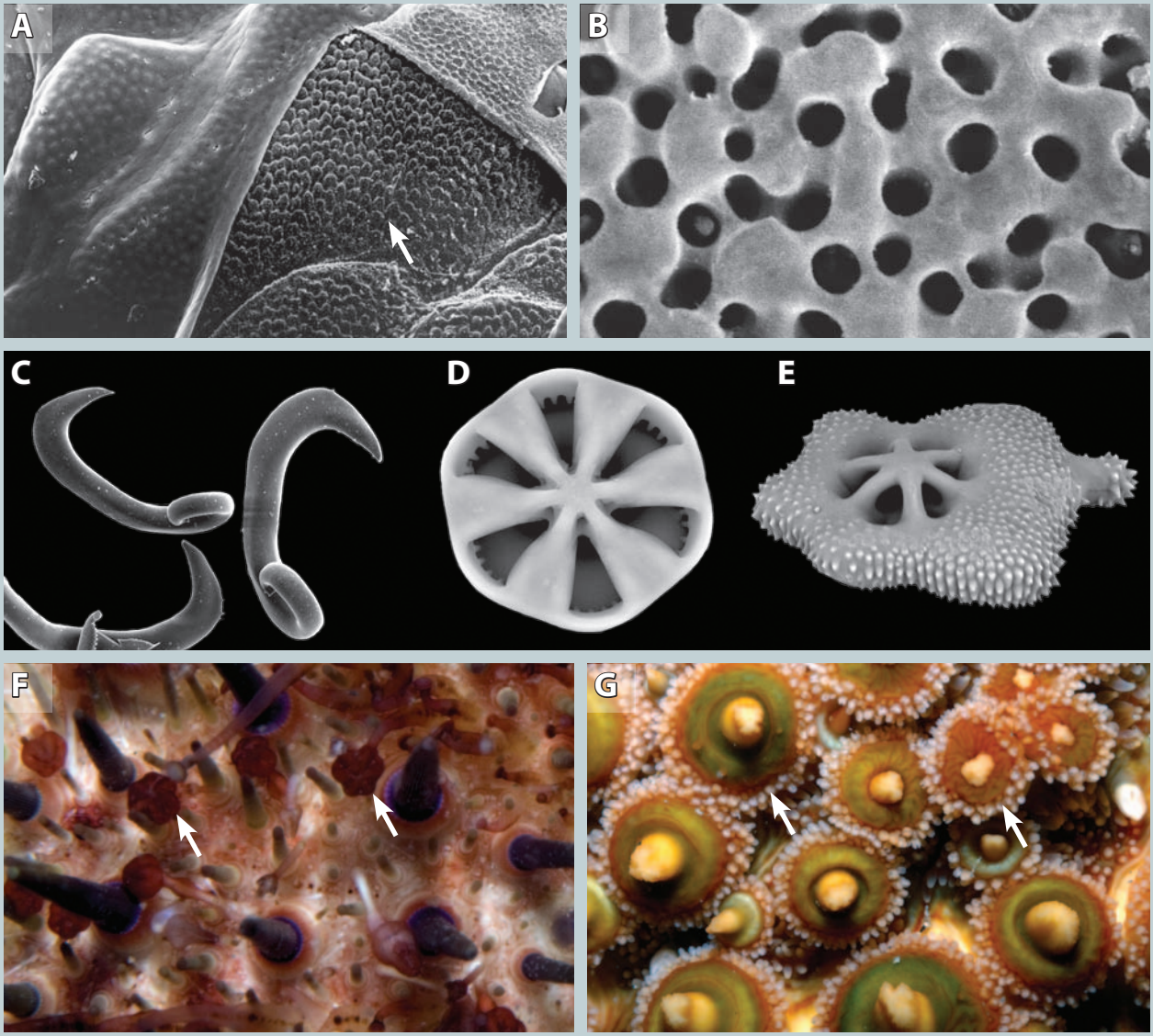


Figure 1.5 Skeletal elements of echinoderms.

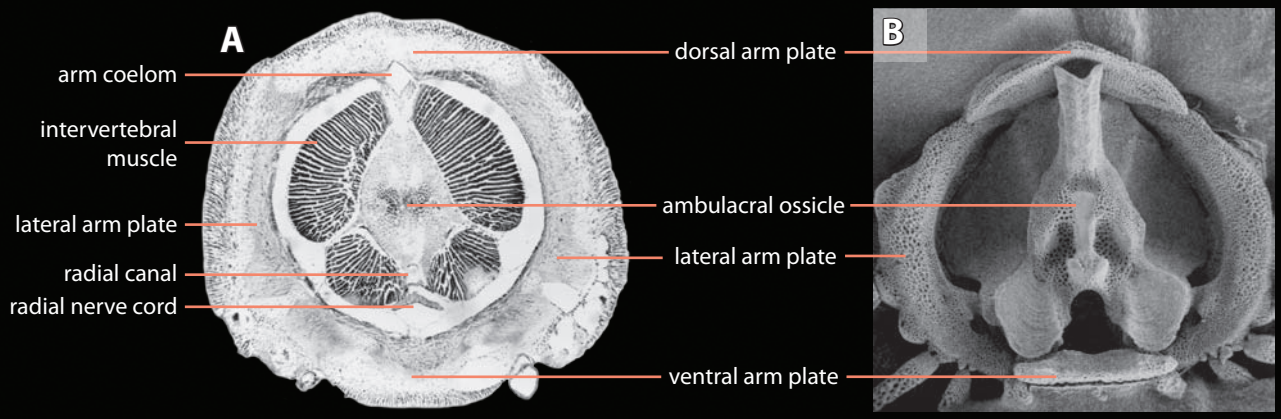
A, **B**, the calcareous skeleton of the brittle star ***Ophionereis schayeri*** (Ophionereididae):
A, skeletal plates (ossicles; see arrow) are revealed when the epidermis is removed from the abactinal surface.
B, microstructure of a plate showing the network of calcium carbonate which forms a three-dimensional porous structure known as a stereom. In life the spaces are filled with dermal cells and extracellular fluids, comprising the stroma.

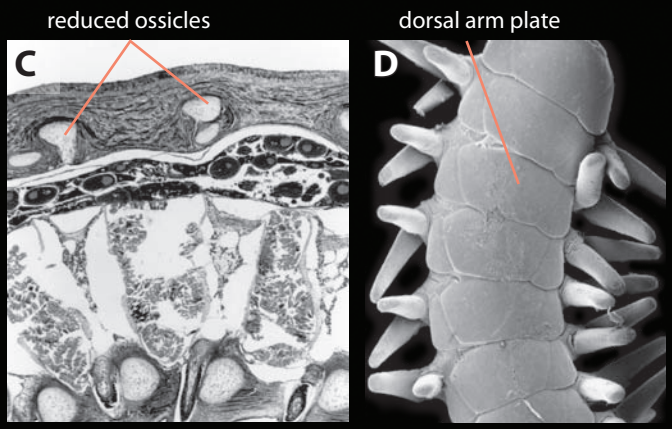
C–E, spicules found in members of the holothurian family Chiridotidae. These microscopic calcareous skeletal elements are present in the body wall of all sea cucumbers and can take widely different shapes, such as wheels, hooks, plates, C-shaped rods and tables; they are a key feature in distinguishing species of holothurians:
C, hook-shaped spicule of ***Taeniogyrus tantulus***.
D, wheel-shaped spicule of ***Taeniogyrus tantulus***.
E, derived wheel-shaped spicule of ***Archedota lapidea***.

F, **G**, pedicellariae, specialised pincer-like skeletal structures, are unique to the two echinoderm classes Asteroidea and Echinoidea:
F, a sea urchin with red tulip-like pedicellariae (arrows).
G, rings of pedicellariae surround the bases of spines of the seastar ***Coscinasterias muricata*** (Asteriidae).

[A, from Byrne 1994; B, M.Byrne, C–E, Museum Victoria; F,G, J.Finn]

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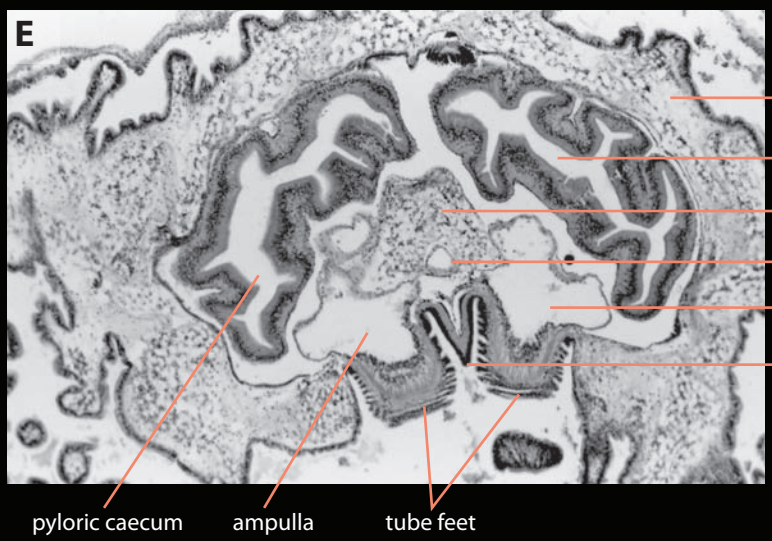


Figure 1.6 Organisation of ophiuroid and asteroid arms.

A, cross-section of an arm of the ophiuroid ***Ophiarachnella ramsayi*** (Ophiodermatidae) showing muscle and skeletal plates.

B, scanning electron micrograph of the arm plates of the ophiuroid ***Ophiothrix fragilis*** (Ophiotrichidae) showing the central ambulacral ossicle surrounded by the dorsal, ventral and two lateral arm plates.

C, longitudinal section of an arm of the snake star ***Astrobrachion constrictum*** (Euryalidae) showing the reduced plates (arrow) embedded in the body wall tissue.

D, scanning electron micrograph of the abactinal surface of the arm of the ophiuroid ***Ophionereis schayeri*** (Ophionereididae) showing the segmented appearance of the large arm dorsal plates.

E, cross-section of an arm of the asteroid ***Parvulastra parvivipara*** (Asterinidae) showing internal structures, the two pyloric caeca part of the digestive tract, the radial nerve cord, tube feet and arm skeleton.

[A,E, from Byrne 2001b; B, from Stauber & Märkel 1988; C, M.Byrne; D, from Byrne 1994]

Box 1.1 Mutable connective tissues: autotomy and catch

An extraordinary and unique feature of echinoderms is their highly specialised mutable connective tissue (MCT), which can undergo rapid, nerve-mediated changes in its mechanical properties. From less than a second to a few minutes, mutable connective tissue can switch between stiffened and compliant states. In extreme events tissue disintegration occurs resulting in autotomy, discarding body parts. In the past, it was assumed that this tissue comprised specialised muscles, but microscopic examination revealed its collagenous, ligament-like nature. Mechanical change in MCTs results from an alteration in the matrix that supports the collagen fibres. Nerve-like processes associated with the tissue are thought to contain a secretory product that gives rise to these changes. Mutability is controlled by an unconventional relationship between the nervous system and the extra-cellular tissue. The involvement of mutable connective tissue in posture control and autotomy reduces the need for energy-demanding muscle cells for these purposes. Two functions of MCTs that are of special interest are autotomy and catch.

Autotomy and Mutable Connective Tissue

Autotomy in echinoderms is caused by disintegration of MCT ligaments. Some ophiuroids, asteroids and crinoids discard or autotomise their arms quite readily, and some sea cucumbers expel (eviscerate) their internal organs following disintegration and detachment of autotomy ligaments (**Figs a–c**). These examples of autotomy are often defensive responses to disturbance. Movement by autotomised body parts distracts predators while the animal escapes. Ophiuroid arm autotomy is accomplished by the rapid breakdown of the autotomy ligament between arm segments, which can occur within one second. Asteroids and crinoids also discard their arms by rupture of specialised MCT ligaments. Splitting of the body during asexual reproduction is also the result of a softening of mutable connective tissue (see **Chapter 3**).

Catch Connective Tissues

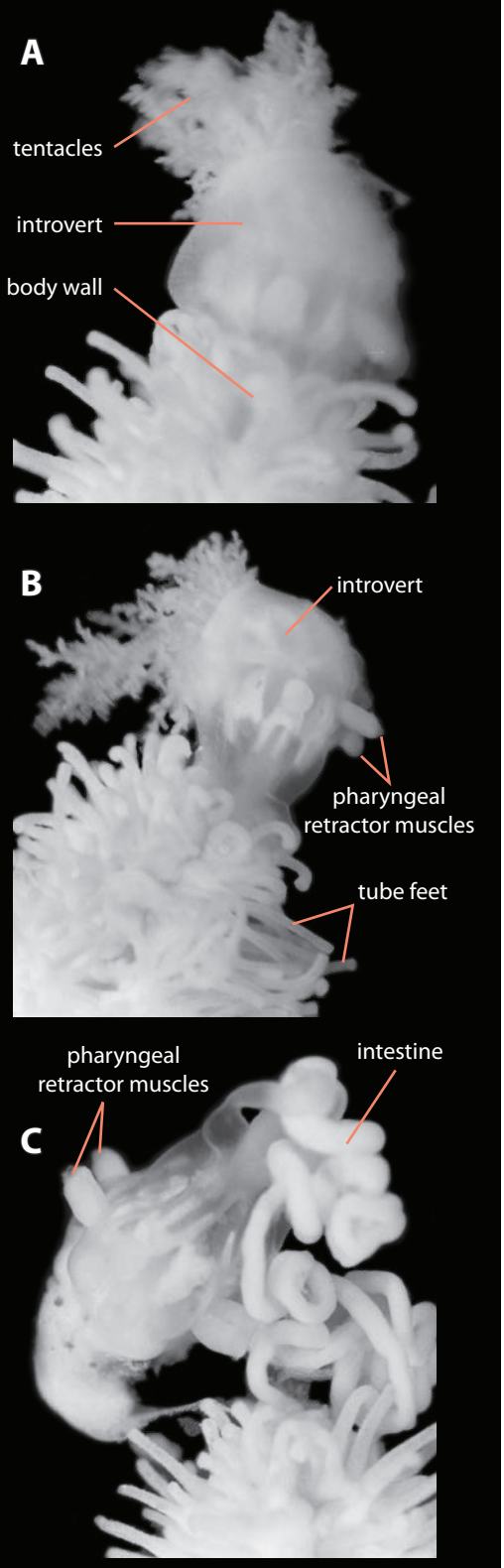
Catch connective tissues, another form of MCT, alternate between the extremes of pliant and extensible, and stiff and inextensible. These changes assist in the maintenance of posture — a stiff and rigid state fixes posture and a pliant state allows posture to be altered. The catch MCT ligament at the base of sea urchin spines is a well-known example. Urchin spines move by muscles and are then held rigidly in place by stiffening of the MCT. Spine catch assists urchins in maintaining their hold in crevices and burrows. Another example of the expression of changes in MCT is found in the sea cucumber body wall. Sea cucumbers in the pliant MCT state alter their body shape to fit into crevices and, once settled, lock their body in place by stiffening the MCT, thus making removal virtually impossible. The catastrophic disintegration of the body wall of the Indo-Pacific sea cucumber *Stichopus chloronotus* is a remarkable manifestation of MCT: if handled roughly, the body wall of this species essentially dissolves.

Further reading Byrne 1985a, 2001a; Fankboner & Cameron 1985; Motokawa & Tsuchi 2003; Wilkie 2005

Figures a–c, a sequence of evisceration in the dendrochirotid north and east Pacific sea cucumber, ***Eupentacta quinquesemita*** (Sclerodactylidae), which involves discarding the tentacular crown and digestive tract; such a process takes about 10 minutes. Most of the gonad, the paired respiratory trees and cloaca remain behind. Evisceration begins by the weakening and then separation of three main body structures: the introvert, the tendons attaching the pharyngeal retractor muscles to the longitudinal muscles (there are five of these; see **Fig. 1.17**), and the intestinal–cloacal junction.

[from Byrne 1985a]

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The extent of development of the skeletal surface varies among echinoderms. The skeleton may be adorned with various tubercles, granules and spines. In asteroids and echinoids, the skeleton also produces small pincer-like structures called pedicellariae (Chia & Amerongen 1975; Ghyoot *et al.* 1987, 1994) that are used in defence and feeding (**Figs 1.5F,G, 2.15, 8.6**). Pedicellariae impale small zooplankton, thereby preventing settlement of fouling organisms. Some asteroids use these structures to catch prey, including small fish. Echinoid pedicellariae have a long moveable stalk terminating in a three-pronged jaw. Spines and pedicellariae of some asteroids and echinoids can induce a painful toxic reaction if touched (**Fig. 2.15**).

Echinoderms vary greatly in their rigidity depending on the extent of development of the endoskeleton. Species with close-knit skeletal plates are relatively firm, whereas those with less densely packed skeletal plates are more flexible. Extremes of this arrangement are exemplified by sea urchins that have a rigid test of fused plates (**Fig. 1.4B**), and sea cucumbers that have a comparatively soft integument in which small skeletal elements called spicules are scattered (**Fig. 1.5C–E**). In crinoids the oral surface, called the tegmen, forms a soft cover with embedded small skeletal elements. The tegmen covers the cup-shaped calyx, the aboral skeleton that houses the body organs.

Echinoderms can be surprisingly nimble, as the connective tissue between skeletal plates allows flexibility for movement and postural change. This dexterity is facilitated by the unusual mutable properties of their connective tissues (**Box 1.1**). The extreme

Figure 1.7 The arms of crinoids are made up of large, well-developed, articulating ossicles which give them a segmented appearance externally (arrow). Each arm is edged with tiny structures called pinnules that give the animal its feathery form.

[J.Finn]

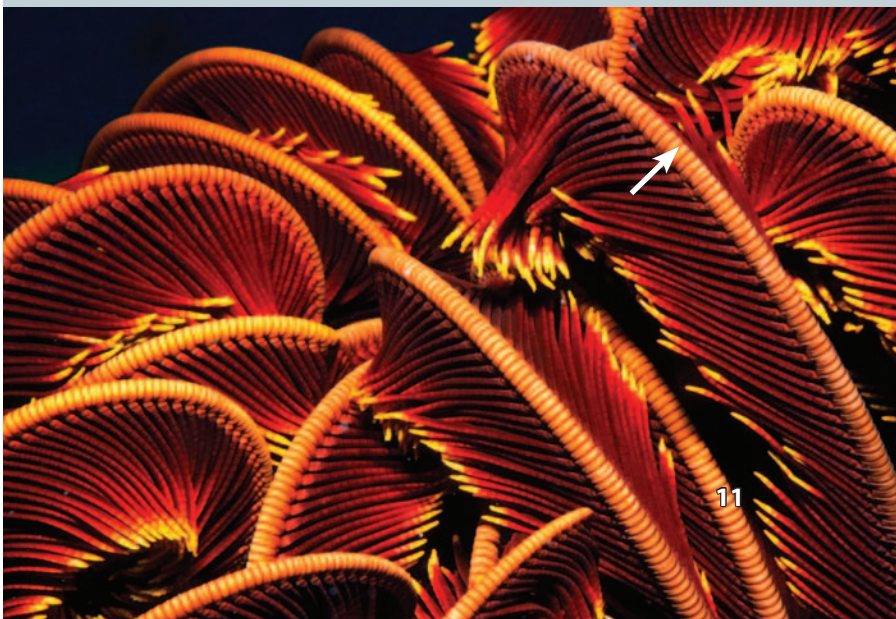




Figure 1.8 Digestion often occurs outside the body for many seastars (Asteroidea).

A, the red seastar ***Odontaster validus*** (Odontasteridea), with its stomach everted to graze the epiphytes growing on the seaweed *Desmarestia antarctica* in Antarctic waters.

B, **C**, the common Indo-Pacific eleven-armed seastar, ***Coscinasterias muricata*** (Asteriidae) is an avid predator of molluscs and mussels in particular (**B**). It also feeds on carrion (**C**) like these dead crabs shown here.

[A, B.Baker; B, D.Paul; C, M.Norman]

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example of connective tissue providing skeletal support is seen in sea cucumbers, where the skeleton is reduced to small spicules embedded in connective tissue (**Fig. 1.5C–E**).

Cross sections of asteroid and ophiuroid arms reveal the plates that support the body. In asteroids, the ambulacral plates protect the radial water canal (**Fig. 1.6E**). These plates are equivalent to the central arm plates (vertebrae) of ophiuroids. In ophiuroids the central arm plates are surrounded by the dorsal (abactinal), ventral (actinal) and lateral arm plates (**Fig. 1.6A,B**). In soft-skinned snake and basket stars the skeleton is reduced to small plates that are embedded in the integument tissue (**Fig. 1.6C**). In other brittlestar families these skeletal elements are well developed and give the arms a segmented appearance (**Fig. 1.6D**). Crinoid arms also have a segmented appearance due to the repeating series of ossicles that support them (**Fig. 1.7**).

Body wall musculature varies greatly in echinoderms. Asteroids and holothuroids, with the most dextrous bodies, have well-developed muscle bands. Echinoids, with their rigid tests, lack body wall muscles. Ophiuroids have a layer of muscle in the disc, but muscular support in the arms is derived largely from the muscles associated with the arm skeleton (**Fig. 1.6A**). In crinoids the major musculature is associated with the arms.

Feeding and digestive system

Echinoderms exhibit almost the full range of feeding strategies seen in marine invertebrates, and although they include predators, herbivores, suspension feeders, deposit feeders and scavengers, there are no parasitic echinoderms (Jangoux & Lawrence 1982). As in other carnivore groups, predatory echinoderms have short digestive systems, whereas herbivores and deposit feeders have comparatively long digestive systems. A typical digestive system consists of a mouth, a short oesophagus, stomach, intestine, rectum and anus. Oral tube feet or tentacles derived from the oral water ring (also known as the oral ring canal) have feeding and sensory roles and are present in the mouth region of asteroids, ophiuroids and holothuroids (**Figs 1.10A, 1.16**). Digestion is largely extracellular, occurring outside the body or in the gut lumen, and is aided by enzymes secreted by the digestive tract. Mucus, also produced by the cells of the digestive tract, lubricates food particles thus facilitating transport. The haemal sinus can store the products of digestion.



Figure 1.9 The small cushion star ***Parvulastra exigua*** (Asterinidae) is found on rocky platforms in the temperate intertidal waters of the southern hemisphere including Australia, where it feeds on microscopic algae by everting its stomach onto the substrate.

[A.Martinez]

Asteroidea

The mouth of seastars is supported by a tough connective tissue membrane (peristomium), and is surrounded by protective moveable spines. The mouth connects with a large stomach that is divided into an outer muscular cardiac stomach and an inner pyloric stomach. Two pyloric caecae, nutrient storage organs, extend along each arm and are connected to the stomach (**Fig. 1.6E**). A short intestine connects the stomach to the rectum. Some asteroids (for example, *Ctenodiscus*) lack an anus and waste solid material is ejected through the mouth.

The feeding biology and ecology of seastars has been well documented (see reviews by Jangoux 1982; Lawrence 2013a; Martinez *et al.* 2017). Many seastars are predators and scavengers, either swallowing their food whole (intraoral feeding) as members in the families Luidiidae and Astropectinidae, or initiating digestion externally (extraoral feeding) as species in the families Asteriidae and Acanthasteridae.

Asteroids that feed intraorally, such as *Luidia* and *Astropecten*, consume bivalves and other invertebrates taken from the upper layer of sandy or muddy seafloors. *Luidia* species are also known to feed on other echinoderms such as heart urchins and ophiuroids, and other smaller asteroids.

Asteroids that feed extraorally extend their stomach through the mouth to surround food and initiate digestion outside the body (**Fig. 1.8A; Box 4.3**). Further digestion either occurs outside the body or the stomach retracts to draw the food back into the body. Extraoral feeding permits seastars to consume food items that are too large to be swallowed directly (**Fig. 1.8B,C**).

The Asteriidae are characteristic extraoral feeders. The powerful suckered tube feet of *Coscinasterias* and *Asterias* wrench open bivalves (**Fig. 1.8B**), the stomach is inserted

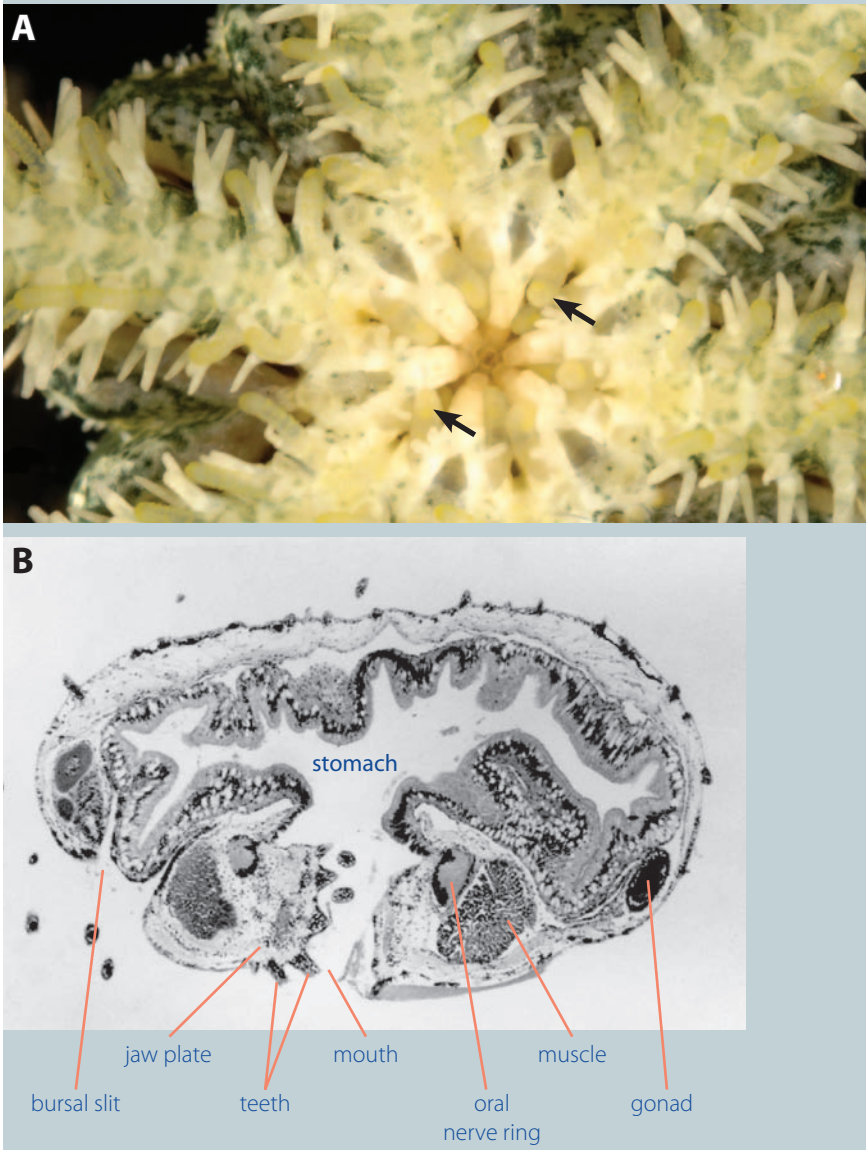


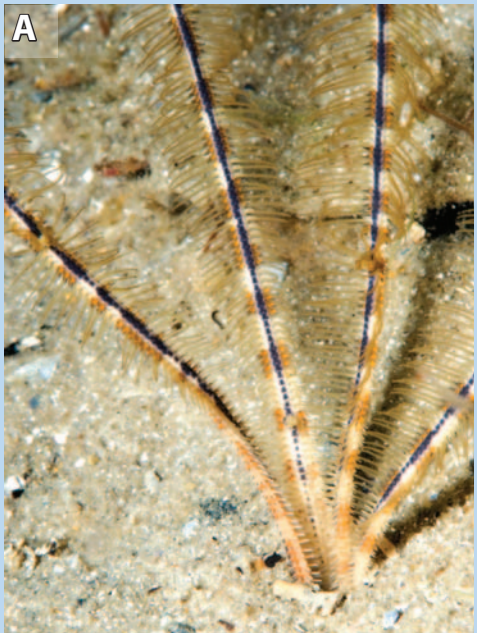
Figure 1.10 Ophiuroid anatomy.

A, actinal view of the central disc of ***Ophiactis*** sp. (Ophiactidae) showing the small tentacles (arrows) protruding from around the mouth.

B, cross-section of the central disc of the ophiuroid ***Ophionereis olivacea*** (Ophionereididae) showing the sac-like stomach, mouth and jaws with attached teeth.

[A, M.Byrne; B, from Byrne 1994]

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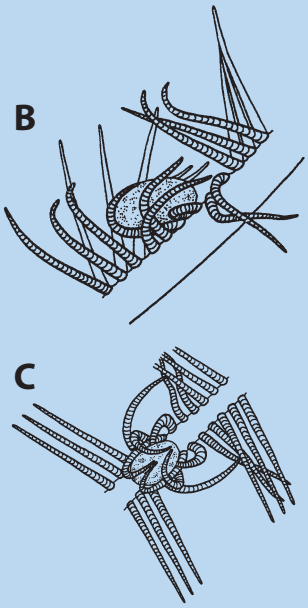


Figure 1.11 Feeding in ophiuroids.

A, a suspension feeding brittle star ***Ophiocentrus pilosus*** (Amphiuridae) with its body buried in the sand and tube feet extended from its outstretched arms.

B, **C**, diagram of tube feet moving a food particle towards the mouth in the suspension feeding ophiuroid ***Ophiothrix fragilis*** (Ophiotrichidae).

[A, J.Finn; B,C, after Warner & Woodley 1975]

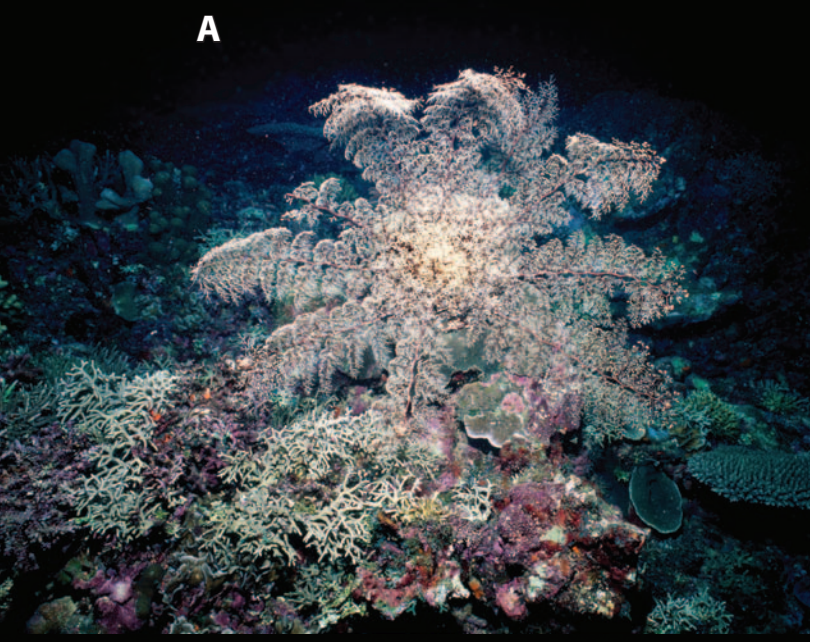
into small gaps between the valves of the prey and the body is digested externally. These seastars also scavenge carrion (**Fig. 1.8C**). Many other asteroids (for example, the Goniasteridae and Ophidiasteridae) feed extraorally on colonial animals such as sponges, bryozoans, ascidians and corals. The extraoral feeder *Acanthaster planci* (the crown-of-thorns seastar) is unusual in being a specialised coral-feeder (see **Chapter 4**).

Some asteroids, such as *Parvulastra exigua* (**Fig. 1.9**), a common species on temperate rocky shores, extrude their stomach over rocks to feed on surface algal and microbial films (Martinez *et al*. 2016). Large tropical oreasterids, such as *Protoreaster*, extrude their stomach tissue to feed on epibenthic films. Deepsea brisingid asteroids are suspension feeders, trapping particles in mucus, but they may also capture prey using their pedicellaria (**Fig. 8.3**). Cilia or tube feet then pass the particles to the mouth. Photographs from submersible craft show brisingids raising their many arms up into the water column to suspension feed, and so these asteroids look superficially similar to ophiuroids (Gage & Tyler 1991; **Figs 2.10, 8.43**). These animals are common on the seamounts to the south of Tasmania, and include species in the genera *Novodinia*, *Brisinga* and *Freyella* (Koslow & Gowlett-Holmes 1998). Many deepsea asteroids are deposit feeders, engulfing micro-organisms and detritus from muddy sediments (Jangoux 1982).

Ophiuroidea

The digestive tract of ophiuroids is comparatively simple, consisting of a star-shaped mouth leading to the short oesophagus and a sac-like stomach that occupies most of the disc (**Fig. 1.10**). There is no intestine or anus. Food is ingested and waste is expelled through the mouth.

Many ophiuroids are suspension feeders, extending their arms with sticky mucus-covered tube feet and spines into the water column away from their perch to capture drifting particles and plankton (**Figs 1.11A, 2.19**). The feeding arms are often seen extending into the water column while the central body of the ophiuroid remains protected in holes in soft sediment or rocks (**Figs 2.19, 9.20D**). Trapped particles are compacted into small mucus-bound balls and passed successively along the arms by the tube feet to the mouth (Warner & Woodley 1975; **Fig. 1.11B,C**). Prey



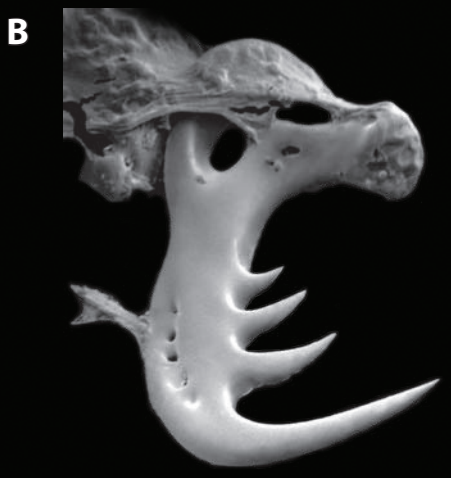


Figure 1.12 Feeding in ophiuroid basket stars.

A, the basket star ***Astroboa nuda*** (Gorgonocephalidae) feeding at night with its highly branched arms spread (up to a metre across) to form a basket to capture food particles. During the day it coils into a tight ball.

B, an electron micrograph of the girdle hooklet of the basket star ***Astrozona*** sp. (Gorgonocephalidae).

[A, A.Flowers & L.Newman; B, S.Stöhr]

items commonly include planktonic copepods, diatoms, Foraminifera, and general detrital material either from the bottom or in suspension. The pan-tropical Indo-Pacific species *Ophiocoma scolopendrina* changes from a suspension feeder to ingesting surface scum at low tides (Magnus 1964; Oak & Scheibling 2006; **Fig. 2.3**).

Basket stars are unusual in being predatory suspension feeders (**Figs 1.12A, 9.1**). They ensnare zooplankton in the hook-bearing, terminal, tendril-like branches of their arms (**Fig. 1.12B**). The arms then curl under the body to bring the food to the mouth (Wolfe 1982). Branched ophiuroids position themselves to feed by climbing out onto a projecting rock, sponge or gorgonian coral to spread and link their arms in a parabolic fan against the current (Warner 1982). Large amounts of water can be filtered by this method. *Astroboa nuda*, with an arm fan area of 0.75 m^2, is capable of filtering 86 m^3 of seawater over eight hours in a 40 mm/s current (Fricke 1966). Some basket stars also use mucus to aid food capture (Patent 1970).

Deposit-feeders, including many *Amphiura* species, collect particles directly from the seafloor, using their sticky tube feet. *Amphiura aster* from New Zealand appears to feed on subsurface sediment particles (Pentreath 1970). Other species, such as *Ophionereis schayeri*, are opportunistic, using a variety of feeding mechanisms.

Carnivorous species, such as ophiodermatids, use an arm-loop capture method, coiling their arms around prey and bringing food directly to the mouth. They have short robust arms that sweep across the substratum searching for food such as copepods, amphipods and euphausiid shrimps. *Ophiura sarsii* will actively hunt moving organisms (Stancyk *et al.* 1998; Harris *et al.* 2009), and the large tropical species *Ophiarachna incrassata* can catch small fish by ambush, lowering its body quickly onto unsuspecting prey hiding under a canopy created by the ophiuroid's arms (**Box 1.2**). This species also scavenges dead animal material. The Antarctic *Ophionotus* species and *Astrotoma agassizii* are primarily carnivorous, but also scavenge dead animal material (Dearborn 1977).

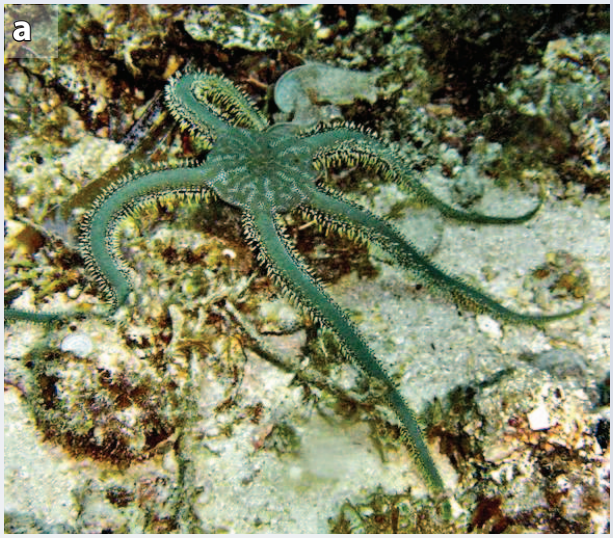
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Box 1.2 *Ophiarachna incrassata*, the fishing ophiuroid

The large, tropical Indo-Pacific brittle star *Ophiarachna incrassata* is a specialist piscivore. This robust, olive-green species emerges from its day-time hiding place at dusk just as the diurnal fish return to the seafloor for rest and shelter (**Fig. a**). The brittle star positions itself at the edge of reefs near shelter sites used by fish. Unsuspecting fish swim into a false crevice formed by the body of the brittle star (**Figs b,c**). As the fish enters the gap between the brittle star's arms, the animal rapidly rotates its arms to imprison the fish in a helical cage. The twilight behaviour, ambush posture and robust arms and spines make *O. incrassata* an efficient fish predator. However, it will also scavenge scraps discarded by other predators such as sharks. In the far north of Australia, around the sea turtle nesting sites at Raine Island, *O. incrassata* eats scraps of turtle meat discarded by sharks.

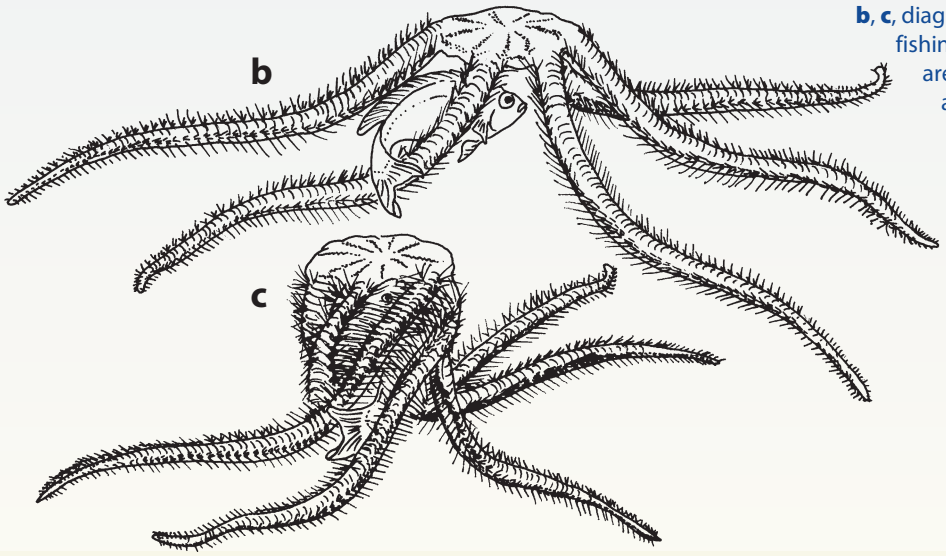
Class Ophiuroidea
Family Ophiodermatidae
Species *Ophiarachna incrassata* (Lamarck, 1816a)

Further reading Morin 1988



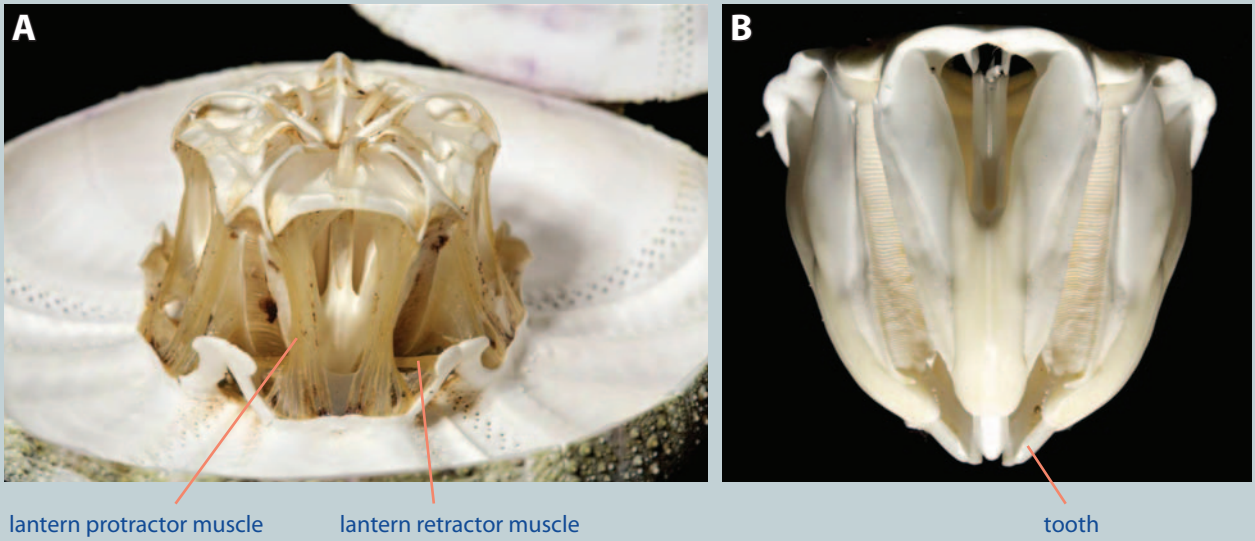
Figures a–c The ophiodermatid ophiuroid ***Ophiarachna incrassata***.

a, the brittle star is readily identified by its green colouring, and the patterning of white spots outlined in black on the disc, and its large size — a disc diameter up to 50 mm and arms up to 250 mm long. It is found mainly on tropical reefs among coral bases and rubble.



b, **c**, diagram of the brittle star's fishing behaviour in which fish are lured under the disc, and then the arms quickly spiral, to trap the fish.

[a, P.&G.Poppe; b,c, B.Patullo from Morin 1988]





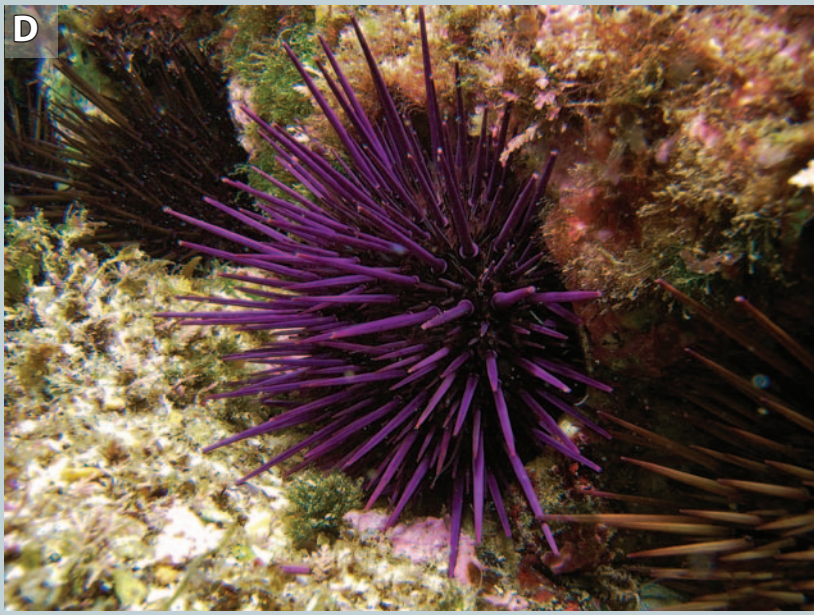


Figure 1.13 Feeding in regular echinoids, commonly called sea urchins.

A, the feeding complex, Aristotle's lantern, within the perignathic girdle of ***Toxopneustes pileolus*** (Toxopneustidae). The internal organs have been removed but the dried muscle tissues of the protractor, postural, interpyramidal, and retractor muscles have been retained.

B, Aristotle's lantern of ***Pseudoboletia indiana*** (Toxopneustidae). The soft tissues (mostly muscle) have been removed from the lantern to show the architecture of the hard plates and the five teeth.

C, five teeth (arrow) of the lantern projecting outside the mouth of ***Temnopleurus alexandri*** (Temnopleuridae).

D, purple and brownish-green spined ***Heliocidaris erythrogramma*** (Echinometridae) in burrows that it has excavated. Excavation takes place as the sea urchin feeds scraping algal film from the rock.

[A–C, A.D.Miskelly; D, J.Hannan]

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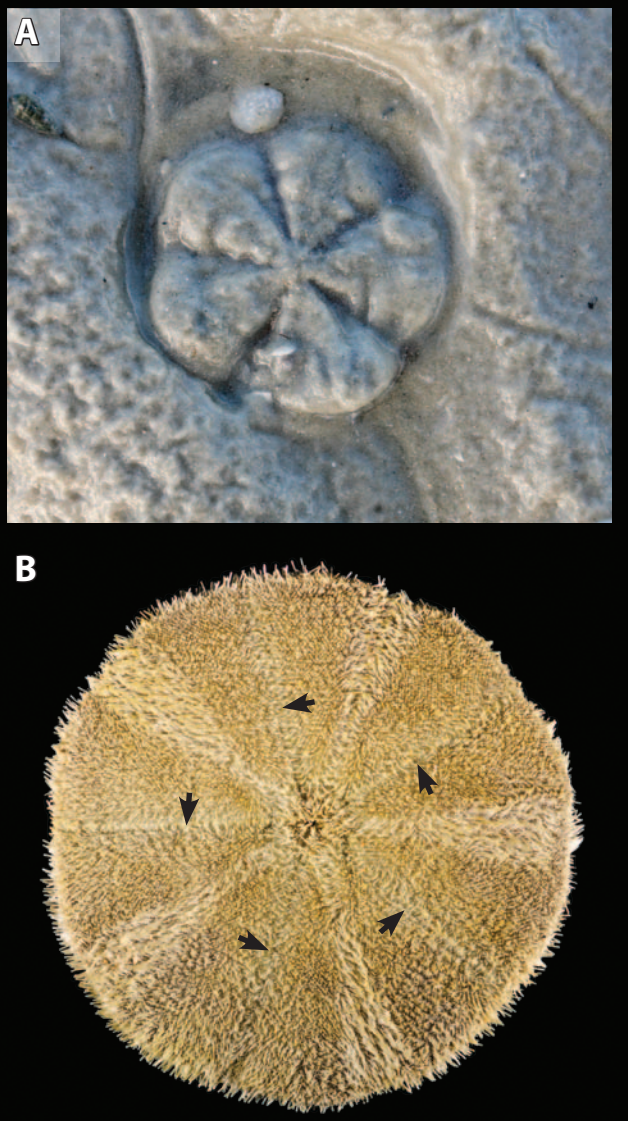


Figure 1.14 Like other sand dollars in the order Clypeasteroida, ***Arachnoides placenta*** (Clypeasteridae) burrow in soft sediments and generally feed on detritus and benthic particulate matter that they gather from among sand grains: **A**, sand dollar feeding on sand flats in northern Australia.
B, actinal view of a test showing the five food grooves (arrows) radiating toward the mouth.
[A, A.D.Miskelly; B, M.Byrne]

Echinoidea

Regular echinoids, the sea urchins (**Figs 1.1E, 1.2L, 10.1**), have an intricate jaw apparatus called the Aristotle's lantern (**Fig. 1.13A–C**), and their feeding ecology is well documented (see Lawrence 2013c). The lantern is a complex of skeletal elements, muscles and ligaments. Externally, five teeth project into the mouth, which is supported by a tough peristomial membrane (**Fig. 1.13C**). The morphology and biomechanics of the Aristotle's lantern have been investigated in several studies (see Candia Carnevali *et al*. 1993; Wilkie *et al*. 1998). Internally the structure is supported by the perignathic girdle, a ring of modified ambulacral and interambulacral plates that serve as attachment surfaces for muscles and ligaments. The major skeletal elements of the lantern include five pyramids (jaws), teeth, rotulae and compasses. The pyramids have a central calcareous band with the tooth at the oral end and the soft dental sac at the opposite end where new tooth material is formed. Teeth are created by the sac at one end and worn down by feeding activity at the other. The rotulae act as braces between adjacent pyramids, and the small compass ossicles connect with the depressor muscles. The lantern has specialised muscles that control protraction and retraction of the teeth during feeding. In sand dollars the lantern is reduced or absent.

In keeping with their algal and particulate diet, the digestive tract of sea urchins and heart urchins is long and coils internally around the test. A pharynx, between the mouth and stomach, is located within the lantern. A small tube (siphon) connects the oesophagus and the intestine, allowing water ingested with the food to bypass the stomach. Symbiotic bacteria that break down cellulose are located in the siphon of heart urchins (De Ridder & Jangoux 1993; De Ridder & Foret 2001). The digestive tract of echinoids is thin-walled and poorly equipped with muscles. Movement of food through the gut is facilitated by continuous ingestion.

Most sea urchins feed on algae harvested by the spines and tube feet. The urchins' hard teeth also enable them to graze on the substratum, removing encrusting organisms and calcareous algae, as well





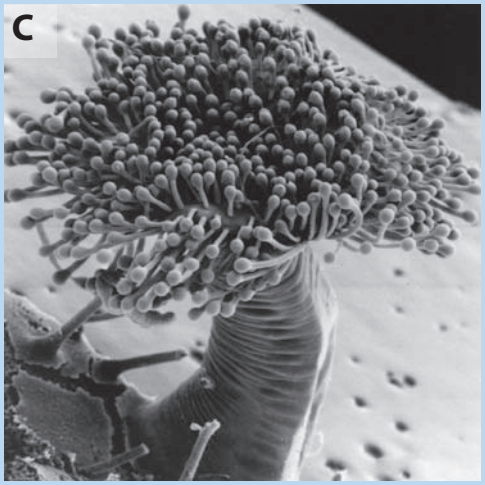


Figure 1.15 Details of the mucus-secreting tube feet of heart urchins (order Spatangoida), irregular echinoids, used to assist feeding.

A, a rosette of structures, around the peristome, bearing the specialised feeding tube feet of ***Spatagobrissus incus*** (Brissidae).

B, feeding tube feet of ***Protenaster australis*** (Schizasteridae).

C, a specialised feeding tube foot from near the mouth of ***Echinocardium cordatum*** (Loveniidae).

[A,B, A.D.Miskelly; C, P.Flammang]

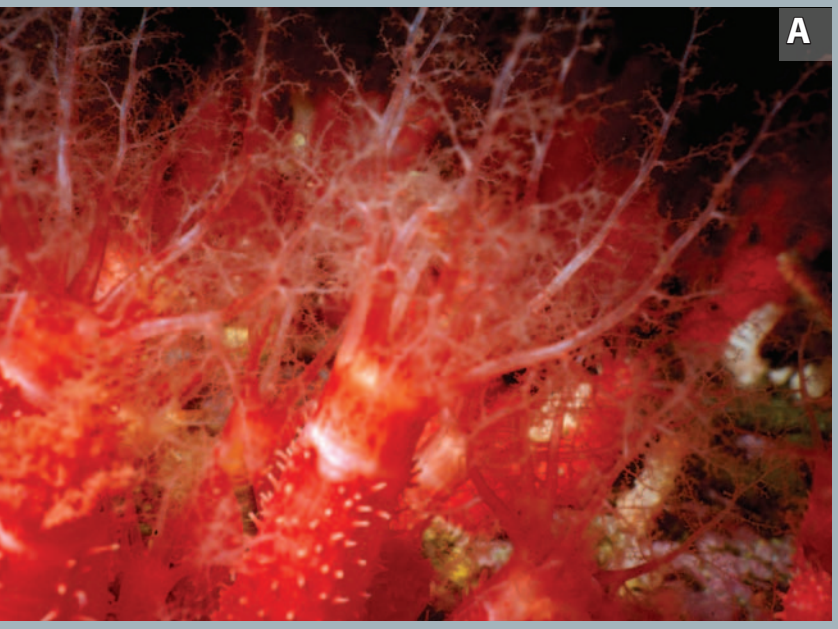
as allowing them to burrow into hard substrates. Many sea urchins, such as *Heliocidaris* in temperate waters and *Echinometra* in tropical waters, play a major ecological role as bioeroders, removing hard substrate, often making burrows for themselves (**Figs 1.13D, 2.9, 4.5E**). Echinoids are often the primary grazers on reefs and can exert a strong influence on community structure (see **Chapter 2**).

Sand dollars (irregular echinoids) feed on benthic deposits, using a complex particle-picking mechanism (Mooi 1986a, 1986b), i.e. thousands of minute tube feet that probe the sediment and gather food particles. Suspension-feeding sand dollars collect particles directly from the overlying water, using their very small sticky tube feet. The particles are passed along the tube feet to food grooves, shallow depressions on the oral surface that converge at the mouth (**Fig. 1.14**). Particles are finally gathered into a mucous cord and directed towards the mouth by tube feet.

The presence of an elongate profile and an anterior-posterior axis in many irregular urchins (heart urchins and sand dollars) is a secondary innovation that is associated with their infaunal (sub-seafloor) burrowing life-style (**Figs 2.36, 10.2; Box 10.6**). In heart urchins the mouth is anterior and the anus posterior, whereas in sand dollars the mouth is situated at the centre of the oral surface and the anus posterior. The feeding tube feet of infaunal echinoids vary in shape from leaf-like to flower-shaped, depending on their roles in feeding and respiration (Fenner 1973; Flammang *et al.* 1991; **Fig. 1.15**). Some infaunal species are known to select and ingest organically rich particles, and they migrate towards the sediment surface to avail themselves of newly settled detritus.

Finally, the cidaroid urchins *Calocidaris* and *Histocidaris* have been found to prey on stalked crinoids off the Bahamas (Baumiller *et al.* 2001); the crinoids can shed their stalks as an escape mechanism (Baumiller *et al.* 2008). Other urchins, such as *Psammechinus miliaris*, consume dead animal tissue and colonial invertebrates such as sponges and bryozoans (Kelly & Cook 2007).

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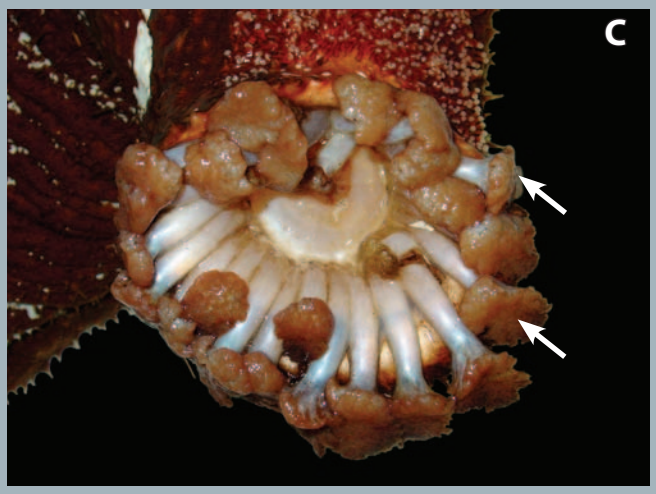




Figure 1.16 Most holothuroids are suspension or deposit feeders that use their mucus-covered, branched buccal (oral) tentacles to collect or trap plankton and decaying organic matter. The shape of the tentacles differs among the various orders of sea cucumbers — from arborescent in Dendrochirotida to peltate in the Aspidochirotida and pinnate in most Elasipodida.

A, the dendrochirotid sea cucumber ***Squamocnus brevidentis*** (Cucumariidae), from New Zealand waters, positioned in the current with its arborescent (dendritic) tentacles extended for feeding; this species is closely related to the Australian animal ***Squamocnus aureoruber*** that occurs in south-eastern Australia.

B, dendrochirotid sea cucumbers like ***Neothyonidium magnum*** (Phyllophoridae) often bury themselves in sand and extend their branched tentacles into the water column to feed; the tentacles are withdrawn rapidly at any sign of danger. One-by-one the tentacles bend over to deposit food into the mouth.

C, the mouth of an aspidochirotid sea cucumber ***Actinopyga*** sp. (Holothuriidae). Members of the genus ***Actinopyga*** have a mouth that is surrounded by a ring of 16–30 flat-ended tentacles with adhesive pads (arrows) which are used to sift sediment for organic matter.

D, the synaptulid sea cucumber ***Synapta maculata*** (Synaptidae) feeds by rhythmically curling and uncurling its pinnate tentacles, collecting food particles from the substrate and delivering them to the mouth for ingestion.

[A, N.Davey; B, C.Bryce; C, M.Byrne; D, G.Bell]

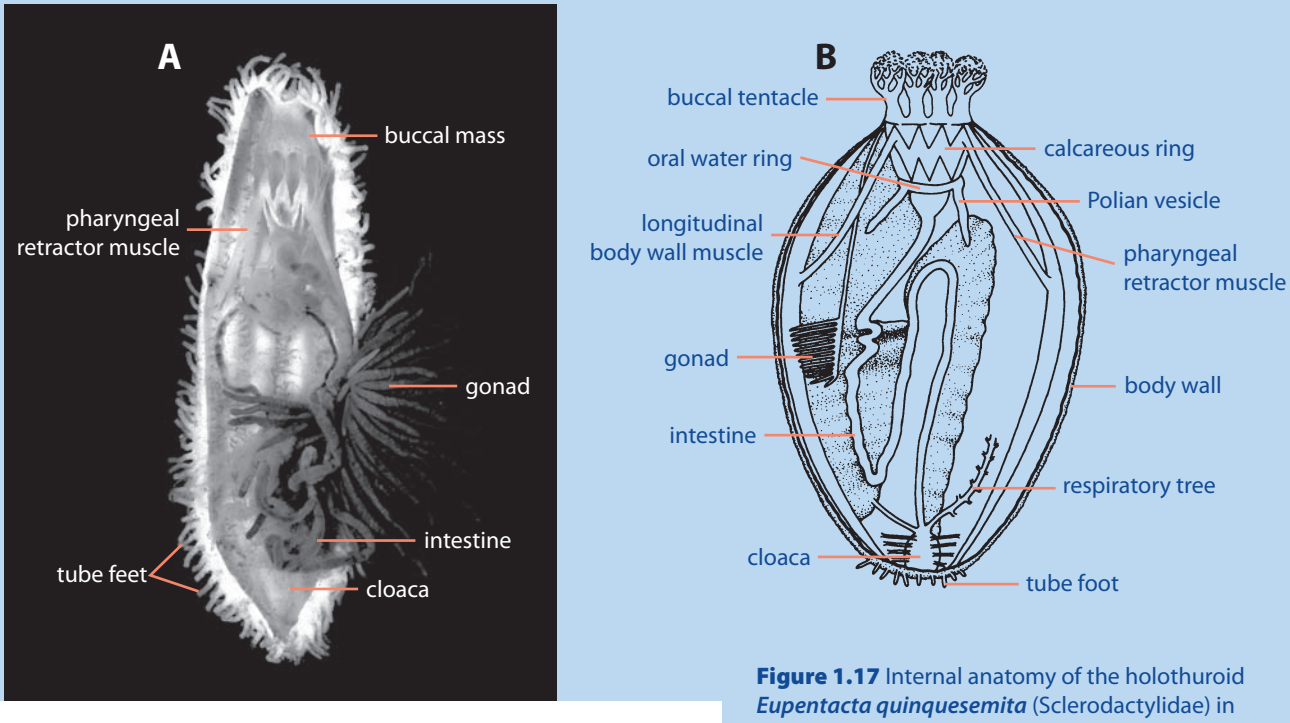


Figure 1.17 Internal anatomy of the holothuroid ***Eupentacta quinquesemita*** (Sclerodactylidae) in longitudinal dissection (**A**) and as a diagram (**B**).

[A, M.Byrne; B, from Byrne 1985a]

Holothuroidea

Holothuroids collect food by means of contractile buccal tentacles (**Figs 1.16, 1.17, 1.28**); if the animal is disturbed, the tentacles are retracted quickly. They are supported internally by a calcareous ring, the largest skeletal element in holothuroids (see **Box 1.1**). The mouth leads to a pharynx within the calcareous ring (**Fig. 1.17**), and the digestive system leads to a small stomach and an elongate intestine divided into descending and ascending portions. Many holothuroids have an intestine connected to a muscular cloaca that opens to the anus; the cloaca also contracts regularly to propel water into respiratory structures called respiratory trees (**Fig. 1.17**).

Dendrochirotid sea cucumbers are suspension feeders. They hold their beautiful arborescent tentacles into the water column, catching particles on minute adhesive papillae that cover the surface of the tentacles (**Fig. 1.16A,B**). The numerous fine branches of these tentacles present a large surface area for food capture. Gut content analyses indicate that these holothuroids feed on diatoms and other planktonic algae and small invertebrates. On the shores of Macquarie Island, vast numbers of the small cucumariid *Pseudopsolus*



Figure 1.18 A sea cucumber expelling faecal pellets.

[L.Newman & A.Flowers]

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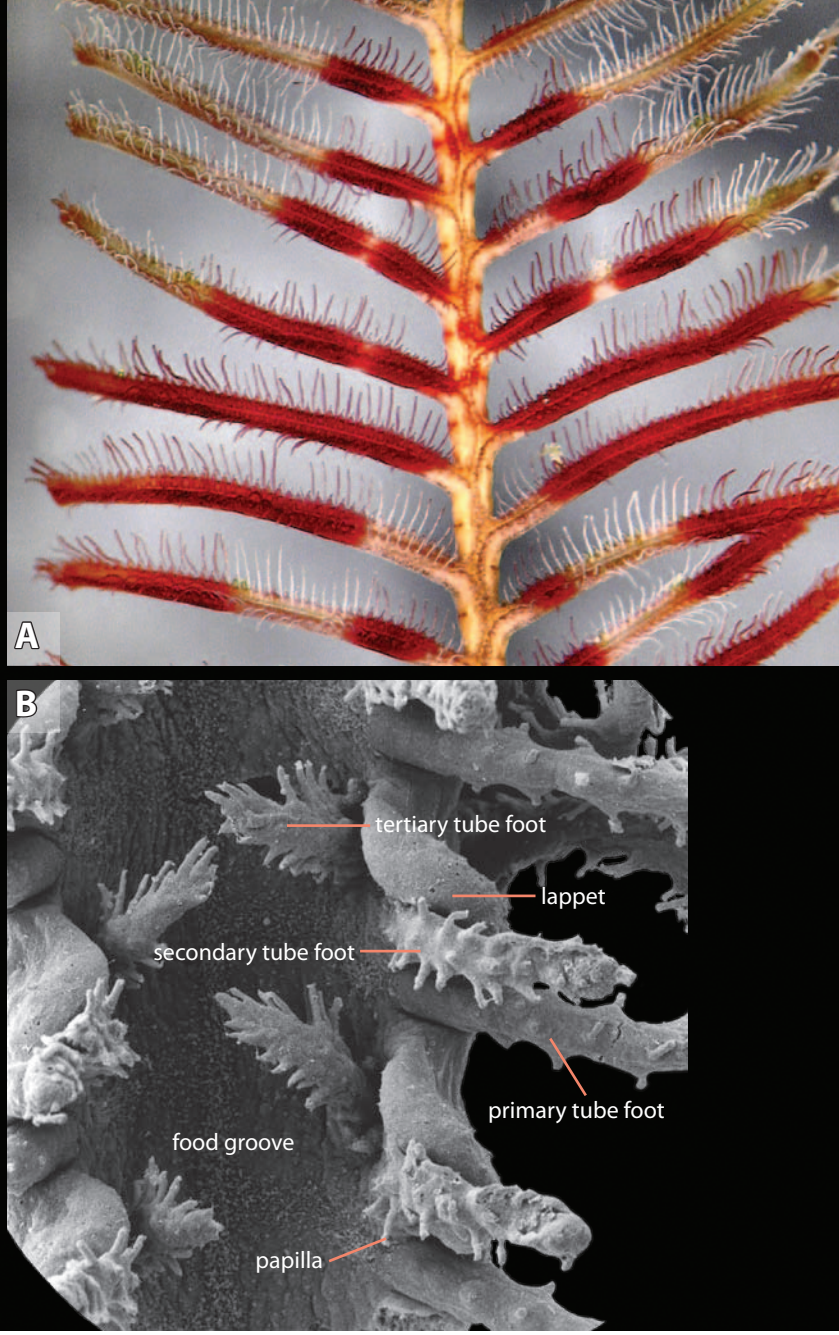


Figure 1.19 Crinoids feed by filtering suspended micro-organisms and detritus from passing water currents with their feather-like arms.

A, rows of translucent primary tube feet extend from pinnules on an arm of ***Stephanometra indica*** (Mariametridae). The long primary tube feet trap drifting food particles by flicking or folding them into the ambulacral (food) groove, where tracts of cilia carry them to the mouth.

B, a section of an ambulacral (food) groove of ***Florometra serratissima*** (Antedonidae) showing tube feet and lappets. Crinoid tube feet occur in groups of three called podial triplets, each with a different morphology and role in food collection — the long primaries collect the food; shorter secondaries collect food and also sort it within the groove, and tertiaries manipulate the particles, once transferred, in the groove. Papillae on the tube feet secrete mucus, to which captured particles initially adhere. In response to disturbance, the tube feet retract within the groove and the lappets fold down, creating a protective roof (see Lahaye & Jangoux 1985).

[A, G.W.Rouse; B, from Byrne & Fontaine 1981]

macquariensis cover the rocks, extending their tentacles briefly to feed on every incoming wave (T.D.O'Hara, personal observation). The dark tentacles of *Thyone* and *Massinium* species can be seen protruding from the sand near rocks around southern Australia, while the large tropical *Plesiocolochirus* species extend their dark tentacles from the sand, usually at dusk.

Aspidochirotid sea cucumbers are deposit-feeders. They extend their tentacles (**Figs 1.16C, 1.28**) across or into the seafloor, either pushing sediment into the mouth or collecting individual particles (Roberts *et al.* 2000; Purcell *et al.* 2016a). The major food items of deposit-feeding holothuroids are sediment bacteria and algae. Large species such as *Stichopus herrmanni* and *Holothuria atra* (**Fig. 11.1**), common on sand flats and lagoonal sediments throughout the tropics, feed on the upper few millimetres of sediment (Uthicke & Klumpp 1998; Uthicke 1999, 2001a). Their large peltate (disc-like) tentacles move sediment particles into the mouth (**Fig. 1.28**). Organic matter is digested from the particles, and the waste is deposited as faecal casts (**Fig. 1.18**). There is conflicting evidence as to whether aspidochirotids can select for sediment particles of a particular size or other characters such as nutrient content. *Holothuria atra* can focus on sediment rich in organic matter (Uthicke 2001a). Aspidochirotid

sea cucumbers such as *Holothuria isuga* and *Actinopyga spinea* are important burrowers, mixing the surface sediment (bioturbation) (**Fig. 2.38**). In general, aspidochirotids play a major ecological role in reworking benthic habitats because they can process large quantities of sediment (Purcell *et al.* 2016a; see **Chapter 2**).

Synaptulid sea cucumbers are surface deposit feeders. They have feather-like tentacles that pick up organic matter from the sediment surface (**Fig. 1.16D**). They do not ingest sediment. To defecate, the synaptulid *Opheodesoma grisea* protrudes its anus above the surface and faeces are expelled in a spray rather than as pellets (Massin 1982b). Deepsea elasipodid sea cucumbers are also surface feeders selecting particles with their tentacles. Burrowing molpadids live with their mouths buried deep in the sediment and ingest sediment from which organic matter is extracted; faecal casts are deposited on the surface of the sediment.

Crinoidea

Crinoids have both the mouth and anus directed upwards. The mouth is formed by the confluence of the ambulacral food grooves, and connects through a short oesophagus to the intestine that has one major loop before it leads to the rectum. The anus is elevated on a small stalk, called the anal cone. The internal anatomy of the crinoid body is shown in **Figure 7.7**.

All crinoids are suspension feeders. They collect food particles with a battery of small tube feet that are located in the food grooves that run along the actinal side of the arms (**Figs 1.19, 7.4**). Crinoids are highly rheophilic, meaning that they orientate their arms to the current with the grooves facing downstream (**Fig. 7.20B**). They often seek feeding positions on reef elevations, and are often seen in large numbers on the reef at night, emerging from their daytime hiding places after dark (**Figs 2.7, 7.1**). Recent studies on the Great Barrier Reef and in Moreton Bay also show populations of crinoids perched on soft bottoms (Messing *et al.* 2006; **Fig. 7.19F**). It is striking to see large populations of feather stars all adopting a similar orientation in areas with unidirectional currents (Byrne & Fontaine 1981, Meyer *et al.* 1984). Sea lilies (**Figs 1.2N, 7.14–7.18**) are elevated above the seafloor by the stalk, and they orientate their arms in a parabolic fan with the food groove downstream (Oji *et al.* 2009). The tube feet of crinoids protrude out of the food groove to catch particles on their sticky surface. The particles are transferred into the food groove with a rapid flicking action (Byrne & Fontaine 1981, 1983). Here, they are compacted by the tube feet and moved towards the mouth by tracts of cilia. The lappets, small skeletal plates along the food groove, assist in the transfer of food from the tube feet to the ciliary track (**Fig. 1.19B**).

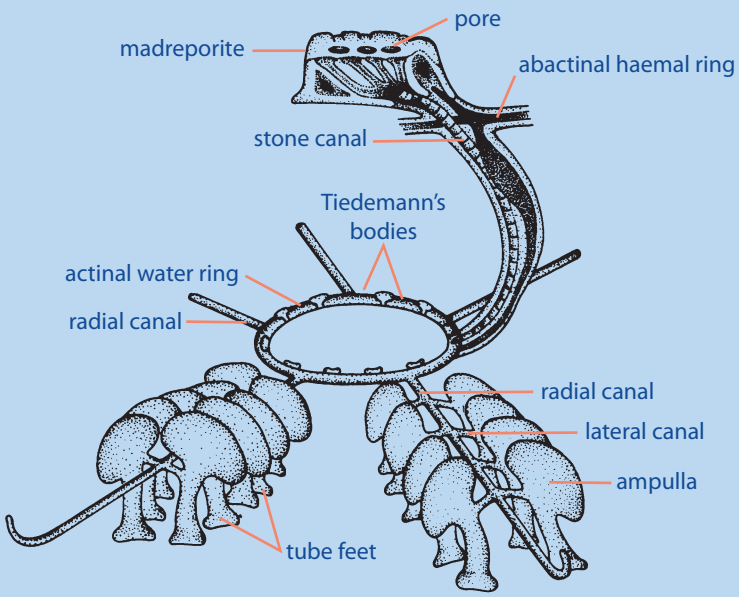


Figure 1.20 Diagram of the water vascular system of the seastar ***Henricia*** sp. (Echinasteridae).
[from Harrison & Chia 1994]

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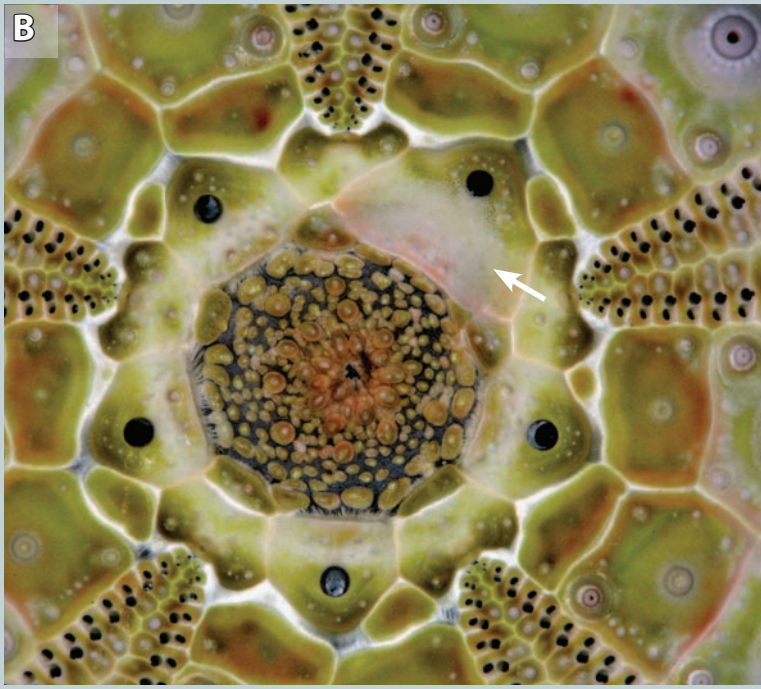


Figure 1.21 The water vascular system of all echinoderms opens to the exterior through a skeletal plate called the madreporite or sieve plate.

A, seastars usually have one madreporite (arrow) on the abactinal surface as shown here for ***Tosia australis*** (Goniasteridae). However, some species do have multiple madreporites.

B, the apical system of a cleaned test of the regular sea urchin ***Centrostephanus rodgersii*** (Diadematidae) showing the placement of the madreporite (arrow) which adjoins the apical plates on the aboral surface. The large pores in the plates are the gonopores.

[A, J.Finn; B, A.D.Miskelly]

Water vascular system

The water vascular system, a unique echinoderm innovation, is formed from the coelom during larval development. It consists of a series of tubes or water canals that form a complex hydraulic system. Externally, the tube feet are the most conspicuous feature of the water vascular system. From their presumed original function as simple respiratory-suspension feeding structures, tube feet have evolved to perform a broad range of functions in feeding, locomotion, respiration, excretion and sensory reception.

The organisation of the water vascular system differs between the classes of echinoderms, and anatomical modifications might have been associated with the generation of new body forms in echinoderm evolution. The water vascular system is most readily illustrated in seastars (**Fig. 1.20**), and its components include the madreporite, stone canal, oral water ring, radial water canals, ampullae and tube feet. The madreporite, a round perforated plate, is the fluid inlet and outlet for the system (**Fig. 1.21**). The fluid in the water vascular system is similar in composition to seawater. Pore canals in the madreporite open into the stone canal, which connects to the oral water ring around the mouth (Tamori *et al*. 1996). The stone canal is thought to function as a pump that drives the circulation of fluid. The oral water ring surrounds the mouth and gives rise to the radial canals running into the arms (**Figs 1.6E, 1.20**). As mentioned above, the ambulacral system of asteroids is open because the radial canal is located external to the skeleton. A series of sacs (Polian vesicles) can connect with the oral water ring and serve as reservoirs of fluid. Small pouches (Tiedemann's bodies) are also associated with the oral water ring and filter water from the stone canal to generate coelomic fluid. Along the arms, the radial canal gives rise to numerous lateral canals that connect to two

or four rows of tube feet and ampullae (**Fig. 1.19**). The ampullae are muscular bulbs that receive fluid from the tube feet when they contract (**Fig. 1.6E**). In many asteroids the tube feet have prominent terminal suckers (**Fig. 1.22A**), and their mobility results from an antagonistic interaction of hydrostatic pressure and muscle contraction. Protraction and retraction are associated with movement of fluid between the tube feet and ampullae. Contraction of an ampulla forces fluid into the tube foot, while contraction of the tube foot shunts water back into the ampulla. Arm spines form a protective cover over the tube feet when they are retracted (**Fig. 1.22B,C**).

With the exception of asteroids, all echinoderms have closed ambulacral systems with an internal radial water canal and tube feet that emerge through pores in the body wall.

In echinoids the madreporite is located at the aboral surface near the anus (**Figs 1.21B, 10.3A**). The oral water ring encircles the Aristotle's lantern and gives rise to the radial canals that run along the inside of the test beneath each of the ambulacral areas. Each radial canal gives off lateral canals that in turn each lead to an ampulla which underlies a tube foot. Unlike other echinoderms, the ambulacral plates of echinoids are perforated by pore pairs through which the tube feet extend; a single tube foot is associated with each pore pair. Regular sea urchins may have single or multiple pore pairs per ambulacral plate (**BoxFig. 10.2c**), and the tube feet have a similar morphology (Nichols 1961). Sand dollars and heart urchins have highly modified tube feet for specific functions including feeding, respiration and locomotion. (Nichols 1959a, 1959b; Mooi 1986a, 1986b; Flammang *et al*. 1991; **Figs 1.15, 2.36**).

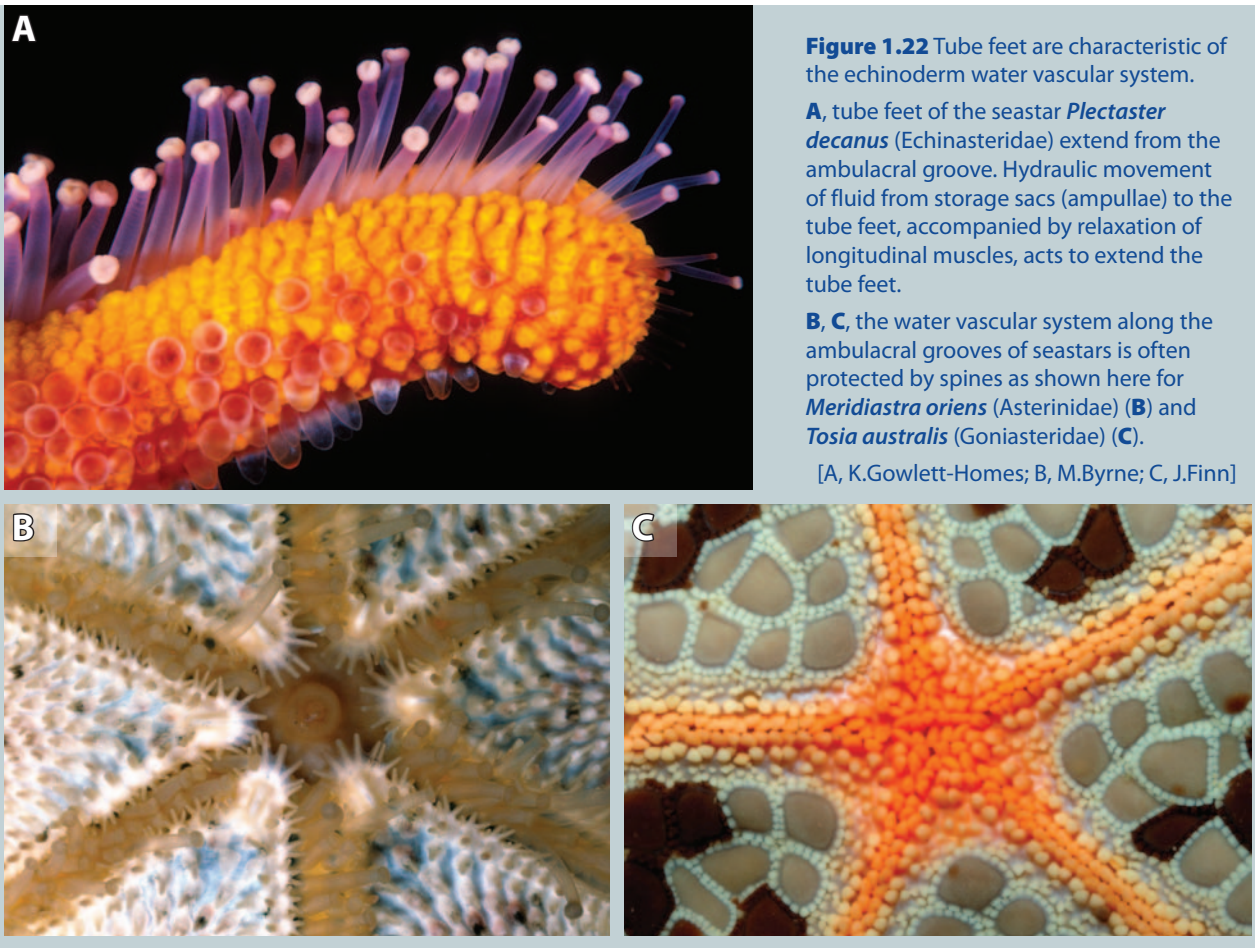


Figure 1.22 Tube feet are characteristic of the echinoderm water vascular system.

A, tube feet of the seastar ***Plectaster decanus*** (Echinasteridae) extend from the ambulacral groove. Hydraulic movement of fluid from storage sacs (ampullae) to the tube feet, accompanied by relaxation of longitudinal muscles, acts to extend the tube feet.

B, **C**, the water vascular system along the ambulacral grooves of seastars is often protected by spines as shown here for ***Meridiastra oriens*** (Asterinidae) (**B**) and ***Tosia australis*** (Goniasteridae) (**C**).

[A, K.Gowlett-Homes; B, M.Byrne; C, J.Finn]

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In ophiuroids the madreporite is located on the oral surface of the disc, and while the tube feet lack ampullae, a basal swelling of the tube feet, or small sacs along the radial canal, function as fluid reservoirs. Contraction of these structures extends the tube feet. The tube feet emerge through the body wall at the base of the lateral arm plates (**Fig. 1.23**). They are often protected by one or more small tentacle scales. Copious amounts of sticky secretions that are produced by the tube feet epithelia assist in feeding and attachment. As shown in **Figure 1.11B,C** the tube feet are very efficient in collecting food particles and mucus, and packing it into small food balls which are then transported by the tube feet along the arm to the mouth (Warner & Woodley 1975).

Holothuroids, unlike other echinoderms, have numerous internal madreporites that communicate with the oral water ring. In this case the water vascular fluid is derived from coelomic fluid rather than from seawater. The water ring encircles the calcareous ring, and uniquely it gives rise to five interradial, longitudinal vessels, from which tube feet arise. The five buccal tentacles are also joined to the water ring. The longitudinal vessels run inside the body wall, and the tube feet (each with an ampulla) extend through the body wall. Tube feet are involved in locomotion and attachment (**Fig. 1.28**). They usually have an adhesive disc at the tip. The papillae that cover some species are modified tube feet that may have a sensory function. Synaptulid sea cucumbers lack tube feet, and their water vascular system is limited to the oral water ring, buccal tentacles and associated Polian vesicles. The unusual deepsea elasipodids walk on their stilt-like tube feet.

Crinoids lack a madreporite. Numerous stone canals on the surface of the tegmen open directly into the coelom (**Fig. 7.7**). From the oral water ring, the radial canal extends along the arms and pinnules (side branches of the arms; **Fig. 1.19**); ampullae are absent. In the pinnules, lateral canals give rise to minute tube feet organised in sets of three (primary, secondary and tertiary; **Fig. 1.19B**) arising from a common base (Byrne & Fontaine 1983). Tube foot movement is generated by contraction of the radial canals. Sticky secretions on the surface of the tube feet are used to entrap food particles.

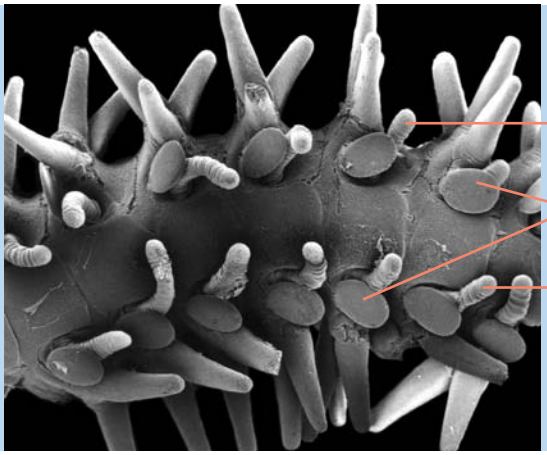


Figure 1.23 In ophiuroids tube feet extend from beneath small circular tentacle scales as seen on the ventral surface of the arm of ***Ophionereis schayeri*** (Ophionereididae).
[M.Byrne]

Respiration and excretion

Echinoderms lack dedicated circulatory and excretory systems. Gas exchange, nutrient transport and voiding of nitrogenous waste usually occur across the general body surface, with the tube feet playing a major role (Lawrence 1987). Ciliated cells in the coelomic lining assist in the circulation of fluid, and asteroids, echinoids and holothuroids have a spacious coelom that plays an important role in gas exchange. Most echinoderms lack respiratory pigments, but some holothuroid and ophiuroid species have haemoglobin-containing cells in the coelom (Christensen *et al.* 2008). These species often inhabit oxygen-poor habitats such as benthic sediments.

Asteroids have numerous small thin-walled extensions (papulae) on the abactinal surface that contain extensions of the coelom and enlarge the surface area for respiratory exchange (**Figs 1.24, 8.7B**). In ophiuroids, ciliated invaginations of the body at the base of the arms, the bursal sacs, are important in respiration (**Figs 1.10B, 1.25**). Ciliated cells in the bursal epithelium generate currents that circulate seawater through the bursal slits located at the base of the arms.

In echinoids tube feet are the primary structures for gas exchange. In sea urchins that live in environments of surface currents, gas exchange is relatively efficient across the tube feet. For those echinoids that live in sediment where oxygen is low, specialised respiratory tube feet are present. These tube feet have very thin walls and are highly flattened to provide a larger surface area for gas exchange. Infaunal echinoids use currents generated by cilia on the body surface to pump oxygenated water from the overlying water into the burrow for gas exchange (Fenner 1973). Some echinoids also have small bushy extensions of the lantern coelom around the mouth called 'gills', but these are unlikely to play a major role in gas exchange.

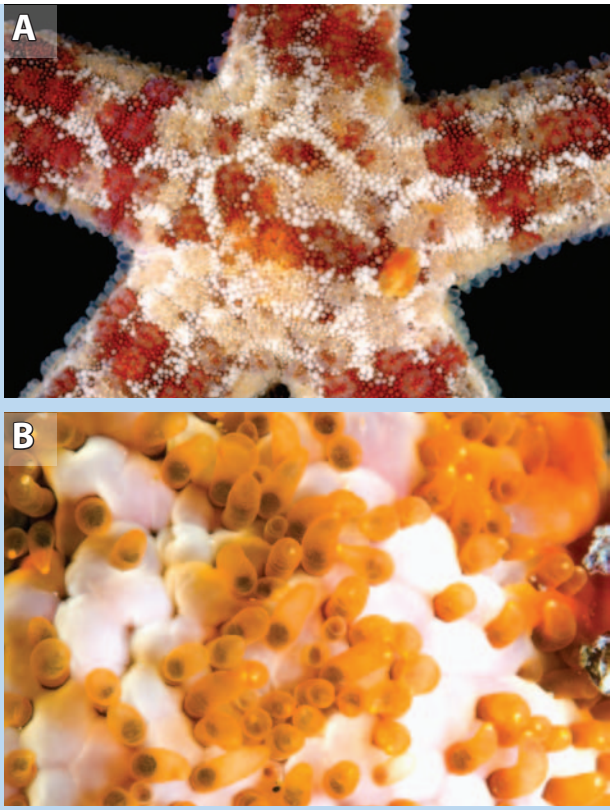


Figure 1.24 The coelom extends beyond the body of sea stars in the form of sacs called papulae to extend the surface area for respiration.

A, transparent papulae extend between red and white plates in the seastar ***Ophidiaster granifer*** (Ophidiasteridae).

B, papulae appearing as orange puffy sacs on the body of the seastar ***Petricia vernicina*** (Asteropseidae).

[A, M.Byrne; B, J.Finn]



Figure 1.25 Bursal slits (arrows) at the base of the arms of the brittle star ***Astrothorax waitei*** (Gorgonocephalidae).

[B.Patullo]

Most holothuroids, apart from synaptulids and elasipodids, have specialised structures for gas exchange, called respiratory trees, associated with the cloaca (**Fig. 1.17B**). These blind-ending tubes extend anteriorly into the coelom, and are periodically inflated with seawater and deflated by muscular contraction of the cloaca. The thin walls of the tubes facilitate respiratory exchange between the oxygenated seawater in the tubes and the coelomic fluid.

Nitrogenous wastes diffuse readily from thin-walled structures such as tube feet and papulae. Phagocytic cells filled with waste material are also voided from these structures. Some sea cucumbers have ciliated channels extending through the body wall connecting the coelom to the exterior, and it is through these channels that phagocytes are expelled (Shinn *et al.* 1990). Evisceration is a unique behaviour that is observed in some sea cucumbers in which the digestive tract is discarded following autotomy of the ligaments anchoring the gut (**Box 1.3**). Some species eviscerate or atrophy their gut

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Box 1.3 Regeneration

Echinoderms have a remarkable ability to regenerate and can readily replace discarded or autotomised body parts. Regeneration to produce a miniature, yet perfectly differentiated version of the lost body part can occur within days, and this is followed by growth to normal dimensions. In a form of asexual reproduction (see **Chapter 3**), some echinoderms can divide their body into two halves, and each half can regenerate into a new individual. In this case a portion of the central disc is required for regeneration to occur. Some asteroids can form a new individual from a single arm.

Adult echinoderms appear to have an almost unlimited source of undifferentiated stem cells available for regeneration throughout life. In cases of massive trauma, differentiated cells such as muscle can revert to an embryonic state, providing a source of stem cells for regrowth. The ability of echinoderms to rapidly replace all tissue types, particularly nervous tissue, has attracted considerable interest as a model system to study neural regeneration. Some species, such as the fissiparous asteroid *Coscinasterias muricata*, are particularly adept at regeneration.

Evisceration, a common phenomenon in sea cucumbers (**Box 1.1**), involves autotomy of mutable connective tissue (MCT) structures that support the feeding tentacles and the digestive system. This event is soon followed by the regeneration of the lost organs and regeneration of a functional digestive tract within days to weeks.

Further reading Candia Carnevali & Bonasoro 2001a; Mazzone & Byrne 2001; Mazzone *et al*. 2003; Mashanov & García-Arrarás 2011



Arm regeneration by the eleven-armed seastar ***Coscinasterias muricata*** (Asteriidae).

[M.Byrne]

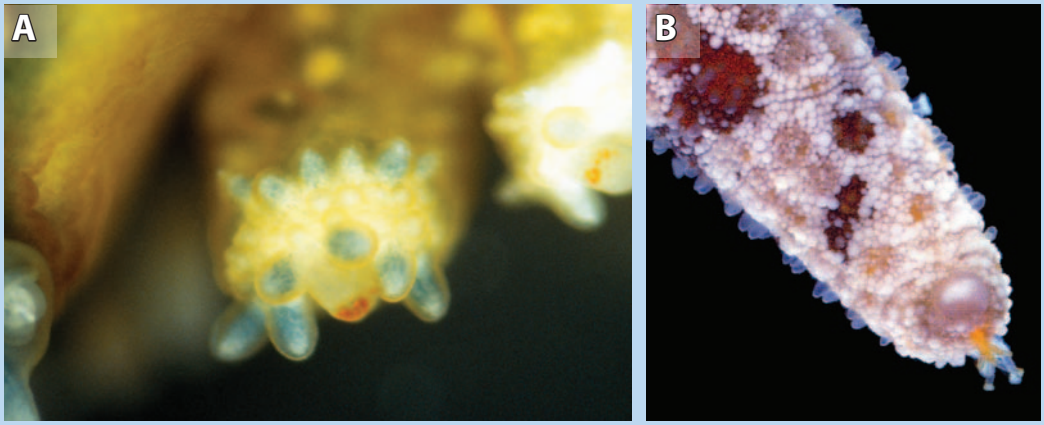


Figure 1.26 Eye spots are the only sensory structures of echinoderms with a suspected photoreceptive function. Eye spots of seastars are found at the tip of the arms as for ***Coscinasterias muricata*** (Asteriidae) (**A**) and ***Ophidiaster granifer*** (Ophidiasteridae) (**B**).

[M.Byrne]

at the end of the summer feeding period, a mechanism suggested to function in elimination of waste material that accumulates as brown deposits in the gut wall (Byrne 1985a; Fankboner & Cameron 1985). Newly regenerated digestive tracts are yellow, but turn brown as waste products accumulate.

Haemal system

Although the name of the haemal system implies a specialisation for circulation, this is not so. The name haemal was used because the fluid in the vessels has an orange/pink colour in some species, but this is not due to the presence of a respiratory pigment. This system functions in nutrient storage, but the mechanisms by which nutrients are circulated in the poorly defined vessels and spaces that characterise the haemal system is not known (Jackson & Fontaine 1984; Harrison & Chia 1994). The role of the haemal system is poorly understood.

Nervous system

The organisation of the nervous system reflects the body plan of echinoderms. A circumoral nerve ring connects radial nerve cords that run along the ambulacrae (**Fig. 1.6A,E**). Despite the pentamerous symmetry of the echinoderm nervous system, recent molecular studies indicate that the echinoderm central nervous system, although highly derived, has homologies linking it with that of chordates (Byrne *et al*. 2006; Raff & Byrne 2006). A conspicuous nerve plexus is found in the basal epithelial layer of the epidermis and contributes to the general body sensitivity of echinoderms. This is well illustrated by the intense sensitivity of echinoderms to light (**Box 1.4**).

Some ophiuroids have giant axons, 20 μm in diameter, which are thought to be important in the rapid reflexes and locomotion exhibited by species such as *Ophiura ophiura* (Cobb & Stubbs 1981). Our understanding of the physiology of the echinoderm nervous system is based largely on research with this species (Cobb 1987, 1990; Cobb & Ghyoot 1993).

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Box 1.4 Sensory receptors and colour change

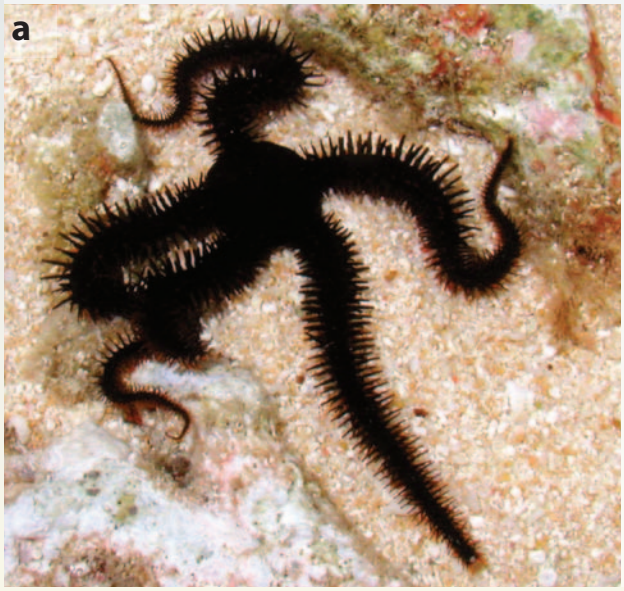
Many echinoderms are highly light-sensitive. Some species reside in daytime hiding places while others such as sea urchins often cover themselves with algae, stones, shells and other material during the day, dropping this cover at night. This behaviour is induced by exposure to ultraviolet light, which can be lethal to echinoderms.

A visit to a temperate or tropical reef after dusk is often rewarded by the sight of echinoderms emerging from their daytime hiding places. During the day nocturnal echinoderms seek out hiding places and shadows when disturbed. Nocturnal activity is thought to be an adaptive strategy to avoid diurnally active predatory fishes, and perhaps to avoid damage from ultraviolet radiation.

It is not known how nocturnally active echinoderms perceive the difference between night and day. The weight of evidence indicates that echinoderms have a general dermal light-sense modulated by surface receptors and neurons along the body surface. The red eyespots at the end of seastar arms are capable of image formation and are important in visually guided behaviour.

Remarkably, some nocturnal tropical ophiocomid brittlestars and diadematid sea urchins change from a uniformly dark colour during the day to a pattern of grey and black banding at night. In Australia, the brittlestar *Ophiocoma erinaceus* exhibits a striking day-night colour change (**Figs a,b**) caused by the migration of pigment cells (chromatophores) in the integument, and this change is associated with day-night patterns of feeding and sensitivity to light. Chromatophores are highly motile cells with abundant pigment-filled cellular processes. These processes change their shape on a day-night cycle. During the day the processes extend over the ophiuroid's surface, at least partially shielding underlying neurons from light stimuli. However, around dusk the processes retract into nests in the skeleton, thereby exposing the neurons to transmitted light. By dawn the animals have switched back to their daytime colour. The skeleton along the surface of colour-changing ophiuroids includes lens-like structures with optical characteristics that transmit incoming light to the underlying neurons.

Further reading Gras & Weber 1983; Hendler & Byrne 1987; Johnsen & Kier 1998; Aizenberg *et al.* 2001; O'Hara *et al*. 2004; Garm & Nilsson 2014





Figures a, **b** The brittle star ***Ophiocoma erinaceus*** (Ophiocomidae). It has two colour patterns depending on the time of day — day colouration (**a**) and night colouration (**b**).

[M.Byrne]

Box 1.5 Swimming, hitchhiking and pelagic echinoderms

Some adult echinoderms can swim up into the water column, although this is usually an escape response to the presence of predators. When disturbed from their perch, feather stars can swim away by moving alternate arms in a fashion resembling the dance of a ballerina (**Figs a–d**). Several deepsea ophiuroids such as *Ophiernus adspersus* swim using their long whip-like arms. These delicate species have a comparatively light skeleton, itself a possible adaptation for swimming. *Ophiernus adspersus* has distinctive, feather-like arm spines that assist in propulsion. Unlike the non-swimming ophiuroids of shallow waters, these deepsea species appear to avoid predators by swimming into the water column rather than by moving into a crevice. Surprisingly, there have even been reports of shallow-water holothuroids swimming to escape predators. For example, the North American sea cucumber *Apostichopus californicus*, when touched by the arm of the predatory seastar *Pycnopodia* lifts off the surface and swims away with an undulating movement.

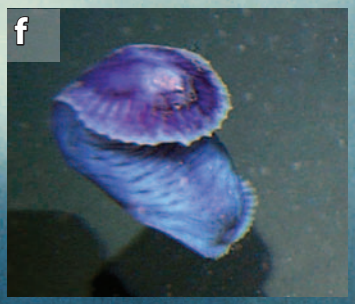
Echinoderms are often collected on floating material such as rafts of kelp. While this is a consequence of the physical removal of the macroalgal habitat from rocky reefs by storms, there have been, however, observations of hitchhiking ophiuroids. *Ophiocnemis marmorata* from Western Australia has been found on jellyfish and other animals that occur on floating objects such as dislodged buoys. In this case, it appears that ophiuroid larvae have settled from the plankton on to these floating homes (**Fig. e**). The association is not an obligatory one, as the ophiuroids are also found on the seafloor, but such hitchhiking has potential as a mechanism for long-distance dispersal.

The only truly pelagic echinoderms are deepsea elasipodid holothuroids. These sea cucumbers are the acrobats of the echinoderm world and some are strikingly coloured red or blue. Elasipodids have morphological adaptations for swimming, such as a veil-like web that connects the tube feet, and the web undulates to propel the animal (**Fig. f**). They swim down to the sediment to collect food and then swim up again. *Pelagothuria natatrix* is the most striking of these sea cucumbers, with its enormous umbrella-like veil (**Fig. g**). The animal appears to drift in the water column, and it can feed on particles that rain down on its veil. Other elasipodids are primarily benthic and only swim in response to disturbance, lifting off the seafloor by a rapid flexing movement of the body.

Further reading Glynn 1965; Mauzey *et al.* 1968; Margolin 1976; Hendler & Miller 1991; Miller & Pawson 1990; Marsh 1998

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Figures a–d, the ballerina-like swimming motions of a feather star.

Figure e, the ophiuroid ***Ophiocnemis marmorata*** (Ophiotrichidae) with a rhizostome jellyfish from off the coast of central Western Australia.

Figure f, the benthic holothuroid ***Benthodytes sanguinolenta*** (Psychropotidae) using its velum of fused tube feet to swim off the 1,000 m seafloor off Ningaloo, Western Australia.

Figure g, the holothuroid ***Pelagothuria natatrix*** (Pelagothuriidae), found at depths of 600–6,800 m in the Atlantic, Pacific and Indian Oceans, is the only true pelagic holothurian.

[a–d, J.Finn; e, C.Bryce; f, CSIRO; g, NOAA]

e

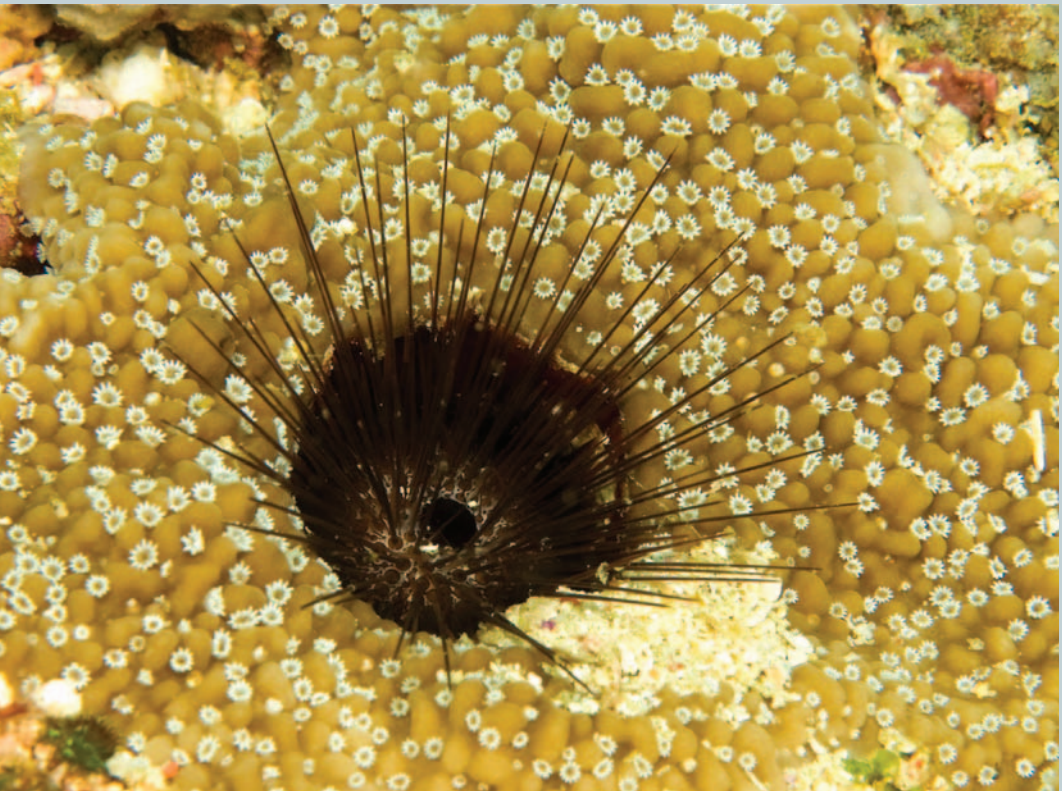


Figure 1.27 The sea urchin ***Echinostrephus aciculatus*** (Echinometridae), found widely across the Indo-Pacific including the tropical waters of northern Australia, lives in coral reef environments where it excavates a living burrow for itself. Individuals may become trapped within their burrows as they grow.

[G.Cranitch]

Sensory structures

In spite of their comparatively complex behaviour, echinoderms lack complex sense organs. The compound eyes at the tip of seastar arms (**Fig. 1.26**) are capable of true image formation. Seastars use these eyes to navigate the reef as shown in a recent study of the tropical blue seastar *Linckia laevigata* (Garm & Nilsson 2014). This is the first demonstration of visually guided behaviour in an echinoderm. Other sensory structures seen in the phylum include the sphaeridia present in the ambulacrae of sea urchins. Sphaeridia are brightly coloured knob-shaped structures that have a possible role in orientation.

Echinoderms apparently use dispersed sensory cells for visual, chemosensory and rheotactic (current-sensing) abilities to locate food and orientate their arms for suspension feeding. They do not have identifiable sense organs to match these functions. Their sensory capabilities appear to depend on superficial sensory cells around the body. Structures around the mouth, such as the oral tube feet and tentacles, are well supplied with nerves and serve a sensory/gustatory role. The tube feet are considered to have a major role in sensory reception and are known to have cells that express genes typical of those active in photoreceptor cells (Agca *et al.* 2011; Ullrich-Luter *et al.* 2011).

Echinoderms are highly sensitive to light. Many species are nocturnal, emerging from their daytime hiding places at dusk or even later. The epidermal nerve plexus appears to underlie what has long been called the general dermal light sense of echinoderms (Millot 1954; Hendler & Byrne 1987; Yerramilli & Johnsen 2010). Interestingly, the diurnal pattern of light sensitivity in some diadematid echinoids and ophiocomid ophiuroids is associated with a day-night change in colouration (**Box 1.4**). This colour change is caused by the migratory activity of skin pigment cells. Movement of these cells covers and uncovers underlying neurons that appear to function as light receptors.

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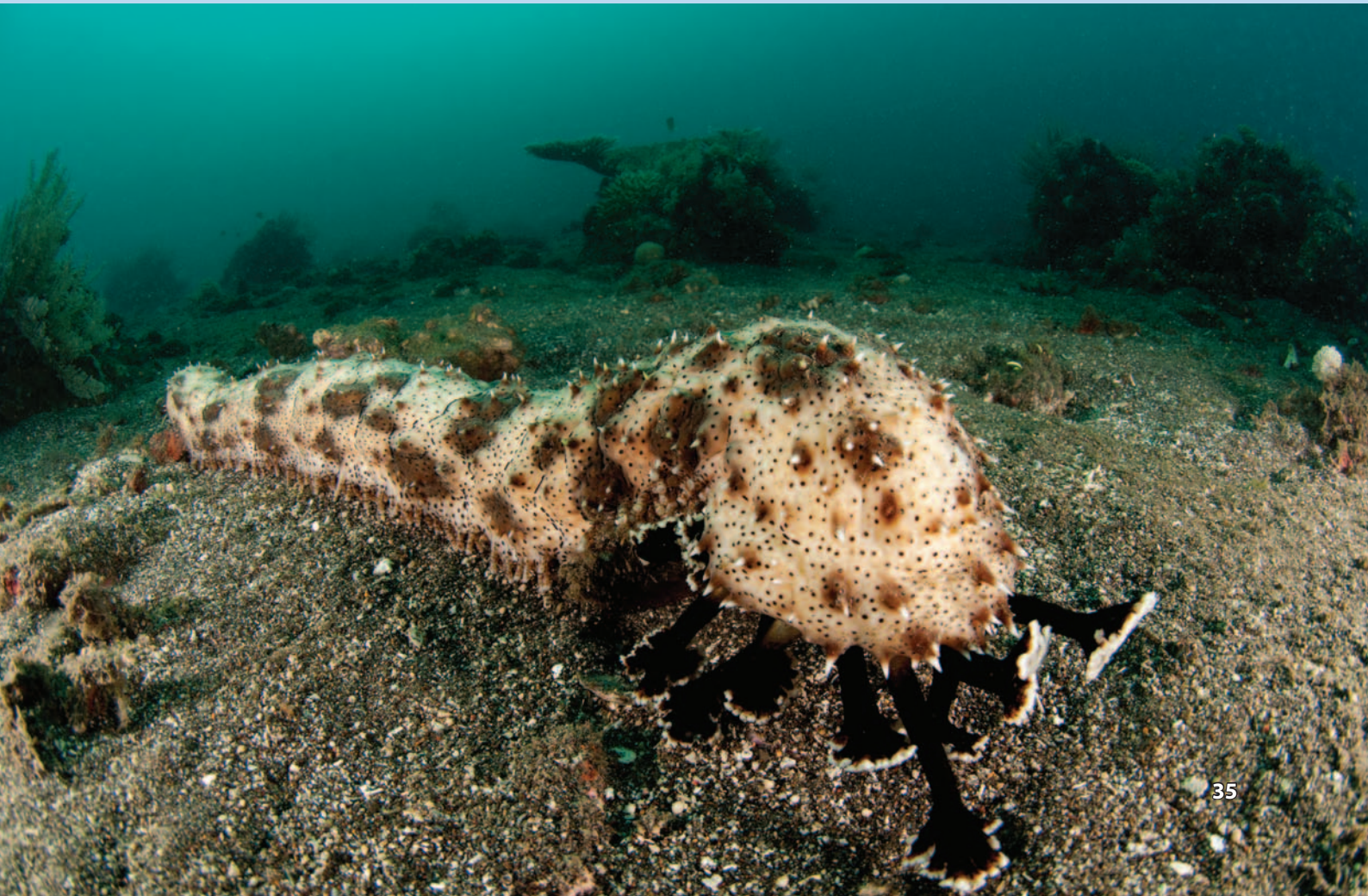
Locomotion

Locomotion is accomplished in echinoderms by structures including arms, tube feet, spines and the body wall. The approach differs among the various classes. Asteroids that inhabit hard substrates have suckered tube feet (**Fig. 1.22A**), and they move efficiently across the seafloor. In contrast, burrowing asteroids have pointed, suckerless tube feet that are used to excavate sediments. Sea urchins move about by means of their spines and tube feet. The spines articulate with a ball-and-socket joint and can move freely. Sediment-dwelling echinoids use their spines in a rowing motion to move through the sediment anterior-end forward; their small tube feet are not used in locomotion (**Fig. 2.36**). Rocky burrow-dwelling echinoids are relatively sedentary with some, such as the tropical Australian *Echinostrephus*, becoming incarcerated as the opening of the burrow is closed due to the growth of calcareous algae (**Fig. 1.27**).

Ophiuroids move over the substratum by a sinusoidal rowing motion of their arms, propelled by muscles working the joints between arm segments (**Fig. 1.6A**). Ophiuroid tube feet rarely play a major role in locomotion, although some species can climb vertical surfaces using their sticky tube feet. Burrowing ophiuroids use their tube feet to displace sediment as they plough into the substratum. Basket stars and

Figure 1.28 Motile sea cucumbers like the aspidochirotid sea cucumber ***Pearsonothuria graeffei*** (Holothuriidae) crawl across the sediment using the three rows of suckered tube feet on the underside. They are deposit feeders and use their peltate tentacles to collect sediment which is then passed to the mouth.

[J.Freund]



snake stars can spend prolonged periods with their arms coiled around corals, sponges or rocks (**Fig. 9.1; Box 9.1**), although they can also use their arms to crawl about. Some ophiuroids can swim over short distances, sometimes with the aid of specialised arm spines (Hendler & Miller 1991; **Box 1.5**).

Locomotion in holothuroids is often related to their feeding habit. Suspension feeders are often sedentary, while deposit feeders can be highly mobile, moving over or through sediments (**Figs 1.28, 2.38**). Locomotion is achieved by the tube feet working with the body wall musculature, or by undulating contractions of the body in species that lack tube feet. The medusa-like, deepsea holothuroids (elasipodids) are remarkable for their spectacular swimming and sailing modes of locomotion, propelled by contraction of the body wall muscles (**Box 1.5**). These are the only truly pelagic echinoderms (**Figs 11.15, 11.17**).

Crinoids move using their arms and, to a certain extent, their cirri and stalk. When disturbed, feather stars exhibit a spectacular swimming response, moving alternate sets of arms in balletic fashion (see **Box 1.5**).

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2: Ecology and Behaviour

Timothy D. O'Hara and Maria Byrne

Echinoderm habitats

Echinoderms are exclusively marine and are probably among the most stenohaline of marine invertebrates (Stickle & Diehl 1987; Barker & Russell 2008; Russell 2013). There are no freshwater or terrestrial species, however a few species can survive in brackish water (8–30‰), such as in the fjords of New Zealand, and the Baltic and Black seas, or in estuaries with fluctuating salinities (Stickle & Diehl 1987; Barker & Russell 2008; Russell 2013). Only crinoids have never been found in low salinity environments (Stickle & Diehl 1987). In general, echinoderms cannot prevent the accumulation of fluids in the coelom in low salinity environments.

Echinoderms occur in all marine benthic habitats from the splash zone of the intertidal to the depths of the oceanic trenches. The ophiuroid *Perlophiura profundissima* was reported from 8,135 m in the Bougainville Trench (Belyaev & Litvinova 1972) and a holothuroid from 10,710 m (Zenkevitch 1963). Some holothuroids (Pelagothuriidae) are even pelagic (**Fig. 11.17; Box 1.4**), swimming in herds above the muddy floors of the deep sea.

Some species (or complexes of species) have been reported to have vast bathymetric ranges — among ophiuroids, *Ophiura irrorata* ranges from 72 to



Figure 2.1 Intertidal pools of Australia's southern rocky shoreline provide a home for hardy echinoderms. Here you will commonly find seastars and sea urchins that are able to cope with the harsh and constantly changing environment of temperature and salinity fluctuations together with powerful wave action, exposure to the sun and the threat of predators. [J.Mallefet]



Figure 2.2 ***Meridiastra calcar*** (Asterinidae), commonly called the carpet seastar, is one of the most widespread seastars of intertidal rock pools in southern Australia. These multi-armed seastars grow to about 50 mm in diameter, and have a highly variable colour pattern, usually with a grey-green background with splashes of orange, yellow or red.

[M.Spencer]

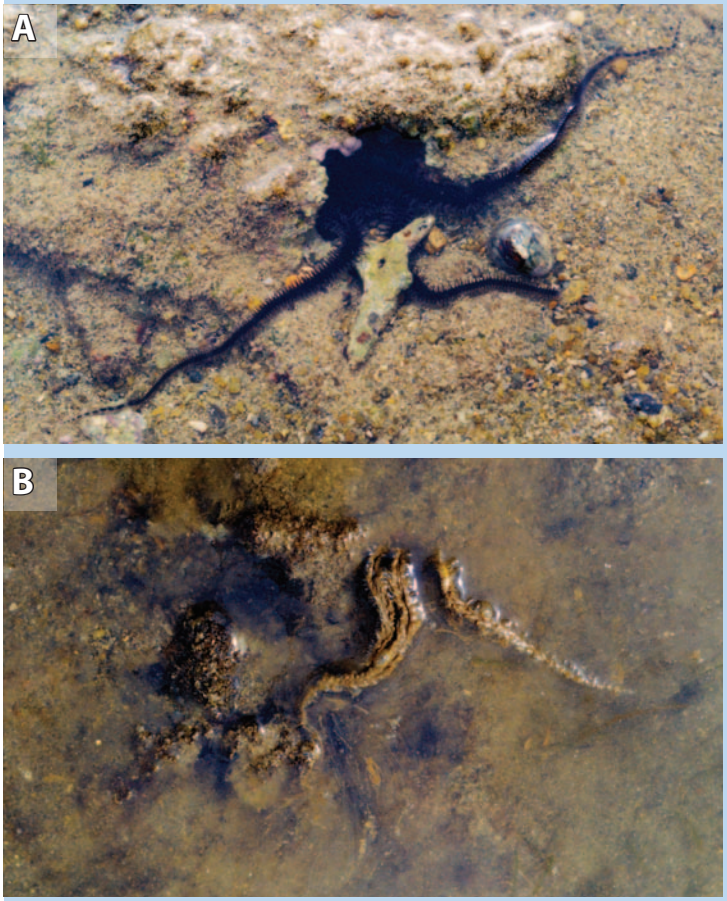


Figure 2.3 In tropical and subtropical waters of the Indo-Pacific and Red Sea the brittle star ***Ophiocoma scolopendrina*** (Ophiocomidae) is a dominant inhabitant of intertidal reef flats, living in small crevices in reef and coral rubble or dense vegetation. This species displays a distinctive feeding behaviour know as 'surface-film feeding':
A, from its crevice on an intertidal flat, ***Ophiocoma scolopendrina*** stretches out its arms at low tide, ready to feed.
B, ***Ophiocoma scolopendrina*** engaged in 'surface-film feeding'. At low tide individuals stretch arms up to the water–air interface and vigorously sweep the interface with the oral surface of the arms, gathering nutrient-rich particulate matter which is then ingested. This method of feeding ends when the water column becomes too deep for the arms to reach the surface; deposit feeding and suspension feeding may then be employed.

[M.Byrne]

5,830 m, *Asteronyx loveni* from 100 to almost 5,000 m (**Fig. 9.7A**), and *Amphipholis squamata* (**Box 9.2**) from the intertidal zone to 1,350 m (T.D.O'Hara, personal observation). There are no gas pockets in the body of echinoderms and, consequently, pressure is not a direct barrier to their distribution (Fell & Pawson 1966a). Temperature is a more potent barrier: polar, temperate and tropical regions have distinctive echinoderm communities (see **Chapter 5**).

Intertidal rock platforms

Relatively few echinoderms have adapted to the extreme environmental variability of the intertidal zone, where species must endure periods of desiccation, high temperatures and high salinities (**Fig. 2.1**). Across southern and eastern Australia asteroids of the asterinid genera *Parvulastra* and *Meridiastra* (cushion stars) can be numerous on intertidal rock platforms (McElroy *et al.* 2012; Nguyen *et al.* 2012; Nguyen & Byrne 2014; Martinez *et al.* 2016; **Figs 1.9, 2.2**). The viviparous

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asterinid seastars (**Boxes 3.1, 4.5**) are among the most tolerant echinoderms with respect to living high on the shore where they are exposed to extremes of temperature and salinity (Byrne 1996a; Byrne & Walker 2007). In eastern Australia the echinometrid sea urchin *Heliocidaris erythrogramma* (**Fig. 4.5A–E**) is common in low intertidal rock pools where it forms burrows in the substrate and catches drifting algae (Keesing 2013).

In tropical Australia, two other echinoderms are ubiquitous under intertidal rocks — the small, black holothuroid *Afrocucumis africana* (**Fig. 11.8**) and the locally super-abundant ophiuroid *Ophiocoma scolopendrina* (Byrne 2008). *Ophiocoma scolopendrina* can be readily observed scooping up the scum left behind by the retreating tide (Oak & Scheibling 2006; **Fig. 2.3**). This species is also abundant under boulders and coral rubble in the Great Barrier Reef where it can occur in very high densities (~100–200 per m^2) (M.Byrne, personal observation). Turfing coralline algae, *Corallina*, and the green alga *Halimeda*, in intertidal rocky areas in temperate and tropical areas, respectively, provide habitat for many echinoderms. They are important recruitment and nursery areas for many species with planktonic larvae and provide a living environment for a number of diminutive species, including the two ophiuroids *Ophiactis resiliens* and *Amphiura constricta* (Falkner & Byrne 2006).

Embayments

The muddy and sandy seafloors of Australia's sheltered bays and inlets support many echinoderms. The most common groups are the filter-feeding amphiurid ophiuroids (**Figs 1.11A, 9.20**), which project their long arms into the water column, and deposit-feeding holothuroids, heart urchins and sand dollars that digest organic particles from the sediment. In Port Phillip Bay, Victoria, some of the most abundant invertebrates are the brittle stars *Amphiura elandiformis* and *A. parviscutata*; the synaptulid sea cucumber *Rowedota allani*; and the heart urchin *Echinocardium cordatum* (**Fig. 2.36; Box 10.6**). Other groups include scavenging ophiuroids, such as *Ophiura kinbergi* and *Ophiomusium* species (**Fig. 9.9**), that skate along the seafloor seeking carrion and prey; and carnivorous asteroids, such as species of *Astropecten* and *Coscinasterias* (**Fig. 1.8B,C**), that favour bivalves. In the tropics, large asteroids including species of *Anthenea*, *Archaster* and *Protoreaster* (**Figs 2.4, 8.16, 8.29, 8.30**) and holothuroids, such as *Holothuria*, can be numerous in sheltered waters (**Fig. 11.1**).

Faunal diversity is generally higher within seagrass meadows, as they include niches not available in muddy and sandy habitats (Waycott *et al.* 2007). Few species eat the unpalatable seagrass fronds, but the ubiquitous

Figure 2.4 Seagrass meadows provide a rich habitat for many marine animals including a variety of echinoderms like these chocolate chip seastars, ***Protoreaster nodosus*** (Oreasteridae), which commonly form aggregations.

[D.Harasti]





Figure 2.5 The temnopleurid sea urchin ***Amblypneustes pallidus*** is found usually attached to seagrass and algal holds in the temperate waters of southern Western Australia and South Australia (see also **Box 10.2**).

[G.Bell]

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algal epiphytes as well as seagrass detritus are consumed by herbivorous echinoids (species of *Holopneustes* and *Amblypneustes*; **Figs 2.5, 2.17**) and omnivorous asteroids, such as *Meridiastra gunnii* and *M. calcar* (**Fig. 2.2**). Ophiuroids and crinoids use the seagrass fronds as perches from which to feed on plankton carried by tidal currents, and deposit-feeding holothuroids feed on the organically enriched sediments present around the seagrass rhizomes (Wolkenhauer *et al.* 2010). The presence of the sea cucumber *Holothuria scabra* (**Fig. 4.3A**) in the subtropical seagrass beds of Moreton Bay can enhance growth of the seagrass, presumably due to enhanced nutrient cycling when this species is present (Wolkenhauer *et al.* 2010). More importantly, seagrasses provide an important nursery resource for juveniles for a number of echinoderms, including the sea urchin *Tripneustes gratilla* and several commercially important species such as the sea cucumbers — sandfish, *H. scabra*, and the black teatfish, *H. whitmaei* (Koike *et al.* 1987; Hamel *et al.* 2001; Vaïtilingon *et al.* 2003; Byrne *et al.* 2004b; **Fig. 4.3B**).

In channels in the embayments, 'mini-reefs' formed from clusters of ascidians and sponges provide shelter and food for echinoderms. Around much of southern Australia, the solitary ascidian *Pyura stolonifera* forms the basis of these clusters, anchored into the sediment by a long rhizome. Sponges, hydroids and bryozoans then colonise these ascidian thickets. Brittle stars, such as ophiotrichids (*Ophiothrix caespitosa* and *Macrophiothrix spongicola*; **Fig. 1.1B**) and ophiactids (*Ophiactis savignyi*; **Fig. 9.21D**) associate with sponges on these 'mini-reefs'. The brittle stars can take advantage of the currents created by the sponges to facilitate their own feeding, and, remarkably, *Ophiothrix* species have been seen to clean the surface of their host, clearing particles that obstruct the flow (Hendler 1984a). The larvae of *O. fragilis* in European waters settle preferentially on sponges (Turon *et al.* 2000) and on the surface of adult *O. fragilis* (Morgan & Jangoux 2004). Australian species such as the ophiuroids *Ophionereis schayeri* and *Ophiomyxa australis*, asteroids *Coscinasterias muricata*, and the holothuroid *Australostichopus mollis,* use these 'mini-reefs' as shelter (**Fig. 2.6**). In the tropics, the ophiuroid *Ophiactis savignyi* can be endozoic, living within the canal system of certain sponges (Caspers 1985).

Shallow-water mangrove habitats also support many echinoderms and are important nursery areas for juvenile asteroids, including *Archaster typicus* (Bos *et al.* 2011; **Fig. 8.16**).





Figure 2.6 In broad coastal bays, small reefs, predominantly covered with sponges and ascidians, provide a safe refuge for a number of echinoderms.

A, the brittle star ***Ophiomyxa australis*** (Ophiodermatidae) frequents both shallow and deep reefs to about 400 m around most of Australia's shores and the Indo-west Pacific.

B, the large eleven-armed seastar ***Coscinasterias muricata*** (Asteriidae) is common in the temperate waters of southern Australia and New Zealand, where it inhabits rocky and sandy areas, under rocks and in the open, to a depth of 150 m.

[A, R.Paton; B, G.Bell]



Figure 2.7 The rich marine environments of tropical coral reefs support an extraordinary number of colourful echinoderms, such as these conspicuous feather stars ***Anneissia bennetti*** (formerly ***Oxycomanthus bennetti;*** Comatulidae). Attached atop a coral bommie, with arms extended, they feed in the strong currents.

[F.Bavendam]

Reefs

Large numbers of filter-feeding echinoderms make use of habitats with high water movement around subtidal rocky and coral reefs; these currents provide a rich source of planktonic food (**Fig. 2.7**). Most notably, these echinoderms tend to be crinoids, basket stars and cucumariid holothuroids (**Figs 1.16A, 9.1**). In southern Australia, kelp holdfasts often contain many ophiuroids (*Ophiactis resiliens*, *Ophiothrix caespitosa*) and holothuroids (*Plesiocolochirus ignavus*). Larger species, such as the ophiuroids *Ophionereis schayeri* and *Clarkcoma canaliculata*, and the crinoid *Cenolia trichoptera*, are found under rocks and in crevices. Sea urchins play a major ecological role grazing algae from rocks and in determining benthic habitat type. *Centrostephanus rodgersii* forms 'barrens', areas completely cleared of foliose algae (Byrne & Andrew 2013; Keesing 2013; **Box 2.1**). This diadematid sea urchin tends to live in crevices during the day, emerging at night to graze on algae, thus forming macroalgal-free areas around its burrow. In south-eastern and southern Australia *Heliocidaris erythrogramma* also forms barrens (Keesing 2013). The temnopleurid sea urchin *Holopneustes purpurascens* is unusual in being a canopy dweller living wrapped in kelp (**Box 10.2**). Some asteroids, such as *Uniophora granifera* and *Coscinasterias muricata* (**Figs 1.8B, 8.39**), are important predators of molluscs on temperate rocky reefs, whereas others, including species of *Pentagonaster*, *Petricia, Fromia* and *Nectria* (**Figs 2.8, 8.19, 8.22D-H**), feed on colonial invertebrates.

Echinoderms are a conspicuous and ecologically important component of coral reef communities (Birkeland 1989a; Byrne *et al.* 2004b; Byrne 2008; Pearse

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2009). Crinoids are particularly diverse and abundant on coral reefs (see **Chapter 11**), taking advantage of the many elevated perches to spread out their arms and feed (**Fig. 2.7**). The most famous echinoderm, however, is the asteroid *Acanthaster planci* (the crown-of-thorns seastar), a predator of coral polyps (**Figs 2.12, 8.15; Box 4.4**). When populations of this species build to large numbers (called outbreaks; see **Chapter 4**) they can consume large quantities of coral polyps on a reef, leaving behind white coral skeletons (**Fig. 4.9B**). Among other large asteroids in tropical regions is the pincushion star, *Culcita novaeguineae* (**Fig. 8.28**), which also eats coral polyps, as well as algae and detritus. Most coral reef seastars belong to the family Ophidiasteridae, which includes the large blue seastar, *Linckia laevigata,* and multicoloured *Fromia*, *Nardoa* and *Tamaria* species (**Fig. 8.25A–F**). These species graze on the surface, eating encrusting sponges and other animals.

Ophiuroids are also diverse on coral reefs, particularly species in the family Ophiocomidae (**Fig. 9.12**). The black *Ophiocoma erinaceus* and various *Ophiomastix* species inhabit coral heads, and a range of other species live under coral rubble and in clumps of the green alga *Halimeda*. Ophiotrichids are also common. Among these, *Macrophiothrix* species (**Fig. 9.22B–D**) extend their long arms from burrows under rocks, and *Ophiothrix* and *Ophiopteron* species can be found at night, wound around tubular soft corals.

Sea urchins are important members of the grazing guild on coral reefs and play a key ecological role in preventing algae from overgrowing coral. Diadematid needle-spined urchins (*Diadema*, *Echinothrix*) typically live in crevices in the coral reef during the day and emerge at night to feed (McClanahan & Muthiga 2013; Muthiga & McClanahan 2013). *Echinometra*, a complex of species across the tropical Indo-Pacific, are major bioeroders of reef substrate, chewing through coral rubble (**Fig. 2.9**). They are often common in very shallow water. In Ningaloo Reef, Western Australia, *Echinometra* species are superabundant in reef habitat where they form extensive burrows in dead coral, habitat generated by the scraping activity of their teeth (**Box 10.3**). In contrast, on the Great Barrier Reef *Echinometra* species are far less abundant (M.Byrne, personal observation).

Coral reefs also support a high diverstity of holothuroids from the families Holothuriidae (for example, *Holothuria*, *Bohadschia*, *Actinopyga*), Stichopodidae (*Stichopus*, *Thelenota*) and Synaptidae (*Synapta*, *Opheodesoma*) (see **Chapter 11**). Many of the large tropical species are commercially important and are harvested in Australia and elsewhere for bêche-de-mer (see **Chapter 4**).

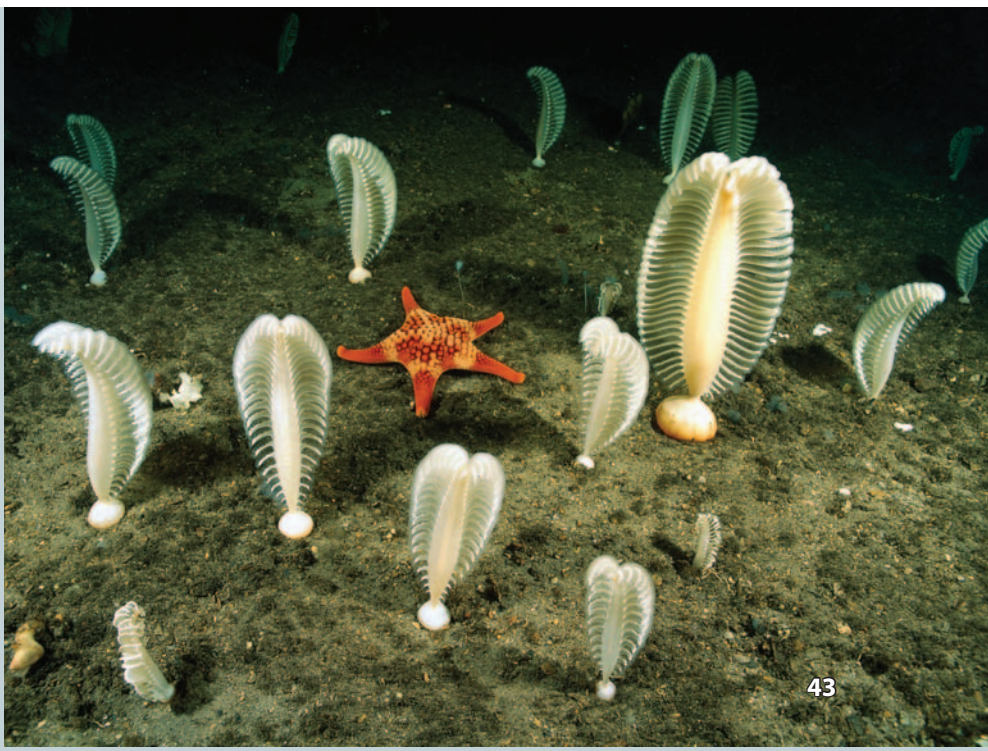


Figure 2.8 The eight species of the endemic genus ***Nectria*** (Goniasteridae) are among the most colourful sea stars found in Australia's southern temperate waters. Living mostly in habitats associated with rocky reefs and shorelines, and sometimes seagrass meadows, from the mid-west of Western Australian to mid-east of New South Wales and Tasmania, they feed primarily on sponges, ascidians, bryozoans and algae. One of the most vibrant sea stars, the ocellate seastar ***Nectria ocellata*** grows to 260 mm; here it crawls among a field of sea pens, ***Sarcoptilus grandis*** (Cnidaria: Pennatulacea), in search of food in the waters of Port Davey, Tasmania.

[F.Bavendam]



Figure 2.9 Members of the sea urchin genus ***Echinometra*** (Echinometridae) are capable of significant bioerosion across the tropical Indo-Pacific. In Australia, ***Echinometra*** species can abrade large quanitities of reef rock/coral while feeding and excavating burrows. Feeding activity is greatest at night. This genus is in need of taxonomic revision and at least four species occur in tropical Australia (see **Box 10.3**).

[C.Bryce]

Numerous closely related species often co-occur on the same reef, especially at tropical latitudes (Byrne *et al.* 2004b). Careful study of these animals has indicated that they have slightly different habitat, feeding or reproductive biology, and that they may not be in direct competition with each other (Sides & Woodley 1983). One of the best known examples of this phenomenon is among *Ophiocoma* brittle stars that dominate shallow tropical reefs. Six to seven species can often be found on reefs across the Indo-west Pacific, including the Great Barrier Reef in the north-east and Ashmore Reef off Western Australia (**Fig. 9.12B,C**). Close examination of some of these indicated the presence of cryptic species and, consequently, even greater diversity than currently appreciated (O'Hara *et al.* 2004). These species inhabit the reef infrastructure or rubble and are often very abundant in rubble areas shoreward of the reef crest (Byrne *et al.* 2004a). On Indian Ocean and Pacific Ocean reefs, including Hawaiian reefs, these animals have been found to have similar feeding strategies, but markedly different microhabitat specialisations. For example, *O. scolopendrina* prefers the high intertidal (**Fig. 2.3**), *O. pica* inhabits live coral heads, and *O. brevipes* lives in sand under rocks (Chartock 1972; Sloan *et al.* 1979).

On deeper reefs, a range of epizoic ophiuroids and crinoids occur on foliose black corals, sea fans and sea whips. Ophiuroids include the basket stars (*Euryale*, *Astroboa*; **Figs 1.12A, 9.1**), the snake stars (*Astrobrachion*; **Box 9.1**), the colourful Ophiotrichidae, and the small Ophiactidae and Ophiacanthidae species. Crinoids are very abundant on deeper reefs in tropical regions, including the striking multi-armed *Anneissia* species (**Fig. 7.1**).

Continental shelf and slope

Below the influence of wave action, the continental shelf shares many species with sheltered embayments. Members of the families Amphiuridae and Ophiuridae dominate the ophiuroid fauna on soft sediments, with species of Ophiotrichidae, Ophiomyxidae and Ophiactidae common among sponges and other colonial invertebrates. Echinoids include pencil urchins such as *Goniocidaris* (**Fig. 10.8C**) and a range of heart urchins including *Brissus* (**Fig. 10.41**).

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An important change in faunal composition takes place between the continental shelf (<200 m) and the continental slope. Numerically, ophiuroids and holothuroids dominate echinoderm slope faunas. The Ophiacanthidae and Ophiuridae are the most diverse ophiuroid families, providing almost two-thirds of the species from the continental slope off south-eastern Australia (T.D.O'Hara, personal observation). Typically, the Ophiacanthidae are filter-feeders, with many species epizoic on cold water corals and sponges. The Ophiuridae generally inhabit the sediments and are deposit feeders or active carnivores.

Deepsea holothuroid families include the Elpidiidae, Synallactidae, Gephyrothuriidae (Aspidochirotida), Laetmogonidae, Deimatidae, Psychropotidae (Elasipodida) and Molpadiidae (Molpadida). Numerous species from these families are known from the east coast of Australia (O'Loughlin 1998a, 1998b), including the elpidiids, which are able to walk across the seafloor on their large tube feet (Pawson 1982a).

Crinoids, asteroids and echinoids are less common, but often attain a larger size and sometimes cluster. Meadows of stalked crinoids of the family Isselicrinidae occur along rocky ridges, and the deepsea asteroids of the families Goniopectinidae, Ctenodiscididae, Porcellanasteridae, Pterasteridae, Benthopectinidae, Brisingidae and Zoroasteridae tend to inhabit soft sediments.

Seamounts, vents and the abyssal plain

The seamounts south of Tasmania were surveyed extensively in 1997 and 2007 before and after the establishment of a deepsea marine protected area (**Fig. 2.10; Box 4.6**). The deeper seamounts with intact *Solenosmilia* coral cover were found to support a diverse and abundant ophiuroid fauna with subantarctic affinities (Koslow & Gowlett-Holmes 1998; O'Hara *et al.* 2008). Most are filter feeders, including numerous members of the Ophiacanthidae. Several stalked crinoids were found that had never been reported previously from Australia (Améziane & Roux 2011). The asteroids included several species of multi-armed Brisingidae such as *Novodinia australis* (**Figs 2.10, 8.43**) and *Brisingella distincta* that lift their arms into the currents to feed. Seamounts affected by trawling were covered with the elongate orange sea urchin *Dermechinus horridus* (**Fig. 10.22E,F; Box 4.6**). Holothuroids were rare. The 2003 NORFANZ expedition discovered a rich echinoderm fauna on seamounts across the Lord Howe Rise and Norfolk Ridge (Williams *et al.* 2006).

The only collections reported from the abyssal plain (>4,000 m depth) around Australia are four trawls taken by the research ship *Galathea* in the Tasman Sea as part of the Danish Deep Sea Expedition 1950–1952.



Figure 2.10 The deepsea benthic communities of the Tasmanian seamounts are diverse and unique. At depths below 1,400 m the benthic floor is mostly dominated by the coral ***Solenosmilia variabilis***, which provides a sheltered environment for a variety of animals such as crabs, fish, sea spiders, brittle stars and seastars like ***Novodinia australis*** (Brisingidae). [CSIRO]

Box 2.1 Urchin barrens and abalone

In many temperate regions of the world, large sea urchins and abalone co-occur and utilise strikingly similar macroalgal food and habitat resources. Abalone and sea urchins also have the same predators, including humans, they have similar life histories with dispersive larvae, and their juveniles recruit to crustose coralline algal habitats near the adults. The ecological overlap and potentially competitive relationship between these fishery species have prompted a number of studies into their ecological interactions.

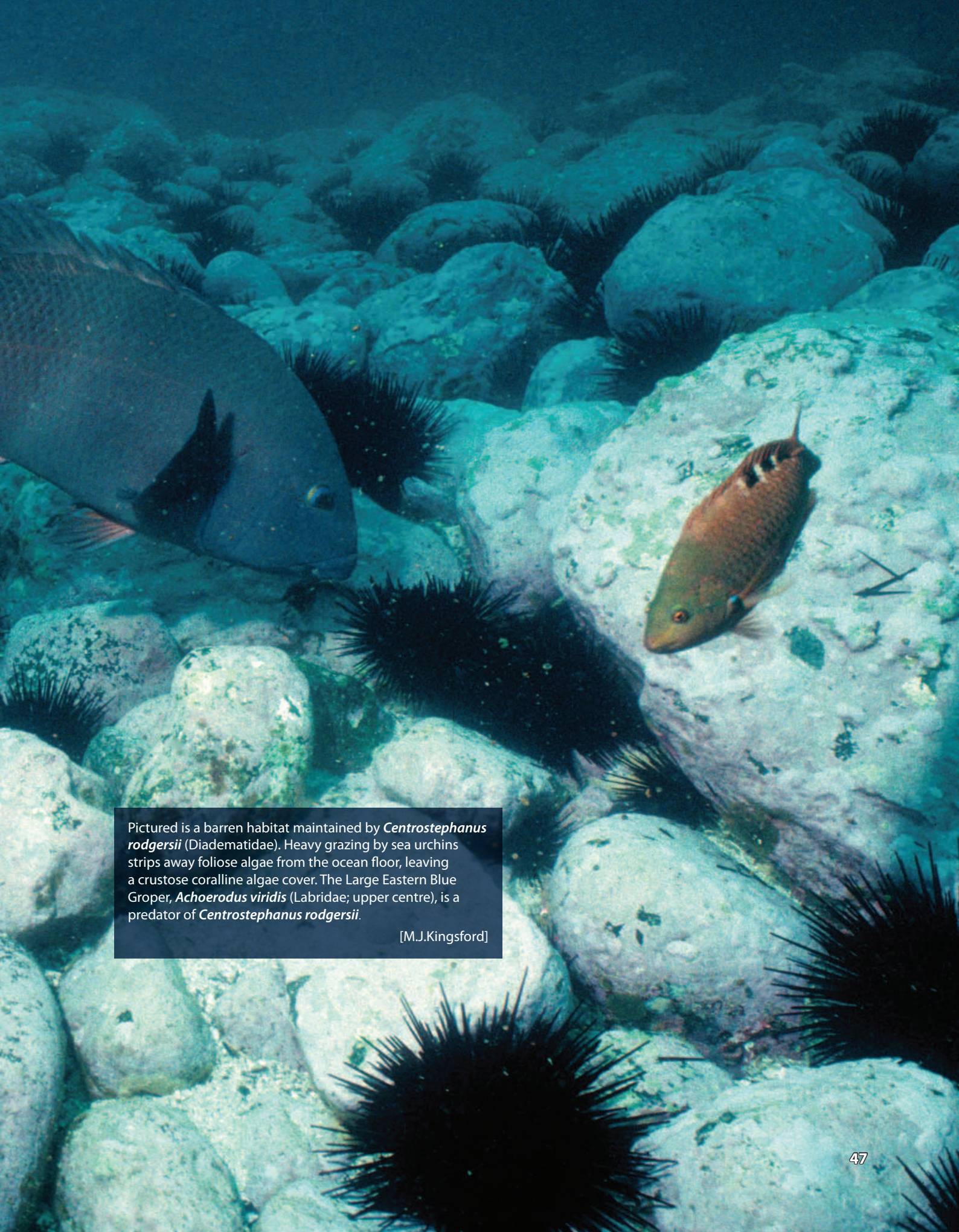
Abalone and sea urchins are major grazers of macroalgae. Sea urchins have a profound influence on the balance between the presence of kelp and barren ground habitats. Along the east coast of Australia, grazing by the sea urchin *Centrostephanus rodgersii* creates a mosaic of these two habitat types. In areas where urchins are numerous and the physical environment allows them to graze away from shelter, the seafloor is devoid of kelp and is covered by encrusting pink coralline algae. Under these conditions urchins are sustained by drift kelp and can maintain this environment; their resilient physiology adjusts body and gonad growth to food availability. In other regions, where urchin foraging is constrained by lower population density or environmental conditions, lush beds of the kelp *Ecklonia radiata* dominate the seafloor. This is so striking that on clear days with good visibility the mosaic of habitats of fringe and barrens can be seen during aerial surveys of the New South Wales coast. The recent spread of *C. rodgersii* to Tasmania has seen the creation of extensive barrens, this invasion having been facilitated by the southerly transport of larvae in the East Australian Current, the circulation of which is being altered by climate change. Interestingly, the Western Australian species *C. tenuispinus* is not known to exert a similar influence on habitat.

With its ability to influence the local availability of food and shelter, *C. rodgersii* can have a profound impact on abalone populations. This appears to be so in New South Wales where abalone are rare in the barrens habitat, and although the interaction in extreme barrens seems to result in direct competitive exclusion of abalone, the relationship is more complex than meets the eye. A similar competive interaction between abalone and *C. rodgersii* is evident in Tasmania following the southern range extension of this urchin from New South Wales.

In some regions, urchins and abalone can have a mutually beneficial interaction, because, by their grazing, urchins maintain patches of encrusting coralline algae, the preferred settlement substrate for abalone larvae. Juvenile abalone also shelter under the spine canopy of urchins, and in South Africa the protection of juvenile abalone from predators such as fish and lobster is essential for sustaining abalone populations. Furthermore, given their ability to ensnare drift kelp, sea urchins provide food for the abalone. The recruitment and early juvenile success of abalone along the west coast of North America appears to be dependent on the grazing and shelter provided by sea urchins.

Further reading Andrew 1993; Andrew *et al*. 1998; Mayfield & Branch 2000; Ridgway 2007; Ling *et al*. 2008, 2009a, 2009b; Strain & Johnson 2009; Byrne & Andrew 2013

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Pictured is a barren habitat maintained by ***Centrostephanus rodgersii*** (Diadematidae). Heavy grazing by sea urchins strips away foliose algae from the ocean floor, leaving a crustose coralline algae cover. The Large Eastern Blue Groper, ***Achoerodus viridis*** (Labridae; upper centre), is a predator of ***Centrostephanus rodgersii***.

[M.J.Kingsford]

Only the holothuroids have been identified, and these included six species of elasipodids (Hansen 1975), many of which also occur on the lower continental slope (O'Loughlin 1998a). However, studies elsewhere in the world have reported small paedomorphic ophiuroids from the family Ophiuridae on the abyssal plain and in the oceanic trenches (Belyaev & Litvinova 1972). No hydrothermal vent or cold hydrocarbon seep faunas have been described from Australia, although several vent-specialist ophiuroids are known from the Atlantic and eastern Pacific oceanic ridges (Tyler *et al.* 1995a; Stöhr & Segonzac 2006).

Interactions

Feeding

Echinoderms exhibit a wide range of feeding strategies reflecting the diverse morphologies and evolutionary histories of the various groups (Jangoux & Lawrence 1982; Lawrence 2007, 2013a, 2013c; Martinez *et al.* 2017). The more important of these strategies are discussed in **Chapter 1** and are further described in **Chapters 7–11**.

Predators

Many echinoderms are predatory, but these, in turn, are consumed by a range of predators. Predation is so important that many specialists believe that it has driven much of the evolution of echinoderms. The diversification of fish in the Mesozoic has been implicated in the elimination of the large aggregations of ophiuroids and stalked crinoids that characterised Palaeozoic seas (Aronson 1987). The decline of the holasteroid and cassiduloid heart urchins in Australia corresponds with the arrival of predatory cassid molluscs (McNamara 1994b). The spiny nature and nocturnal habits of many echinoderms are adaptations

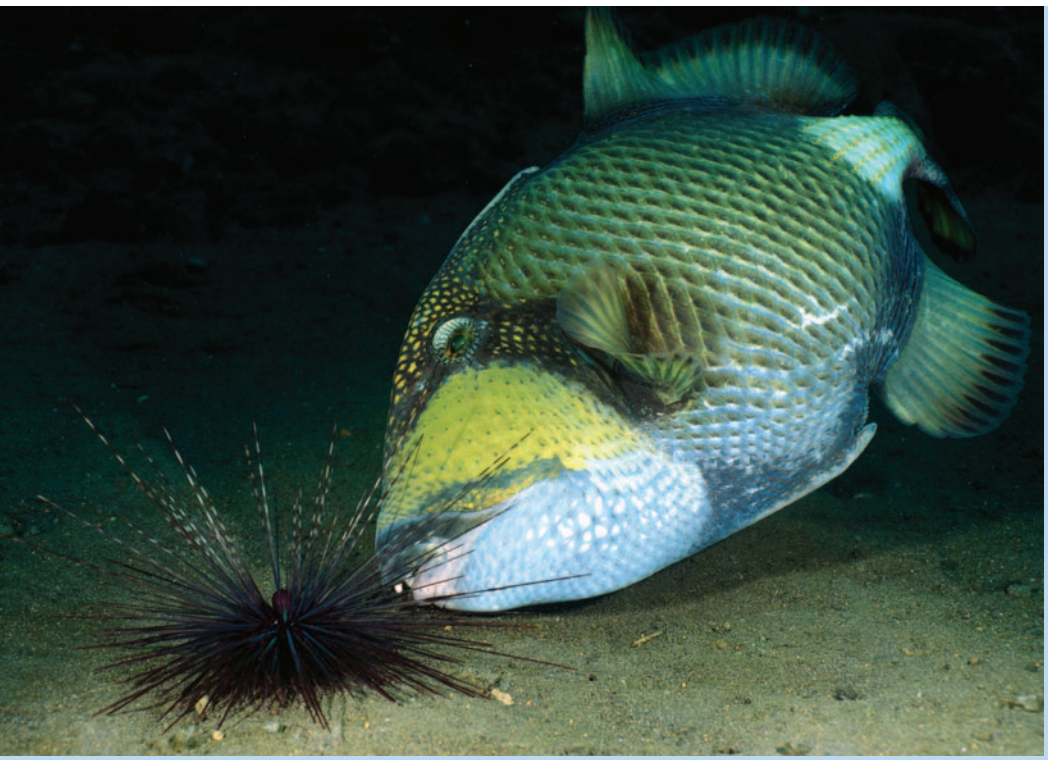


Figure 2.11 A Titan Triggerfish, ***Balistoides viridescens*** (Balistidae), attacks a long-spined sea urchin, ***Diadema setosum*** (Diadematidae), it has dislodged from between rocks. Titan Triggerfish use their strong jaws and prominent chisel-like teeth to flip over sea urchins and crack the tests on the aboral surface where there are fewer spines; they also feed on corals, crabs, molluscs and tube worms. Titan Triggerfish are also territorial and have been seen to remove ***Linckia*** seastars from their province; the Triggerfish picks up the seastar in its mouth and drops it some distance away (M.Byrne, personal observation). [F.Bavendam]

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Figure 2.12 The giant triton, ***Charonia tritonis*** (Ranellidae), is one of the few predators of the crown-of-thorns seastar, ***Acanthaster planci*** (Acanthasteridae); see also **Box 4.4**.

[G.Bell]

affording defence against predation (Keesing & Halford 1992a, 1992b). Many echinoderms also occupy chemically rich habitats such as those which include sponges and algae that are unpalatable to fishes; this may be another predator avoidance mechanism for echinoderms (Hendler & Littman 1986; Falkner & Byrne 2006).

Fish, gastropods, octopus, crabs and lobsters are the major predators of adult echinoderms in many environments (**Figs 2.11, 2.12, 10.5**). Two of the best known molluscan predators are the giant triton (*Charonia tritonis*) which preys on the crown-of-thorns (*Acanthaster planci*; **Fig. 2.12**) and the pincushion seastar (*Culcita novaeguineae*), and the helmet shell (*Cassis cornuta*) that preys on urchins (**Fig. 10.5**). At the other extreme are coral polyps that can capture small echinoderms (Hendler & Littman 1986). Asteroids and cidaroid urchins also prey on other echinoderms. For example, the asteroid *Mediaster australiensis* has been recorded as a significant predator of the ophiuroid *Ophiacantha fidelis* on the continental slope of eastern Tasmania (Blaber *et al.* 1987), and the deepsea cidaroid sea urchins can attack and consume stalked crinoids (Baumiller *et al.* 2001, 2008). On temperate rocky shores *Parvulastra exigua* (**Fig. 1.9**) is preyed on by *Meridiastra calcar* (**Figs 2.2, 8.17F**), and this may be a factor in the separation of these two species into the mid and low intertidal zones, respectively (Stevenson 1992).



Figure 2.13 The sea urchin ***Heliocidaris erythrogramma*** (Echinometridae) with bald spot disease. Lesions, most likely caused by a bacterial infection, develop on the test causing necrosis and loss of spines. This can result in the death of the individual.

[B.Mos]

Diseases

Echinoderms are host to a range of diseases caused by microorganisms (Jangoux 1987a), often seen as bald or darkened patches on the body. These diseases are caused by bacteria. Bald spot disease of sea urchins, where necrotic lesions of tissue develop on the test, is common in Australian species and many other species around the world (**Fig. 2.13**). This disease is lethal and appears to be caused by pathogenic bacteria (*Vibrio*) (Gilles & Pearse 1986; Becker *et al*. 2007; Girard *et al*. 2012; Wang *et al*. 2013; Sweet *et al*. 2016). The test loses its spines at the 'spot' and weakens as necrosis develops. In the terminal stages of the disease the bald spots may develop a green colour as the naked test patch is colonised by algae. Sea urchin bald spot disease appears to be on the increase due to climate-driven increases in sea temperature (Girard *et al*. 2012; Sweet *et al*. 2016; Brothers *et al*. 2016a). In New South Wales increased incidence of bald spot disease in *Heliocidaris erythrogramma* and *Holopneustes purpurascens* is correlated with increasing sea temperatures (Sweet *et al*. 2016).

Mass mortalities of urchins have occurred in the North Pacific (*Strongylocentrotus purputatus*), North Atlantic (*Strongylocentrotus droebachiensis*) and the Caribbean (*Diadema antillarum*) in the 1980s (Gilles & Pearse 1986; Scheibling & Hennigar 1997; Lessios 1988, 1995, 2005; Muthiga & McClanahan 2013; Scheibling & Hatcher 2013). The disease in the North Atlantic was caused by an amoeboid agent, whereas an unknown organism was responsible for the Caribbean event. The die-off of *Diadema* was catastrophic: the sea urchin disappeared from most of the region which resulted in an ecological shift from coral reefs to algal reefs. Thirty years later the *Diadema* populations are only present in patches and they seem unlikely to recover to previous densities due to low spawner density preventing successful reproduction (Levitan *et al*. 2014). Mass mortalities of *Strongylocentrotus purputatus* and *Paracentrotus lividus* (Atlantic and Mediterranean) were due to bald spot disease (Gilles & Pearse 1986; Girard *et al*. 2012). As sea urchins are considered to be the most important group of consumers living in shallow water, these mass mortalities have major ecological implications (Steneck 2013).

Microbial infections of crown-of-thorns seastars have been described from juveniles, but do not appear to influence the population size of this seastar. The most recent echinoderm disease-driven mass mortality is from the seastar wasting disease. This has resulted in the death of thousands of asteroids along the west coast of North America (Hewson *et al*. 2014). The disease attacks many species causing the seastars to degenerate and then fall apart; a number of asteroid species have disappeared from extensive areas of coastline. The disease is transmissible and the disease-causing agent appears to be a virus (Hewson *et al*. 2014).

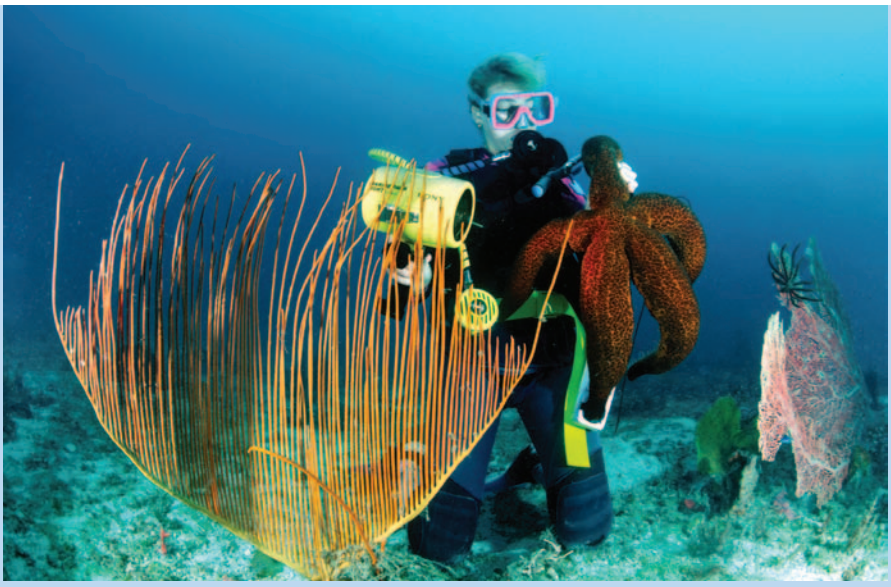


Figure 2.14 ***Thromidia catalai*** (Mithrodiidae), sometimes called the giant seastar, can reach a span of 600–650 mm and weigh up to 6 kg. It is found across the Indo-Pacific and in Australia it lives in the tropical waters of Queensland and Western Australia.

[G.Bell]

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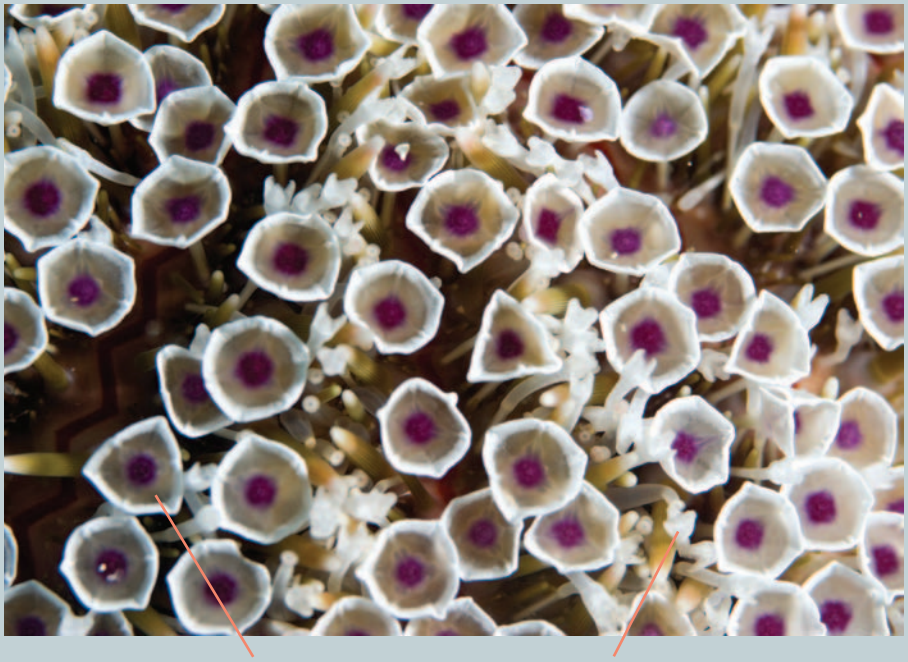


Figure 2.15 The flower urchin, ***Toxopneustes pileolus*** (Toxopneustidae), can be easily identified by the presence of conspicuous and abundant venomous, stalked globiferous (flower-like) pedicellariae scattered among the spines. Comprising three valves, each of which ends in a fang-like tip, the white 'circular' ends of the pedicellariae act like jaws, snapping shut when touched; they are effective against predators and larger ectoparasites. Smaller ophicephalous pedicellariae are also abundant; they resemble tube feet, but end in three small valves, and are responsible for removing encrusting organisms and debris.

[M.Spencer]

Defence against predators

Echinoderms have developed a number of defensive strategies against predators, and these are reviewed below.

Size

The large size attained by some holothuroids and asteroids is effective protection against predators (**Fig. 2.14**). Such echinoderms cannot be consumed whole, and they can rely on their amour, spines and toxins to deter attempts to remove pieces of their flesh. Species that have few predators as adults, such as the crown-of-thorns seastar or the holothuroid *Holothuria scabra*, live cryptically as juveniles when they are more vulnerable to predation (Keesing & Halford 1992a, 1992b; Hamel *et al.* 2001). In general, the early benthic stages of echinoderms are cryptic, although the ecology of juveniles of most species is poorly understood.

Toxins, spines and mucus

Many crinoids, asteroids and holothuroids have in their skin toxic or unpalatable chemical compounds which deter predation. Skin extracts have been found to cause distress, disorientation and death of fish, and paralysis in mice (Rao *et al.* 1985), but not in predatory molluscs or crustaceans (Yamanouchi 1955). These compounds include terpenes and saponins. Research on the chemistry of protective compounds produced by echinoderms has focused on northern hemisphere or Antarctic species, including species found in Australian Antarctic waters (McClintock 1989). Many common Australian echinoderms are likely to be toxic, given their bright colours and ability to feed undeterred in the open during daylight hours.

The spines of some asteroids and echinoids are tipped by venomous skin (Marsh & Slack-Smith 1986), and this venom is injected when the spine penetrates a victim's body. The crown-of-thorns seastar can inflict a painful reaction when touched. Sea urchins of the family Diadematidae have needle-like spines tipped with toxins, and the hollow spines of *Diadema*,

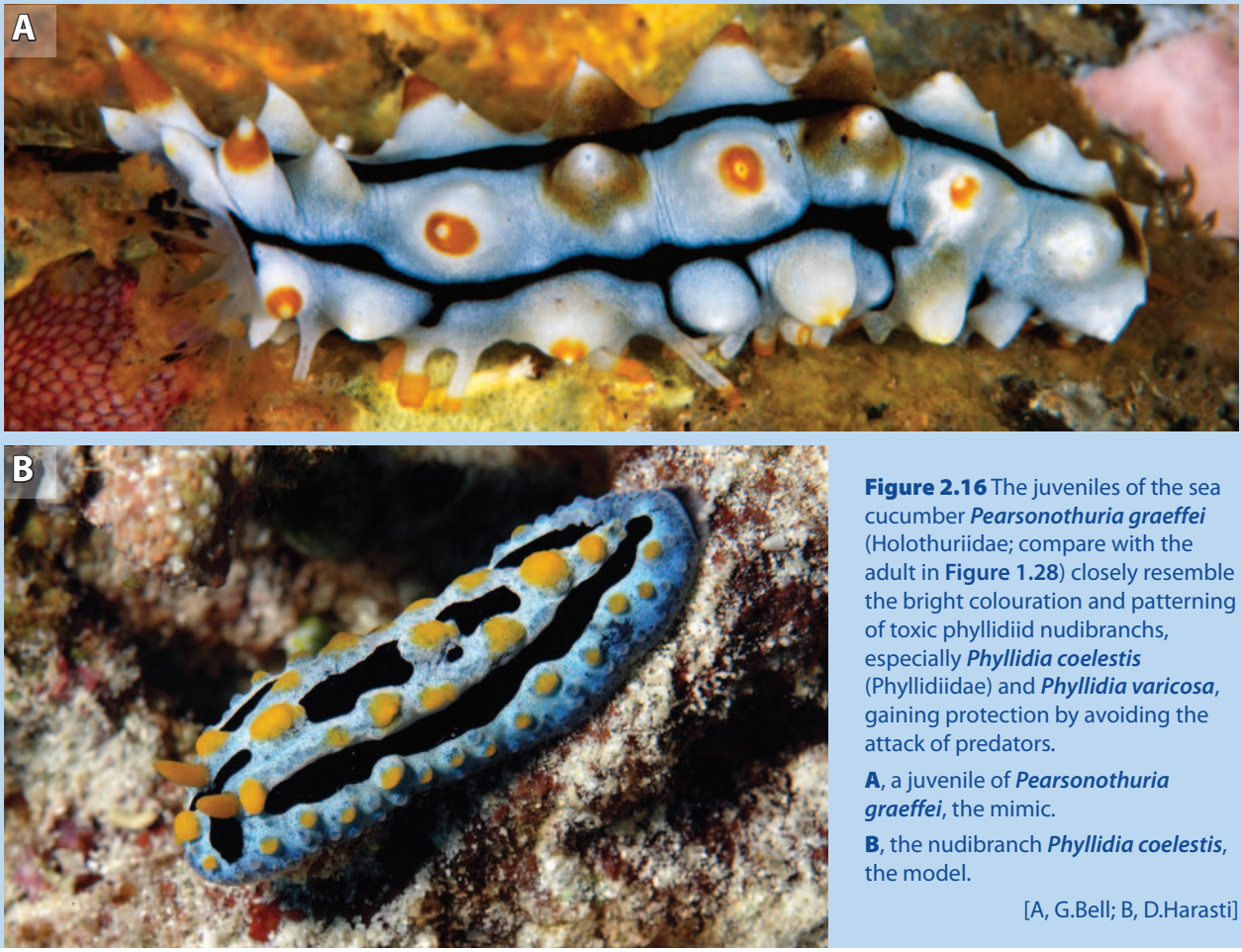


Figure 2.16 The juveniles of the sea cucumber ***Pearsonothuria graeffei*** (Holothuriidae; compare with the adult in **Figure 1.28**) closely resemble the bright colouration and patterning of toxic phyllidiid nudibranchs, especially ***Phyllidia coelestis*** (Phyllidiidae) and ***Phyllidia varicosa***, gaining protection by avoiding the attack of predators.

A, a juvenile of ***Pearsonothuria graeffei***, the mimic.

B, the nudibranch ***Phyllidia coelestis***, the model.

[A, G.Bell; B, D.Harasti]

following penetration of a victim, may fragment into pieces. When threatened, *Diadema* bunch their spines together, pointing them towards the disturbance. Spines of *Echinothrix* sea urchins have terminal barbs that are very difficult to remove once they are embedded in a victim's surface tissue.

In sea urchins, toxins are not only restricted to spines. Toxic pedicellariae, rather than spines, occur in urchins of the family Toxopneustidae. The large flower-like pedicellariae of *Toxopneustes pileolus* (**Figs 2.15, 10.23F**) have fang-like tips that can inject venom, causing serious pain in humans.

While the toxins released by echinoderms cause a painful sting-like reaction the pain is short lived. Echinoderm toxins are not known to have long-term effects on humans.

Some ophiuroids, such as *Ophionereis schayeri* and *Ophioderma devaneyi*, produce copious quantities of mucus when disturbed; this is a stress response and possibly a defensive mechanism (Hendler & Miller 1984a; Christensen *et al*. 2011). *Ophiocoma* species are also reported to have defensive mucous secretions (Fontaine 1964).

Camouflage

Whereas some species use toxins to fend off or discourage predators, others have evolved strategies to avoid being seen, and both strategies can occur within the same genus. For example, *Stichopus chloronotus* is an olive-green holothuroid that is conspicuous on coral reef flats and toxic to fish (Bakus 1981), while the sympatric *S. monotuberculatus* and *S. horrens*

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Figure 2.17 Many echinoderms have adopted strategies to blend with the environment to avoid being noticed by predators. The southern Australian endemic sea urchin ***Holopneustes inflatus*** (Temnopleuridae) wraps itself in seagrass, becoming less readily visible. [M.Norman]



Figure 2.18 A leopard fish, ***Bohadschia argus*** (Holothuriidae), ejects Cuvierian tubules from its anus as a defensive response to disturbance. These tubules are very sticky and can ensnare the intruder.

[G.Bell]

take cover by day under coral slabs and presumably are not as toxic. Juvenile holothuroids of the species *Pearsonothuria graffei* appear to mimic nudibranchs (**Fig. 2.16**). Some ophiuroids can change colour from day to night, presumably enhancing their camouflage or altering the exposure of photosensitive tissue to light and thus allowing the animal to detect and escape to darkened crevices at night (**Box 1.4**). Other species are bioluminescent, perhaps deterring predators with a flash as the predator bumps into the arms, or autotomising an arm that flashes to serve as a decoy (**Box 2.2**).

Some echinoderms enhance their camouflage by covering themselves with sediment or detritus. *Holopneustes* sea urchins, common on southern Australian reefs and seagrass beds, encase themselves in pieces of algae and seagrass during the day and often drop this cover at night (**Fig. 2.17**). Sea urchins such as *Temnopleurus alexandri* and *Pseudoboletia indiana* cover their surface with shells. Holothuroids such as *Holothuria atra* use their tiny tube feet to cover themselves with sand. For *H. atra*, however, this sand-covering behaviour may also convey some photo-protection in its sunny environment.

Photophobia and escape reactions

Many echinoderms avoid predation by fish by hiding during the day and emerging at night to feed. They exhibit a strong negative reaction to light and a positive reaction to touching the substratum (Reese 1966). Light, touch and chemical substances are detected by specialised tube feet or cells spread throughout the skin (Pentreath & Cobb 1972; Sloan & Campbell 1982). Sea urchin tube feet have an extensive system of photoreceptors (Agca *et al*. 2011; Ullrich-Luter *et al*. 2011). Typically shelter is found under rocks, in crevices, or by burrowing into the seafloor. In contrast, deepsea species, living without light below the depths where visual predators forage, often remain permanently exposed (see **Box 4.6**).

The escape behaviour of some tropical holothuroids takes the form of 'bounding' away from molluscan predators (Kropp 1982; **Box 1.5**). When attacked, *Stichopus chloronotus* tries to shake off the predator, roll away and then escape by arching its body, followed by successive peristaltic waves. Other species, such as *Holothuria cinerascens*, contract lengthwise and swell centrally, forming a spherical shape that prevents the predator gaining a hold when the holothuroid is sheltering in a crevice; others escape by means of a short burst of swimming (**Box 1.5**). The seastar *Parvulastra exigua* exhibits a fleeing response if touched by the sympatric sea star *Meridiastra calcar*. This latter species preys on *P. exigua* (Stevenson 1992). Aggressive behaviour can also occur, and several *Ophiocoma* brittle stars are known to actively defend their crevices (Sides 1985).

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Box 2.2 Bioluminescence

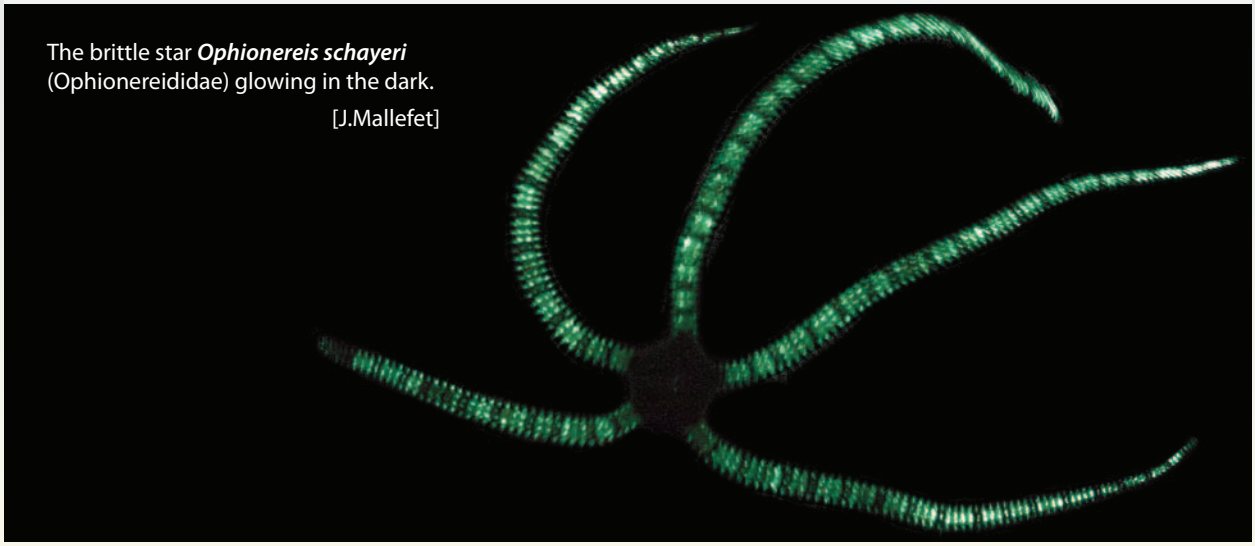
Bioluminescence is known to occur in all echinoderm classes except the echinoids. The most spectacular fireworks-like displays are seen in certain ophiuroids — the impressively bioluminescent species of *Ophiopsila*, which extend their arms at night to feed on suspended particles, emit small flashes when the arms are touched by passing plankton. A bright green flash extends down the length of the arm from the point of contact, and this rapid response (50–100 ms) is thought to be achieved by specialised neuronal cells known as photocytes. The action of these cells appears to be controlled by nerves that run along the length of the arms. The conduction velocity of 450 mm/s indicates the involvement of giant fast-acting axons.

Recent investigations of the physiology of luminescence have concentrated on the cosmopolitan ophiuroid *Amphipholis squamata* (Mallefet 1999). When disturbed, the arms of *A. squamata* exhibit a luminescent glow. Each colour morph of this species has a different pattern of luminescence. The response involves calcium ions and is modulated by a number of neurotransmitters including acetylcholine.

Luminescent ophiuroids in Australia include *Ophiopsila pantherina*, which forms extensive populations off the Great Barrier Reef; this species displays the intense green flashes characteristic of the genus. In temperate Australia, luminescent species include *Ophionereis schayeri*, *Amphiura constricta*, *Ophiactis resiliens*, *Ophioplocus bispinosus* and *Ophiacantha alternata*. *Ophionereis schayeri* exhibits the most dramatic response, with green flashes travelling down the arm from the disc. In other species, the response is more of a glow rather than a flash.

The function of bioluminescence is unclear. It may serve as a lure on an autotomised arm, distracting the predator from the retreating animal. Experimental evidence, however, indicates that bioluminescence in *Amphipholis squamata* increases the risk of predator attack. In this case bioluminescence may attract secondary predators that prey on the predator threatening *A. squamata*. Other uses may be to attract or stun prey or to advertise unpalatability.

Further reading Brehm & Morin 1977; Shimomura 1986; Herring 1995; Mallefet 1999; Dupont 2002; Byrne 2009; Woolsey *et al*. 2013



The brittle star ***Ophionereis schayeri*** (Ophionereididae) glowing in the dark. [J.Mallefet]





Figure 2.19 Aggregations of ophiuroids.

A, offshore ***Ophiothrix fragilis*** (Ophiotrichidae) of the eastern Atlantic and Mediterranean sometimes aggregates in vast numbers — up to 2,000 individuals have been reported in a square metre (Warner & Woodley 1975). It suspension feeds, raising its arms to catch particles floating by.

B, at the shelf edge of the Great Barrier Reef vast dune fields support huge numbers, of over 400 individuals per square metre, of the brittle star ***Ophiopsila pantherina*** (Amphiuridae; Woolsey *et al*. 2013). With the disc buried in a sand burrow, they extend their arms to feed in the water current.

[A, K.Hiscock; B, M.Byrne]

Autotomy

The 'lizards' tail' approach is also common among echinoderms (**Box 1.1**). Some ophiuroids, crinoids and asteroids readily drop parts of their arms (autotomy) in response to a predator attack (Emson & Wilkie 1980; Wilkie 2005). The arm fragment, which can maintain independent movement for some time, distracts the predator, allowing the animal to escape. The echinoderm subsequently regenerates the lost arm (**Fig. 3.7C; Box 1.3**).

Sublethal predation associated with autotomy can be very important for some species. For example, predators often consume the autotomised arms of filter-feeding ophiuroids (Bowmer & Keegan 1983).

Arms are not the only body structure that can be shed. Some amphiurid brittle stars shed their discs, including gonads and stomach and, amazingly, they regrow all of these structures from the skeletal oral ring. It has been suggested that for a Florida species, *Ophiophragmus filograneus*, this behaviour is a response to predation by stingrays which readily consume the nutritious discarded discs (Turner *et al.* 1982), but equally it could be just a general stress response. The holothuroids *Stichopus chloronotus* and *S. horrens* can shed a piece of body wall that will satisfy a predatory gastropod (Kropp 1982). These species will completely disintegrate if handled for any length of time (Motokawa & Tsuchi 2003). Other holothuroids autotomise their digestive tract, a phenomenon called evisceration (see below), in response to a predatory attack (**Box 1.1**). Following evisceration the digestive tract is regenerated.

Holothuroids — Cuvierian tubules and evisceration

Some aspidochirotid holothuroids have specialised defensive structures called Cuvierian tubules (**Fig. 2.18**). These are long white slender tubules that

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are ejected from the anus when the animal is disturbed, and they can become strongly adhesive on contact with seawater. In some species (for example, *Holothuria leucospilota*) these tubules are thread-like, while in *Bohadschia* species they are thicker (**Fig. 2.18**). There has been much interest in the underwater 'super-glue' produced by the Cuvierian tubules as a structural biomaterial (De Moor *et al.* 2003). The function of these structures has been debated for over a century (Hamel & Mercier 2000), and although they seem capable of ensnaring predators and have been observed to catch crabs in the laboratory (Flammang *et al.* 2002), there is a lack of field evidence to support this conclusion. Their sudden ejection and toxic nature may also act as a diversion or a repellent to predators.

Holothuroids that eviscerate their intestines do so through the anus (aspidochirotids) or mouth (dendrochirotids) (**Box 1.1**). Southern Australian representatives of these groups include *Australostichopus mollis* and *Thyone okeni* respectively (Dawbin 1949; Tracey 1972). Many of the *Holothuria* species in tropical Australia also eviscerate (M.Byrne, personal observation). Evisceration involves the loss of the gut, the haemal system and the water vascular system. Dendrochirotids also lose their tentacle crown and aspidochirotids their respiratory trees. This action can be a response to a disturbance, or it can be a seasonal occurrence. Seasonal evisceration may be involved in the elimination of waste material that has accumulated as brown deposits in the gut wall (Byrne 1985a; Fankboner & Cameron 1985) or may play a role in the expulsion of parasites (Byrne 1985b). It is debatable if evisceration is a defensive response as it tends to happen too long after the disturbance for it to be effective against most predators (Tracey 1972) with the exception of predatory seastars (Byrne 1985a).

Aggregations

Some echinoderms form dense aggregations of many individuals (Warner 1971, 1979; **Figs 1.16A, 2.4, 2.19, 9.11G**). Boom and bust cycles are observed in some populations and, consequently, aggregations can vary over time (Uthicke *et al.* 2009). They can last as long as 50 years or more, or they can be short-lived (days to weeks). The size and longevity of aggregations in echinoderms can be cyclical or seasonal (Uthicke *et al.* 2009). Although this phenomenon tends to occur in areas of high prey or nutrient availability, such events can be more than merely a response to food and habitat. The benefits of aggregation include the increased likelihood of reproductive success, protection against predation, stability in fast-flowing currents, and increased deposition of suspended food particles through disturbance of the benthic water movement (Warner 1984). An aggregation can be actively maintained by the individuals involved, so that the European brittle star *Ophiothrix fragilis* will actively seek an aggregation of the same species if moved into nearby bare areas (Broom 1975; **Fig. 2.19A**). Aggregations of this species are maintained over successive generations for at least 50 years by the preference of larvae to settle on the bodies of adults (Warner 1984). Similar long-term stable aggregations are characteristic of amphiurid brittle stars in soft bottom habitats in the North Atlantic (O'Connor *et al.* 1983, 1986). Off the Great Barrier Reef, aggregations of the brittle star *Ophiopsila pantherina* form vast beds on underwater sand dunes at depths of 70 m, extending their arms to feed (Byrne 2009;

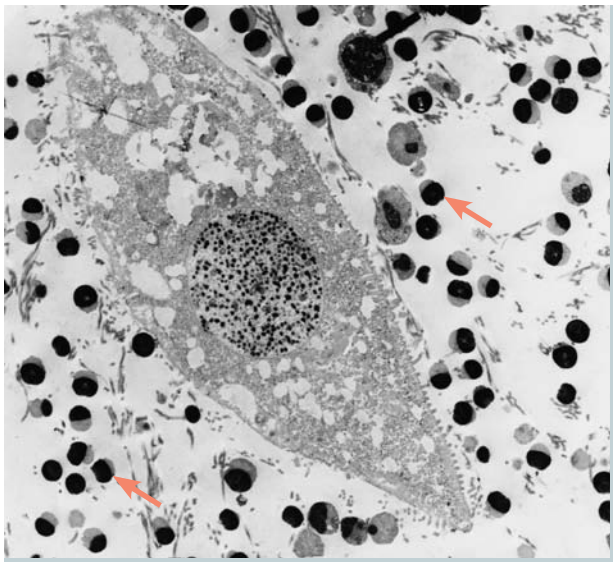


Figure 2.20 The testes of the Northern Pacific seastar, ***Asterias amurensis*** (Asteriidae), can become infested with the ciliate *Orchitophyra stellarum*. Here the protist is surrounded by seastar sperm (arrows) which it ingests, thus reducing fertility and in some cases castrating the male seastar.

[M.Byrne]

Woolsey *et al.* 2013; **Fig. 2.19B**). Stable aggregations of *Centrostephanus* sea urchins in barrens are a conspicuous feature of the shallow subtidal in south-eastern Australia (**Box 2.1**) and may be related to the reduction in numbers of sea urchin predators (Byrne & Andrew 2013).

Off south-eastern Australia, the ophiuroids *Ophiothrix aristulata, Ophiocamax applicatus* (**Fig. 9.11G**) and *Ophiacantha fidelis* occur in enormous numbers on the continental slope (Madsen 1967; Blaber *et al.* 1987; O'Hara 1990). For the latter, species densities of 261–522 animals per square metre have been measured at 420–580 m off Maria Island, Tasmania, from underwater photographs, giving an average biomass of 52.2 grams per square metre.



Figure 2.21 Most members of the molluscan family Eulimidae are highly specialised and exclusively parasitic on echinoderms. Most attach permanently like this blue eulimid limpet, ***Thyca crystallina***, living on the oral surface of the blue seastar ***Linckia laevigata*** (Ophidiasteridae). It is the female limpet that is visible, the dwarf male lives under the shell of the female.

[J.Freund]

Echinoderm parasites and associates

Parasites

Echinoderms are host to a range of parasitic organisms (Jangoux 1987a, 1987b, 1987c). Sporozoan protists infest the coelom and tissues of many echinoderms. The ciliate *Orchitophyra stellarum* infests the testes of seastars, including the Japanese species *Asterias amurensis* (Northern Pacific seastar), causing partial or complete castration (**Fig. 2.20**). In cases of a high parasite load the testes become infertile. However, the possibility of using *Orchitophyra* as a biological control against populations of *A. amurensis* in Australia has been rejected because it is not host-specific, and it could parasitise native stars (Byrne *et al.* 1997a).

A parasitic nematode, *Echinomermella matsi*, infects the coelom of urchins and can occupy the whole body space causing rapid mortality (Jones & Hagen 1987). Many flatworms, mostly belonging to the family Umagillidae, occur in the coelom and digestive tract of echinoderms (Shinn 1981, 1983a, 1983b, 1985). The relationship between these worms and their echinoderm host is not well understood. However, due to the ingestion of host coelom cells and intestinal tissue by umagillids in sea cucumbers and sea urchins, they can be considered parasitic (Shinn 1981, 1983a, 1983b). Dissections of *Meridiastra* species (Asterinidae) usually reveal small red umagillids living in the body coelom (M.Byrne, personal observation). Nothing is known about host-worm relationships for Australian echinoderms.

Parasitic snails of the family Eulimidae prey almost exclusively on echinoderms and include ecto- and endoparasitic species (**Figs 2.21, 10.31A; BoxFig. 7.1e**). Victorian populations of the common temperate seastar *Meridiastra calcar* can host large numbers of the eulimid *Apicalia brazieri* (Hales 2006). These snails commonly parasitise aspidochirotids with soft body walls, such as the tropical species *Holothuria fuscorubra* (syn. *Holothuria isuga*) (Byrne 2008). Surface-dwelling eulimids insert their proboscis through the body wall into the host's coelom and haemal system (Egloff *et al.* 1988). The proboscis functions like a straw, sucking up host body fluids as a food source. Endoparasitic eulimids include gall-forming species, one of which induces the formation of large lumps along the arms of *Linckia multifora* (**Fig. 8.26**), a seastar common along the Great Barrier Reef. This seastar readily discards arms, but those infected by the snails cannot be

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Figure 2.22 Some of the more unusual associates of crinoids are the polychaetous myzostome worms (now all assigned to the one family, Myzostomidae). Myzostomes may be free-living with vagile forms which move freely over the host, or external sessile forms; others live in skeletal crypts, soft tissue cysts or pinnule galls and some are internal parasites. Except for some endoparasitic and stalk-dwelling myzostomes, all feed on food particles trapped in the ambulacral grooves of the host's pinnules, arms or centrodorsal. In Australian seas, myzostomes are most numerous in tropical waters, with only a few species recorded from the temperate coasts.

A, **B**, Two myzostomes recorded from Lizard Island, Great Barrier Reef, Queensland.
A, ***Myzostoma furcatum***, a vagile form, living on the arms and pinnules of the crinoid ***Himerometra robustipinna*** (Himerometridae).
B, ***Myzostoma*** sp., a sessile form, living on the centrodorsal of a comasterid crinoid.

[G.W.Rouse]

autotomised because the parasite, by some unknown mechanism, suppresses the response (Davis 1967). Eulimid parasites of sea cucumbers are bizarre worm-like organisms. These gastropods have lost all of their free-living features, including their shell. Much of the female body is occupied by a massive ovary (Byrne 1985b). The female is accompanied by a dwarf male. Their gastropod affinity is seen in the reduced veligers brooded by the females (Byrne 1985b; Altnöder *et al.* 2007). An eulimid, likely to be a new species, parasitises *Holothuria atra* in tropical Australia (M.Byrne, personal communication).

Myzostomes are striking animals and have a long history of association with crinoids, the two often being found together as fossils. Myzostome polychaetes are usually specialised associates of crinoids (**Fig. 2.22; Box 7.1**), although a few species are associated with asteroids and ophiuroids. The ectoparasitic forms are disc-shaped worms that move rapidly along the crinoid arms, stealing food. The endoparasitic forms feed on host tissues.

Crustaceans can also parasitise echinoderms. Ecto- and endoparasitic copepods are common and conspicuous, especially in ophiuroids where they can occupy the gonads and bursa. *Cancerilla* copepods often occur on

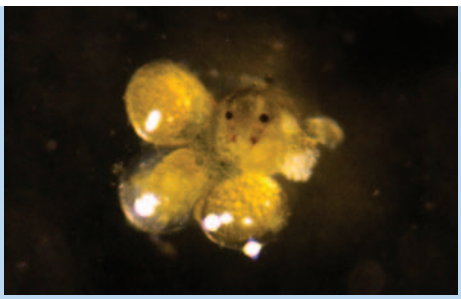


Figure 2.23 Eggs of one of the marine caddisflies removed from the coelom of the intertidal temperate seastar ***Parvulastra exigua*** (Asterinidae); the embryonic insect with two black eyes can be seen. The caddisfly larvae escape from the echinoderm and live and feed on calcareous algae in the intertidal pools. However, since large numbers of the caddisfly eggs are laid into the tufts of the calcareous algae, it is likely that their occurrence within the seastar coelom is accidental (Leader & Bedford 1979).

[M.Byrne]

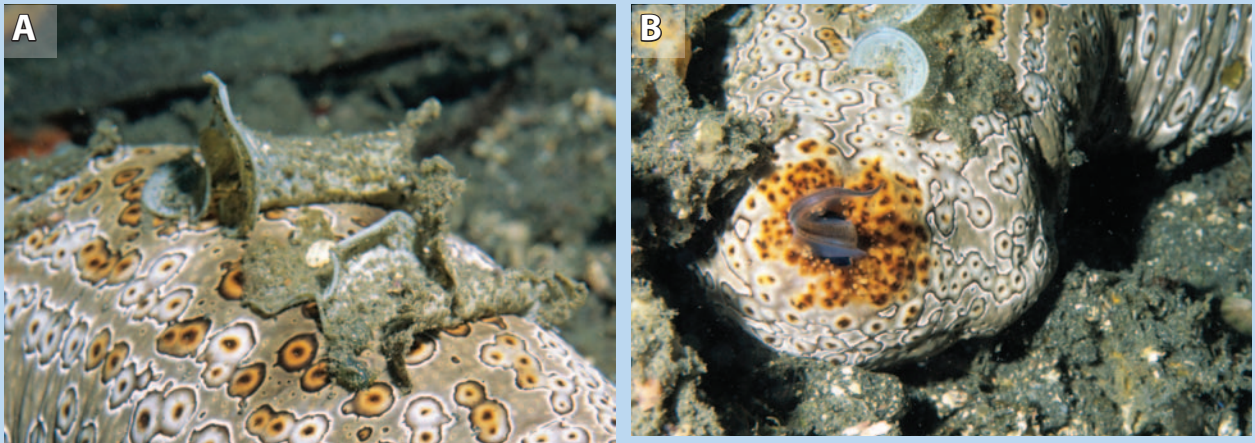


Figure 2.24 Silver Pearlfish, ***Encheliophis homei*** (Carapidae) swimming near its host, the holothuriid sea cucumber ***Bohadschia argus*** (**A**). By day, the pearlfish lives inside the sea cucumber, entering through the anus (**B**), but at night it leaves to feed. The 30 or so pearlfish species are highly modified, lacking scales and pelvic fins. Most live in the body cavites of sea cucumbers, giant clams and pearl oysters in a putatively commensal relationship, not harming their host. Some species, however, are parasitic on sea cucumbers, eating their gonads.

[C.Marshall]

the oral surface of *Amphipholis squamata*. *Cucumaricola* copepods have been identified from the coelom of the southern Australian holothuroid *Cucuvitrum rowei* (O'Loughlin & O'Hara 1992). Copepods can also induce gall-formation in the body wall, with galls evident as lumps on the skin. Other crustacean parasites include small pinnotherid crabs that feed on the surface of echinoids and others that encyst in the respiratory trees of sea cucumbers (Hamel *et al.* 1999). Some surface-dwelling copepods are cryptically coloured, matching their host, as in the species on the tropical asteroid *Echinaster luzonicus* (**Fig. 8.38F**).

Ascothoracid 'naked' barnacles live as ectoparasites on crinoids and ophiuroids and as endoparasites in asteroids and echinoids. The endoparasitic species can take over the body, feeding on host cells and fluid. These grow to be enormous females, accompanied by a dwarf male, and their presence may castrate their host.

Intertidal asterinid seastars serve as hosts for the larvae of caddisflies. Adult caddisflies deposit eggs in the coelom of seastars (Anderson *et al.* 1976). Dissection of the seastar *Parvulastra exigua* can reveal the surprise of 'beads' of developing caddisfly embryos with pairs of black eyes evident through their egg cases (**Fig. 2.23**).

The most unusual parasites of echinoderms are pearlfishes that live in the coelom of tropical sea cucumbers and in the body cavity of tropical seastars (Van Meter & Ache 1974; Parmentier & Das 2004; Parmentier & Vandewalle 2005; **Fig. 2.24**). Some are permanent residents in the coelom while others repeatedly enter and exit the host via the anus. The permanent residents are harmful, consuming the host's viscera, particularly the gonads, while pearlfishes that emerge appear to forage outside their holothuroid home. Dissection of large sea cucumbers can reveal that the only contents are pearlfish which have consumed all of the viscera (M.Byrne, personal observation). It is not known if sea cucumbers can recover from such devastating consumption of their body parts. Considering their large size, pearlfishes are likely to have a deleterious effect on their host. To communicate, pearlfishes make a grunting sound that transmits

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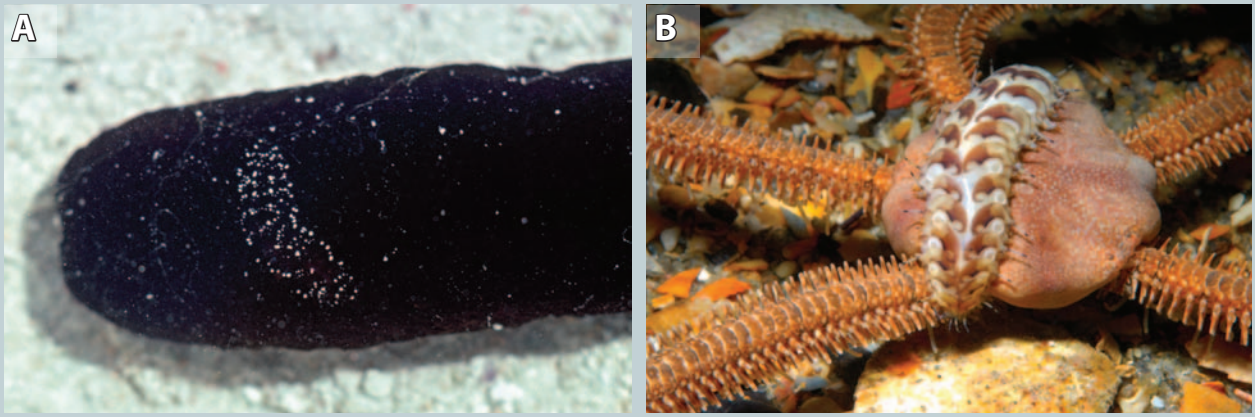


Figure 2.25 A number of scale worms live on echinoderms where they are typically found in the feeding grooves of arms, or if found on holothurians, firmly attached to the body wall; most closely resemble their host, having similar colouration and patterning. **A**, a black scale worm with white spots attached to the sea cucumber ***Holothuria atra*** (Holothuriidae) from the Great Barrier Reef. The colour of the worm matches that of the sea cucumber's body and the white spots mimic sand grains. **B**, the polychaete scale worm ***Lepidonotus melanogrammus*** (Polynoidae) riding on the disc of the southern Australian ophiuroid ***Ophionereis schayeri*** (Ophionereididae).

[A, M.Byrne; B, J.Finn]

throught the body wall of the host. Thus these fishes may call to each other from within the relative safety of their sea cucumber host (Parmentier *et al.* 2006).

Commensal associations: excluding Crustacea

Many invertebrates use the surface of echinoderms as a substrate and source of shelter (David *et al.* 2009; Purcell & Eriksson 2015). Some of the better known examples can be symbiotic polychaete scale worms (Polynoidae). These commensals are amazingly camouflaged — for example, the black scale worm, occasionally with white spots that resemble sand grains, is barely discernible on the surface of black sea cucumbers (**Fig. 2.25A**). Only a trained eye can detect them easily. The southern Australian scale worm *Lepidonotus melanogrammus* has a very similar colour pattern to its associate, the banded ophiuroid *Ophionereis schayeri* (**Fig. 2.25B**).

Echinoderms can be host to sessile epizoic animals such as sponges and bryozoans (**Fig. 2.26**). The



Figure 2.26 The distinctive spines of the eastern slate-pencil urchin, ***Phyllacanthus parvispinus*** (Cidaridae), are often covered with colonial animals such as sponges, bryozoans and hydroids.

[D.Harasti]



Figure 2.27 Babysitting ophiocomid ophiuroids on the Great Barrier Reef — the juveniles of ***Ophiomastix caryophyllata*** settle on the adults of ***Ophiomastix janualis***. Juveniles are found attached to the disc or lie in the bursa of the adult, and once a certain disc size is reached they leave their host. [J.Finn]

spines of cidaroid sea urchins are not covered by epithelium and hence they are often covered by encrusting animals (David *et al*. 2009). They are an important habitat for these associates. Commensal galeommatoid bivalves are commonly associated with sediment-dwelling echinoderms such as the sea urchin *Eupatagus valenciennesii* (**Fig. 10.44C**). The common Antarctic ophiuroid *Ophiurolepis gelida* is usually densely covered by an epizoic sponge *Iophon radiatus* (Dearborn 1977), and the Antarctic deepsea holothuroid *Pseudostichopus spiculiferus* is also covered by a sponge (O'Loughlin & Ahearn 2005). The tropical nudibranch *Plakobranchus ocellatus* lays its egg masses on the surface of *Holothuria atra*, where the developing young may be able to develop in an environment that is chemically protected due to the presence of toxins in the body wall of its host (Mercier & Hamel 2005). The holothuroid *Stichopus herrmanni* hosts many epibiont species, including some echinoderms — ophiuroids, asteroids and synaptid sea cucumbers (Purcell & Eriksson 2015).

One of the most interesting associations is exhibited by the baby-sitting brittle stars (**Fig. 2.27**). Typically, these are ophiocomid species in which the larvae of one species settle in the bursae of another species and remain associated with the bursae and the surface of the new surrogate parent until they reach an advanced juvenile stage (Hendler *et al.* 1999a; Fourgon *et al.* 2007).

Other associates reside within and under the spine canopy of sea urchins and the arms of feather stars, and in the burrows created by heart urchins or sea cucumbers. These include fishes (**Fig. 2.28**), molluscs (such as bivalves, abalone and small squid) and even other echinoderms (**BoxFig. 7.1f**) An association between the brittle star *Amphipholis linopneusti* and a spatangoid heart urchin has recently been recorded from the continental slope off Fiji (Stöhr 2001). In temperate Australia, the ophiuroid *Clarkcoma pulchra* is often associated with the sea urchin *Centrostephanus rodgersii* during the day (Byrne & Andrew 2013). This urchin is active nocturnally and as it emerges to feed the two species separate. In intertidal rock pools gobies shelter among the spines of sea urchins (Griffiths 2003). Several fish are similarly camouflaged, barely visible against the surface of their crinoid hosts (**Figs 2.28, 2.29**).

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Figure 2.28 Close relationships between fish and echinoderms are not unusual. Fish are often found sheltering among the arms of feather stars or the spines of sea urchins.

A, the clingfish ***Discotrema monogrammum*** (Gobiesocidae) lives among the arms of feather stars in tropical Indo-Pacific waters, such as Hibernia Reef, Western Australia. Size of fish: *ca*. 20 mm.

B, the striped clingfish ***Diademichthys lineatus*** (Gobiesocidae) is often found in association with sea urchins. It is widespread across tropical Indo-west Pacific including northern Australia and Papua New Guinea. Size of fish: *ca*. 50 mm.

C, Ornate Ghostpipefish, ***Solenostomus paradoxus*** (Solenostomidae), are found solitary or paired among branches of feather stars, gorgonians and floating weeds. Widespread in waters of the Indian and western Pacific oceans including Australia, they are very well camouflaged and often difficult to find. Size of fish: to 120 mm.

[A, C.Bryce; B, D.Harasti; C, G.Bell]

Commensal associations: Crustacea

by Peter J.F. Davie

Many marine crustaceans live in association with echinoderms. Among these are shrimps, squat lobsters and crabs.

CARIDEA — Shrimps

Though the majority of commensal marine shrimps live in association with cnidarians, more than 50 species of shrimp are known to associate with over 70 species of echinoderms (Bruce 1982) in the Indo-west Pacific region (**Fig. 2.29; Box 7.1**). Crinoids and echinoids have the greatest number of symbionts — their numerous feathered arms or spines offer well-concealed niches that are not provided by most holothurians, ophiuroids and many asteroids. Echinoids also tend to have space below them close to the substrate that can provide a suitable living area for animals such as shrimps and other small decapods. Asteroids host a few pontoniine shrimps, and some holothurians are used by a small number of pontoniine or gnathophyllid shrimps. Of the ophiuroids, only the basket stars have attracted a single species of shrimp commensal, *Lipkemenes lanipes* (**Fig. 2.29A**).

Most echinoderm shrimp symbionts belong to two families: the Palaemonidae (specifically the subfamily Pontoniinae) and the Alpheidae. The small families Hymenoceridae and Gnathophyllidae contain several species considered as either commensals or as predators, with perhaps the best known being *Hymenocera picta*, *Phyllognathia ceratophthalma*, and the bumble-bee shrimp *Gnathophyllum americanum* and its close relative *G. taylori*. The only other shrimp associated with echinoderms is a stenopid, *Odontozona* species, found on crinoids. With the exception of the genus *Periclimenes*, all the other shrimp genera are associated with a single class of host. However, peculiarly, the pontoniine shrimp *Conchodytes tridacnae*, normally found in the branchial cavities of giant clams, has also been recorded from the cloaca of holothurians.

Figure 2.29 Numerous shrimps live in close association with echinoderms, receiving protection from predators and scavenging food particles from their hosts.

A, the shrimp commensal ***Lipkemenes lanipes*** (Palaemonidae) has been reported from six species of gorgonocephalid basket stars, including the Indo-Pacific ***Astroboa nuda*** (Gorgonocephalidae) that is also found in the tropical waters of northern Australia. Size: to 8 mm length.

B, the urchin shrimp ***Stegopontonia commensalis*** (Palaemonidae) is well camouflaged with its striped purple/black and white colouration against the long spines of the sea urchin ***Diadema setosum*** (Diadematidae). Size: to 30 mm length.

C, the crinoid shrimp ***Laomenes amboinensis*** (Palaemonidae) lives hidden among the arms of feather stars. Often well comouflaged, taking on the colours and pattern of their host, they are difficult to detect as they lie motionless. Size: to 15 mm length.

D, the sea urchin shrimp ***Periclimenes colemani*** (Palaemonidae) lives in pairs on the venomous fire sea urchin ***Asthenosoma varium*** (Echinothuriidae) throughout the Great Barrier Reef, Queensland, and the Indo-Malaysian region. Size: to 20 mm length.

E, the emperor shrimp ***Periclimenes imperator*** (Palaemonidae) lives on a number of different hosts like this sea cucumber, ***Bohadschia*** species, on the Great Barrier Reef, Queensland. Size: to 20 mm length.

F, the snapping shrimp ***Synalpheus carinatus*** (Alpheidae) resting underneath a feather star; the body is translucent, revealing the inner organs and gonads. This species is found in the seas of the east Indo-west Pacific. Size: to 20 mm length.

[A, C.Marshall; B–D, F, G.Bell; E, D.Harasti]

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A
B
C
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Figure 2.30 The squat lobster ***Allogalathea elegans*** (Galatheidae) lives among the arms of feather stars throughout the Indo-Pacific, including Australian waters. These lobsters have several body colour patterns, ranging from a single uniform colour to variations of longitudinal stripes. The colour and patterning of the lobsters often match their host. Size: body to 15 mm length.

[D.Harasti]

Very little is known about the nature of shrimp–echinoderm associations. Pairs of more than one genus or even several genera may be present upon a single host depending on its size. *Periclimenes imperator* is almost invariably found in pairs on holothurians (**Fig. 2.29E**), as are the species of *Synalpheus* found in crinoids (**Fig. 2.29F**). However, a crinoid such as *Comanthus timorensis* may accommodate only a pair of the larger *Palaemonella pottsi* or *Parapontonia nudirostris*, but may also shelter four or five of the smaller *Periclimenes commensalis*. Large hosts, such as the nocturnal basket stars, often host a considerable shrimp population — *Astroboa nuda* has been known to host 56 specimens of *Lipkemenes lanipes*.

Each shrimp genus typically has its own particular niche on the body of the host. *Athanas* species are usually on the oral surface of the test of their host echinoids, or on the substrate below. *Synalpheus* species sit together on the dorsal surface of the disc of their crinoid hosts. Species of *Tulearіocaris* and *Stegopontonia* cling to the spines of their hosts (**Fig. 2.29B**), whereas *Periclimenes* species are on the aboral surface of the test. *Periclimenes colemani* pairs occupy a bare area on the surface of their host's test that they have cleared of pedicellaria and smaller spines, creating their own living space (**Fig. 2.29D**). Virtually nothing is known about the food materials utilised by the shrimps that feed *in situ* on the host, rather than on the substrate. Those living on spines of echinoids such as *Diadema* or *Echinothrix* may be able to feed from passing currents; some may scrape the host's spines, while others probably subsist on a diet of mucus, or mucus and entrapped particles. The free-living predatory *Gnathophyllum americanum* browses on the extended papulae on the dorsal surface of asteroids.

Where commensal shrimps are exposed on their host they usually mimic the colour and patterns of their host, but colour can also vary according to regional host differences or between host species. *Periclimenes soror* when found on *Culcita*, *Protoreaster* or *Pentaceraster* is usually a deep purple-red, but when found on *Acanthaster* it is typically bright red with a conspicuous white dorsal stripe. Most of the shrimps found on *Diadema* or *Echinothrix* are a dark blue-black colour, often with a fine longitudinal white line. *Athanas indicus* from *Echinothrix* is almost a uniform black colour. *Periclimenes colemani*, found in *Asthenosoma intermedium*, also closely matches its host's colour pattern, being white with large red spots. In deeper water, *Periclimenes hertwigi* is red, with white tips to the chelae of the second pereiopods and the telson. All show a clear resemblance to their host animals. Some of the species found on crinoids also enhance their cryptic colour patterns by having large parts of their bodies completely transparent. The dorsal and ventral surfaces of the body are pigmented,

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so that the shrimp is distinctly visible when viewed from above, but the tissues between are transparent, so that the shrimp is much less easily seen when viewed from the side. This form of colouration is found in *Palaemonella pottsi*, *Periclimenes commensalis* and *Periclimenes tenuis*.

ANOMURA

Galatheidae and Chirostylidae — Squat lobsters

Galatheids are typically mostly free-living, however, worldwide forty-four species occur in symbiotic relationships, commonly with cnidarians (mostly hard and soft corals and gorgonians). Sixteen species have been recorded in association with echinoderms (Baeza 2011), mostly on crinoids (**Fig. 2.30**), but one with an holothurian, one on echinoids and one on an asteroid. The crinoid symbionts typically live camouflaged among the feathery cirri, the basal parts of the arms, or between the substrate and the body. They most likely steal food in the form of organic particles trapped by the crinoid arms. They occur both in heterosexual pairs or as single males or females.

In Australian waters, species of *Allogalathea* (see Cabezas *et al.* 2011) are probably the best known and most common and have been recorded on a variety of crinoids including *Capillaster multiradiatus*, *Comanthina schelegeli*, *Comanthina parvicirrus*, *Anneissia bennetti* (formerly *Oxycomanthus bennetti*) and *Stephanometra spicata*. Two other species of the genus *Galathea* have also been reported: *G. genkai* on *Heterometra savignii* and *Decametra chadwicki*; and *G. inflata* on 13 different host species.

The commensal species of Chirostylidae are similar to the Galatheidae in host preferences. In Australian waters only one echinoderm symbiont has been recorded — *Uroptychus babai*, which lives on the crinoid *Glyptometra inaequalis* (Ahyong & Poore 2004).

BRACHYURA — True Crabs

A number of brachyuran crabs from three families, Pilumnidae, Portunidae and Pinnotheridae, live in close association with various species of echinoderms.

Pilumnidae: Eumedoninae

The crab family Pilumnidae contains an interesting small subfamily, the Eumedoninae, the members of which apparently live exclusively as symbionts on and within echinoderms (**Figs 2.31, 2.32**). Eumedonines can be relatively common on tropical reefs, but they are mostly small (typically around 10 mm carapace length), and their cryptic habits mean that they are seldom encountered or collected. Species are often, but not always, host specific. Of the 13 genera currently recognised, ten genera and 17 species



Figure 2.31 The three species of zebra crabs live, often in pairs, among the spines of sea urchins throughout the Indo-Pacific — like this species ***Zebrida adamsi*** (Pilumnidae) on the fire sea urchin ***Asthenosoma varium*** (Echinothuriidae). These crabs typically have a brown and white zebra pattern, and can grasp the spines of the host firmly by the modified hooked-shaped ends of the walking legs. Size: carapace length 20 mm.

[G.Bell]

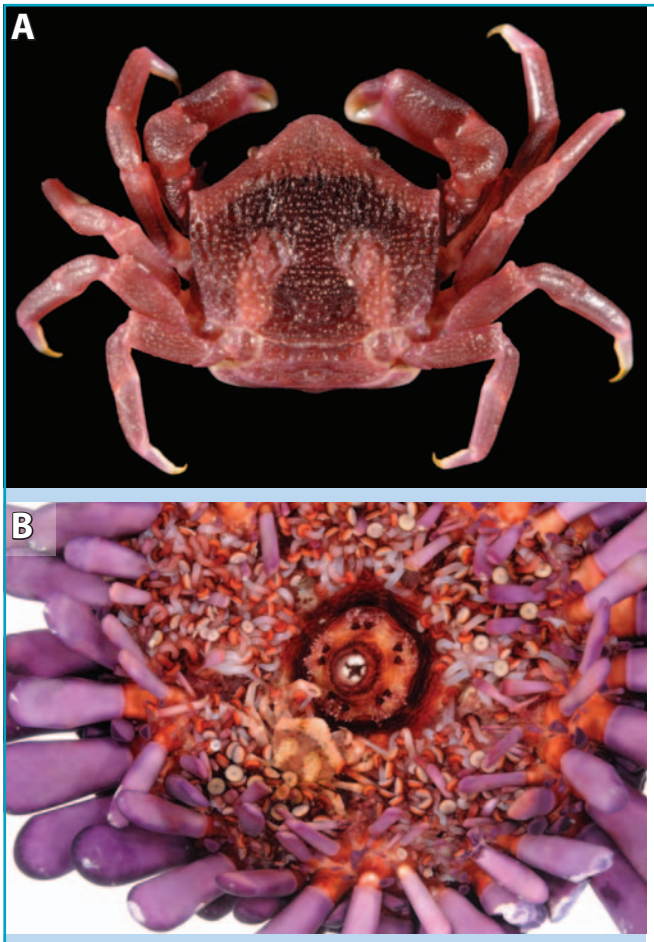


Figure 2.32 This urchin crab ***Echinoecus sculptus*** (Pilumnidae) (**A**) was named by Australian carcinologist Melbourne Ward in 1935, and is still only known from Christmas Island. It lives exclusively under the coastal helmet sea urchin, ***Colobocentrotus atratus*** (Echinometridae) (**B**).

[Tan Heok Hui]

occur in Australian waters, with the monotypic genus *Zebridonus* (*Zebridonus mirabilis*) apparently indigenous to the Gulf of Carpentaria (Chia *et al.* 1995).

Six genera are obligate symbionts of feather stars (crinoids): *Ceratocarcinus*, *Harrovia*, *Permanotus*, *Tauropus*, *Tiaramedon* and *Rhabdonotus*, with *Rhabdonotus* species specialised symbionts on comatulid crinoids (*R. pilipes* known from Australia; Chia & Ng 1995). A further five genera are symbionts of sea urchins, *viz. Echinoecus*, *Eumedonus*, *Gonatonotus*, *Zebrida* and *Zebridonus* (Chia *et al.* 1995; Chia & Ng 1998).

Cyclocarcinus pinnotheroides (more commonly known as *Hapalonotus reticulatus*) is an obligate symbiont of sea cucumbers (*Holothuria scabra*) that lives in a gall in the wall of the respiratory cavity. It has not yet been recorded from Australia, but is known from the north-eastern coast of New Guinea, and as the host is common in tropical Australia, it is possible it may be discovered in the northern Great Barrier Reef waters in the future.

In terms of the exact nature of the symbiotic relationship, it seems that it varies between symbiont and host. For example, the urchin symbionts of the genus *Zebrida* tend to act more as parasites or micro-predators — typically a heterosexual pair of crabs feed on epithelial tissues, and although their impact on the host urchin is usually slight, it has sometimes been reported as more significant (Suzuki & Takeda 1974). In contrast, the crinoid symbiont *Harrovia albolineata* is probably a simple commensal, using its host as a permanent shelter and feeding by taking food in the form of organic particles caught on the crinoid cirri.

Portunidae: Caphyrinae

Portunid crabs are normally free-living, active predators, however a few species of *Lissocarcinus* are known to live commensally with echinoderms. *Lissocarcinus orbicularis* is easily the best known, and is widespread in the Indo-west Pacific oceans from South Africa to Japan and Hawaii (**Fig. 2.33**). It lives associated with large holothurians (such as *Holothuria*, *Actinopyga*, *Stichopus* and *Bohadschia* species), often in mated pairs. The crabs feed mainly on bottom-dwelling organisms and are most common in the oral tentacles where they have ready and protected access to the substrate, however they are also found on the outer surface, or even hiding within the anus. They seem to prefer holothurians with more pronounced surface papillae (such as *Holothuria atra*) because they are able to grasp tightly to the skin and are more difficult to dislodge. The colour pattern of *L. orbicularis* varies from a white background with maroon to almost black spotting, to a dark background with white spotting; and the colouring has been experimentally shown to be able to change after moulting to better blend with the host (homochromy).

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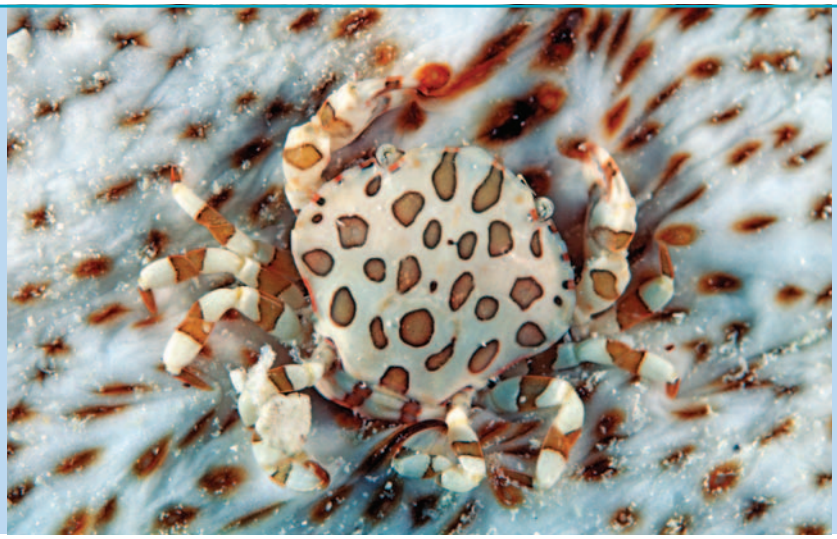


Figure 2.33 The harlequin crab ***Lissocarcinus orbicularis*** (Portunidae) lives in association with sea cucumbers. It is often seen walking over the body of its hosts, but it often shelters within the gut cavity, or near the oral tentacles and anus. Size: carapace length to 30 mm.

[G.Bell]

Pinnotheridae

Pinnotheridae are a highly diverse group of small crabs that mainly live commensally with other invertebrates (Ahyong & Brown 2003; Ahyong 2010). They are found associated with a variety of hosts, but particularly inside the shells or tubes of bivalve molluscs, ascidians and polychaete worms. However, worldwide there are also numerous records of pinnotherids living in association with echinoderms. In particular they inhabit the atrial cavity of a variety of holothurians, across six families: Caudinidae, Cucumariidae, Holothuriidae, Phyllophoridae, Stichopodidae and Synaptidae. The pinnotherid genus *Holotheres* includes six species that are all obligate symbionts of holothurians (Ng & Manning 2003). One species, *Holotheres danielae*, an endemic to Western Australia, inhabits a species of *Haplodactyla* (Ahyong 2010). *Ostracotheres holothuriensis* (**Fig. 2.34**), another crab species, is known from temperate Australia and is apparently commensal inside an unidentified holothurian and in the ascidian *Herdmania momus* (Pregenzer 1988).

Pinnotherids are also known to associate with echinoids and have been recorded living on the tests of a variety of echinoids covering at least eight families: Arbaciidae, Echinidae, Strongylocentrotidae, Echinometridae, Brissidae, Clypeastridae, Echinarachniidae and Mellitidae. However, until now there have been no records of echinoid associations with pinnotherid crabs in Australia.



Figure 2.34 ***Ostracotheres holothuriensis*** (Pinnotheridae) is a temperate Australian species known to occur commensally inside an unidentified holothurian, as well as in the ascidian ***Herdmania momus***.

[J.L.Baker]



Figure 2.35 Sand seastars are adapted to life in sand, mud or loose gravel environments. ***Astropecten*** species (Astropectinidae) emerge to feed on detritus and any other edible items at low tide.

[D.Harasti]

Burrowing and boring

Asteroids such as *Luidia*, *Astropecten* and *Bollonaster* burrow into sand or mud during the day, presumably as a defence measure (**Figs 2.35, 8.9, 8.13**). These species have pointed tube feet, adaptive for life in soft sediments. A star-shaped depression on the surface of the sediment indicates the presence of a seastar below.

Ophiuroids of the family Amphiuridae often live in burrows (**Fig. 9.20D**). The disc remains buried in the sediment, and the long arms extend out to feed. Burrowing can be rapid; tube feet dig around the arm bases, the tips of the arms are thrust into the sediment and the disc is pulled under (Lawrence 1987). The arm spines are often flattened to assist digging. The tube feet maintain the burrow wall with the help of mucous secretions, and the burrow is ventilated by vertical undulations of the arms (Woodley 1975). The large brittle star *Ophiopsila pantherina* lives in burrows in tropical Australia (Byrne 2009; **Fig. 2.19B**). These ophiuroids maintain their disc in a burrow and extend their arms to feed in strong current areas (Woolsey *et al.* 2013).

Among echinoids, heart urchins and sand dollars live in sediments (**Figs 1.14A,B, 2.36; Box 10.6**). Spatangoid heart urchins can burrow tens of centimetres, even in muddy sediments. They have modified spines on the ventral surface and ribbon-like organs (fascioles) that secrete mucus which prevents mud from smothering the respiratory tube feet. Spines, fascioles and tube feet work in combination to construct tunnels to the surface at the anterior and posterior ends, the anterior tunnel for respiration and the posterior to eliminate waste. Occasionally, a notch running down the anterior edge of the test enhances water flow to the mouth (Chesher 1963). These urchins move horizontally through the sediment, periodically constructing new tunnels. Some species emerge at night, using light-sensitive tube feet to control the timing of their emergence (McNamara 1984b). In response to anoxia, heart urchins will also emerge at random times from their burrows (Chesher 1970). Sand dollars usually live in shallower burrows than heart urchins, often positioning the surface of the test just below the sediment surface (**Fig. 1.14**). Their flattened shape includes a number of hydrodynamic modifications, including indentations and depressions, which prevent them from being overturned in strong currents (Telford 1981, 1983). Aggregations of the sand dollar *Arachnoides placenta* (**Fig. 2.37**) are common in the sandy beaches of northern Australia.

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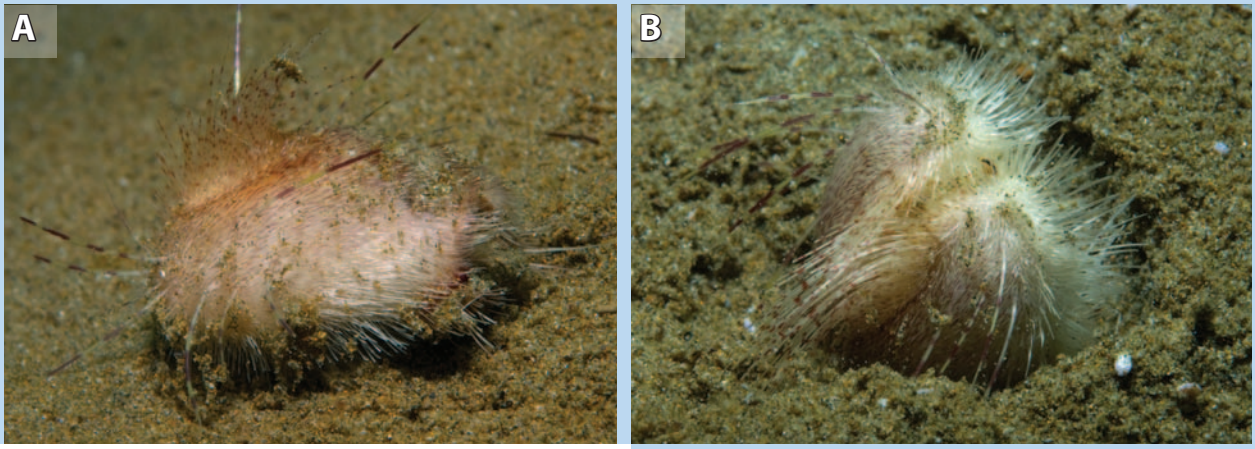


Figure 2.36 The upper sediment layer of the seafloor may be strongly reworked by the cosmopolitan burrowing heart urchin ***Echinocardium cordatum*** (Loveniidae). Superbly adapted for burrowing, it moves through the sediment at a depth of 100–150 mm in sand or sandy-silt in sheltered environments, ingesting large quantities of sediment. In Australia, the heart urchin is commonly found in estuaries along the southern coast from Sydney, New South Wales, to Western Australia and Tasmania: **A**, the spines of ***Echinocardium cordatum*** form a dense coat, with most spines directed posteriorly to aid burrowing. The longer spines of the upper surface push the substrate away and aid burial, and the curved spoon-shaped spines on the oral surface assist the animal to sink further into the sediment. **B**, ***Echinocardium cordatum*** burrowing into the sediment. [J.Finn]

Regular echinoids can create depressions or bore cavities in rocky substrates (**Figs 1.13D, 2.9; Box 10.3**). They use their spines and teeth to scrape and wear the rock away, and these holes are widened as the urchin grows. Occasionally, an urchin can outgrow the small entrance formed when it was younger, and it must rely on water movement to supply food to the burrow. In the tropics, *Echinostrephus* species are characteristic rock borers and can become incarcerated in their burrow (**Fig. 1.27**), while in temperate Australia, *Heliocidaris erythrogramma* gradually forms shallow hollows in rock (**Figs 1.13D, 4.5E**).

Ecological engineers

Some echinoderms are 'ecosystem engineers' through their activities that cause bioerosion, bioturbation and formation of barren habitats (**Box 2.1**) or by influencing species composition of marine communities. Some echinoderms can have a profound influence on their habitat — large populations of crown-of-thorns seastars can consume the majority of corals on a reef (see **Chapter 4**). Top predators on temperate rocky reefs such as the introduced seastar *Asterias amurensis* (Northern Pacific seastar) play a major role in determining the biodiversity of habitats (Byrne *et al*. 2013a).

The burrowing and grazing activities of echinoids can substantially modify rock and coral reefs. For example, grazing *Echinometra* species remove a significant amount of calcium carbonate from coral reefs (Conand *et al.* 1997), while the grazing activities of some urchins can also remove all of the foliose macroalgae, creating a 'barrens' habitat (**Box 2.1**). *Centrostephanus rodgersii* is responsible for the formation of barrens on subtidal reefs along the southern coast of New South Wales. The barrens can range in size from small patches created by a single urchin to large areas of many hectares (Andrew 1993; Andrew & Constable 1999; Byrne & Andrew 2013). All that remains in such habitats are encrusting coralline algae, sponges, limpets and sabellid worms. Another urchin, *Heliocidaris erythrogramma*, can form

large populations in sheltered bays along Australia's southern coast, occasionally forming a dense line or 'front' across seagrass beds, consisting of up to 180 individuals per square metre (Andrew & Constable 1999; Andrew & Byrne 2007).

Burrowing echinoderms can play a significant role in the reworking (bioturbation) of seafloor sediments by mixing particles of different grain size, releasing organic substances into the water, and circulating oxygenated water down into the sediments. For example, the burrowing and feeding activities of the heart urchin *Echinocardium cordatum* have a measurable effect on the recycling of nutrients in semi-enclosed bays such as Port Phillip Bay, Victoria (Bird *et al.* 1999). Several studies have emphasised the key role of bioturbation played by *Echinocardium cordatum* (**Fig. 2.36**) and amphiurid ophiuroids in soft bottom habitats (Vopel *et al.* 2003, 2007; Solan *et al.* 2004).

The feeding activities of deposit-feeding and burrowing by holothuroids (**Figs 1.18, 2.38**) can also rework sediments and are likely to play an important role in recycling nutrients (Massin 1982a, 1982b; Purcell *et al.* 2016a). Species with downward-orientated mouths bring sediments up from deeper layers while others defecate below the surface, taking sediments back down under the surface. Faecal pellets are rich in nutrients, but can bury surrounding organisms and clog the feeding apparatus of nearby filter feeders. Tropical deposit-feeding holothuroids are ecologically important in bioturbation of carbonate sediments and nutrient recycling (Uthicke & Klumpp 1998; Uthicke 1999, 2001a, 2001b), and play a role in the carbonate balance of local reefs, potentially ameliorating on a local scale the negative impacts of ocean acidification on coral calcification (Schneider *et al.* 2012). *Holothuria atra* and *Stichopus chloronotus*, two such holothuroids, rework ~4,600 kg of sediment per hectare per year on a reef flat near Lizard Island on the Great Barrier Reef, which is equivalent to the upper 5 mm of sediment in this area (Uthicke 1999). Horizontal movement of sediment through the feeding and ploughing activities of holothuroids such as *Holothuria isuga* (**Fig. 2.38**) plays a major role in turning over lagoon sediments.

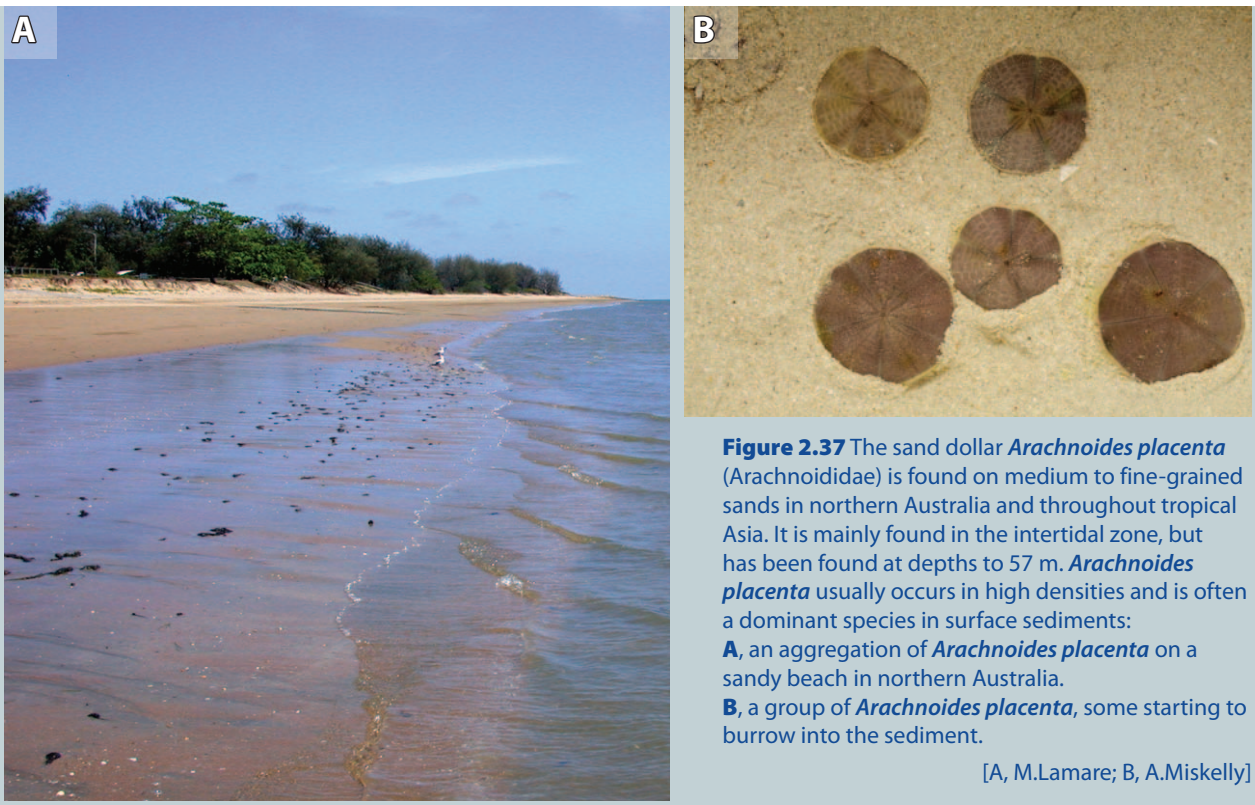


Figure 2.37 The sand dollar ***Arachnoides placenta*** (Arachnoididae) is found on medium to fine-grained sands in northern Australia and throughout tropical Asia. It is mainly found in the intertidal zone, but has been found at depths to 57 m. ***Arachnoides placenta*** usually occurs in high densities and is often a dominant species in surface sediments:
A, an aggregation of ***Arachnoides placenta*** on a sandy beach in northern Australia.
B, a group of ***Arachnoides placenta***, some starting to burrow into the sediment.

[A, M.Lamare; B, A.Miskelly]

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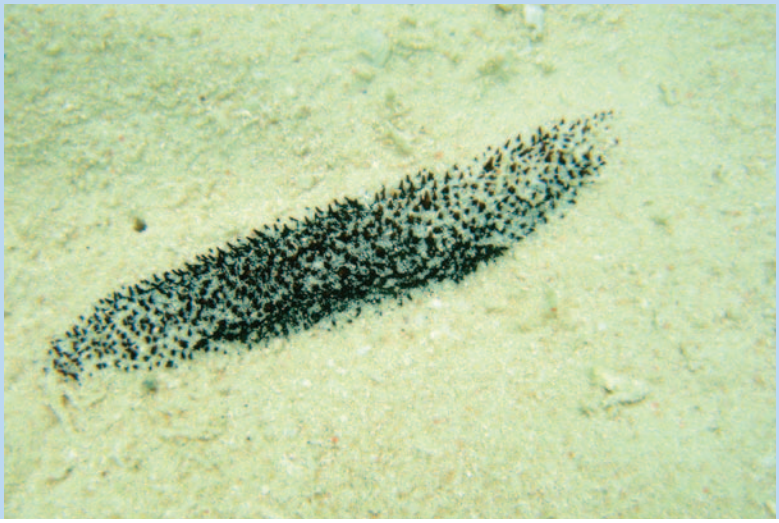


Figure 2. 38 Sea cucumbers are significant bioturbators in marine environments. Their activities of ingestion and defecation of sediment particles, and burrowing play a major role in shifting and mixing the top layers of the sea bed and recycling detrital matter, thus allowing oxygen to penetrate the sediment. ***Holothuria isuga*** (Holothuriidae) is a well-known bioturbator living in abundance on the southern Great Barrier Reef, Queensland; this sea cucumber can extend to a metre in length as it burrows just beneath the surface of the sand.

[A.Weiss]

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3: Echinoderm Life Histories

Maria Byrne and Timothy D. O'Hara

Echinoderms exhibit the full range of life history strategies seen in marine invertebrates, from the broadcasting of gametes into the water column to various types of parental care, such as brooding, to asexual propagation (Giese *et al.* 1991; Byrne *et al.* 1999; **Figs 3.1, 3.5, 3.7, 3.8, 8.41; Boxes 3.1, 8.1, 8.3, 10.4**). Most echinoderms have separate sexes, and free-spawn their gametes for external fertilisation in the water column (**Figs 3.1, 3.2**), followed by development through a dispersive feeding larval stage (**Fig. 3.11; Box 3.1**). This type of life history is considered to represent the ancestral state for echinoderms (Strathmann 1985; Raff & Byrne 2006). However, echinoderms also exhibit various specialised reproductive processes. Some are hermaphroditic, with short-lived, non-feeding larvae that may or may not spend time in the plankton, while other species completely lack a larval phase (**Box 3.1**). The evolution of different life history traits appears to have been a major influence underlying speciation within some echinoderm clades (**Box 3.1**). Careful examination of the life history of apparently widely distributed species and of species in poorly researched habitats has led



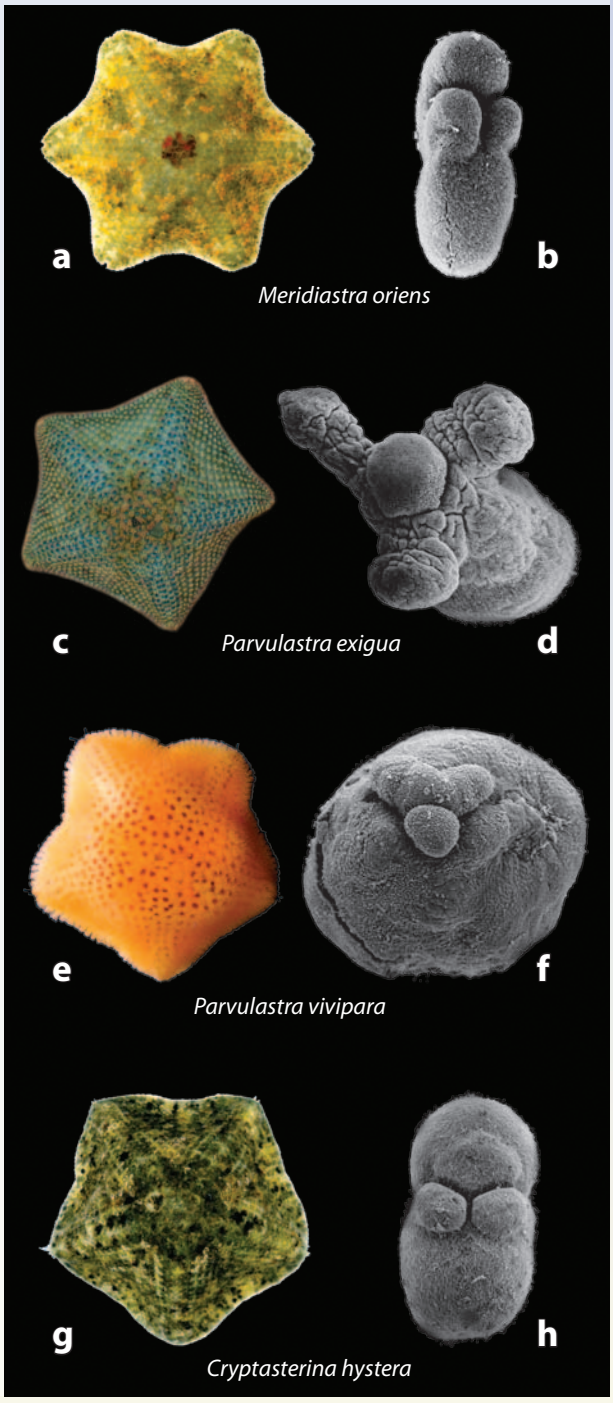
Figure 3.1 A female brittle star, ***Clarkcoma pulchra*** (Ophiocomidae), perched on the tips of its arms with the central disc raised, releases thousands of green eggs into the surrounding water column. The eggs develop in the gonads located in the central disc of the brittle star. Initially they are shed into the bursa. They are then released through the bursal slits which open on the oral surface of the disc between the arm bases.

[D.Harasti]

Box 3.1 Life history, evolution and speciation

Diversification of life history strategies has markedly influenced speciation among echinoderms, and a careful study of apparent colour morphs of varieties of some shallow-water echinoderms has revealed cryptic species with specialised life histories. Australian *Heliocidaris* urchins and asterinid seastars have been used as model organisms to investigate the evolution of development. These echinoderms include species with ancestral-type feeding larvae and various forms of highly derived non-feeding larvae (see **Box 10.4**).

The remarkable life history diversity among Australian asterinid seastars includes the full range seen in the Echinodermata, with planktotrophic development (in *Patiriella regularis*) at one end of the spectrum and intragonadal development (in *Parvulastra vivipara*) at the other. The strikingly different larval morphologies contrast with the apparent uniformity of the adults (**Figs a–h**). *Patiriella regularis* spawns small eggs (150 µm diameter), and has typical feeding bipinnaria and brachiolaria larvae (**Fig. 3.10**). Other species



Figures a–h Larval diversity in Australian asterinid seastars. Adult seastars (left) and non-feeding lecithotrophic brachiolaria larvae (right). Larvae of this type occur only in Asteroidea (seastars).

a, **b**, adult ***Meridiastra oriens*** and its planktonic larva. Adult 40 mm diameter (from tip of arm to opposite interambulacrum); larva 450 µm long.

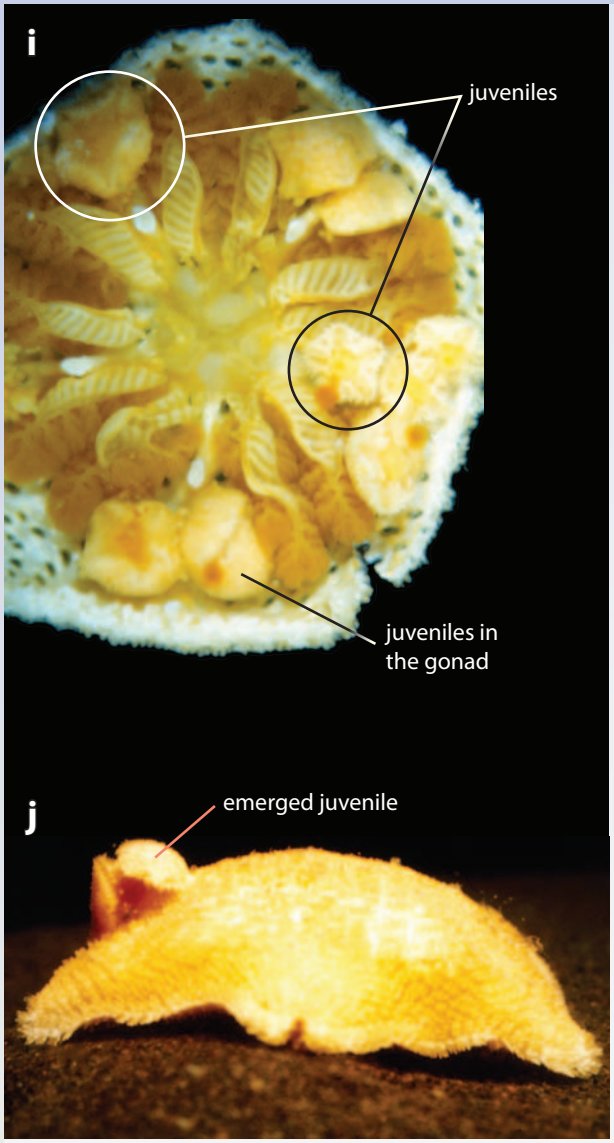
c, **d**, adult ***Parvulastra exigua*** and its benthic tripod-shaped larva. The attachment complex of three arms and the central adhesive disc is clearly seen. Adult 20 mm diameter; adhesive disc of larva 100 µm.

e, **f**, adult ***Parvulastra vivipara*** and its intragonadal larva with the vestigial attachment complex evident. Adult 10 mm diameter; larva 120 µm long.

g, **h**, adult ***Cryptasterina hystera*** and its intragonadal larva. Adult 20 mm diameter; larva 400 µm long.

[a,b,d–h, M.Byrne; c, J.Finn]

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Figures i, j In ***Parvulastra vivipara***, a small viviparous asterinid seastar endemic to Tasmania, embryos develop in the gonads to an advanced juvenile stage.
i, oral view of the gonads with advanced juveniles; a number of juveniles have been removed from the gonads. The top circled juvenile is approximately 2 mm in diameter.
j, after a year or so the well-developed juveniles emerge from the gonads via the gonopores on the aboral surface of the adult. The juveniles are approximately 5 mm in diameter.

[i, M.Byrne; j, from Hoggins 1976]

have lecithotrophic development. *Meridiastra calcar*, *M. gunnii*, *M. oriens* (**Figs a,b**) and *Cryptasterina pentagona* spawn large eggs (*ca.* 400 µm diameter) and have planktonic lecithotrophic brachiolaria. The bipinnaria stage has been omitted, but the attachment complex is retained because it is essential for benthic settlement. *Parvulastra exigua*, a small species that lays large eggs (340 µm diameter) onto the substratum, has a highly modified tripod-shaped larva (**Figs c,d**). Its brachiolar complex serves as a tenacious attachment device.

Viviparous asterinids have the most highly derived life history pattern seen in the Echinodermata. These asterinids are hermaphrodites and retain their eggs in the gonad where fertilisation and development occur. Among asteroids, viviparity is known only for five species, all of which occur in the family Asterinidae: *Cryptasterina pacifica*, a species endemic to Japan, and four species endemic to Australia, *Parvulastra vivipara* (Tasmania), *Parvulastra parvivipara* (South Australia), *Cryptasterina hystera* (Queensland) and *Cryptasterina* sp. from the Great Barrier Reef.

In temperate Australia, *Parvulastra vivipara* (**Figs e,f**) and *P. parvivipara*, some of the smallest of the known seastars, have secondarily reduced the size of their eggs (120 µm diameter) from an ancestral species that had a larger egg. The minute vestigial brachiolaria larvae of these species metamorphose as tiny juveniles. While in the gonad, these juveniles grow by cannibalising their siblings, an unconventional approach to maternal provisioning. Only the largest juveniles emerge through the gonopore a year or more after fertilisation (**Figs i,j**). In contrast, viviparous *Cryptasterina* species from tropical regions have large eggs (*ca.* 400 µm diameter) and their brachiolariae swim in the gonads and resemble those of *Cryptasterina* species that have planktonic larvae (**Figs g,h, 3.6D**). With their extremely non-dispersive mode of development, it is not surprising that the viviparous asterinids have the most restricted distributions of any echinoderm.

Further reading Byrne & Barker 1991; Byrne 1992, 1995, 1996a, 2005, 2006; Raff & Byrne 2006; Puritz *et al*. 2012; Keever *et al*. 2013

to the discovery of new taxa (Dartnall *et al*. 2003; Hart *et al*. 2003, 2006; O'Loughlin & Rowe 2005, 2006; Byrne & Walker 2007; Puritz *et al*. 2012). The only detectable differences between some morphologically similar cryptic species are to be found in the larvae. Across the Echinodermata there appears to be a trend towards evolution of non-feeding larvae, which may have been influenced by the differential extinction of species with feeding larvae over evolutionary time (Uthicke *et al*. 2009).

Sexual reproduction

Sexual reproduction is the most common mode of propagation among echinoderms, with most species having separate sexes (**Figs 3.2, 3.3, 3.6A,B**). Smaller echinoderms are often hermaphroditic, and these can have ovaries and testes or ovotestes (**Fig. 3.6D,E**). Sequential hermaphrodites first mature as male or female and then change sex later in their life. Echinoderms that change sex, such as the Indo-Pacific ophiuroid *Ophiopeza spinosa* (Byrne *et al*. 2008c), are usually protandric, maturing first as a male and subsequently becoming female. Simultaneous hermaphrodites, such as the viviparous *Parvulastra*, are potentially self-fertile. Some individuals of the intertidal seastar *Parvulastra exigua*, an egg-laying species common on the shores of eastern and southern Australia, can fertilise their own eggs, and this may contribute to the fine-scale population genetic structure that characterises this species (Barbosa *et al*. 2012, 2013). The more common mode of fertilisation for this species is cross fertilisation in aggregations of individuals that make a communal egg mass (Byrne 1992). Many hermaphrodites are small secretive animals only one or two centimetres in diameter, living in algal turfs or hidden away in the infrastructure of reefs (O'Loughlin 1994).

Most echinoderms show no external morphological differences between the sexes. Some sea urchins and sea cucumbers have genital papillae that protrude from the anterior end of the body, and these assist in differentiating the sexes (Chia 1977; O'Loughlin 2001), the male papillae are often longer than those of females. During spawning these papillae resemble elevated cones with eggs and sperm emerging from their apices (**Fig. 3.2E**). In some cucumariid holothuroids the males have long genital papillae that appear to be used to transfer sperm into the marsupia of females where the eggs are fertilised and the young develop (O'Loughlin 2001). Sexual dimorphism is marked in some sea urchins that brood their young. Female *Abatus* heart urchins from Antarctica develop prominent invaginations of their test where the young develop (**Fig. 3.4**); these invaginations are lacking in males.

The deepsea asteroid *Xyloplax* is unusual in exhibiting marked differences between males and females: males have a penis-like projection that is likely to serve as a copulatory organ (Rowe *et al.* 1988, 1994; **Fig. 8.44B**). Spermatogenesis in *Xyloplax* is also unique among echinoderms in the production of filiform spermatozoa (**Fig. 3.9C**) rather than the round-headed

Figure 3.2 Most echinoderms have separate male and female individuals and reproduce sexually. This often occurs by releasing (spawning) eggs or sperm into the water column, where the eggs, once fertilised, develop into larvae that will later settle, generally, on the seafloor. Spawning is usually a seasonal or annual event, but some echinoderms are capable of spawning throughout the year. Factors which induce spawning are complex and may include water temperature, light or the phase of the moon (Mercier & Hamel 2009).

A, ***Tosia magnifica*** (Goniasteridae), a biscuit star, releases gametes from the interambulacral gonopores between adjacent arms.

B, echinoderms often adopt raised postures to spawn, thus facilitating the dispersal of gametes, like ***Fromia indica*** (Goniasteridae) where streams of whitish gametes are being released.

C, the flower urchin, ***Toxopneustes pileolus*** (Toxopneustidae), which is usually fully covered by coral rubble, emerges to spawn. Gametes are released from the five gonads through five gonopores located on the aboral surface.

D, in crinoids (feather stars) recognisable gonads are found in the pinnules, located in the more proximal part of the ray (arm). Feather stars may adopt a raised position to broadcast their gametes; the gonads lie in the swollen bases of the pinnules and either eggs or sperm are released by rupturing of the pinnule wall.

E, the leopard sea cucumber, ***Bohadschia argus*** (Holothuriidae), adopts an elevated position to release eggs or sperm. The spawning event of this female sea cucumber on the Great Barrier Reef took less than 30 seconds; males are known to take much longer, perhaps an hour.

[A, J.Finn; B, N.Coleman; C, A.Chen; D, R.Babcock; E, B.Saunders]

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A


B


C


D


E

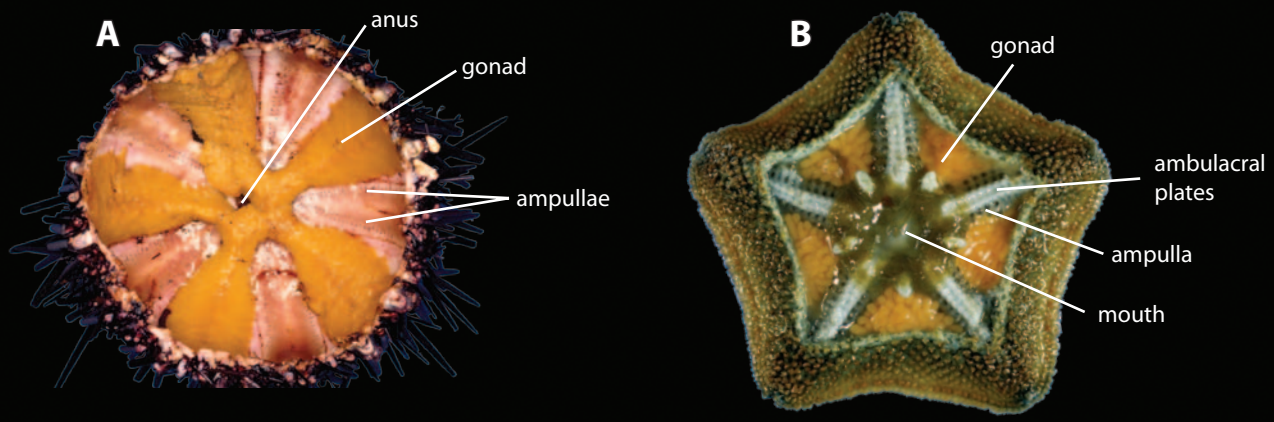


Figure 3.3 Radial organisation of echinoderm gonads.
A, aboral (abactinal) view of the sea urchin ***Centrostephanus rodgersii*** (Diadematidae).
B, oral (actinal) view of the seastar ***Parvulastra exigua*** (Asterinidae).
[M.Byrne]

spermatozoa seen in other asteroids (Healy *et al.* 1988). Sperm morphology can also be useful as a taxonomic character, as shown for the *Echinometra* '*mathaei*' species complex (Landry *et al.* 2003).

Sexual differences between small and large echinoderms are also correlated with spawning mechanisms. Thus, large species such as *Acanthaster planci*, the crown-of-thorns seastar, and an introduced species, *Asterias amurensis*, the Northern Pacific seastar, release millions of small eggs and vast quantities of sperm into the water (see **Fig. 3.6A,B; Box 3.2**). By contrast, the smallest echinoderms produce comparatively few eggs. Furthermore, species that care for their young release their eggs into brood chambers on or within the body. These brood chambers include gonads, stomach pouches and the space just below the mouth or on the body surface (**Figs 3.4A–C,E, 3.6D; Boxes 3.1, 7.2, 8.1, 8.3**). Embryonic development occurs in these chambers (**Figs 3.4, 3.5A, 3.6D, 3.12; Box 8.3**). Among species that care for their young are the hermaphroditic ophiuroids such as *Amphipholis squamata* (**Fig. 3.5; Box 9.2**) and *Amphiura constricta* that are common and widespread on Australian coasts, the Antarctic heart urchin *Abatus ingens* (**Fig. 3.4**), the endemic seastar *Smilasterias multipara* from south-eastern Australia (**Box 8.3**) and the endemic crinoid *Aporometra wilsoni* from South Australia (**Fig. 3.12; Box 7.2**).

Reproductive anatomy

In general, reproductive anatomy reflects the pentamerous organisation of the echinoderm body (**Fig. 3.3**). Seastars have two gonads in each arm, and each opens to the outside through gonopores. Sea urchins have one large elongate gonad along each interradius (**Fig. 3.3A**), and gametes are released through gonopores in the genital plates that surround the anus (**Figs 1.4B, 1.21B, 3.2C**). Acquisition of a secondary bilateral shape in the heart urchins (for example, *Abatus*; **Fig. 3.4**) and sand dollars is accompanied by a decrease in the number of gonads.

The reproductive anatomy of most ophiuroids is associated with 10 respiratory bursae, one on either side of the base of each arm (**Figs 1.10B, 1.25**). These sac-like invaginations of the body wall project into the coelom and, depending on the species, each can have one or several gonads associated with it. The gametes are released into the bursae and exit through the bursal slit

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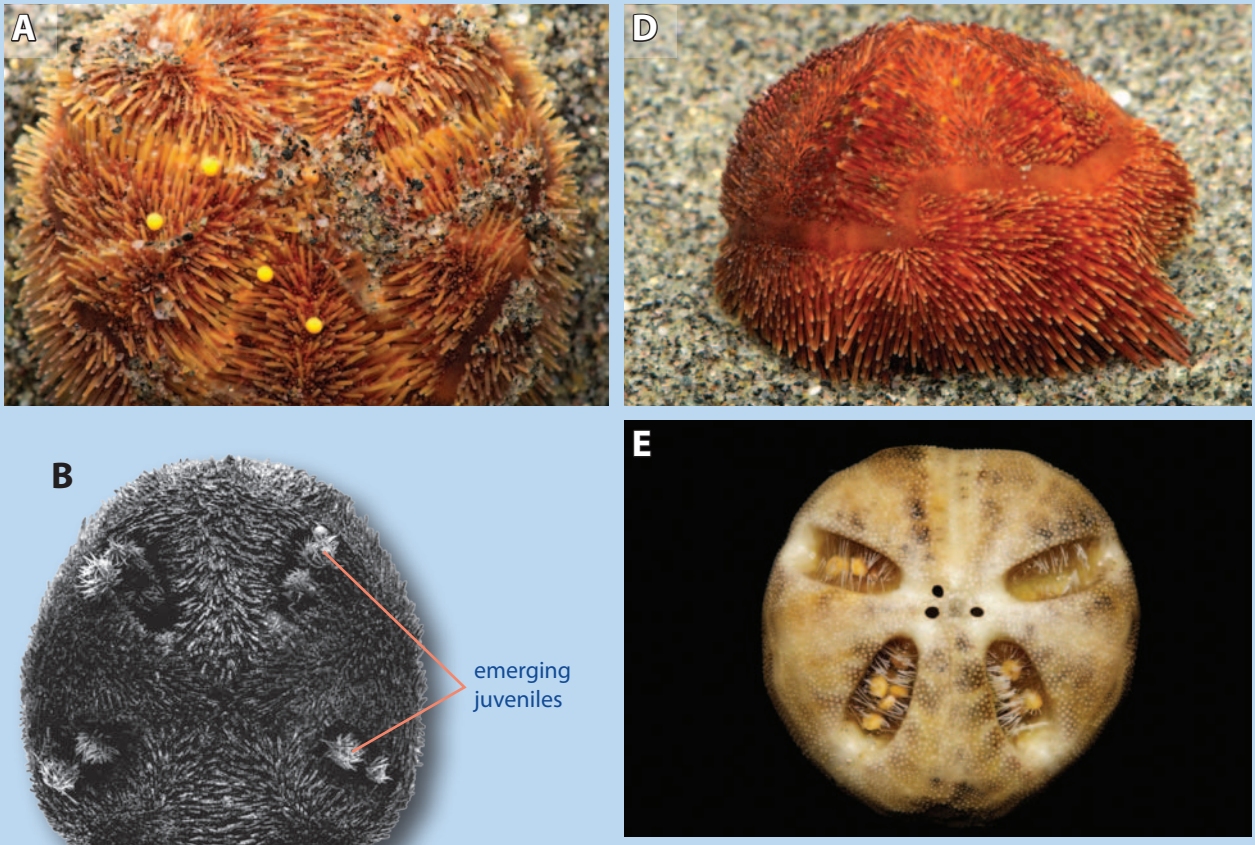


Figure 3.4 Among echinoderms brooding appears to be particularly common in Arctic and Antarctic species as well as those from the deep sea. In echinoids, brooding is more common in the regular cidaroids, and the irregular spatangoids. All known members of the subantarctic and Antarctic spatangoid genus ***Abatus*** (Schizasteridae) brood their young inside four aboral ambulacral pouches.

A, ***Abatus ingens***, a brooding female with eggs released from the brood pouches following disturbance; aboral view. They brood most of the year with juveniles taking almost a year to develop.

B, **C**, ***Abatus nimrodi***:
B, juvenile sea urchins exit the pouches on the aboral surface of the female. Embryos are at different stages of development in each pouch with less developed embryos at the bottom of the pouch and nearly 'fledged' juveniles near the exit. Adult test 50–60 mm diameter.
C, the inside of the upper half of a female test showing the invaginated brood pouches where the embryos develop.

D, **E**, ***Abatus shackletoni***:
D, lateral view of an adult male showing spine canopy.
E, female with spines removed to show brood pouches, juveniles and large gonopores that connect to three gonads. The eggs are transferred from the gonopore to the brood pouch by tube feet and spines. The eggs are fertilised in the pouch.

[A,D,E, A.Miskelly; B,C, M.Byrne]

at the base of the arms (Fig. 3.1). Species that brood their young (Fig. 3.5) retain the eggs in the bursal sac, the location of fertilisation and development. The gonads of some snake stars, such as *Astrobrachion constrictum*, lie in the arm coelom, like those of asteroids (Fig. 3.6C). This feature, once thought to be an ancestral trait linking ophiuroids and asteroids (Mortensen 1932), is probably a specialised feature of euryalid brittle stars (see Chapter 9).

Crinoids have a multitude of small gonads located in the pinnules, the delicate side branches of the arms (Figs 3.2D, 7.5). The secondarily bilateral holothuroids differ in having one or two elongate gonads located in the coelom (Fig. 1.17A). The gonads are either richly branched with elongate tubules or in small tuft-like arrays. A gonoduct opens on the anterior surface adjacent to the tentacles.

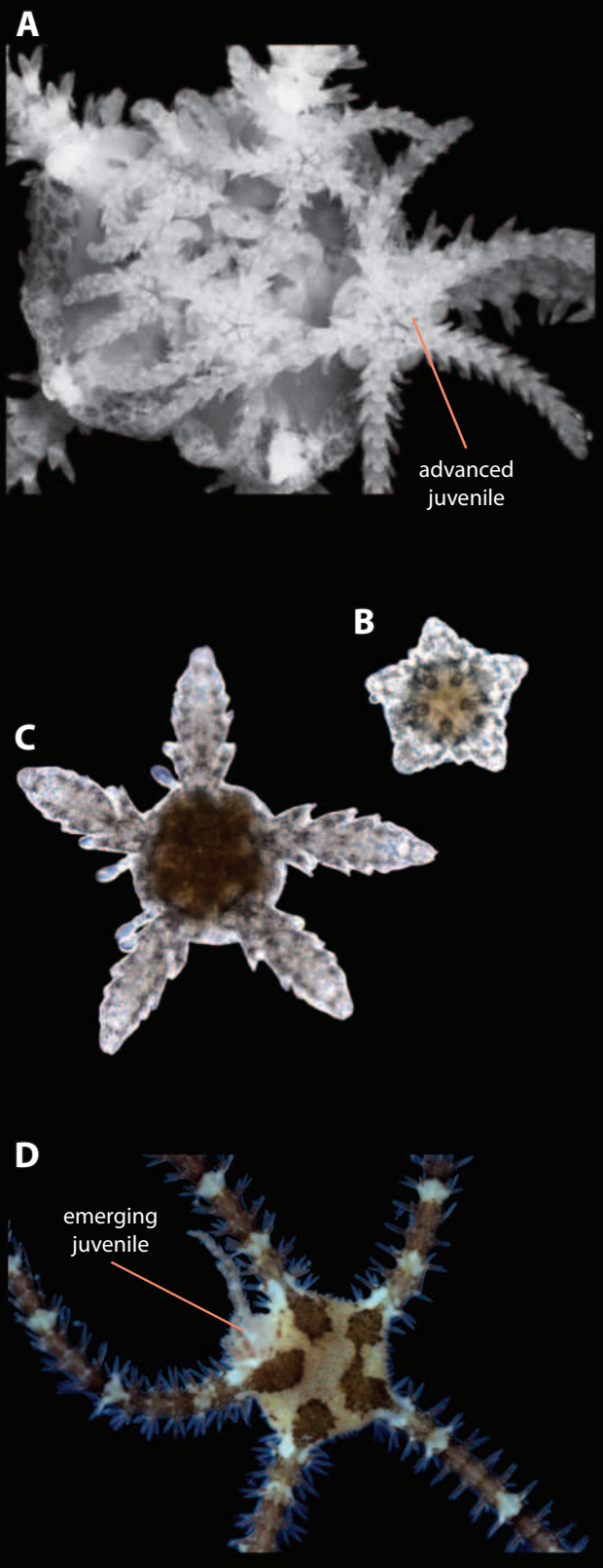


Figure 3.5 A feature common to many small-bodied brittle stars is that they brood their young, effectively giving birth to live young. Often these species are simultaneous hermaphrodites — the male and female gonads of an individual release sperm and eggs through the gonopore into the bursal sac where internal fertilisation takes place. Embryos develop in the bursal sacs in specialised brood pouches located in the central disc. When fully developed, juveniles emerge through the bursal slits found at either side of the arm bases.

A, fertile year-round, the diminutive, cosmopolitan viviparous brittle star ***Amphipholis squamata*** (Amphiuridae), is able to brood a number of embryos at different stages of development. Embryos receive nourishment from the adult, with brooding continuing until the crawl-away juvenile stage. Removal of the aboral portion of the central disc reveals a number of rather advanced juveniles; they are estimated at <1 mm disc diameter.

B, **C**, photomicrographs of young at different developmental stages, taken from a single adult of ***Amphipholis squamata***:
B, small juvenile that was connected to the brood pouch (*ca*. 200 µm diameter).
C, a more advanced juvenile with arms.

D, a fully developed juvenile emerges from the bursal brood pouch via the bursal slit in the brittle star ***Ophiurochaeta littoralis*** (Ophiodermatidae), which is known from the warm waters of the Caribbean Sea and the Gulf of Mexico. The adult is 2.5 mm disc diameter.

[A,D, M.Byrne; B,C, A.Clark]

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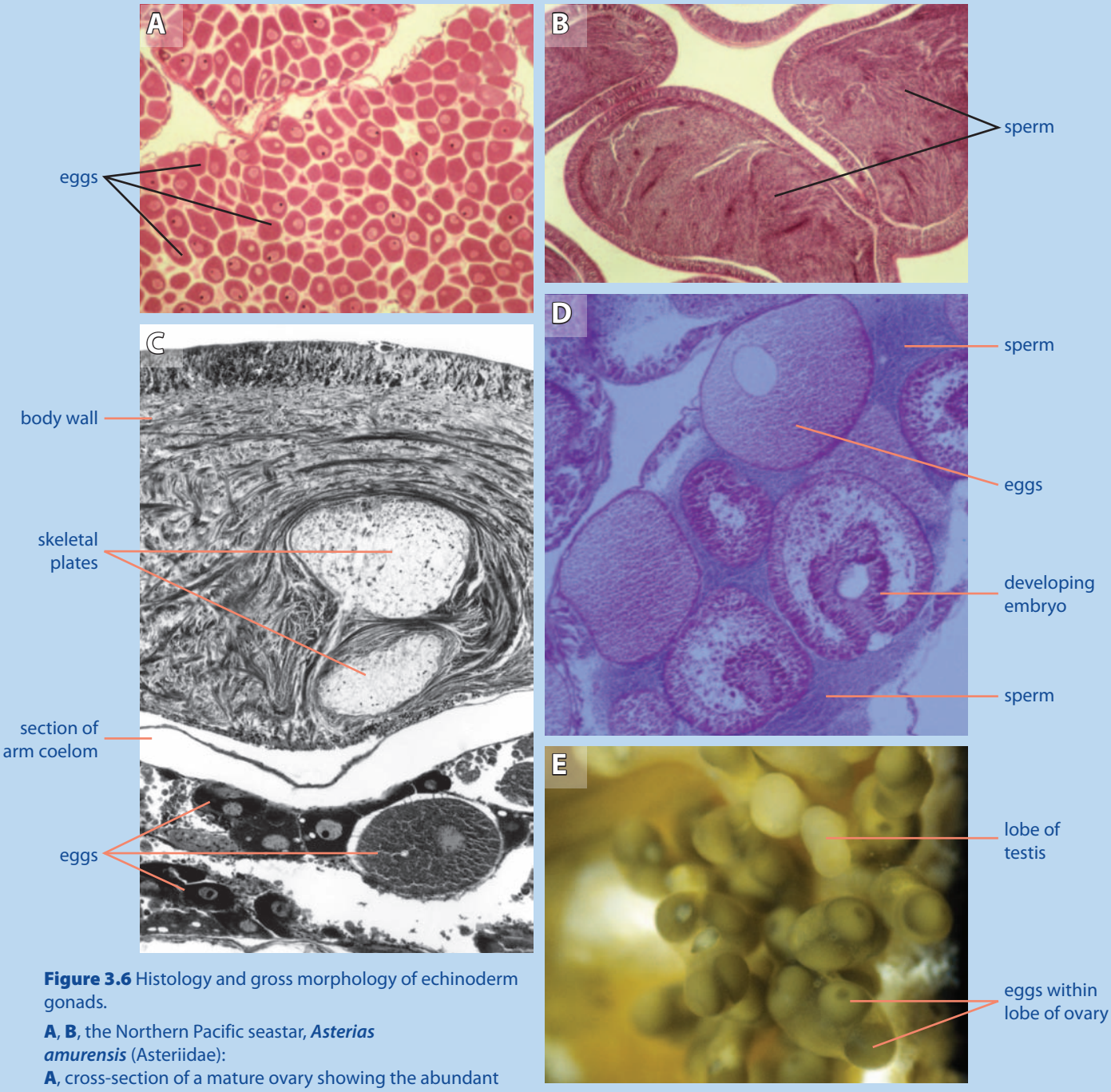


Figure 3.6 Histology and gross morphology of echinoderm gonads.

A, **B**, the Northern Pacific seastar, ***Asterias amurensis*** (Asteriidae):
A, cross-section of a mature ovary showing the abundant small eggs just prior to spawning. The eggs are *ca.* 100 µm diameter.
B, cross-section of a mature testis filled with sperm.

C, cross-section through the arm of a female brittle star (snake star) ***Astrobrachion constrictum*** (Euryalidae), showing the eggs developing in the tubular ovaries. This ophiuroid is unusual in that the gonads are located in the arms, and the skeletal plates are reduced and are embedded in body wall connective tissue. The eggs are *ca.* 350 µm diameter.

D, **E**, the viviparous, self-fertilising hermaphroditic seastar ***Cryptasterina hystera*** (Asterinidae):
D, cross-section of ovotestes showing sperm (darker blue-purple colour), eggs and developing embryos.
E, details of ovotestes showing some lobes containing green eggs and the pale-coloured lobes containing sperm. The eggs are 440 µm diameter.

[M.Byrne]

Asexual reproduction

The remarkable ease with which echinoderms can divide their bodies is based on the mutable properties of their connective tissue (**Fig. 3.8; Boxes 1.1, 1.3**). During fission or arm autotomy the connective tissue along the breakage plane softens irreversibly, resulting in the separation of body parts.

Asexual reproduction occurs in asteroids, ophiuroids and holothuroids (**Figs 3.7, 3.8, 8.41C–E; Box 1.3**). Some asexual species rarely, if ever, develop gonads, so entire populations can be completely clonal. In asteroids and ophiuroids asexual reproduction is exhibited by multi-armed species that reproduce by division or fission of the body (**Fig. 3.7; Box 1.3**). Transverse fission is also common in tropical sea cucumbers (**Fig. 3.8**). Division of the body is followed by regeneration of each half into a new and complete individual, although mortality of one half is also reported (Lee *et al.* 2008a; Thorne & Byrne 2013; Thorne *et al.* 2013). The asteroid *Linckia multifora*, a common tropical species, has remarkable

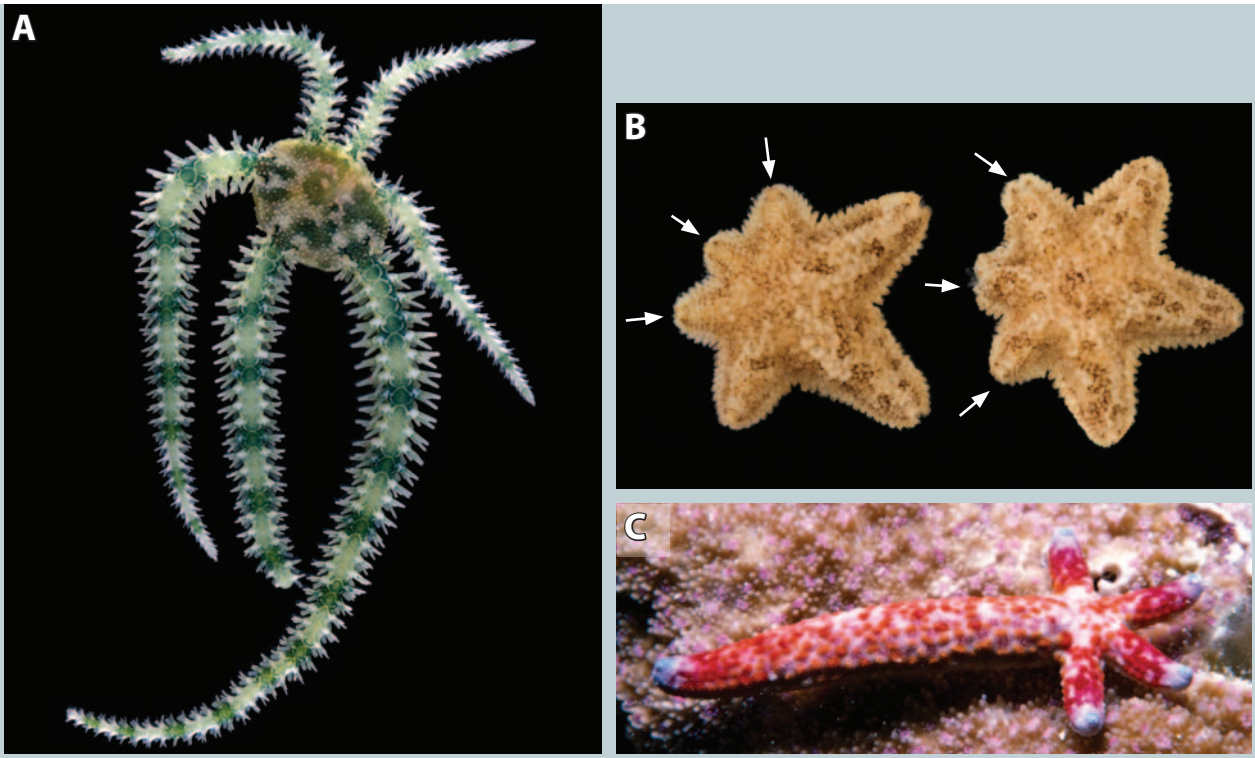


Figure 3.7 Asexual reproduction and regeneration in echinoderms. While most echinoderms are capable of regenerating lost parts, asexual reproduction by fission occurs only in some asteroids, ophiuroids and holothuroids.

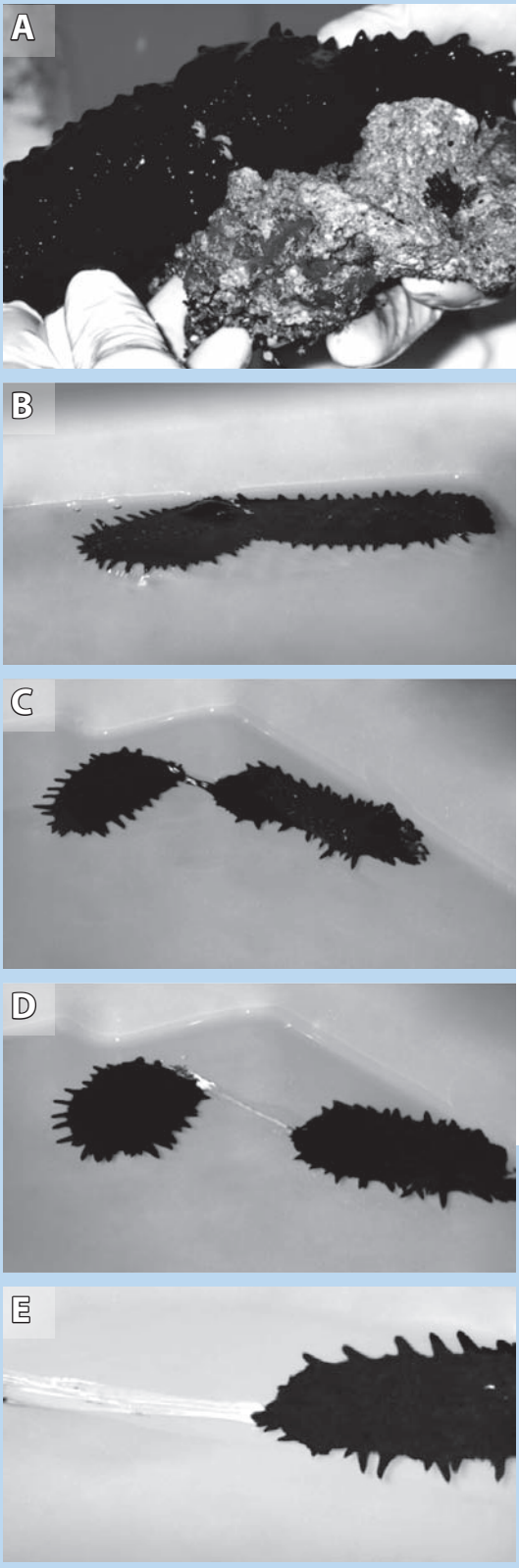
A, the fissiparous six-armed brittle star ***Ophiocomella sexradia*** (Ophiocomidae) in an advanced state of regeneration following fission of the central disc; the three small arms at the 'top' are the newly developed regenerating arms. In this species the disc divides in two, each half usually with three arms; each half then forms an entirely new animal by regeneration. The disc is 5 mm diameter.

B, body profiles of two individuals of the fissiparous seastar ***Ailsastra*** sp. (Asterinidae) following division. Regeneration of three arms is well-advanced for each seastar (arrowed); as for most echinoderms regeneration can only occur if a substantial portion of the central disc remains.

C, unlike most other echinoderms the seastar ***Linckia multifora*** (Ophidiasteridae) can regenerate an entire individual from a single arm, thus forming a comet-like individual during the regeneration stage.

[A,B, M.Byrne; C, A.Flowers & L.Newman]

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regenerative capabilities: it can grow a complete individual from a single arm, forming comet-like shapes (**Fig. 3.7C**). This is the only asteroid known to be able to form new individuals from such small portions of the body, an extreme form of reproductive cloning in adult echinoderms.

Some asteroids and holothuroids, including the common temperate seastar *Coscinasterias muricata* and the tropical sea cucumber *Holothuria atra*, reproduce asexually early in life and later, at a larger size, they switch to sexual reproduction (Crump & Barker 1985; Uthicke 1997; Lee *et al.* 2008a). It is not clear if some populations are maintained by sexual propagules while others are derived from asexual reproduction. A recent genetic study indicates that a mixture of asexual and sexual reproduction maintains populations of *H. atra* on the Great Barrier Reef (**Fig. 3.8**) and elsewhere across its broad Indo-Pacific range (Uthicke *et al.* 1998). The conditions under which these methods of reproduction are favoured are unknown. In tropical habitats, asexually reproducing echinoderms such as *H. atra*, *Stichopus chloronotus*, the 6-armed ophiuroid *Ophiocomella sexradia* or the multi-armed asteroid *Ailsastra* species, can be the numerically dominant invertebrates (**Figs 3.7, 3.8**). The ability of the planktonic larvae of some asteroids, ophiuroids and echinoids to give rise to clonal larvae by budding off parts of their tissue is likely to be an important phenomenon in the connectivity of populations, but this is, as yet, not fully understood (Byrne 2013).

Figure 3.8 Asexual reproduction by transverse fission (self division) is known for about nine sea cucumbers including the tropical ***Stichopus chloronotus*** (Stichopodidae) found on the Great Barrier Reef. The process of fission begins with a mid body constriction in the intact animal (**A**). Following 'softening' of the constricted region due to changes in the connective tissue, the body separates into two parts (**B**, **C, D**), the mouth anterior end and the anal posterior end. Each part then regenerates to form an intact individual. The remains of the fragmented and disintegrated body wall connective tissue are seen as white fibres (**E**).

[from Uthicke 2001c]

Echinoderm gametes

Echinoderm eggs range in diameter from 60 to 1000 µm. Species that have small eggs (60–150 µm diameter) develop through feeding (planktotrophic) larvae. These echinoderms are often large bodied and highly fecund, producing many thousands to millions of eggs (**Fig. 3.6A**). Conversely, echinoderms with large eggs (200–1000 µm diameter) develop through non-feeding (lecithotrophic) larvae that are fully provisioned by the egg (**Fig. 3.6C,D**). These species are often small bodied and have low fecundity. An even more extreme situation is seen in viviparous species that produce only a few eggs at a time. A secondary reduction in egg size has occurred in the viviparous asteroid *Parvulastra vivipara* and the ophiuroid *Amphipholis squamata* (Fell 1946; Byrne & Cerra 1996).

All echinoderms, apart from echinoids, have round-headed sperm (**Fig. 3.9A**). Echinoid sperm have a conical head (**Fig. 3.9B**), while *Xyloplax* has uniquely filiform spermatozoa (Healy *et al.* 1988; **Fig. 3.9C**).

Reproductive cycles and temporal cues

Most echinoderms reproduce in a discrete and predictable annual cycle of gonad growth and gamete release (Mercier & Hamel 2009). The pattern of gonad growth is often assessed through calculating a 'gonad index', the weight of the gonad relative to the weight of the body. To determine the precise timing of gamete release, gonad development is also often documented by histological section (**Fig. 3.6A–D**). Seasonal spawners, such as the seastars *Meridiastra calcar* and *Acanthaster planci* and the sea urchins *Centrostephanus rodgersii* and *Heliocidaris erythrogramma*, have synchronous gonad development with an annually predictable season of reproductive maturity across populations (Mercier & Hamel 2009). This pattern is reflected in the synchronicity of gamete development and a reduction in the gonad index once spawning is under way. In contrast, echinoderms that have extended spawning periods or non-seasonal reproduction, such as *Parvulastra exigua* and the sea urchins *Holopneustes purpurascens* and *Heliocidaris tuberculata*, have advanced gametes in the gonads for much of the year and a relatively constant gonad index (Laegdsgaard *et al.* 1991; Byrne 1992; Williamson & Steinberg 2002). Furthermore, some species, such as *Acanthaster planci*, that have annual spawning seasons in Australia where there is some environmental seasonality have the potential in populations closer to the equator where there is minimal seasonality to have prolonged continuous reproduction (Cheney 1974; Babcock & Mundy 1992; Pratchett *et al*. 2014).

Echinoderm reproduction is controlled by a complex and interacting suite of endogenous and environmental factors. Depending on the species, seasonally variable factors such as photoperiod, temperature and food availability can be important regulators of reproduction (Pearse *et al.* 1986). Control of reproduction by photoperiod is best documented for asteroids, and the introduction of *Asterias amurensis* to Tasmania provided an opportunity to test the photoperiod hypothesis (see **Box 3.2**). Many tropical echinoderms spawn during the annual coral spawning period, with several species spawning simultaneously (Babcock *et al.* 1992). Spawning is also influenced by pheromones (communication chemicals) produced by sexually mature individuals (Mercier & Hamel 2002).

Echinoderm reproduction is usually not associated with complex behaviour. Mating behaviour as seen in the close spatial association of males and females occurs in several species, including *Archaster typicus* and *A. angulatus* (**Fig. 8.16A**), and this undoubtedly facilitates fertilisation (Young *et al.* 1992; Run *et al.* 1988; Keesing *et al*. 2011a; Lawrence *et al*. 2010). As mentioned above, some brooding echinoderms have copulatory structures. Where population density is high and spawning is synchronous, fertilisation success is likely to be high. Many echinoderms, however, do not live close to other members of their species, and fertilisation appears to be a more haphazard event (Levitan 1995). An exception is the high fertilisation

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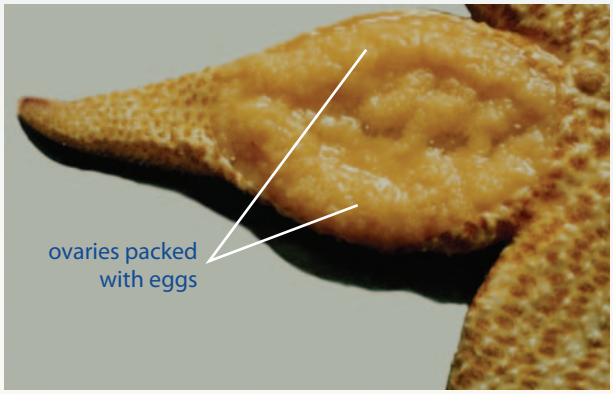
Box 3.2 Northern Pacific seastar — seasonal reproduction in the northern and southern hemispheres

There was a sense of considerable alarm in 1993 when large numbers of the seastar *Asterias amurensis*, commonly known as the Northern Pacific seastar, were discovered in the Derwent River Estuary in Tasmania. Possibly introduced in ship ballast waters, this northern Pacific species rapidly proliferated under apparently ideal conditions for reproduction (see **Chapter 4**).

In its natural environment in the north-eastern Pacific, *A. amurensis* is known from latitudes spanning those of its current south-eastern Australian distribution. Reproduction in asteroids is thought to be controlled by photoperiod and, consequently, the introduction of *A. amurensis* to the Derwent provided a unique opportunity to test this hypothesis. In Japan *A. amurensis* was known to be a winter spawner, releasing gametes at sea temperatures (9–12°C) not unlike those in the Tasmanian winter (10–13°C). The reproductive cycle of *A. amurensis* in Tasmania is identical to that of Japanese populations and, as predicted by the photoperiod hypothesis, the timing of reproduction in Tasmania was six months out of step with that in Japan. The similarity of the temperature regimes in Japan and Tasmania indicate that temperature might also play an important role in regulating reproduction, perhaps by modulating the onset of spawning activity. *Asterias amurensis* is a highly fecund seastar, producing large gonads and releasing up to 20 million eggs. Given the similarity of environmental factors in Tasmania and Japan, it is not surprising that *A. amurensis* has been a spectacularly successful invasive species in Tasmania.

Class Asteroidea
Family Asteriidae
Species *Asterias amurensis* (Lütken, 1871)

Further reading Byrne *et al.* 1997a,1997b, 2013a, 2016b; Pearse & Walker 1986; Pearse *et al*. 1986



A female Northern Pacific seastar, ***Asterias amurensis,*** with part of the body wall removed from one of the arms showing the two large ovaries which contain hundreds of thousands of eggs.

[M.Morrice]

rates reported for *Acanthaster planci* in eggs several metres from a spawning female (Babcock & Mundy 1992). For this seastar, the sheer mass of sperm (*ca.* 100 g) released by individual males in a single spawning event, and the large numbers of eggs released by females, estimated to be *ca.* 60 million for large females in New Caledonia (Conand 1985) and over 100 million for individuals on the Great Barrier Reef (R.C.Babcock, personal communication), almost certainly contribute to the success of fertilisation. During spawning some echinoderms adopt an elevated posture. Thus, asteroids and ophiuroids 'stand' on the tips of their arms, and some sea cucumbers rise up in a cobra profile, moving back and forth as sperm or eggs are released (**Figs 3.1, 3.2**).

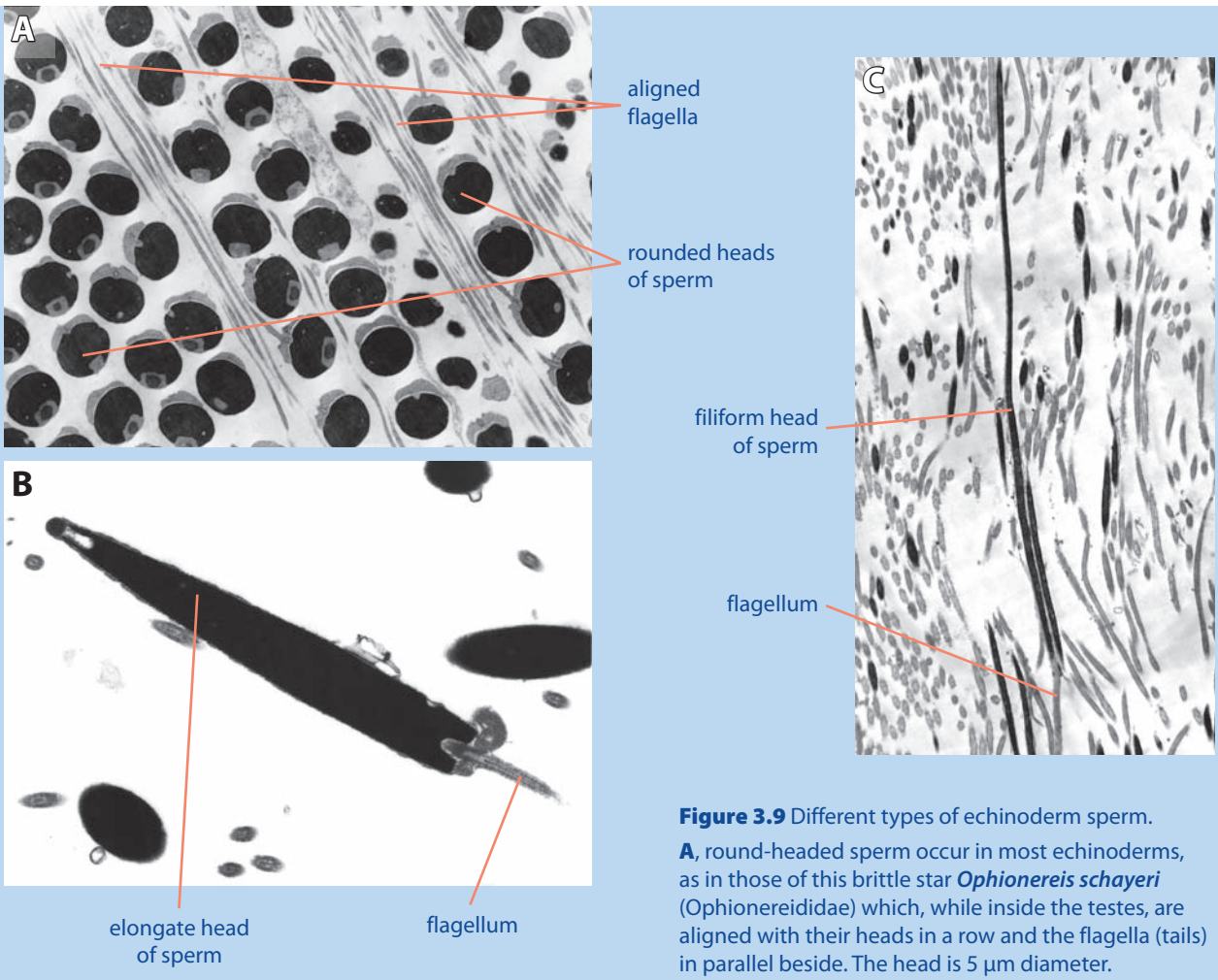


Figure 3.9 Different types of echinoderm sperm.

A, round-headed sperm occur in most echinoderms, as in those of this brittle star ***Ophionereis schayeri*** (Ophionereididae) which, while inside the testes, are aligned with their heads in a row and the flagella (tails) in parallel beside. The head is 5 µm diameter.

B, sea urchins have sperm with conical tips, like this from ***Heliocidaris erythrogramma*** (Echinometridae). The head is 7 µm long.

C, the extremely elongate filiform head of the sperm of ***Xyloplax*** (Xyloplacidae) is unique in the Echinodermata. The head is *ca.* 15 µm long.

[A,B, M.Byrne; C, J.Healy]

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Development

Most echinoderms are free-spawners, and fertilisation and development occur in the water column (**Figs 3.1, 3.2**). By contrast, *Parvulastra exigua* deposits its eggs in sticky masses on rocks of coastal reefs and tide pools (Byrne 1992), and the embryos complete their development unattended by the adult. Other species retain their eggs and care for their young (**Figs 3.5D, 3.4, 3.5A**). On the shores of islands in the Southern Ocean, *Anasterias*, a common intertidal seastar, holds its young around its mouth while they develop (Simpson 1982). The temperate seastar *Smilasterias multipara* incubates its embryos in its stomach (O'Loughlin & O'Hara 1990; **Box 8.3**). In this species the released eggs are picked up individually by the tube feet and transferred to the mouth. Consequently, the parent seastars cannot resume feeding until approximately a month later when the offspring have dispersed.

Brooding ophiuroids, such as *Amphipholis squamata* and *Ophiopeza spinosa*, retain their progeny in respiratory bursae until the young emerge as crawl-away juveniles (**Fig. 3.5**). A recent high resolution study of juveniles brooded in the bursae of *A. squamata* and *Ophioderma wahlbergii* (from South Africa) showed that all the juveniles were orientated with their mouth against the wall of the bursa, strengthening the hypothesis that the bursal wall provides nutrients to the developing young (Landschoff & Griffiths 2015).

Viviparous asterinid seastars do not spawn at all — rather, they retain their eggs in the gonads where they are fertilised (**Box 3.1**). As these animals have ovotestes, self-fertilisation is possible (**Fig. 3.6D,E**).

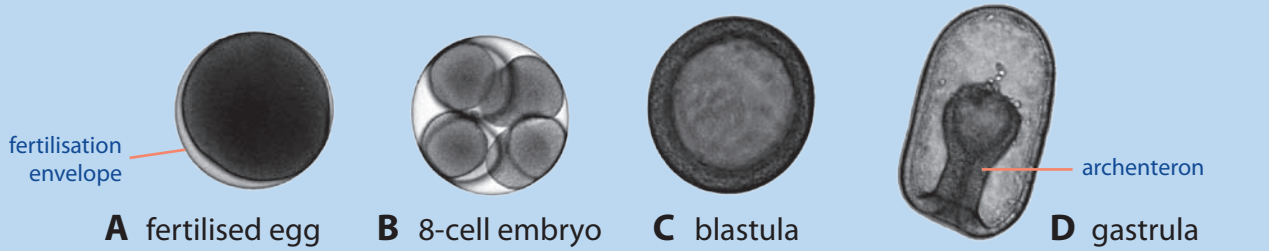
Brooding also occurs in crinoids (Messing 1984; Haig *et al*. 2012). *Aporometra wilsoni* from South Australia broods its young inside the maternal genital pinnules until they emerge as doliolaria larvae (**Fig. 3.12; Box 7.2**). Some crinoids brood their young to the advanced stalked pentacrinoid stage with their progeny attached to the female body (**Fig. 7.30A**).

Following early cell divisions, echinoderm embryos develop through blastula and gastrula to larval stages (**Figs 3.10, 3.11**). The presence of a feeding larva is considered to be the ancestral state for modern Echinodermata (Raff & Byrne 2006; **Fig. 3.11A–F**). Feeding (planktotrophic) larvae have well-developed digestive tracts and an intricate array of ciliated bands that are used to capture phytoplankton. Such larvae appear to have occurred in the early evolution of echinoderms. In contrast, non-feeding (lecithotrophic) planktonic or benthic larvae lack a functional gut and have comparatively simple ciliation (**Fig. 3.11G,H; Boxes 3.1, 8.1**). Evolution of a large egg freed larvae from the necessity to feed, resulting in the reduction and loss of feeding structures (Raff & Byrne 2006).

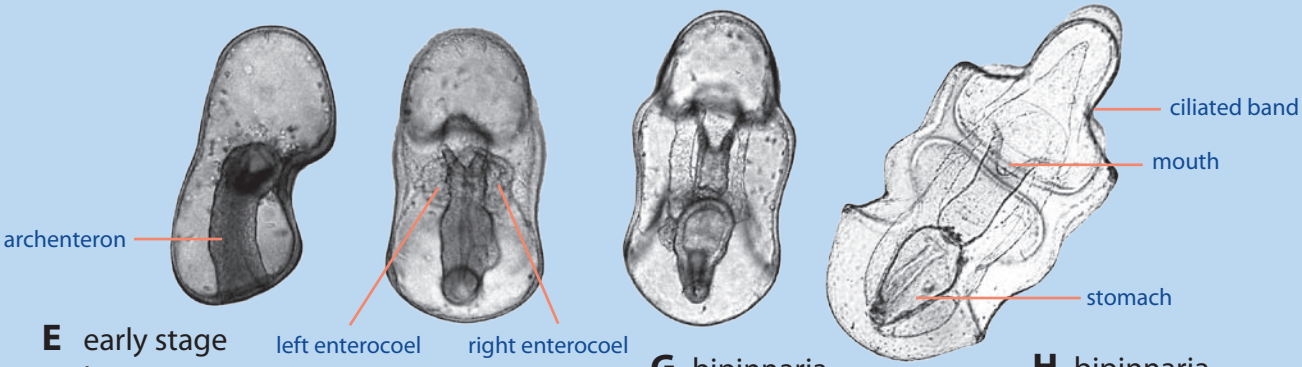
The presence of vestigial feeding structures such as a non-functional gut and a reduced pluteal skeleton in some non-feeding larvae provide evidence that lecithotrophy is a derived state in echinoderms (Emlet 1995a; Selvakumaraswamy & Byrne 2000a). Having non-feeding larvae is a trait often associated with a suite of life history attributes including decreased adult size, a large egg, hermaphroditism, internal fertilisation and parental care of the young. The evolutionary significance of the linkage of these traits has been a subject of extensive discussion, and while many hypotheses have been proposed, none provides a widely applicable explanation.

The different types of echinoderm larvae tend to be class specific (Raff & Byrne 2006; Young *et al.* 2006; Byrne 2013). Thus, most asteroids have planktotrophic bipinnaria and/or brachiolaria larvae, whereas ophiuroids and echinoids generally have pluteal larvae (**Figs 3.10, 3.11A–E**). The holothuroids have an auricularia larva (**Fig. 3.11F**) that is virtually identical to the tornaria larva of hemichordates (Byrne *et al.* 2006, 2007; Raff & Byrne 2006; Swalla 2006). Crinoids are not known to have a feeding larva — they have doliolaria larvae (**Figs 3.11I, 3.12; Box 7.2**). Significantly, the discovery of vestigial feeding ciliary band structures in the development of stalked crinoids (**Fig. 3.11I**) provided an important indication of the feeding larval life history in this most ancient group of echinoderms (Nakano *et al.* 2003).

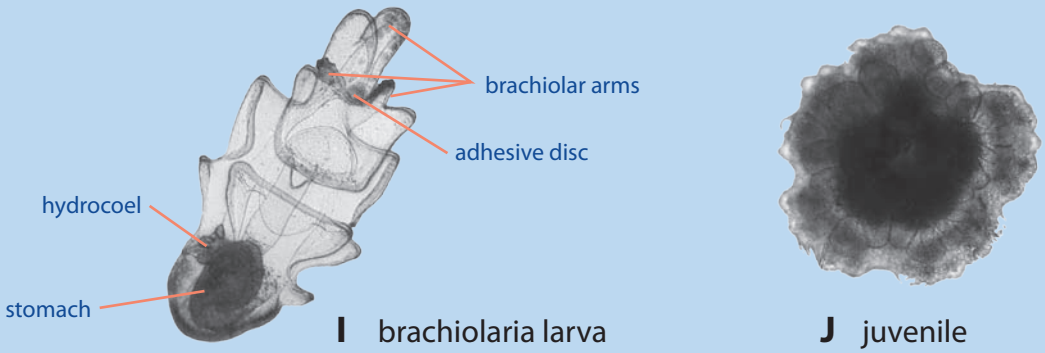
Asteroid bipinnaria have two ciliary bands that loop around the body and, as metamorphosis approaches, they can give rise to brachiolaria larvae with the



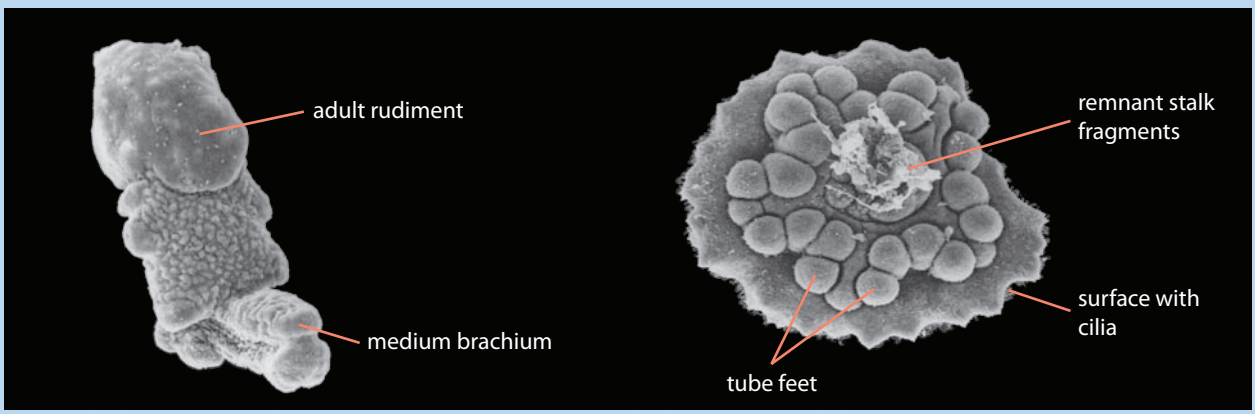
A fertilised egg **B** 8-cell embryo **C** blastula **D** gastrula



E early stage bipinnaria larva **F** mid stage bipinnaria larva **G** bipinnaria larva **H** bipinnaria larva



I brachiolaria larva **J** juvenile



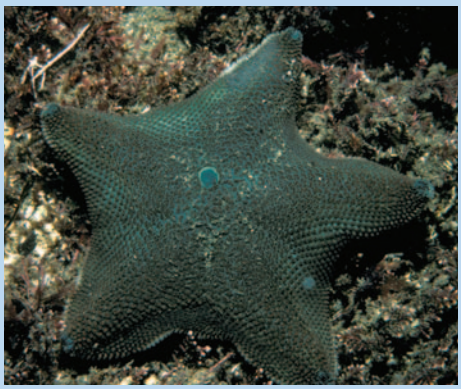
K metamorphosing larva **L** newly metamorphosed juvenile

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developing juvenile at the posterior end (**Fig. 3.10I,K**). These larvae have three sticky arms and an adhesive disc at the anterior end, all of which are used for benthic attachment by larvae ready to settle. However, paxillosidan seastars, such as *Luidia*, are the exception. They do not develop through a brachiolaria stage; instead the bipinnaria gives rise to the juvenile while in the plankton. In these asteroids the juvenile tube feet are used for settlement. Asteroids with non-feeding development have a simple brachiolaria larva with similar attachment structures (**Fig. 3.11G; Box 3.1**). The brachiolaria of the recently discovered species *Tosia neossia* is unusual in being non-swimming benthic larvae (Naughton & O'Hara 2009; **Box 8.1**).

The pluteal larvae of echinoids and ophiuroids have a ciliary band that follows the contour of the larval arms (**Fig. 3.11C–E**). Ophioplutei and echinoplutei have up to four and up to six pairs of arms, respectively, with a skeletal rod supporting each arm. The similarity of

Figure 3.10 Developmental stages of the New Zealand cushion seastar, ***Patiriella regularis*** (Asterinidae). Development in ***Patiriella regularis*** is through planktotrophic bipinnaria and brachiolaria larvae. Settlement and metamorphosis into juveniles occurs after 9–10 weeks. This species has separate sexes and spawns small eggs and sperm into the water column where fertilisation takes place:
A–J, light micrographs.
K–L, scanning electron micrographs.



M adult

A, newly fertilised egg with fertilisation envelope.

B, 8-cell cleavage stage embryo at 2–2.5 hours after fertilisation.

C, late blastula at about 16 hours.

D, advanced gastrula with the primitive gut, the archenteron, forming at *ca.* 35 hours. Advancement to the gastrula larval stage occurs when the blastula hatches through the rupture in the fertilisation envelope; the gastrula becomes a free-swimming larva.

E, early stage bipinnaria larva, the archenteron (primitive gut) is forming at *ca.* 47 hours.

F, mid stage bipinnaria larva with the right and left enterocoel forming by outpocketing of the archenteron (typical of echinoderms and chordates); *ca.* 55 hours after fertilisation.

G–H, more advanced bipinnaria; 75 hours to 4 weeks.

I, advanced brachiolaria (the second larval stage) at 8 weeks, with an attachment complex at the anterior end comprising three well-developed brachiolar arms and an adhesive disc, and an adult rudiment, with the five lobes of the hydrocoel evident at the posterior end. The attachment complex is used to attach the larva to the benthos when it settles.

J, metamorphosing larva from the aboral surface; it is the developing adult rudiment that is visible, at 9 weeks.

K, late brachiolaria, ventral view, in the exploratory/attachment posture with the median brachium extended at 90° to the larval body and a distinct adult rudiment at the posterior end. After 9–10 weeks the advanced brachiolaria extends its brachia (arms) and attaches to the substrate, at first undertaking a temporary attachment/exploratory phase. During this exploratory phase the brachiolaria may detach and swim away or 'walk' over the substratum. Following this phase, the larva attaches permanently using the brachia and adhesive disc and starts to metamorphose. During metamorphosis the larval body is shortened and resorbed to a thin stalk. The adult rudiment develops with formation of the pentamerous shape.

L, post-metamorphosing larva detached from its stalk, oral view. Remnants of the stalk are visible centrally, and two pairs of tube feet are present on each of the five rays. The future adult surface is covered in cilia. The post-larva breaks free of its attachment stalk and takes up an independent existence at a diameter of 450–500 µm, five to six days after settlement. Development continues with the completion of the adult digestive tract; the newly detached post-larva does not have a mouth or an anus.

M, adult New Zealand cushion seastar.

[A–L, from Byrne & Barker 1991; M, K.Gowlett-Holmes]

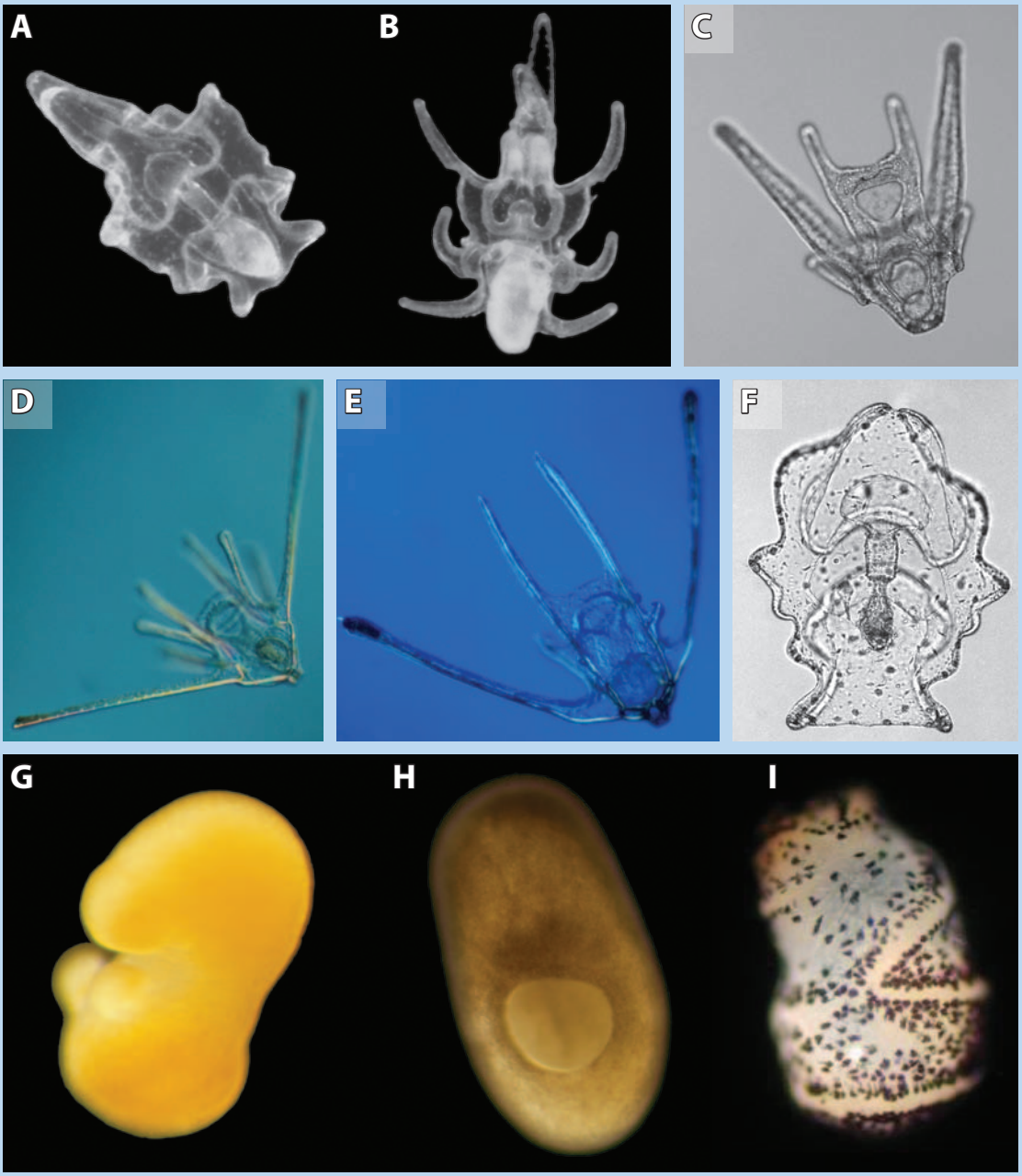


Figure 3.11 Echinoderm larvae. **A–F**, feeding planktotrophic larvae. **G–I**, non-feeding lecithotrophic larvae.

A, late bipinnaria larva of the crown-of-thorns seastar ***Acanthaster planci*** (Acanthasteridae); 700 µm long.

B, brachiolaria larva of ***Acanthaster planci***; 1.5 mm long.

C, echinopluteus larva of the sea urchin ***Temnopleurus alexandri*** (Temnopleuridae); 200 µm long.

D, ophiopluteus larva of the brittle star ***Macrophiothrix spongicola*** (Ophiotrichidae); 350 µm long.

E, ophiopluteus larva of the brittle star ***Ophiactis resiliens*** (Ophiactidae); 400 µm long.

F, auricularia larva of the sea cucumber ***Holothuria scabra*** (Holothuriidae); 750 µm long.

G, brachiolaria larva of the seastar ***Cryptasterina pentagona*** (Asterinidae); 550 µm long.

H, vestibula larva of the sea urchin ***Holopneustes purpurascens*** (Temnopleuridae); 700 µm long.

I, doliolaria larva of the sea lily ***Metacrinus rotundus***; 500 µm long.

[A,B, J.Keesing; C,F,G, M.Byrne; D,E, P.Selvakumaraswamy; H, M.Ricketts; I, H.Nakano]

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ophioplutei and echinoplutei was taken to suggest a close relationship between echinoids and ophiuroids. However, it is now accepted that these larvae are a striking example of parallel (independent) evolution. The juvenile sea urchin develops in the posterior region of the larva as the larva settles to the seafloor. In contrast, brittle stars metamorphose in the plankton, with the juvenile supported by the remaining larval arms. Echinoids with lecithotrophic development, such as *Heliocidaris erythrogramma* and *Holopneustes purpurascens*, can have reduced plutei or a simple spherical larva with no pluteal structures (Morris 1995; Byrne *et al*. 2001; Byrne & Selvakumaraswamy 2002; Raff & Byrne 2006; **Fig. 3.11H; Box 10.4**). Ophiuroids with non-feeding development, such as *Ophionereis schayeri*, *Ophiopeza spinosa* and *Ophiarachnella gorgonia*, typically have vitellaria larvae characterised by distinct ridges of cilia (Byrne & Selvakumaraswamy 2002; Cisternas *et al*. 2004; Cisternas & Byrne 2005; Byrne *et al*. 2008a). The non-feeding larvae of echinoids range from the larva of *Heliocidaris erythrogramma* which has a reduced larval skeleton and a ciliated band (**Box 10.4**) to the vestibula larva of *Holopneustes purpurascens* (**Fig. 3.11H**) which has lost all traces of the pluteus larva (Morris 1995).

Holothuroid auricularia have a single ciliated band that loops around the body, resembling the asteroid bipinnaria (**Fig. 3.11F**). As metamorphosis approaches, the auricularia gives rise to a non-feeding doliolaria larval stage by reorganisation of the ciliated bands. All crinoids have non-feeding development through a doliolaria larva (**Figs 3.11I, 3.12**).

A striking feature of echinoderm development is the metamorphosis of a bilaterally symmetrical larval stage into a radially symmetrical adult. Echinoderms arose from a bilateral ancestor, and the radial adult body plan is a highly derived feature. Explaining this evolution has been a challenge to scientists, but the consensus from recent molecular research indicates that the feeding larval stage was interposed between the adult and the juvenile stage of formerly direct-developing ancestral echinoderms (Raff & Byrne 2006). Metamorphosis involves a complex of morphogenetic changes when the larval body is fully or partially reabsorbed as the juvenile forms. There is great interest in the extent to which larval structures contribute to the adult body and how this differs among the classes (David & Mooi 1998; Arnone *et al*. 2015; Byrne *et al*. 2016a). These data have implications for how we interpret the evolution and phylogenetic relationships of the classes.



Figure 3.12 A doliolaria larva emerges from a genital pinnule via the genital pore of a female ***Aporometra wilsoni*** (Aporometridae); note that the doliolaria larva lacks ciliary bands and thus is unable to swim (see **Box 7.2**). This feather star, like the only other two ***Aporometra*** species, is a brooder that retains embryos at various stages of development within the maternal genital pinnules; the doliolaria larva (*ca*. 400 µm long) emerge from the female through a pore on the genital pinnule.

[G.W.Rouse]

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4: Management: Fisheries, Ferals and Conservation

Timothy D. O'Hara and Maria Byrne

Fisheries

Sea cucumbers – trepang

Holothuroids, known commonly as sea cucumbers, have been fished and eaten by the peoples of East Asia for at least a thousand years (**Figs 4.1–4.3**). The processed body wall of the sea cucumber is known by a variety of names, including bêche-de-mer (according to MacKnight (1976) a corruption of the Portuguese 'bicho da mar' or sea worm), trepang (Indonesian), hai-sum (Chinese) and iriko (Japanese). Throughout East Asia bêche-de-mer is considered a delicacy and added to soups and stews or pickled. In China it is a luxury sea food item and is regarded as a culinary treasure (To & Shea 2012; Purcell *et al*. 2013). It has a reputation as an aphrodisiac or anti-inflammatory agent, although the former is possibly based more on the shape of the animal than any

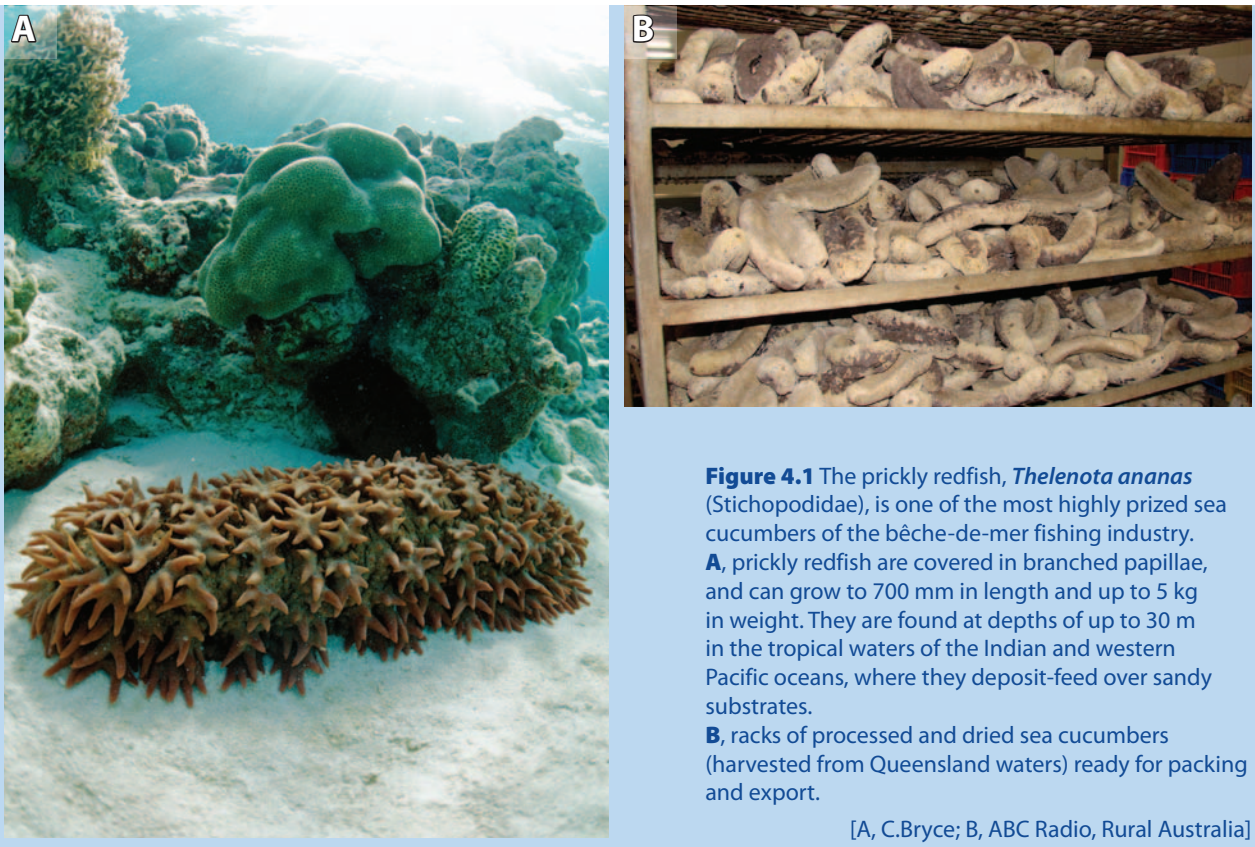


Figure 4.1 The prickly redfish, ***Thelenota ananas*** (Stichopodidae), is one of the most highly prized sea cucumbers of the bêche-de-mer fishing industry.
A, prickly redfish are covered in branched papillae, and can grow to 700 mm in length and up to 5 kg in weight. They are found at depths of up to 30 m in the tropical waters of the Indian and western Pacific oceans, where they deposit-feed over sandy substrates.
B, racks of processed and dried sea cucumbers (harvested from Queensland waters) ready for packing and export.

[A, C.Bryce; B, ABC Radio, Rural Australia]

Box 4.1 The changing names of sea cucumbers

In recent times, several fished sea cucumbers have been subjected to a particularly confusing series of name changes. One remarkable account concerns the commercially valuable species known by its commercial name as the black teatfish (*Holothuria whitmaei*). Although fishers have long observed two colour forms, for much of the second half of the twentieth century taxonomists adhered to the view held by eminent German taxonomist Albert Panning (1944) that they represented a single, variably coloured species, *Holothuria nobilis*, described by Selenka in 1867. It was not until the late 1970s that French scientists in New Caledonia recognised that local black and white and black forms had different reproductive patterns. The name *nobilis* was retained for the black form and Cherbonnier in 1980 newly described and named *Holothuria fuscogilva* (the black and white form).

Subsequently, Rowe (in Rowe & Gates 1995:296) examined Selenka's original description and type specimens and found a mixture of black and black and white animals. He was convinced that Selenka had two species before him when he described *nobilis*, a black and white form (collected from Zanzibar, East Africa) and a black form (collected from Hawaii). Rowe then considered that the black and white form, including the recently described *fuscogilva*, represented the species Selenka had named *nobilis*, whereas he identified the black form as another closely related species, *Holothuria whitmaei*. More recently, a molecular study (Uthicke *et al*. 2004a) demonstrated that there are at least three species: black animals with white 'teats' from Africa (*H. nobilis*), white animals with black markings that range across the Indo-Pacific (*H. fuscogilva*) and a mainly black animal from the western Pacific (*H. whitmaei*). Geographic variation within *H. fuscogilva* may be indicative of further cryptic species; the so-called 'pentard' variety of teatfish harvested as *H. fuscogilva* in the north-eastern Indian Ocean is likely to be a new species.

Other recent name changes are listed in **Table 4.1**. Unfortunately, this is not the end of name changes for fished holothuroids, as there is some uncertainty regarding other Indo-Pacific species of *Holothuria*, *Actinopyga*, *Bohadschia* and *Stichopus* which will only be resolved through molecular and morphological analyses of live animals and preserved type specimens in museums. Although the common names used by fishers and natural resource managers are reasonably descriptive, it is clear that some commercial fishery names include several species. For example, the curryfish group comprises three species, *Stichopus herrmanni*, *S. ocellatus* and *S. vastus*. Also, the *Stichopus horrens* group comprises numerous species, including *S. horrens* (*sensu stricto*), *S. naso* and *S. monotuberculatus*, with the last taxon representing a species complex. Determination of the identity of harvested species is critical for species management, conservation and identification of species in need of protective measures.

Establishing and changing the scientific names of these holothurians, as for all species, is governed by a series of rules and guidelines known as the *International Code of Zoological Nomenclature*. The *Code* aims to bring stability to scientific names, removing the confusion that may occur when different common names are used for the same species. However, scientific name changes can be equally bewildering, especially in cases where two or more scientific names have been applied to one species, or, as in the case of *Holothuria nobilis*, where the 'species' is found to comprise several distinct species. Many of the commercial species are now listed as vulnerable or endangered by the International Union for Conservation of Nature (IUCN).

Further reading Selenka 1867; Panning 1944; Cherbonnier 1980; Rowe & Gates 1995; Uthicke *et al*. 2004a, 2010; Byrne *et al*. 2010; Conand *et al*. 2014

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pharmaceutical evidence (Cannon & Silver 1986). The major consumer of bêche-de-mer (or trepang) is China, followed by Korea and Japan, and much of the trade is channelled through dealers in Hong Kong, Singapore and Taiwan (Conand 2001; To & Shea 2012). The animals are collected for export from all around the Indo-Pacific oceans, from Madagascar to Ecuador and Canada to New Zealand. In Australia, established fisheries are found across the tropical north, and there is interest in starting a small temperate fishery in the south-east. The most important fishery in Australia is the Queensland Sea Cucumber Fishery operating on the Great Barrier Reef (Eriksson & Byrne 2015). In addition to dried and frozen product, fermented sea cucumber intestines are sold in large bottles in Samoa (Eriksson *et al.* 2007), and pickled sea cucumber intestines and body wall are consumed in Japan.

Australia's first modern industry

Trade in bêche-de-mer was Australia's first modern industry (MacKnight 1976). Prior to 1700, Indonesian fishers from Macassar (Ujung Pandang) in southern Sulawesi used the December–February monsoonal winds to sail south-east to (now) Arnhem Land to gather and dry the sea cucumbers that were abundant in the shallow waters of the coastal north. The Macassans set up camps to process and smoke the harvest before catching the April–May winds to return home. In Macassar, the catch was bought by Chinese merchants and shipped back to China on trading junks.

The Indonesian fishers, according to nineteenth century European observers (MacKnight 1976), appear to have collected mostly the light-coloured *Holothuria scabra* (sandfish or chalkfish; **Fig. 4.3A**) and a dark-coloured



Figure 4.2 Traditionally sea cucumbers are processed into a dried product known as bêche-de-mer (or trepang). Today, sea cucumbers are also available as a frozen product. White teatfish, ***Holothuria fuscogilva*** (Holothuriidae), collected from the tropical waters of Australia, is one species which is processed for delivery as a frozen product to local and Asian markets. One of the largest import and export markets is in Hong Kong.
A, processing commences on fishing vessels with gutting and freezing as seen for these sea cucumbers.
B, bagged sea cucumbers awaiting final treatment following delivery to the processing plant from fishing vessels.
C, sea cucumbers are further treated onshore in dedicated processing plants with the product undergoing a brine bath, further gutting as required, boiling and freezing. Once processed, the frozen sea cucumber product is packed into boxes for shipment to wholesale markets. This product may be used in various enterprises including the restaurant trade and retail sales.
[R.Kuiter; courtesy of Tasmanian Seafoods]

Table 4.1 Commercial holothuroids in the waters of tropical Australia.

* commercial species harvested in Australia.
EN endangered as defined by the IUCN (1994).
VU vulnerable as defined by the IUCN (1994).
§ names from Russell & Vail 1988a.
§§ information from Conand 1998a; Kinch *et al.* 2008; Department of Sustainability, Environment, Water, Population & Communities 2011.
† states and territories of Australia: NSW, New South Wales; NT, Northern Territory; QLD, Queensland; TAS, Tasmania; VIC, Victoria; WA, Western Australia.

Species	Common name	Indonesian name §	Current value	Notes §§ †
Actinopyga echinites * VU	deep water redfish		medium	Minimum size in WA and NT is 120 mm, and in QLD is 150 mm.
Actinopyga lecanora	stonefish	obor or kapok	medium	Generally highly fecund with early sexual maturity. *Actinopyga* species are not distinguished once processed.
Actinopyga miliaris * VU	blackfish		medium	Minimum size in QLD is 200 mm; marketed as Long Blackfish.
Actinopyga spinea *	burrowing blackfish			Minimum size in QLD is 200 mm; marketed as long blackfish.
Actinopyga sp. (formerly *Actinopyga mauritiana*)	surf redfish	kasut	medium	The fishery for surf redfish was closed in the Torres Strait in January 2007.
Bohadschia argus	leopard fish	getak	low	*Bohadschia* species are generally not distinguished after processing; their biology is poorly known.
Bohadschia marmorata (sometimes confused with *Bohadschia vitiensis*)	brown sandfish		low	
Bohadschia ocellata	leopard fish	getak	low	
Bohadschia similis	brown spotted sandfish		low	
Holothuria atra *	lolly fish	cerah	low	Traditionally harvested; minimum size limit across northern Australia is 150 mm, but in QLD is 200 mm.
Holothuria coluber	snake fish	kasut	low	
Holothuria edulis	pinkfish	karet	low	
Holothuria fuscopunctata *	elephant trunkfish		low	Although of low value, vulnerable to over-exploitation by divers because of low fecundity and late sexual maturity; minimum size in QLD is 400 mm.
Holothuria leucospilota	white threads fish		low	Low value species because of cuvierian tubules and thin skin.

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Species	Common name	Indonesian name §	Current value	Notes §§ †
Holothuria fuscogilva * VU	white teatfish	koroh susu	high	Extensively harvested by divers, late sexual maturity and low fecundity, stocks declining across its range, vulnerable to over-exploitation; minimum size in WA and NT is 320 mm, 400 mm in QLD.
Holothuria lessoni * EN (formerly *Holothuria scabra versicolor*)	golden sandfish		high	Extensively harvested, high potential fecundity; minimum size in QLD is 200 mm.
Holothuria scabra * EN	sandfish		high	Extensively fished, potential for aquaculture due to wide environmental tolerance, high fecundity and early sexual maturity; minimum size in WA and NT is 160 mm, 200 mm in QLD.
Holothuria whitmaei * EN (formerly *Holothuria nobilis*)	black teatfish	koroh batu	high	Extensively harvested on reef flats, low fecundity and late sexual maturity, stocks declining across its range, vulnerable to over-exploitation; minimum size in WA is 260 mm and NT is 320 mm; fishing in Torres Strait was suspended in January 2007.
Stichopus chloronotus	greenfish	japong	low	Occasionally harvested, biology poorly known; minimum size in QLD is 200 mm.
Stichopus naso (mistakenly called *Stichopus horrens*)	peanutfish		low	
Stichopus ocellatus *	curryfish		high	Member of the curryfish group, minimum size in QLD is 350 mm.
Stichopus vastus *	curryfish		high	Member of the curryfish group, minimum size in QLD is 350 mm.
Stichopus herrmanni * VU (historically referred to as *S. variegatus*)	curryfish	gama	high	An important species in the QLD fishery; minimum size is 350 mm. This and other species in the curryfish group are now considered high value species due to modifications in processing. Once these animals were rarely harvested as they would readily disintegrate.
Thelenota ananas * VU	prickly redfish	nanas	high	Extensively harvested by divers, vulnerable to over-exploitation due to low potential fecundity and late sexual maturity, stocks declining; minimum size in WA and NT is 300 mm, 500 mm in QLD.
Thelenota anax *	amberfish	duyung	low	Harvested by divers; vulnerable to over-exploitation.

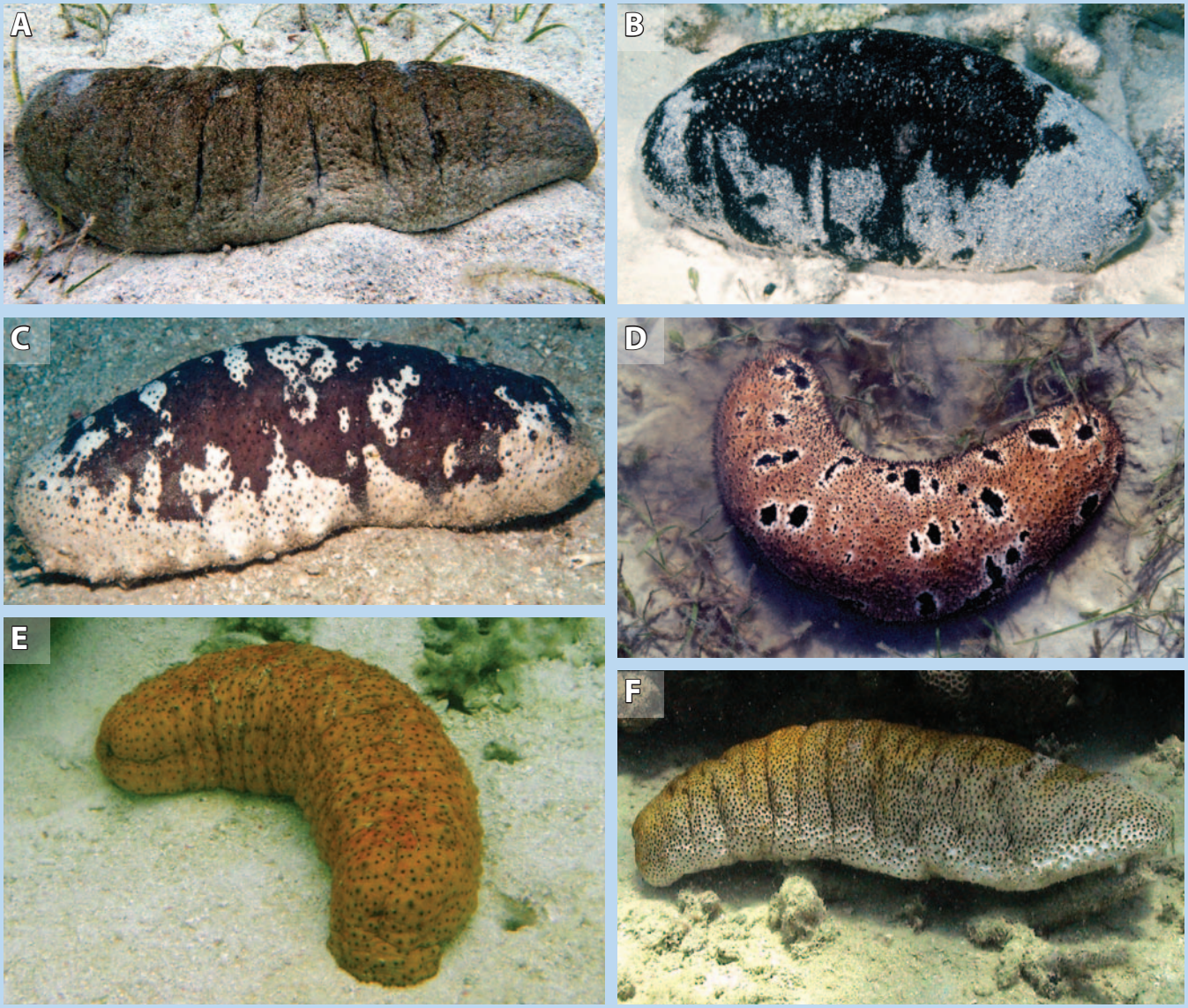


Figure 4.3 Although some 200 species of sea cucumbers have been described from Australian waters, only about 20 have been fished for commercial or traditional purposes. The commercial value of a species is generally determined by its size and the thickness and consistency of the body wall.

High value species include:

A, sandfish, ***Holothuria scabra*** (Holothuriidae);

B, black teatfish, ***Holothuria whitmaei*** (Holothuriidae);

C, white teatfish, ***Holothuria fuscogilva*** (Holothuriidae);

D, golden sandfish, ***Holothuria lessoni*** (Holothuriidae); and

E, curryfish, ***Stichopus herrmanni*** (Stichopodidae).

Low value species include:

F, elephant trunkfish, ***Holothuria fuscopunctata*** (Holothuriidae).

[A, S.W.Purcell; B, C.Bryce; C, G.R.Allen; D, L.Newman & A.Flowers; E, M.Byrne; F, A.Hoggett]

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species, possibly *Actinopyga miliaris* (blackfish) or *Holothuria whitmaei* (black teatfish; **Fig. 4.3B**). Animals were collected in the shallows at low tide, by hand or with a short spear, by divers who could free-dive down to 20 m, or by a simple dredge pulled by several canoes.

Sea cucumbers require considerable preparation to produce a marketable product and that process can vary considerably among species. The dense skeletal ossicles in the skin require specific processing techniques, many of which have been in use for hundreds of years and are still used today in India, Indonesia and throughout the South Pacific (Hamel *et al*. 2001). In general, processing begins by the removal of the viscera and sand from inside the sea cucumber followed by the body wall being rinsed in sea water; this may occur on board fishing vessels. The body wall product is then boiled in water for a short time and is then further processed for one to three weeks in salt and water. Following this, the body wall is dried in the sun for a few days or smoked in specially constructed huts. Modern processing in Australia is conducted on an industrial scale following many of the traditional processing steps. However, following the boiling of the body wall it may be frozen and shipped clearly labelled as frozen bêche-de-mer product (To & Shea 2012).

MacKnight (1976) documents the history of the trepang trade in Australia. At its height, the Australian trepang trade may have reached 600 tonnes of dried product or 6 million animals per annum. In 1882, the South Australian State Government, which had jurisdiction over what is now the Northern Territory, introduced licences and imposed customs duties on the Macassans, and in 1906 it closed the trade in favour of local fishers. However, the local industry failed to reach the scale of the Macassan trade due to the higher costs of labour. A fishery in Queensland and in the Torres Strait fared better. It first started in 1827 and produced up to 542 tonnes per annum in the early 1900s, including the flesh of a valuable reef-dwelling holothuroid, the black teatfish. The local industry in Western Australia was never large, and always secondary to the pearling trade. For Indonesians who traditionally fish the coral reefs and banks off north-western Australia, holothuroids are only part of the target catch, along with shark fin, fish, trochus shell and clam meat. The Queensland fishery declined during the 1930s due to over-exploitation of stocks in the Torres Strait and the beginning of World War II. From 1948 to the 1980s this fishery did not operate.

Current status

The most recent review of the Australian trepang fishery is provided by Kinch *et al*. (2008); see **Table 4.1**. A surge in demand and a marked global expansion in the holothuroid trade occurred after 1980 (Conand & Byrne 1993). In 1992 approximately 11,400 tonnes of dried product were recorded from Australia, which equates to a fresh catch of around 120,000 tonnes (Conand 1998b). Serious over-exploitation of the high value species has occurred in many parts of the world, including Australia (Uthicke 2004; Uthicke *et al*. 2004b; Skewes *et al*. 2006; Eriksson & Byrne 2015). As populations of high value species have diminished, there has been a shift to harvesting of what was once considered to be medium to low value species and to the exploitation of stocks in deeper water, below 30 m (Conand 2001), as seen in the Great Barrier Reef fishery (Eriksson & Byrne 2015; **Fig. 4.4**).

The traditional, high-value species from the Indo-Pacific are the black teatfish (*Holothuria whitmaei*), white teatfish (*H. fuscogilva*) and, to a lesser extent, the prickly redfish (*Thelenota ananas*) (**Figs 4.1, 4.2, 4.3B,C**). All three species are large, but slow growing, and are easily collected. Consequently, they are biologically vulnerable to over-exploitation (Conand 1998a), and have been placed on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 1994) as endangered (*H. whitmaei*, *T. ananas*) and vulnerable (*H. fuscogilva*). Thirteen species have now been placed on the IUCN Red List (Conand *et al*. 2013). An inevitable decline in the stocks of these species, particularly the black teatfish, saw a shift to other species, most notably the two sandfish species (*Holothuria scabra* and *H. lessoni*) and *Actinopyga* species (Hamel *et al*. 2001). Sandfish quickly became the prime target species in the Indo-Malay and South Pacific regions, and by the late 1990s, intense exploitation had already depleted stocks in the waters of New Caledonia, Malaysia, Papua New Guinea,

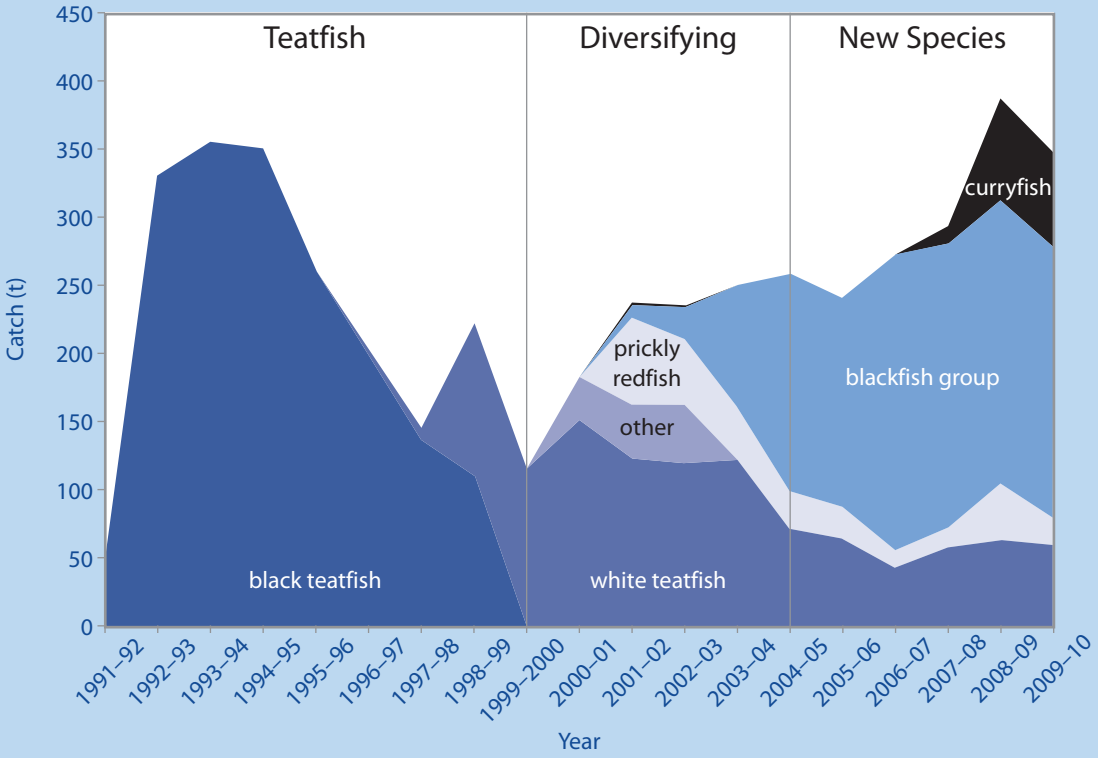


Figure 4.4 Catch records from the Queensland East Coast Bêche-de-mer Fishery. The blackfish group is predominantly burrowing blackfish (***Actinopyga spinea***) and a small amount of blackfish (***A. miliaris***). The three sections are conceptual periods in the fishery based on the composition of catch. A rotational zoning scheme for a portion of the fishery was implemented in 2004.

[from Erikisson & Byrne 2015]

Fiji and Mozambique (Hamel *et al.* 2001). In recent times the sea cucumber fisheries of many Indo-Pacific nations including Palau, Papua New Guinea, Samoa, Solomon Islands, Tonga and Vanuatu have been closed due to overfishing (FAO 2013; Purcell *et al.* 2013).

In Australia, holothuroid fisheries are located in northern Western Australia, the Northern Territory and Queensland, and around offshore islands and reefs in the Coral Sea and Indian Ocean. Over-exploitation led to the 1996 closure of the Torres Strait fishery for sandfish, and recent surveys (2004) indicate no population recovery (Skewes *et al.* 2006). The Torres Strait fishery for black teatfish and surf redfish (*Actinopyga* species, formerly *A. mauritiana*) was closed in January 2003 leaving only white teatfish, prickly redfish and some low value species to be harvested. Following local declines of *Holothuria whitmaei* in harvested areas in the Great Barrier Reef Marine Park (Uthicke 2004), the Queensland East Coast Bêche-de-mer Fishery for black teatfish was closed in 2002. Size limits for all species were introduced in all states in 1996 in an effort to protect brood stock (see **Table 4.1**).

The Total Allowable Catch (TAC) of the Queensland East Coast Bêche-de-mer Fishery changed from 380 tonnes gutted wet weight to 361 tonnes based on an agreed weight conversion (Queensland Department of Primary Industries and Fisheries 2007a; Fisheries Queensland 2010). It is not clear how this new reporting relates to the original TAC of 380 tonnes gutted wet weight with respect to tonnage landed. In 2007, 284 tonnes of a mixed species were harvested, reported as gutted wet weight. In the 2010 report, the TAC of 361 tonnes comprised 64 tonnes of white teatfish and 297 tonnes of 'all other species' (Fisheries

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Queensland 2010). In 2009–2010 the commercial harvest was 235 tonnes landed form (salted/frozen or boiled product) with burrowing blackfish (*Actinopyga spinea*) (marketed as long blackfish) contributing 70% of the total catch, white teatfish 20% and curryfish 9% of the catch. The value of the commercial harvest in 2009–2010 was $4.9 million; the primary market was China. The most recent assessment of the Queensland East Coast Bêche-de-mer Fishery indicates that the catch approached 400 tonnes in 2011 with a value of $5.4 million (Eriksson & Byrne 2015).

Two species have been listed under the name 'blackfish', the majority of the catch being the deeper water (>30 m) burrowing blackfish. In recent years, harvesting of animals from the curryfish group (*Stichopus herrmanni*, *S. vastus*) has increased. Once, species in the curryfish group were not considered to be commercially viable, as the body wall would easily disintegrate on collection. However, the move by industry towards frozen product (Fisheries Queensland 2010) has resulted in a higher value product. In recent activity *Stichopus herrmanni* has become a significant part of the catch with harvest focused on the Capricorn Bunker region of the southern Great Barrier Reef. In 2007–2008, about 11,000 individuals of curryfish were extracted from 12 zones. In 2008–2009, this number rose to 64,500 individuals extracted from 40 zones, and in 2009–2010 about 61,000 individuals were extracted from 43 zones (Fisheries Queensland 2011). In total, at least 155 tonnes of curryfish (that is 136,500 individuals multiplied by the reported individual mean weight of 1.14 kg in Roelofs (2004)) were harvested between 2007 and 2010 (Eriksson & Byrne 2015).

A portion of the fished area in the Queensland fishery is managed on a three-year rotational zoning system with time limits in each zone introduced to reduce local fishing pressure (Lowden 2005; Plagányi *et al.* 2015). However, Burrowing Blackfish Zones are not managed through the three-year rotational zone plan. Management of this fishery, the most important component of the Queensland sea cucumber harvest, relies on allocated zone-specific total allowable catches. From 2004, burrowing blackfish have dominated the catch with over 1.2 million individuals harvested in 2006–2007, declining slightly in subsequent years (Fisheries Queensland 2011). Fishers are also allowed to fish beyond the rotational time limits and in unallocated prospecting zones for curryfish which are considered an 'underutilised taxon' (Fisheries Queensland 2011). The major curryfish species fished in Queensland waters, *Stichopus herrmanni*, is now listed as vulnerable to extinction by the IUCN (1994), Conand *et al*. (2013) and Purcell *et al*. (2013, 2014). This species has suffered a 60–90% decline in over 50% of its range (Conand *et al*. 2014; Purcell *et al*. 2014).

The short-lived Moreton Bay Fishery had a TAC of 45 tonnes, but in 2007 this fishery harvested only 20 tonnes, entirely of sandfish (Queensland Department of Primary Industries and Fisheries 2007b). The developing fishery in the Coral Sea was limited to two operators who could collect up to 75 tonnes by hand. The fishery started again in the Northern Territory in 1992, while in the northern region of Western Australia, between Exmouth Gulf and the Northern Territory border, three operators took 78 tonnes of six species in 2005 (99% sandfish) (Hart & Murphy 2006). The average size caught suggested that a review of the Legal Minimum Length (160 mm) of sandfish was required. In the Northern Territory, 170 tonnes were collected in 2006, again mostly inshore sandfish (Northern Territory Government 2006). There was no apparent trend to the collection of lower value species.

Off north-western Australia, Indonesian fishers have been permitted to collect sea cucumbers from offshore reefs using traditional methods under a Memorandum of Understanding (MoU) signed between the Australian and Indonesian governments in 1974. The area covered by this MoU includes Ashmore Reef, Seringapatam Reef, Scott Reef and the surrounding reefs of Cartier Island and Browse Island. Most Indonesian fishers sail in traditional praus from the island of Roti off the coast of Kupang, West Timor. High value species, such as black teatfish, white teatfish and prickly redfish, were over-exploited on Ashmore and Cartier reefs by 1988 (Russell & Vail 1988b). In 2000, population densities of black teatfish were possibly only 0.4% of unfished stocks (Smith *et al.* 2000). Ashmore Reef and Cartier Island have since been declared marine reserves, and sea cucumbers can no longer be fished in these areas (Commonwealth of Australia 2002). However, illegal fishing has persisted, and sea cucumbers are found on some of the foreign

fishing vessels apprehended each year across Australian waters (Australian State of the Environment Committee 2001; Australian Fisheries Management Authority 2008).

A temperate species, *Australostichopus mollis* (**Fig. 1.1D**), forms the basis of a small fishery in New Zealand (Morgan & Archer 2000), and there have been proposals to harvest it in Victoria and Tasmania. However, these proposals have not come to fruition due to difficulties in calculating sustainable harvest levels and concerns over the potential bioaccumulation of heavy metals, including cadmium (Barry & Parry 1993).

The ecological effects of the sea cucumber fishery are largely unknown. Fishery-independent data for Australian sea cucumber fisheries is lacking and no biomass information is available from before the onset of harvesting. Thus, it is impossible to understand the full implications of harvest landing data. Harvesting is mostly by hand in Australia, thus avoiding dredging techniques that damage the seafloor biota. A sea cucumber fishery is unlikely to have much impact on predator numbers as most fished species have biotoxins that deter predation. However, sea cucumbers do play an important ecological role in the mixing of sediments across sand-flats; they also host numerous commensal animals (Purcell *et al.* 2016a). In addition, recent research indicates a key role for sea cucumbers in the calcium carbonate balance of coral reefs (Schneider *et al.* 2012; Wolfe *et al.* 2016). By breaking up calcium carbonate sand in the gut, the digestive process increases the pH of surrounding water. This source may contribute to buffering of changes in seawater pH associated with increasing atmospheric CO_2 at least locally. Thus, natural processes in the sea cucumber's gut may counter the negative effects of ocean acidification on coral growth.

The rezoning of the Great Barrier Reef in 2003 increased the area of no-take regions to 30% and, although many protected areas have low populations of commercial sea cucumbers due to pre-zoning harvest activity, they have the potential to support increased populations in the future. The critical importance of sanctuaries for the conservation of high value species such as the black teatfish is attested by the large populations of this species in no-take zones and their rarity in fished areas (Byrne *et al.* 2004b; Uthicke 2004).

Are sea cucumber fisheries sustainable?

Holothuroid fisheries throughout the tropical Indo-Pacific have been poorly managed (Conand 2001; Lovatelli *et al.* 2004; Toral-Granda *et al.* 2008; Purcell 2010; Friedman *et al.* 2011; Purcell *et al.* 2013, 2014). Basic population and catch data are lacking, and the biology of most species is largely unknown (see **Table 4.1**). In many cases, the most accessible species on reef flats are harvested, regardless of their size or value. There has been a serial depletion of valued species, including in Australia (**Fig. 4.4**). Even when management regulations are in place, supervision is poor and illegal fishing flourishes. Many high value species are characterised by slow growth, density-dependent fertilisation, low larval survival and ease of collection, making them particularly vulnerable to over-exploitation. It is doubtful whether a sustainable fishery can be maintained under these circumstances. Even countries such as Australia, with relatively well-managed and supervised resources, have had to close certain fisheries, and it could take up to 50 years for stocks to recover following cessation of fishery activity (Conand & Byrne 1993). The rotational zoning scheme applied to a portion of the Great Barrier Reef fishery is controversial (Plagányi *et al.* 2015; Purcell *et al.* 2015, 2016b), and as yet its success is not clear.

Working groups have been successful in the recent listing of commercial holothuroid species in Appendix II of the CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) convention on trade on endangered species (United States Fish and Wildlife Service 2002; Lovatelli *et al.* 2004; Toral-Granda *et al.* 2008). Furthermore, protection and conservation of many commercial species has been strengthened recently by their listing on the IUCN Red List of Threatened Species (Conand *et al.* 2014).

Stock enhancement or aquaculture may be the only long-term, sustainable way of maintaining a holothuroid industry. The most promising species for cultivation is the sandfish, which has a relatively high reproductive potential and can tolerate a range of environmental conditions. This has been successfully spawned and reared in captivity, although brood stock are still collected from the wild (Hamel *et al.* 2001). This species has distinct genetic stocks in different regions (Uthicke & Benzie 2001) and differences between the Indian

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and Pacific Oceans indicate the presence of cryptic species (Eriksson *et al*. 2011). The stock enhancement program in the Solomon Islands has been careful to use only local brood stock in order to maintain local and regional genetic diversity (Battaglene 2000).

Sea urchins

Sea urchins are harvested for their roe (gonads; **Fig. 3.3A**), which are considered to be a delicacy in Japan, and in other parts of eastern Asia and France (Andrew *et al*. 2002). Worldwide production is over 60,000 tonnes (wet weight) but, like sea cucumbers, sea urchins have been over-exploited in many areas, and the industry is experimenting with aquaculture (Andrew & Constable 1999). Typically, fisheries have been characterised by explosive growth leading to overfishing and, finally, decline.

Three species of sea urchin are currently harvested in temperate Australia: *Centrostephanus rodgersii* (Diadematidae), *Heliocidaris erythrogramma* and *H. tuberculata* (Echinometridae) (**Fig. 4.5**; **Box 10.4**; see also **Table 4.2** for a list of common names). The roe is removed from the test by processors in Australia, and air-freighted fresh or chilled to Japan. The sea urchin fishery began in Tasmania in the 1970s, and expanded rapidly until 1988 when 358 tonnes (live) of *H. erythrogramma* were harvested from sheltered bays along the east coast. The industry has declined since then; many formerly productive beds now appear to have been over-exploited, and divers have to collect from deeper, more inaccessible locations. A new management plan for the Tasmanian industry was introduced in 2005 (Department of Primary Industries, Water and Environment 2005). *Heliocidaris erythrogramma* and *H. tuberculata* are vulnerable to shore collectors due to accessibility of their shallow-water habitats.

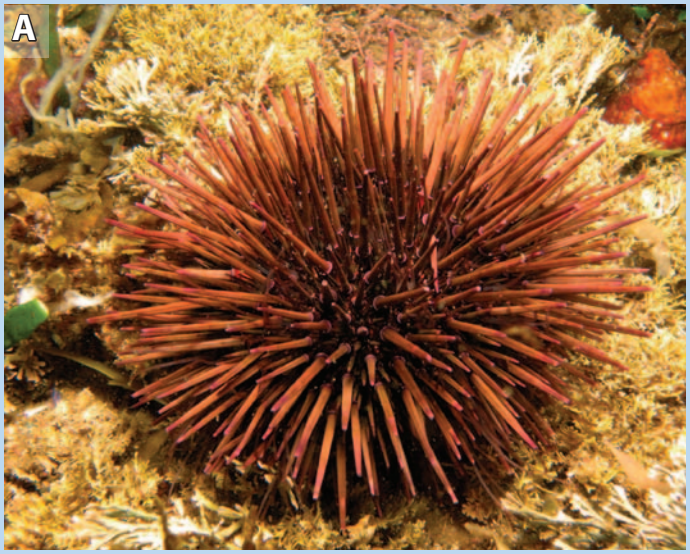
In Victoria, two species are harvested commercially: *Heliocidaris erythrogramma* and *Centrostephanus rodgersii*. For management and permit purposes the Victorian fishery is divided into two sectors based on locality: coastal waters of eastern Victoria and Port Phillip Bay (Victorian Department of Primary Industries — Fisheries 2011). Catches of *H. erythrogramma* have been variable, ranging from 4 to 38 tonnes for the period from 1995 to 2004. In the subsequent period, 2005–2010, the catch ranged from 12 to 4 tonnes from eastern Victoria and 18 to 13 tonnes from Port Phillip Bay (Victorian Department of Primary Industries – Fisheries 2011). Catches of *C. rodgersii* from the far east of the state rose sharply to 53 tonnes during 1995–1998, declining to 20 tonnes in 2004. In the subsequent period, from 2005–2010, the range was from 25 to 11 tonnes from eastern Victoria and 2 to 0 tonnes from Port Phillip Bay (Victorian Department of Primary Industries — Fisheries 2011).

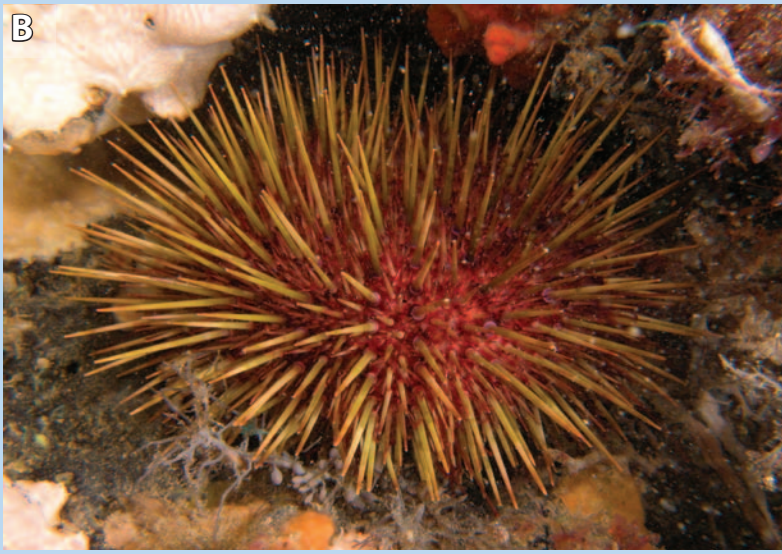
In New South Wales, a small fishery harvesting *C. rodgersii* and *H. tuberculata* (Andrew & Byrne 2007) expanded rapidly from less than 2 tonnes a year in 1998 to 120 tonnes in 2000; there is also a small fishery for *H. erythrogramma*. In 2015, the harvest,

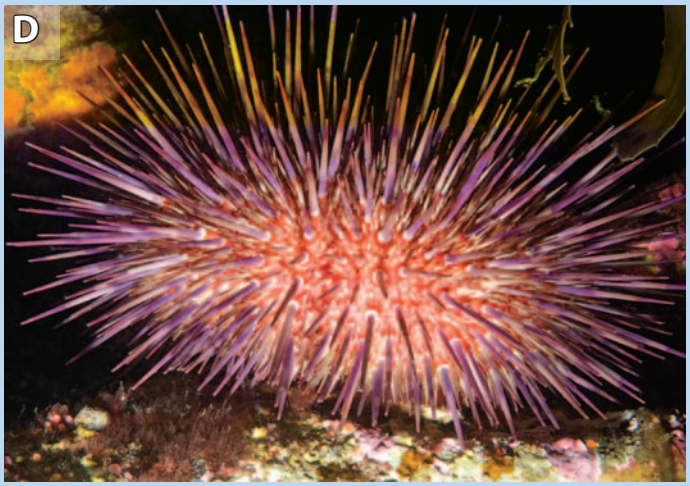
Table 4.2 Standard names used for the three commercial species of sea urchins.

§ In Tasmania *Heliocidaris erythrogramma* is commonly referred to by its generic name *Heliocidaris*.

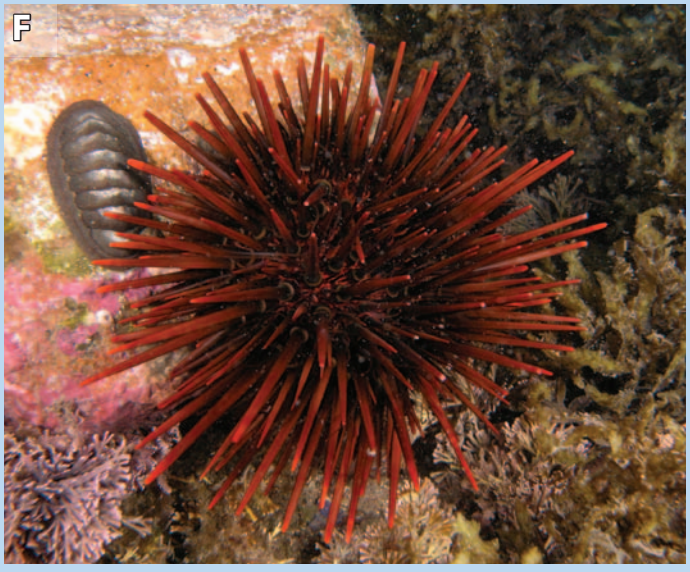
Scientific name	Fishery standard names	Other standard names
Centrostephanus rodgersii	purple sea urchin (NSW) black sea urchin (VIC) long-spined sea urchin (TAS)	long spine sea urchin
Heliocidaris erythrogramma	green sea urchin (NSW) white sea urchin (VIC) *Heliocidaris* (TAS)§ purple sea urchin (SA)	
Heliocidaris tuberculata	red sea urchin (NSW)	

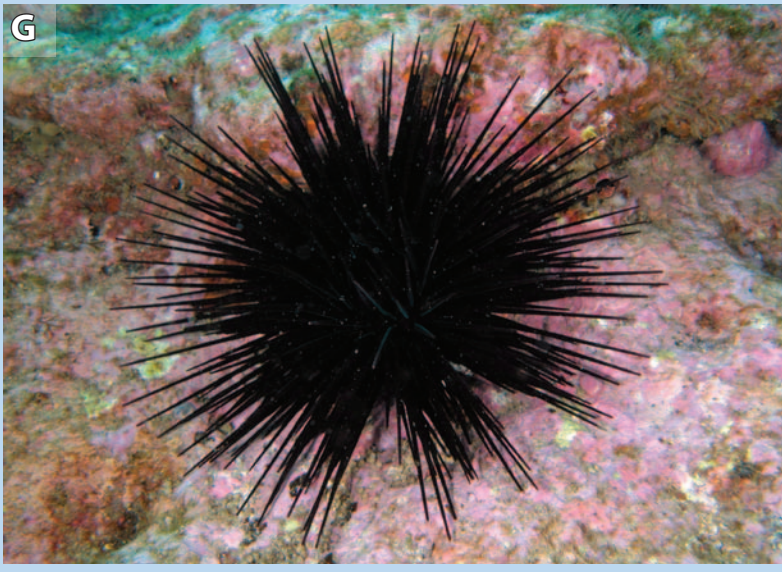












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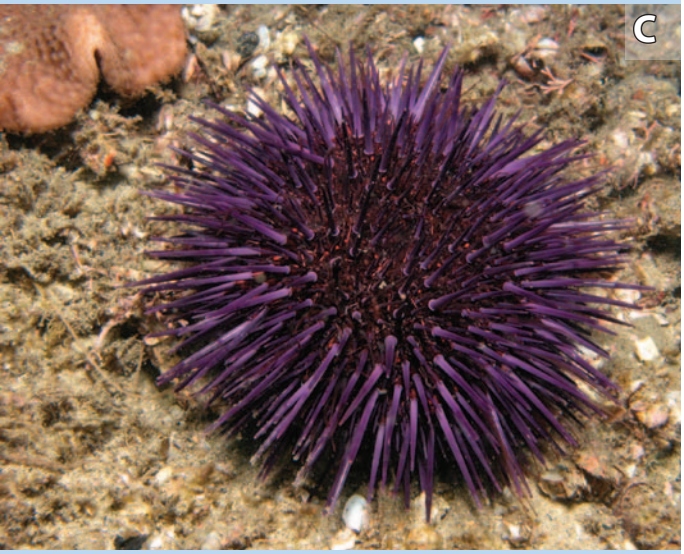


Figure 4.5 Three species of sea urchins are harvested commercially in temperate Australia. Commercial fishers hand collect sea urchins from intertidal rocky reefs using surface supplied air (hookah) or compressed air diving equipment.

A–**E**, different colour morphs of ***Heliocidaris erythrogramma*** (Echinometridae); animals from New South Wales (**A**–**C**) and Victoria (**D**,**E**). In New South Wales and South Australia very small catches are taken of this sea urchin, but in Victoria more significant harvests are made in the Port Phillip Bay zone. These urchins grow to a maximum test diameter of 105 mm, and are widely distributed around southern Australia.

F, ***Heliocidaris tuberculata*** (Echinometridae) occurs from southern Queensland to southern New South Wales, but is only harvested in New South Wales. These urchins grow to a maximum test diameter of 115 mm.

G, ***Centrostephanus rodgersii*** (Diadematidae) is abundant along the south-eastern coast from mid-northern New South Wales to eastern Victoria. This is the main sea urchin harvested in New South Wales, and in Victoria landings form a significant catch. These urchins grow to a test diameter of about 100 mm.

[A–C,F,G, D.Harasti; D,E, J.Finn]

dominated by *C. rodgersii,* is estimated to be 75–78 tonnes with a value of ~$100,000 (New South Wales Department of Primary Industries 2015). The fishery for *H. tuberculata*, both commercial and recreational, is a cause for concern. Due to questions on the suitability of *H. tuberculata* as a fishery species, this urchin was originally excluded from the commercial fishery, but the zero allowable catch was lifted and a fishery began in 1999 (New South Wales Department of Primary Industries 2015). The peak catch of *H. tuberculata* was recorded in 2000 at 48–83 tonnes, it subsequently declined to 10–16 tonnes in 2002–2009 and to 4–5 tonnes in 2013–2014 (Worthington & Blount 2003; New South Wales Department of Primary Industries 2015). *Heliocidaris tuberculata* is endemic to the east coast of Australia, limited to the region from just north of the Queensland border to mid New South Wales (**Box 10.4**). This species is recruitment and growth limited with slow to no recovery of fished populations and there is evidence of serial depletion (Worthington & Blount 2003). Overharvesting of this species has caused the demise of local populations.

A small fishery for *H. erythrogramma* is located in South Australia, in the areas surrounding Streaky Bay and Coffin Bay (Agriculture Food and Fisheries Division of Primary Industries & Resources 2004; Fisheries and Aquaculture Division of Primary Industries and Resources



Figure 4.6 Recreational harvest of ***Centrostephanus rodgersii*** (Diadematidae) from the coast of New South Wales. Recreational fishers are subject to a bag limit of 10 urchins (all species combined). Catch sizes from recreational collection of sea urchins is not known, but they can be locally substantial (M.Byrne, personal observation).

[B.Kelaher]

Box 4.2 New Zealand cushion star

Diagnostic features The New Zealand cushion star (*Patiriella regularis*) has a near-pentagonal shape, usually with five short triangular arms extending from the flattened disc. It can grow up to 75 mm in diameter. In New Zealand the colour is predominantly a mottled olive-green with yellow, orange, mauve and brown hues. In Tasmania the olive-green colour dominates.

Distribution This species is native to New Zealand, where it is found at depths down to 92 m around the North and South Islands, and the offshore Stewart and Chatham Islands. It was introduced into south-eastern Tasmania where it has spread as far as Bruny Island and the Tasman Peninsula. It is thought to have arrived in Tasmania after 1930 in crates of live oysters imported from New Zealand.







Figures a–c Colour variations in the New Zealand cushion star, ***Patiriella regularis***.
a, in its native waters of New Zealand this common species occurs in an array of colours from orange-red to blue, yellow and green.
b, **c**, in Tasmania, Australia, where the New Zealand cushion star is invasive, colouration varies from dark green (**b**) to olive-brown with a lighter margin (**c**).

[a, M.Byrne; b,c, K.Gowlett-Holmes]

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Other specimens exist in museum collections taken from Stanley (north-western Tasmania), Sydney and Newcastle (New South Wales) and Rockhampton (Queensland). These were collected between 1930 and 1976 and appear not to have formed permanent and sustainable populations.

Biology In New Zealand, *P. regularis* is one of the most common seastars on coastal platforms and shallow subtidal habitats where it grazes the microalgal film on rocks. The sexes are separate, and spawning occurs in late spring and early summer; planktotrophic larvae can live for up to 9–10 weeks before settlement; see **Figure 3.10** for details of developmental stages. Animals with four or six to eight arms are sometimes found.

The environmental impact of *P. regularis* has not been assessed, but it is likely to be substantial because it is a very opportunistic feeder. It can consume algal films, extruding its stomach over the substratum, and will take easy prey, engulfing small molluscs. *Patiriella regularis* will also aggregate around dead animals, quickly scavenging this food source.

Similar species *Patiriella regularis* differs from other five-armed Australian asterinid species in having a combination of an olive-green colour and gonopores on the aboral surface of the body. The plates are not in regular rows down the dorsal sides of the arm, and the spaces between the plates are large with numerous respiratory papulae.

Class Asteroidea
Family Asterinidae
Species *Patiriella regularis* (Verrill, 1867)

Further reading Byrne & Barker 1991; O'Loughlin *et al*. 2002; O'Loughlin & Waters 2004

South Australia 2011). Catch data are not available for this fishery.

Maintenance of a viable sea urchin industry has been hampered by the varying quality of the roe and the failure of stocks to recover sufficiently quickly after harvesting. Market prices depend on the colour, texture and quantity of roe (Department of Primary Industries, Water and Environment 2002; Fisheries and Aquaculture Division of Primary Industries and Resources South Australia 2011), which, in turn, are influenced by the reproductive condition and diet of the sea urchins. Roe can comprise up to 15% of the live body weight of *C. rodgersii* just before spawning (Andrew & Constable 1999). For *H. erythrogramma* in Tasmania, the average amount of roe per animal varied from 3 to 5.5% during the 1990s (Department of Primary Industries, Water and Environment 2002). The quality is generally poorest after spawning, but urchins forming dense populations or occupying less favourable habitats also have roe of poor quality (Byrne *et al*. 1998). This is a serious problem for *C. rodgersii* fisheries, as the majority of accessible animals occur in 'barrens habitats' where food levels are low (Andrew & Constable 1999). Moreover, entire crates of sea urchins have been rejected by processors if even only the first few animals are considered to have low quality roe (Department of Primary Industries, Water and Environment 2002).

Although recruitment for black sea urchins, *C. rodgersii*, tends to be sporadic (Andrew & Byrne 2007), large populations of this urchin have recently become established in Tasmania, through larval recruitment from New South Wales populations (Ling *et al*. 2008; Byrne & Andrew 2013). Recruitment of this urchin to Tasmania is attributed to its long duration as a planktonic larva (3–5 months) and strengthening of the East Australian Current due to climate change (Andrew & Byrne 2007; Ling *et al*. 2008). The decline in abundance of predators on sea urchins, such as rock lobsters and fishes, is also considered to have contributed to the successful range

Box 4.3 Northern Pacific seastar

Diagnostic features The Northern Pacific seastar (*Asterias amurensis*) has the classic seastar form with five long arms, each up to 250 mm. These radiate from a small central disc and gradually taper to a pointed tip. The convex dorsal surface is covered in irregular longitudinal rows of small spinelets. The ventral surface is flat, with a single row of spines on the adambulacral plates along the furrow and four rows of suckered tube feet. The colour is mainly yellow with purple hues, particularly near the arm tips.

Distribution This species is known in the northern Pacific from Japan around to Alaska, including the Chinese, Korean and Siberian coastlines. In Australia, the first animals were collected in 1986, and now large populations occur in the Derwent Estuary in Tasmania and Port Phillip Bay in Victoria. There are also ongoing sightings from other locations on the coasts of Tasmania and Victoria.

Biology *Asterias amurensis* is a voracious carnivore that prefers bivalves, but will eat a range of prey from heart urchins and ascidians to fish carcasses. It is even cannibalistic when food is scarce. These seastars are enormously fecund — females can release up to 20 million eggs. Larvae can live up to 90 days, and can be swept to remote locations by currents.

Similar species Within Australia, *Asterias amurensis* is often confused with *Uniophora granifera* which also has five elongate arms and purple hues. The latter can be distinguished by the relatively robust 'knobbed' spinelets on the dorsal surface and the blunter tips to the arms.

Interaction with humans In Japan, *Asterias amurensis* is considered a major problem on cultivated bivalve beds, and the seastar is removed by dredging. In China dried *A. amurensis* are used to flavour soups. The massive numbers of these animals in Australian populations and the very high density of larvae in the invasive range of this species ensure that the risk of translocation to other localities along the southern Australian coast remains high. Under ocean warming scenarios, however, the distribution of *A. amurensis* in Australia is modelled to contract while suitable habitat for this species in the Southern Ocean and Antarctica will increase.

Class Asteroidea
Family Asteriidae
Species *Asterias amurensis* (Lütken, 1871)

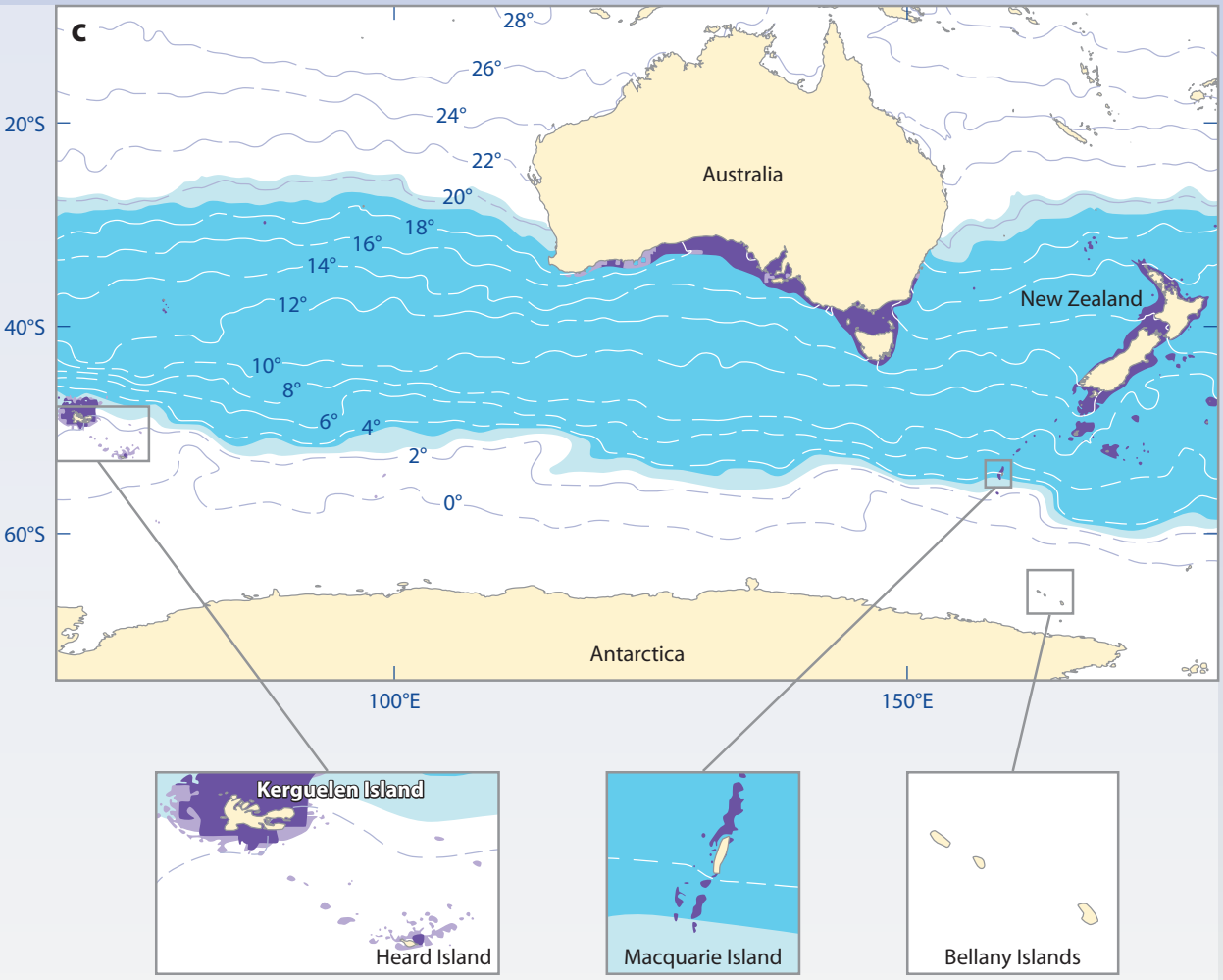
Further reading Furlani 1996; Byrne *et al*. 1997b, 2013a, 2016b; Lockhart & Ritz 2001a, 2001b





Figures a–c ***Asterias amurensis.***
a, Northern Pacific seastars devour mussels displaced from the hulls of ships.
b, a seastar engulfs a bivalve mollusc, holding it in position, pressed against its mouth by its podia. This seastar is an extraoral feeder. It everts its stomach, sliding it between the two valves of the bivalve, and using digestive enzymes, liquefies the bivalve soft-body parts prior to nutrient absorption. Once absorption is complete the stomach is retracted and the empty shell is discarded.
[a, M.Byrne; b, J.Finn]

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dark purple	=	highly suitable area for the benthic adult stage
light purple	=	suitable area for the benthic adult stage
blue	=	optimal area for larval development
light blue	=	marginal area for larval development

c, potential distribution of ***Asterias amurensis***, and regional Sea Surface Temperature (SST) isotherms. Purple regions represent highly suitable areas and light purple regions represent suitable areas for the benthic adult stage based on current mean winter and summer seafloor temperatures. Blue regions represent the areas where SST is optimal for larval development (blue) and marginal (light blue). Isotherms represent current mean sea surface temperature (°C) during winter. The suitability of the vast areas of coastline in Australia and New Zealand as well as Australian islands in the Southern Ocean shows that vigilance is needed to prevent the further spread of this apex predatory seastar.

[from Byrne *et al*. 2016b]

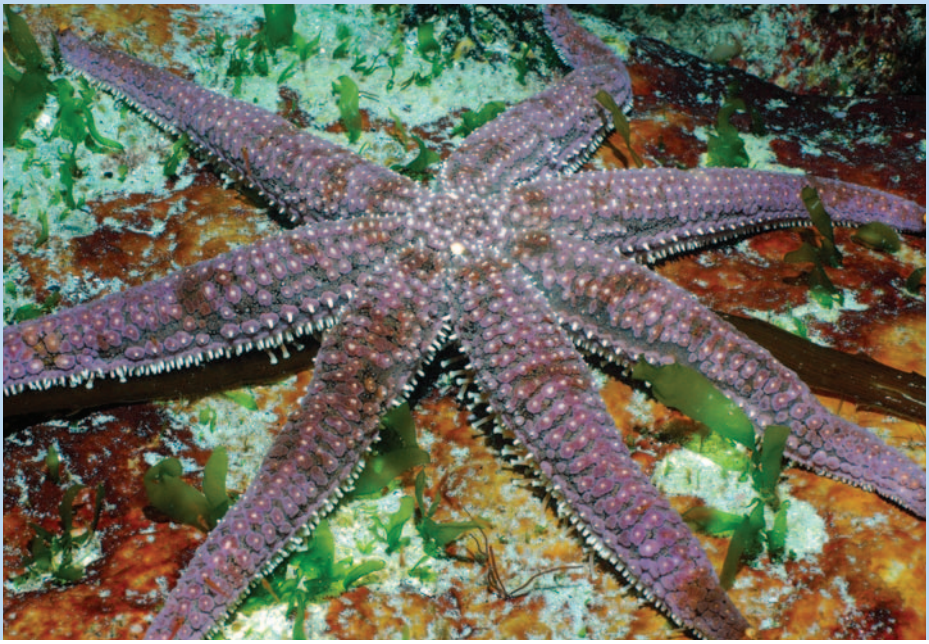


Figure 4.7 The exotic New Zealand seven-armed seastar ***Astrostole scabra*** (Asteriidae), once found only in Tasmania, was recently reported from Victoria. It is New Zealand's largest native seastar, growing up to 750 mm, and most voracious, eating sea urchins and molluscs such as abalone. [G.Edgar]

extension of *C. rodgersii* to Tasmania (Ling *et al*. 2010). The abundance of *C. rodgersii* may prompt a fishery for this species in Tasmania. Availability of shelter also seems to be a factor limiting the number of new recruits to a population. Survivorship of juvenile *C. rodgersii* appears also to be dependent on the availability of shelter which may limit the number of new entrants into a population (Byrne & Andrew 2013).

Problems of variable roe quality and irregular recruitment have prompted research into ranching, aquaculture or artificial manipulation of natural populations (Andrew *et al*. 2002). Ranching involves the collection of wild animals which are then held in sea cages, tidal pools or onshore tanks and fed an artificial diet until harvest. In this way the quality and quantity of roe can be controlled to ensure a high-value, consistent product, and leads to a reduction in the cost of processing, while maintaining natural populations through the retention of low quality catches. Furthermore, there have been proposals to manipulate natural population densities to ensure an adequate diet for harvestable urchins. These proposals include selectively removing large older urchins or transplanting of juveniles to more productive habitats. However, urchins are key herbivores on rocky subtidal reefs and manipulation of urchin populations can have adverse consequences for other herbivores such as abalone (Andrew & Constable 1999).

Sea urchins are also harvested by recreational fishers (**Fig. 4.6**). In a number of Australian states including Queensland, New South Wales and Victoria, fishers are subject to a bag limit ranging from a maximum of 5 to 20 sea urchins per person per day, but fishing beyond these limits is commonly observed. Little information is available on the recreational harvest of sea urchins.

Introduced species

In comparatively recent times, three species of echinoderm appear to have been introduced into Australian waters by human activity. All three are shallow-water asteroids that were first seen in Tasmania. Two, *Patiriella regularis* (the New Zealand cushion star) and *Astrostole scabra* (the New Zealand seven-armed seastar), were introduced from New Zealand (**Fig. 4.7; Box 4.2**). The third, *Asterias amurensis* (the Northern Pacific seastar), is considered, on the basis of genetic studies, to have originated in Japan (**Box 4.3**).

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New Zealand cushion star

Patiriella regularis was the first introduced echinoderm recognised for Australia (**Box 4.2**). The New Zealand origin of the Tasmanian population has been confirmed by recent analysis of their mitochondrial DNA (O'Loughlin *et al*. 2002). It is likely to have arrived in crates of live oysters imported from the South Island of New Zealand (Dartnall 1969a). Imports of New Zealand oysters into Hobart were common during the early part of the nineteenth century and until the 1930s. Crates of oysters were stored in the sea near the Hobart wharf until they were sold. In addition to *P. regularis*, several other invasive New Zealand invertebrates appear to have been introduced to Tasmania through this trade, including the rosy screw shell, *Maoricolpus roseus*, and a crab, *Cancer novaezelandiae* (see Dartnall 1969a).

It is likely that the introduction occurred after 1930, because in 1929 the renowned echinoderm taxonomist H.L.Clark visited Hobart, and it is most unlikely that he would have overlooked this species if it were common. By the late 1960s, however, *Patiriella regularis* was the most abundant asteroid in the Derwent Estuary, occurring on rock platforms from the D'Entrecasteaux Channel to the Tasman Peninsula (Dartnall 1969a). It remains largely confined to this area, although occasional specimens have been collected from northern Tasmania and the east coast of Australia.

The impact of *Patiriella regularis* on the shallow-water marine environment around Hobart has not been quantified, but is likely to have been considerable. It has been implicated in the extinction of what might have been a local endemic species, *Marginaster littoralis*. *Patiriella regularis*, however, is not recognised nationally as an invasive pest species and there are no plans to attempt to control the existing population. It is unlikely that the more recent introduction of the Northern Pacific seastar will reduce the population of *P. regularis* as they prefer different habitats and have different diets.

New Zealand seven-armed seastar

Astrostole scabra, New Zealand seven-armed seastar, was first reported from Tasmania in the late 1960s by Alan Dartnall, former Curator of Marine Invertebrates at the Tasmanian Museum and Art Gallery (Dartnall 1969a; **Fig. 4.7**). He recorded its presence on rocky reefs at depths down to 30 m, all along the east coast of Tasmania, and he also cited unconfirmed reports of its presence along the west coast. A single animal reported from Collaroy (Town 1979), north of Sydney, New South Wales, was later re-identified as *Astrostole rodolphi*, which is also known from Lord Howe Island and Norfolk Island (Rowe & Gates 1995). *Astrostole scabra* appears to be increasing its range, as apparent from 2003 discoveries in Victorian waters off Point Hicks and Portland (T.D.O'Hara, unpublished data).

Although it is not certain whether *A. scabra* was introduced to Australia by human activity, molecular analyses indicate that it is very similar to New Zealand populations (O'Loughlin *et al*. 2002). It may have been introduced accidentally along with *Patiriella regularis* among live New Zealand oysters in the first half of the twentieth century. This species is never very abundant. It is not currently considered to be a major marine pest, and there are no plans to actively control it. However, its recent arrival in Victoria might indicate a potential to spread throughout south-eastern Australia. This would be a concern to the abalone industry, as this species is known to eat large shellfish in New Zealand.

Northern Pacific seastar

The Northern Pacific seastar, *Asterias amurensis,* is a native of the north-western Pacific Ocean (**Boxes 3.2, 4.3**). The biology and ecology of this species and its introduction to Australia are reviewed in Byrne *et al*. (2013a). *Asterias amurensis* was first collected in Australia in 1986, and was initially thought to be a variant of a native species, *Uniophora granifera* (knobbed seastar; **Fig. 8.5**). It was not until 1992 that researchers from the South Australian Museum identified the seastars as *A. amurensis*. By then it was abundant near the Hobart Wharf (Turner 1998). Concerns about the potentially devastating impacts of the introduced Northern Pacific seastar on the local marine fauna led the Tasmanian Government to establish the 1993 National Seastar Taskforce to undertake research and monitoring activities. In an attempt to control the Northern Pacific seastar population, two public dives



Figure 4.8 To reduce the numbers of Northern Pacific seastars ***Asterias amurensis*** (Asteriidae) in the early 1990s, several community dives were organised. In the winter of 1993, one 'star busting' event was held at Sullivans Cove, Hobart. A community committee in conjunction with CSIRO and the Tasmanian Department of Primary Industries and Fisheries (DPIF) organised the collection of Northern Pacific seastars by scuba diving. About 24,000 individuals were collected, and later composted by the University of Tasmania. This hardly put a dent in the population, then estimated at around 30 million.
A, Northern Pacific seastars stranded on a beach at low tide.
B, community members counting the Northern Pacific seastars after collection.

[CSIRO]

were organised to collect the seastars; the second dive collected some 24,000 individuals from Sullivans Cove (Turner 1998; Fig. 4.8). However, these control measures had little impact on the population, then estimated to be 30 million.

In 1995, solitary individuals were reported from Port Phillip Bay in Victoria (O'Hara 1995a), and in January 1998, 105 juveniles were found on a mussel farm near Dromana (Garnham 1998). This now appears to have been part of a larger settlement that ranged along the eastern shore of Port Phillip Bay from Mornington to the Port of Melbourne (Parry *et al.* 2000). The estimated population in Port Phillip Bay initially increased exponentially, from an estimated 300,000 in 1997, to 30 million in 1998, 90 million in 1999, and 165 million in 2000 (Parry & Cohen 2001). By 2004, numbers had declined to an estimated 35.5 million. Aggregations had become patchy, perhaps in response to the reduced availability of food (Parry *et al.* 2004).

It is unclear how this species was introduced into Tasmania and then across Bass Strait to Port Phillip Bay. Genetic analyses indicate that the source of the Tasmanian population is likely to have been central or southern Japan (Ward & Andrew 1995; Murphy & Evans 1998). Early discussions implicated ships' ballast water as the likely vector, with larvae being taken up in a Japanese harbour and discharged at the Hobart wharf. It is possible that live adult seastars could have

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been transported to Australia from Japan. Live seastars have been found in sea-chests (the ballast water filtration system) of ships leaving Hobart (R.Thresher, personal communication), and a live seastar fell out of a coil of rope on a visiting vessel at the port of Burnie in 2002 (A.Morris, personal communication). Small populations in Georges Bay and Hendersons Lagoon on the north-eastern coast of Tasmania may have been translocated accidentally as part of the live fish trade, before being discovered and eradicated in 2001 (R.Thresher, personal communication). It seems likely that the source of the Victorian infestation of *A. amurensis* was larvae transported from Hobart in ship's ballast (Dunstan & Bax 2007). Also it could have been introduced in association with the trade in live fish between Hobart and Melbourne that was active during the period when this seastar was introduced to Port Phillip Bay (T.D.O'Hara, unpublished data). By whatever means the Northern Pacific seastar was introduced into Tasmania, the success of this invader was facilitated by environmental conditions (temperature, day-length) in the Derwent River being similar to those of the source population in Japan (Byrne *et al*. 1997b). Both localities are at similar latitudes, but in different hemispheres. Moreover, the disturbed condition of the Derwent River may have facilitated its establishment, such disturbance being a common feature of many marine introductions (Fields *et al*. 1993; Stachowicz *et al*. 2002).

The Northern Pacific seastar is currently recognised as one of Australia's most significant marine pest species (National Taskforce on the Prevention and Management of Marine Pest Incursions 1999; Byrne *et al*. 2013a), and is considered to be one of the most ecologically damaging in the world (Lowe *et al*. 2000). A recent analysis of its potential distribution in Australia, with respect to its natural habitat and thermal regime in the Northern Hemisphere, and the thermal tolerance of the larvae (**Box 4.3**), indicates that *A. amurensis* has the capacity to flourish from Albany in Western Australia to Mallacoota in Victoria (Byrne *et al*. 2016b). As the waters of southern Australia continue to increase in temperature due to global warming, the distribution of this species is modelled to contract, in parallel with the increased risk that it may invade the Southern Ocean and Antarctica (Byrne *et al*. 2016b).

While it thrives on sandy or muddy seafloors in sheltered bays, in the Northern Pacific *A. amurensis* is also known from the continental shelf down to 200 m. A female can produce between 5 and 20 million eggs, and the free-swimming larvae, which can live for up to 60 days before settling, potentially can be spread over long distances in ocean currents (Byrne *et al*. 1997b).

Because of its ability to form massive populations, the potential impact of the Northern Pacific seastar on Australia's marine fauna is considerable (Lockhart & Ritz 2001a, 2001b; Ross *et al*. 2002, 2004). The total biomass of the Northern Pacific seastar in Port Phillip Bay in 2001 was estimated to be 2000–3000 tonnes, approximately half that of all demersal fish (G.Parry, personal communication). Potentially it could alter the ecological processes that recycle nutrients throughout the bay, especially because it preys heavily on bivalves, a molluscan group with a key role in nutrient recycling (Parry & Hirst 2016). The Northern Pacific seastar is a generalist feeder, preferring bivalves, but opportunistically eating heart-urchins, and small seastars to ascidians, and it will feast on dead flesh if available. The overlap in diet between *A. amurensis* and several fish species is suggested to have contributed to the decline of eagle rays, globe fish and the Eastern Shovelnose Stingaree from Port Phillip Bay (Parry & Hirst 2016).

Asterias amurensis is quite mobile, and readily migrates to wharfs from surrounding areas to feast upon mussels dislodged from pylons by boats or from ships' hulls in dry dock (**Box 4.3**). In Japan it can consume up to 80% of benthic prey species (Hatanaka & Kosaka 1959), and in the Derwent Estuary it has significantly reduced the population of once-common bivalves such as *Fulvia tenuicostata* (Ross *et al*. 2002). There is some concern for species that are endemic to the south-eastern Tasmanian region, including the endangered Spotted Handfish (*Brachionichthys hirsutus*). The handfish lays its eggs around the base of ascidians, and the Northern Pacific seastar is believed to consume both the eggs and the ascidians.

In Port Phillip Bay, the explosive growth of the Northern Pacific seastar population was assisted partly by the vast numbers of molluscan bivalves that live on the sandy seafloor around the eastern rim of the bay, including the introduced species *Corbula gibba*



A crown-of-thorns seastar, ***Acanthaster planci***, feeding on coral polyps. [G.Bell]

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Box 4.4 Crown-of-thorns seastar



Diagnostic features The crown-of-thorns is one of Australia's largest seastars, with arms growing up to 300 mm in length. It can have up to 21 arms, although 15–18 are more usual. The soft skin of the upper surface of the arms and the central disc is protected by long (15–30 mm) conical spines. The arms have two rows of suckered tube feet along each ambulacral groove. Numerous madreporites are present on the disc. The colour is variable, often rust-coloured, or purplish blue with yellow suckers on the tube feet.

Distribution In Australian waters it is found on coral reefs from Port Maud, Western Australia, across northern Australia to North Solitary Island, New South Wales, and Lord Howe Island at depths to 30 m (Rowe & Gates 1995). It also occurs in the Red Sea and throughout the Indian and Pacific oceans from Africa to Panama, and north to Japan, at depths to 65 m.

The distinct genetic structure of Indian Ocean and Pacific Ocean populations of *Acanthaster planci* were thought to reflect historic patterns of ocean circulation, but recent molecular taxonomic investigation has revealed that this is due to incipient speciation of different *Acanthaster* clades, promoted by historic sea level change. There may be at least four species within the nominal taxon *Acanthaster planci*.

Biology The adult seastar feeds on hard corals by extruding its stomach from the mouth and pressing it against the coral. Digestive enzymes are released from the stomach surface, and, within 3–5 hours, the soft tissue of the coral is liquefied and nutrients may be absorbed. The affected coral is reduced to a white skeleton (**Fig. 4.9B**).

The crown-of-thorns is usually found at low densities, less than one animal per hectare. These are non-outbreak populations, and in these populations the seastars often hide during the day in the reef infrastructure and emerge at night to feed. However, numbers can increase rapidly, with a resultant population 'outbreak'. They usually prefer to eat *Acropora* corals, and during outbreaks can consume up to 95% of hard corals on a reef.

Large females can produce hundreds of millions of eggs. Along the Great Barrier Reef, spawning occurs at night in December. The swimming larvae feed on microscopic algae for several weeks before settling onto rubble areas at the base of reefs. Juveniles feed on coralline algae, remaining well concealed until they reach six months of age, when they switch their diet to coral and start growing rapidly. They can live for 12–14 years, although during outbreaks many die prematurely from starvation as their coral food declines.

Adult crown-of-thorns seastars are taken by few predators, however the giant triton mollusc and several large fish such as the maori wrasse, puffer fish, trigger fish and emperors will prey on the seastar.

Similar species *Acanthaster brevispinus* also lives on the Great Barrier Reef from Townsville to the Capricorn Group, and around some of islands in the Tasman Sea. It can be distinguished from *A. planci* by the much smaller spines on the disc (2 mm high), and by its preferred habitat, which is sandy areas between reefs, where it feeds on molluscs.

Interaction with humans The covering of the crown-of-thorns spines produces a toxin called saponin, and when humans are impaled by the spines the toxin is released into the wound causing severe pain, as well as nausea and swelling. The crown-of-thorns also has the potential to destroy popular coral viewing sites, damaging the tourist trade in these areas. Human activities may have increased the frequency of outbreaks.

Class Asteroidea
Family Acanthasteridae
Species *Acanthaster planci* (Linnaeus, 1758)

Further reading Kenchington 1978; Potts 1981; Conand 1985; Moran 1986, 1988; Johnson 1992a; Engelhardt & Lassig 1997; Benzie 1999; Vogler *et al*. 2008, 2012; Uthicke *et al*. 2009; Haszprunar & Spies 2014; Pratchett *et al*. 2014; Wolfe *et al*. 2015a, 2015b

(G.Parry, personal communication). The Northern Pacific seastar is implicated in the failure of populations of the scallop *Pecten fumatus* to recover following cessation of scallop dredging in 1996. Finally, the enormous numbers of larvae of the Northern Pacific seastar in the plankton, up to 1100 per cubic metre in the Derwent, the highest recorded for any echinoderm, is likely to have a major impact on the planktonic ecosystem (Bruce 1998).

The Northern Pacific seastar has an economic impact on shellfish fisheries and aquaculture, posing a direct threat to scallop fishing and mussel aquaculture. Farmers of the mussel *Mytilus galloprovincialis* in Port Phillip Bay have had to alter their activities considerably to protect their cultures, ensuring that ropes are kept off the seafloor, cleaned regularly to remove settled seastars, and bathed in fresh water (toxic to seastars) when transported to locations outside the bay (Parry *et al*. 2000).

In 1999, Federal and State governments in Australia adopted a national control plan for the Northern Pacific seastar (National Taskforce on the Prevention and Management of Marine Pest Incursions 1999). This plan has had two principal aims, firstly to reduce the risk of the pest being spread elsewhere in Australia by human activity and, secondly, to develop controls for the seastar populations, possibly leading to its eradication. Preventing the spread of the Northern Pacific seastar is particularly difficult as there are numerous ways this vagrant species could be translocated. The most likely methods are transport of larvae in ships' ballast water, adults in ship sea-chests or fishing gear, and larvae or adults along with live seafood. A suite of regulations, codes of practice and education programs are required to minimise the risk posed by each of these activities.

Controlling existing populations of *Asterias amurensis* in Australia is also problematic. Removing animals by hand, or with mechanical devices such as dredges, or chemically by injecting animals with toxins, has proved effective only in small areas. Established populations are often so large that cleared patches are rapidly re-colonised. These types of control measures tend to succeed only for small populations, such as an outbreak at a new location. In late November 2003, for example, several live Northern Pacific seastar individuals were found washed up at Point Norman near Inverloch, Victoria (Holliday 2005). It took several months to find the living population, which was on a small sponge-covered reef just inside Andersons Inlet. The source of the infestation was unknown. The Victorian Department of Sustainability and Environment coordinated a team of 450 volunteers to remove the entire population at this location by hand. After 800 dives over 15 months, 282 individuals were removed, and the population appeared to have been eradicated by 2006. The recent 2015 findings of populations of *A. amurensis* in Gippsland, south-eastern Victoria, at Tidal River (Wilsons Promontory) and Anderson Inlet (Inverloch), show that this species is capable of spreading from Port Phillip Bay (Richardson *et al*. 2016).

In terrestrial situations, pests and weeds have been controlled effectively using biological agents. This involves deliberately introducing a predator, parasite or disease of the pest from its native range. Researchers have identified a minute ciliate (*Orchitophyra stellarum*) that attacks the gonads of male Northern Pacific seastars, often rendering them sterile. Unfortunately this ciliate is a generalist parasite that infects a number of seastars from different families and genera and so is likely to parasitise native species (Byrne 1996b; Byrne *et al*. 1997a; Stickle *et al*. 2001a, 2001b; Sunday *et al*. 2008) and is therefore inappropriate as a biocontrol method.

Control of pest populations by environmental manipulation appears to be more promising. Suggestions have included removing key sources of food (for example, keeping wharves and jetties free of mussels) or artificially increasing the numbers of predators. Known predators of the Northern Pacific seastar include the native eleven-armed seastar (*Coscinasterias muricata*), the giant spider crab (*Leptomithrax gaimardii*) and various leatherjackets (fish).

We may have to await future technologies to provide a permanent solution. Although genetic controls, including stocking populations with sterile males or preventing the production of female offspring could be considered, development of these methods for biocontrol requires identifying the mechanism(s) of sex determination in seastars, a challenging pursuit in itself.

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Crown-of-thorns seastar

The crown-of-thorns seastar, *Acanthaster planci* (often abbreviated as COTS), is probably the most infamous native echinoderm in Australia (**Box 4.4**). It is viewed as a destroyer of coral reefs, and a considerable effort has been invested in researching, monitoring and controlling outbreaks of this seastar on the Great Barrier Reef. However, despite decades of research, the causes and spread of outbreaks remain poorly understood. Although it appears that eutrophication associated with agriculture is a factor (Brodie *et al*. 2005; Uthicke *et al*. 2009; Fabricius *et al*. 2010; Brodie & Waterhouse 2012; Fabricius 2013; Pratchett *et al*. 2014), it is clear that outbreaks occurred periodically on the Great Barrier Reef before land clearing and agriculture (De Vantier & Done 2007), and many outbreaks occur in remote regions, such as the middle of the Indian Ocean, far from the influence of agricultural eutrophication (Pratchett *et al*. 2014; Roche *et al*. 2015).



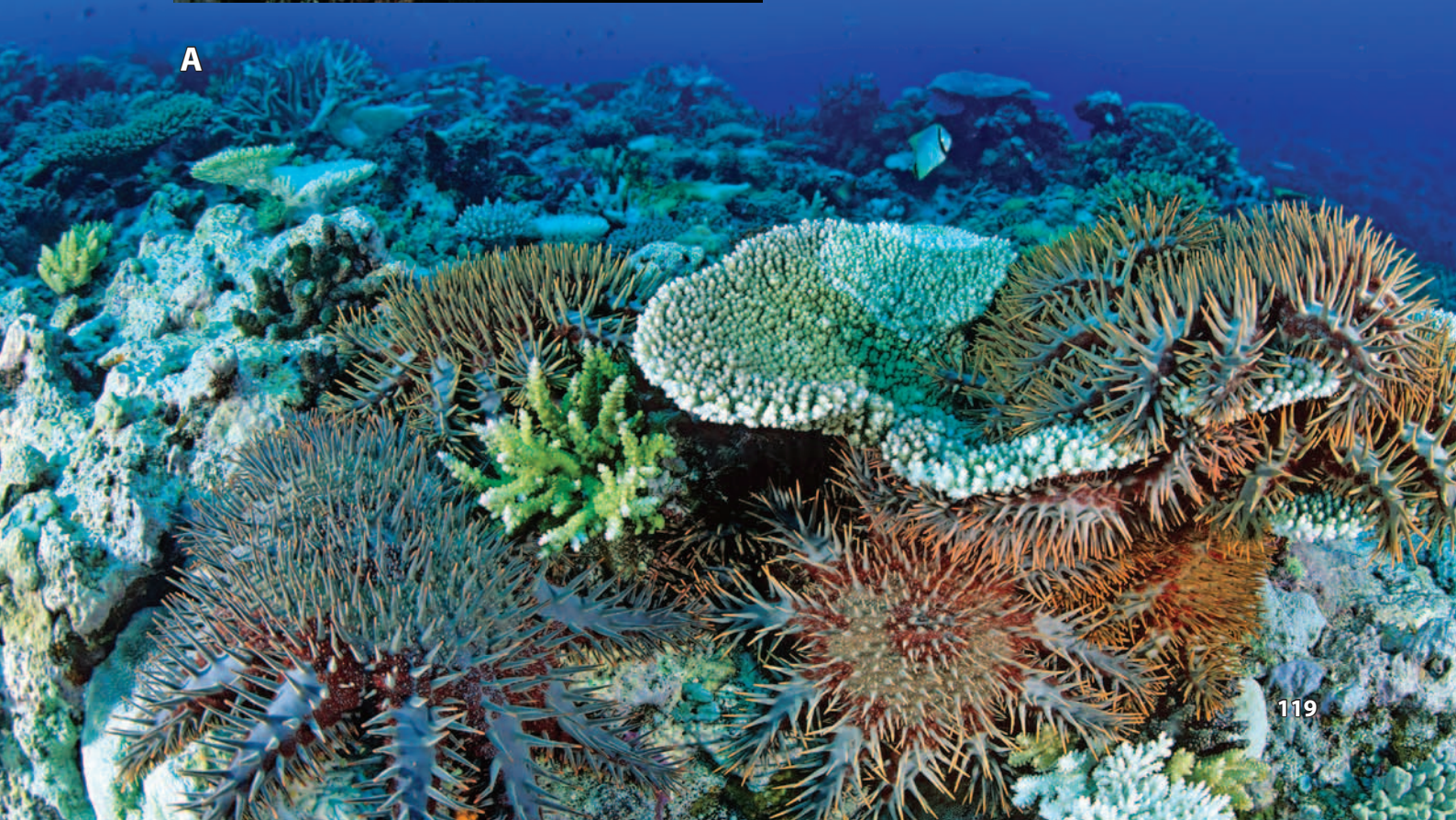


Figure 4.9 The notorious crown-of-thorns seastar, ***Acanthaster planci*** (Acanthasteridae). **A**, seastars feeding on a coral reef in Queensland; during feeding the stomach is everted through the mouth and spread over the coral, releasing digestive enzymes to dissolve the coral polyps prior to nutrient absorption. **B**, all that remains once the crown-of-thorns seastars remove the soft coral polyps are the barren, white coral skeletons.

[A, G.Bell; B, W.Boyle]

It is likely that crown-of-thorns has been present across the Indo-Pacific oceans for at least 3 million years (Benzie 1992), although it is now known to be a complex of at least four species, with the '*planci*' clade being Western Indian Ocean (Vogler *et al*. 2008, 2012; Haszprunar & Spies 2014). The population at Christmas Island belongs to the northern Indian Ocean form, where as Cocos Keeling Island populations belong to the southern Indian Ocean clade (Vogler *et al*. 2008). Interestingly, populations from coral reefs along the north-western Australian coast appear to have originated from Queensland (perhaps 8,000 years ago) not from elsewhere in the Indian Ocean. The Queensland *Acanthaster* are part of the Pacific clade. *Acanthaster* is not known from the Caribbean, presumably because the ancient seaway between North and South America was closed by the time the seastar colonised Panama.

Distinctive feeding scars on corals caused by crown-of-thorns predation provide evidence that outbreaks occurred along the Great Barrier Reef prior to 1960 (De Vantier & Done 2007). *Acanthaster planci* spines have been found in seafloor sediments 3000–7000 years old, although it is unclear whether these remains derived from an outbreak (Engelhardt & Lassig 1997).

Discovery

Acanthaster planci is a conspicuous member of coral reef communities (**Fig. 4.9**). It was one of the first seastars to be described scientifically, and was well known to indigenous peoples throughout the Indo-Pacific (Moran 1988). Most coastal peoples know to stay clear of the venomous spines of crown-of-thorns. *Acanthaster planci* occurs in low density non-outbreak populations and active outbreak populations (>15 per hectare of reef) (Fabricius 2013). Outbreaks are also defined as the density of *A. planci* at which the rate of their predation on corals exceeds long-term growth capacity of the prey to allow recovery (Fabricius 2013). The inherent characteristic of *A. planci* as being a boom and bust echinoderm species underlies its major role in altering the state of coral reef ecosystems (Uthicke *et al*. 2009).

With the advent of scuba diving in the 1950s, divers reported large numbers of *A. planci* at some reefs, firstly at the Ryukyu Islands, southern Japan in the late 1950s and then at Green Island, northern Great Barrier Reef in 1962. These outbreaks often caused extensive coral death and the presence of so many seastars close to popular tourist destinations caused alarm. But attempts to eradicate or control them were largely unsuccessful. A two-year control program at Green Island in the 1960s, which removed 44,000 crown-of-thorns, failed to stop the destruction of a small coral viewing area (Moran 1988). The Japanese Government spent an equivalent of almost US$6 million removing approximately 13 million crown-of-thorns from the Ryukyu Archipelago (Yamaguchi 1986), but this barely impacted on the amount of coral death on reefs in this region. It is possible that these removal measures only enhanced food availability and thus the success of the remaining, now lower density, crown-of-thorns, which, due to their very high fecundity, can be a source of larvae for new outbreaks. In Australia, large-scale protracted outbreaks along the Great Barrier Reef which, began in 1962, 1979 and 1993, and the most recent outbreak which is still underway (2016), reduced coral cover on many reefs (Fabricius *et al*. 2010; Hughes *et al*. 2011; Pratchett *et al*. 2014).

The Australian Commonwealth and Queensland governments initiated a series of committees to investigate the crown-of-thorns issue. However, opinions among the scientists varied with regard to whether management intervention was necessary or desirable. Some scientists believed the outbreaks are a natural phenomenon, nature's way of ensuring that the reef community remains diverse and does not become overrun by a few dominant species. After the *A. planci* outbreak at Green Island in 1979, the Crown of Thorns Starfish Advisory Committee was formed in 1985 to oversee research and monitoring. Significant government funding for research was allocated, starting in 1986, focusing on the reproduction, dispersal and recruitment of *Acanthaster*. By 1992 funding for this primary research had largely ceased, although long-term and more detailed short-term monitoring have continued under the auspices of the Australian Institute of Marine Science. The COTSWATCH

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monitoring program began in 1993 to encourage and coordinate sightings of crown-of-thorns by scientists and the general public, within Australia and across the Indian and Pacific oceans. The most recent (2016) outbreak of *A. planci* along the Great Barrier Reef has resulted in extensive damage to many reefs including many visited by tourist operators and this, along with the UNESCO threat of an endangered status for this World Heritage Area, has prompted renewed funding for research on this species.

A report, based on analysis of data for three stressors (bleaching, cyclones, COTS outbreaks), implicates *A. planci* as being responsible for 42% of the estimated loss of corals from the Great Barrier Reef in the past 27 years (De'ath *et al*. 2012). The model used in this study did not consider a number of factors that are involved in the decline in coral cover, including reduced calcification due to stress from ocean acidification and warming, algal overgrowth due to anthropogenic nutrient enrichment, sedimentation, large flood events associated with La Niña, diseases, overfishing of predators and other ecologically important species (for example, sea cucumbers), the impact of ocean waves not related to cyclones and change in the demography of coral larvae (Harvell *et al*. 2002; Hughes *et al*. 2011; Frieler *et al*. 2012; Tan *et al*. 2012; Tran *et al*. 2012; Eriksson & Byrne 2015). A recent time-series analysis of coral growth over the last 60 years indicated a major decrease in coral calcification on the Great Barrier Reef which is likely due to global change (Silverman *et al*. 2012). In addition, ocean waves generated by distant disturbances (such as earthquakes) are likely to have caused a decline in coral cover on reefs in the southern Great Barrier Reef (Woolsey *et al*. 2012). The decline in coral cover and recruitment failure on inner reefs of the Great Barrier Reef is strongly influenced by increased turbidity, sedimentation and nutrient-driven increase in macroalgae (Fabricius & De'ath 2001; Hughes *et al*. 2011; Tran *et al*. 2012). Most importantly, the manta tow technique used to generate data for the model assessment is not suitable for estimating absolute densities of *A. planci* and cannot accurately distinguish mortality events caused by bleaching, disease or predation by this seastar, especially when observations are taken some time after the mortality event (Fernandes *et al*. 1990; Hughes *et al*. 2011). Although it is clear that outbreaks of *A. planci* have been a major factor in the decline in coral cover on the Great Barrier Reef, the 42% decline attributed to the influence of this species in De'ath *et al*. (2012) is undoubtedly an overestimate, as there are many other stresses to consider.

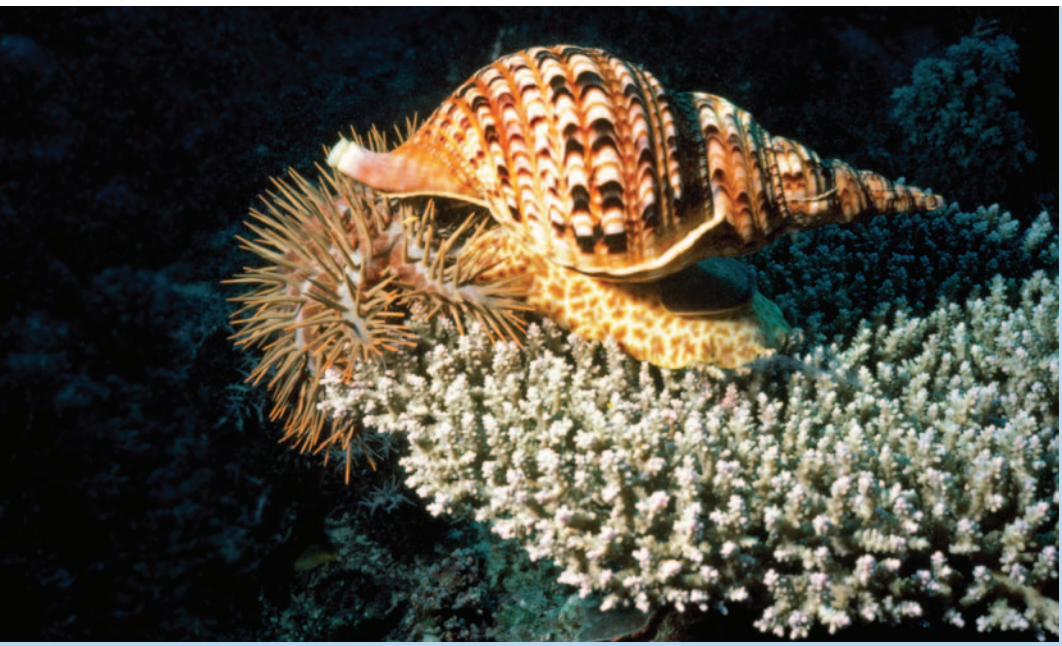


Figure 4.10 The crown-of-thorns seastar, ***Acanthaster planci***, has few predators. Of some 11 species that have been reported to prey on these seastars, the giant triton, ***Charonia tritonis***, is the best known. A giant triton can eat about one crown-of-thorns per week.

[Great Barrier Reef Marine Park Authority]

Spread of the outbreaks

A crown-of-thorns 'outbreak' occurs when coral is being consumed faster than it can grow, i.e. when there is a net decrease in coral cover. Outbreaks may arise from a single mass recruitment event or from a series of successful recruitment events from multiple years and cohorts (Stump 1994; Pratchett 2005). Outbreaks of *A. planci* on the Great Barrier Reef appear to follow a predictable pattern. A primary outbreak established by one or a series of successful recruitment events on reefs at latitude 14–16°S near Cooktown and Cairns, an area called the 'initiation box' (Pratchett *et al.* 2014), gives rise to secondary outbreaks in cohorts of larvae that spread in a southerly direction at about 60–90 km a year in a stepping-stone fashion (Moran *et al.* 1992; Lourey *et al.* 2000). This southerly spread comes to a halt at about 20°S, near the Whitsunday Islands, although there have been some independent outbreaks at the Swain Reefs (22°S) and as far south as Elizabeth and Middleton Reefs (29–30°S). The direction of seastar outbreaks is consistent with larvae being carried south by the currents. The reason for the build up of *A. planci* in the 'initiation box' and for infestations halting at about 20°S are not known, but are likely to be related to oceanographic currents (Hock *et al.* 2014; Pratchett *et al.* 2014). The secondary outbreak hypothesis suggests that *A. planci* in these 'down stream' populations should be genetically similar to each other and there is some evidence for this in an allozyme study along a 750 km section of the northern Great Barrier Reef (Benzie & Stoddart 1992). A more recent molecular genetics investigation, however, indicated that *A. planci* in outbreak populations are genetically diverse, suggesting that outbreaks are not generated in a 'down stream' model by a rogue genetic subset of a greater population (Timmers *et al.* 2012).

Outbreak populations of *A. planci* have major ecological impacts, altering coral reef community structure and affecting fish populations (Williams 1986; Colgan 1987; Fabricius 2013; Pratchett *et al.* 2014). Although fish populations can be negatively affected by *A. planci*, meta-analysis of stressors on fish populations indicate that storm damage has





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a much greater impact (Wilson *et al*. 2006). There can be up to a million seastars on a reef during an outbreak and they can consume and destroy up to 95% of the hard corals. *Acropora* species are the favoured food, but a range of other coral species can become prey, including massive, slow-growing *Porites* colonies (Engelhardt & Lassig 1997). Eventually, the amount of available food declines, many seastars starve, and the outbreak comes to an end for that particular reef. Reefs can take 10–25 years to recover, although massive slow-growing species will take longer (De'ath & Moran 1998). If repeated outbreaks occur in quick succession, then some species, particularly massive corals, do not recover (Colgan 1987).

Although the crown-of-thorns is also found in northern Western Australia and southern Queensland, it rarely forms outbreaks at these locations. High numbers were recorded (up to 170 per hectare) on reefs off Dampier in the 1970s and 1980s (Wilson & Marsh 1974, 1975); cyclone damage slowed down the recovery of these reefs.

Causes

Three main hypotheses have been postulated to explain primary outbreaks of crown-of-thorns. These focus on the seastar's natural reproductive capacity, the reduction and removal of predators from some reef systems, and the influence of runoff from land (Birkeland 1982; Johnson 1992b; Engelhardt & Lassig 1997; Brodie *et al*. 2005; Fabricius *et al*. 2010; Fabricius 2013; Pratchett *et al*. 2014).

The hypothesis that outbreaks might be explained by natural causes is based on the seastar's spectacular ability to reproduce and special features of its planktonic life stage. Natural fecundity (large females producing at least 60 million eggs a year; Conand 1985) is complemented by an extraordinary fertilisation rate, with up to 50% of eggs capable of being fertilised when males and females are 30 m apart and 25% fertilisation at 60 m (Babcock & Mundy 1992). On the Great Barrier Reef, *A. planci* mass spawns at the same time as the coral, and this synchronous spawning facilitates reproductive success. These spawning aggregations are thought to give rise to the waves of larvae that recruit to downstream reefs. The larvae are also robust, having been well provisioned by the maternal parent producing comparatively large eggs (that

Figure 4.11 Culling crown-of-thorns seastars, ***Acanthaster planci***, on the Great Barrier Reef, Queensland.
A, divers searching and retrieving crown-of-thorns seastars from among a reef of staghorn coral.
B, a diver injects a crown-of-thorns seastar with sodium bisulfate, a biodegradable chemical that is deadly to the seastars, but does little harm, in low doses, to the surrounding reef ecosystem. This technique is very labour-intensive and expensive and is only used to eradicate crown-of-thorns from small or critical areas of reef. To ensure a fatal dose of sodium bisulfate is delivered, each seastar is injected multiple times. With this method 70,000 crown-of-thorns over 10 months were culled during the late 2012/2013 outbreak to protect tourism hotspots in the northern and middle sectors of the Great Barrier Reef.

A new more effective method for controlling localised crown-of-thorns seastar outbreaks involves injecting them with a protein solution that includes yeast extract and ox bile. This kills the seastars within 24 hours by inducing a disease that causes discoloured and necrotic skin and copious mucus accumulation at the spine tips (Rivera-Posada *et al*. 2011, 2012). Only a small single injection of the protein solution is needed to kill an individual crown-of-thorns seastar, a significant improvement on the administration of multiple sodium bisulfate injections. Caution, however, is needed as the disease was transmitted to non-target seastars in aquarium trials (Rivera-Posada *et al*. 2011, 2012). Injection of household vinegar can also be used to kill crown-of-thorns.

[courtesy of the Association of Marine Park Tourism Operators]

are loaded with toxins that deter planktonic predators) (Yamaguchi 1975). In laboratory cultures the larvae of *A. planci*, given favourable feeding conditions such as would be expected in a plankton bloom, can develop quickly (*ca.* 2–3 weeks) to the competent larval stage. In addition to food availability, larval survival is also influenced by water temperature and salinity. On the reef a number of climatic or oceanographic factors may influence larval survival and settlement, from global events such as the El Niño-La Niña Southern Oscillation to localised variations in current, which in turn lead to the retention of larvae around particular reefs (Black *et al.* 1995; Engelhardt & Lassig 1997).

It has also been suggested that outbreaks might be facilitated by overfishing of the predators of crown-of-thorns (Endean 1977). Larvae are likely to be preyed upon by a range of invertebrates and fish, but are chemically protected and distasteful to many predators (Yamaguchi 1975). Small juveniles are eaten by small crabs, shrimps and lobsters (Keesing & Halford 1992a, 1992b), and adults are food for large gastropod molluscs such as the giant triton (*Charonia tritonis*; **Figs 2.12, 4.10**) and fish species such as emperor fishes, pufferfishes, triggerfishes and Maori Wrasse. However, all these predators have declined since the 1950s (Endean 1977). The giant triton was collected for its shell, but has been fully protected throughout Queensland since 1969. Nonetheless, this snail appears unlikely to be a major predator because it can only consume on average one crown-of-thorns per week (Endean 1969).

Until 2004, only 4.5% of the Great Barrier Reef Marine Park was protected from fishing and a recent survey showed that crown-of-thorns are less numerous and less damaging in protected reefs (Sweatman 2008; McCook *et al.* 2009). The lower impact of crown-of-thorns in no-take zones is suggested to be due to the presence of fish species that prey on juvenile seastars. The Redthroat Emperor fish (*Lethrinus miniatus*), targeted by recreational fishers, feeds on juvenile seastars although they are not a favoured prey (Engelhardt & Lassig 1997). It appears that predation on juveniles might be a significant factor in regulating outbreaks but it is difficult to account for the episodic nature of the outbreaks solely from a general reduction in predators (Keesing & Halford 1992a, 1992b).

Finally, the 'terrestrial runoff hypothesis' or the 'larval survival hypothesis' suggest that outbreaks are linked to input into marine habitats of nutrients from the land, leading to enhanced levels of the phytoplankton consumed by the larvae of *A. planci* (Birkeland 1982, 1989b; Lucas 1982). This is exacerbated by land clearing and intensive agriculture, particular for sugar cane (Birkeland 1982). Larval survival is modelled to increase nine-fold with every doubling of available phytoplankton (Okaji *et al.* 1997; Brodie *et al.* 2005), and outbreaks of crown-of-thorns on the Great Barrier Reef tend to occur three years after exceptionally heavy rains disperse excess nutrients across the reef. The most recent outbreaks on the Great Barrier Reef may have been influenced by recent La Niña conditions that caused major flooding and nutrient run off along the coast of Queensland (Brodie & Waterhouse 2012). Spawning in December, near the start of the wet season in tropical Australia, would also ensure that the larvae were in the plankton to benefit from nutrient delivery from the land and enhanced phytoplankton levels. It appears that increased survival of larvae and juveniles is more important than adult survival in facilitating an outbreak (Brodie *et al.* 2005; Fabricius *et al.* 2010; Fabricius 2013). However, recent reviews suggest that an increase in phytoplanktonic food sources for larvae may not be the cause of *A. planci* outbreaks elsewhere in the Pacific (Lane 2012; Pratchett *et al.* 2014). Finally, while it might be expected that increased food should also enhance population success of other species with planktotrophic larvae, this has not been observed.

For the Great Barrier Reef, the weight of evidence supports the nutrient hypothesis as the most important factor leading to periodic outbreaks of crown-of-thorns (Brodie *et al.* 2005; Fabricius *et al.* 2010; but see Pratchett *et al.* 2014 for a discussion of other possible factors). The fundamental boom and bust population biology of *A. planci* is likely to be an an important factor (Uthicke *et al.* 2009). These characteristics include the enormous investment in gamete production, longevity of spawned gametes, ability of the larvae to capitalise on pulses of phytoplankton, chemicals in the eggs that deter fish predators, resilience of larvae and fast development (Lucas *et al.* 1979; Babcock & Mundy 1992; Okaji *et al.* 1997; Brodie *et al.* 2005; Pratchett *et al.* 2014; Wolfe *et al.* 2015a, 2015b).

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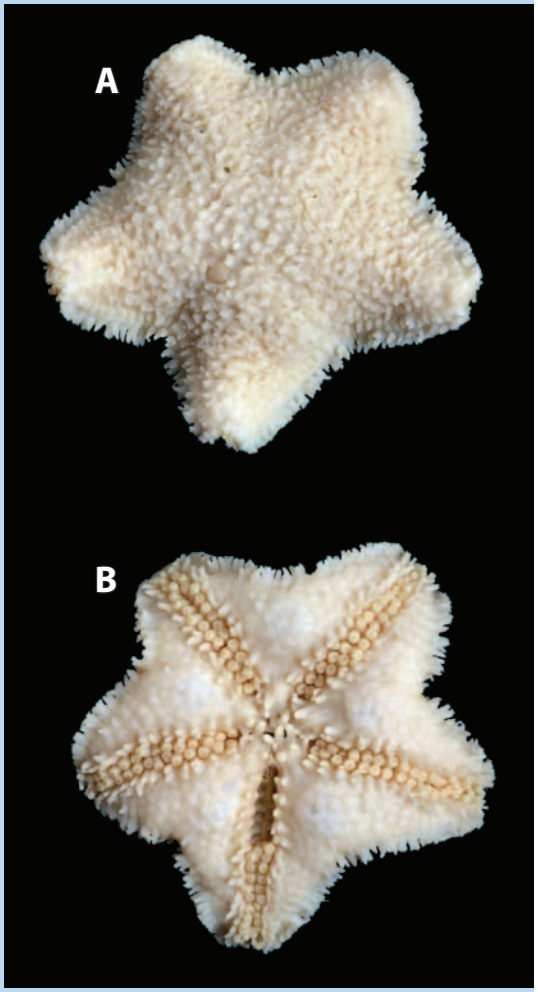


Figure 4.12 The Derwent River seastar, ***Marginaster littoralis*** (Poraniidae), was first described by A.J. Dartnell in 1970 as a native of Australia, but the validity of the species status is in question as it may have been a short-lived introduced species. In life the small seastar was up to 25 mm across and teal-green in colour with a pale off-white margin on the outer edge. A number of specimens are housed in Australian museums, but it may be extinct as it has not been seen in the wild for many years.

Preserved specimens, from the Museum Victoria collection, that have lost their body colour.
A, dorsal view.
B, ventral view.

[B.Patullo]

Current situation

Outbreaks are currently ongoing (2016) in the north and middle sections of the Great Barrier Reef. This has led to renewed calls for management and control of *A. planci*. The frequency of successful recruitment events leading to outbreaks may indicate the development of a chronic infestation, similar to those on some Fijian and Japanese reefs.

Significant improvements have been made in the methods used to kill *A. planci* seastars directly. One such method is by the injection of 'dry acid' (sodium bisulfate) into individual seastars by scuba divers. Dry acid is toxic to *A. planci*, but is harmless to other organisms when properly handled and does not affect corals (**Fig. 4.11**). However, this method is not cost effective for large areas of reef and its use is limited to small-scale operations around sites of high tourist or conservation value. Artificially increasing the number of predators is not desirable, because the predators of the crown-of-thorns are generalists that are also likely to target more vulnerable seastars such as the pincushion seastars (*Culcita* species) and the blue star (*Linckia laevigata*) (Keesing & Halford 1992a). Currently, there is no obvious candidate for biological control (Cannon 1975; Brodie *et al.* 2005; Fabricius *et al.* 2010). The most recent outbreak has greatly renewed interest in the search for disease and biocontrol agents to directly control population densities of *A. planci* (see Rivera-Posada *et al.* 2011, 2012; Caballes *et al.* 2012). In experiments by Rivera-Posada *et al.* (2011, 2012), injections of bile protein extract were trialled as a means to induce disease in *A. planci*. However, caution needs to be applied as there are no species-specific disease agents for asteroids and control of released agents in the marine environment is intractable (see Byrne *et al.* 1997a, 2013a). Indeed, experimental induction of necrosis in *A. planci* led to infection of another tropical seastar *Linckia guildingi* housed in the same tanks (Rivera-Posada *et al.* 2012). Use of biological control in the aquatic environment is also risky. Agents that influence seastar population densities are rarely species specific as shown for the protistan parasite of asteriid seastars which, although it was suggested to be a useful biocontrol agent for *Asterias amurensis,* is now known to parasitise at least six species (Byrne *et al.* 1997a, 2013a).

Key measures to stem crown-of-thorns outbreaks include reduction in agricultural runoff, overfishing and sedimentation of reefs. Recent water quality guidelines to stem and manage nutrient runoff from the land are an important aspect of the management response to the problem. In addition, the increase in no-take fishing zones to more than one-third of the Great Barrier Reef is also a measure to address environmental factors that contribute to generation of outbreaks (Great Barrier Reef Marine Park Authority 2002b; Fernandes *et al*. 2005).

Conservation issues

Echinoderms, and other marine animals and plants, are subject to human-induced pressures ranging from global (for example, climate change) to more localised in their effect (for example, habitat destruction). This section will describe some of the conservation issues affecting echinoderms in Australia.

Introduced species

Exotic organisms are acknowledged to be one of the principal threats to Australia's marine habitats and their biodiversity. A comprehensive study of the marine plants and animals introduced into Port Phillip Bay in Victoria estimated that between 300 and 400 species have been introduced accidentally or deliberately, with two or three new exotic species becoming established annually in the bay (Hewitt *et al*. 1999). This represents 10–20% of the total species diversity in the bay, making Port Phillip Bay one of the most invaded marine ecosystems in the world (Hewitt *et al*. 1999). Although other areas have not been surveyed as extensively, conspicuous marine pests have been found in most ports around Australia. Reducing the impact of these pests and minimising the risk of new introductions are among the most important challenges for managers of the marine environment. Some of these invaders have the potential to affect native echinoderm species.

Introduced species can be detrimental to native animals in many ways. They can efficiently hunt and kill vulnerable species; invasive plants or sedentary animals can proliferate across a landscape, crowding out less competitive animals and plants; and introduced parasites and diseases can cause rapid population declines of previously healthy native species. All of these processes have occurred in marine environments around Australia.

One potentially irreversible effect of a marine introduction in Australia was the possible extinction of a small Tasmanian seastar, *Marginaster littoralis* (**Fig. 4.12**). First described in 1970, it was thought to be confined to two sites in the Derwent Estuary, near Hobart (Dartnall 1970). Subsequently, the populations of *M. littoralis* declined, and a detailed survey in 1993 failed to find any specimens (Materia 1994). Interestingly, over the same period there was a gradual increase in the introduced New Zealand cushion star, *Patiriella regularis*. While this may represent one of the few documented examples of a modern marine invertebrate extinction, and the first echinoderm extinction (Roberts & Hawkins 1999), there are uncertainties associated with the appearance and apparent disappearance of this enigmatic species (Materia 1994). Firstly, there has been some confusion over the identity of specimens of *M. littoralis*, as it is superficially similar in morphology and colour to *P. regularis*. Secondly, it is unclear whether its decline was related to competition from *P. regularis*, hybridisation with that species, or environmental factors. Moreover, there are some specimens intermediate in colour and morphology between *M. littoralis* and *P. regularis*, although these have proved to be identical to *P. regularis* in allozyme studies (Materia 1994). Thirdly, *M. littoralis* may itself be an introduced species. The type locality, the Powder Jetty in the Derwent River Estuary, had a long history of ship visits and was also a disturbed environment, due to bridge construction, pollution and ship traffic, conditions known to facilitate the establishment of pest species. Moreover, Clark (1938) did not record this species in the early surveys of the echinoderms of Tasmania.

The rate of marine introductions appears to be increasing (Hewitt *et al*. 1999). This can be attributed

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Box 4.5 Tasmanian cushion star

Diagnostic features *Parvulastra vivipara*, commonly called the Tasmanian cushion star or the Tasmanian live-bearing seastar, grows on average to a radius of 10 mm, occasionally to 15 mm. It is pentagonal and uniformly yellow-orange in colour.

Distribution Restricted to approximately 11 isolated sites in south-eastern Tasmania between Bruny Island and the Tasman Peninsula, in depths to 1 m.

Biology *Parvulastra vivipara* is found on intertidal rock platforms under loose rocks or among mussel clumps during the day. It emerges to feed at night or in dull light conditions. When feeding, it everts its stomach to graze the micro-algal/bacterial film growing on rocks. It is one of only four seastars known to be viviparous, nurturing young within the gonads. The young reach quite a large size before birth (on average 38% of adult size) by cannibalising their smaller siblings within the gonad. The juveniles that survive this competition emerge through the gonopore on the top surface of the parent, and immediately move away to live an independent life. Individuals have survived for up to eight years in aquaria and given rise to juveniles, indicating that the young can be generated by self fertilisation.

Similar species Two other species of *Parvulastra*, *P. exigua* and *P. parvivipara*, also have five arms, a single row of spines on the actinal plates, and small aboral spinelets on the disc (0.2–0.3 mm high). *Parvulastra exigua* is blue-green and lays egg vases via gonopores on the oral surface. The reddish yellow *P. parvivipara* also has aboral gonopores and gives birth to live young. However, this species is smaller than *P. parvivipara* (to 5 mm radius), one of the smallest seastars in the world, and is known only from the west coast of the Eyre Peninsula, South Australia.

Interaction with humans Because of its small populations and restricted range, *P. vivipara* has been listed as 'endangered' under the *Tasmanian Threatened Species Protection Act 1995*. The main threats are from coastal development and poor water quality. The seastar does not survive close to sewage outfalls, and can also be affected by siltation. One large population occurred along a causeway carrying a major road. Alterations to this road required relocation of large numbers of seastars to unaffected localities. Ten years later there is little sign of the seastars at the translocation sites. Fortunately, the areas where *P. vivipara* live are not the preferred habitats of the introduced predatory Northern Pacific seastar (*Asterias amurensis*).

Class Asteroidea
Family Asterinidae
Species *Parvulastra vivipara* (Dartnall, 1969b)

Further reading Byrne 1996a; Prestedge 1998, 1999, 2001



An adult and two juveniles of the Tasmanian cushion star, ***Parvulastra vivipara***.

[M.Byrne]

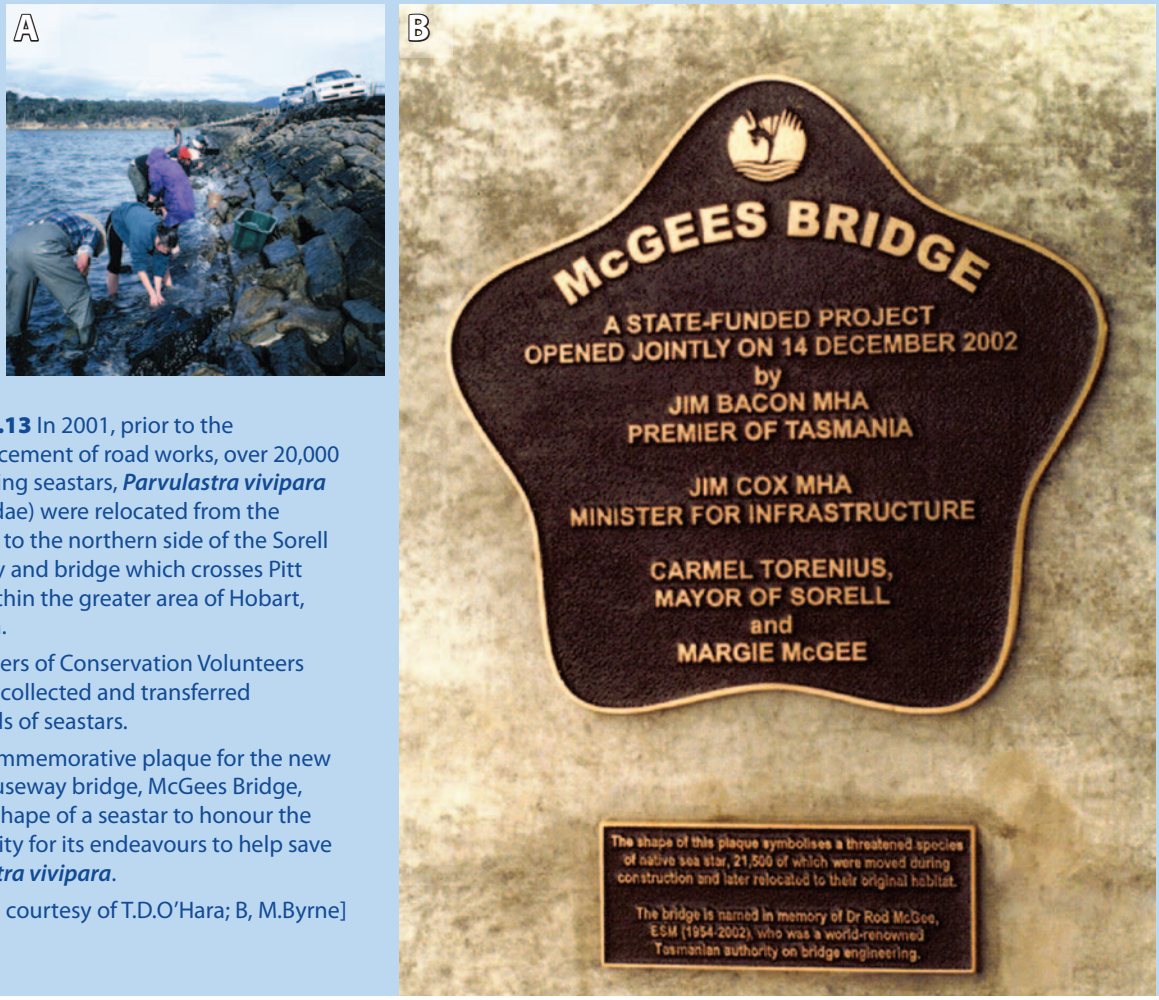


Figure 4.13 In 2001, prior to the commencement of road works, over 20,000 live-bearing seastars, ***Parvulastra vivipara*** (Asterinidae) were relocated from the southern to the northern side of the Sorell causeway and bridge which crosses Pitt Water within the greater area of Hobart, Tasmania.

A, members of Conservation Volunteers Australia collected and transferred thousands of seastars.

B, the commemorative plaque for the new Sorell causeway bridge, McGees Bridge, is in the shape of a seastar to honour the community for its endeavours to help save ***Parvulastra vivipara***.

[A, courtesy of T.D.O'Hara; B, M.Byrne]

in part to increased detection of exotic organisms, but possibly also to faster voyages and changing patterns of trade. Consequently, as pollution is reduced in many estuaries and bays, the natural communities are not returning to their former state. Rather, they are being modified by introduced species (Fields *et al*. 1993; Stachowicz *et al*. 2002; Coles *et al*. 2006). This is particularly true of Port Phillip Bay in Victoria, where introduced species now dominate the top ten most abundant animals in the bay (Wilson *et al*. 1998).

One positive development is the fact that the threat of introduced marine species is now recognised by local, state and Federal governments in Australia. Protocols and procedures have been put in place for surveying port environments in an effort to minimise the introduction of new pests from ships and aquaculture, and for the eradication of new infestations as quickly as possible (National Taskforce on the Prevention and Management of Marine Pest Incursions 1999). However, while minimisation of the impact of new introductions has been comparatively effective, little has been achieved towards the eradication of established pests (see Northern Pacific seastar above). Unfortunately, a lack of consensus among Australian states has hindered the establishment of a system to prevent the transportation of marine pests between Australian ports. Indeed, by 2008, only Victoria had comprehensive marine biosecurity arrangements (State of Victoria 2004).

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Intertidal habitat destruction

Intertidal organisms must cope with the hazards of life between the high and low tides, including periodic exposure, substantial variations in temperature, salinity and ultraviolet radiation, and contact with terrestrial and airborne predators. The intertidal habitat is also vulnerable to human pressures, such as harvesting of food and bait species, trampling, pollution, and destruction through the building of seawalls, ports, piers and roads (O'Hara 2002). Oil pollution can cause the local extinction of shallow-water species (Crump & Emson 1998). Intertidal areas near Australian cities are often degraded (Australian State of the Environment Committee 2001).

Cushion seastars (*Parvulastra* and *Cryptasterina* species) are among the few echinoderms that specialise in intertidal habitats. They can also have some of the most restricted ranges of any Australian marine invertebrates, making them of particular conservation concern. *Parvulastra parvivipara* is known from only five to seven localities along the west coast of the Eyre Peninsula in South Australia, and *P. vivipara* is known from nine to 11 sites near Hobart, Tasmania (**Box 4.5**). The latter is listed as endangered under the *Tasmanian Threatened Species Act* (1995). The more recently discovered species *Cryptasterina hystera* is only known from four locations (Dartnall *et al*. 2003; Puritz *et al.* 2012).

Concern over the future of *Parvulastra vivipara* led to two almost certainly unprecedented efforts to relocate seastar populations when road works and bridge construction threatened some of their habitats (**Fig. 4.13**). One of the largest populations of *P. vivipara* occurred along a causeway across Pitt Water, to the east of Hobart, where it lived under small sandstone rocks that flank the causeway. Ahead of repair to the causeway, the first effort to relocate seastars was made in October 1988, when staff and volunteers of the Threatened Species Unit of the Tasmanian Parks and Wildlife Service spent a morning collecting 3,500 of the tiny seastars and moving them in buckets from a section of the causeway that required repairs. They were relocated to a nearby cove with a similar environment. Plans to return the seastars were never executed as seastars that were left repopulated the repaired section of the causeway naturally.



Figure 4.14 Thousands of chocolate chip seastars, ***Protoreaster nodosus*** (Oreasteridae), are harvested each year from Indo-Pacific waters, then dried and processed for the souvenir and home decoration markets. These seastars mostly live in shallow sandy/muddy habitats at depths of 1–30 m across the tropical Indo-Pacific region, including northern Australia. This is usually a common seastar, but the pressures of continuous harvesting have caused significant population declines in some areas. These seastars may grow to a 200–250 mm diameter, although commonly they are much smaller in areas where they are harvested.

[J.Freund]

Box 4.6 Seamount biological communities and fishing

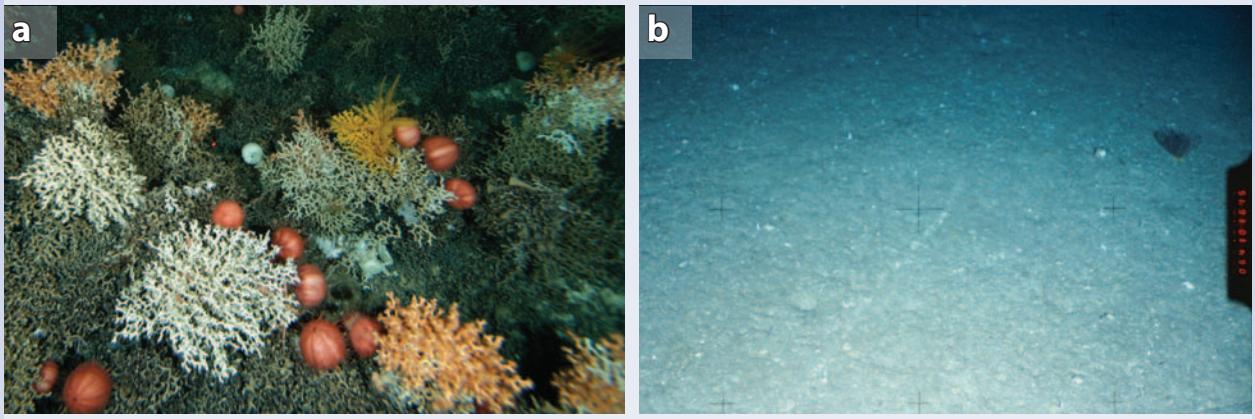


Figure a, **b** Off southern Tasmania the Huon Commonwealth Marine Reserve, declared in 2007, protects the unique and vulnerable seamount communities. Covering some 10,000 km^2 and ranging from 70 to over 3,000 m below sea level, the reserve contains a remarkable cluster of submerged seamounts, the remnants of volcanoes.

a, on many of the untouched deep-water seamounts the stony coral ***Solenosmilia variabilis*** forms extensive thickets that provide habitat for a host of animals including the sea urchin ***Dermechinus horridus*** (Echinidae); depth: 1,291–1,406 m.

b, commercial trawl fishing largely removes the stony coral habitats from shallow seamounts; they may take decades to recover. Scrape marks made by heavy trawls can be seen on the ocean floor.

[a, from CSIRO Survey and monitoring for South East Marine Protected Areas (SS11/2006); b, from CSIRO Tasmanian Seamounts Study 1997 (SS01/97, station 32)]

Corals reefs are usually thought to be exclusively associated with shallow-water tropical environments. However, they can also occur in the deep sea, although the species that occur there are quite different from those that dominate shallower habitats. Deepsea coral reefs are characteristic of seamounts or other rocky surfaces that experience some water flow. Seamounts occur all around Australia, but they are particularly numerous in the Great Australian Bight, around Tasmania and on the Lord Howe Rise and the Norfolk Island Ridge in the Tasman Sea. The faunal communities that grow on seamounts can be diverse, different from those of the surrounding seafloor, and have a limited capacity to regenerate if disturbed. They are also targeted by trawl fishers who catch large numbers of valuable fish, which, in southern Australia, was Orange Roughy.

The fauna of the seamounts to the south of Tasmania has been studied in detail. The main coral is *Solenosmilia variabilis*, and it forms a thick interleaving lattice. Only the tips of the slow-growing coral are alive, but the dense matrix provides shelter for a myriad of smaller creatures, including brittle stars, sea urchins and squat lobsters.

The contrast between fished and unfished seamounts is stark. Unfished seamounts support diverse *Solenosmilia* reefs, whereas fished seamounts are mostly covered in bare rock (up to 90%) with some gorgonians, sea urchins and holothuroids. The coral cover appears to have been removed in the early days of the fishery; the seamounts are now surrounded by coral rubble and sand.

The vulnerability of the southern Tasmanian seamounts was first recognised by the Australian Government in 1999 with the creation of a marine reserve, the Tasmanian Seamounts Marine Reserve, prohibiting bottom trawling. Later, in 2007, the small Tasmanian Seamounts Marine Reserve was incorporated into a much larger protected area, the Huon Commonwealth Marine Reserve. However, seamount faunas in other areas differ from those to the south of Tasmania, which are influenced by subantarctic conditions. Australian seamount communities will only be adequately protected by a comprehensive system of seamount reserves or the introduction of new technology to ensure that trawl nets are not dragged over the seafloor.

Futher reading Rogers 1994; Richer de Forges *et al*. 2000; Koslow *et al*. 2001; O'Hara 2007; O'Hara *et al*. 2008; Althaus *et al*. 2009; Rowden *et al*. 2010

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The widening of the causeway with construction of a bridge required a much larger relocation during 2001–2004. With the help of Conservation Volunteers Australia, the Department of Transport organised the transfer of 21,500 seastars from the southern to northern side of the causeway over five days. The design of the new causeway specified that the intertidal environment of the causeway would be similar to that of the old structure to create a new habitat for the seastars (Aquenal 2005). Since the massive translocation there is little indication of the thousands of seastars that were moved, and there has also been a decline in numbers of *P. vivipara* at the type locality near Midway Point (M.Byrne, unpublished data). In addition to the uncertainty of the success of the translocation exercise, there has been a widespread deterioration in the habitat quality at Pitt Water due to extensive siltation, and a change in the fauna with an increase in fouling suspension feeding worms, ascidians and sponges that cement rocks together. Years of observations of *P. vivipara* from Pitt Water indicates that this species requires clean rock surfaces to support its nightly feeding forays to the upper surfaces of rock to graze on microalgae (Prestedge 1998). Conservation measures are needed to protect *P. vivipara* in this region.

More studies are required before we fully understand the effects of these relocations. These translocations were undertaken without any knowledge of the suitability for or carrying capacity of the new sites for *P. vivipara*, and many of the sites had no previous populations of *P. vivipara*. It is clear that the *P. vivipara* did not fare well at many of the transfer locations. In cases where *P. vivipara* were added to an existing population mortality may have occurred if the combined numbers exceeded the carrying capacity of the habitat. Although there was a concern that mixing of populations might affect genetic diversity within the species, genetic studies indicate little if any genetic difference between populations of viviparous asterinid species (Keever *et al.* 2013). Nevertheless, it is significant that society recognises the need for invertebrate conservation.

Trawling and dredging

Damage to habitat can be caused by trawling and dredging (Thrush *et al.* 1998; Watling & Norse 1998). Bottom trawling for fish and prawns occurs on the continental shelves and on the upper continental slopes (<1,000 m) around much of the Australian coast and the coasts of offshore tropical and subantarctic islands. Bottom trawl nets typically have a beam or



Figure 4.15 The warty sea cucumber, ***Cercodemas anceps*** (Cucumariidae), is a popular aquarium species. It is found across the Indo-west Pacific and in Australia, from southern Western Australia across the north to southern Queensland. This species has a short body and colourful, retractable feeding tentacles.

[C.Bryce]

board at the front of the net which is dragged across the seafloor, forcing bottom-dwelling fish or prawns back into the net. Dredging for scallops occurs in bays and on the continental shelf, and involves a metal cage being dragged across the seafloor to collect the scallops from the surface layer of the sediment. Finally, shipping channels are regularly cleared and deepened by means of specialised dredges that move great quantities of sand and mud from the channels to 'spoil' dumping grounds nearby (Brodie & Waterhouse 2012). In support of mining exports, shipping and dredging activity has significantly increased leading to concerns for the health of the Great Barrier Reef (Brodie & Waterhouse 2012; Davey 2012) as well as its World Heritage status (UNESCO 2012). This dredging activity prompted a UNESCO reactive monitoring mission to assess the overall state of conservation of the the Great Barrier Reef and its potential for listing as 'in danger' (UNESCO 2012). With the Great Barrier Reef in decline (De'ath *et al*. 2012), and in response to the State Party Report (Australian Government 2013) concerns for the health of this World Heritage Area continue (UNESCO 2013), especially in light of the most recent (2016) bleaching that impacted most of the northern region (Ainsworth *et al*. 2016).

All the activities listed above remove the larger, habitat-forming colonial animals, such as corals, sponges and sea whips, that host echinoderms. The hard, brittle, slow-growing species such as deepsea black, gold and bamboo corals or glass sponges are particularly vulnerable to dredging and trawling operations (see **Box 4.6**). This has a flow-on effect on the echinoderms that live on these colonial animals, such as snake stars and crinoids, and many smaller species that occur in and around sponges and corals near the seafloor.

Apart from the target species, trawling also collects other animals from the seafloor. Mechanical damage caused by the net, changes in temperature and pressure as animals are brought to the surface, and exposure on the trawl deck, kill many of the animals in the so-called 'bycatch', most of which is then discarded. On average, 1–4 kg of echinoderms are collected per trawl in the South-east Australian Trawl Fishery (Barratt *et al*. 2001); echinoderms form about 3% of the bycatch in the Northern Trawl Fishery (Barratt *et al*. 2001).

The Australian fishing industry has recognised the need to reduce bycatch and habitat damage (Australian Fisheries Management Agency 2000). Bycatch reduction devices are now available for high-profile species such as turtles and dugongs, and action plans to reduce bycatch have been prepared for many Australian fisheries. Unfortunately, much of the damage occurred in the early days of the fisheries and, in the short term, there remains a need to identify and protect vulnerable or refuge communities in marine reserves or introduce other management measures. In the longer term, we require even more reliable and environmentally sensitive fishing methods to prevent continuation of damage to seafloor habitats and communities.

No doubt trawling and dredging can result in echinoderms and other organisms being greatly affected by changes in the community structure on the seafloor. Although predators, competitors and/or prey are removed, often in large quantities, we know comparatively little of the biological consequences of these events. However, research on Tasmanian inshore rocky reefs indicates that when 'no-take' marine reserves are created, there can be a dramatic change in the relative abundance of fish, echinoids and large brown algae (Edgar & Barrett 1997, 1999).

Over-exploitation

In addition to their exploitation as food, echinoderms are also collected for the aquarium trade, and as decorations and souvenirs (**Fig. 4.14**). Colourful seastars such as *Linckia laevigata* (**Fig. 8.25A**), sea cucumbers such as *Pseudocolochirus violaceus*, (**Figs 1.2G, 11.9A**) and *Cercodemas anceps* (**Fig. 4.15**), and brittle stars, such as *Ophiarachna incrassata* (**Box 1.2**) and *Ophiarachna megacantha* (**Fig. 9.13D**), are popular aquarium species. Typically, these animals are collected in Queensland for small domestic and export markets.

Dried and painted seastars are occasionally seen for sale in souvenir and gift shops. These are generally species of the tropical genera *Linckia*, *Astropecten*, *Protoreaster*, *Pentaceraster* and *Fromia*. Pencil sea urchins are also sold as decorations and wind chimes. Very little has been published about the origin of these specimens,

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but most come from the Indo-Pacific, possibly from the Philippines and south-western Pacific islands. The most common sea urchins for sale as decorations are sand dollars, most of which are collected off North America.

This trade is of concern because it appears to be completely unregulated, and virtually no information is available about the population status of these species. The trade often includes juveniles under breeding age, and it is unlikely that they are being collected sustainably. The result may be the localised extinction of popular species, for example Caribbean populations of *Oreaster reticulatus* (Scheibling & Metaxas 2001).

Water quality

The fauna and flora of many Australian estuaries, bays and coastal waters are adversely affected by poor water quality. This can be characterised by increased nutrients from sewage outfalls and agriculture runoff; elevated levels of sediment (increased turbidity) from stream erosion, vegetation clearing, urban and port development and seagrass dieback; pollutants originating from urban and industrial sources; altered salinity from draining of swamps and changes to the overall hydrology of an estuary; increased water temperatures caused by outflows from power stations; and increased nutrient levels and sedimentation. These were implicated in the massive die-off of seagrasses in the coastal environment in the last 25 years of the twentieth century (Larkum *et al.* 1989). Although progress has been made in addressing point-source pollution, diffuse pollution from historical land clearing, land-use changes and urban stormwater remain an issue (Australian State of the Environment Committee 2011).

Environmental stressors have an impact on the diversity and abundance of echinoderms in sheltered waters of bays and coastal inlets (O'Hara 2002). Since many of the changes are widespread, they may result in the global extinction of vulnerable species (Roberts & Hawkins 1999). Some echinoderms, such as the small black holothuroid *Trochodota shepherdi* and the ophiuroid *Ophiocomina australis* (O'Hara 2002), appear to be restricted to seagrass habitats in southern Australia, although the relationship between these species and seagrass has yet to be determined.

There is also strong evidence that increased sedimentation and eutrophication from agricultural sources are adversely affecting coral reefs on the Great Barrier Reef (Fabricius & De'ath 2001; Hughes *et al.* 2011; UNESCO 2013). Elevated nutrients promote an increase in macroalgal cover on inner reefs of the Great Barrier Reef (Hughes *et al.* 2011), and there is strong evidence that elevated nutrients contribute to crown-of-thorns outbreaks. Inorganic nitrogen, often bound to fine sediments, is by far the largest source of nitrogen entering the Great Barrier Reef; recent modelling suggests that the total nitrogen discharge into the area has increased from 20,077 tonnes annually in the late 1800s to 35,053 tonnes, and total phosphorus has increased from pre-European settlement loads of 2,727 tonnes annually to 5,849 tonnes (Great Barrier Reef Marine Park Authority 2014). The Reef Water Quality Protection Plan 2013 (see State of Queensland 2013) aims to achieve a 50% reduction in dissolved inorganic nitrogen loads entering the Great Barrier Reef by 2018. There has been a recent 42% fall in pesticide and herbicide concentrations around Mackay and the Burdekin River, which previously exceeded water quality guidelines, due to Government-funded initiatives to reduce discharge from sugar-cane agriculture (Great Barrier Reef Marine Park Authority 2014).

The management of water catchments and estuaries has been recognised as fundamental to the health of Australia's inshore marine environments (Australian State of the Environment Committee 2001). Management action plans have been developed for many Australian catchments in order to lower nutrient and sediment levels to acceptable levels. Sewage outfall is directed away from rivers and bays, stream erosion is curtailed and agricultural runoff is being addressed. For example, a plan for river catchments draining onto the Great Barrier Reef is being implemented (Great Barrier Reef Marine Park Authority 2002b). However, many of Australia's river systems are sufficiently degraded, and agricultural practices sufficiently entrenched, to require considerable levels of funds to fully address the impact on marine environments (Australian State of the Environment Committee 2001).

Climate change

Global warming is causing the waters of the oceans to simultaneously warm, decrease in pH and increase in the partial pressure of carbon dioxide (pCO_2) (Intergovernmental Panel on Climate Change 2013). All these factors will have deleterious impacts on physiological function in marine biota (Caldeira & Wickett 2003; Harley *et al*. 2006; Brierly & Kingsford 2009; Hofmann & Todgham 2010; Byrne 2011; Przeslawski *et al*. 2015). Increased seawater temperatures have the potential to become the most damaging threat to Australia's marine ecosystems (Polaczanska *et al*. 2007), and recent reviews have assessed the potential impact of climate change on echinoderms (Przeslawski *et al*. 2008; Byrne 2010, 2011; Byrne & Przeslawski 2013; Przeslawski *et al*. 2015). Water temperatures around Australia are projected to rise by 2–3°C at the surface and by 0.5–1.0°C at a depth of 500 m; the pH to decline by 0.2 units; the ocean mixed-layer depth to rise by a metre; surface currents to decrease by 0–1.2 m/s; and sea level to rise by 0.18–0.59 m (Hobday & Lough 2011; CSIRO & Bureau of Meteorology 2015). Already, a global rise of 0.1°C was detected for waters between 0 and 700 m from 1961 to 2003 (Bindoff *et al*. 2007). South-eastern Australia is a global climate change hotspot where sea temperatures have been increasing for decades due to changes in circulation patterns, in particular of the East Australian Current (Polaczanska *et al*. 2007; Ridgway 2007; Hobday & Lough 2011; Hobday & Pecl 2014). Global sea level is currently rising at the maximum rate (3 mm/year) projected by the International Panel on Climate Change (IPCC) mainly through thermal expansion of the oceans (Solomon *et al*. 2007). Modelling has shown that polar environments are particularly vulnerable to the deleterious effects of climate change, with major change in ocean conditions modelled to occur within the next two decades (McNeil & Matear 2008).

Climate change will affect marine and coastal ecosystems in various ways. Ocean acidification will impact on the ability of marine calcifiers (including echinoderms) to incorporate calcium carbonate (due to the decreased availability of this mineral) into their skeletons as reported for sea urchin and brittle star larvae, including several Australian species (Kurihara & Shirayama 2004; Dupont *et al*. 2010; Sheppard Brennand *et al*. 2010; Doo *et al*. 2012; Byrne *et al*. 2013b). However, calcification in regenerating ophiuroid arms was not reduced in low pH seawater (Wood *et al*. 2008). Climate change stressors will not operate in isolation, and a recent study indicated that early development in the sea urchin *Heliocidaris erythrogramma* would be more seriously affected by near-future projected ocean warming than ocean acidification, and that those embryos that survived the early bottleneck of mortality due to warming would be somewhat buffered from the deleterious effects of acidification (Byrne *et al*. 2009, 2011a, 2011b). Sea urchin echinopluteus larvae reared in ocean acidification conditions are smaller, although as shown for the larvae of the tropical species *Tripneustes gratilla*, a moderate increase in temperature can reduce the negative effect of decreased pH/increased pCO_2 on calcification (Sheppard Brennand *et al*. 2010; Byrne *et al*. 2013b). For the intertidal seastar *Meridiastra calcar*, increased temperature, not decreased pH, was the most important climate change stressor for larval development in this species (Nguyen *et al*. 2012). The interactive effects of ocean warming and acidification are complex, as shown for sea urchin calcification and for seastar and brittle star respiration (Sheppard Brennand *et al*. 2010; Byrne *et al*. 2011b; Christensen *et al*. 2011; McElroy *et al*. 2012; Carey *et al*. 2016). More multistressor studies are needed to understand how echinoderms and other marine taxa will fare in a changing ocean (Byrne & Przeslawski 2013; Przeslawski *et al*. 2015).

Rising seawaters will inundate coastal environments, forcing mangroves, salt marshes and seagrass beds to relocate to higher ground. However, human infrastructure and coastal topography such as cliffs and barrier reef islands will prevent this happening in many places, with consequent loss of these habitats (Beaman *et al*. 2008; CSIRO & Bureau of Meteorology 2015). This could impact adversely on echinoderms and other species currently living at sea level, including several localised endemics (Byrne 2006;

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Byrne & Walker 2007; Puritz *et al*. 2012). Increased occurrences of severe storms due to climate change is also likely to have a negative impact on echinoderm populations as observed in the disappearance of an entire coastal population of the seastar *Cryptasterina pentagona* from northern Queensland due to a cyclone (Dartnall *et al*. 2013).

Echinoderms and associated animals and plants will be forced to shift their distributional ranges according to their temperature tolerances, potentially causing major changes in ecosystems, although some species may have a certain adaptive (genetic change) or phenotypic (acclimation) capacity to tolerate change (Przeslawski *et al*. 2008; Sunday *et al*. 2011; Foo *et al*. 2012; Foo & Byrne 2016). As temperatures increase beyond tolerance limits it is expected that, in the absence of adaptation/acclimation, echinoderm populations nearer to the equator will decline and species may follow changing marine isotherms by migrating toward temperate regions. In the southern hemisphere, the general shift in species distribution will be to the south, with tropical taxa occurring at what are now subtropical latitudes, and subtropical species moving into what are currently temperate habitats. Of greatest concern are those species now confined to cool-temperate south-eastern Australia, as there will be no refuge for these species south of Tasmania in a warming world (Edgar *et al*. 1997). Such range-shifts have happened before in response to natural climatic variations. Temperatures at the peak of the last interglacial period (125,000 years ago) were approximately 1°C higher than today, and at that time reef-building corals occurred as far south as Newcastle in New South Wales and Albany in Western Australia (see **Chapter 5**). Antarctic species, which do not have the option for southerly migration, are particularly vulnerable.

The decline in coral reef health will severely affect the distribution of echinoderms and associated coral reef biota (Attrill *et al*. 2004). Because many corals live close to the limits of their temperature tolerance, sea temperature increases of as little as 1°C can cause coral bleaching: the coral's symbiotic algae is ejected and, as a result, the host dies (Hoegh-Guldberg 1999; Johnson & Marshall 2007). Several major bleaching events have occurred over the past decade, and even earlier. It is estimated that about one-sixth of the world's corals died in a massive bleaching event in 1998 (Global Coral Reef Monitoring Network 2000; Przeslawski *et al*. 2008). Another massive bleaching event occurred in 2010. Some heavily bleached reefs such as those in the Keppel Islands have recovered from bleaching in the past, perhaps because of a generally healthy local ecosystem (Great Barrier Reef Marine Park Authority 2002a; Carilli *et al*. 2009). However, with many other reefs damaged through increased sedimentation and nutrient pollution, over-exploitation, blast- and cyanide-fishing, mining and tourism, it is estimated that effectively 27% of the world's corals were lost by 2000 and by 2100 this loss could reach 40% (Wilkinson 2004). In the third major global coral bleaching event (2016), ~90% of coral reefs in the northern Great Barrier Reef have exhibited bleaching (Ainsworth *et al*. 2016; Australian Coral Reef Society 2016).

A further consequence of global warming might involve changes to the deepsea circulation of oceanic waters. Currently, oxygenated water sinks to the deep sea near the Antarctic and Arctic, driving a current that slowly winds its way across the seafloor of the globe (Tomczak & Godfrey 1994). However, during warmer periods in the Earth's history (such as the early Eocene 50 mya), the deep sea was comparatively stagnant, perhaps even anoxic at times (Prothero 1994). Any alteration to the deepsea circulation might have a profound impact on life in the oceans.

Although the Earth has experienced periods of unusually higher temperatures in the past, current and projected increases in global temperatures caused by human-induced climate change might be too rapid and too severe for many species to either relocate or adapt.

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5: Biogeography

Timothy D. O'Hara

Australia is one of the world's great centres of biodiversity. This fact has long been recognised for the terrestrial environment, with most people aware of Australia's unique mammals, and its terrestrial flora. However, the marine fauna and flora are similarly diverse, ranging from the vast tropical reefs of the north, to the rich algal beds of the south coast, to the ice-fauna of Australia's Antarctic territories, to the extensive muddy plains of the deep sea and the species-diverse slopes of seamounts.



Figure 5.1 The shallow-water marine environment of Australia is divided into two major biotic regions, the tropical Northern Australian Region and the temperate Southern Australian Region. To the east and west of the continent transition zones exist where tropical and temperate floras and faunas overlap. Winter sea-surface temperatures are shown (°C).

[redrawn after Wilson & Allen 1987]

Biogeographical patterns

Biogeographers have long recognised that the shallow-water Australian marine environment can be divided into two principal regions based on temperature (Ekman 1953; Wilson & Allen 1987; **Fig. 5.1**). Sea temperatures of the tropical north range from about 18°C in winter to 30°C in summer. Many species that occur here are also spread throughout the tropical Indian and Pacific oceans, from the coast of Africa to the Hawaiian Islands. In contrast, the southern coast is temperate, with sea-surface temperatures ranging from approximately 11°C in winter to 22°C in summer, and supports a largely endemic fauna. The eastern and western coasts are transition zones, supporting a mix of tropical and temperate species, as well as some that are found only in these zones.

Species composition also changes dramatically between the continental shelf (<200 m depth) and the continental slope (200–3,500 m) (O'Hara *et al.* 2011). While the abyssal plain (>3,500 m) is presumably also distinctive, there has been virtually no research on this habitat around Australia.

Biogeographical patterns for Australian echinoderms can be illustrated with the aid of an ordination diagram that demonstrates the relationship between species distribution and diversity and geographical location (**Fig. 5.2**). Each point on the diagram in **Figure 5.2A** represents a region, with the distance between points indicating the number of species shared between regions. Therefore points that are close together share most species, whereas those that are far apart have different communities of echinoderms. All regions that include only the continental slope and abyssal plain (>200 m) cluster apart from all those from shallower waters, as faunas differ significantly between shallow and deeper waters (O'Hara *et al.* 2011).

The pattern for the shallow-water regions shows a gradient between the tropical north and the temperate south, with the eastern and western coasts intermediate in their species composition (**Fig. 5.2A**). Interestingly, on the upper continental slope (200–2,000 m) the ophiuroid fauna shows a similar pattern, despite there being far less environmental variability at these depths (O'Hara *et al.* 2011).

Northern Australia

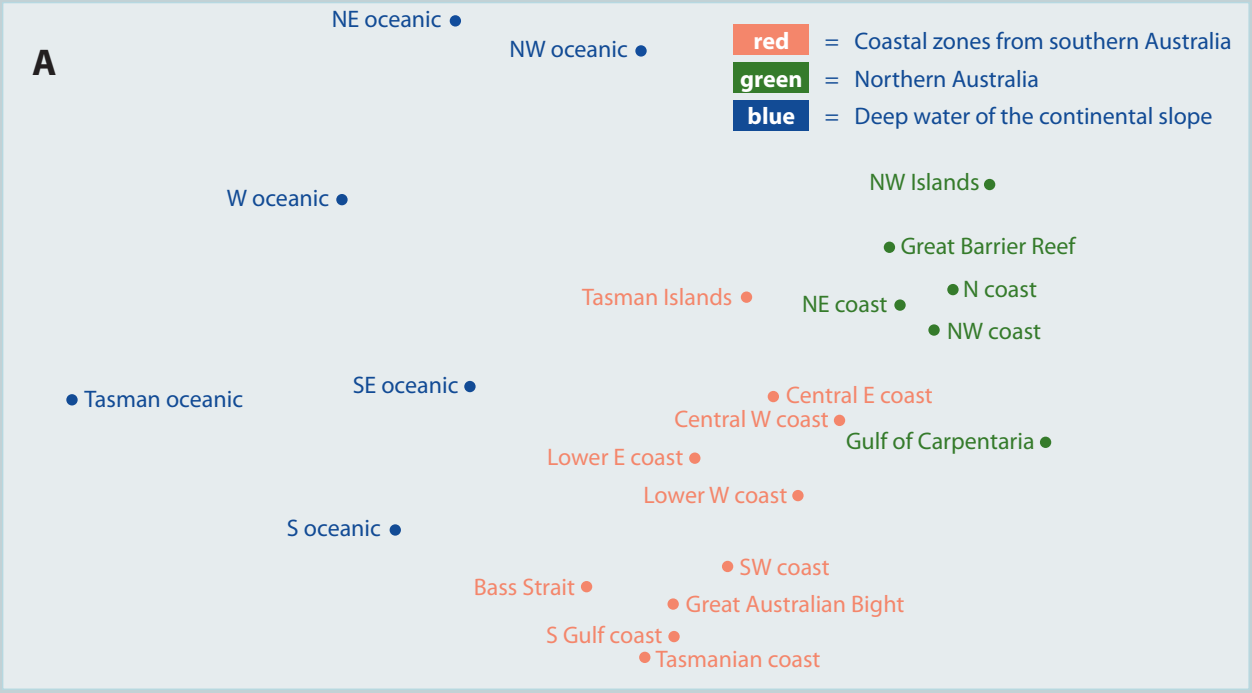
In tropical Australia, the north-western, northern and north-eastern faunas (i.e., NW coast, N coast and NE coast; **Fig. 5.2A**) group closely together, a little offset from the Great Barrier Reef and the offshore reefs and remote NW Islands off the north-western coast (for example, Ashmore, Scott and Mermaid). The difference between a mainland and reef suite of species has been recognised for some time (Endean 1957), although this is ecological rather than biogeographical, as there tends to be a lack of muddy and rocky habitats around coral reefs (Marsh & Marshall 1983; Rowe 1985a; Wilson & Allen 1987). The Gulf of Carpentaria stands apart from the other regions, principally because of the paucity of coral reef species (Post *et al.* 2006), but perhaps also attributable to the comparative lack of research on the area. The Tasman islands (Lord Howe Island, Norfolk Island and Elizabeth and Middleton reefs) stand slightly apart, having a combination of species from the east and north-eastern coasts and New Zealand, as well as a few endemics.

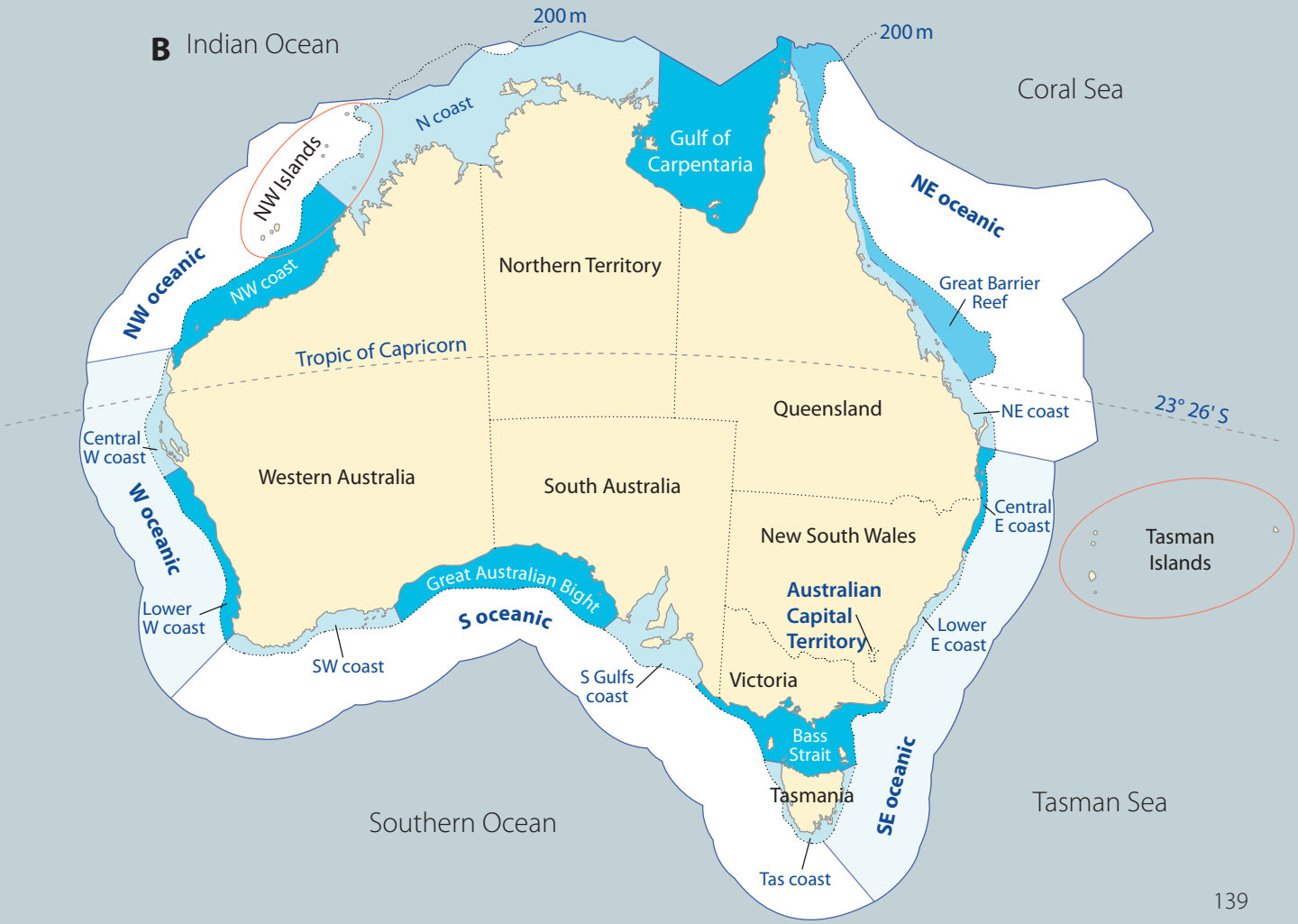
Figure 5.2

A, Ordination of the presence and absence of echinoderm species in marine zones from around Australia as shown in **B**. Coastal zones from southern Australia are shown in red, northern Australia in green and those from deeper water of the continental slope in blue. **B**, Marine zones of Australia's waters from the coast to the edge of the Exclusive Economic Zone. Tasman Islands include Norfolk and Lord Howe islands and Elizabeth and Middleton reefs. NW Islands include Ashmore and Cartier islands, Scott and Seringapatam reefs and Rowley Shoals.

[A, T.D.O'Hara, personal data; B, modified after Rowe & Gates 1995]

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A
red = Coastal zones from southern Australia
green = Northern Australia
blue = Deep water of the continental slope
NE oceanic
NW oceanic
W oceanic
NW Islands
Great Barrier Reef
Tasman Islands
NE coast
N coast
NW coast
Tasman oceanic
SE oceanic
Central E coast
Central W coast
Gulf of Carpentaria
Lower E coast
Lower W coast
S oceanic
SW coast
Bass Strait
Great Australian Bight
S Gulf coast
Tasmanian coast


B Indian Ocean
200 m
200 m
Coral Sea
N coast
NW Islands
Gulf of Carpentaria
NE oceanic
NW oceanic
NW coast
Northern Territory
Great Barrier Reef
Tropic of Capricorn
Queensland
23° 26′ S
NE coast
Central W coast
Western Australia
South Australia
W oceanic
Central E coast
New South Wales
Tasman Islands
Great Australian Bight
Australian Capital Territory
Lower W coast
S oceanic
Lower E coast
SW coast
S Gulfs coast
Victoria
Bass Strait
Tasmania
SE oceanic
Tasman Sea
Southern Ocean
Tas coast

Southern Australia

Along the southern coast, the ordination shows the western regions slightly separated from those of the east (**Fig. 5.2A**). This coast has been studied in greater detail by O'Hara & Poore (2000) who found the following. Both the western and eastern extremes have endemic species, with only 17% of the fauna shared by Albany in Western Australia and Eden in New South Wales. The principal dividing lines appear to be through Spencer Gulf and Gulf St Vincent in South Australia and around Wilsons Promontory in Victoria. This divides the southern coastline into a western warm-temperate region, a cool-temperate region including eastern South Australia, western Victoria and Tasmania, and a warm-temperate region from eastern Victoria to southern New South Wales.

It must be emphasised, however, that these regions are not completely distinct, many species are shared by the regions, and even those species that are endemic to a particular region do not necessarily share the same distribution limits. There have been attempts to identify biogeographical boundaries (where the distributional ranges of many species coincide) around major habitat breaks, such as the lack of rocky reef habitats along the sandy coastlines of eastern South Australia or eastern

Table 5.1 Species richness and endemicity of shallow-water echinoderms around Australia; derived from Rowe & Gates (1995).

* see **Fig. 5.2B** for location of the regions.

Region*	No. of species	No. of endemic species	Endemicity %
Northern Australia			
NW coast	431	23	5
NW Islands	179	0	0
N coast	374	4	1
Gulf of Carpentaria	75	0	0
NE coast	392	6	2
Great Barrier Reef	354	12	3
Tasman Islands	192	6	3
Southern Australia			
Central E coast	193	4	2
Lower E coast	247	9	4
Bass Strait	175	3	2
Tas coast	125	6	5
S Gulfs coast (Spencer Gulf & Gulf St Vincent)	144	5	3
Great Australian Bight	114	3	3
SW coast	121	1	1
Lower W coast	242	10	4
Central W coast	248	4	2

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Victoria (Wilson & Allen 1987; Hidas *et al.* 2007). However, these regions have rarely been studied in detail, and often there are low rocky reefs offshore (remains of old submerged shorelines) that would provide a migration route for many species. The lack of definite boundaries indicates that the old notion of dividing Australia into discrete biogeographical 'provinces' (see Wilson & Allen 1987) is not really an accurate interpretation. Instead, the situation is more of a gradient, so that, for example, across southern Australia, the warm-temperate faunas of the west and east (which also include some tropical species at the edges of their ranges) gradually merge into the cool-temperate fauna of the far south (**Fig. 5.2A**).

Subantarctic islands and Antarctica

Further south in the Southern Ocean, the shallow water fauna is completely different from that of Tasmanian waters. Macquarie Island has a mixture of shallow-water subantarctic species, and deeper-water species from New Zealand and/or Antarctica (**Box 5.1**). Not surprisingly Heard Island, lying 4,000 km to the west, shares most species with nearby Kerguelen and Marion islands. Only 10% of the Heard Island echinoderm species are shared with Macquarie Island (T.D.O'Hara, unpublished data). The fauna of the Australian territory in eastern Antarctica is broadly similar to that of other parts of Antarctica, although some regional differences exist (O'Loughlin *et al.* 1994, 2011a).

Diversity and endemism

The diversity of echinoderms is far higher in the tropics than in temperate regions (**Table 5.1**) — although data from Rowe & Gates (1995) are somewhat out of date they do give an indication of diversity of the region and the number of endemics. North-western Australia is the most speciose region, closely followed by the northern and north-eastern coasts. Apart from the anomalous Gulf of Carpentaria, the regions of lowest diversity are the comparatively poorly studied Great Australian Bight and Tasmania. Australian echinoderms appear to follow the general trend of species richness decreasing with distance from the tropics (Gaston 2000; O'Hara & Poore 2000).

Of the 1026 shallow-water echinoderm species recorded from Australia by Rowe & Gates (1995), 26% are endemic to Australia and its remote oceanic islands. Of the 566 species occurring in southern Australia (including the west and east coasts, but excluding the Tasman Sea islands), 29% are endemic. This is more than double the percentage that are endemic to the north (12% of 690 species). At the regional level (**Table 5.1**), north-western Australia and Tasmania, somewhat surprisingly, have the highest rates of endemicity (5%), although many of these species are very poorly known and may in the future be found elsewhere. Clusters of short-range endemic species are also found on the south-eastern and south-western coasts.

Historical explanations

Past events have played an important role in determining the distribution of echinoderms along the modern Australian coastline. For example, a species that evolved on the eastern coast may never have had the opportunity to colonise Western Australia, even though environmental conditions are suitable, because waters along the southern coast have been too cold and those along the northern coast too warm to allow migration from one side to the other.

This section will examine two main issues: the origins of the Australian marine fauna and the processes that have led to high species richness within the region.

Box 5.1 Rafting to remote Macquarie Island

Speciation is hypothesised to occur following differentiation of populations in isolation. The method by which these populations become isolated was the subject of an acrimonious scientific debate in the 1980s between biogeographers who believed that the isolated populations originated through the occasional colonisation of remote sites (long-distance dispersal) and those who believed that they were derived from populations separated by the movement of continental plates (vicariance). This is unfortunate because both processes are likely to be important. The significance of long-distance dispersal can be illustrated by examining the origins of the fauna of remote islands.

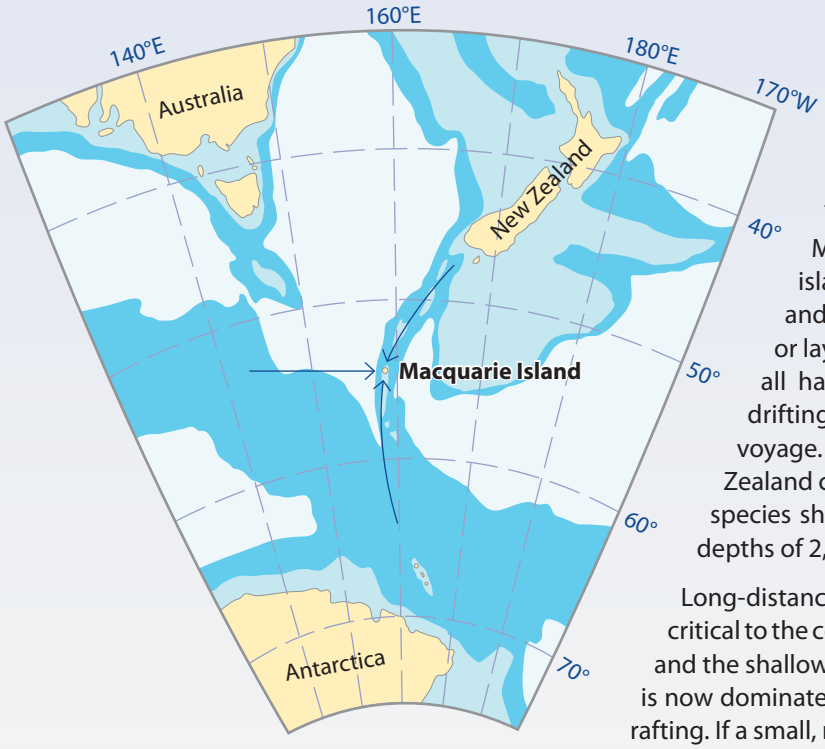
Macquarie Island lies mid-way between New Zealand and eastern Antarctica. It sits atop a long submerged ridge that is being pushed up by the collision of the Australian and Pacific continental plates. The island appears to have emerged only 600,000 years ago, and has never been contiguous with neighbouring continents. More than 50 species of echinoderms have been reported from around this island. How did they get there?

There appear to be three obvious routes. The first two run along the submerged ridges to the north and south of the island, from New Zealand and Antarctica, respectively, while the third utilises the circumpolar currents that flow west to east across the Southern Ocean. The nearest lands to the west of Macquarie Island are the isolated islands of Kerguelen and Heard, more than 5000 km away. Echinoderms could disperse over this distance if they have very long-lived larvae (the current is estimated to take 260 days to travel this distance) or by hitchhiking on floating seaweed or other materials.

It should be possible to correlate species distribution patterns with the life history and habitat required for dispersal via each of the three routes. For example, only shallow-water rocky reef species could raft on drifting kelp, as kelp only grows on shallow rocky reefs. Moreover, species dispersing along the ridge would need to tolerate a wide range of depths since

The evolution of Australia's marine fauna and environment over time are informed by two main sources of data: fossil and DNA evidence. The geological record is the primary data source; **Figure 5.3** shows the geologic time scale for the past 70 million years, from the Cretaceous to the present, along with various geological events which have helped to shape the fossil record. Fossils provide information on species occurrence in the past, and, by assuming that extinct species preferred the same environmental conditions as similar species that are living today, we can make some generalisations about past environmental conditions. Other geological evidence provides some indication of the geographic position of Australia over time and an overall timeframe for the fossil record. Secondly, much information can be gained from living organisms. Analyses of differences in morphology or DNA can generate a tree of species relationships which yields information leading to hypotheses about how and where species have evolved. The separation date of two closely related species can be estimated by comparing sections of DNA that are assumed to mutate at a modelled rate (the so-called 'molecular clock').

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Possible dispersal routes for marine fauna colonising the relatively recently emerged Macquarie Island via surface currents from the west or submerged oceanic ridges from Antarctica and New Zealand.

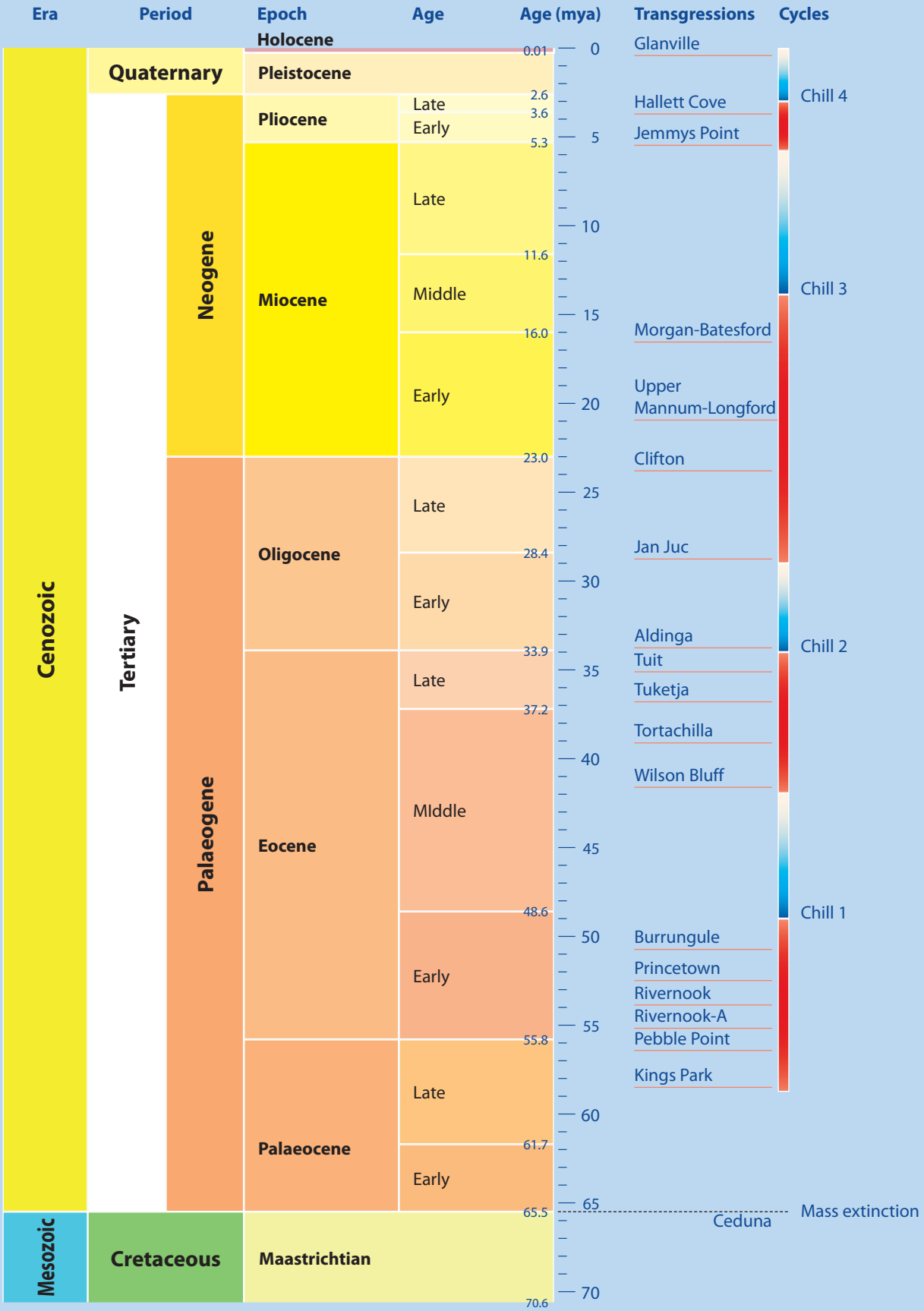
much of the northern ridge to New Zealand is below 100 m, and much of the southern ridge to Antarctica is more than 2000 m deep.

This is exactly the pattern that emerges. The 20% of the echinoderms shared by Macquarie Island with Kerguelen and Heard islands are shallow-water, rocky reef asteroids and holothuroids. They either brood their young or lay egg cases (they lack long-lived larvae), and all have large suctorial tube feet that can grip drifting kelp firmly enough to survive the long voyage. The 56% of species that also occur in New Zealand can tolerate depths to 100 m, and the 15% of species shared with eastern Antarctica can survive at depths of 2,000 m.

Long-distance dispersal in this situation is obviously critical to the colonisation of the coasts of Macquarie Island, and the shallow-water echinoderm fauna around the island is now dominated by species that appear to have arrived by rafting. If a small, recently formed island receives a substantial proportion of its total fauna by this means, how many species over time have reached a continent like Australia?

Further reading Fell 1962c; O'Hara 1998, 1999a; O'Hara *et al.* 2013

Both methods have their problems. The fossil record, even for well-known groups, such as echinoids or molluscs, is very incomplete. As most marine fossils have been recorded from locations that are now on land, we have information mainly from times of elevated sea levels and warm temperatures, or from areas that have been uplifted subsequently from the sea by geological forces. Fossil beds from the last 65 million years (since the beginning of the Tertiary period; see **Fig. 5.3**), are only accessible across western and southern Australia, there is little from the north and east coasts, or from much of Tasmania (**Fig. 5.4**). No location provides a complete record from all periods (McGowran *et al.* 2000). Even where there is a good record, different marine habitats may have been preserved at different locations or periods, making comparisons difficult. For example, the middle Miocene fossil beds (15 mya) of southern Australia are typically representative of continental shelf faunas, whereas later deposits contain fossils from coastal habitats (Darragh 1985). Unfortunately, cores of sediment from the deep sea, which have a more complete stratigraphical record, do not often contain complete fossils of larger animals such as echinoderms, although our understanding of



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how to classify disarticulated microfossils is expanding (for example, Thuy *et al*. 2012). A consequence of this incomplete record is that the record of absence of a species from a particular fossil stratum is ambiguous. The species may really have been absent, it may not have been fossilised, or it may not have been discovered.

The problem of relying on the relationships between modern species to determine the origin of a fauna is that it does not take into account species that have become extinct or species' distributions that have shifted over time. The latter is of particular concern for marine systems which contain fewer barriers to distribution than terrestrial ones. Modern taxa reflect recent events more strongly than distant events; evolutionary events become increasingly obscured over time (Rosen & Smith 1988).

The use of a 'molecular clock' is controversial. It is unclear whether mutation rates are constant across time or species. The molecular clock has been calibrated by dating the divergence of marine species separated by the creation of the Isthmus of Panama in Central America. However, the joining of the North and South American continents at Panama was not necessarily a single event. It appears to have taken place in stages with the creation of shallow seas and shoals long before the seaway was finally closed. Haug & Tiedemann (1998) suggest a gradual closure from 13 to 1.9 mya, with significant changes in the planktonic fauna occurring at 6.8, 4.6, 2.5 and 1.9 mya.

Despite these difficulties, much information can be gleaned from these various sources of data. The most powerful analyses test hypotheses with several independent datasets. Unfortunately, to date many biogeographical studies have been inductive; an author creates a plausible (although often untestable) scenario from a few (often disconnected) facts (Ball 1975).

Of all the echinoderms only the sea urchins (Echinoidea) have a substantial Tertiary record in Australia. Consequently, the following discussion also draws on examples from the Mollusca, Foraminifera (single-celled protists enclosed in a test), Ostracoda (small crustaceans), as well as echinoids.

Origin of the shallow-water Australian marine fauna

The fauna and flora of tropical Australia are similar to the fauna and flora of the tropical Indo-Pacific. Many northern Australian species range from Africa to Hawaii. One species, the sea urchin *Echinothrix diadema*, even occurs as far as the eastern Pacific (Lessios *et al.* 1998). In two seastar species complexes, *Acanthaster planci* (crown-of-thorns) and *Linckia laevigata* (blue seastar), a genetic break occurs between the Indian and Pacific Ocean populations, indicating the presence of a long-term barrier to dispersal between the two oceans (Williams & Benzie 1998; Benzie 1999; Vogler *et al.* 2008). Interestingly, populations on the north-western Australian coast are more similar to Great Barrier Reef populations than those elsewhere in the Indian Ocean. This could be due to a recent colonisation of the north-western reefs from the Great Barrier Reef or the presence of a long-term barrier to dispersal between Australia and the rest of the northern Indian Ocean (including the Cocos-Keeling Islands).

The origin of the fauna of southern Australia is quite complex. It includes taxa that appear to be:

1. endemic (termed Palaeoaustral or Gondwanan),
2. derived from an Indo-Pacific (Tethyan) fauna, or
3. derived from elsewhere in the Southern Ocean (Neoaustral) (Knox 1980; O'Hara & Poore 2000; Phillips 2001).

Figure 5.3 Geological sequences from the Cretaceous through Tertiary to the present. The major marine transgressions in southern Australia over the Cenozoic are aggregated into several major climate cycles characterised by relatively high temperatures and elevated sea levels (red bars). These are separated by periods of cooler temperatures and lower sea levels (blue bars) that produced few if any accessible marine fossil beds. The Holocene (or Recent) is represented by a pink line.

[redrawn and modified with permission from McGowran *et al.* 2000]

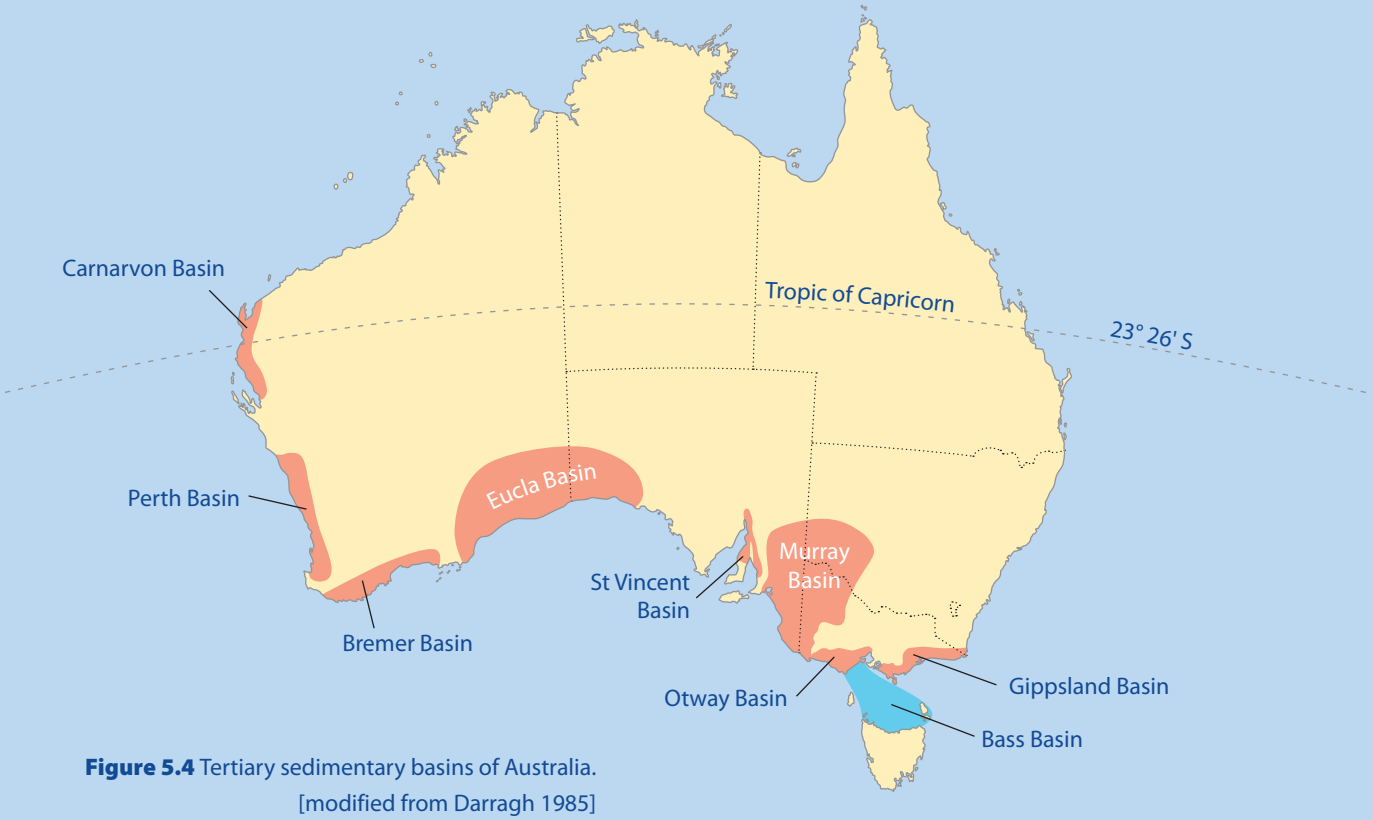


Figure 5.4 Tertiary sedimentary basins of Australia. [modified from Darragh 1985]

Southern Palaeoaustral component

The endemic component of the current southern Australian fauna can be traced with confidence through fossil beds of south-eastern Australia back to the late Eocene (40 mya). Few, if any, species have persisted from this period to the present, however some Late Eocene genera are still extant, and many others persisted until the mid Miocene (15 mya), to be replaced by related genera. Few endemic genera have been found in fossil beds earlier than the Late Eocene. The preceding Cretaceous, Late Palaeocene and Early Eocene beds have different faunas (Darragh 1985; McNamara 1998; Irwin 2001). Most phylogenies of Australian fossil echinoids or molluscs can be traced back to only the late Eocene (Darragh 1985; Irwin 2001). There are a few exceptions. The extant regular echinoid genus *Goniocidaris* has been found in late Cretaceous beds near Perth (McNamara 1986) and the lineage of the Australian endemic bivalve genus *Neotrigonia* (Late Miocene to Recent), can be traced back through the fossil genus *Eotrigonia* (Palaeocene to Middle Miocene) to the Mesozoic *Trigonia* (Middle Jurassic to Late Cretaceous) (Darragh 1986).

Unfortunately, the answer to the really interesting question of the origin of the Palaeoaustral component is elusive. Interpreting geological data using the theory of plate tectonics suggests that, in the Late Cretaceous to early Eocene, Australia was connected to Antarctica via Tasmania, forming, with South America, the last fragment of the super-continent Gondwana (Veevers 1986). The southern Australian coastline is suggested to have been part of a long narrow bay that emptied to the tropical Tethys Sea near what is now south-western Australia. The coastline of eastern Australia was contiguous with the coastline of eastern Antarctica and eventually with what is now

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Chile in South America. Australia is believed to have been orientated at right angles to its present position, leading to the suggestion that what is now the south-western Australian coast was warmer than the present day eastern coast.

If this interpretation is correct, there appear to be three choices for the origin of the current fauna; it could be derived from:

1. an earlier warm water fauna that lived along what is now Australia's south-west coast,
2. a cool-water fauna that lived along the eastern coast and invaded southern Australia when the seaway opened between Tasmania and Antarctica, or
3. an entirely new fauna that dispersed to Australia after the breakup of Gondwana.

Unfortunately the Australian marine fossil record in the Late Cretaceous is very sparse. There is some evidence from outside Australia that widespread marine faunas began to become regionally differentiated during the Late Cretaceous as the Earth cooled (Zinsmeister 1982). The best fossil records for this period in Australia are from the Carnarvon Basin in the north-west (Darragh & Kendrick 1991, 1994). The mollusc fauna appears to be indicative of a warm water environment, although perhaps not tropical, as many taxa, such as reef-building rudist bivalves typical of the tropics, are absent. Fossil records are absent from Australia's eastern coast from this time, although this has not prevented some researchers from speculating that eastern Australia shared a regional fauna (termed 'Weddellian') with New Zealand and the Antarctic Peninsula (Zinsmeister 1979).

The Palaeocene to Early Eocene fossil record is also poor. Echinoids, mainly holasterids and spatangoids, are known from the Carnarvon and Perth basins (**Fig. 5.4**). Holasteroids suffered a world-wide decline in diversity from the Palaeocene to Late Eocene so they are not a useful pointer to the origin of the later fauna, although one genus, *Giraliaster*, later reappears in the Late Eocene of southern Australia (McGowran *et al.* 2000). The spatangoids were largely cosmopolitan (McGowran *et al.* 2000). Palaeocene molluscs are known from the Pebble Point Formation in Victoria, but are not closely related to either the tropical or New Zealand faunas of that time (Darragh 1994, 1997).

There is also little evidence from fossils of a sudden opening up of a seaway between Tasmania and Antarctica, permitting Australian east coast or New Zealand species to invade southern Australia, or vice versa. Although the apparently sudden appearance of Australian planktonic Foraminifera in New Zealand in the late Early Oligocene has been used as evidence of the opening of an oceanic seaway (Jenkins 1993), more recent research has either located these species earlier in the New Zealand fossil record or attributed the distributions to global environmental change (McGowran *et al.* 2000). Possibly, a shallow water connection existed across Bass Strait or south of Tasmania intermittently back into the Cretaceous (Coleman 1980). Many Tasmanian magnetic anomalies from that time have been destroyed by faulting (Royer & Rollet 1997) so perhaps we will never know when the seaway first opened.

Consequently, there is no strong evidence to link the current marine fauna to either the western or eastern coast of Gondwana. It is possible that it is not related exclusively to previous Gondwanan faunas at all, as there were two global extinction pulses during this period. The largest occurred between the Cretaceous and Palaeocene (the so-called K/T extinction event at 65 mya), when major groups such as the dinosaurs, plesiosaurs and ammonites totally disappeared. It is unclear from the fossil record whether these extinctions were gradual (over a few hundred thousand years) or catastrophic. The cause was almost certainly climate change, possibly from an intense period of volcanism, a spatial rearrangement of continents, or an asteroid impact (Courtillot 1999). Estimates of marine species loss as a whole range from 70% to 76% (Jablonski 1995). Approximately 33% of echinoids became extinct (Jeffery & Smith 1998). Recovery from this event was variable. For some taxonomic groups the entire fauna was replaced, for others new species evolved from populations that survived in local refuge areas (Jagt 2000). There are no accessible fossil beds that show what happened during the K/T extinction event in Australia.

A second period of global faunal change occurred during the Middle Eocene, when there was a period of intense global cooling. There is a complete absence of fossil beds for seven million years (McGowran 1991). The fauna that emerged in the warm conditions of the late Eocene was quite different. As mentioned earlier, the previously common holasteroid echinoids suffered a worldwide decline. Other groups such as scleractinian corals diversified greatly again after considerable Middle Eocene extinctions (Veron 1995). Similarly, there was a considerable turnover in ostracod species that was global in extent (Benson 1979). Since these changes were global in nature, it is possible that much of the Palaeoaustral Australian fauna is derived from refuge areas outside the region.

In summary, the origin of the Palaeoaustral fauna is unclear. The use of the term Gondwanan to describe this fauna appears to be inappropriate as it is difficult to trace the current fauna back to the period when Australia was connected to other southern continents.

Southern Indo-Pacific component

Tropical Indo-Pacific faunas have invaded southern Australia episodically during periods of warm temperatures, pushing the endemic cool-temperate fauna back to the south-east. The warmer the period, the further east and south the tropical species penetrated. During the Late Eocene to Early Oligocene period (41–33 mya) of global warming, similar mollusc assemblages occurred from south-western Australia

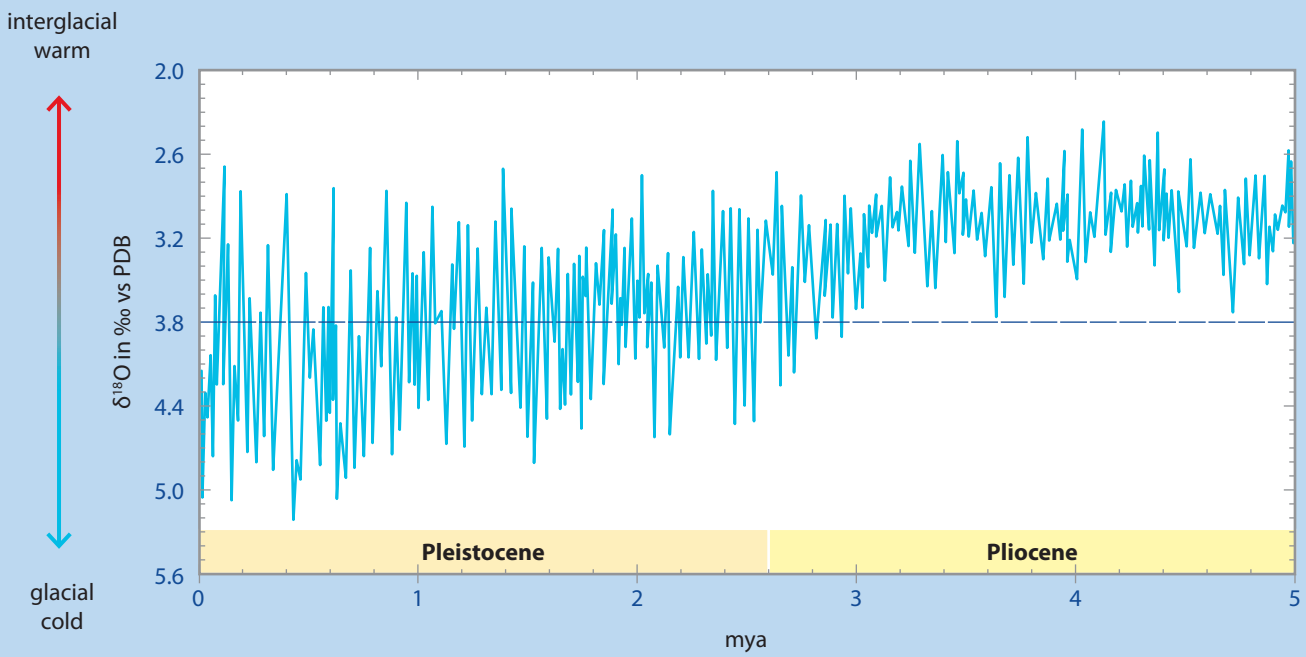


Figure 5.5 Sea level changes over the last 5 million years inferred from the deepsea isotope record of Tiedemann *et al*. (1994). The dashed horizontal line provides a reference for the opening (flooding) and closing of Bass Strait; it is roughly the depth at which Bass Strait floods and the part of the graph that falls below this line indicates the periods when the Strait was fully closed. Bass Strait opened and closed many times as the sea level fluctuated, reflecting glacial periods. Early in the Pleistocene *ca*. 40,000 year glacial cycles dominated, but more recently 100,000 year cycles have been more common. The left axis is the ratio of the isotopes ^{18}O:^{16}O in benthic Foraminifera compared to a standard (PDB) and is a proxy for changes in sea level.

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(Bremer Basin) all the way to Victoria (Otway Basin) (McGowran *et al.* 2000). For other groups, such as echinoids and foraminiferans, some regional differentiation is evident as not all tropical species appear to have reached Victoria (McGowran *et al.* 2000). This period of global warming was terminated by a sudden global 'chill' at 33.7 mya, possibly due to the initiation of circumpolar currents around Antarctica as the seaway opened between Antarctica and South America.

The next cycle of global warming, from the Late Oligocene to Middle Miocene, was not quite as prominent. The echinoid and mollusc faunas differentiated into a tropical fauna (known from Carnarvon in the north-west), a subtropical fauna occurring along south-west and southern coasts (from the Perth to Murray basins, termed the 'Austral' province), and a cool-temperate fauna in the south-east (Darragh 1985; McGowran *et al.* 2000; Irwin 2001). This period was terminated in another great global chill that occurred over the Late Miocene.

Finally the Pliocene to Pleistocene periods are characterised by continual climatic oscillations between glacial and interglacial periods every 40–100,000 years (Tiedemann *et al.* 1994; **Fig. 5.5**). The Pleistocene (beginning 2.6 mya) is marked by an increased severity of the cycles and lower average temperatures. Each glacial period brings cooler sea temperatures and lower sea levels. That the current period (the Holocene) is just the latest of a series of interglacial periods partly explains the number of tropical species that occur along the southern coast (O'Hara & Poore 2000). During the last interglacial, 125,000 years ago, which was warmer than at present, reef-building corals occurred as far south as Newcastle in New South Wales and Albany in Western Australia (Marshall & Thom 1976; Kendrick *et al.* 1991).

These long- and short-term cycles, periodically, have allowed many tropical species to invade southern Australia. Presumably, many taxa now considered characteristic of the southern fauna are those that adapted to the cooler conditions together with their descendants. It has been estimated that up to 70% of current southern Australian echinoderms have an Indo-Pacific origin (Rowe & Vail 1982).

Southern Neoaustral component

Some taxa appear relatively recently in the Australian fossil record and seem to be immigrants from elsewhere in the Southern Ocean. The most plausible dispersal mechanism for cool-water species is west to east drift on the powerful circumpolar currents to the south of Australia (Fell 1962c). Organisms can disperse either through long-lived pelagic larvae or as adults attached to floating kelp holdfasts (**Box 5.1;** Scheltema 1971; O'Hara 1998). A deepwater 'supergyre' has been discovered linking the Indian and Pacific Oceans south of Australia (Ridgway & Dunn 2007) which possibly could have had a major influence on the dispersal of bathyal animals.

Several examples of sudden appearances of mollusc genera in the fossil record are well documented. According to Murray-Wallace *et al.* (2000) the most plausible ancestor for the common Australian east coast bivalve *Anadara trapezia*, which first appeared in the fossil record of Australia and New Zealand in the middle Pleistocene, is *A. bravardi*, a Middle Miocene species from Argentina. The common scallop *Pecten fumatus*, which first appears in the Australasian fossil record in the early Pleistocene, is closely related to Miocene *Pecten* species from Europe. Beu & Darragh (2001) state that ancestors of *Pecten fumatus* possibly arrived via South Africa, first spreading across the tropical Atlantic Ocean during a period of cold temperature, and then westward across the Southern Indian Ocean, a route apparently common for Southern Ocean molluscs.

Other immigrants appear to have arrived more recently. The blue mussel *Mytilus planulatus*, common on jetties across southern Australia and long considered a native species, has been found to be genetically similar to *Mytilus galloprovincialis* from Europe (McDonald *et al*. 1991; Geller *et al*. 1993). This species has no fossil record in Australia, but some specimens have been found in coastal aboriginal shell middens (Lamprell & Healy 1998), which suggests that it arrived in the last 6000 years (when the sea level stabilised after the last glacial period). Genetic data suggests that Australian blue mussels first diverged from European forms at least 1.4 mya, crossing the equator in the Atlantic Ocean (Hilbish *et al*. 2000).

Dispersal can occur across the tropical Indo-Pacific oceans as well. The fossil record of the widespread echinoid Indo-west Pacific species complex *Echinometra 'mathaei'* (**Box 10.3**) suggests that it arose in the Middle Miocene in Europe and then spread across the Indian Ocean via the Red Sea, probably reaching south-western Australia during the Pleistocene (McNamara 1992). A similar route may have been taken by tropical scallop species (Beu *et al.* 1997; Beu & Darragh 2001).

Some echinoids appear suddenly in the fossil record. The first records of the speciose genera *Amblypneustes* and *Microcyphus* are from the South Australian Roe Calcarenite (Irwin 2001), now considered to be of Late Pliocene age (Kendrick *et al.* 1991). Some important southern Australian genera have no fossil record in Australia at all, including the regular sea urchins *Heliocidaris* and *Holopneustes*, and the irregular echinoid *Echinocardium*. *Echinocardium cordatum* is a species complex that occurs in temperate shallow seas in both hemispheres (**Box 10.6**). The Australian/New Zealand population (*E. australe*) diverged from North Atlantic forms at least 4 mya (Egea *et al.* 2016).

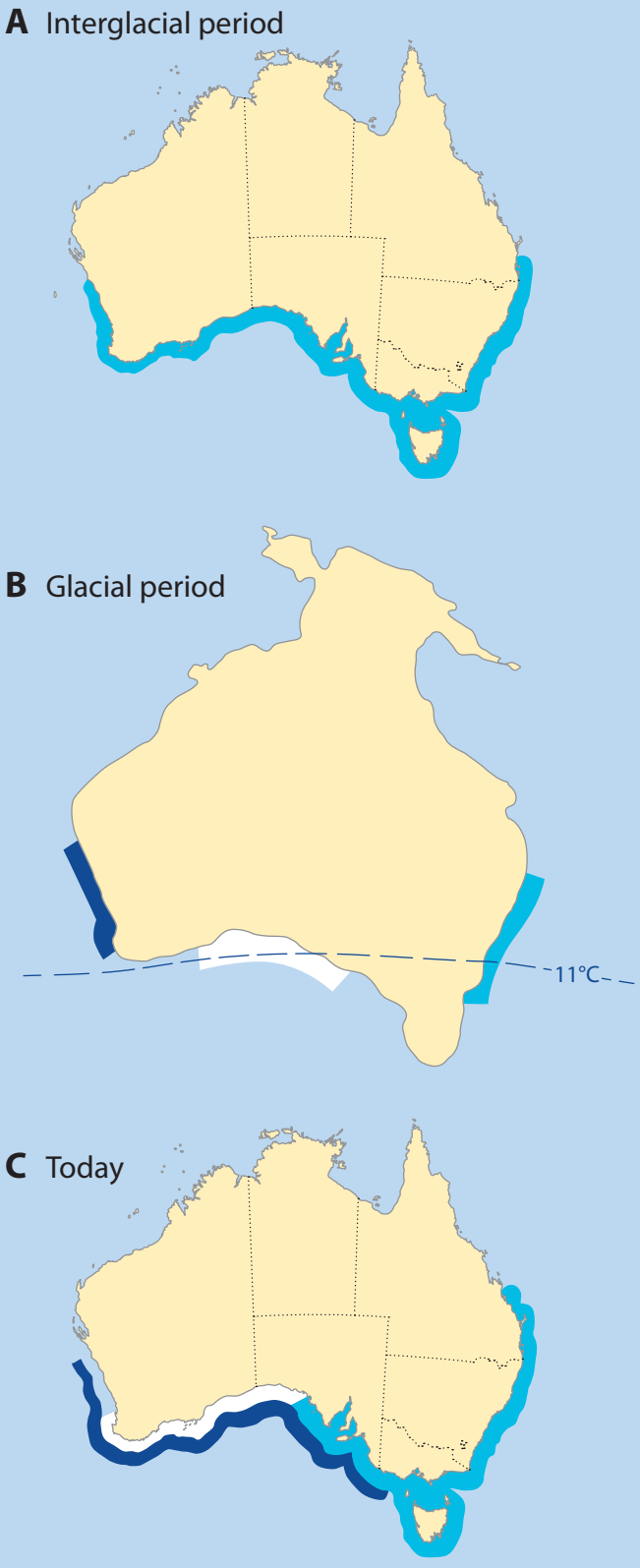


Figure 5.6 A model of allopatric speciation for the shallow-water southern Australian marine environment. Species with continuous distributions during interglacial periods (**A**) are split into allopatric populations during glacial periods (**B**). Barriers to dispersal are formed by a combination of lowered sea surface temperatures and sea levels particularly across the Bassian Isthmus in south-eastern Australia. One or two pairs of these allopatric populations speciate and then become partially sympatric in succeeding interglacial periods, such as today (**C**). The distributions shown in (**C**) are based on three sister species in the asteroid genus ***Patiriella*** (see Waters *et al.* 2004).

The 11°C glacial isotherm depicted in **B** is based on reconstructions by Barrows *et al.* 1996 for the last glacial period (16 kya).

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Summary

No single origin can be determined for the southern Australian marine fauna. Instead, successive waves of immigrants have arrived over time, supplementing an ancient Palaeoaustral fauna. The southern Australian marine environment cannot be regarded as a biogeographic 'island' that has developed separately from the rest of the world. Dispersal to and from Australia has been a frequent and important biogeographical process.

Nevertheless, once arrived, these taxa have adapted to their new environment and have become distinct from their parental stock; some have then speciated further. Consequently, although generic or family-level endemism is relatively low for echinoderms, species endemism is relatively high.

Although it is likely that at least some southern Australian species are descended from an ancient Gondwanan fauna, the fossil evidence is inconclusive. Perhaps future genetic studies will be able to differentiate between speciation resulting from the breakup of Gondwana and that derived from long-distance dispersal via ocean currents.

Diversity of the Australian fauna

The southern Australian marine fauna and flora exhibit high levels of species richness (Poore 1994; Phillips 2001). This is particularly true for some taxonomic groups such as algae, molluscs, crustaceans and sponges. This high level of regional diversity may also explain the apparent high levels of local diversity (number of species per square metre) discovered for southern Australian marine environments (Coleman *et al*. 1997).

The faunal or floral diversity of a region is related to rates of speciation, immigration, and extinction (Gaston 2000). For higher than average diversity, speciation or immigration rates need to be higher than for other regions, or extinction rates lower. The contributions of these three processes are discussed in the next section.

Speciation

The process of speciation has long fascinated biologists. The main mechanism proposed is allopatric speciation, which occurs when two populations of a species are isolated by a barrier (**Fig. 5.6**). Over time, through genetic mutation, natural selection and genetic drift, the two populations differentiate until they can no longer interbreed, and are deemed to be separate species. The barrier may later disappear and the species may spread out and overlap.

Consequently high rates of speciation may occur in regions where species distributions are regularly fragmented by barriers created by variable environmental conditions. Evidence for this process would include radiation of species within genera and identifiable barriers to dispersal.

Radiation appears to have occurred in relatively few southern Australian marine genera. For example, in echinoderms and decapods (crabs, shrimps, lobsters, etc.) there is an average of two species per genus (O'Hara & Poore 2000). Moreover, many genera are widespread and the southern Australian representatives are often not closely related. The overall picture suggests that species in the same genus have derived from multiple immigration events, not from local radiation. A few exceptions exist, including the asteroid genus *Nectria* (8 species) (Rowe & Gates 1995), the echinoid *Amblypneustes*/*Holopneustes* complex (11+) (Rowe & Gates 1995; Miskelly 2002; Jeffery *et al*. 2003) and the crinoid *Cenolia* (6) (Naughton *et al*. 2014a). The asteroid genus *Patiriella* (formerly with 6 species) is now known to contain representatives of several genera (Hart *et al*. 1997; O'Loughlin & Waters 2004).

The Bass Strait region has long been proposed as an intermittent barrier to species dispersal in southern Australia (Dartnall 1974; Wilson & Allen 1987; Waters 2008). The theory is that during Pleistocene glacial periods, low sea levels closed Bass Strait and low water temperatures prevented the dispersal of warm temperate species around the southern tip of Tasmania. This would create separate east and west populations that might diverge to become distinct species over ime.

Fossils that might test this hypothesis are not available, as the Pleistocene record from southern Australia is intermittent, consisting mainly of remains from the last two interglacial peaks. Instead the evidence for this proposal comes mainly from the current distribution of closely related species that appeared to be split into eastern and western species across Bass Strait (Dartnall 1974). However, subsequent research has shown that many of these species are not closely related or have more extensive distributions. For example, the three species of '*Asterina*' listed by Dartnall (1974) as overlapping in the Bass Strait region are now placed in separate genera, *viz. Meridiastra atyphoida*, *Indianastra inopinata* and *Aquilonastra scobinata* (O'Loughlin & Waters 2004). The proposal also dates from a time when researchers believed there were only four Pleistocene glaciations. We now know there have been at least 60. The cycles are relatively brief (40–100,000 years between interglacial maxima), perhaps too brief for the classic allopatric speciation model. This is not much time for the evolution of barriers to reproduction.

Indeed, the limited molecular and fossil data suggest that many modern species arose much earlier than recent Pleistocene glacial cycles. For example, the asteroids *Parvulastra vivipara* and *P. parvivipara* are estimated to have diverged 1.3–2.1 mya (Hart *et al*. 1997), and *Meridiastra oriens*, *M. medius* and *M. occidens* approximately 2.1–2.4 mya (Waters *et al*. 2004). The two species of *Cryptasterina*, the Indo-Pacific *C. pentagona* and the Queensland endemic *C. hystera*, may have diverged as recently as 6,000 years ago (Puritz *et al*. 2012). Three species-pairs of fish with

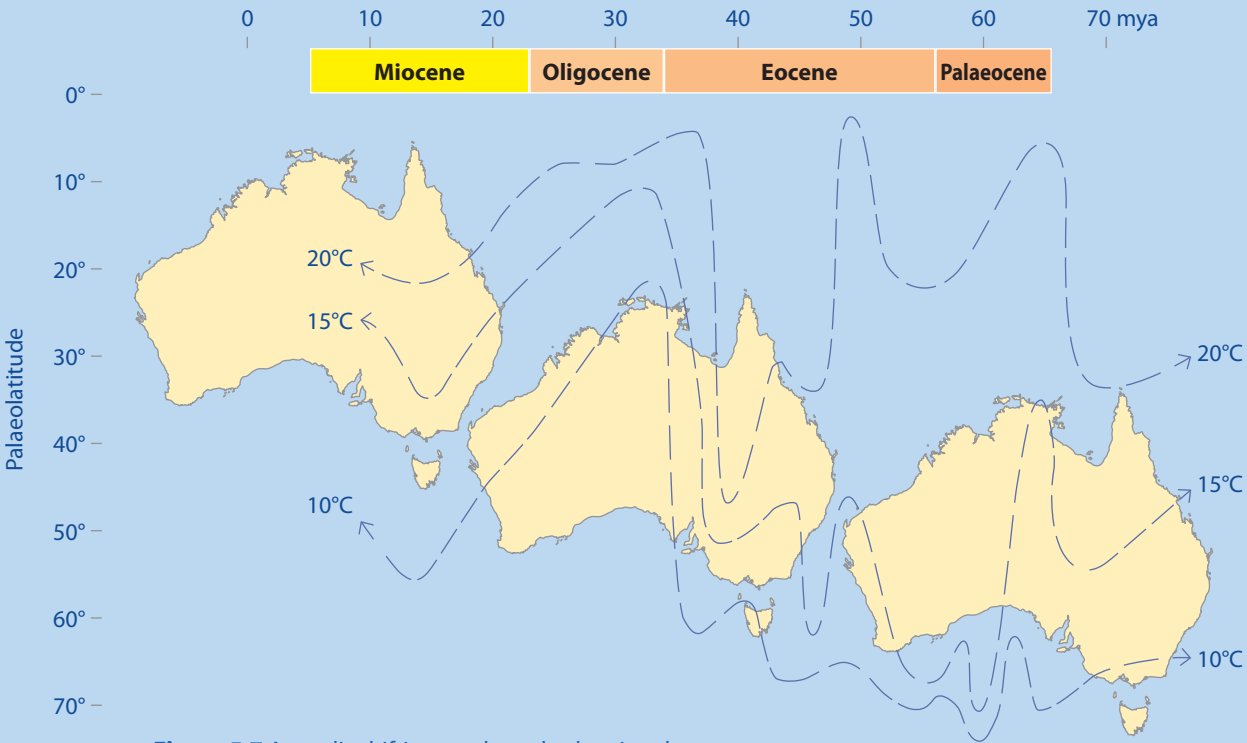


Figure 5.7 Australia drifting northwards, showing that oceanographic temperature changes over time have been larger than those expected from tectonic movement.

[redrawn with permission from McGowran *et al*. 2000]

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allopatric distributions across southern Australia are dated at 2.7–3.8, 7.0–10 and 7.8–11.2 mya respectively (Burridge 2000). Fossil data also suggest that a minor extinction/speciation pulse occurred at the beginning of the Pleistocene, with subsequent climatic cycles causing shifts in species distributions along with changing sea temperatures, but relatively few extinctions (Jackson 1995; O'Hara & Poore 2000).

Molecular phylogenetic analyses often reveal discrete lineages of Pleistocene (Avise 2000) or even Holocene age (Puritz *et al.* 2012) that are difficult to distinguish morphologically. Whether or not these lineages represent separate biological species (often termed 'cryptic species') is difficult to determine. For example, the ophiuroid species in the southern Australian genus *Clarkcoma* include distinct genetic lineages that can be distinguished by subtle differences in colour and oral plating (Naughton *et al.* 2014b). The most recent lineages are allopatric; the others show a degree of sympatry, consistent with populations being occasionally isolated (for example, by sea level changes) and then subsequently reconnected (Naughton *et al.* 2014b). In summary, while many of the recognisable 'species-pairs' historically used to promote the idea of marine species diverging across a Bass Strait land-bridge may predate the Pleistocene (or not be closely related at all), much of the subsequent genetic diversification arising from the climatic cycles can be obscured by the limited morphological evolution that has occurred since these relatively recent events.

Extinction and immigration

Extinction events are a regular feature of the fossil record. Major extinction events may involve up to 85% of all species (Jablonski 1995). Usually these events are tied to major climatic changes. Consequently, lower than average rates of extinction might arise from environmental stability. It has been suggested that Australia's slow continental drift into warmer northern waters over the last 50 million years may have offset the effect of overall global cooling, creating a continuously equitable climate (Nix 1982; Phillips 2001). However, this is unlikely to have been the case, as fluctuations in global temperatures appear to have greatly exceeded the effect of Australia's northward drift (**Fig. 5.7**).

A lower than average extinction rate may also eventuate if species can persist in refuges during extremes of climate. Australia's long eastern and western coastlines would have allowed species to shift their range north or south depending on changes in local seawater temperatures. We know from the fossil record that a cool-temperate fauna persisted in south-eastern Australia even during the warmest periods of the Tertiary (Darragh 1985). Few Australian fossil records are available from the coolest periods, however Australia appears not to have experienced the widespread extinctions (for example, among brachiopods and molluscs) that occurred in New Zealand during the late Miocene chill (McGowran *et al.* 2000; Beu & Darragh 2001).

As documented above, frequent changes of climate have facilitated successive waves of immigration into southern Australia. Australia's drift northwards towards the Indo-Pacific may have facilitated above-average immigration, although this has not been tested in any quantitative analysis.

Summary

The cause of Australia's high shallow-water species richness is debatable. However, a plausible scenario is that the fauna has been supplemented repeatedly by immigrations from the tropics and the Southern Ocean. These immigrant taxa evolved over time to give rise to endemic members of the regional fauna, and in some cases diversified into several separate species. Rates of extinction may have been lower than for other regions, as temperature-specific species have found refuge along Australia's extensive coastline during the extremes of the climatic cycles.

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6: Phylogeny and Geological History

Andrew B. Smith

Adult echinoderms, with their pentaradial body plan, look superficially so very different from other invertebrate groups that their origins and relationships are not immediately apparent. However, a less cursory assessment shows that they nest high within the Bilateria. Although not bilateral as adults, echinoderms do start life as bilaterally symmetrical organisms, and so their status as members of the Bilateria is not as anomalous as would first seem. Indeed, bilateral fossil echinoderms have been recently discovered from the early middle Cambrian of southern Europe (Zamora *et al*. 2012). Traditionally, Bilateria have been divided into two groups, the protostomes and deuterostomes, according to whether the mouth arises directly from the larval blastopore (protostomes) or forms secondarily as a separate opening (deuterostomes). On this criterion echinoderms are clearly deuterostomes, and this has been confirmed by recent molecular phylogenetic analyses (Philippe *et al*. 2005; Dunn *et al*. 2008; Cannon *et al*. 2009).

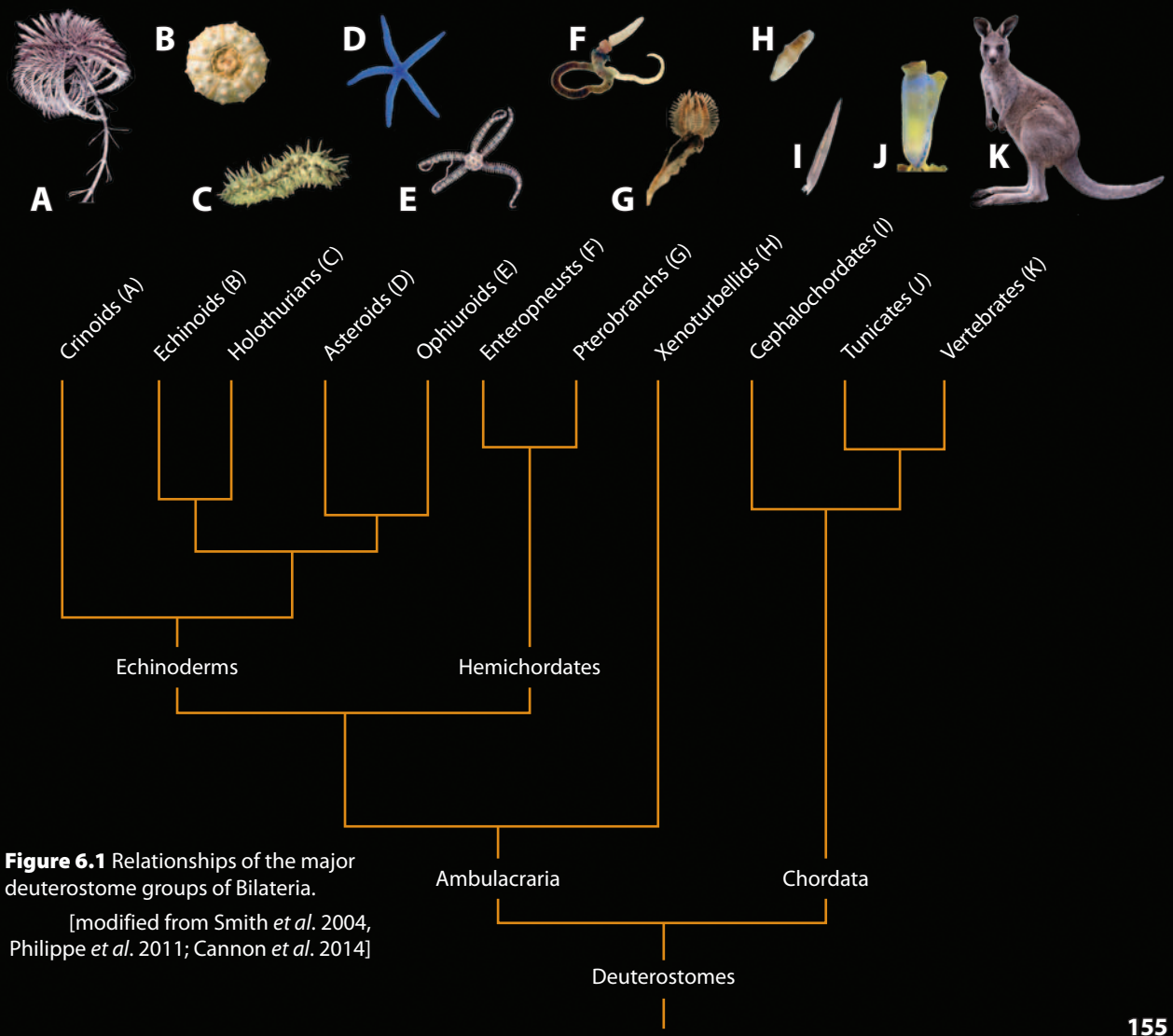
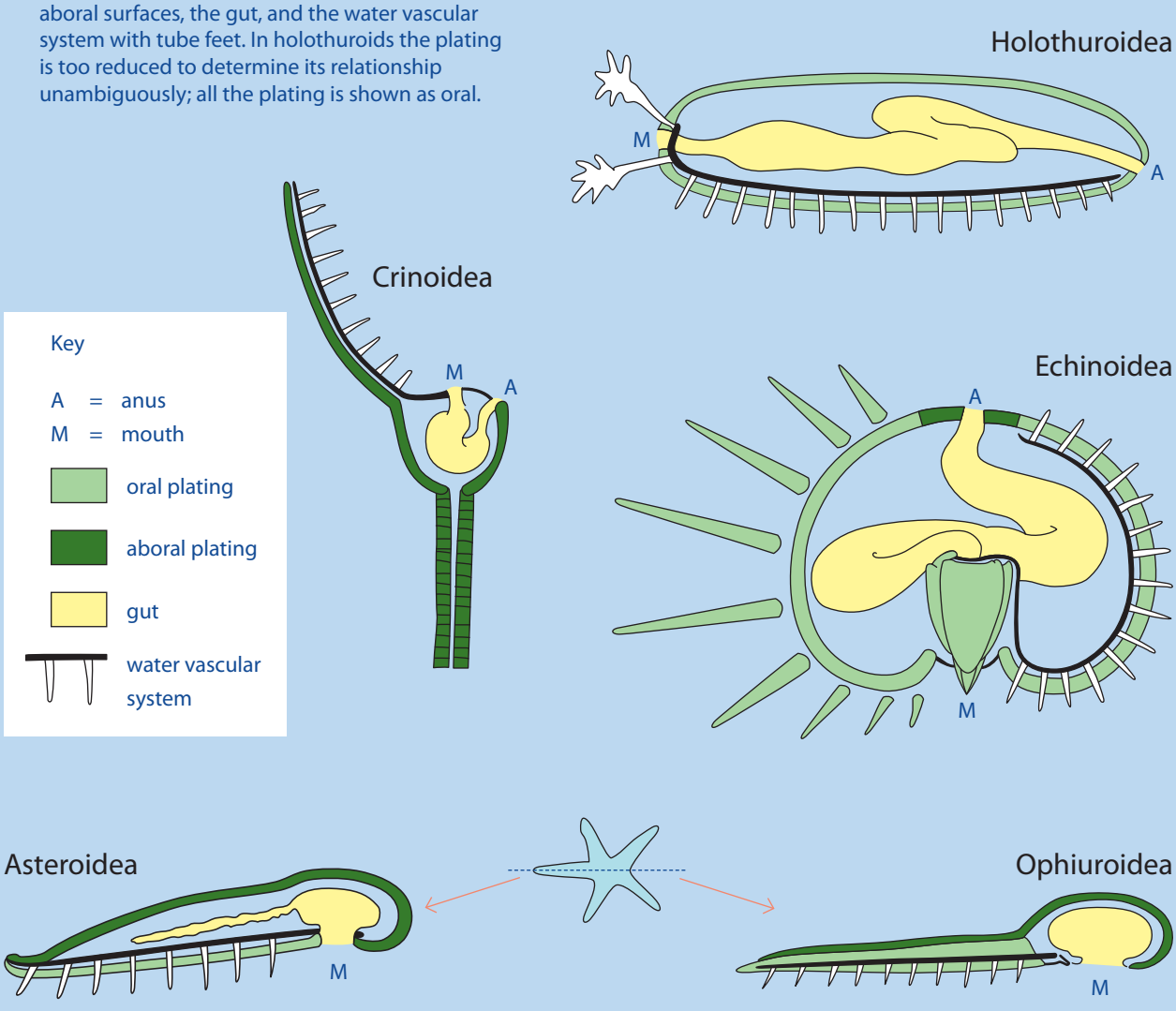


Figure 6.1 Relationships of the major deuterostome groups of Bilateria.

[modified from Smith *et al*. 2004, Philippe *et al*. 2011; Cannon *et al*. 2014]

The Deuterostomia comprises two other groups in addition to echinoderms, the chordates and hemichordates (Fig. 6.1). The relationships of these three taxa have proved particularly difficult to resolve on the basis of morphological evidence. This is because echinoderms show closest similarity with hemichordates when larval characters are compared, but chordates seem more similar to hemichordates when adult characters are considered. The larvae of indirect-developing echinoderms and hemichordates are very similar in appearance. Indeed, for many years after it was discovered in the plankton, the larvae of enteropneust hemichordates were thought to be the larval stage of some unknown seastar. They share a complexly folded ciliary band that surrounds the mouth and is used in feeding, and both have a very similar tripartite gut. Similarities even extend to the molecular level and the way set-aside cells are laid down (Peterson *et al.* 2000). Conversely, the presence of gill slits in the adults of both chordates and hemichordates, together with their obvious bilateral organisation, have been sufficient to convince most workers that they are sister taxa.

Figure 6.2 Schematic body plans of the five living classes of echinoderms showing orientation to the substratum, placement of the oral and aboral surfaces, the gut, and the water vascular system with tube feet. In holothuroids the plating is too reduced to determine its relationship unambiguously; all the plating is shown as oral.



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Recent research on morphology (Peterson & Eernisse 2001) and gene sequence data (Bromham & Degnan 1999; Winchell *et al.* 2002; Bourlat *et al.* 2006; Dunn *et al.* 2008; Cannon *et al.* 2014) has clearly demonstrated that hemichordates and echinoderms group together as sister taxa to the exclusion of chordates. Both hemichordates and echinoderms share an identical tripartite body plan, with a single anterior coelom (the axocoel), followed by paired mesocoels and paired somatocoels. However, whereas all these body coeloms are retained in the adult hemichordate, echinoderms undergo a radical developmental transformation in which the right mesocoel is lost and the remaining coeloms become stacked vertically (Peterson *et al.* 2000; see **Fig. 6.3**). Echinoderms and hemichordates also, uniquely, have a closely similar metanephridium or protokidney, the axial organ, which is used for pressure filtering the primitive haemal system fluid.

The pairing of echinoderms and hemichordates was first recognised by Metchikoff in the nineteenth century, and it was he who initially proposed uniting them under the name Ambulacraria. This has some interesting implications for phylogeny. Firstly, since both hemichordates and chordates have gill slits, these structures must be primitive to deuterostomes as a whole, and so their loss in the extant echinoderms is a derived character. It also suggests that their ontogenetic transformation from bilaterality through asymmetry to pentaradiality might correspond to an evolutionary transformation (Smith 2005). Comparing echinoderm ontogeny and developmental gene-signalling patterns with those of hemichordates suggests that an evolutionary switch from posterior facultative to anterior obligate larval attachment may have proved the critical trigger in the evolution of the echinoderm body plan (Smith 2008). Anterior attachment necessitated introducing a phase of torsion during early growth, and this caused the axis of the developing adult echinoderm to become rotated 90° out of alignment with *Hox* and other body-patterning genes. Consequently, the developing echinoderm rudiment came to receive a complex mosaic of anterior-posterior gene-signalling patterns, allowing extensive co-option of gene-signalling pathways to take place, and a radically new body plan organisation to emerge. The fossil record of echinoderms is particularly illuminating as it preserves a series of primitive, pre-radiate forms critical for understanding the early stages of evolution (see **Box 6.1**).

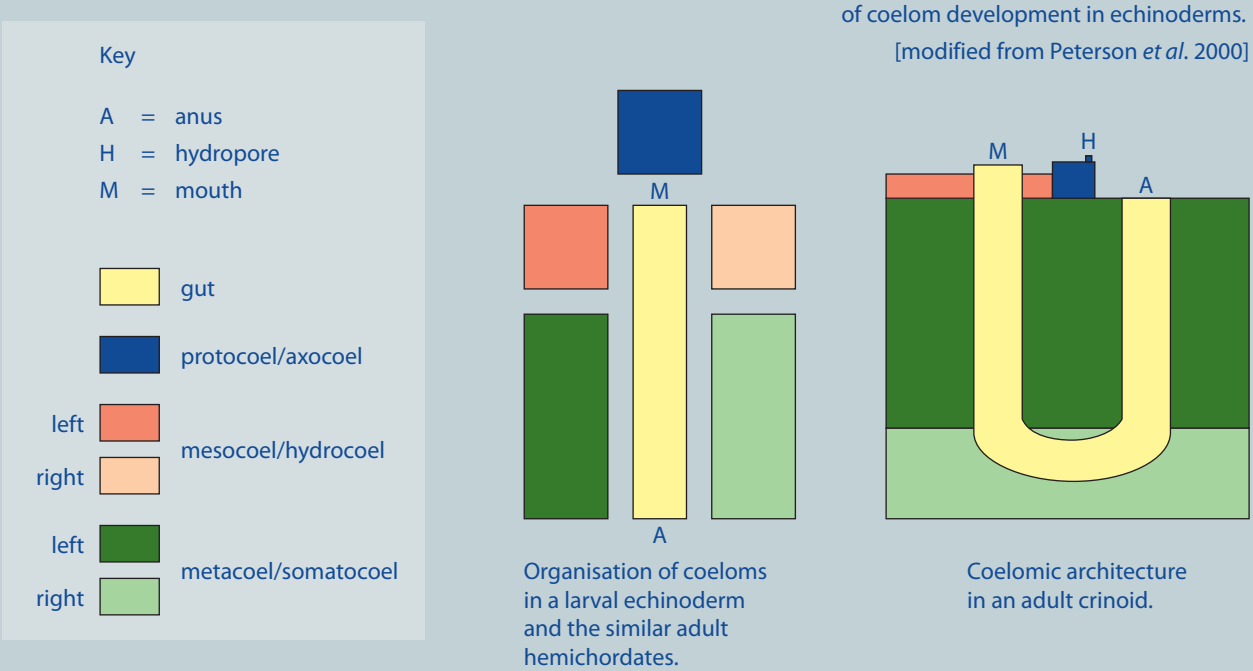
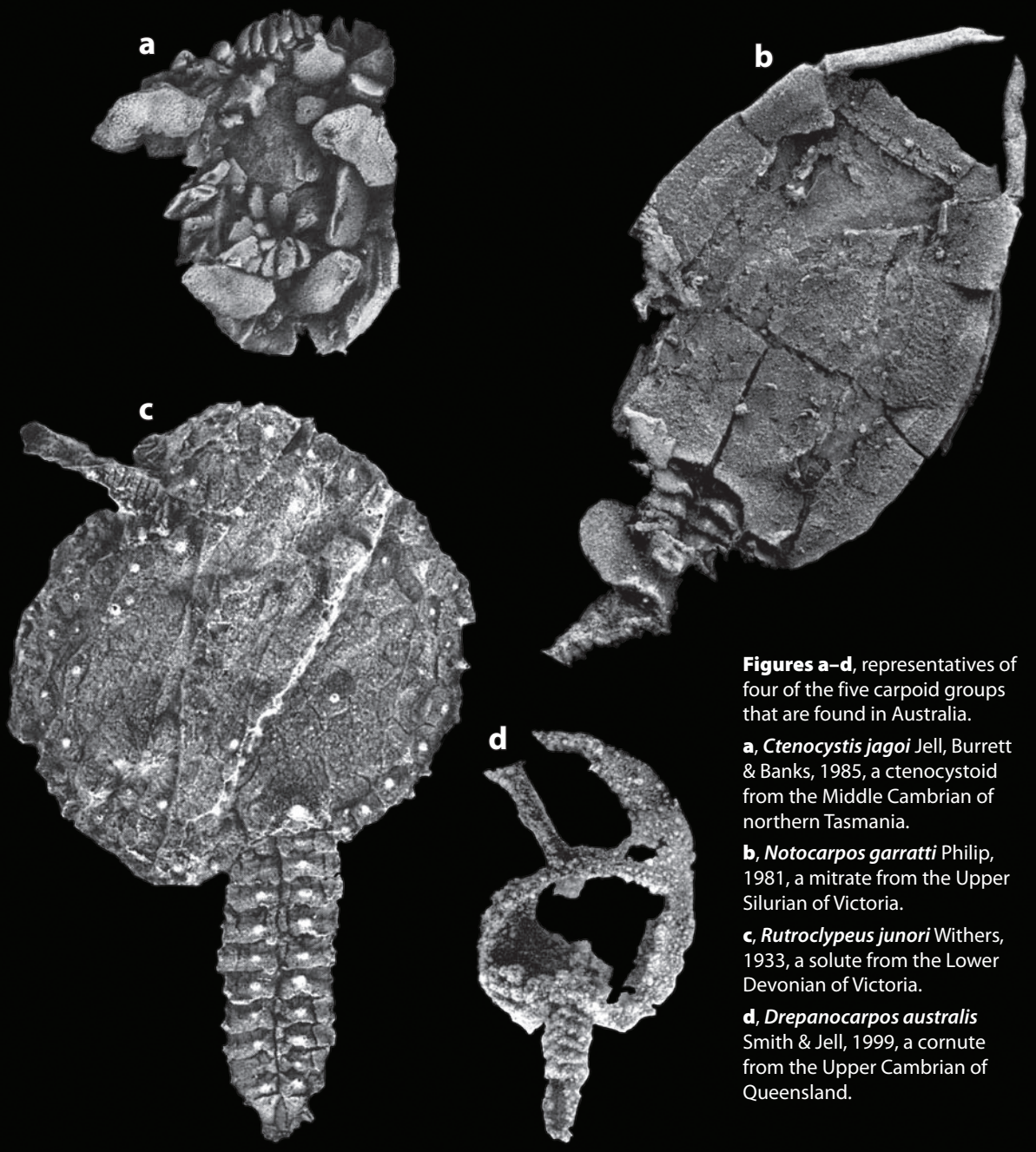


Figure 6.3 Diagrammatic representation of coelom development in echinoderms. [modified from Peterson *et al.* 2000]

Organisation of coeloms in a larval echinoderm and the similar adult hemichordates.

Coelomic architecture in an adult crinoid.

Box 6.1 Carpoids and their importance to echinoderm phylogeny



Figures a–d, representatives of four of the five carpoid groups that are found in Australia.

a, ***Ctenocystis jagoi*** Jell, Burrett & Banks, 1985, a ctenocystoid from the Middle Cambrian of northern Tasmania.

b, ***Notocarpos garratti*** Philip, 1981, a mitrate from the Upper Silurian of Victoria.

c, ***Rutroclypeus junori*** Withers, 1933, a solute from the Lower Devonian of Victoria.

d, ***Drepanocarpos australis*** Smith & Jell, 1999, a cornute from the Upper Cambrian of Queensland.

[a, from Jell *et al*. 1985; b, from Ruta & Jell 1999b; c, from Jell & Holloway 1983; d, from Smith & Jell 1999]

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The term 'carpoid' signifies a small but highly controversial group of fossil animals with a plated body from which one or two appendages project. Carpoids have variously been interpreted as specialist crown-group echinoderms (Sumrall 1997; David *et al*. 2000; Sumrall & Wray 2006), stem-group echinoderms (Ubaghs 1975; Paul & Smith 1984; Smith 2005) or stem-group chordates (Jefferies 1986). Australian representatives include ctenocystoids (Jell *et al*. 1985), solutes (Jell & Holloway 1983), mitrates (Ruta & Jell 1999a, 1999b) and cornutes (Smith & Jell 1999). Few groups can have engendered such heated debate over their interpretation, and there remain fundamental disagreements about what constitutes anterior and posterior, which openings represent mouth and anus, and whether the appendages should be interpreted as attachment stem, feeding arm or motile tail. With such a lack of consensus even about basic aspects of anatomy, one might think these fossils are best passed over without comment. Yet the group may be phylogenetically very important to our understanding of the origins of echinoderms.

Although there are major areas of uncertainty with regard to the interpretation of certain anatomical structures of carpoids, some observations seem indisputable:

(i) Carpoids have a calcitic mesoskeleton composed of stereom, identical to that of echinoderms.

(ii) The hydropore, where recognised, is always single, not paired, and indeed the body form is usually strongly asymmetrical. There is never a trace of tri- or pentaradiate symmetry.

(iii) Most have a complex series of specialised openings on the body (for example, operculum in cinctans, lamelliorgans in cornutes) that are distinct from the mouth and anus, and that are functionally designed as one-way valves allowing water outflow from the interior of the body. In mitrates there are internal bars that closely resemble in structure and position the gill-bars of tunicates (Dominguez *et al*. 2002).

(iv) There is a complex and well-developed internal system of nerves that is arranged bilaterally and centred on the point where the appendage joins the body.

(v) The carpoid appendage is highly muscular, unlike the stalk of modern echinoderms (Clausen & Smith 2005).

(vi) One group of carpoids, the solutes, have both a single ambulacrum and a stem. They attached themselves by their stem and possibly underwent budding. Their stem skeleton is mesodermal, yet it is clear that small juveniles were attached to the stems of adults, without forming abnormal stereom growth (Daley 1996).

The first two features (stereom skeleton and asymmetry of development) are features shared uniquely with echinoderms. The well-developed, endothelial nervous system is also characteristic of crinoids (which similarly can have nerve passageways embedded in the basal skeleton around the chambered organ at the base of the cup) and distinct from the more derived eleutherozoan groups in which the major nerves are ectodermal. Although not all scholars would agree, all evidence seems to point to the one-way valve openings being gill-slits. The most functionally coherent interpretation is that these animals were pharyngeal feeders, drawing water in via the mouth, through an internal filtration system, and expelling the filtrate through the outflow openings in the body wall. If this is correct, then carpoids possessed pharyngeal openings. As pointed out above, this feature is primitive for both deuterostomes as a whole and for the Ambulacraria.

So, carpoids have some, but not all, of the derived character states of echinoderms, yet retain primitive features such as pharyngeal openings and possibly even stem budding. Thus, they are best interpreted as stem group echinoderms that separated after echinoderms and hemichordates had diverged, but before echinoderms lost their pharyngeal openings and acquired pentaradiality (i.e. well before crown-group divergence). Carpoids first appear in the Lower Cambrian (515 mya) at the same time as the first pentaradiate echinoderms, and the groups persist through to the late Carboniferous, about 300 mya.

Echinoderms share four distinctive features that distinguish them as a monophyletic group:

(i) They have a mesoskeleton composed of calcium carbonate constructed in a very distinctive manner; it forms a three-dimensional lattice structure (called stereom).

(ii) They have a complex and highly developed system of enclosed tubes that derives from one of the larval coeloms (the left hydrocoel); this forms the water vascular system and tube feet of the adult (**Figs 6.2, 6.3**).

(iii) In the transformation from larva to adult the originally bilaterally symmetrical larval rudiment undergoes torsion, first becoming asymmetric and later pentaradiate. During this process only the right hydrocoel is lost while the left hydrocoel develops as a crescent and gives rise to lateral outgrowths that go on to form the five radial water canals.

(iv) They do not have pharyngeal gill slits.

The phylogenetic relationships of the echinoderm classes

From both morphological and molecular perspectives extant echinoderms fall into five clearly differentiated and readily distinguished classes (Littlewood *et al*. 1997; Janies 2001; Smith *et al*. 2004). These are the sea lilies and feather stars (Crinoidea), seastars (Asteroidea), brittle stars (Ophiuroidea), sea urchins (Echinoidea) and sea cucumbers (Holothuroidea). A sixth class, sea daisies (Concentricycloidea), was proposed for a deep-water New Zealand echinoderm, *Xyloplax*, but more recent molecular work has shown *Xyloplax* to nest deep within the class Asteroidea (see **Box 6.2**).

Crinoids stand apart from the other four classes in several respects:

(i) They are primitively sessile and attach to the seafloor by a stem or by finger-like cirri (feather stars lack a stem as adults, but they attach as juveniles and shed their stem during development). Other extant echinoderms are free-living, and lack a stem at all stages of their development.

(ii) They have a U-shaped gut with the mouth and anus both opening on the same surface, facing away from the seafloor, unlike (with rare exceptions) other echinoderm groups (**Figs 6.2, 6.3**).

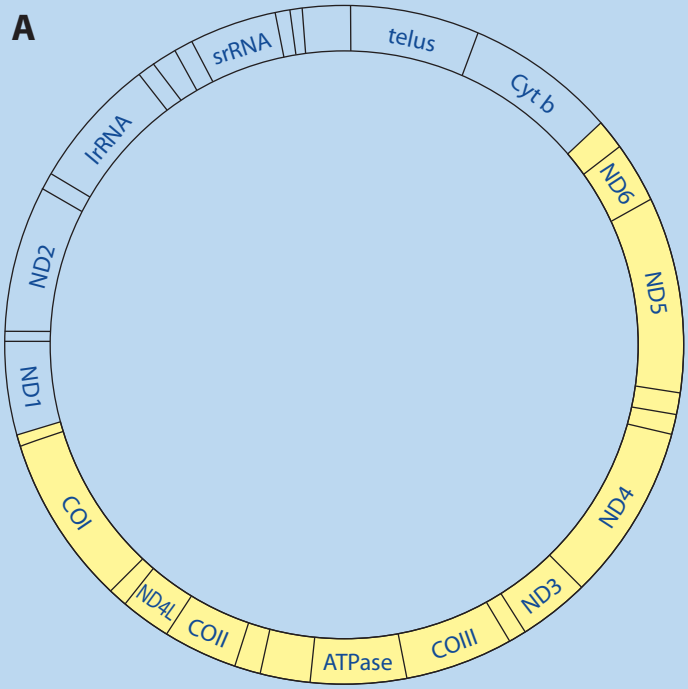
(iii) Their arms are highly developed and branch to form a parabolic fan that is used for suspension feeding. Other suspension-feeding echinoderms do not use this mechanism.

(iv) In other echinoderms with robust skeletons the water vascular system is floored by ambulacral ossicles, but these are absent in crinoids. In crinoids, the skeleton supporting the arms is derived from the aboral skeleton (**Fig. 6.2**), as is evident not only from the elements overlain by the water vascular system (hydrocoel), but also by extensions of the internal body coelom. In asteroids, ophiuroids and echinoids the body coelom and hydrocoel are separated by ossicles of the ambulacral system (Mooi & David 1997, 2000).

(v) The crinoid nervous system is dominated by the hyponeural element. In other echinoderms it is the ectoneural element that dominates (Heinzeller & Welsch 2001).

(vi) Echinoids, asteroids, ophiuroids and holothuroids all share a calcified, scroll-like stone canal and madreporite, at least primitively. Crinoids lack a madreporite; instead their tegmen is perforated by minute pores, known as hydropores (or madreporic canals), which serve the same function (**Figs 6.3, 7.7**).

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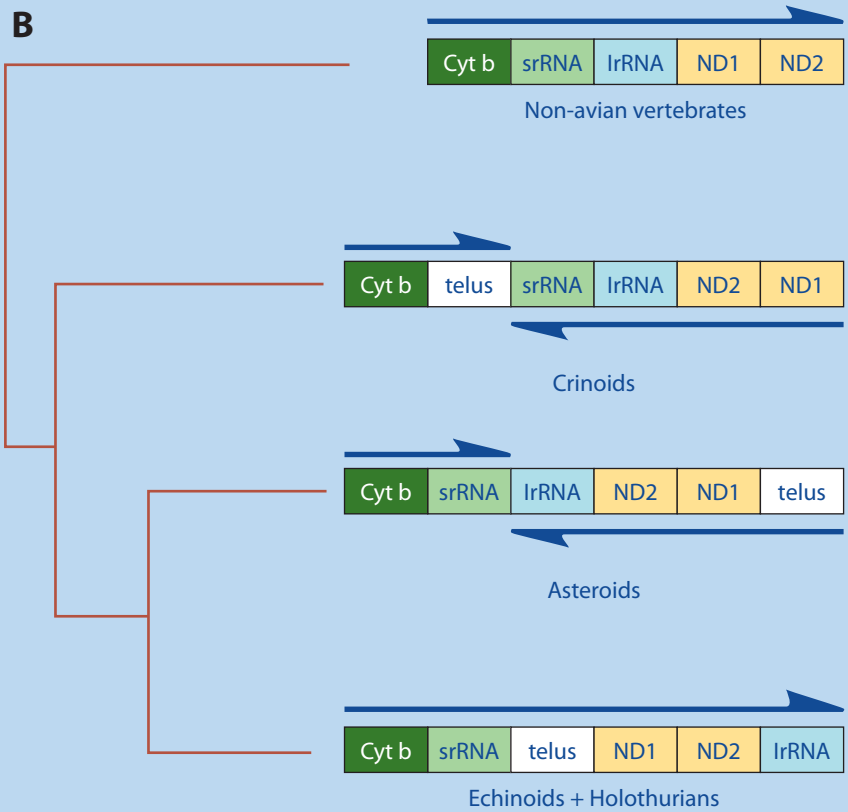


Figure 6.4 Mitochondrial gene order in echinoderms.

A, mitochondrial genome map of the crinoid ***Florometra serratissima*** (Antedonidae): circular DNA of 16,005 base pairs. The white zone denotes the genes from *Cyt b* and *ND1*, the more variable mitochondrial genome segments which are further illustrated in **B**. The gene order encompassing *COI* to *ND6* is conserved across four of the five echinoderm classes, Ophiuroidea being the exception.

B, mitochondrial gene order arrangements between *Cyt b* and *COI* of basic echinoid+holothurian, asteroid and crinoid patterns and a non-avian vertebrate outgroup pattern. Arrows indicate transcription polarity.

[after Smith *et al*. 2004 following Scouras & Smith 2001]

Box 6.2 Sea daisies

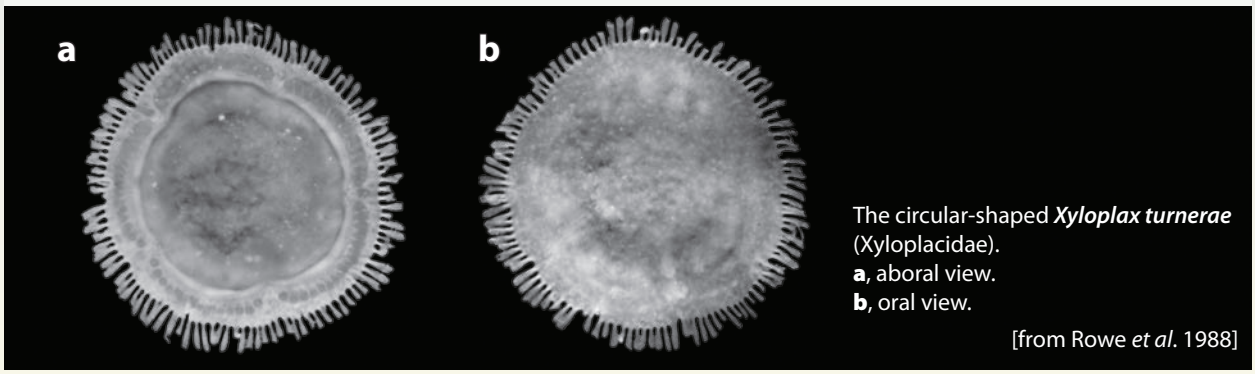
Timothy D. O'Hara

In 1983, some tiny and unusually discoid, deepsea echinoderms were found by marine biologists in deep water off New Zealand. Their unique morphology was readily apparent, and within three years of being discovered they were described in the scientific literature as belonging to an entirely new class of Echinodermata, the Concentricycloidea or sea daises, the first new class of living echinoderms to be described since 1821 (Baker *et al*. 1986). The new species, no more than 9 mm in diameter, was named *Xyloplax medusiformis*. Subsequently two more species have been described from sunken wood from abyssal depths off the Bahamas (*X. turnerae* by Rowe *et al*. 1988; **Figs a,b**) and from the north-eastern Pacific Ocean (*X. janetae* by Mah 2006a).

The species of *Xyloplax* are certainly unusual (**Fig. 8.44**). They have no arms, and two of the species, *X. medusiformis* and *X. janetae*, have no stomach or gut, only a thin velum covering the skeleton on the ventral surface, which can presumably digest nutrients directly from the environment. The shape and flexibility of *X. medusiformis* indicates that it may be able to swim like a jelly-fish, pulsating from one food source to another. Genital organs appear to be used for copulation, and the resulting juveniles are brooded within the gonads. But it was the internal anatomy of the sea daisies that at first seemed to be most revolutionary. The mouth frame appeared to be derived from the usual asteroid ambulacral ossicles, and was surrounded by two water vascular rings (all other echinoderms have only one) and only one ring of tube feet. The double ring appears to have been derived from the splitting of the radial longitudinal vessels (see **Chapter 1**).

However, not all researchers were happy with the conclusion that sea daises represented a new class of Echinodermata. Initial cladistic analyses suggested they were specialised asteroids, perhaps related to the equally aberrant deepsea Caymanostellidae (Smith 1988a). Evidence to support this alternative view has continued to mount. The unusual oral frame was eventually reinterpreted as constructed from modified oral (not ambulacral) plates (Mooi *et al*. 1998). Questions have also been raised about the true nature of the inner of the two water vascular rings, suggesting that it may be part of the haemal system (Janies & Mooi 1999). Janies *et al*. (2011) determined by microscopic examination of brooded juveniles of *X. janetae* that early development of the water-vascular system is consistent with that found in other asteroids, and in the same work gave molecular evidence that support the view of Janies & Mooi (1999) that *Xyloplax* is an asteroid.

Despite disagreements over just how aberrant these animals are, their discovery has highlighted our poor understanding of deepsea environments and the exciting species they contain.



The circular-shaped ***Xyloplax turnerae*** (Xyloplacidae).
a, aboral view.
b, oral view.
[from Rowe *et al*. 1988]

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These differences imply that crinoids represent the most basal of extant echinoderms, and indeed this is supported by all published molecular analyses (Mallatt & Winchell 2007; Swalla & Smith 2008; Janies *et al.* 2011; O'Hara *et al.* 2014b). Thus, there is sound support for dividing echinoderms into two major clades, the Pelmatozoa, for crinoids and their fossil relatives, and the Eleutherozoa, for the remaining four classes.

Eleutherozoa traditionally have been divided into two groups based on overall body form: the Asterozoa, for the star-shaped asteroids and ophiuroids, and the Echinozoa for the basically globular echinoids and holothuroids (Fell 1967). However, hypotheses of relationships between these four classes have been controversial. Firstly, seastars with their extensive aboral plated surfaces are closer to the primitive echinoderm body plan than echinoids. In echinoids the homologous aboral surface is reduced to just the genital and periproctal plates (Smith 1984b; Mooi & David 1996; **Fig. 6.2**). Consequently, it is possible that the grouping of asteroids with ophiuroids could be based on a shared primitive character state (or symplesiomorphy). Secondly, the highly reduced and modified holothuroid skeleton has made it difficult to establish unambiguous skeletal homologies with other classes.

Some researchers have considered the Asterozoa to be a paraphyletic grouping, with brittlestars more closely related to the Echinozoa (echinoids and holothuroids) than to seastars (Smith 1984a). This was based on the similarity of larval form, jaw apparatus construction, internal coelom arrangement, and the enclosure of the radial nerve and water vessel in ophiuroids and echinoids. Analyses of morphological data supported this view (Littlewood *et al.* 1997; Janies 2001; Smith *et al.* 2004) as did a detailed analysis of the echinoderm nervous system (Heinzeller & Welsch 2001). Ophiuroids, echinoids and holothuroids all share the derived condition of having neurulated radial nerves. In all three taxa the radial nerve lies fully enclosed within the mesoderm with an overlying epineural sinus. Since both asteroids and crinoids have an external nerve that remains un-neurulated, this strongly implies sister-group relationships of ophiuroids, echinoids and holothuroids.

An alternative view is that Asterozoa are monophyletic and that asteroids and ophiuroids pair together (David & Mooi 1996, 1999; Mooi & David 1997; Sumrall 1997). Just two morphological synapomorphies support this grouping: the presence of a saccate gut, and the presence of a system of adambulacral ossicles. However, strong support for this grouping came initially from mitochondrial genome order (Marshall 1994).

Mitochondrial gene order seemed to provide a clear solution to relationships (**Fig. 6.4**). A 4.6 kilobase section of the echinoderm mitochondrial genome was found to be inverted in asteroids and ophiuroids compared to that in echinoids and holothuroids (Smith *et al.* 1993; **Fig. 6.4B**). Furthermore, it was the echinoid-holothuroid arrangement that was closest to that of the gene order seen in chordates. The conclusion drawn naturally was that the asteroid-ophiuroid arrangement represents an evolutionary novelty and identifies the pair as a monophyletic clade (Mooi & David 1997). At that time the order of genes in crinoid mitochondria was unknown, but recent research has shown that the story is not so simple (Scouras & Smith 2001; Perseke *et al.* 2008). The mitochondrial gene order in crinoids is also partially inverted, like that of asteroids and ophiuroids. In other aspects the ophiuroid mitochondrial gene order is very different from that of other echinoderms. So, unfortunately, mitochondrial gene order does not provide a clear resolution of the relationship of the eleutherozoan classes.

Ribosomal genes have also been used to try to resolve the relationships of echinoderm classes (Littlewood *et al.* 1997; Janies 2001; Smith *et al.* 2004). Molecular data has been analysed on its own and in combination with morphological data. These studies find strong molecular support for a pairing of echinoids and holothuroids, even though this is only weakly supported by the limited morphological data. The key question of how ophiuroids are related has, however, proved difficult to resolve because reconstructing relationships of groups that radiated rapidly deep in geological time can be particularly difficult (Pisani *et al.* 2012). Weak evidence in favour of ophiuroids grouping either with asteroids or with echinoids plus holothuroids was found, depending upon the precise details of the phylogenetic technique applied to tree-building.

The most recent genetic data, derived from hundreds of nuclear genes, strongly support the original palaeontological view that the crinoids are a sister group to the other four classes, that asteroids are sister to the ophiuroids, and that holothurians are sister to the echinoids (Cannon *et al.* 2014; O'Hara *et al.* 2014b; Telford *et al.* 2014; see **Box 6.3**).

A brief overview of the fossil record of echinoderms with reference to Australia

Australia has a rich fossil record for echinoderms that spans their entire history, from the Cambrian to the Pleistocene; see **Figure 6.5** for examples of fossils from the Palaeozoic. From the late pre-Cambrian Ediacaran fauna of the Flinders Ranges one small disc-like organism called *Arkarua* has been described as an echinoderm (Gehling 1987). Although *Arkarua* shows an apparent five-fold symmetry, it lacks a skeleton of stereom and shows no definitive evidence for having had a water vascular system. Its position as an echinoderm is thus highly questionable.

The skeletal record of echinoderms begins in the Lower Cambrian about 540 million years ago. From the start, carpoids (and very late stem group radiate echinoderms such as the triradiate helicoplacoids) (Dornbos & Bottjer 2000) are accompanied by clearly pentaradiate primitive pelmatozoans and eleutherozoans, showing that the basal divergences must already have taken place before the appearance of the oldest fossils. In northern Queensland, Tasmania and New South Wales there are good faunas of Middle and Late Cambrian age that show an increasing diversity of echinoderms through this interval. Particularly well represented are the edrioasteroids. These are discoidal to subglobular forms that lived mouth-upwards and attached to firm substrates, like crinoids, but that lacked free arms (Smith & Jell 1990; **Fig. 6.5B**). Edrioasteroids had true ambulacral plates that formed an integral part of the body wall as in asteroids and echinoids, but their aboral plating was reduced to a small aboral attachment pad.

The first primitive representatives of modern classes appear in the fossil record in the Early Ordovician (*ca.* 495 mya). At the same time we find the earliest true crinoids, and the earliest asteroids and ophiuroids. Sea urchins appeared slightly later, in the Middle Ordovician (*ca.* 450 mya; Smith & Savill 2002), along with the first holothuroids (Reich 2001). However, these early records of holothuroids are based on isolated body-wall spicules; the first undisputed holothuroid body fossil comes from the Pridolian of Victoria and is Late Silurian in age (*ca.* 420 mya). Lower Palaeozoic faunas tend to be dominated by crinoids (**Fig. 6.5C**) and their relatives the cystoids, both of which were stalked. Cystoids resemble crinoids in many ways: both have skeletal outgrowths bearing their water vascular system and forming a filtration fan, but the detailed construction of the arms differs. Crinoid material, in the form of disarticulated disc-shaped elements of the stalk, cup and arms, can form a significant constituent of many Devonian limestones in eastern Australia, confirming that they were a major component of the marine benthic fauna. Articulated skeletons are more restricted in occurrence, but support the view that the pelmatozoan fauna was highly diverse at this time. These faunas were extensively described and monographed by Jell *et al.* (1988), Jell (1999) and Jell & Jell (1999).

Because the skeleton of asteroids and ophiuroids is composed of ossicles embedded in soft tissue it tends to disintegrate rapidly upon death. Consequently, it is only when there are special sedimentary conditions (for example, where normal bacterial decomposition has not occurred) that articulated skeletons of these groups become preserved in the rock record. Therefore, just a few such special deposits (known as 'Lagerstatten'), yielding fossil seastars and brittle stars exist. One important Lagerstatte, in the Late Silurian of the Melbourne Basin, has yielded a diverse assemblage of asterozoans (Withers & Keble 1934a; Jell & Holloway 1983). Even rarer are Palaeozoic sea urchins, which, unlike their modern relatives, have a membrane-embedded skeleton; only the occasional isolated specimen has been reported from Australia (Brown 1967).

One particularly noteworthy group of extinct echinoderms are the ophiocistioids, an eleutherozoan group intermediate between holothuroids and echinoids. Ophiocistioids were subglobular animals with large, plated tube feet, an internal jaw apparatus closely resembling the Aristotle's lantern of echinoids, and a triple-column ambulacral structure. The ophiocistioid *Gillocystis* (**Fig. 6.5D**) is found in the early Devonian of Victoria (*ca.* 400 mya) (Jell 1983). Ophiocistioids first appear in the Middle Ordovician

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Box 6.3 Recent results from the phylogenomic revolution

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Several phylogenomic papers on echinoderms have now taken advantage of the latest next-generation sequencing technologies — see Cannon *et al*. 2014; O'Hara *et al*. 2014b; Telford *et al*. 2014. These new methods can sequence millions of short DNA sequences simultaneously, facilitating the creation of robust phylogenetic trees from hundreds of genes across hundreds of species. These publications will revolutionise our understanding of the relationships between and within the echinoderm classes.

Although, sequencing technologies are becoming much cheaper, it is still very expensive to sequence and annotate (work out the function of each section of DNA) a whole genome from scratch. Consequently, various technologies are used to target specific sections of the genome. One useful method is to target messenger-RNA; effectively this focuses the sequencing effort on genes that code for proteins that were being expressed by the animal when the tissue sample was taken. Complementary strands of DNA (cDNA) are created from RNA fragments and sequenced. A collection of sequenced cDNA strands is called a transcriptome after 'transcription', the first step in gene expression.

The first three phylogenomic papers on echinoderms (Cannon *et al*. 2014; O'Hara *et al*. 2014b; Telford *et al*. 2014) all have used transcriptome data to investigate the relationships between the classes. All unequivocally support the grouping of asteroids and ophiuroids (Asterozoa) and the grouping of echinoids and holothurians (Echinozoa). The hypotheses that the ophiuroids were more closely related to the echinoids and holothurians than the asteroids received no support. Thus the latest technology supports the old palaeontological view of the class relationships, suggesting that the pluteus larva present in both ophiuroids and echinoids evolved independently, and refuting conclusions based on early genetic data (which in retrospect had far too little information to infer relationships going back almost 500 million years).

and, by the Early Devonian, the body wall skeleton of some groups was reduced to such an extent that it was composed of just microscopic plates and elements. In these taxa, the wheel-shaped body elements are indistinguishable from those of later holothuroids.

Stalked crinoids flourished through the Carboniferous and Permian, and are represented in Australia by scattered records across the continent (Webster 1987; Webster & Jell 1999a, 1999b). The Australian fauna at that time shows strongest affinities with faunas described from Timor and North America. It is in the Permian that we begin to see the first representatives of modern (crown-group) echinoderms. Thus, Australia has some of the earliest isocrinoids, a group of modern stalked crinoids, today confined to relatively deep-water settings (Webster & Jell 1999b). Also in the Permian we

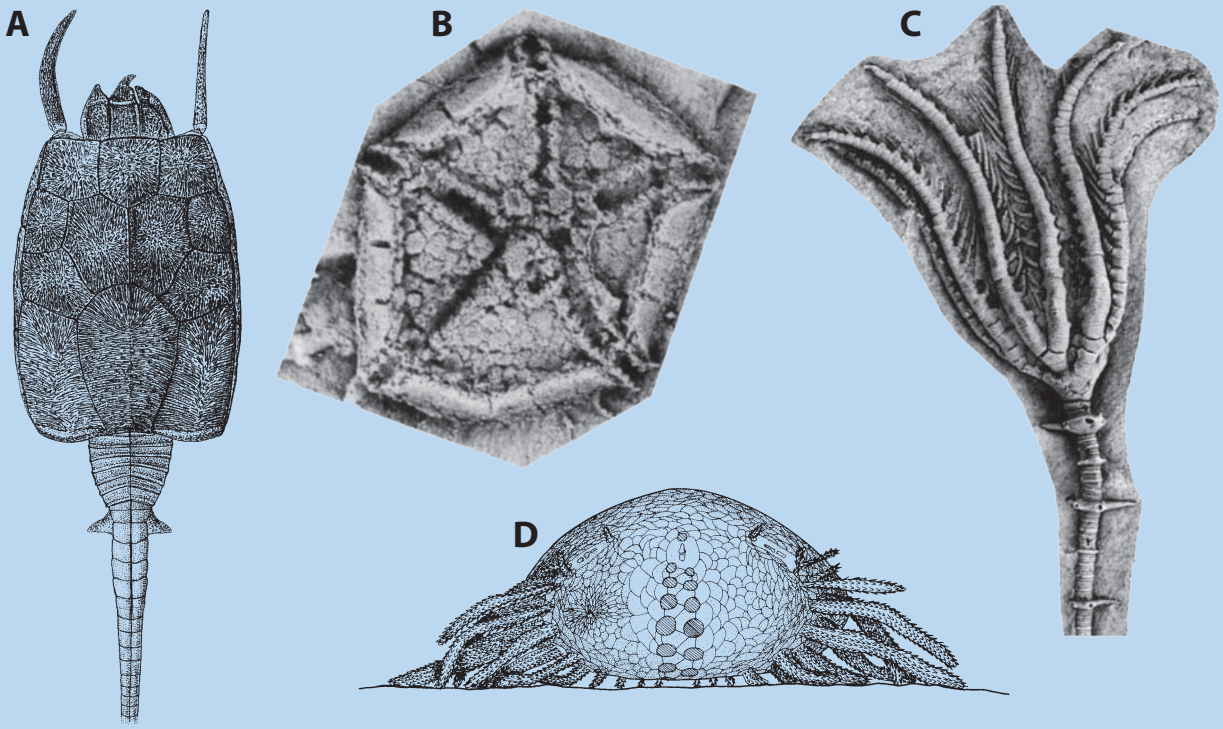


Figure 6.5 Some important echinoderm groups from the Palaeozoic of Australia.

A, ***Protocytidium elliottae*** Ruta & Jell, 1999a, a mitrate carpoid from the Ordovician of central Victoria.

B, ***Cambraster tastudorum*** Jell, Burrett & Banks, 1985, an edrioasteroid from the Middle Cambrian of northern Tasmania.

C, ***Dendrocrinus saundersi*** Jell & Holloway, 1983, from the Late Silurian-Early Devonian of Victoria, one of the many fossil crinoids from the Lower Palaeozoic of Australia.

D, ***Gillocystis polypoda*** Jell, 1983, an ophiocistioid from the Early Devonian of Victoria.

[A, from Ruta & Jell 1999a; B, from Jell *et al*. 1985; C, from Jell & Holloway 1983; D, from Jell 1983]

find the first relatively modern-looking asteroids, the Monasteridae (Kesling 1969); their greatest abundance is in the Permian of Western Australia.

Worldwide Early Triassic faunas are comparatively rare, and the composition of marine communities had changed significantly by the start of the Jurassic when fossil echinoderms once again become common. None of the cystoid groups survived into the Triassic and, although crinoids remained important, only one of the four major Palaeozoic groups survived into the Mesozoic. A similar bottleneck appears to have affected asteroids, ophiuroids and echinoids in the Late Permian and Early Triassic, with only one or two lineages surviving to give rise to the modern fauna. (The record of fossil holothuroids is too poor to be confident of evolutionary patterns.) It is from this point onwards that echinoids become a much more obvious component of marine benthic communities. To a large extent this probably reflects a change in preservation potential, since it coincides with sea urchins evolving a rigid test, a factor more conducive to fossilisation.

During the Jurassic the major lineages of modern asteroids, ophiuroids and echinoids became established. At this time the first irregular echinoids appear and the five major extant asteroid groups also make their first appearance. Unfortunately, there is only a very sparse record of echinoderms from this time interval in Australia (Rose & Olver 1980).

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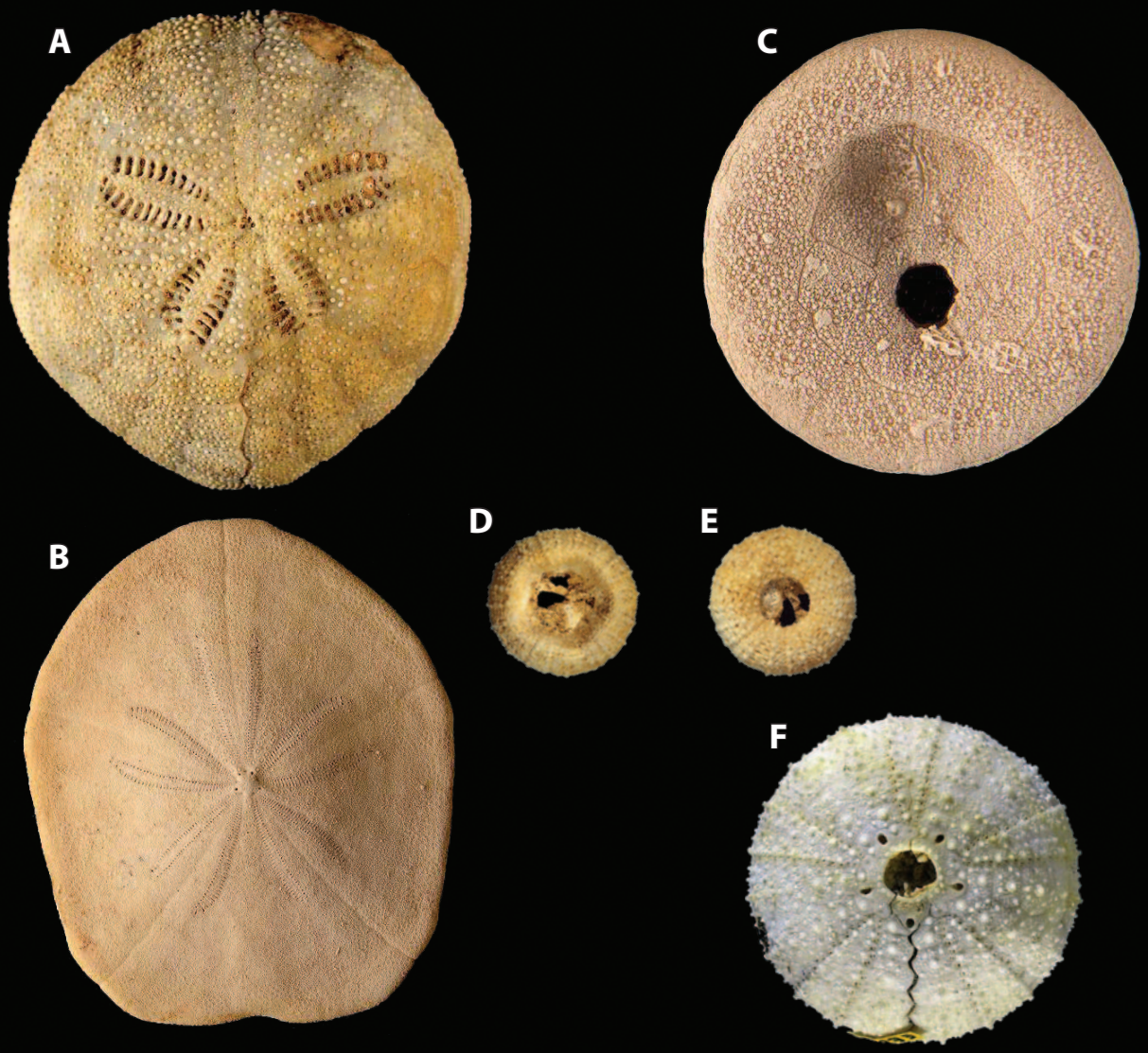


Figure 6.6 Echinoids from the Tertiary of Australia.

A, ***Spatagobrissus laubei*** (Duncan, 1877), a heart urchin of the order Spatangoida, apical view; Port Campbell Limestone Formation, Miocene, Port Campbell Township, Victoria, Australia. Test length 38 mm. (specimen NHM E7770)

B, ***Monostychia australis*** Laube, 1869, a sand dollar of the order Clypeasteroida, apical view; Late Miocene, base of Morgan Limestone, Blanchetown, Murray River, South Australia. Test length 50 mm. (specimen NHM EE606)

C, ***Willungaster scutellaris*** Phillip & Foster, 1971, a sand dollar of the order Clypeasteroida, oral view; Lower Miocene, Longfordian, Port Vincent Limestone, Yorke Peninsula, South Australia; the large depression in front of the peristome is the brood pouch. Test length 10.3 mm. (specimen NHM E76219)

D, **E**, ***Paradoxechinus novus*** Laube, 1869, a regular echinoid of the order Camarodonta: **D**, apical view; **E**, oral view; Mannum Formation, Miocene, Murray River, South Australia; the upper surface is deeply depressed around the apical disc forming a brood pouch. Test diameter 10 mm. (specimen NHM EE1074)

F, ***Cryptechinus humilior*** (Bittner, 1892), a regular echinoid of the order Camarodonta, oral view; Late Miocene, Morgan Limestone, Blanchetown, South Australia. Test diameter 23 mm. (specimen NHM EE584)

[from Smith & Kroh 2011]

In contrast, the record for the most recent 65 million years, from the Palaeocene onwards, is outstanding, with large and important echinoderm faunas reported from all time intervals. By now stalked crinoids had become rare in shelf environments, and they had been replaced by feather stars which were locally both diverse and abundant, as in the Miocene of the Murray River Basin. However, there are no Lagerstatten, and asteroid and ophiuroid remains of this period are almost entirely fragmentary. Sand dollars make their first appearance in the Eocene (about 50–55 mya), and forms such as *Monostychia* (**Fig. 6.6B**) and *Clypeaster* became locally common. At the same time, a major diversification of heart urchins was underway, with many endemic taxa evolving in Australia (**Fig. 6.6A**). Amongst the commonest of fossils are the heart urchin *Lovenia*, and regular echinoids (**Fig. 6.6D–F**) are also common at this time. The extensive fossil-echinoid literature was monographed by Holmes (1993).

A noteworthy feature of the Australian fauna in the early Tertiary is the preponderance of marsupiate echinoid species (Philip & Foster 1971; McNamara 1994a; **Fig. 6.6C–E**). The greatest diversity of brooding echinoids (forms with lecithotrophic development) occurs in the Early Tertiary. In the Late Oligocene (25 mya) up to 15% of the total echinoid fauna are brooders, but by the Pliocene (2 mya) there were none left living in Australia. Brooding is most frequently found at high latitudes (McNamara 1994a). At the start of the Eocene, Australia lay at high latitude and was connected to Antarctica. Tectonic activity resulted in Australia splitting from Antarctica during the Eocene, and the continent started to move rapidly northwards to its present day latitude. This decline in brooding echinoids in Australia fits very well with the northward palaeogeographic migration of the Australian continent over time.

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Part 2:
Echinoderm Diversity



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7: Class CRINOIDEA

Charles G. Messing, Anne K. Hoggett, Lyle L. Vail, Greg W. Rouse and Frank W.E. Rowe

General introduction

Crinoids, commonly known as sea lilies and feather stars, have five rays, usually branched and featherlike, that arise from a cup-like central body (theca). Unlike other living echinoderms, the body in most crinoids anchors to the seafloor via a stalk and orientates with the oral surface away from the substrate. Feather stars are those crinoids that detach from a postlarval stalk and take up a free existence (**Figs 1.1A, 7.1, 7.2**), but they do not represent a monophyletic group (Hemery *et al.* 2013; Rouse *et al.* 2013). By contrast, some cyrtocrinids have lost the stalk completely and attach via the stump-like base of the theca (**Figs 7.3E, 7.15C,D**). **Figure 7.3** illustrates the breadth of form among living crinoids. All living crinoids are epibenthic suspension feeders.

The theca consists of a skeletal calyx that encloses or supports the central visceral mass, and an overlying, occasionally calcified, membrane, the tegmen, that bears the mouth, anus and hydropores, and defines the oral surface. Five ambulacral food-collecting grooves radiate from the central mouth across the tegmen onto the rays and their branches (**Fig. 7.4**). Simple side branches (pinnules) that alternate on opposite sides along the rays provide the primary food-collecting surface and give the rays their feather-like appearance (**Figs 1.7, 7.1**). Specialised genital pinnules bear the gonads (**Figs 3.2D, 7.5**), and some pinnules near the bases of the rays (oral pinnules) may be modified with possible roles in protecting (**Fig. 7.6A**) or cleaning (**Fig. 7.6B**) the tegmen rather than contributing to



Figure 7.2 Two families of feather stars are endemic to Australia: Ptilometridae and Aporometridae. Both occur along the southern coast, but ***Ptilometra australis*** reaches southern Queensland. Like other species in its family, ***Aporometra wilsoni*** (Aporometridae) (above) is an ovoviviparous brooder that retains developing embryos inside the maternal genital pinnules (**Box 7.2**). This small species (ray length to 30 mm) has been recorded from Victoria and South Australia, and clings to brown algae, including ***Cystophora*** and ***Sargassum*** species. It completes its entire life cycle in one year.

[G.W.Rouse]

Figure 7.1 Almost a quarter of all living crinoid species occur in Australian seas. Dozens dwell on shallow tropical reefs, although most are either partly or completely hidden during the day. ***Anneissia bennetti*** (formerly called ***Oxycomanthus bennetti***; Comatulidae), which appears in a wide range of brilliant colours, is one of the few species that clings completely in the open both day and night, usually on prominent perches such as this barrel sponge, ***Xestospongia testudinaria***. This species may have 50 or more feathery arms that reach up to 200 mm in length.

[G.Bell]

food capture. Unlike most seastars, urchins and sea cucumbers, crinoid tube feet (podia) lack a terminal sucker. Instead, they are tiny, less than 1 mm long, finger-like, and arranged in triplets of a long primary, medium secondary, and short tertiary tube foot along the ambulacra (**Fig. 1.19**).

The water vascular system consists of a circum-oesophageal ring canal from which five radial canals arise, paralleling the ambulacra along the ray branches to their tips (**Fig. 7.7**). Structures aligned with these canals and their surrounding skeleton are considered radial; those between are interradial. The stone canal ends blindly with no external madreporite; instead, numerous ciliated funnels (madreporic canals or hydropores) pierce the tegmen, establishing a connection between the coelom and the external environment. The coelom is reduced, subdivided, and envelops the coiled digestive tract. A well-developed haemal system consists of numerous interconnecting lacunae that, according to Heinzeller & Welsch (1994), are chiefly limited by basement membranes of adjacent epithelia, but sometimes pass uninterrupted into adjacent connective tissue. No true heart exists, and the system likely does not carry out typical haemal functions. Similarly, the axial gland contains glandular tubes not found in other echinoderms. The spongy organ lies oral of the axial gland and consists chiefly of haemal tubes lined with coelomic epithelia (**Fig. 7.7**).

Unlike the arrangement in other living echinoderms, the primary component of the crinoid nervous system is aboral, with a large ganglion (aboral nerve mass, or centre) within the basal ring in stalked forms and within the centrodorsal in feather stars (Hyman 1955; Heinzeller & Welsch 1994; Heinzeller 1998; Bohn & Heinzeller 1999; Nakano *et al*. 2009). The hyponeural system is continuous with and part of the aboral system. The ectoneural system is relatively inconspicuous and is 'integrated in the base of the food collecting epithelium' (Bohn & Heinzeller 1999:241; **Fig. 7.7**).

An extensive mesodermal endoskeleton, consisting chiefly of articulated series of calcareous pieces called ossicles (**Fig. 7.8**), largely determines morphology and forms the basis of much of crinoid taxonomy. Each part of the body is composed of a different type of ossicle, *viz*., the stalk (or column) of columnals, the rays of brachials, pinnules of pinnulars, and hook-like anchoring cirri of cirrals. The calyx consists of a ring of five interradially orientated basal ossicles (which may be modified, reduced or lost) and five (rarely ten) radial ossicles, which orientate with the radial water vascular canals and from which the rays arise (**Figs 7.9, 7.10**). Some sea lilies retain a ring of five small, radially-orientated infrabasal ossicles hidden at the base of the calyx, but these are absent in most living species. Rays may remain undivided (**Figs 7.9A, 7.34**) or branch at ossicles called axils (or axillaries) (**Figs 7.9C, 7.10**). An arm is the unbranched series of brachials following the last axil (although the term is sometimes used synonymously with ray, especially by palaeontologists) (**Fig. 7.3C**).

Stalked crinoids anchor to the seafloor by a terminal attachment disc, a radix of segmented rootlets, or prehensile cirri that arise at intervals along the stalk (**Fig. 7.3**). After losing the postlarval stalk, feather stars cling to the seafloor or to sessile macrobenthos by means of a ring or cluster of cirri arising from a large, central, aboral ossicle, the centrodorsal (**Figs 7.3C, 7.8A, 7.10**), although a few species lack cirri and rest on the seafloor on their rays (**Figs 7.11B, 7.19F**). The centrodorsal ranges from disc-like to conical, and may represent several fused stalk ossicles. The term centrodorsal derives from an older designation of the mouth-bearing surface as ventral and the opposite surface as dorsal, in agreement with most other living echinoderms. However, because crinoids generally live with the mouth uppermost, functional and anatomical landmarks of orientation conflict. As a result, we use aboral and oral (or adoral: toward the mouth) instead of dorsal and ventral, respectively. In the cyrtocrinids *Holopus* and *Cyathidium* the stalk is absent, and the calyx cements directly to the substrate (**Figs 7.3E, 7.15**).

In addition to aboral and oral, two other pairs of terms describe the location of structures on a crinoid. Distal and proximal indicate a direction or position away from versus toward the central aboral/oral axis, that is, toward the tip versus the base of a ray, arm, cirrus or pinnule, or toward the anchoring versus upper end of the stalk (**Fig. 7.3D**). For example, proximal pinnules arise near the bases of the rays; the attachment disc is on the distal end of the stalk. Interior versus exterior refer to positions toward or away from the midline of a ray or ray branch drawn from the preceding fork (**Fig. 7.10**).

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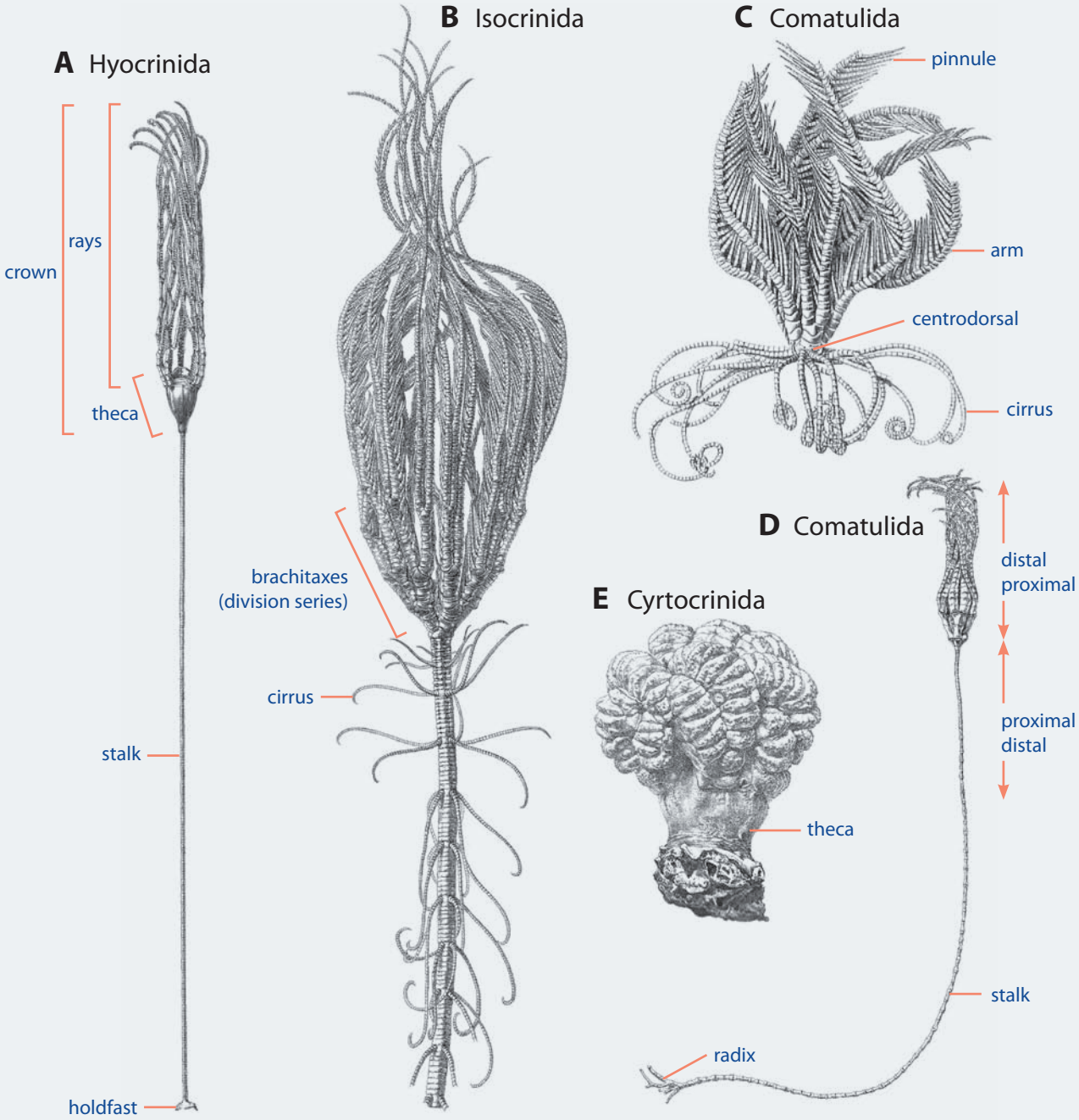


Figure 7.3 Diversity of form in living crinoids.

A, order Hyocrinida. ***Hyocrinus bethellianus***. The theca label overlaps the base of the rays because it includes the tegmen atop the calyx. The distal stalk has been estimated.

B, order Isocrinida. ***Metacrinus varians***.

C, order Comatulida. ***Ptilometra macronema***.

D, order Comatulida. ***Bathycrinus aldrichianus***.

E, order Cyrtocrinida. ***Holopus rangii***.

(A,D, SW Indian; B, W Pacific; C, S and W Australia; E, W Atlantic[1])

[A,B, modified from P.H.Carpenter 1884; C, from P.H.Carpenter 1888; D,E, from P.H.Carpenter 1884]

1 where locations are provided in figure captions they refer to the site(s) at which the photographic image was taken or the specimen collected for the line drawings.



Figure 7.4 Oral surface (tegmen) of a feather star, ***Dichrometra brachypecha*** (Mariametridae), showing the ambulacral groove trunks converging on the central mouth, with the anal papilla displaced to one side in an interambulacral area. (W Pacific)

[C.G.Messing]

Skeletal features—the structure and arrangement of ossicles, and the various articulations that join them—have contributed importantly to understanding crinoid taxonomy, phylogeny and ecology. Successive ossicles are joined by ligaments or combinations of muscles and ligaments that anchor in depressions called fossae on the articular faces of the ossicles. In many cases, the fine skeletal structure, or stereom, differs between fossae anchoring ligaments and muscles (Meyer *et al.* 1978a). Living crinoids have four basic articulations. A synarthry is a general term for a ray or stalk articulation crossed in any direction by a fulcral ridge. Muscular synarthries between ray ossicles are the most numerous and bear pairs of muscle bundles and

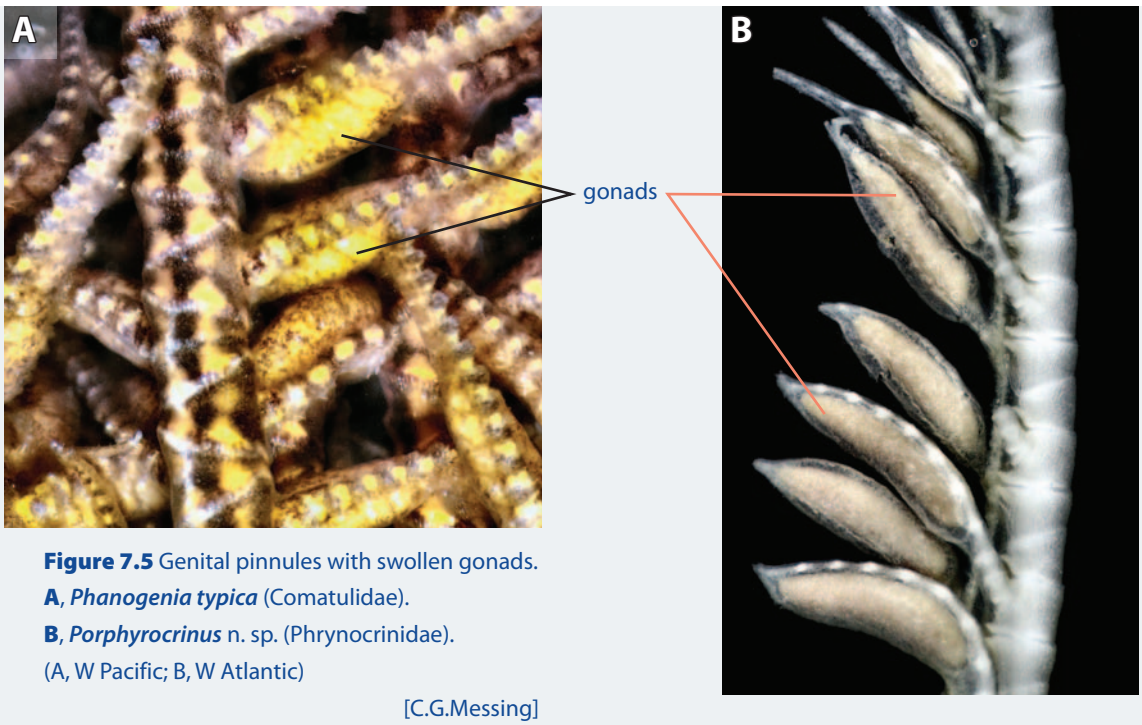


Figure 7.5 Genital pinnules with swollen gonads.
A, ***Phanogenia typica*** (Comatulidae).
B, ***Porphyrocrinus*** n. sp. (Phrynocrinidae).
(A, W Pacific; B, W Atlantic)

[C.G.Messing]

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mutable collagenous ligaments on the ambulacral side of a usually diagonal fulcral ridge, and a large ligament on the other side (**Figs 7.8D, 7.10**). Contraction of the muscles curls or bends the arms inward, collapsing the feeding posture when, for example, the current is perhaps either too weak or too strong. When the muscles relax, the ligaments can become rigid, allowing the arms to maintain an extended feeding posture without expending energy. In ligamentary synarthries, found in some stalks and the bases of the rays, a pair of large ligaments flanks a fulcral ridge, permitting limited side-to-side flexibility (**Figs 7.8C, 7.10**). A symmorphy is a modified ligamentary synarthry in which one facet is deeply concave and the other convex (**Fig. 7.9B**). The three other articulation types contain only ligaments. A synostosis, which appears externally as a straight or gently curved suture between stalk ossicles or the proximal ossicles of a ray, is a rigid joint; its articular faces are smooth and united by relatively few, short ligament fibres. In a syzygy, which is also rigid, radiating ridges and grooves on the two joint faces appose each other so that the external suture resembles a perforated line (**Figs 7.8E, 7.10**). They occur in the rays of most members of order Comatulida. In a symplexy, found only between columnals in some stalked crinoids, ridges (culmina) on one joint face interlock with corresponding grooves (crenellae) on the apposed face, and the articulation appears externally as a wavy suture (**Fig. 7.8F**). Ligamentary articulations, chiefly between columnals or proximal ray ossicles, may be modified during development or with growth into several secondary forms that may converge on other articular types, for example a symplexy into a synostosis, or a ligamentary synarthry into a more rigid cryptosynarthry (**Fig. 7.10**) or cryptosyzygy. Detailed treatments of articulations and their variations with ontogeny and evolution can be found in Roux (1974, 1980), Meyer *et al*. (1978a), Messing *et al*. (2000), Roux *et al*. (2002), Améziane & Roux (2005), Hess & Messing (2011a) and Roux & Lambert (2011).

Diagnostic components of ray branching patterns, which have been taxonomically important at familial and generic levels, may include the number of branches and the number of ossicles and their articulations between successive brachitaxes—the series of ossicles following one axil and including the next (or following

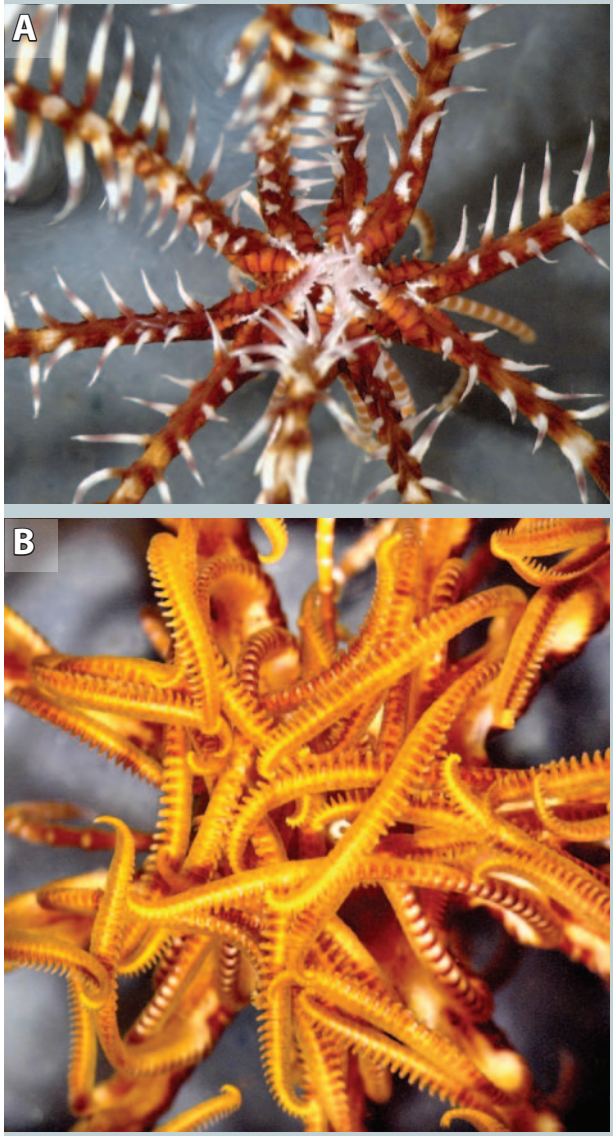


Figure 7.6 Modified oral pinnules.

A, thick and spinose in ***Oligometra carpenteri*** (Colobometridae).

B, flagellate and bearing a terminal comb in ***Alloeocomatella pectinifera*** (Comatulidae).

(A, Great Barrier Reef, Australia; B, W Pacific)

[C.G.Messing]

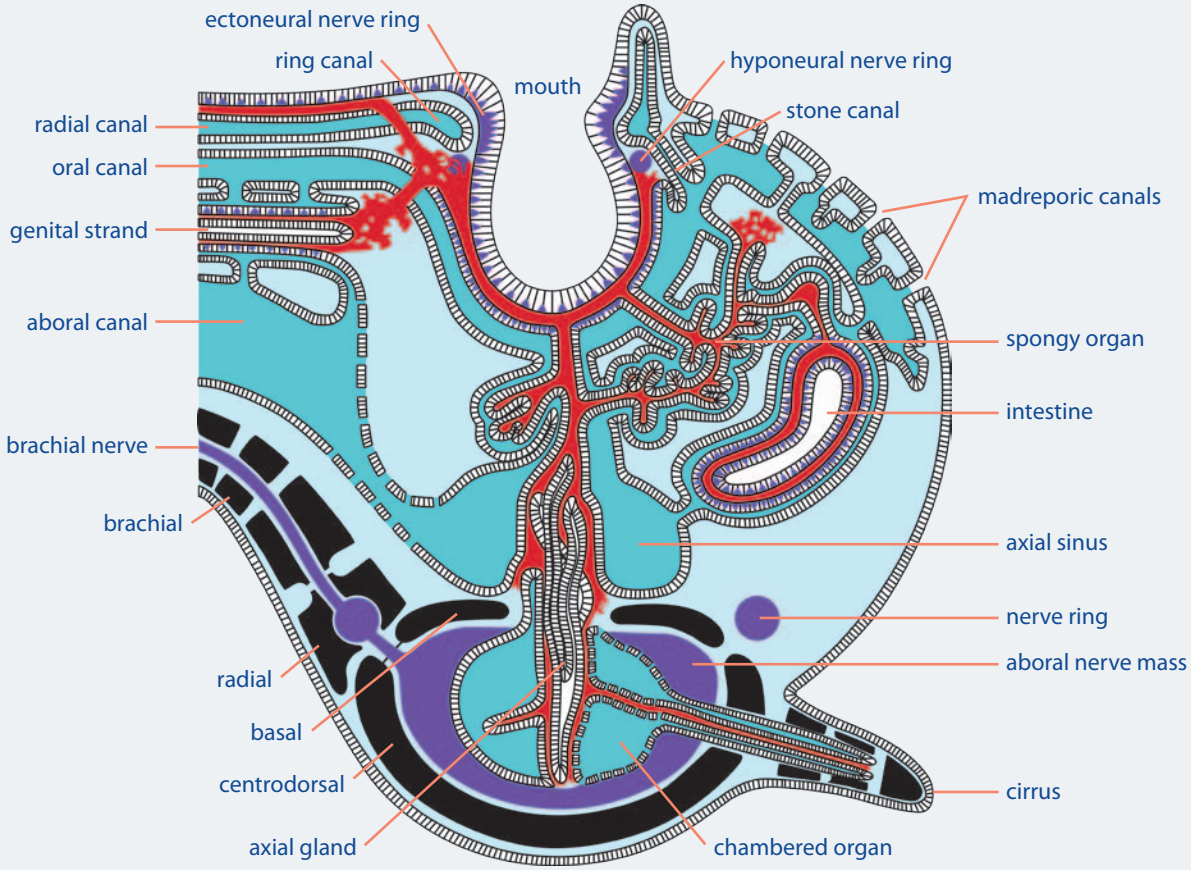


Figure 7.7 Simplified schematic cross-section of crinoid (feather star) anatomy in vertical section through a ray (left) and interray (right) with oral surface at top (not to scale), showing skeletal components (black), coelomic spaces (blue), haemal lacunae (red), nervous tissue (purple), and connective tissue (pale blue). Neural plexuses in epithelia are represented by rows of purple triangles. Nerves associated with the hyponeural ring are not shown.

[modified from Heinzeller & Welsch 1994]

the radial at the base of the ray and including the first axil) (**Figs 7.9, 7.10, 7.11**). Brachitaxes and their component ossicles are identified in order from the base of the ray, for example the primibrachial series (composed of two primibrachial ossicles, or primibrachs, in most living crinoids) arises from the radial ossicle, and is followed by the secundibrachial series (composed of secundibrachs), and so on. However, it is important to note that recent phylogenetic reconstructions based on molecular data have upended numerous taxa based on morphological features and that some sequence-based clades are so far unsupported by corresponding morphological characters (for example, Hemery *et al.* 2013; Rouse *et al.* 2013; Summers *et al.* 2014).

Because crinoids are modular organisms with numerous repeated skeletal parts, their diagnoses and descriptions are greatly shortened by symbols and abbreviations (**Figs 7.9C, 7.10, 7.11**). Brachitaxes are abbreviated Br preceded by a Roman numeral counting from the base of the ray, and an Arabic numeral indicating the number of component ossicles; br with an Arabic subscript indicates an individual brachial; ax an axil, and + a syzygy. Details vary for different

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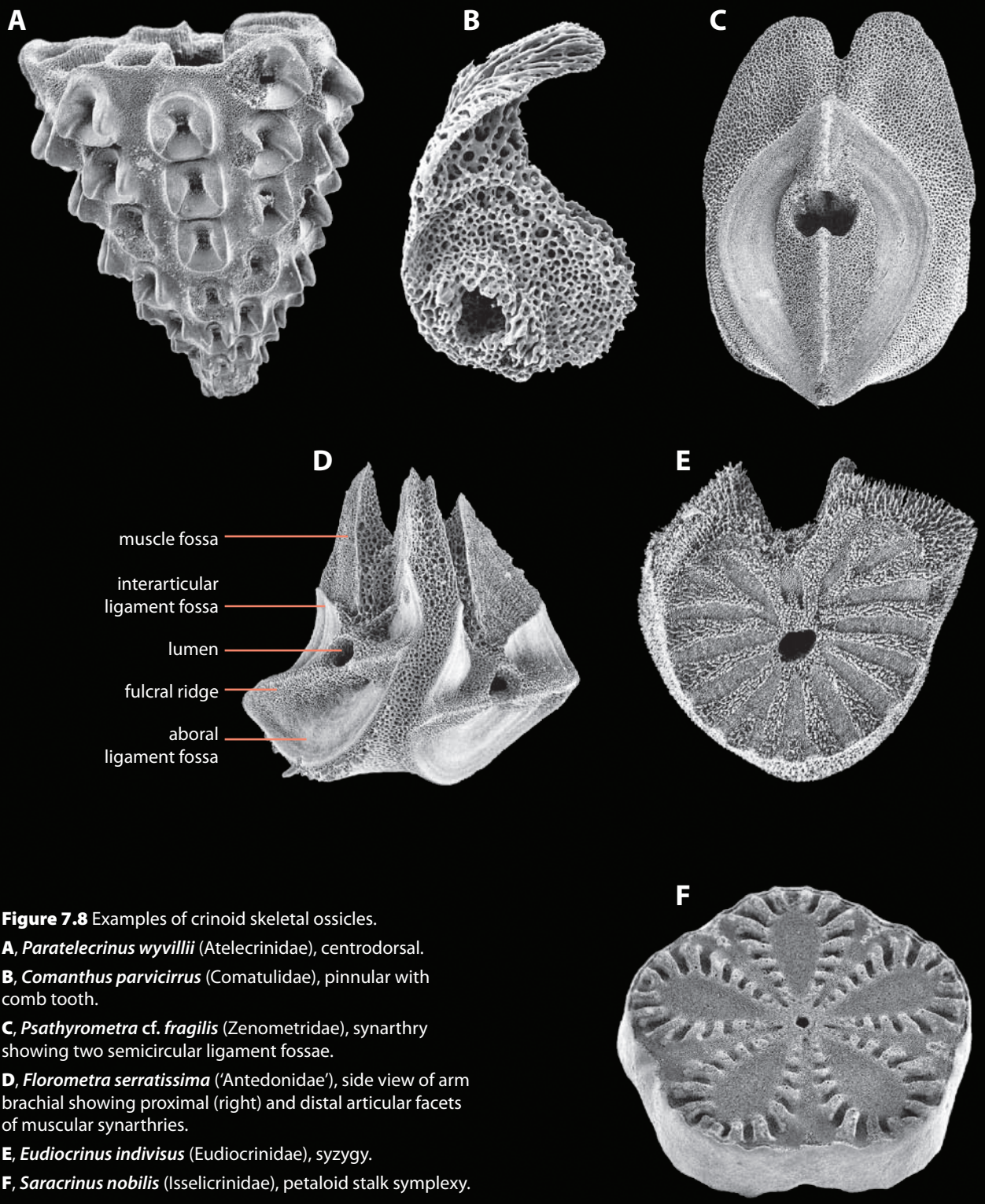


Figure 7.8 Examples of crinoid skeletal ossicles.

A, ***Paratelecrinus wyvillii*** (Atelecrinidae), centrodorsal.

B, ***Comanthus parvicirrus*** (Comatulidae), pinnular with comb tooth.

C, ***Psathyrometra* cf. *fragilis*** (Zenometridae), synarthry showing two semicircular ligament fossae.

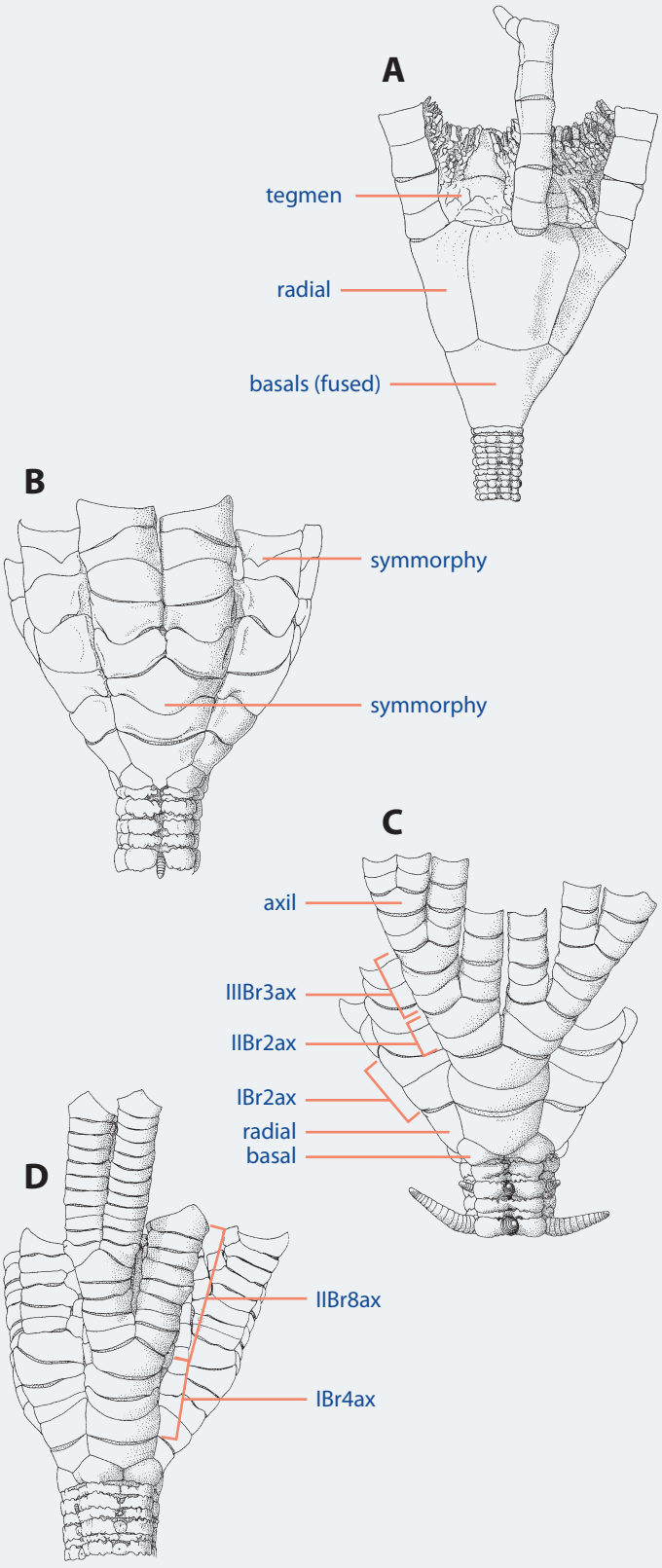
D, ***Florometra serratissima*** ('Antedonidae'), side view of arm brachial showing proximal (right) and distal articular facets of muscular synarthries.

E, ***Eudiocrinus indivisus*** (Eudiocrinidae), syzygy.

F, ***Saracrinus nobilis*** (Isselicrinidae), petaloid stalk symplexy.

(All W Pacific except C and D, NE Pacific)

[A–E, C.G. Messing; F, courtesy of M.Roux]



taxonomic groups, but, for example, in a feather star, IIBr4(3+4) indicates the second brachitaxis (or secundibrachial series) from the base of a ray composed of four ossicles with the third and fourth joined by syzygy (**Fig. 7.11A**), and IIax2 is an axil—the second ossicle of a second brachitaxis (**Fig. 7.11E**); in Isocrinida, IIBr8ax indicates a second brachitaxis composed of eight ossicles ending in an axil (**Fig. 7.9D**). Messing (1997), Roux (2002) and Hess (2011a) give more detailed discussions of crinoid skeletal morphology and nomenclature.

Crinoids do not generate their own filtration currents, but rely on extrinsic water movement to bring food particles to them. However, they are active participants to the extent that they modify arm and pinnule postures, and mobile feather stars and isocrinids seek preferred feeding stations, to take advantage of prevailing and changing flow patterns and velocities (for example, Macurda & Meyer 1974; Meyer & Macurda 1980; Byrne & Fontaine 1981; Meyer 1982b; Meyer *et al.* 1984; Messing *et al.* 1988; **Figs 7.1, 7.2, 7.17H, 7.19E, 7.20, 7.21**). Most species are rheophilic ('current-loving') and depend on horizontal water movements for food delivery, even at hadal depths (Oji *et al.* 2009). Such species array their arms in radial (**Figs 7.21B, 7.22D**), parabolic (**Figs 7.14A, 7.17H, 7.20B, 7.21A**), conical (**Fig. 7.37**), or arcuate fans (**Figs 7.19E, 7.22A**). Some feather stars are rheophobic—either cryptic within, or extending their arms from, irregular rocky and reef substrates—relying on weak multidirectional water movements

Figure 7.9 Theca and ray bases of stalked crinoids.
A, ***Hyocrinus cyanae*** (Hyocrinidae).
B, ***Hypalocrinus naresianus*** (Isocrinidae).
C, ***Endoxocrinus parrae*** (Isselicrinidae).
D, ***Saracrinus nobilis*** (Isselicrinidae).
See text for explanation of abbreviations.
(A, SW Pacific; B,D, W Pacific; C, W Atlantic)
[from Roux *et al.* 2002]

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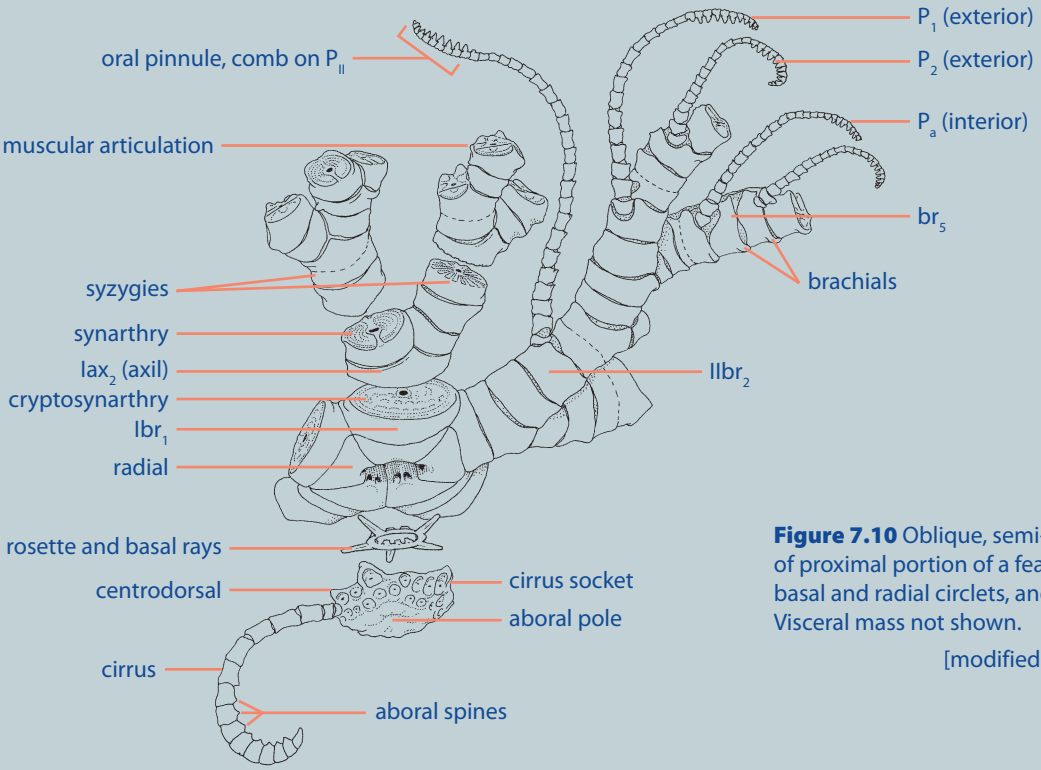


Figure 7.10 Oblique, semi-exploded view of proximal portion of a feather star showing basal and radial circlets, and bases of two rays. Visceral mass not shown.

[modified from Messing 1997]

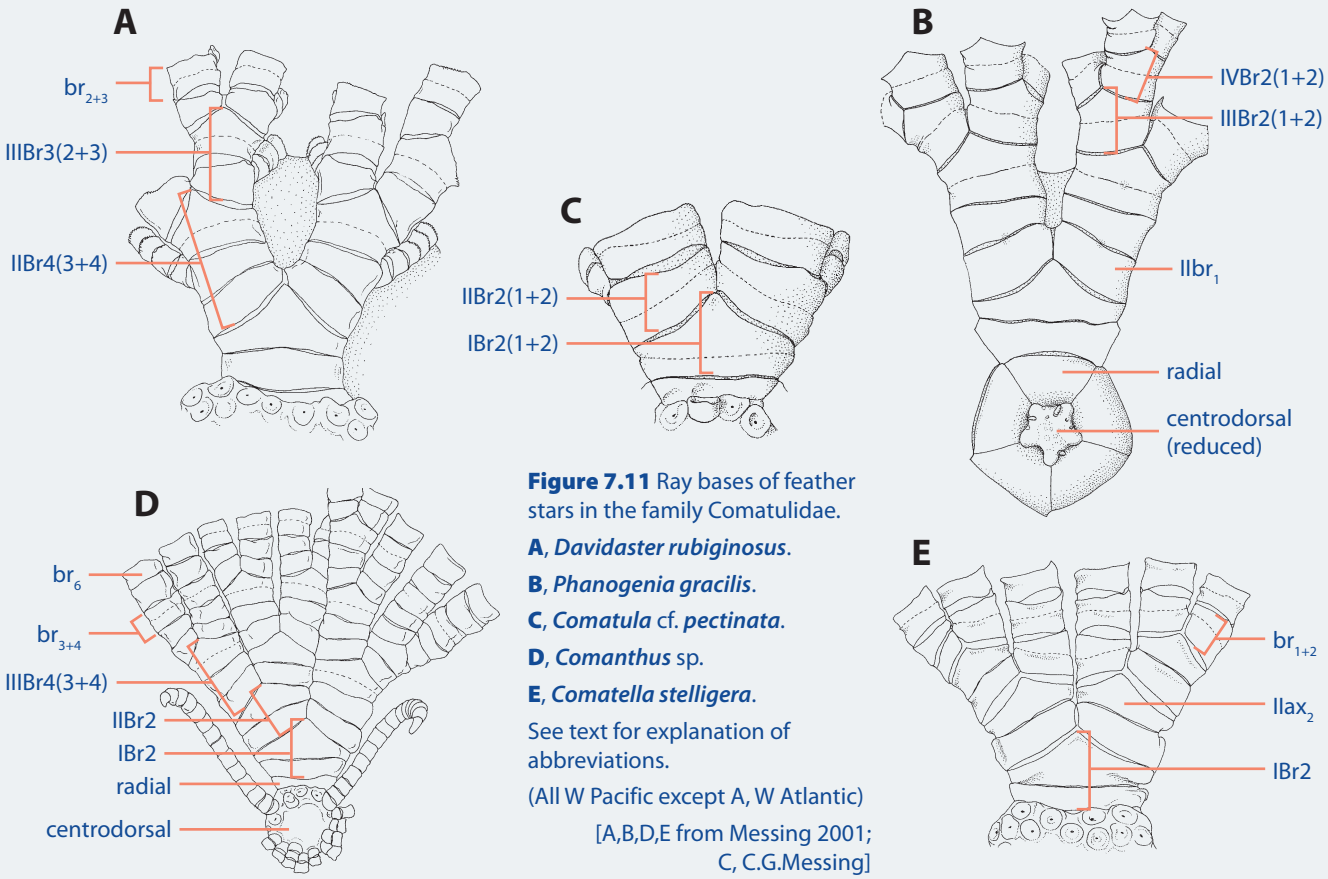


Figure 7.11 Ray bases of feather stars in the family Comatulidae.

A, ***Davidaster rubiginosus***.

B, ***Phanogenia gracilis***.

C, ***Comatula*** cf. ***pectinata***.

D, ***Comanthus*** sp.

E, ***Comatella stelligera***.

See text for explanation of abbreviations.

(All W Pacific except A, W Atlantic)

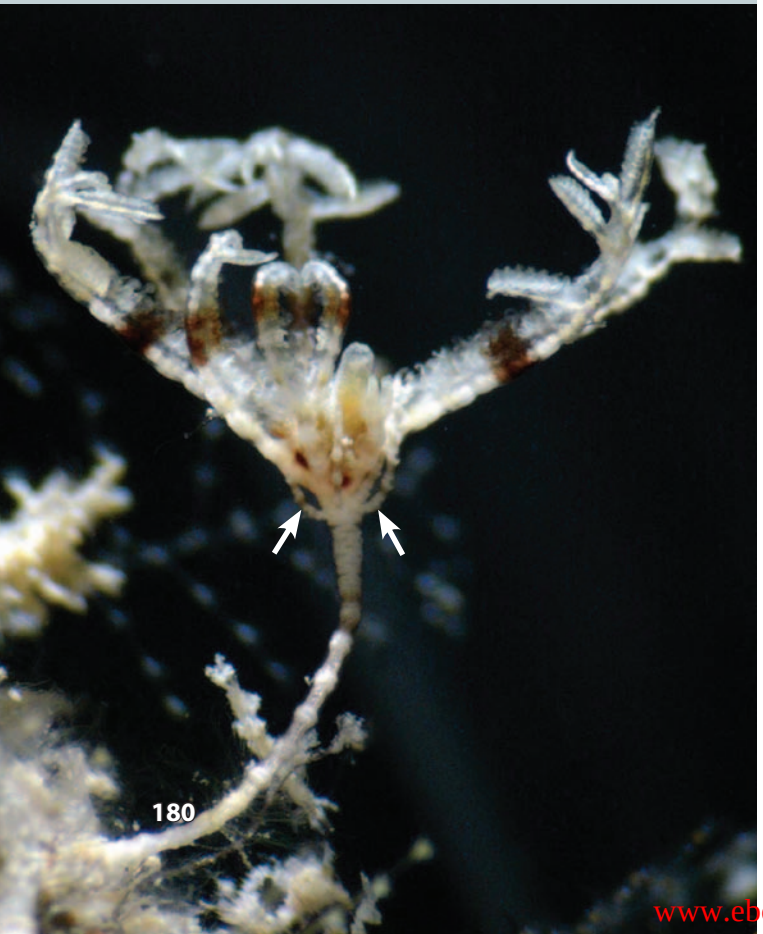
[A,B,D,E from Messing 2001; C, C.G.Messing]

(**Figs 7.19C, 7.23**). Although it is possible that crinoids at all depths can capture sinking particles during periods of slack water, it is not known if they actively feed under such conditions. *In situ* photographs show crowns tilted to intercept horizontal water movement, even at depths exceeding 9,000 m (Oji *et al*. 2009). During periods of negligible flow or slack conditions, crinoids assume distinct, ostensibly non-feeding, postures, for example oral surface upward and arms drooping, or arms curled meridionally inward or in a cone (Macurda & Meyer 1974; Byrne & Fontaine 1981; Meyer *et al*. 1984; **Figs 7.17C, 7.20A**).

The longer podia (**Fig. 1.19**) flick passing suspended particles into the food groove, where they are wrapped into boluses with mucus and carried, conveyor-belt style, via cilia along the pinnule, and down the arm to the central mouth. The shorter tube feet often scrape food off the long tube feet and retain it in the groove.

Figure 7.12 Advanced stalked pentacrinoid postlarva of a feather star. The most proximal pinnules have not yet developed, but the initial slender cirri are visible (arrows), curved upward from the centrodorsal at the top of the stalk, just under the bases of the arms.

[G.W.Rouse]



Adjacent tube feet may coordinate to capture larger food particles (Nichols 1960; Byrne & Fontaine 1981; LaHaye & Jangoux 1985; Holland *et al*. 1986; Lawrence 1987; Leonard 1989; Baumiller 1997).

Current information on crinoid diets derives from examination of gut contents and faecal material, which include protists (for example, diatoms, dinoflagellates, foraminiferans, radiolarians, and tintinnid ciliates), invertebrate larvae (for example, veligers), small crustaceans (especially copepods), detritus and inorganic grains (for example, sediment, spicules). Large proportions of benthic taxa (for example, diatoms) reflect the importance of resuspended material to the diets of some species (Gislén 1924; Rutman & Fishelson 1969; La Touche 1976). Inorganic grains indicate that particle capture is non-selective and may not reflect digestibility. Crinoids may also capture soft-bodied plankton (for example, non-loricate ciliates) that may be destroyed by digestion or unidentifiable in faeces. However, Holland *et al*. (1991) found that particles ingested by the feather star *Oligometra serripinna* (Colobometridae) pass through the gut rapidly and, by one hour after ingestion, accumulate in the extreme hind end of the intestine and rectum, where they suggested most digestion takes place. They also suggested that, at least in the generally low particulate organic carbon (POC) environment of coral reefs, gluttonous feeding during brief episodes of elevated POC (for example, during spawning of other invertebrates) might contribute significantly to crinoid nutrition.

Detritus constitutes a significant component of gut contents in some crinoid species (La Touche 1976; La Touche & West 1980; Featherstone *et al*. 1998), which makes assessment of diet and nutrition more difficult. Any contribution by microorganisms in the detritus to crinoid nutrition remains unquantified, and captured detritus may not be distinguishable from faeces. However, La Touche (1976) found that *Antedon bifida* ('Antedonidae') could not digest most of the diatoms and dinoflagellates found in its gut, suggesting that detrital microbes might provide the primary source of nutrition. West (1978) and D.F.Smith *et al*. (1981) documented uptake of dissolved organic material by crinoids, but its relative contribution to nutrition likewise remains unknown.

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Identifiable dietary components vary among crinoid species with availability (for example, seasonality, locality and activity rhythms), tube foot morphology and spacing (Meyer 1979, 1982a, 1982b), ambulacral groove width, and crown elevation (see below). Most information derives from studies on shallow-water feather stars (Comatulida). As examples, ciliates, foraminiferans and radiolarians contribute 50–87% of *Lamprometra klunzingeri* (=*Dichrometra palmata*) (Mariametridae) gut contents (Rutman & Fishelson 1969; Meyer 1982b); chiefly faecal, re-suspended detritus makes up 53–85% of *A. bifida* food (La Touche & West 1980); diatoms and dinoflagellates contribute 54–57% of faecal samples of *Anneissia bennetti* (Comatulidae) and *Pontiometra andersoni* (Colobometridae) (Meyer 1982b). For deeper water taxa, unidentifiable detritus contributes 59.2–69.0% by area of gut contents of stalked *Endoxocrinus parrae* and *Neocrinus decorus* (Isselicrinidae) (Featherstone *et al*. 1998), whereas Kitazawa *et al*. (2007) found that inorganic particles dominated gut contents of five deep-water crinoids, the feather stars *Chondrometra rugosa* and *C. robusta* (Charitometridae) and stalked *Endoxocrinus alternicirrus*, *Metacrinus wyvillii* (Isselicrinidae) and *Hypalocrinus naresianus* (Isocrinidae), with diatom frustules more common in long-stalked *M. wyvillii* and *H. naresianus*, and chlorophyll derivatives (probably from faecal pellets of zooplankton or dinoflagellates) in the feather stars and short-stalked *E. alternicirrus*. However, Meyer (1982b) noted that faecal content from different individuals of the same species taken on a single dive differed significantly, reducing the usefulness of interspecific comparisons, although rank abundance and presence/absence data remained useful.

Food particle size also varies among species, but the great majority of items range from about 20 to 150 μm (La Touche & West 1980; Liddell 1982; Meyer 1982a). Mucus-covered tube feet act as an adhesive filter and can capture particles smaller than the spaces between them. Leonard (1989) successfully fed *Antedon mediterranea* coccolithophores ~11 μm across. Ambulacral groove width ranges from 75 to 300 μm in different species and is often cited as setting the upper size limit of particles that crinoids can successfully retain (Fell 1966a; Rutman & Fishelson 1969; La Touche & West 1980). However, items larger than groove widths have been recorded. Although Meyer (1982b) recorded a 200 μm groove width in *Lamprometra* (=*Dichrometra*) *palmata* with maximum least dimension of virtually all particles <200 μm, he also recorded items 350–550 μm in *Capillaster multiradiatus* (Comatulidae), clearly larger than groove width. Similarly, La Touche & West (1980) noted that *A. bifida* (in aquaria) could convey particles substantially larger than groove width (to 1 mm diameter) to the mouth in still water.

Meyer (1979, 1982a, 1982b) suggested that variations among species in length and spacing of their primary podia contribute to dietary differences and that longer primary podia may permit larger particle capture (relative to co-occurring species with similar groove widths), or that ambulacra may stretch to accommodate larger particles in some species. Another possibility is that arms with wider grooves may contribute more to particle capture in some species than in others that use only their pinnules.

The best documented predators on living crinoids are fishes, sea urchins and seastars. Most predation, at least on feather stars in shallow water, appears to be chiefly sublethal grazing by non-specialist fishes that take pinnules, visceral masses, arms, or parts of arms (Meyer & Ausich 1983; Meyer 1985). One or two fish species in each of nine families include feather star predators: Balistidae, Chaetodontidae, Ephippidae, Labridae, Lutjanidae, Monacanthidae, Notacanthidae, Sparidae and Tetraodontidae. Of these, only the sparid *Chrysophrys auratus* is known to feed on numbers of whole feather stars (Meyer 1985). A photograph in Conan *et al*. (1981) appears to show a boarfish (Caproidae) feeding on the arms of the stalked isselicrinid *Annacrinus* (=*Endoxocrinus*) *wyvillethomsoni*. However, although some caproids often shelter among stalked crinoids (Colin 1974; C.G.Messing, personal observations), they feed on crustaceans, molluscs and worms (Quéro 1986), and the supposedly missing arms appear to be recurved toward the lens. On the other hand, isselicrinids (for example, *Neocrinus decorus*, *Endoxocrinus parrae*) are prey to cidarid pencil urchins such as *Calocidaris micans* and *Histocidaris nuttingi* — gut contents of the latter may

Box 7.1 Associates and symbionts

Crinoids play host to a wide variety of associated organisms including crustaceans such as copepods, isopods, amphipods, caridean shrimps (**Figs 2.29C,F; BoxFig. 7.1a,b**), galatheid squat lobsters (**Fig. 2.30**), and crabs, eulimid gastropods (**Fig. e**), ophiuroids (**Fig. f**), nematodes, annelid scaleworms, gobiesocid clingfish *Lepadichthys* and *Discotrema* (**Fig. 2.28A**) and pipefish (**Fig. 2.28C**) (Humes & Ho 1970; Bruce 1982; Zmarzly 1984b; Fabricius & Dale 1993; Deheyn *et al*. 2006). However, most unusual are the myzostomes, strange worms that, except for their planktonic larval stages, are almost exclusively associated with echinoderms, chiefly crinoids (**Figs 2.22; BoxFig. 7.1c,d**). Although now considered aberrant annelids, they have previously been placed with groups as different as flatworms (Eeckhaut *et al*. 2000) and rotifers (Zrzavý *et al*. 2001). About 90% of the approximately 150 described species are ectosymbionts on feather stars, but others infest the integument, coelom, digestive system or gonads of a variety of crinoids, with about a dozen species associated with ophiuroids and asteroids (Summers & Rouse 2014), two with black corals (Antipatharia) (Bo *et al*. 2013) and one recorded from a sponge (Okada 1920). After a larva settles, the host crinoid usually surrounds it with a tissue cyst, although *Myzostoma alatum*, which attaches to the tegmen of the 'antedonid' *Leptometra phalangium* in European waters, does not appear to elicit any physical deformation in the host (Eeckhaut & Jangoux 1992). Most species leave the cyst and become mobile on the surface of their host. These are mostly disc-shaped or elongated and are frequently camouflaged with the same colours and patterns as their host, or body extensions that resemble host structures such as pinnules. Though mobile, they cannot leave to move over the substrate to another host. Other species remain within a tissue cyst or induce their host to generate a hard surrounding gall of skeletal material along a food groove or within the mouth, digestive system, coelom or gonads. Except for those found within the coelom and gonads that probably consume host tissues as true parasites, most myzostomes, whether mobile or ensconced in cysts or galls, steal food collected by their hosts, for example, by inserting their proboscis into a food groove (Summers & Rouse 2014). Most myzostomes are known from shallow tropical reefs, which support the greatest crinoid diversity, although some species have been reported from abyssal depths. Skeletal deformations on fossil crinoids dating to the Jurassic (Radwanska & Radwanski 2005; Hess 2010) and possibly even the Palaeozoic (Brett 1978; Meyer & Ausich 1983) have been attributed to myzostomes.

Grygier (2000) stated that museum collections house about 70 myzostome species, described and undescribed, from Australian waters. Of these, 60 are tropical, occurring from the Great Barrier Reef, Queensland, across the Northern Territory to Western Australia north of Shark Bay. He noted only about 13 species from temperate waters — between Fraser Island, Queensland, and Perth, Western Australia. Only two species are currently known from South Australian waters: *Myzostoma australe* on *Ptilometra macronema* (Ptilometridae) (Rouse 2003), and *M. seymourcollegiorum* on *Cenolia trichoptera* and *C. glebosus* (Comatulidae) (Rouse & Grygier 2005). Most recently, Rouse *et al*. (2016) described three new Australian species of *Mesomyzostoma* from the feather stars *Dichrometra* sp. (Mariametridae), *Comaster* species, and *Clarkcomanthus albinotus* (Comatulidae). Members of this genus infest either the coelom or gonads.

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Figures a–f Associates of crinoids.
a, alpheid shrimp on ***Phanogenia gracilis*** (Comatulidae).
b, caridean shrimp on ***Amphimetra tessellata*** (Mariametridae).
c, myzostome on ***Clarkcomanthus*** sp. (Comatulidae).
d, pair of striped myzostomes on a mariametrid.
e, eulimid gastropod on ***Dorometra nana*** ('Antedonidae').
f, ophiuroid ***Ophiomaza cacaotica*** on ***Dichrometra*** cf. ***palmata*** (Mariametridae).
[A,C,E, C.G.Messing; B,D, G.W.Rouse; F, R.Tan]

consist chiefly of crinoidal material (Baumiller *et al.* 2008) — and hyocrinids succumb to both asteroids and echinoids (Bowden *et al.* 2011; **Fig. 7.14B,C**).

Sublethal predation pressure on reef-dwelling feather stars appears to be relatively low, with chiefly one to five arms missing or regenerating in fewer than half of specimens studied, and cryptic and semicryptic species exhibiting less damage (Meyer 1985; Schneider 1988). However, Mladenov (1983) reported that 80% of *Florometra serratissima* off Vancouver Island had one or more regenerating arms. He attributed the arm loss to the crab *Oregonia gracilis* and the asteroid *Pycnopodia helianthoides*. At least some attacks by fish may be directed at the numerous associates (commensals and parasites) resident among crinoid arms (Meyer 1985) (see **Box 7.1**). Behavioural, morphological and visual camouflage by associates suggests that they represent a potential food source and that their hosts provide significant shelter.

Possible defences against predation include cryptic or semicryptic behaviour; large spine-like oral pinnules or a dense thicket of arms and pinnules to shield the visceral mass; incorporation of distasteful or toxic compounds; rapid regeneration of arms and visceral mass, and crawling/swimming (Rideout *et al.* 1979; Bakus 1981; Meyer & Ausich 1983; Mladenov 1983; Meyer 1985, 1988; but see McClintock *et al.* 1999). All feather stars are at least potentially mobile, although members of only some families can swim (for example, Mariametridae, 'Antedonidae', but not Comatulidae), and isselicrinids and most other Isocrinida can potentially escape from benthic predators by arm crawling and shedding the distal portion of the stalk (Messing *et al.* 1988; Baumiller *et al.* 2008, 2010). Oji & Okamoto (1994) demonstrated how the ray branching pattern and distribution of autotomy points (syzygies) in a shallow-water feather star (for example, *Oxycomanthus* (=*Anneissia*) *japonicus*) approached a theoretically ideal pattern for minimising effects of arm loss via predation, whereas the pattern in deep-water *Metacrinus rotundus* approached an arrangement ideal for harvesting food in a low-predation environment.

Crinoids are gonochoric and only rarely hermaphroditic (Holland 1991; Obuchi *et al.* 2010). The sexes are usually indistinguishable, although gonads packed with mature gametes can be recognisable as ovaries or testes (Vail 1987a; Holland 1991; Heinzeller & Welsch 1994), and females of a few species brood their offspring in marsupia (Hyman 1955; Fell 1966a). Gonads lie on the ambulacral side of the genital pinnules or at their bases on the rays (Ubaghs 1978; Lawrence 1987; **Fig. 7.5**). Most species appear to broadcast gametes (**Fig. 3.2D**). A few brood their juveniles or are considered ovoviviparous or even possibly viviparous (**Figs 7.2, 7.30A**), although the mechanism of transfer of sperm to ovary is not known. In those feather stars in which development is known, a non-feeding doliolaria larva metamorphoses through stalked cystidean and pentacrinoid postlarval stages prior to stalk loss (**Fig. 7.12; Box 7.2**). However, *Metacrinus rotundus*, the only stalked crinoid for which early development is known, passes through an auricularia-like larval stage before becoming a doliolaria (Nakano *et al.* 2003, 2004).

Crinoids occur in most seas (except the Black Sea and Baltic Sea) and from the lower intertidal zone to abyssal depths, although stalked forms are restricted to depths below 100 m. Current taxonomy recognises approximately 664 species in 183 genera and 32 families (see **Table 7.1** for the classification of extant families within Crinoidea followed in this chapter). Of these, about 100 species in 35 genera and 13 families retain a stalk throughout life; six species in two genera of one family attach directly via the calyx, and the rest are feather stars that lose the stalk following a postlarval stage. The tropical Indo-west Pacific region harbours almost half of the known species, with just over 100 species known from shallower depths of less than 50 m and a similar number from depths of 100–1,000 m in the East Indian Archipelago, Southeast Asia (Clark & Rowe 1971; Messing *et al.* 2000). By contrast, only about 55 species are known from the next richest area, the tropical western Atlantic. Globally, more than 300 feather star species occur shallower than 200 m, disputing the traditional view that living crinoids are primarily deepsea organisms (McConnaughey & Zottoli 1983; Thurman & Webber 1984).

Feather stars are abundant in a variety of marine habitats, particularly on shallow Indo-western Pacific reefs. Maximum densities can reach 18 individuals per square

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Table 7.1 Classification of living Crinoidea modified from Hess & Messing (2011a).

* indicates families known from within Australia's Exclusive Economic Zone (EEZ) and extended continental shelf (ECS) waters.

† Comatulidae was formerly placed, as Comasteridae, in superfamily Comasteroidea. However, a superfamily designation for a single included family is redundant. Comatulidae is listed first rather than with the families *incertae sedis*, as it includes the most common, diverse and abundant of crinoids found in Australian waters.

Class Crinoidea

Subclass Articulata

Order Hyocrinida
- Family Hyocrinidae *

Order Cyrtocrinida
- Family Eudesicrinidae
- Family Sclerocrinidae
- Family Holopodidae

Order Isocrinida
- Family Isocrinidae
- Family Cainocrinidae *
- Family Isselicrinidae *
- Family Proisocrinidae

Order Comatulida
- Family Comatulidae * †

Superfamily Himerometroidea
- Family Himerometridae *
- Family Colobometridae *
- Family Mariametridae *

Superfamily 'Tropiometroidea'
- Family Tropiometridae *
- Family Calometridae *
- Family Ptilometridae *
- Family Asterometridae *
- Family Charitometridae *
- Family Thalassometridae *

Superfamily Notocrinoidea
- Family Notocrinidae *
- Family Aporometridae *

Superfamily 'Antedonoidea'
- Family Antedonidae *
- Family Zenometridae
- Family Pentametrocrinidae *

Superfamily *Incertae sedis*
- Family Atopocrinidae
- Family Eudiocrinidae *
- 'Bourgueticrinines'
- Family Bourgueticrinidae
- Family Bathycrinidae *
- Family Phrynocrinidae *
- Family Septocrinidae
- Family Atelecrinidae
- Family Guillecrinidae

Incertae sedis
- Family Caledonicrinidae

metre on the Great Barrier Reef, Queensland (Vail 1987a) and 115 per square metre at Madang, Papua New Guinea (Messing 1994). Stalked crinoids and feather stars are often abundant in a variety of deep-water assemblages, for example, on hard grounds at depths of 350–600 m in the Bahamas, on Antarctic knolls at 580–600 m, below 1,000 m in the north-eastern Atlantic and on the flanks of seamounts off California, and on rocky trench floors in over 9,000 m (Conan *et al*. 1981; Messing *et al*. 1990; Messing 2004; Oji *et al*. 2009; Bowden *et al*. 2011). **Figure 7.17H** indicates that crinoids may also be abundant in deep Australian waters.

About 150 species have been recorded from Australian waters, about 60 from shallow tropical waters and 19 restricted to Australian Antarctic Territorial waters (AAT). **Table 7.1** includes 20 families from Australia's Exclusive Economic Zone and the Extended Continental Shelf.

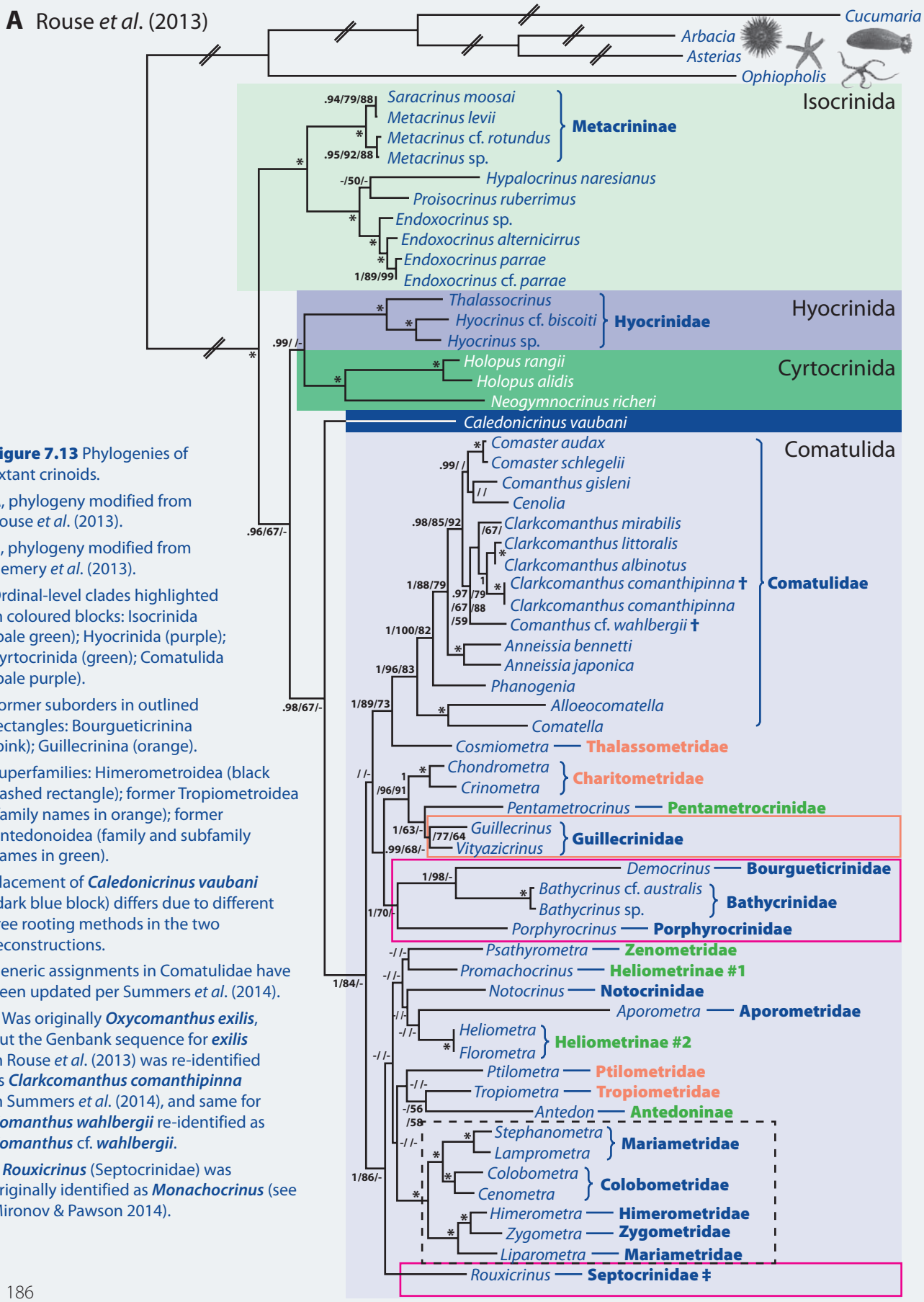


Figure 7.13 Phylogenies of extant crinoids.

A, phylogeny modified from Rouse *et al*. (2013).

B, phylogeny modified from Hemery *et al*. (2013).

Ordinal-level clades highlighted in coloured blocks: Isocrinida (pale green); Hyocrinida (purple); Cyrtocrinida (green); Comatulida (pale purple).

Former suborders in outlined rectangles: Bourgueticrinina (pink); Guillecrinina (orange).

Superfamilies: Himerometroidea (black dashed rectangle); former Tropiometroidea (family names in orange); former Antedonoidea (family and subfamily names in green).

Placement of ***Caledonicrinus vaubani*** (dark blue block) differs due to different tree rooting methods in the two reconstructions.

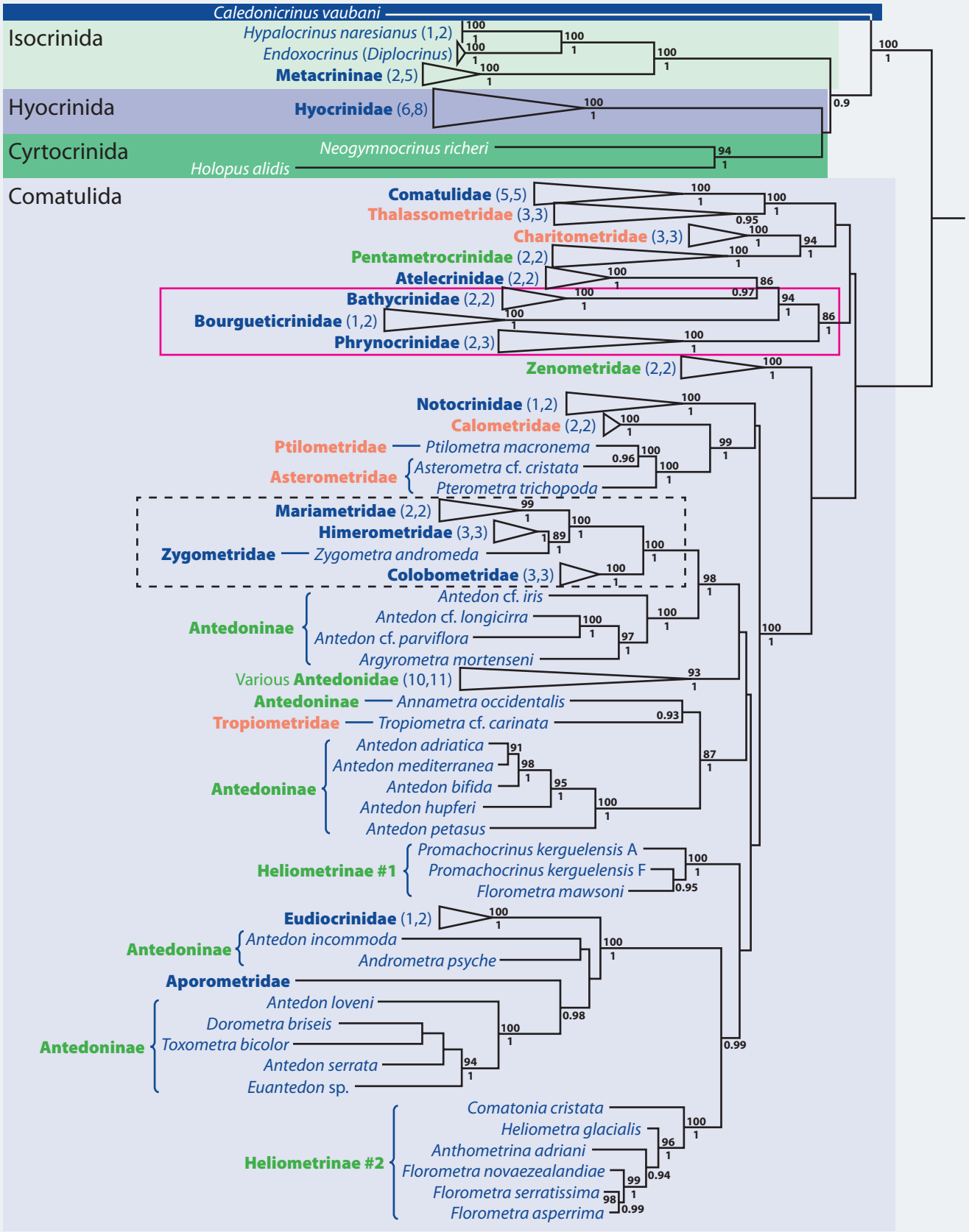
Generic assignments in Comatulidae have been updated per Summers *et al*. (2014).

† Was originally ***Oxycomanthus exilis***, but the Genbank sequence for ***exilis*** in Rouse *et al*. (2013) was re-identified as ***Clarkcomanthus comanthipinna*** in Summers *et al*. (2014), and same for ***Comanthus wahlbergii*** re-identified as ***Comanthus*** cf. ***wahlbergii***.

‡ ***Rouxicrinus*** (Septocrinidae) was originally identified as ***Monachocrinus*** (see Mironov & Pawson 2014).

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B Hemery *et al*. (2013)



Fossils

Although crinoids are the least studied of living echinoderm groups, their skeletal remains are among the most abundant and important of fossils. More than 6,000 fossil species have been described (Hess *et al*. 1999). Forms definitively recognisable as crinoids first appeared during the Early Ordovician. They underwent several major radiations during the Palaeozoic and became major carbonate-producing organisms. Crinoid skeletal remains constitute the primary components of extensive carbonate shelves in many Palaeozoic and Mesozoic settings (Ausich 1997b). The Keokuk and Burlington limestones of the American Midwest, for example, consist chiefly of crinoid remains in layers up to 53 m thick spanning an area of more than 74,000 square kilometres (Ausich 1997a; Hess *et al*. 1999). Short stratigraphic ranges of many species make them important as at least local biostratigraphic index taxa.

Crinoid fossils are well known from Australia (Philip 1964a; Campbell & Bein 1971), but their discussion is beyond the scope of this chapter.

Phylogeny

All extant crinoids have been placed in subclass Articulata, characterised in the most recent morphological classification as having the calyx composed of five infrabasal, basal and radial ossicles, but with infrabasals reduced or absent in most groups; no anal plates or compound radial ossicles; mouth exposed on the tegmen surface; axial nerves enclosed in a canal penetrating the basals, radials and brachials; brachials generally connected by articulations that include muscle bundles, but non-muscular, exclusively ligamentary articulations present in most species, and arms with pinnules, except in some extinct microcrinoids (Hess 2011b). Hess & Messing (2011b) treated all post-Palaeozoic crinoids as articulates using a modified version of the widely used arrangement of Rasmussen & Sieverts-Doreck (1978). They included four orders with extant taxa (Hyocrinida, Cyrtocrinida, Isocrinida, and Comatulida) and four exclusively Mesozoic orders (Holocrinida, Encrinida, Millericrinida and Roveacrinida).

Several alternative hypotheses have also been proposed. According to Roux (1987), recurrent paedomorphosis led to skeletal simplifications and architectural and functional constraints that generated convergent features; he suggested that the Articulata is an artificial and probably paraphyletic construct. On the other hand, Webster & Jell (1999a) recognised the presence of syzygial brachial pairs in the arms (with alternating muscular and cryptosyzygial ligamentary articulations) as the defining synapomorphy. They broadened the group to include a variety of Late Palaeozoic taxa with Mississippian *Corythocrinus* as the earliest stem articulate. Within Articulata, Heinzeller (1998) combined short-stalked (avoiding the term stalkless) feather stars and long-stalked isocrinids in a taxon Cirrata, based on neuroanatomical evidence.

The first higher-level phylogenies to incorporate molecular data used similar datasets of eight to ten terminals in six to seven families and four nominal orders (Cohen *et al*. 2004; Eléaume 2006). Both returned well-supported isocrinid and cyrtocrinid clades, and close relationships among a feather star (Comatulida) and stalked *Bathycrinus* and *Guillecrinus*. Two more recent reconstructions have incorporated many more taxa (**Fig. 7.13**). Rouse *et al*. (2013), using five genes (COI, 16S, CytB, 18S, 28S) from 59 terminals in 44 genera, 24 families and six orders and suborders, returned well-supported hyocrinid, cyrtocrinid and isocrinid clades, with two stalked groups — Guillecrinidae and most 'Bourgueticrinina' — nested within an otherwise monophyletic Comatulida, supporting the hypothesis that bourgueticrinines arose from feather star ancestors via paedomorphosis (Rasmussen 1978). Basal relationships among the major clades were not well supported, though Isocrinida was recovered as the sister group to the remaining Articulata, and Hyocrinida and Cyrtocrinida formed a clade. Within Comatulida, the abundant and diverse reef-dwelling Comatulidae (formerly Comasteridae) and Himerometroidea (formerly Mariametroidea) returned as monophyletic, whereas Antedonoidea and Tropiometroidea were polyphyletic. Hemery *et al*. (2013) sequenced four genes (COI, 16S, 28S, 18S) from 105 terminals in 74 genera, 25 families and five orders and suborders, and returned the same four major clades (Isocrinida,

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Cyrtocrinida, Hyocrinida, Comatulida), with 'Bourgueticrinina' again nested within Comatulida, but with some differences in mutual relationships among major clades relative to Rouse *et al.* (2013), owing to their rooting their tree based on the midpoint method rather than an outgroup. Their phylogeny again returned monophyletic Himerometroidea (except for Eudiocrinidae, not included in Rouse *et al.* 2013) and Comatulidae, and polyphyletic Antedonoidea and Tropiometroidea. Placement of *Caledonicrinus vaubani*, treated as Bathycrinidae on morphological grounds, differed because of the rooting between the two molecular phylogenies but did not group with other bathycrinids in either case. Feather stars in the family Atelecrinidae nested among stalked 'bourgueticrinines' in Hemery *et al.* (2013), suggesting that the stalk has been repeatedly lost and retained among some extant crinoid lineages.

Published sequence-based phylogenies have in most cases not included formal taxonomic revisions, and the classification in Hess & Messing (2011b) is not formally phylogenetic. The following classification therefore remains subject to revision. Taxa that molecular analyses suggested to be poly- or paraphyletic are retained within quotation marks ('…') for convenience pending formal revision. Alternative taxonomic hypotheses are discussed under each group. The descriptions of each group refer only to extant members, except where indicated.

Order HYOCRINIDA

This order contains one family.

Family Hyocrinidae

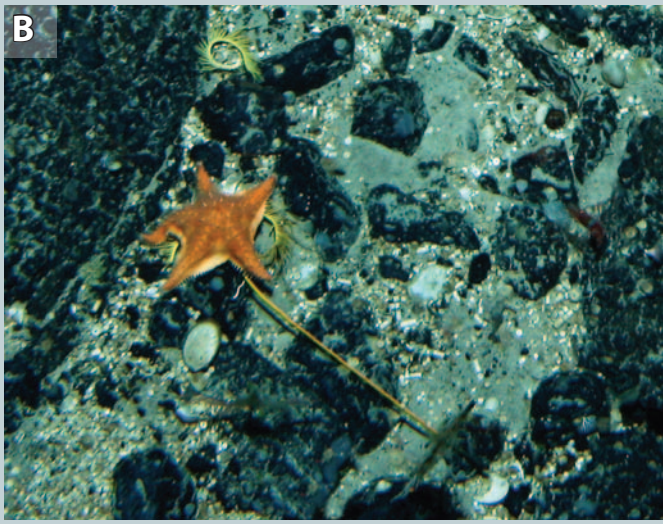
Figure 7.14

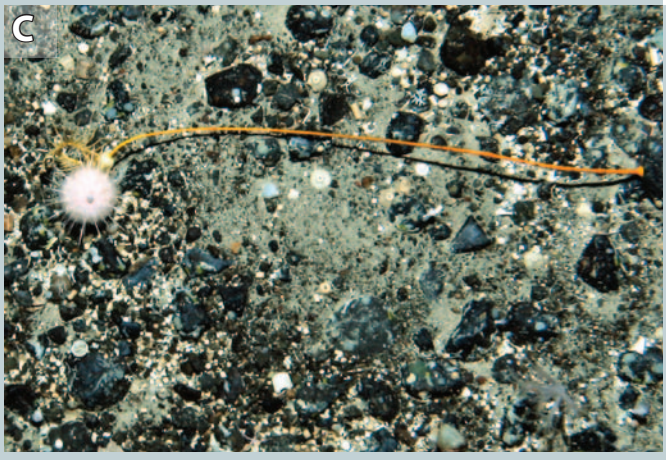
Although the resemblances are superficial, hyocrinids among all living crinoids most closely summon the image of the Palaeozoic 'living fossil': a long, slender homeomorphic stalk, *viz.*, one composed of numerous similar disc-like columnals, attached to the substrate by a terminal anchoring plate, and supporting a large globular or conical calyx with feather-like arms (**Figs 7.3A, 7.9A, 7.14A**). The proximal columnal articulations are symplexies with radiating crenellae arranged in more than five groups (except in pentamerous *Laubiericrinus*). Crenellae may be reduced on distal facets, and cirri and nodals are absent. The calyx is hollow, thin-walled and composed of basals and five radials; basals are fused or with one to three sutures. Infrabasals are absent. Rays are unbranched (except in *Calamocrinus*), with no syzygies; non-muscular articulations are smooth (synostoses). The arms are narrower than the radials and are separated laterally from each other. The tegmen is plated.

Mironov & Sorokina (1998) first raised hyocrinids to ordinal status and recognised 10 extant genera in four subfamilies of the single family Hyocrinidae. More recent work has reorganised the family, omitting subfamilies and recognising 27 species in eleven genera and subgenera: *Hyocrinus* (5 species), *Anachalypsicrinus* (2), *Belyaevicrinus* (1), *Calamocrinus* (1), *Dumetocrinus* (2), *Feracrinus* (3), *Gephyrocrinus* (2), *Laubiericrinus* (1), *Ptilocrinus* (*Ptilocrinus*) (3), *Ptilocrinus* (*Chambersaecrinus*) (3) and *Thalassocrinus* (4) (Roux & Pawson 1999; Roux 2002, 2004; Roux *et al.* 2002; Améziane & Roux 2011; Eléaume *et al.* 2011, 2012; Hess 2011c; Roux & Lambert 2011). Rouse *et al.* (2013) returned three hyocrinids as a monophyletic group sister to Cyrtocrinida, with both forming a clade sister to *Caledonicrinus*+Comatulida (including the other bourgueticrinines and Guillecrinidae). Hemery *et al.* (2013) returned nine species in six genera (11 terminals) as a monophyletic group again sister to Cyrtocrinida, but with their combined clade sister to a monophyletic Isocrinida (**Fig. 7.13**), although this was a rooting artefact (G.W.Rouse, unpublished data).

Hyocrinidae occur in all major ocean basins, chiefly at depths below 700 m (range 450–6,290 m) (Mironov & Sorokina 1998; Roux 2004; Tunnicliffe *et al.* 2015). Améziane & Roux (2011) described the first hyocrinids from Australian waters: *Feracrinus koslowi*, *P.* (*Chambersaecrinus*) *tasmaniaensis* and







P. (*Ptilocrinus*) *australis*, all from seamounts south of Tasmania in depths of 1,400–1,815 m. Bowden *et al.* (2011) described an assemblage dominated by a large hyocrinid up to 500 mm tall, later described as *P.* (*P.*) *amezianeae* (Eléaume *et al.* 2011), on knolls at the base of the Admiralty and Scott seamounts south-east of Tasmania near the Balleny Islands in 580–600 m (**Fig. 7.14A**). The crinoids occur in patches spanning 20–50 m^2 with mean densities of 2.6±1.7 individuals per square metre separated by expanses of coarse sediment and barren rock. Numerous stalk bases on rocks (including those barren of living crinoids), and sediments composed chiefly of crinoid ossicles, suggest that the assemblages have persisted for a substantial length of time. Bowden *et al.* (2011) also reported the first direct observations of echinoderms — the asteroid *Glabraster antarctica* (**Fig. 7.14B**) and the echinoid *Sterechinus antarcticus* (**Fig. 7.14C**) — preying on stalked crinoid crowns, in this case *P.* (*P.*) *amezianeae*.

Since then, Eléaume *et al.* (2014a) recorded *Feracrinus heinzelleri* and *Hyocrinus bethellianus* in Australia's Antarctic Territorial waters. *Ptilocrinus stukalinae*, known from the north-western Pacific, Antarctic Peninsula and off southern New Zealand (Macquarie Island) in 4,664–6,145 m, and *Belyaevicrinus latipinnulus*, from the Scotia Arc and Pacific Ocean in 3,056–5,530 m, also likely occur in Australian Territorial waters (Mironov & Sorokina 1998; Eléaume *et al.* 2014a).

Figure 7.14 Family Hyocrinidae.
Ptilocrinus (Ptilocrinus) amezianeae from Antarctic waters reaches a height of 500 mm.
A, a group from the south-east knoll of Admiralty Seamount, east of the Balleny Islands off Antarctica.
B, preyed upon by the asteroid ***Glabraster antarctica*** (Poraniidae).
C, preyed upon by the echinoid ***Sterechinus antarcticus*** (Echinidae).
[A, courtesy of D.A.Bowden; B,C, from Bowden *et al.* 2011, courtesy of Elsevier]

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Order CYRTOCRINIDA

Figure 7.15

Cyrtocrinids differ from typical sea lilies in having the stalk usually reduced to one or a few columnals (**Fig. 7.15A,B**), or completely absent with the calyx attached directly to the substrate by an expanded base (**Fig. 7.15C,D**). Cirri are absent. The calyx is sometimes asymmetrical, composed of five stout radial ossicles in extant taxa, and occasionally with its aboral component interpreted as a fused basal circlet or modified or fused columnal(s). Radials are often developed as protective structures. Syzygies are absent. Rays divide at primibrachs 1 or 2, and further in *Neogymnocrinus*.

Simms (1988) placed the group within the Millericrinida as a suborder (Cyrtocrinina) sister to Millericrinina based on their common reduction in tegmen height and cryptic infrabasals. He considered them a millericrinine offshoot adapted to hardgrounds or reefs and characterised by fused or indistinguishable basals. However, Hess (2011d) treated cyrtocrinids as a separate order (leaving Millericrinida extinct), noted that their origins remain obscure, and pointed out several features unknown in millericrinids: tall radials with articular facets sunken between interradial projections, and neither synarthrial nor syzygial articulations between

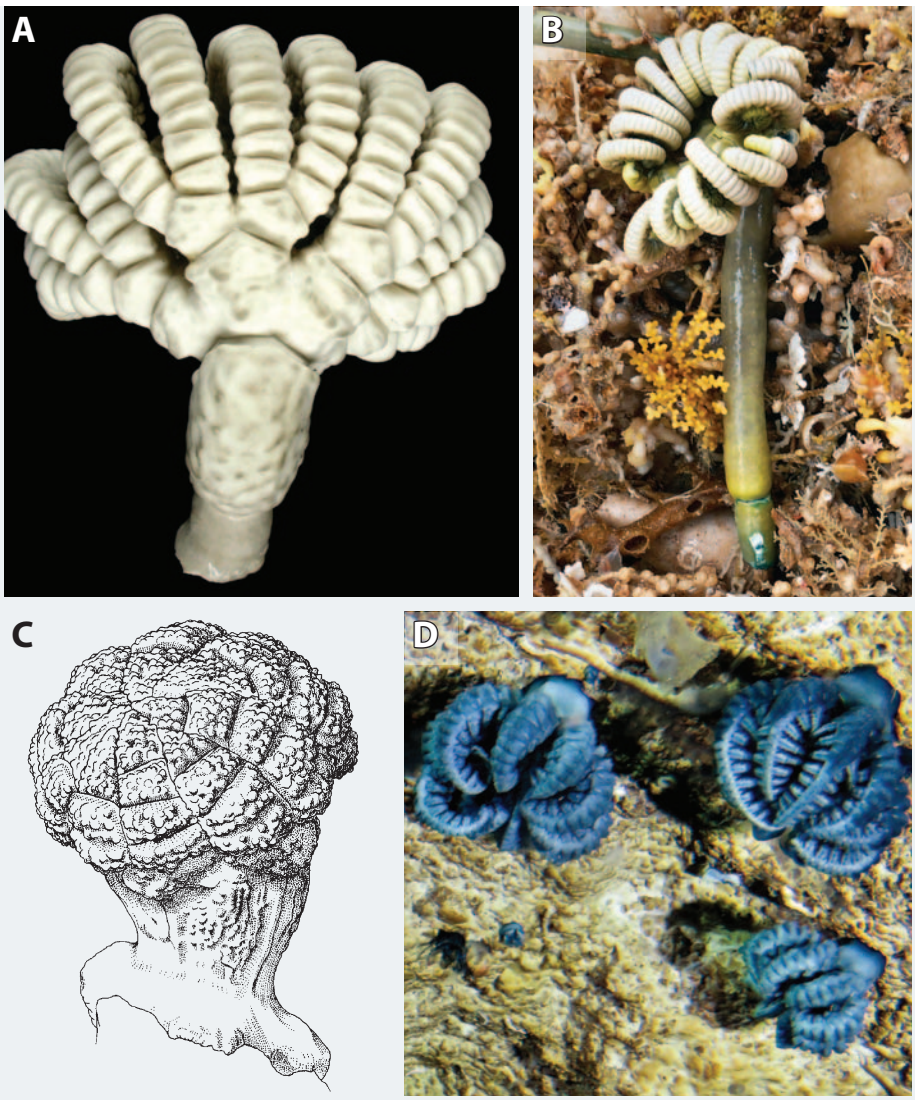


Figure 7.15 Cyrtocrinida.

A, **B**, family Sclerocrinidae. ***Neogymnocrinus richeri***: **A**, a preserved specimen. **B**, specimen from the Loyalty Seamounts north-east of New Caledonia during the 2011 R/V Alis EXBODI cruise.

C, **D**, family Holopodidae. **C**, ***Holopus alidis*** with arms curled tightly over the tegmen; this species is known from the south-west tropical Pacific including New Caledonia at depths of 350–470 m. **D**, three large ***Holopus mikihe*** from Isla Roatán, Honduras, at a depth of 421 m, flanked by two tiny bluish juveniles and one ***Cyathidium pourtalesi*** (blackish with short rays at left).

[A, N.Améziane; B, B.Richer de Forges; C, from Roux *et al*. 2002; D, C.G.Messing & T.K.Baumiller]

arm ossicles. He identified 15 families in two suborders, which occur from the Lower Jurassic to Recent, and noted that they may have been the most diverse group of crinoids during the Mesozoic.

Eight extant species are distributed among four genera in three families: *Holopus* (3 species) and *Cyathidium* (3) in Holopodidae, *Neogymnocrinus richeri* (formerly *Gymnocrinus*, family Hemicrinidae) in Sclerocrinidae, and *Proeudesicrinus lifouensis* in Eudesicrinidae (Bourseau *et al*. 1991; Améziane *et al*. 1999; Roux *et al*. 2002; Hess 2006; Donovan & Pawson 2008). Both Rouse *et al*. (2013) and Hemery *et al*. (2013) returned *Holopus* and *Neogymnocrinus* species as a monophyletic Cyrtocrinida sister to Hyocrinida.

Circumstantial evidence has suggested that cyrtocrinids may feed on relatively large prey (described both as raptorial and passive predatory feeding), as well as by suspension feeding. The arms of both *Holopus* and *Cyathidium* have strong interbrachial muscles and can close over the oral surface quite rapidly in response to disturbance, perhaps trapping larger prey; specimens of both genera have been found with proportionately large crustacean remnants, up to several hundred micrometers across, in their guts (Grimmer & Holland 1990; Wisshak *et al*. 2009).

Although no cyrtocrinids are currently known from Australian waters, *Holopus alidis* (**Fig. 7.15C**), *N. richeri* (**Fig. 7.15A,B**) and *P. lifouensis* have all been recorded from New Caledonia and adjacent waters at moderate depths (375–530 m, with one record of *P. lifouensis* from 960 m). *Holopus* and *Cyathidium* attach directly by means of an expanded stump-like calyx. In *Holopus*, the arms, when not extended, curl tightly over the tegmen like a fist (**Fig. 7.15C**); in *Cyathidium* (**Fig. 7.15D**), the primi- and secundibrachial ossicles form a tight lid over the incurled arms. *Neogymnocrinus richeri* has a two-ossicle stalk with strongly asymmetrical rays that extend, if unrolled, in a fan-like array. *Proeudesicrinus lifouensis* is known only from dissociated ossicles (Bourseau *et al*. 1991; Roux *et al*. 2002).

Order ISOCRINIDA

All two dozen or so living representatives of this group except the monotypic Proisocrinidae have a completely heteromorphic stalk, *viz*., composed of nodal columnals, each bearing a whorl of up to five cirri, alternating with a series of internodal columnals without cirri (**Fig. 7.3B**). The stalk may be pentalobate, pentagonal or circular in cross-section. Columnal articulations are symplexies, in which crenellae and culmina are arranged in five petaloid areas (**Fig. 7.8F**). Juveniles attach by a terminal disc (**Fig. 7.17C,D**), but adults lose the attachment and anchor by means of the cirri, either just the terminal whorl (**Fig. 7.17A,B**), or by several to many whorls along a portion of the stalk that lies along the substrate (**Fig. 7.17E,F**). The calyx is a low cup composed of five basals, five radials (**Fig. 7.9C**) and, in some genera, internal infrabasals. Basals typically appear externally as rhombic bulges or triangles below and between the radials. The visceral mass rests on the calyx and surrounding ray bases, and the tegmen is plated. The rays branch at primibrach 2 or between primibrachs 4–7, and often beyond, so that arms number 10 to about 50 (**Figs 7.9C,D, 7.17G**). Brachial articulations have well-developed muscular fossae, and non-muscular ligamentary articulations include synostoses, synarthries and symmorphies; syzygies are absent. The order extends from the Triassic to Recent, although Webster & Jell (1999b) include Late Permian *Archaeoisocrinus*. Stalk length in Lower Jurassic *Seirocrinus subangularis* (Pentacrinitidae) exceeded 20 m in length, the longest recorded for any crinoid. Extant isocrinid stalks rarely exceed l m in length (Rasmussen & Sieverts-Doreck 1978; Fell 1982; Lawrence 1987).

Several species with completely heteromorphic stalks have been observed to release the anchoring grip of their cirri and crawl with their arms, although none yet in Australian waters (Messing *et al*. 1988; Baumiller *et al*. 1991; Birenheide *et al*. 1994). Their locomotion, which can reach 30 mm per second, combined with active shedding of a distal portion of the stalk, appears to be an escape response to cidarid echinoid predators (Baumiller *et al*. 2001, 2008, 2010; Baumiller & Messing 2007).

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The classification of this order has been revised repeatedly and remains controversial (**Table 7.2**). Rasmussen & Sieverts-Doreck (1978) recognised two families with extant members; Simms (1988) expanded the order to include the comatulids and their immediate Mesozoic antecedents. He distinguished Isocrinida from Millericrinida by synarthrial articulations in the postlarval stalk and the (plesiomorphic) retention of cirri in the former. Subsequently, Simms *et al*. (1993) treated Isocrinina as an order consisting of four families, and removed Mesozoic Pentacrinitidae to Comatulidina. An alternative arrangement assigned all extant Isocrinida (*sensu* Rasmussen & Sieverts-Doreck 1978) except Proisocrinidae to Pentacrinitidae (following Clark 1923) based on stalk and crown articulations and proximal ray patterns as they reflected ontogenetic trends and heterochronic gradients (Roux 1981, followed by Bourseau *et al*. 1991; Roux *et al*. 2002; David *et al*. 2006). Most recently, Hess' (2011e) revision dispersed the living genera based chiefly on patterns of proximal ray articulations and included two suborders, six families and four subfamilies.

Although Roux (1980) removed monotypic Proisocrinidae (*Proisocrinus ruberrimus*) to Millericrinidae, Rouse *et al*. (2013) recovered this species within Isocrinida, as sister to *Hypalocrinus*. Both Hemery *et al*. (2013) and Rouse *et al*. (2013) recovered trees with a Metacrininae clade (*Metacrinus* and *Saracrinus*) as sister to a clade containing *Endoxocrinus* and *Hypalocrinus*. These results render Isselicrinidae of Hess (2011e) paraphyletic by nesting *Hypalocrinus* (Isocrinidae, Isocrininae) within Isselicrinidae. The following treatment uses the isocrinid families of Hess (2011e) pending formal revision.

Family Isocrinidae

As noted above, all extant crinoids with a completely heteromorphic stalk bearing whorls of cirri along its entire length and an autotomy plane (a cryptosymplectial to synostosial articulation) beneath the cirrus-bearing nodals have often been placed in this family, which has been variously known as Isocrinidae (Rasmussen 1978; Roux 1981; Simms 1988; Oji 1990, 1998; Rowe & Gates 1995), Pentacrinidae (Clark 1923; Roux 1974, 1985a, 1987; Bourseau & Roux 1989; David & Roux 2000) or Pentacrinitidae (Roux *et al*. 2002, 2009; David *et al*. 2006; Hemery *et al*. 2013). Hess (2011e) restricted this family to species with a synarthry between primibrachs 1–2. Monotypic *Hypalocrinus naresianus* (**Fig. 7.9B**) is known from the Kermadec Islands, Fiji, Indonesia and the Philippines, although not yet Australia. It is also generally the deepest-living Pacific isocrinid (*sensu lato*), with most records below 900 m (to 2,468 m) (Clark 1923; Bourseau & Roux 1989). Two species of *Neocrinus* occur in the tropical western Atlantic.

Family Cainocrinidae

Figure 7.16

Hess (2011e) distinguished this family on the basis of a cryptosyzygy or synostosis between primibrachs 1–2, a flat synarthry between secundibrachs 1–2, and a cryptosyzygy or symmorphy between secundibrachs 3–4. No specimens have been included in phylogenies using molecular data. *Teliocrinus springeri* (**Fig. 7.16**) is the only extant species and is known only from the northern Indian Ocean with one specimen possibly from Northern Territory waters (Rowe & Gates 1995). It has also been placed in the isocrinid (or pentacrinitid) subfamily Diplocrininae (Roux 1981; Roux *et al*. 2009). Roux *et al*. (2009) recognised two bathymetrically allopatric subspecies.

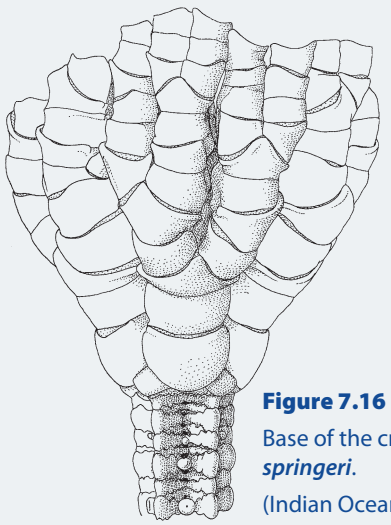


Figure 7.16 Family Cainocrinidae. Base of the crown of ***Teliocrinus springeri***. (Indian Ocean). [from Roux *et al*. 2002]

Table 7.2 Recent taxonomic arrangements of order Isocrinida. Only genera with extant species are included.

† indicates fossil higher-level taxa.

* Simms *et al.* (1993) did not list genera.

Rasmussen & Sieverts-Doreck (1978)	Roux (1981)	Simms (1988)
Order Isocrinida	**Family Pentacrinidae**	**Order Isocrinida**
Holocrinidae †	**Isocrininae**	**Holocrinidae** †
Pentacrinitidae †	*Cenocrinus*	**Pentacrinitidae** †
Isocrinidae	**Balanocrininae**	**Suborder Comatulidina**
Isocrinus (=*Neocrinus* part)	*Hypalocrinus*	**Suborder Isocrinina**
Annacrinus (=*Endoxocrinus* part)	*Neocrinus*	**Isocrinidae**
Cenocrinus	**Diplocrininae**	*Isocrinus* (=*Neocrinus* part)
Chladocrinus (=*Neocrinus* part)	*Diplocrinus*	*Chladocrinus* (=*Neocrinus* part)
Endoxocrinus	*Endoxocrinus*	**Cainocrinidae**
Hypalocrinus	*Teliocrinus*	*Teliocrinus*
Metacrinus	**Metacrininae**	**Isselicrinidae**
Teliocrinus	*Metacrinus*	*Annacrinus* (=*Endoxocrinus* part)
Proisocrinidae	*Saracrinus*	*Cenocrinus*
Proisocrinus	**Pentacrinitinae** †	*Diplocrinus* (=*Endoxocrinus* part)
		Endoxocrinus
		Metacrinus
		Saracrinus
		Marsupitidae †
		Unitacrinidae †
		Suborder Bourgueticrinina

Family Isselicrinidae

Figure 7.17

Primibrachs 1–2 articulate via a cryptosyzygy or synostosis, and secundibrachs 1–2 are joined by either a cryptosyzygy or muscular articulation. The two extant subfamilies, Diplocrininae and Metacrininae, include the majority of isocrinids *sensu lato* (18 species plus 4 subspecies). The former is the most widely distributed group of Isocrinida: in the western Atlantic and western and central Pacific oceans (Roux *et al.* 2002; David *et al.* 2006), chiefly at depths of 200–900 m, with one species (*Endoxocrinus wyvillethomsoni*) in the deep north-eastern Atlantic (1,200–2,070 m). Metacrininae is restricted to the Indo-western Pacific. *Metacrinus rotundus* has been collected as shallow as 100 m off Japan.

Both subfamilies are known from Australian waters. In Diplocrininae, brachitaxes usually have fewer than five brachials beyond the primibrachs, no transverse primibrachial synarthry, and stalk symplexies with lanceolate areolas opened outward and with relatively few crenellae (usually fewer than eight per interpetaloid zone). *Endoxocrinus* includes western Pacific *Endoxocrinus alternicirrus* (**Fig. 7.17A–D**). Subspecies *E. a. sibogae* is known from eastern Tasmania north to Tonga and the Philippines at depths of 364–970 m.

Subfamily Metacrininae (**Figs 7.3B, 7.17E–H**) includes *Metacrinus* and *Saracrinus* and is characterised by

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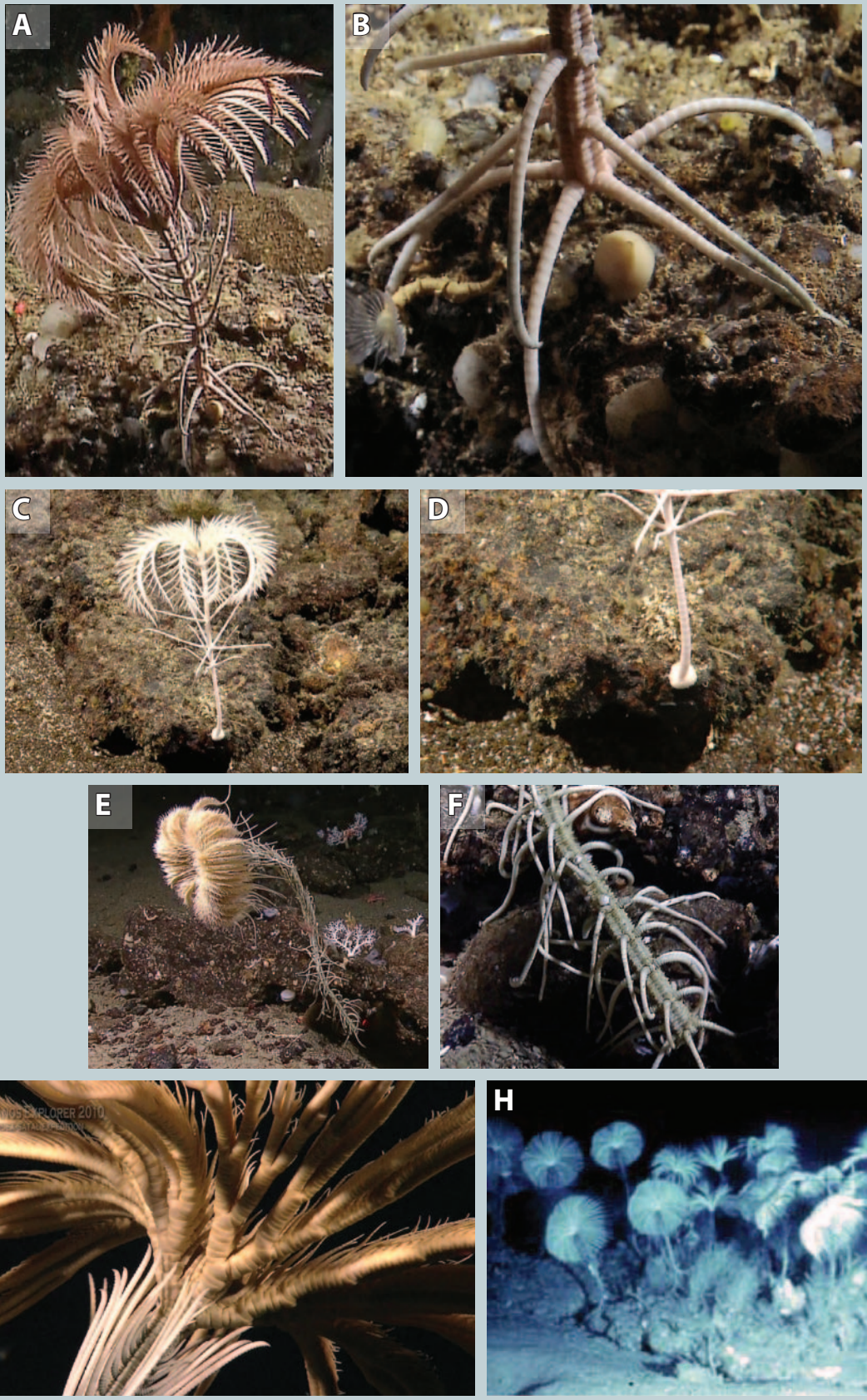
Klikushin (1992)	Simms *et al.* (1993) *	Hess (2011e)
Order Pentacrinida	**Order Isocrinina (*sic*)**	**Order Isocrinida**
Holocrinidae †	**Isocrinidae** (paraphyletic)	**Suborder Pentacrinitina**
Pentacrinidae †	**Cainocrinidae** (paraphyletic)	**Pentacrinitidae** †
Isocrinidae	**Isselicrinidae**	**Eocomatulidae** †
Balanocrininae †	**Proisocrinidae**	**Suborder Isocrinina**
Diplocrininae		**Isocrinidae**
Annacrinus		**Isocrininae**
Diplocrinus		*Hypalocrinus*
Endoxocrinus		*Neocrinus*
Teliocrinus		**Balanocrininae** †
Isocrininae		**Cainocrinidae**
Hypalocrinus		*Teliocrinus*
Neocrinus		**Isselicrinidae**
Isselicrininae †		**Isselicrininae** †
Metacrininae		**Diplocrininae**
Cenocrinus		*Cenocrinus*
Metacrinus		*Endoxocrinus*
Saracrinus		(incl. *Annacrinus*, *Diplocrinus*)
		Metacrininae
		Metacrinus
		Saracrinus
		Proisocrinidae
		Proisocrinus

primibrachial series of 4–7 ossicles (**Figs 7.9D, 7.17G**). Eight species have been recorded in Australian waters (Rowe & Gates 1995). Améziane-Cominardi (1991) treated the best known, *Metacrinus cyaneus*, as a junior synonym of *M. rotundus*, otherwise known from Japan and the south China Sea. This species has been collected along the eastern and south-eastern coasts from Lady Musgrave Island, Queensland, to Cape Everard, Victoria, and off Port Hedland, Western Australia. It is distinctively coloured either uniformly blue or with a blue stalk and pale yellow-white crown tinged with orange. It forms extensive patches on ridges off eastern Bass Strait (**Fig. 7.17H**). Améziane & Roux (2001) mentioned specimens of *Metacrinus* aff. *wyvillii* and *Saracrinus nobilis* from seamounts south of Tasmania. Three other species are known only marginally from Australian waters, *viz.*, *Metacrinus interruptus* from the Timor Sea, *M. nodosus* off Norfolk Island, and *Saracrinus varians* from Wanganella Bank in the Tasman Sea.

Family Proisocrinidae

Figure 7.18

The sole species, *Proisocrinus ruberrimus*, differs from other isocrinids in having only the proximal (upper) portion of the long stalk heteromorphic with nodals that bear only rudimentary cirri, and columnals that alternate in size (**Fig. 7.18**). The middle and distal stalk consists of similar columnals without nodals. All stalk



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Figure 7.17 Family Isselicrinidae.

A–**D**, ***Endoxocrinus alternicirrus***.
A, specimen clinging to the seafloor using only distal cirri.
B, closeup of distal stalk in **A**.
C, juvenile still attached to the seafloor via terminal holdfast.
D, closeup of distal stalk and holdfast in **C**.

E, **F**, unidentified species in subfamily Metacrininae from Indonesia.
E, specimen with crown orientated relative to a weak horizontal flow from the right, but not with fully expanded parabolic filtration fan.
F, closeup of distal stalk showing multiple whorls of cirri used for anchoring.

G, base of the crown of a member of subfamily Metacrininae, possibly ***Saracrinus angulatus***.

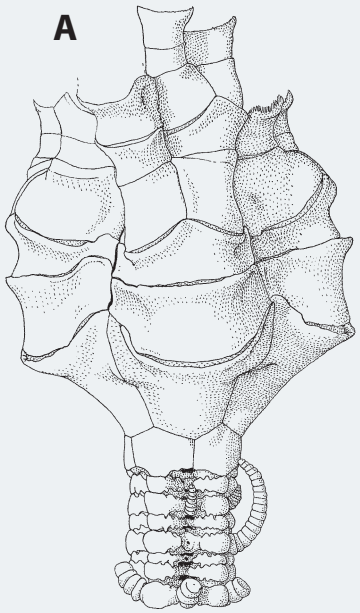
H, a crowd of ***Metacrinus rotundus*** (formerly ***M. cyaneus***) from the rim of a canyon in eastern Bass Strait, Australia, at about 200 m depth; 1996.

(A–G, Indonesia; H, Australia)

[A–G, courtesy of V.Tunnicliffe from Tunnicliffe *et al*. 2015; H, CSIRO]

articulations are symplexies with no cryptosymplexies between nodals and infranodals. It anchors via a terminal attachment disc. Non-muscular articulations between primibrachs and secundibrachs 1–2 are synostoses; all other ray articulations are muscular.

Rasmussen (1978) placed *P. ruberrimus* in a monotypic Proisocrinidae in order Isocrinida. Roux (1980) and Bourseau *et al*. (1991) considered it an extant representative of Millericrinidae due to the absence of cryptosymplexies, the multiradiate facets in the distal column, and the resemblance to the Jurassic millericrinids *Angulocrinus* and *Millericrinus*. However, sequence data offer strong support for placement within Isocrinida (Rouse *et al*. 2013). The species is known from the East China Sea, Philippines, Indonesia, and from New Caledonia to French Polynesia at depths of 800–1,900 m (Bourseau *et al*. 1991; Tunnicliffe *et al*. 2015).



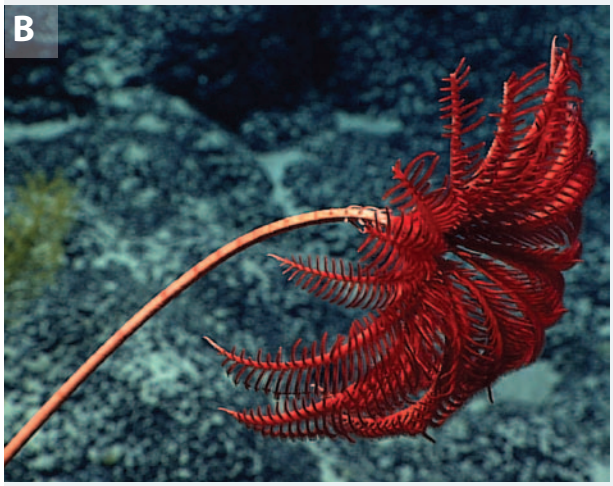


Figure 7.18 Family Proisocrinidae.

Proisocrinus ruberrimus is found in the tropical western Pacific in deep water.
A, base of the crown.
B, specimen showing the rudimentary cirri along the proximal stalk.

[A, from Roux *et al*. 2002; B, NOAA Okeanos Explorer 2015, Hohonu Moana: Exploring the Deep Waters Off Hawaii]

Order COMATULIDA

Comatulids traditionally included those living crinoids that shed the stalk following an attached postlarval (pentacrinoid) stage (**Fig. 7.12; Box 7.2**) and retain only the topmost ossicle, the centrodorsal, which typically bears whorls of anchoring cirri (for example, **Figs 7.3C, 7.10, 7.11D, 7.19E, 7.20B,C, 7.26, 7.27, 7.32**). They are informally referred to as feather stars, or incorrectly as 'unstalked' crinoids. However, recent molecular phylogenies nest members of two former stalked crinoid suborders, Bourgueticrinina and Guillecrinina, within Comatulida, so that the only morphological feature that currently unites the group is a postlarval stalk with synarthrial articulations that may persist in an adult stalk lacking true cirri (Hess & Messing 2011c). The feather stars are thus paraphyletic. However, juvenile Isocrinida also have synarthrial stalk articulations (Simms 1989), so it remains unclear what morphological feature uniquely unites members of Comatulida. The order diversified substantially through the Cenozoic Era and now represents the most diverse extant crinoid group with ~591 accepted species (542 feather stars plus 49 stalked). However, the Cenozoic fossil record consists largely of fragmentary and dissociated remains (for example, Moore & Vokes 1953; Meyer & Macurda 1977; K.J.S.Purens, unpublished data; K.J.S.Purens & T.K.Baumiller, unpublished data).

In feather stars, the centrodorsal develops as an enlarged uppermost columnal, but fossil forms suggest that it originated from a series of fused columnals. The basal ossicles form a complete circlet in postlarvae and some juveniles, but almost always become modified as a delicate internal ossicle (the rosette) that roofs the centrodorsal cavity (**Fig. 7.10**). The rosette can be accompanied by five rod- or tongue-like basal rays that lie between the centrodorsal and radial circlet. Members of Atelecrinidae retain a complete basal circlet as adults (**Fig. 7.40A**). The visceral mass rests on the radial circlet and ray bases; it can be naked, plated or variously invested with small ossicles. Rays are undivided in members of three families (**Figs 7.33–7.35**); in other groups they divide one or more times to produce 10–200 arms. Ray length varies from 30 to 500 mm. Pinnules and cirri vary widely in form and size, and have provided important diagnostic characters at several taxonomic levels.

Anatomy and development were treated in detail and summarised by Hyman (1955), Holland (1991) and Heinzeller & Welsch (1994). Feather stars are the only extant crinoids that occur in shallow water, but they can be found from intertidal to abyssal depths. They occur in all the world's oceans and seas except the Baltic Sea and Black Sea (Clark 1931). Many are brightly coloured, and some can swim by means of graceful arm undulations. Colour patterns can be specific or highly variable.

In the former bourgueticrinine stalked crinoids, articulations between columnals are synarthries, although shorter, often discoidal columnals near the top of the stalk can articulate via synostoses or symplexies (**Fig. 7.3D**). The stalk terminates in either an irregular attachment disc for hard substrates or a root-like radix arising from several distal columnals for anchoring in sediments. Some species can develop either form. Cirri are absent, and the calyx ranges from low and wide through conical, to tall and cylindrical. The five basal ossicles can be distinct, fused, internalised or reduced. There are five radials, although occasional specimens can have fewer or more, and *Porphyrocrinus daniellalevyae* from the western Atlantic may develop at least 15 (Messing 2016). Rays are undivided or divide once at primibrach 2 or distally. Ligamentary articulations in the rays exhibit several forms, but syzygies are absent. Fossils date to the Upper Cretaceous.

Gislén (1924) first suggested that Bourgueticrinidae (treated by him as an extinct family ancestral to extant Bathycrinidae) arose from Early Cretaceous Thiollericrinidae. Rasmussen (1978) and Simms (1988) specified a paedomorphic origin, but the former suggested a comatulid ancestor and the latter either an isocrinid or comatulid ancestor; Simms *et al.* (1993) later focused on a comatulid ancestor. However, Roux (1977) and Pisera & Dzik (1979) retained them within Millericrinida following Gislén (1938). Molecular phylogenies (Hemery *et al.* 2013; Rouse *et al.* 2013) have nested these stalked taxa within Comatulida, reinforcing the paedomorphic hypothesis (**Fig. 7.13**). Similarly, molecular data nest stalked Guillecrinidae, placed in its own suborder Guillecrinina by Hess

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(2011g), within Comatulida as sister to the feather star *Pentametrocrinus*, leading Rouse *et al*. (2013) to eliminate the suborder.

Unlike other articulate crinoids, classification of Comatulida is based largely around superfamilies (Clark 1931, 1947; Clark & Clark 1967; Rasmussen 1978). As with Isocrinida, higher-level taxonomy remains unsettled (for example, Rasmussen 1978; Simms *et al*. 1993). The most recent morphological classification (Hess & Messing 2011c) recognised six extant superfamilies and 24 families (including stalked forms). A.H.Clark's monumental, seven-part monograph (1915, 1921, 1931, 1941, 1947, 1950, 1967; the last co-authored by A.M.Clark) forms the foundation for current taxonomy at species to family levels. Molecular phylogenies have returned some family-level taxa as monophyletic clades and others as polyphyletic (Hemery *et al*. 2013; Rouse *et al*. 2013; **Fig. 7.13**). Among extant forms, only Comatulidae (formerly Comasteridae), which dominates reef environments worldwide, has been subjected to substantial recent revision (Hoggett & Rowe 1986a; Rowe *et al*. 1986; Messing 2001; White *et al*. 2001; Summers *et al*. 2014). All others are clearly in need of reappraisal. Morphological taxa dissolved by sequence data are therefore indicated below in quotation marks ('…') pending formal revision. Sixteen morphological families occur in Australian waters.

H.L.Clark (1938, 1946) carried out the first major research specifically on the Australian fauna. Subsequent taxonomic work includes that of A.M.Clark (1966, 1975), Rowe & Pawson (1977), Hoggett & Rowe (1986a) and Rowe *et al*. (1986). Clark & Rowe's (1971) key to shallow-water Indo-west Pacific echinoderms is a useful guide to those feather stars that fall within its geographical limits, although their treatment of the Comatulidae is now obsolete (see Hoggett & Rowe 1986a; Rowe *et al*. 1986; Messing 2001; Summers *et al*. 2014). Feather stars are conspicuous and diverse members of the invertebrate fauna on the Great Barrier Reef, and the ~57 species recorded from Lizard Island represent the greatest concentration of crinoid species of any site on Earth. Recent work has also described crinoid assemblages on sediment substrates in Moreton Bay (Stevens & Connolly 2003) and Lizard Island (Messing *et al*. 2006).

Family Comatulidae

(formerly Comasteridae)
Figure 7.19

Sequence-based phylogenies return this family as monophyletic and sister to family Thalassometridae ('Tropiometroidea') (Hemery *et al*. 2013; Rouse *et al*. 2013). Under its former name, it was placed alone in a superfamily Comasteroidea. At least one pair of oral pinnules bear one or a pair of blades or knobs on the distal segments that together produce a comb-like structure (**Figs 7.6B, 7.10**). A calcareous deposit plugs the central lumen of the radial circlet. Uniquely among feather stars, the mouth in most species lies near the margin of the oral surface, whereas the anal papilla is central, reflecting a unique configuration of the gut (**Fig. 7.19A**). In other feather stars, which have a central mouth, the intestine makes a single clockwise coil from the mouth to the off-centre anal papilla (**Fig. 7.4**). In comatulids with a marginal mouth, the intestine first runs to the centre of the visceral mass, then angles to the margin from where it runs inward in four clockwise coils to the central anus (A.H.Clark 1915). In at least some taxa, the posterior arms (opposite the mouth) are substantially shorter and bear the gonads (or at least better-developed ones); whereas the anterior arms, that arise closest to the mouth, are longer and are the primary feeding appendages. The centrodorsal is usually disc-shaped with marginal cirri, although several genera include species with a reduced, often pentagonal or stellate centrodorsal and few or no cirri (**Fig. 7.11B**). Most also feel 'sticky' when handled due to the numerous proximally-directed hooks on the middle and distal pinnules. Species range from small, delicate and ten-armed to massive forms with up to 200 arms (**Fig. 7.19B**). Ten-armed *Alloeocomatella pectinifera* has anterior rays up to 500 mm long, the longest of any extant crinoid (although its posterior rays are only about 200 mm long) (**Fig. 7.19C**). Important taxonomic characters have included ray branching patterns (**Fig. 7.11**), locations of proximal syzygial articulations, form and distribution of combed pinnules, and number and form of cirri. However, Summers *et al*.'s (2014) sequence-based reconstruction has reduced the usefulness of some of these features and returned several clades that so far lack any morphological synapomorphies.

The family currently includes ~95 accepted species in 21 genera. Summers *et al*. (2014) recognised two subfamilies. Comatellinae (4 genera) and Comatulinae, the latter divided into five tribes: Comatulini (2), Capillasterini (1), Comasterini (5), Neocomatellini (2), and Phanogeniini (3). Four other genera were not included and treated as *incertae sedis*. Three other species cannot yet be assigned satisfactorily to genus.

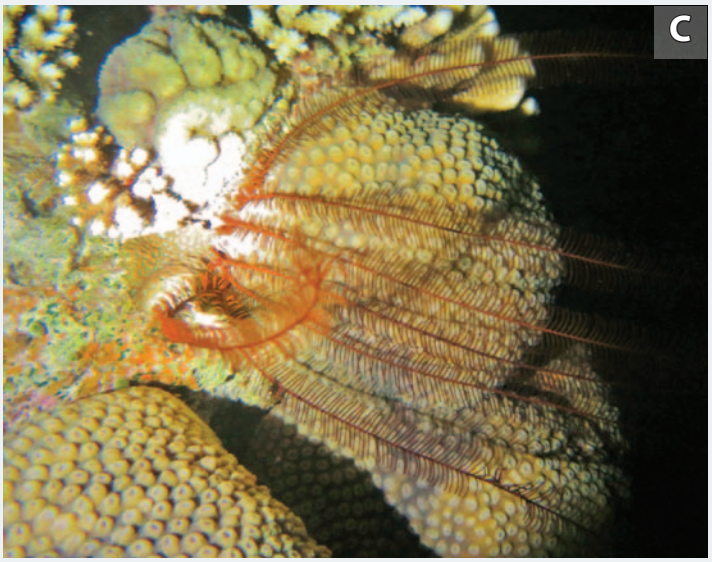
Thirteen genera are restricted to the tropical Indo-west Pacific: *Alloeocomatella*, *Anneissia*, *Aphanocomaster*, *Capillaster*, *Clarkcomanthus*, *Comatula*, *Comaster*, *Comatella*, *Comanthus*, *Comatulides*, *Palaeocomatella*, *Phanogenia*, *Rowemissia*, and the three species *incertae sedis*. *Cenolia* is chiefly confined to the southern coast of Australia, New Zealand and Lord Howe Island. *Comatulella* is endemic to southern Australia. *Nemaster*, *Davidaster* and *Comatilia* occur in the tropical western Atlantic Ocean, and *Neocomatella* occurs both there and in the north-eastern Atlantic and Mediterranean Sea. *Comissia* and *Comactinia* are the only genera currently recognised to occur in both the tropical western Atlantic and Indo-west Pacific. However, *Comissia* is heterogeneous and likely does not represent a clade (Messing 2001, 2003a).

The Australian fauna includes 45 species in 12 genera, both subfamilies and all tribes (Messing 1995, 1998; Rowe & Gates 1995; Summers *et al*. 2014). All of the tropical Indo-west Pacific genera, except *Comatulides*, *Aphanocomaster*, *Palaeocomatella*, *Rowemissia* and the three species *incertae sedis*, occur in Australian waters. All are found in the relatively shallow waters of the continental shelf (<200 m), with many reaching the lower intertidal zone and only a few extending beyond shelf depths. In a molecular phylogenetic examination of the five *Cenolia* species that dominate the southern Australian shallow crinoid fauna, Naughton *et al*. (2014a) removed *C. benhami* to *Oxycomanthus* (now *Anneissia*), resurrected *C. novaezealandiae* from synonymy, and added three undescribed species, almost doubling the number of *Cenolia* species in the region. The other named species are *C. trichoptera*, *C. tasmaniae* and *C. glebosus*. The former two are understood to occur across the entire southern Australian coastline (Byron Bay, New South Wales, to Trigg Island, Western Australia) and *C. glebosus* from Mooloolaba, Queensland, to Broughton Island, New South Wales, including Lord Howe Island (Rowe & Gates 1995).





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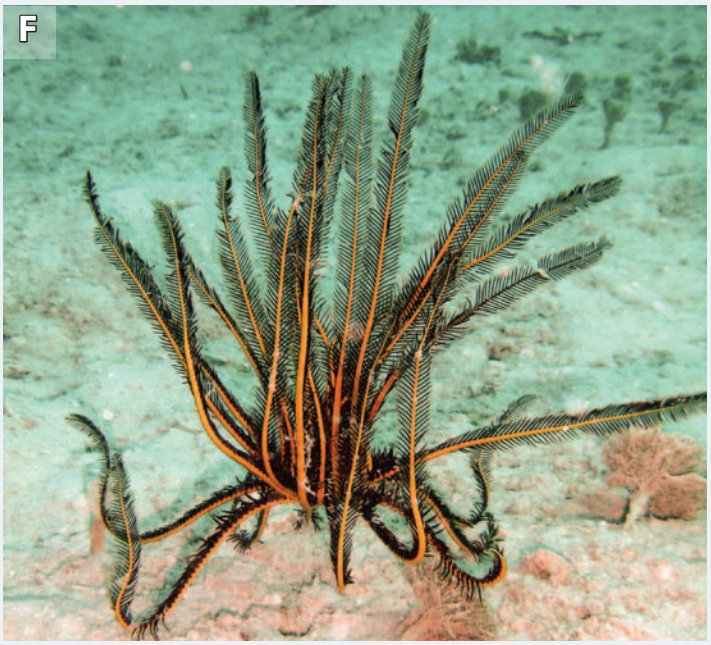


Figure 7.19 Family Comatulidae.

A, ***Comatula*** cf. ***pectinata***, oral surface (disc) showing excentric mouth, marginal ambulacral groove, and central anal papilla.

B, ***Comaster schlegelii*** develops as many as 200 arms that it arrays in a series of irregular overlapping bushy fans. Moderately developed cirri are lost in larger specimens that use some of their arms and pinnules for anchoring.

C, ***Alloeocomatella pectinifera*** is completely cryptic during the day. It extends several of its ten arms, which may reach 500 mm in length, from a crevice at night.

D, ***Phanogenia gracilis*** is a rheophobic, semicryptic species that hides its central body and shorter arms in a crevice or under a ledge and extends its longer arms for feeding, typically with pinnules arranged in four directions (multidirectional 'tetrad' posture).

E, ***Anneissia bennetti*** typically perches fully exposed on elevated reef topography and arrays its arms in a multi-layered arcuate fan. The cirri are longer and more robust than in any other Australian comatulid.

F, ***Comatula rotalaria*** lacks cirri and dwells on inter-reef sediment substrates. It elevates its calyx by flexing five to eight of its ~10 long interior arms to form shallow U- or V-shapes, while its ~10 shorter exterior arms orientate more or less upward as a central tuft. A few other long arms flex slightly, but do not touch the bottom. It is unique among extant crinoids in having exterior arms that develop from the first pinnule and remain shorter than interior arms.

(A, Singapore; B,F, Lizard Island, Great Barrier Reef, Queensland; C, Maldives Islands; D, Raja Ampat, Indonesia; E, Great Barrier Reef, Queensland)

[A,D, C.G. Messing; B,F, G.W. Rouse; C, F.Ducarme; E, G.Bell]

Comatulidae reaches greatest diversity in coral reef habitats and often constitutes a large proportion of the crinoid fauna (Fabricius 1994; Messing 1994), for example, 27 of the 57 species recorded at Lizard Island, Great Barrier Reef (A.Hoggett & L.L.Vail, unpublished data). Many species are semicryptic within the reef infrastructure, at least during the day, typically exposing only their longer anterior arms and orientating their pinnules in a tetrad, multidirectional posture not found in other feather star families (for example, *Clarkcomanthus littoralis*, *Phanogenia gracilis* (**Fig. 7.19D**) (Meyer & Macurda 1980). Others, which are fully or mostly exposed at all times (for example, *Anneissia bennetti*, *Clarkcomanthus alternans*, *Comaster schlegelii*, and *Comaster audax*) (**Fig. 7.19B,E**) or perch completely in the open at night (*Alloeocomatella polycladia*), tend to have symmetrical rays. Continuously exposed species appear to regulate their feeding activity according to current flow (Meyer & Macurda 1980). They include species that anchor using numerous strong cirri (for example, *A. bennetti*) and others that lack cirri and use arms and pinnules for attachment (for example, *Comanthus alternans*). Semicryptic species tend to become more exposed at night, whereas a few that are completely concealed during the day become partially exposed at night (*Clarkcomanthus comanthipinna* and *Alloeocomatella pectinifera* (Vail 1987b; Messing 1995; **Fig. 7.19C**). At Enewetak Atoll, Zmarzly (1984a) found that population distributions (including perch fidelity) of exposed *A. bennetti* and *Comaster schlegelii* remained virtually constant over a six-month study, with no recruitment, mortality or emigration, and only three instances of immigration into the study sites.

Reproduction has been studied thoroughly only in the Japanese *Anneissia japonica* (formerly *Comanthus japonica*), but this species is unusual in having females that contain viable gametes on only one day each year (Holland 1991). On the Great Barrier Reef, isolated spawning events have been observed at night in *Phanogenia gracilis*, *Comanthus parvicirrus*, *Comanthus wahlbergii* and *Comatella nigra* during summer (Babcock *et al*. 1992), and in *A. bennetti* during winter (Meyer *et al*. 1984). At Lizard Island, feather stars settle into artificial reef interstices throughout the year, although numbers of settling individuals are much lower during winter (June to August), and settlement density varies markedly between sites (A.Hoggett, unpublished data).

As in other echinoderm groups, feather stars associated with coral reefs are normally restricted to that habitat. However, an inter-reef, soft-bottom fauna at Lizard Island includes species typical of reefs (*Comatella nigra* and *Comaster schlegelii*) as well as some that are never found on reefs (*Comatula rotalaria*; **Fig. 7.19F**) (Messing *et al*. 2006). Most temperate Australian species occur on rocky substrates. *Cenolia* species are partially concealed during the day (Rowe *et al*. 1986), whereas *Comatulella brachiolata* uses its highly modified pinnules and cirri to cling to other organisms (Clark 1931).

Superfamily HIMEROMETROIDEA
(formerly Mariametroidea)

The morphology-based classification includes five families: Himerometridae (5 extant genera), Mariametridae (7), Colobometridae (18), Zygometridae (2) and Eudiocrinidae (1) (Clark 1941, 1947). Miocene *Discometra* has also been placed in Himerometridae. Most characters listed by Hess & Messing (2011c) are either found in some other groups of Comatulida (for example, centrodorsal low hemispherical to discoidal; aboral apex cirrus-free; centrodorsal cavity narrow to moderate; radial circlet with a calcareous plug), are treated as diagnostic by their absence (for example, no aboral star; no pinnule comb; genital and distal pinnules not carinate), or are variable (keel on basal segments of proximal pinnules present or not). Other features are listed with exceptions (for example, radial articular facet with wide midradial furrow with or without median ridge, except in *Cyllometra*). Hemery *et al*.'s (2013) molecular phylogeny returned the superfamily as monophyletic except for Eudiocrinidae. Of the two genera formerly included in Zygometridae, molecular data nest *Zygometra* within Himerometridae and separate *Catoptometra* as a non-himerometroid (Taylor 2015; K.Taylor, C.G.Messing & G.W.Rouse, unpublished data). Representatives of Himerometridae (including *Zygometra*), Mariametridae and Colobometridae all have shallow radial coelomic depressions or radiating furrows on the adoral centrodorsal surface and corresponding aboral radial ossicle surface, which may represent a synapomorphy; neither Eudiocrinidae nor *Catoptometra* exhibit these

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features (A.H.Clark 1915). Many genera have one or more enlarged or stiffened oral pinnules that ostensibly contribute to protecting the visceral mass, but the feature is widely variable. Mutual relationships of the four families based on molecular data differ in Rouse *et al*. (2013) versus Hemery *et al*. (2013), but their trees include only seven and nine terminals, respectively.

Most species occur from southern Japan to Australia; a few reach the Red Sea and South Africa, and one colobometrid occurs in the tropical western Atlantic (Clark 1947). All four families recognised within Himerometroidea here have Australian representatives.

Family Himerometridae

Figure 7.20

Himerometrids have primibrachs united by synarthry (syzygy in *Zygometra*; **Fig. 7.20C**), cirrals smooth or with a median aboral spine or carina, IIBr series usually of four ossicles, usually extremely short, almost disc-like brachial ossicles, and more than ten arms. The family includes four genera: *Himerometra* (3 species), *Heterometra* (28), *Homalometra* (1), *Craspedometra* (1), and *Zygometra* (5). Many species are distinguished on the basis of minor, variable morphological characters, and over a third were described from only three or fewer specimens. Taylor (2015) and K.Taylor, C.G.Messing & G.W.Rouse (unpublished data) returned three *Zygometra* species (formerly in Zygometridae) as a clade nested within Himerometridae and sister to several species of *Heterometra*. Morphologically, *Zygometra* species differ from *Himerometra* only in having a syzygy rather than a synarthry in the IBr2 series. They also returned *Amphimetra*, included in Himerometridae by Clark (1941), within Mariametridae. Unlike other himerometrids, *Amphimetra* species develop only ten arms. In the rare cases in which specimens develop more than ten arms, the IIBr series consist of two ossicles as in Mariametridae, although specimens often exhibit extremely short, disc-like brachials as in *Himerometra robustipinna*.

The family ranges from the Red Sea and East Africa to Japan, Australia and the south-western Pacific Ocean (Fiji, Tonga and New Caledonia), but it has not been

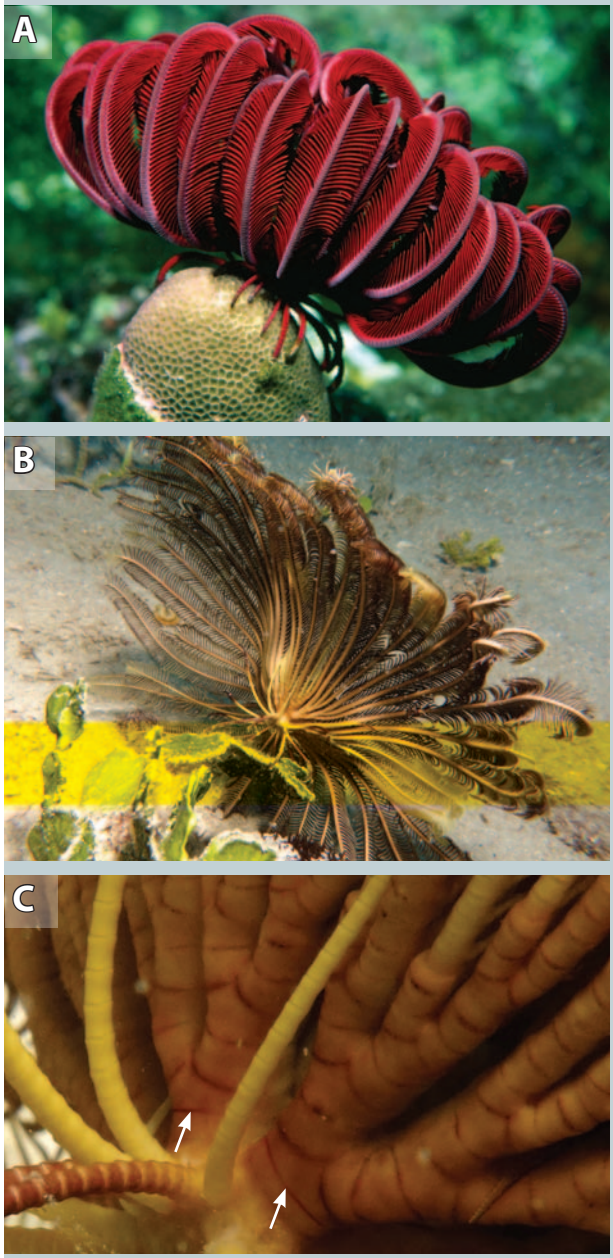


Figure 7.20 Family Himerometridae.

A, ***Himerometra robustipinna*** with its arms curled in a meridional posture, reflecting weak flow conditions.

B, **C**, ***Zygometra microdiscus***:
B, animal with arms arrayed in a parabolic fan clinging to calcareous green alga, ***Halimeda*** sp., on sediment and rubble substrate between reefs at Lizard Island, Great Barrier Reef, Queensland.
C, close-up of same animal with arrows indicating the diagnostic syzygies in the primibrachial series IBr2(1+2).
(A, Indonesia)

[A, G.Bell; B,C, L.L.Vail]

recorded from Palau or Micronesia. Himerometridae includes 37 nominal species in five genera but, as with the other himerometroid families, species-level distinctions are often based on ontogenetically variable features or minor morphological distinctions (Clark 1941), so that many taxa could prove to be synonymous. Eleven species in four genera are known from tropical Australia: *Himerometra* (2), *Heterometra* (4), *Homalometra* (1) and *Zygometra* (4). The single species of *Homalometra*, *H. denticulata*, is known only from the Arafura Sea off the Northern Territory and eastern Indonesia (Rowe & Gates 1995).

Himerometra is represented in Australian waters by *H. robustipinna* (including its junior synonyms *H. magnipinna*, *H. martensi* and *H. bartschi*) (Rouse *et al*. 2006; Taylor 2015; K.Taylor, C.G.Messing & G.W.Rouse, unpublished data), which is common on upper and mid-reef slopes (Vail 1989b), perching in the open day and night on elevated corals or rock substrates that are often subject to substantial currents and surge (**Fig. 7.20A**). The arms either curl in above the disc, or extend in a deep bowl or funnel, or a radial or biplanar fan. A specimen attributed to *Himerometra persica* recorded from Lizard Island (Rowe & Gates 1995) is probably a juvenile *H. robustipinna*. Another, from Heron Island (USNM E34998) is a small *Zygometra* cf. *punctata*. The type specimens of *H. persica* are correctly placed in *Heterometra* (Taylor 2015; K.Taylor, C.G.Messing & G.W.Rouse, unpublished data).

Heterometra comprises 28 nominal, often poorly circumscribed, tropical Indo-West Pacific species, four of which have been recorded from Australia, *viz*., *H. crenulata*, *H. nematodon*, *H. quinduplicava* and *H. sarae* (Rowe & Gates 1995). Records of *H. crenulata* extend from Montebello Island, Western Australia, to Double Island Point, Queensland, chiefly in less than 20 m (Clark 1941; Rowe & Gates 1995). *Heterometra sarae* is known only from Ashmore Reef in the Timor Sea, and *H. nematodon* and *H. quinduplicava* occur in Queensland waters at depths less than 40 m. Only *H. crenulata* has been observed *in situ* in Australia. A single specimen found coiled beneath rubble on sediment off Lizard Island flexed its arms aborally upon exposure (Messing *et al*. 2006).

In Australian waters, four species of *Zygometra* — *Z. microdiscus* (including *Z. elegans*), *Z. comata*, *Z. andromeda* and *Z. punctata* — range chiefly from around Fremantle, Western Australia, across the north coast, and down the east coast to Sandon Bluffs, New South Wales, at depths less than 50 m. However, *Z. andromeda*, previously known only from Sri Lanka (Clark 1941), has been collected off the North West Shelf, Western Australia, at depths of 50–146 m (Rowe & Gates 1995). It is distinguished from *Z. comata* only by having the distal edges of the proximal ray ossicles thickened, everted and finely scalloped or tuberculate (Clark 1941).

Specimens attributed to the smaller species (<40 arms; <40 cirrals), *Z. punctata* and *Z. comata*, on the northern Great Barrier Reef either cling near the bases of gorgonians, to the edge of soft corals, or extend their arms from crevices. By contrast, Messing *et al*. (2006) observed *Z. microdiscus* at Lizard Island clinging to macroalgae and small rocks on a sediment bottom in 16–17 m with arms orientated in a parabolic filtration fan with some lower arm tips touching the sediment (**Fig. 7.20B,C**). C.G.Messing & G.W.Rouse (personal observation) observed a large *Z. microdiscus* walking on its arm tips on sediment at night, its centrodorsal elevated enough to permit clearance for its long (>50 mm) cirri. Crinoids provisionally identified as *Z. microdiscus* reach local densities of 20 per square metre on sediment bottoms in Moreton Bay, southern Queensland (Stevens & Connolly 2003).

Family Colobometridae

Figure 7.21

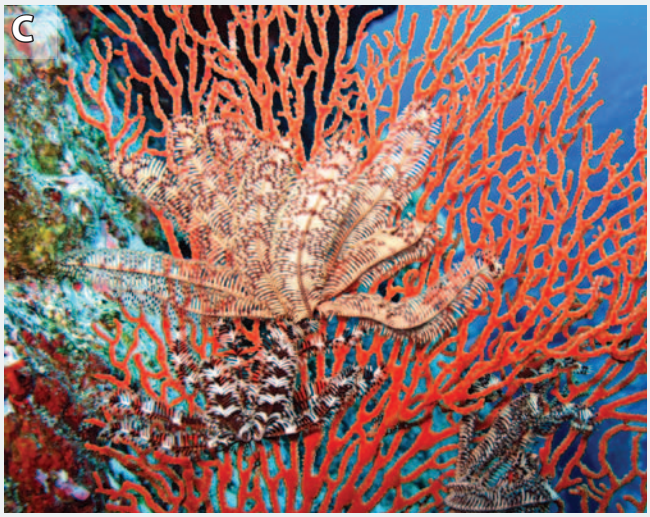
Taxonomy of Colobometridae based on morphology distinguishes 18 genera and approximately 48 species worldwide (A.H.Clark 1947; A.M.Clark 1951; Hess & Messing 2011c). However, species in genera containing multiple species (for example, *Iconometra*, *Decametra*, and *Cyllometra*) are again largely based on minor, variable characters, for example numbers and proportions of cirrals, and relative lengths and numbers and proportions of pinnulars of proximal pinnules. Size and form vary markedly, from small 10-armed taxa (for example *Decametra* and *Oligometra* species) to *Pontiometra andersoni*, which has as many as 120 arms up to 180 mm in length (Clark 1947).

Recent molecular data have altered the composition of the family to the point that the primary morphological

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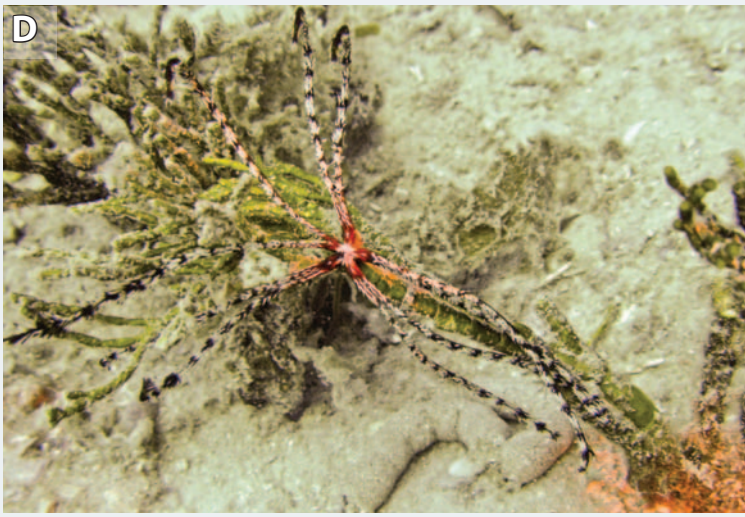


Figure 7.21 Family Colobometridae.

A, two ***Cenometra bella*** clinging to an octocoral with arms arrayed in a parabolic filtration fan (current flow from right to left).

B, three ***Colobometra perspinosa*** clinging to an octocoral with arms arrayed in a radial filtration fan.

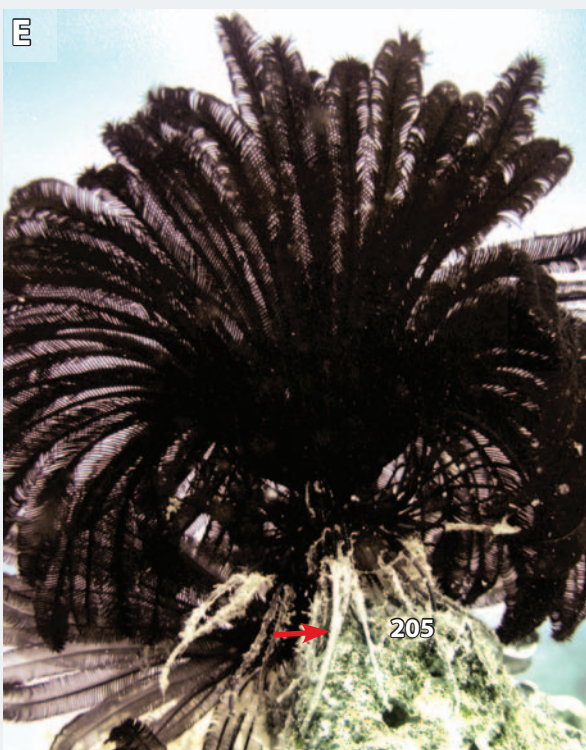
C, three ***Oligometra serripinna*** clinging to an octocoral fan with arm orientations suggesting flow upward from below.

D, ***Oligometra carpenteri*** clinging to the green alga ***Halimeda*** sp. on sediment between reefs, with pinnules pressed against arms, and pairs of adjacent arms chiefly orientated roughly in parallel along algal axis.

E, ***Pontiometra andersoni*** clinging to a rock pinnacle with arms arrayed in a parabolic filtration fan. Arrow indicates one of many long cirri (this one covered with sediment).

(All images from Lizard Island, Great Barrier Reef, Queensland)

[G.W.Rouse]



character — at least some cirrus segments with a pair of transversely orientated aboral spines or tubercles, or one or two transverse ridges, is no longer diagnostic of all genera. Remaining characters are found among a wide range of feather stars, for example 10 or more arms, radial articular facets steep, and IIBr and following brachitaxes of two or four ossicles, or vary within the family, for example interarticular ligament fossae moderate and triangular to large and high (Clark 1941; Hess & Messing 2011c). Hemery's (2011) trees placed *Iconometra anisa* (the only member of the genus examined) outside Colobometridae as sister to Aporometridae, and this clade sister to a group of Antedonidae.

Of the genera included on morphological grounds, *Pontiometra*, *Basilometra*, *Cenometra*, *Colobometra*, *Decametra*, *Iconometra*, *Oligometrides*, *Oligometra* and *Petasometra* are tropical Indo-west Pacific, chiefly at depths less than 50 m. Some species penetrate to about 150 m. *Alisometra*, *Clarkometra*, *Cyllometra* and *Epimetra* occur in the same region but at depths of about 70–200 m; *Embryometra* and *Gislenometra* occur off south and south-eastern Africa at 238–567 m; *Austrometra* is endemic to south-eastern Australia, and *Analcidometra* is restricted to the tropical western Atlantic Ocean. The last four genera are all monotypic (Clark 1947).

Fourteen species in 10 genera are known from Australian waters: *Austrometra* (1 species), *Basilometra* (1), *Cenometra* (1), *Colobometra* (1), *Decametra* (3), *Iconometra* (1), *Oligometra* (2), *Oligometrides* (1), *Petasometra* (2), *Pontiometra* (1). All are tropical shelf taxa except *Austrometra thetidis*, which is restricted to the temperate eastern coast from central New South Wales to Tasmania in waters 60–360 m deep (Rowe & Gates 1995).

Cenometra bella (**Fig. 7.21A**), *Colobometra perspinosa* (**Fig. 7.21B**), *Basilometra boschmai*, *Oligometra serripinna* (**Fig. 7.21C**), *O. carpenteri* (**Fig. 7.21D**), *Petasometra clarae*, *Oligometrides adeonae* and *Pontiometra andersoni* (**Fig. 7.21E**) have been observed *in situ* and, in Australian waters, cling fully exposed to elevated perches. The first four typically form radial fans and cling to gorgonian octocorals, although *O. serripinna* also attaches to soft corals and other benthos (Vail 1988, 1990). *Pontiometra andersoni* forms a parabolic filtration fan atop prominent coral heads or pinnacles and uses its extremely long cirri to further elevate itself (Meyer & Macurda 1980; Messing 2007). *Petasometra clarae* displays a clear preference for soft corals (Vail 1989b), and at Madang, Papua New Guinea, it forms biplanar arcuate or irregular radial fans, the latter when subject to substantial surge (C.G.Messing, unpublished data). *Oligometrides adeonae* clings to algae on sediment bottoms with its ten arms arranged in a radial or shallow parabolic fan. *Oligometra carpenteri*, which is more abundant in deeper water than *O. serripinna* (22–25 m compared to 6–19 m), can assume a radial fan posture, but it usually extends its arms in pairs parallel to the branches of its octocoral or macroalgal perch, with the pinnules pressed against the arms, at least during the day, perhaps as a means of camouflage (Vail 1990; Messing *et al*. 2006).

Oligometra serripinna is the best studied and perhaps most common shallow-water colobometrid in Australian waters. Vail (1988) recorded densities reaching 200 individuals per 100 square metres in northern Australia. Limited data suggest that adult specimens are at least two years old (Vail 1989a). This species is gonochoric with a 1:1 male:female sex ratio. At Lizard Island it probably has a bimodal reproductive cycle with peaks around February and June (Vail 1987b). Studies of its feeding behaviour include a description of the gut by transmission electron microscopy (LaHaye & Holland 1984), tube foot morphology relative to prey capture (Meyer 1979), effects of current direction on prey capture (Holland *et al*. 1987) and mechanisms of food particle capture and transport (Holland *et al*. 1986).

Family Mariametridae

Figure 7.22

Diagnostic characters of mariametrids include IBr2 united by synarthry, cirrals smooth or with a median aboral spine or carina, IIBr and following brachitaxes of two ossicles only, and usually more than ten arms (Clark 1941; Hess & Messing 2011c). However, the taxonomy and composition of this family is in a state of flux. As examples, molecular sequence data include the former himerometrid *Amphimetra* (Hemery 2011),

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Figure 7.22 Family Mariametridae.

A, ***Dichrometra*** sp. exhibiting nocturnal feeding posture, an arcuate filtration fan.

B, **C**, two specimens attributed to ***Dichrometra brachypecha*** collected at the same location on the same dive at Palau, showing highly variable concentric colour patterns.
B, aboral view of green and white specimen.
C, oral view of orange and white specimen.

D, ***Amphimetra tessellata*** clinging to the green alga ***Udotea*** sp. on sediment between reefs at Lizard Island, Great Barrier Reef, Queensland. It is exhibiting a radial filtration fan posture.

(A, Solomon Islands)

[A, J.Maragos; B,C, C.G.Messing; D, G.W.Rouse]

and place *Lamprometra* and *Liparometra* in synonymy under the senior *Dichrometra* (Taylor 2015; K.Taylor, C.G.Messing & G.W.Rouse, unpublished data).

Mariametrids occur from the Red Sea to Micronesia (a report from the Hawaiian Islands was never confirmed) from the lower intertidal to at least 245 m (Clark 1941). Larger specimens can have 12–50 (usually 15–40) arms up to 150 mm long. Again, many species within genera are currently distinguished on the basis of characters that may vary with growth or environment (for example, numbers of arms, numbers and proportions of cirrals, relative lengths of proximal pinnules), so the actual number of taxa remains unclear.

As an example, Rankin & Messing (2008) reduced six nominal species of *Stephanometra* to two: *S. indica* and *S. tenuipinna*. At least seven species in three genera occur in Australian waters: *Dichrometra* (including *Lamprometra* and *Liparometra*) (4), *Stephanometra* (2) and *Amphimetra* (1). All are restricted to shallow tropical environments. A few older trawl records from deep water are likely to be inaccurate.

Species of *Dichrometra* and *Stephanometra* are nocturnal, usually hiding under ledges, rubble or in crevices during the day with rays coiled, and crawling a metre or more to reach exposed perches at dusk. The typical feeding posture is a biplanar arcuate filtration fan, that is, with the arms of the down-current part of the fan rotated so that the ambulacral grooves face down-current (Meyer & Macurda 1980; **Fig. 7.22A**), although sometimes the arms can be spread in a radial posture more-or-less parallel to the substrate (C.G.Messing, unpublished data). Large individuals sometimes assume feeding postures during the day under reduced light levels under ledges or in tunnels (Meyer & Macurda 1980; Messing 2007). Most night-active individuals are sensitive to light, as even brief illumination from a torch sends them back to their daytime resting places. During a study spanning almost two months, N.G.Wilson (2005) found that 80% of mariametrids consistently returned to the same nocturnal perch.

Colour varies widely, even among specimens attributed to the same species, but most patterns display concentric bands of contrasting colours (**Fig. 7.22B,C**). H.L.Clark (1921) found a group of four *Lamprometra* (now *Dichrometra*) *brachypecha* under a rock at Mer Island, Torres Strait, and wrote: 'When the rock was overturned, the arms would be more or less closed over the mouth, the whole animal appearing like a tuft of green sea-weed, but on being touched the arms instantly and all together were laid back flat against the rock and the broad white band flashed into view. The immediate effect was obliterative and one's first thought was that the animal had vanished. That this reaction is protective seems possible.'

By contrast, *Amphimetra tessellata* occurs exposed almost exclusively, and sometimes abundantly, on sediment substrates between reefs where it clings to macroalgae, sponges or bryozoans and forms a radial or shallow parabolic fan (**Fig. 7.22D**). When disturbed, or perhaps when flow drops below a threshold, the arms close into a funnel, and the pinnules may press against the arms (Messing *et al.* 2006). Multiple partial arm loss in several specimens may represent instances of predation (Schneider 1988). *Amphimetra pinniformis*, recorded in Australia from a single dubious record from Holothuria Banks, off the northern coast of Western Australia (elsewhere only Papua New Guinea), is distinguished from the senior *A. tessellata* only on the basis of smaller size and minor (and overlapping) differences in proportions of cirrus segments (Clark 1941). A few specimens collected at Lizard Island have the more prominent synarthrial tubercles characteristic of *A. laevipinna*, otherwise known only from three specimens of uncertain locality (probably Japan) (Clark & Clark 1967). Both are probably variants of *A. tessellata*.

'Superfamily TROPIOMETROIDEA'

Members of this superfamily have distinctive pinnules that are triangular in cross-section (prismatic) and keeled aborally, and the arms appear to end abruptly with small distal inwardly curving brachials. However, most other characters (for example, ambulacral plates, centrodorsal radial pits and aboral star) do not occur consistently; many features are widely variable (for example, centrodorsal shape, radial exposed surface, radial articular facet, and adoral muscle fossae). The keeled prismatic pinnules also occur in Isocrinida (Hess 2011e) and are thus likely plesiomorphic. Both Hemery *et al.* (2013) and Rouse *et al.* (2013) returned the group as polyphyletic within Comatulida, with Thalassometridae sister to Comatulidae, and Charitometridae close to the antedonoid Pentametrocrinidae. Placements of other tropiometroid families differed between the two reconstructions, for example Hemery *et al.* (2013) returned representatives of three tropiometroid families (Calometridae, Ptilometridae and Asterometridae) as a clade sister to the non-tropiometroid Notocrinidae, and Tropiometridae nested within a clade of antedonids, whereas Rouse *et al.* (2013) returned an *Antedon*/Ptilometridae/Tropiometridae as sister to Himerometroidea.

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The six extant families (whatever their final phylogenetic distribution) include 31 genera, with one fossil record dating to the Miocene (Shibata & Oji 2007) and another possibly Pliocene (Sieverts 1933). Three fossil families with eleven genera extend from Upper Jurassic to Miocene (Hess & Messing 2011c). All six families with extant taxa are represented in Australian waters (Clark 1947, 1950; Rasmussen & Sieverts-Doreck 1978; Fell 1982; Rowe & Gates 1995).

Family Tropiometridae

Figure 7.23

Species in the single genus *Tropiometra* have 10 arms, the longest reaching 260 mm in length. Unlike other 'tropiometroids', pinnule ambulacra lack conspicuous side or covering plates. The centrodorsal is thick, discoid to low-columnal, with stout, smooth cirri that lack any aboral ornament. Rouse *et al*. (2013) returned the genus as sister to *Antedon mediterranea* ('Antedonidae'), and Hemery *et al*. (2013) returned it as sister to the 'antedonid' *Annametra occidentalis*, and this clade as sister to a clade of Atlanto-Mediterranean *Antedon* species (including *A. mediterranea*). *Tropiometra* currently includes three nominal species: *T. carinata* (tropical western Atlantic around southern Africa to south-western India and Sri Lanka), *T. magnifica* (Gulf of Aden) and *T. afra* (Clark 1947). Substantial sequence differences between *T. afra afra* (Australia to the Philippines, New Caledonia) and *T. afra macrodiscus* (South China Sea to Japan) suggest that the latter deserves separate species status (Rouse *et al*. 2006). Almost all records are from shallow water, although the single specimen of *T. magnifica* was collected in 73–220 m (Clark 1947).

Tropiometra afra occurs in Australian waters from Fremantle, Western Australia, across the north coast and south to Fish Rock, New South Wales. It also is found at Lord Howe Island in the Tasman Sea (Rowe & Gates 1995). Specimens are usually semi-cryptic on reefs, with the arms forming an irregular array of monoplanar fans (**Fig. 7.23**). It is usually dark purplish brown (black *in situ*) but can also be uniformly yellow or banded dark purplish brown and yellow.

Family Calometridae

Figure 7.24

Calometrids (**Fig. 7.24**) are easily recognised by their globose visceral mass, which is completely plated and easily lost; the small, delicate first pinnule (P1) with enlarged basal two segments, and muscular fossae on the radial facets forming short curved bands. Each distal cirrus bears an aboral spine. Seventeen nominal species in five genera (*Calometra*, *Gephyrometra*, *Neometra*, *Pectinometra* and *Reometra*) occur in the tropical Indo-west Pacific from the Bay of Bengal to Japan, Australia and New Caledonia at depths of 20–600 m (Clark 1947; Messing *et al*. 2000).

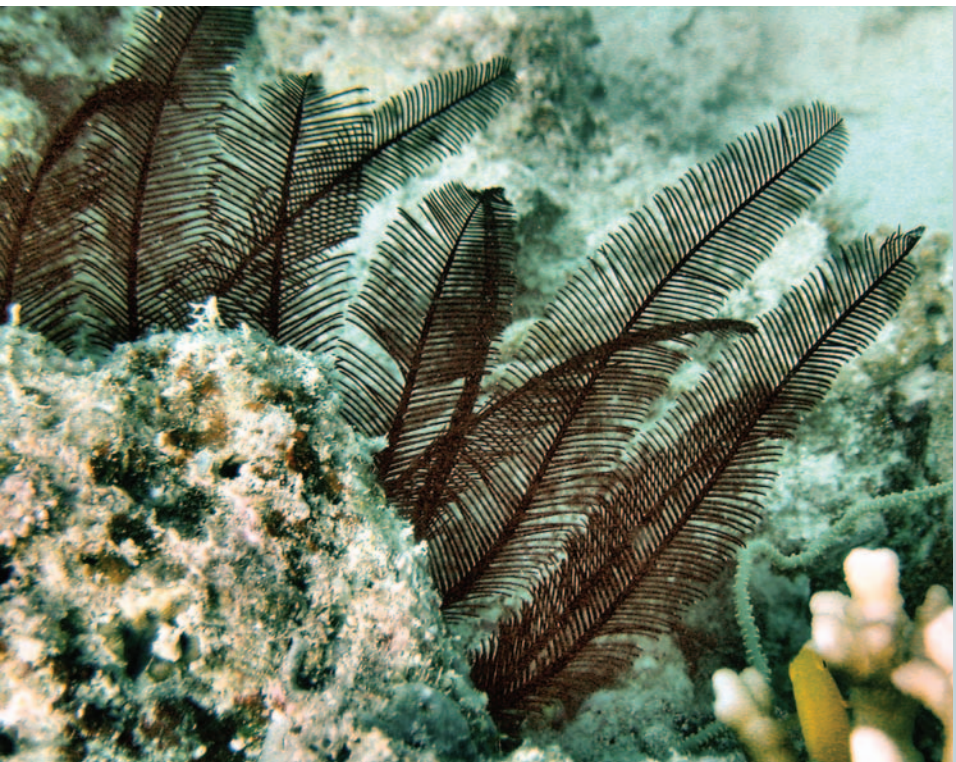


Figure 7.23 Family Tropiometridae. ***Tropiometra afra*** extends its ten arms from under a rock, with pinnules in a monoplanar pinnate array. Lizard Island, Great Barrier Reef, Queensland. [G.W.Rouse]



Figure 7.24 Family Calometridae.

Calometra callista clinging to an octocoral off the Ryukyu Islands of southern Japan. It has its arms arrayed in a radial fan, and the characteristic stiffened proximal and middle pinnules can be seen.

[Ryukyu University Museum (Fujukan)]

Two genera occur in Australian waters: *Reometra* and *Neometra*. *Reometra mariae* has been found at depths of 46–51 m between Swains Reef on the Great Barrier Reef and Double Island Point, Queensland (Rowe & Gates 1995). It has also been reported at depths of only 30 m in New Caledonia (Meyer 1986). *Neometra conanimis* and *N. gorgonia* are endemic to the west coast of Australia at depths of 92–219 m; Messing *et al*. (2000) suggested that they might be synonyms. *Neometra multicolor* ranges from Shark Bay, Western Australia, to Moreton Bay, Queensland, but it also extends northward to Japan. *Neometra diana*, known from the eastern part of the Indian Ocean, has been recorded from the North West Shelf, Western Australia (Rowe & Gates 1995). Because several diagnostic characters, for example numbers of arms, cirri and cirrus segments, vary with growth, the actual number of species in the genus is uncertain (Messing *et al*. 2000).

Family Ptilometridae

Figure 7.25

The sole genus *Ptilometra* contains two species, both endemic to southern Australian coasts. The long slender cirri are as long as or longer than the arms, and most segments bear an aboral spine. P1 is shorter and smaller than P2 and lacks the enlarged basal segments of calometrids. Radial muscular fossae are much wider than tall but, unlike those of calometrids, are not strongly curved. The large centrodorsal is disc-like or columnar with numerous cirri (30–60 in fully developed specimens) in 15–20 columns. *Ptilometra australis* ranges from southern Queensland to Bass Strait, and *P. macronema* occurs from the north-western coast of Tasmania westward to Geraldton, Western Australia (**Fig. 7.25**). Both occur from the subtidal to about 110–113 m depth (with most records shallower than about 70 m), and they share similar varied colour patterns that include cream, pink and purple (Clark 1947; Rowe & Gates 1995; Edgar 1997). Diagnostic features are chiefly minor differences in proportions of

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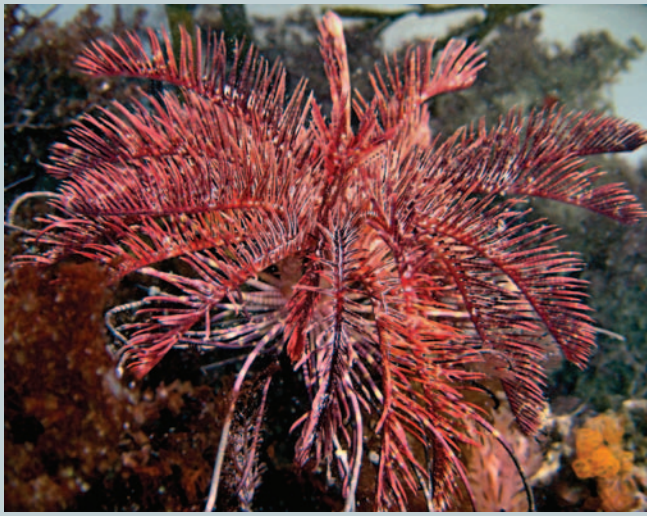


Figure 7.25 Family Ptilometridae.

The sole genus ***Ptilometra*** contains two species, both endemic to Australian waters. ***Ptilometra australis***, with its arms spread in a meridional posture, is found only from southern Queensland to Bass Strait, here photographed at Nelsons Bay, New South Wales.

[G.W.Rouse]

cirrus and pinnule segments, so it is unclear whether they represent two species or not. Rouse *et al.* (2013) returned *Ptilometra* with weak support as sister to a *Tropiometra*/*Antedon* clade, whereas Hemery *et al.* (2013) returned it nested within an Asterometridae clade (not included in Rouse *et al.* 2013).

Family Asterometridae

Figure 7.26

Asterometrids (**Fig. 7.26**) resemble ptilometrids, but have a much smaller, pentagonal centrodorsal usually with a conical tip, interradial ridges and fewer cirri (usually 15–30) in ten columns. The adoral surface of the centrodorsal bears multiple, narrow, deep radial pits similar to those of Notocrinidae that may form canals connecting to the aboral star in juveniles. The muscular fossae of the radials are more-or-less rhombic, steep and narrow. The family ranges from southern Japan to tropical Australia and includes 11 nominal species in three genera (*Asterometra*, *Pterometra* and *Sinometra*). Four nominal species occur in Australian waters at depths of 60–200 m: *A. anthus* (Sahul Bank, Timor Sea), *A. mirifica* (Sahul Bank to Melville Island, Northern Territory), *P. pulcherrima* (Rowley Shoals and off Bedout Island, Western Australia) and *P. trichopoda* (Carnarvon to near Rowley Shoals, Western Australia) (Rowe & Gates 1995). As with Calometridae, the true number of species is uncertain. *Asterometra mirifica*, *A. cristata* and *A. macropoda* are distinguished chiefly by the strength and extent of the proximal carination on the rays (Clark 1947; see also Messing *et al.* 2000). Molecular data suggest that the family may be paraphyletic. Hemery *et al.* (2013) returned *Pterometra trichopoda* as sister to a *Ptilometra macronema* (Ptilometridae)/*Asterometra* cf. *cristata* clade.



Figure 7.26 Family Asterometridae.

A specimen of ***Asterometra*** sp., from Papua New Guinea, with its characteristically long cirri.

[G.W.Rouse]

Family Charitometridae

Figure 7. 27

In Charitometridae (**Fig. 7.27**), as in ptilometrids and asterometrids, P1 is more slender than the following pinnules. However, unlike the cirri of those families and thalassometrids, those of charitometrids are short and usually composed of fewer than 25 similar unpolished segments that are smooth, weakly carinate or bear a low aboral tubercle. Genital pinnules taper from a broad base or have two to four middle segments abruptly broadened. Rouse *et al*. (2013) returned a clade of two charitometrids as sister to Pentametrocrinidae and the stalked crinoids *Vityazicrinus* and *Guillecrinus*. Hemery *et al*. (2013) found the same sister relationship between Charitometridae and Pentametrocrinidae, but did not include the two stalked genera.

About 32 species in eight genera occur in the tropical and subtropical Indo-west Pacific and tropical Atlantic oceans, mainly at depths of 150–1,500 m (with one record in 2,194 m). Three genera and six species are known from Australian waters: *Charitometra basicurva* (Wanganella Bank, Tasman Sea), *Glyptometra crassa* (off Norfolk Island, South Pacific Ocean) *G. inaequalis* (Newcastle to Ulladulla, New South Wales), *Monachometra patula* (Sahul Bank, Western Australia, Timor Sea), *M. robusta* (Sahul Bank to Melville Island, Northern Territory) and *M. kermadecensis* (off New South Wales). The latter may represent an undescribed species distinct from *M. kermadecensis*, which was collected in the Kermadec Islands (Rowe & Gates 1995).



Figure 7.27 Family Charitometridae.
Possibly ***Glyptometra*** sp., illustrating the typical robust cirri.
[Indonesia, NOAA Okeanos Explorer Program, INDEX-SATAL 2010]

Family Thalassometridae

Figure 7.28

In the Thalassometridae (**Fig. 7.28**), as in ptilometrids and asterometrids, the cirri are long and slender with aboral spines. However, P1 is always longer and stouter than P2, the distal cirrus segments are highly polished, and the radial muscular fossae are taller than wide. The centrodorsal varies from discoid to conical or columnar. Arm number in different genera ranges from 10 to 30. The family includes 14 genera and over 60 species and is widely distributed in the Atlantic, Indian and Pacific oceans, chiefly at depths of 150–1,000 m (with two dubious records in less than 100 m). Several genera penetrate to abyssal depths (1,500–2,900 m) (Clark 1950). Molecular data (Hemery *et al*. 2013; Rouse *et al*. 2013) consistently returned representatives of the family as sister to Comatulidae, with which thalassometrids share no known synapomorphies.

Seven genera and eight species are known from Australian waters. Three appear to be endemic: *Cosmiometra dasybrachia* (Bass Strait), *C. woodmasoni* (Sahul Bank, Timor Sea) and *Stiremetra spinicirra* (Broken Bay to off Batemans Bay, New South Wales). Rowe & Gates (1995) added four species previously known from the East Indies: *Daidalometra arachnoides* (Port Denison, Queensland), *Crotalometra rustica* (Dampier to Rowley Shoals, Western Australia), *Parametra compressa* and *Stenometra snelliusi* (both Port Hedland, Western Australia) and *Thalassometra gracilis* (Cape Hawke to Shoalhaven Bight, New South Wales). Messing *et al*. (2000) synonymised *Stenometra snelliusi* under *Stenometra cristata*, and Clark (1950:23) noted that 'there appear to be no real

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Figure 7.28 Thalassometridae.
An unidentified thalassometrid illustrating the typically long slender cirri with well-developed aboral spines, and an associated unidentified ophiacanthid ophiuroid.
[Indonesia, NOAA Okeanos Explorer Program, INDEX-SATAL 2010]

differences between [*Daidalometra* and *Stenometra*] other than in the number of arms'. Two other species likely occur in subantarctic Australian waters: *Thalassometra bispinosa*, currently known from the southern Indian Ocean (Marion and Crozet islands) and off Peru in 2,925–4,265 m, and *T. villosa*, known from Campbell Island south of New Zealand, and the Aleutian Islands in 1,860–1,940 m (Eléaume *et al.* 2004, 2014a).

Superfamily NOTOCRINOIDEA

Extant representatives of the two families appear to be united by having radially orientated pits in the centrodorsal, although their relationships to other Comatulida is unclear. Rouse *et al.* (2013) nested a paraphyletic Notocrinoidea with a representative of each family (*Notocrinus virilis* and *Aporometra wilsoni*) within a clade of three Heliometrinae and one zenometrid (both 'Antedonoidea'). However, Hemery (2011) returned a monophyletic Notocrinidae (*N. virilis* and *N. mortenseni*) as sister to a large Calometridae/Ptilometridae/Asterometridae clade and *Aporometra* sp. at a substantial distance as sister to the supposed colobometrid *Iconometra anisa* within a large clade of various 'antedonids' The pinnules are shorter than in most other comatulids, and proximal brachial syzygy placement is variable. Most other diagnostic features are found in at least some representatives of other superfamilies, for example pinnules round in cross section, tegmen plated, saccules present, 10 arms only, and ambulacral plates present or absent. Of the seven genera, one is known from the Lower Jurassic to the Eocene, four from the Cretaceous, and two are exclusively Recent (Rasmussen & Sieverts-Doreck 1978; Fell 1982).

Family Notocrinidae

Figure 7.29

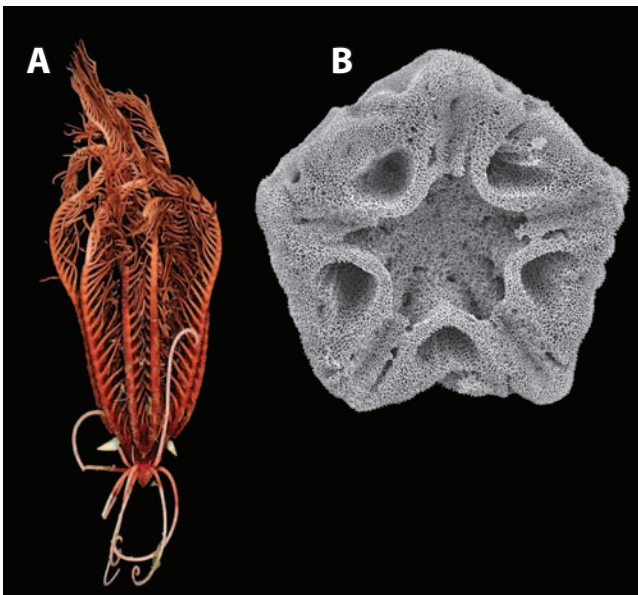


Figure 7.29 Family Notocrinidae.
Notocrinus virilis, from Antarctic waters.
A, entire specimen with ectoparasitic gastropods on the bases of two of its arms.
B, scanning electron microscope image of the oral face of the centrodorsal showing five deep radial pits surrounding a central cavity.
[A, S.Schiaparelli; B, C.G.Messing]

The only extant genus, *Notocrinus*, occurs in Antarctic waters in depths of 80–700 m and includes two species: *N. virilis* (**Fig. 7.29A**) and *N. mortenseni*. Both occur in Australian Antarctic Territorial waters. Juveniles of the two extant species have five pits arranged radially around the aboral centrodorsal apex (radial star). The adoral side of the centrodorsal is deeply excavated by five large radial pits (**Fig. 7.29B**). Adult arm length can exceed 100 mm, and cirri number 30 to more than 60. Pinnule ambulacra bear large side plates and small covering plates, and the gonads are located on the arms rather than on the pinnules. Development is direct, with embryos developing in marsupial pouches — only a few per pouch in *N. virilis*, but up to 92 in *N. mortenseni* (Mortensen 1920; Clark & Clark 1967). Five additional genera attributed to the family are known only from European fossil deposits dating chiefly to the Cretaceous (one Jurassic). Baumiller & Gaździcki (1996) described *Notocrinus seymourensis* from the Eocene, Antarctic Peninsula.

Family Aporometridae

Figure 7.30

Unlike notocrinids, aporometrids (**Figs 7.2, 7.30; Box 7.2**) lack the radial star and ambulacral plates, but the adoral side of the centrodorsal bears shallow radial pits. Arms reach 30 mm in length; cirri number 25 at most but may be as long as the arms, and the gonads and marsupia lie on the pinnules, not on the arms. The cirri have uniquely flattened aboral surfaces. The systematic position of the family is uncertain. A.H.Clark (in Clark & Clark 1967) linked it to the Notocrinidae on the basis of disc plating, viviparity, and several shared features of the centrodorsal, pinnules and radials. However, A.M.Clark, in the same publication (p. 23), noted that aporometrids had 'no more in common with the Notocrinidae than they do with any other comatulid family.' Both gonad placement (on the arms in *Notocrinus*; on the pinnules in *Aporometra*) and reproductive mechanisms differ substantially, and do not indicate a close relationship.





Figure 7.30 Family Aporometridae.

A, a female ***Aporometra paedophora*** with pentacrinoid postlarvae attached to its pinnules.

B, oral view of ***Aporometra wilsoni*** showing the central mouth and a large pale anal papilla. A few long cirri are visible between some rays.

[A, K.Nolan; B, G.W.Rouse]

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The single genus, *Aporometra*, includes three nominal species endemic to the southern Australian coast: *A. wilsoni*, *A. occidentalis* and *A. paedophora*. They are ovoviviparous brooders that retain developing embryos within maternal genital pinnules. The sexes are separate, but the details of internal fertilisation and possible sperm storage remain unknown. Their status and development is discussed in **Box 7.2**.

'Superfamily ANTEDONOIDEA'

Molecular data clearly indicate that Antedonoidea is polyphyletic (Hemery *et al*. 2013; Rouse *et al*. 2013). Putative diagnostic morphological features are widely variable, although the radial ossicles of most genera have large muscle fossae developed as thin flanges. The three families, Antedonidae, Pentametrocrinidae and Zenometridae, are treated together here for convenience pending formal taxonomic revision; the first two are represented in Australian waters (Clark & Clark 1967; Rasmussen & Sieverts-Doreck 1978; Fell 1982; Rowe & Gates 1995; Messing & White 2001).

'Family Antedonidae'

Figure 7.31

As with Antedonoidea, molecular data indicate that Antedonidae is polyphyletic (Hemery *et al*. 2013; Rouse *et al*. 2013), but no formal taxonomic revision has been undertaken. Of the five nominal subfamilies, only Isometrainae has some molecular support. The others are either para- or polyphyletic. Both Antedoninae and the genus *Antedon* return as polyphyletic, with Atlanto-Mediterranean *Antedon* species forming a clade but Indo-western Pacific species polyphyletic. Heliometrinae is paraphyletic, with a clade including Eudiocrinidae, Aporometridae and several antedonines nested within (Hemery *et al*. 2013). However, the heliometrine genera form two well-supported clades, each supported by morphology. *Florometra mawsoni*, ten-rayed *Promachocrinus kerguelensis* (**Fig. 7.31B**) and *Solanometra antarctica* (the latter not included in molecular analyses) (Heliometrinae #1) have one pair of canals in the radials and lack basal rays, whereas *F. serratissima*, *F. magellanica*, *Heliometra glacialis*,

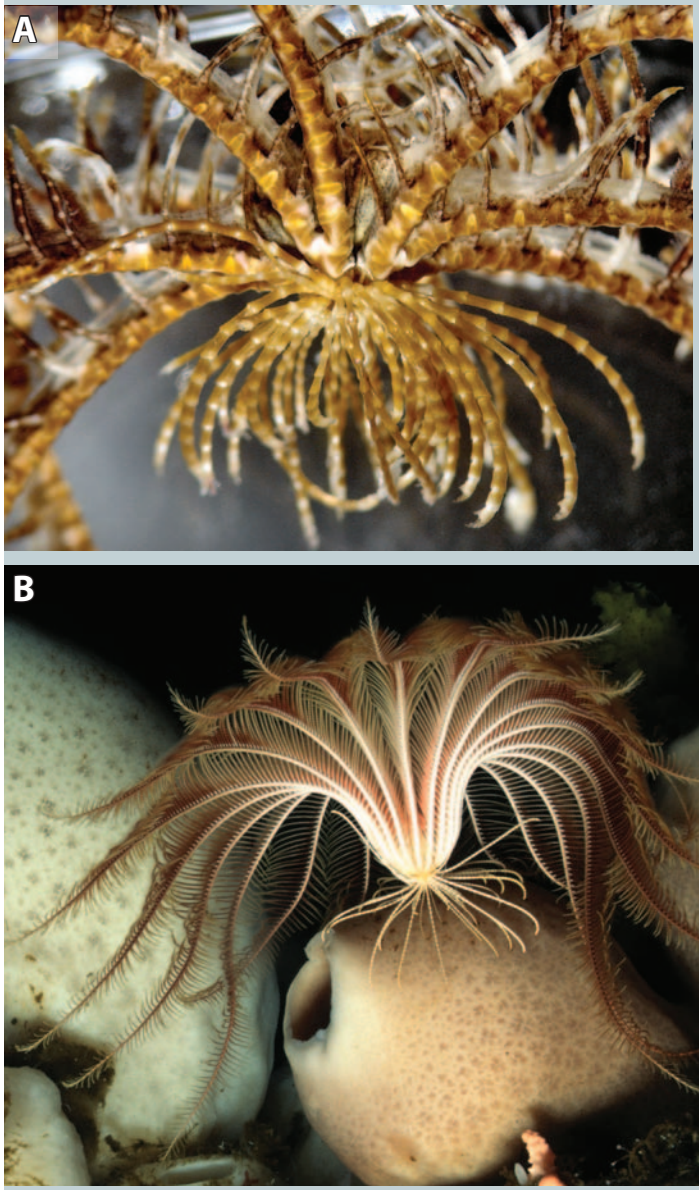


Figure 7.31 Family 'Antedonidae'.

A, ***Dorometra nana*** illustrating the numerous slender cirri, axils with strongly projecting proximal angles, and slender, elongated, cylindrical pinnulars. This species is found from the eastern Indian Ocean to the Bonin, Marshall, and Tonga islands, including northern Australia.

B, the heliometrine ***Promachocrinus*** is one of only two living crinoid genera that develops ten radial ossicles; each gives rise to two arms. The single named species, ***P. kerguelensis***, is circum-Antarctic, although molecular data suggest that at least five species exist (Wilson *et al*. 2007).

(A, Lizard Island, Great Barrier Reef, Queensland)

[A, G.W.Rouse; B, N.Wu]

Box 7.2 The curious case of *Aporometra*

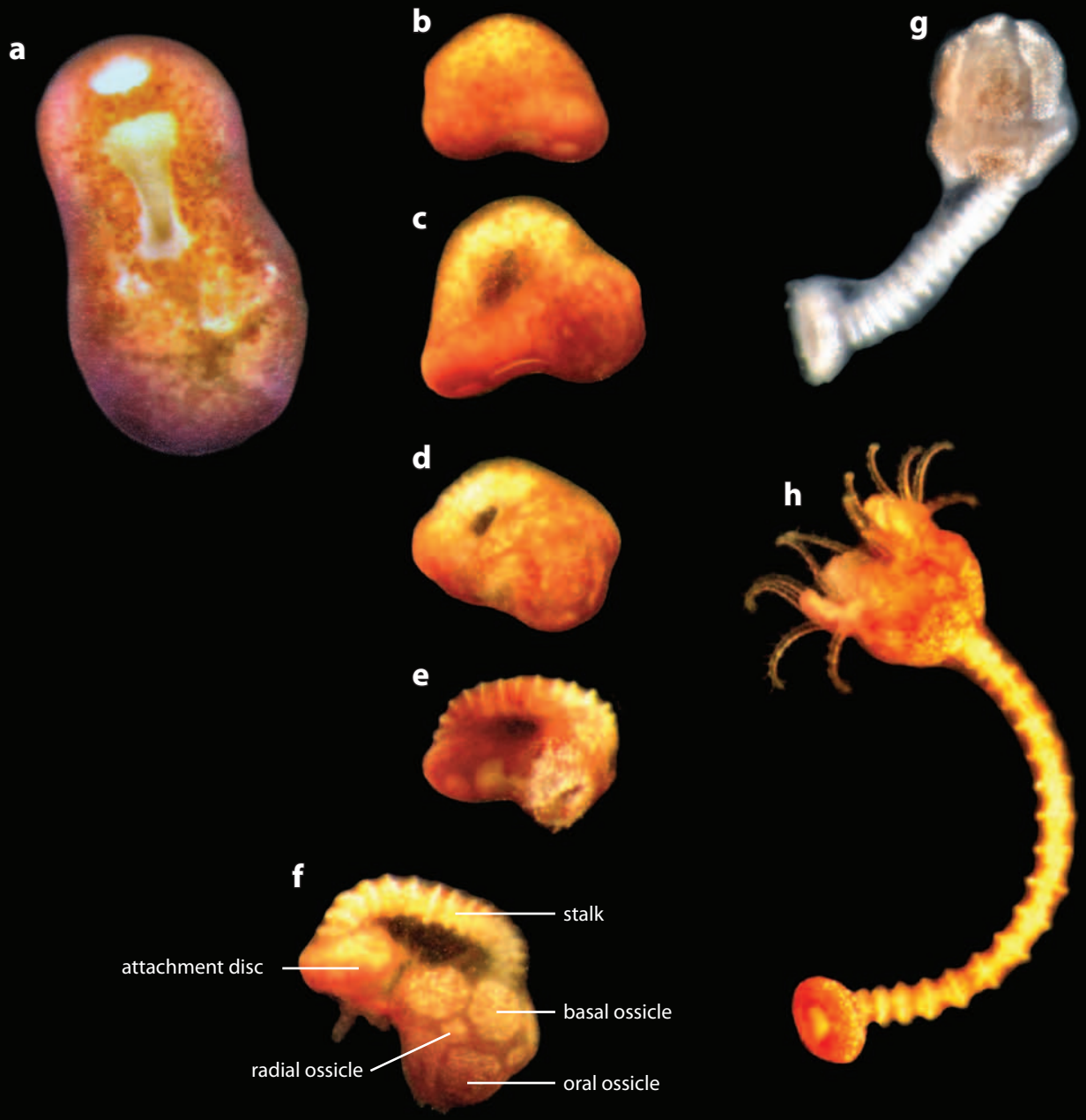
Aporometra is restricted to temperate Australian latitudes. *A. wilsoni* (**Fig. 7.30B**) occurs from Perth, Western Australia, to Gabo Island, Victoria, from the intertidal to a depth of 18 m in association with brown algae (*Cystophora* and *Sargassum* spp.), whereas *A. occidentalis* is currently known definitively only from the Recherche Archipelago and Koombana Bay (possibly to Fremantle), Western Australia, in ~9–15 m, on brown algae and the seagrass *Cymodocea* sp. The status of *A. paedophora* (**Fig. 7.30A**), known from Bass Strait and off the Manning River, New South Wales, at a depth of 40 m, remains unresolved (Clark & Clark 1967; Helgen & Rouse 2006; Haig *et al*. 2012). Morphologically, the three are very similar. Although molecular sequences satisfactorily separate *A. wilsoni* and *A. occidentalis*, the two can only be distinguished reliably by the distally directed spines on segments of the oral pinnules in *A. wilsoni*, which are absent in *A. occidentalis* (Helgen & Rouse 2006). A.H.Clark & A.M.Clark (1967) distinguished *A. paedophora* only on the basis of fewer stouter cirrus segments, but these characters vary both geographically and with specimen size.

Aporometra wilsoni is the only crinoid known to complete its entire life cycle in one year. Females begin developing eggs in February, males first appear in March, brooded larvae appear in females by May, and sperm in males by July. Females continue to brood larvae through December, when both sexes begin to senesce (Haig *et al*. 2012). Haig & Rouse (2008) estimated that a female might potentially bear as many as 2,640 larvae over the reproductive season. New recruits first appear by November and constitute most of the population by January (Haig *et al*. 2012).

White, late-stage eggs remain within the ovaries, whereas uniformly ciliated, pink larvae of about the same size occur outside the ovaries but still within the pinnules. Here, they first develop into a red doliolaria stage before exiting via the genital pore (**Figs a–c, 3.12** (emerging doliolaria)). The doliolariae lack ciliary bands, so emerging larvae apparently fall from the female and attach to adjacent substrates to complete development. The stalk and holdfast appear well developed before being released (**Figs d–f**) so that the free cystidean stage can attach to the substrate (**Fig. g**). The postlarva is considered a pentacrinoid when the oral surface opens, podia are exposed, and feeding can begin (**Fig. h**). By contrast, stalked postlarvae remain attached to the pinnules of *A. paedophora* through the pentacrinoid stage (Clark 1909; Helgen & Rouse 2006; Haig & Rouse 2008; **Fig. 7.30A**). Clark (1938) noted eggs and embryos in the genital pinnules of the third species, *A. occidentalis*, but made no mention of any later stalked cystidean or pentacrinoid stages.

Order	Comatulida
Superfamily	Notocrinoidea
Family	Aporometridae
Species	*Aporometra occidentalis* Clark, 1938
	Aporometra paedophora (Clark, 1909)
	Aporometra wilsoni (Bell, 1888)

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Figures a–h larval development of ***Aporometra wilsoni***.
a, doliolaria larva of ***Aporometra wilsoni*** showing oval adhesive pit at top and elongated V-shaped vestibule. A pair of pale oral ossicles are visible below the vestibule.
b, late doliolaria, side view.
c–e, late doliolariae through early metamorphosis, showing development and gradual separation of the stalk and attachment disc.
f, metamorphosing larva before attachment.
g, free cystidean.
h, pentacrinoid with open oral surface and exposed podia.
(Not all to scale)

[J.Haig]

Anthometrina adriani and *Comatonia cristata* (Heliometrinae #2) have basal rays (vestiges in *C. cristata* (Messing 1981)) and two pairs of canals (Eléaume 2006; Hemery *et al*. 2013; C.G.Messing, unpublished data).

Because no detailed morphological examination has been undertaken in the light of molecular data, it remains unknown whether features formerly used to diagnose the family are plesiomorphic or homoplastic. All are found in other Comatulida, for example retention of apical cirri (Atelecrinidae, Thalassometridae), large centrodorsal cavity (Zenometridae, Atelecrinidae, Pentametrocrinidae), first arm syzygy at br3+4 (most feather stars), and second at br9+10 (widespread in different families). *Dorometra nana* (**Fig. 7.31**), known from the eastern Indian Ocean to the western central Pacific Ocean and tropical Australia, exhibits several of the features that characterise many 'typical antedonids': numerous slender cirri; axils with proximal angles strongly projecting toward the ray base; second syzygy at br9+10, and slender, elongated cylindrical pinnule segments. Members of the genera *Comatonia*, *Ctenantedon*, *Microcomatula*, *Anthometrina*, *Florometra* and *Solanometra* develop oral pinnule combs that may resemble those of family Comatulidae. Distribution by any taxonomic level above genus is likewise largely uncertain. The seven nominal species of *Isometra* (Isometrainae) are restricted to Antarctic waters and the south-western Atlantic. Heliometrinae #1 is restricted to the Southern Ocean, but members of Heliometrinae #2 also occur around the Pacific Rim, in the Arctic, North Atlantic and tropical western Atlantic. Many species occur in shallow water, whereas *Bathymetra abyssicola* was collected at a depth of 5,301 m (Clark & Clark 1967).

Common, shallow-water European species of *Antedon* have been the subjects of classical through recent studies of reproduction (Carpenter 1866; Ludwig 1880; Barrois 1888; Seeliger 1892; Harvey 1931; Holland 1976; Nichols 1994a, 1994b), development (Thompson 1830; Bury 1888; Jangoux & Lahaye 1990), anatomy (Carpenter 1866; Chadwick 1907; Holland 1969; Bals *et al*. 1990), regeneration (Candia Carnevali & Bonasoro 1995, 2001b), behaviour and functional morphology (Nichols 1960; Lahaye & Jangoux 1985), and ultrastructure (Welsch *et al*. 1990; Erlinger *et al*. 1993; Heinzeller & Welsch 1994). *Isometra* and *Phrixometra* from the temperate South Atlantic to the Antarctic are viviparous.

Rowe & Gates (1995) recorded 15 species in six genera from Australian waters, including Lord Howe Island and Norfolk Island: *Antedon*, *Bathymetra*, *Dorometra*, *Euantedon*, *Nanometra* and *Toxometra*. Most species have restricted geographic ranges. Thus, *Antedon loveni* is endemic to south-eastern Australia, and *Euantedon paucicirra* ranges from Port Phillip, Victoria, to Gulf St Vincent, South Australia. *Antedon incommoda* is a predominantly southern Australian species, but it ranges from the Dampier Archipelago in the north-west, to Norfolk Island, in the South Pacific Ocean. *Antedon detonna* (Norfolk Island), *Bathymetra carpenteri* (west of Tasmania), *Nanometra duala* (Norfolk Island), *N. johnstoni* (east of Tasmania), and *Toxometra bicolor*, *T. lepta*, *T. nomina* and *T. poecila* (all from the north-west coast) are chiefly known from their type localities, while *Antedon iris*, *A. parviflora*, *Dorometra nana* and *D. parvicirra* are tropical species with broader distributions in the Indo-west Pacific. Although the combination of small size, fragility, and (in at least some cases) cryptic behaviour of many of these taxa have limited the collection of specimens, both *A. loveni* and *A. incommoda* from the southern coasts can be common and offer ample material for comparative research with putative northern hemisphere congeners.

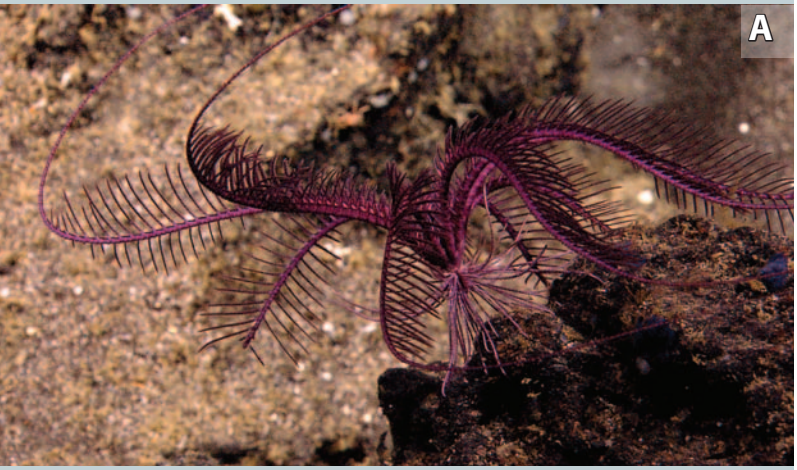
Twelve additional 'antedonid' species are known from Australian Antarctic Territorial waters: *Anthometrina adriani*, *Florometra mawsoni*, *Promachocrinus kerguelensis*, *Solanometra antarctica*, *Isometra graminea*, *I. johanni*, *Anisometra frigida*, *Eometra antarctica*, *Eumorphometra aurora*, *E. concinna* and *Tonrometra spinulifera* (Eléaume *et al*. 2014a).

Family Zenometridae

Figure 7.32

Messing & White (2001) raised three genera formerly included in the antedonid subfamily Zenometrinae to family rank on the basis of several apparently unique features, for example a large completely hollow centrodorsal lacking pockets or pits along the narrow oral

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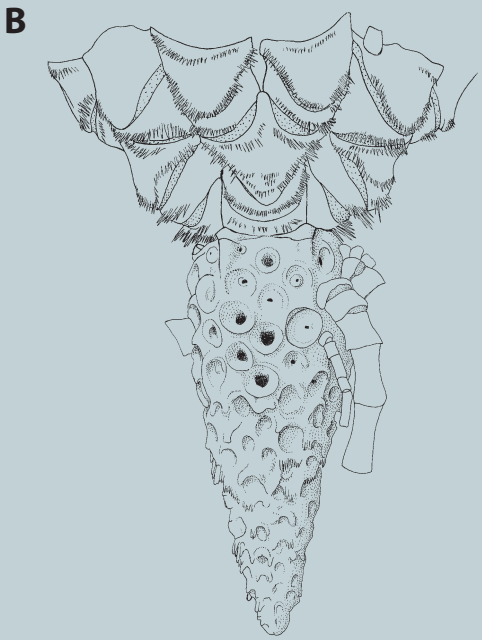


Figure 7.32 Family Zenometridae.

A, zenometrid, at a depth of 714 m, probably ***Sarametra triserialis***, showing numerous long cirri and arms terminating in a slender filament with reduced pinnules.

B, ***Sarametra triserialis***, tall narrow centrodorsal with cirrus sockets in columns, and spinose ray bases.

(A, Indonesia; B, New Caledonia)

[A, NOAA Okeanos Explorer Program, INDEX-SATAL 2010; B, modified from Messing & White 2001]

rim, cirrus sockets with a concave fulcral bowl around the lumen, and flat tongue-like basals forming a ring with a large central lumen. The centrodorsal is usually taller than wide at the base with cirrus sockets arranged in columns (**Fig. 7.32**). All species have five rays that divide once to produce 10 arms. Two genera (*Zenometra* and *Sarametra*) are monotypic, while *Psathyrometra* comprises three imperfectly circumscribed species. The family is widely distributed across the Indian, Pacific and North Atlantic oceans in deep water (439 to at least 3,465 m; chiefly 500–1,000 m). Rouse *et al*. (2013) returned a single zenometrid (*Psathyrometra fragilis*) as sister to *Promachocrinus*, *Florometra+Heliometra*, or *Notocrinus* in different analyses. Hemery *et al*. (2013) returned a zenometrid clade (*Sarametra triserialis*, *Psathyrometra* n. sp.) as basal to a large group of Comatulida including Himerometroidea, Notocrinidae, several tropiometroid families and all former Antedonidae. Although no zenometrids have been



Figure 7.33 Family Pentametrocrinidae.

Pentametrocrinus atlanticus from off St Augustine, Florida, USA. The arrow indicates the diagnostic syzygy joining the fourth and fifth brachial ossicles.

[courtesy of Southeastern Regional Taxonomic Center (SERTC)]

recorded from Australian waters, *Sarametra triserialis* has been collected from eastern Indonesia and New Caledonia and could be expected to occur in Australia.

Family Pentametrocrinidae

Figure 7.33

The two genera have either five or ten undivided arms that arise from five (*Pentametrocrinus*) (**Fig. 7.33**) or ten (*Thaumatocrinus*) radial ossicles, respectively (except for branching arm fragments identified as *T. investigatoris*) (Clark & Clark 1967). The first brachial syzygy lies at br4+5, with subsequent syzygies at variable intervals. *Pentametrocrinus* includes about nine species, and *Thaumatocrinus* six. The genera are widely distributed in deep water (250–3,300 m), but they are unknown from the Arctic and South Atlantic oceans. In phylogenetic analyses based on molecular data, Rouse *et al.* (2013) returned a *Pentametrocrinus*+Guillecrinidae clade sister to Charitometridae, and Hemery *et al.* (2013) returned a Pentametrocrinidae+Charitometridae clade (but did not include Guillecrinidae). *Pentametrocrinus semperi* is the only species recorded from Australian waters, from the western end of the Great Australian Bight east to between Port Jackson and Newcastle, New South Wales, and off north-eastern New Zealand, at depths of 1,279–1,736 m (Rowe & Gates 1995).

Superfamily *Incertae sedis*

Family Atopocrinidae

Figure 7.34

Atopocrinus, previously known from a single specimen (*A. sibogae*) (**Fig. 7.34**) collected in Indonesia at a depth of 1,633 m, was formerly placed in Atelecrinidae based on its conical centrodorsal with cirrus sockets flanked by prominent tubercles, which resemble those of *Atelecrinus* (Clark & Clark 1967). Messing (p. 146 in Hess & Messing 2011c) removed the genus to the new family Atopocrinidae based on a new specimen from Japan, apparently representing a new species. The centrodorsal of this specimen has a narrow central cavity; the basals are flat and tongue-like rather than forming an unmodified circlet as in atelecrinids, although there appears to be no rosette; small perforations between cirrus sockets connect the centrodorsal cavity with the exterior; and cirrus sockets (arranged in 15 columns rather than 10 as in *A. sibogae*) initially arise as tubes along the adoral surface of the centrodorsal. The five rays are undivided, with a synarthry between brachials 1 and 2 and a syzygy at br4+5 (as in Pentametrocrinidae), with few radiating ridges. The first pinnule is on brachial 2.

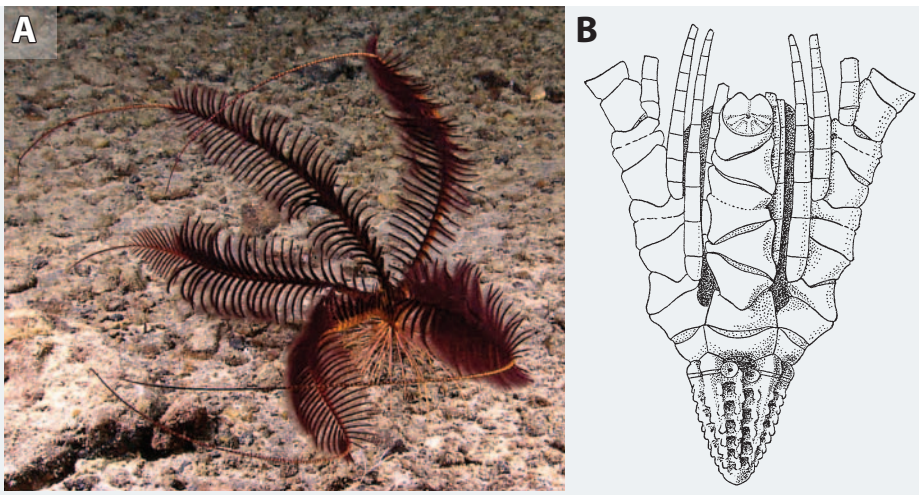


Figure 7.34 Family Atopocrinidae.

A, an unidentified atopocrinid from Indonesia showing five undivided rays and, previously undescribed, arms terminating in long filaments.

B, bases of three rays and centrodorsal of the holotype of ***Atopocrinus sibogae*** collected from north of Ceram, Indonesia.

[A, NOAA Okeanos Explorer Program, INDEX-SATAL 2010; B, from A.H.Clark 1915]

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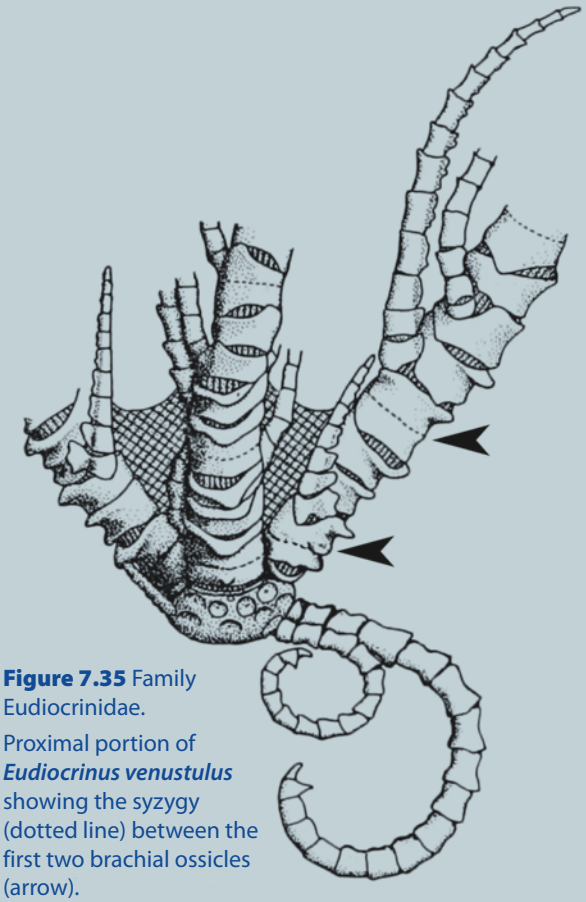


Figure 7.35 Family Eudiocrinidae.
Proximal portion of ***Eudiocrinus venustulus*** showing the syzygy (dotted line) between the first two brachial ossicles (arrow).
(south-west of the Mergui Archipelago, Burma)
[from A.M.Clark 1972]

Family Eudiocrinidae

Figure 7.35

Eudiocrinidae, formerly placed in Himerometroidea, differs from all other Comatulida in having five unbranched rays with primibrach ossicles joined by syzygy (**Fig. 7.35**). Hemery *et al*. (2013) returned a clade of two *Eudiocrinus* species as basal to a large clade containing several 'antedonids' and Aporometridae, and this entire clade nested within Heliometrinae.

The only genus, *Eudiocrinus*, includes 13 nominal species and ranges from the Maldive Islands to Japan, Australia, and the Marshall Islands to a depth of 183 m. The shallowest record is approximately 10–30 m for *E. tenuissimus* from Enewetak Atoll. Because the primary specific diagnostic characters are the proportions of cirrus segments and the shape of oral pinnules (Clark 1941), several species could represent infrasubspecific variants (Clark 1975), for example Clark (1941:146) stated that 'whether *E. ornatus*, *E. philenor* and *E. serripinna* are to be regarded as species or as forms of *E. indivisus* is more or less a matter of personal opinion.' Most records are of trawled or dredged specimens from 'sand and coral' bottoms (Clark 1941), although Zmarzly (1984a) found *E. tenuissimus* under a reef ledge, and Messing (2007) reported one *E. venustulus* clinging to an antipatharian.

A single imperfect specimen of *E. serripinna* from Swain Reefs, southern Great Barrier Reef in 64–73 m, is the only Australian record of the family (Clark 1975). Its colour in life was light and dark brown. The next closest record of this and several other *Eudiocrinus* species is from Kepulauan Kai, in Maluku, Indonesia (A.H.Clark 1941; A.M.Clark 1975).

'Bourgueticrinines'

These stalked crinoids have been treated variously as a separate order Bourgueticrinida (Rasmussen 1978), and as a suborder within orders Millericrinida (Roux 1977), Comatulidina (Simms *et al*. 1993; Jagt 1999) and Comatulida (Hess 2011f). Different arrangements have recognised one (Simms *et al*. 1993), two (Clark 1907; Gislén 1924, 1925; Roux 1977), or four families (Rasmussen 1978). Recent discoveries combined with molecular data make the latter figure more likely, although the taxonomic arrangement, when formalised, will differ from earlier schemes (Mironov 2000; Mironov & Pawson 2010, 2014; Hemery *et al*. 2013; Rouse *et al*. 2013). All have been linked by the lack of true cirri (some have a basal root-like radix composed of cirrus-like structures) and by xenomorphic stalks (divisible into proximal, middle and distal sections of different ossicle forms or articulations) composed chiefly of columnals articulated by synarthries, except near the apex (Hess 2011f). The most recent morphological arrangement recognised 46 extant species in 13 genera and four families: Bathycrinidae [*Bathycrinus* (11 species), *Cingocrinus* (1), *Discolocrinus* (2), *Monachocrinus* (7), *Naumachocrinus* (1), and *Caledonicrinus* (1)], Bourgueticrinidae [*Conocrinus* (6), *Democrinus* (10)], Phrynocrinidae [*Phrynocrinus* (1), *Porphyrocrinus* (3)], and Septocrinidae [*Septocrinus* (1), *Rouxicrinus* (1)

and *Zeuctocrinus* (2)]. Molecular reconstructions place most former bourgueticrinines within Comatulida, supporting the idea that their stalk retention is the result of paedomorphosis (Rasmussen 1978, Simms 1988, 1999, 2011; Simms *et al.* 1993). Rouse *et al.* (2013) returned terminals representing four genera from Bathycrinidae, Bourgueticrinidae and Phrynocrinidae as a clade sister to a clade containing both feather stars (Charitometridae, Pentametrocrinidae) and stalked Guillecrinidae (**Fig. 7.13**). Hemery *et al.* (2013) returned seven terminals representing five genera in the same three families as a clade sister to a (Pentametrocrinidae+Charitometridae/ Comatulidae+Thalassometridae) clade. Accepted families including multiple terminals returned as monophyletic. However, *Caledonicrinus vaubani* returned as a distant branch in both reconstructions; the septocrinid *Rouxicrinus vestitus* (misidentified as *Monachocrinus caribbeus* — see Mironov & Pawson (2010, 2014)) also returned separately in Rouse *et al.* (2013), and the feather star family Atelecrinidae returned within a 'bourgueticrinine' clade in Hemery *et al.* (2013). The placement of the latter suggests that the stalk has been regained and lost repeatedly and eliminates the lack of cirri as a diagnostic character for the group. Mironov & Pawson (2014) described knobby processes on the interior surface of primibrachial ossicles in Bathycrinidae (*Bathycrinus*, *Cingocrinus*, *Discolocrinus*, *Monachocrinus*) and Bourgueticrinidae (*Democrinus*), that correspond with those in Atelecrinidae (Messing 2003b, 2013), but do not occur in Septocrinidae, Caledonicrinidae or Phrynocrinidae. These features reflect molecular reconstructions that placed Phrynocrinidae sister to a Bourgueticrinidae+(Bathycrinidae+Atelecrinidae) clade, and returned both Septocrinidae and Caledonicrinidae as separate branches (Hemery *et al.* 2013; Rouse *et al.* 2013). Rouse *et al.* recommended following Simms *et al.* (1993) and synonymising Bathycrinidae and Phrynocrinidae under the senior Bourgueticrinidae. However, because molecular data now also includes Atelecrinidae (Hemery *et al.* (2013), we withhold revision pending additional information.





Figure 7.36 Family Bourgueticrinidae.

A, ***Democrinus brevis*** from off Isla Roatán, Honduras; one specimen is missing its arms.

B, **C**, ***Conocrinus lofotensis,*** from the North Atlantic, showing details of the crown (**B**) and whole animal (**C**).

[A, C.G.Messing & T.K.Baumiller; B,C, from Carpenter 1884]

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Family Bourgueticrinidae

Figure 7.36

The calyx is usually elongate, cylindrical to conical, with basals taller than radials. The five rays are undivided (**Fig. 7.36**). The basals can be fused, and the broad radial articular facet bears large muscle fossae. Brachials 1 and 2 are joined by cryptosynarthry or synostosis, and brachial 4 bears the first pinnule. A proximale, an enlarged topmost columnal (or series of fused columnals) attached to the calyx, is present in fossil genera and in the juveniles of some extant species. The topmost columnals are cylindrical and shorter than those below, or are similar to the more distal columnals which have elliptical synarthrial articular facets and can be cylindrical, barrel- or hourglass-shaped. The family is widely distributed in the northern and western Atlantic and Pacific oceans, and it has also been recorded from the western Indian Ocean. Depth records range from about 100 m (possibly shallower for western Atlantic *Democrinus rawsonii*) to more than 2,000 m (Meyer *et al*. 1978b; Roux *et al*. 2002). None of the 15 extant species have been found in Australian waters, although three *Conocrinus* and two *Democrinus* species have been collected in Indonesia, and *D. aoteanus* is known off New Zealand (McKnight 1973; Roux *et al*. 2002).

Family Bathycrinidae

Figure 7.37

The calyx is conical, funnel-shaped, cylindrical, or with a median constriction (**Fig. 7.3D**). Basals are fused or not, and form a low ring. The five rays divide once at primibrachial 2 to produce ten arms (**Fig. 7.37**). The broad flat primibrachs are joined by cryptosynarthry, as is every second or third following articulation. The first pinnule arises from brachial 4 to 14; the pinnulars are V-shaped in cross-section and bear cover plates. The ambulacra lack large rodlike spicules. Usually ten or more of the topmost columnals are low and discoidal in adults. Mesistele columnals are elongated except in *Cingocrinus*. The stalk anchors via a rootlike radix or, in *Naumachocrinus*, a terminal disc. *Caledonicrinus vaubani*, which was formerly included in this family but which differs substantially morphologically and has been removed, is discussed below. Its removal leaves behind a more cohesive Bathycrinidae.



Figure 7.37 Family Bathycrinidae. ***Bathycrinus*** sp. from the Ross Sea. [NIWA, New Zealand International Polar Year and Census of Antarctic Marine Life, Ross Sea Biodiversity Vogage 2008]

Bathycrinids are found in all oceans including the Arctic, chiefly below 1,000 m, although *Naumachocrinus hawaiiensis* has been collected between 570 and 920 m (Bourseau *et al*. 1991; Tunnicliffe *et al*. 2015). *Bathycrinus volubilis*, the deepest known crinoid identified to species, was collected as deep as 9,070–9,345 m in the Kuril-Kamchatka Trench (Mironov 2000; Oji & Kitazawa 2008), whereas Belyaev (1966) noted a *Bathycrinus* species from 9,715-9,735 m in the Japan Trench (see also Oji & Kitazawa 2008).

Of the 22 extant species in five genera [*Bathycrinus* (11), *Monachocrinus* (7), *Naumachocrinus* (1), *Cingocrinus* (1) and *Discolocrinus* (2)], only *Bathycrinus australis* has been reported from Australian Antarctic waters (Eléaume *et al*. 2014a). Several others occur nearby: *B. sibogae* in Indonesia; *B. australis*, *B. australocrucis* and *M. aotearoa* off New Zealand; *M. mortenseni* off New Caledonia, and *N. hawaiiensis* from Indonesia, New Caledonia and the Solomon Islands (McKnight 1973; Bourseau *et al*. 1991; Mironov 2000, 2008; Roux *et al*. 2002; Tunnicliffe *et al*. 2015).

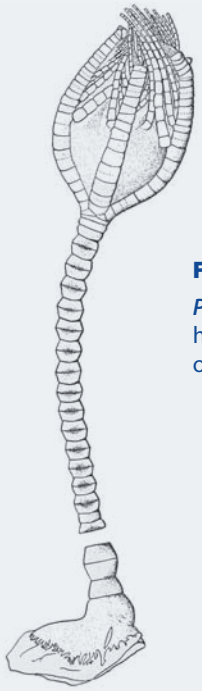


Figure 7.38 Family Phrynocrinidae.
Phrynocrinus nudus, drawing of the holotype, from off Japan at a depth of 1,187 m.
[from Clark 1907]

Family Phrynocrinidae

Figure 7.38

The small calyx consists of five short unfused basals and five taller radials (**Fig. 7.38**). The radial circlet ranges from slightly to much broader than the basal circlet, and the rays are undivided or divide distally up to three times. Primibrachs 1 and 2 are joined by synostosis, and the first pinnule arises on brachial 8 to 10. Few to many proximal columnals are thin and discoid in adults and the following columnals are joined by synarthries that are circular to elliptical in cross-section. The stalk terminates in an irregular attachment disc.

The two eastern Atlantic species of *Porphyrocrinus* are restricted to deep water (1,300–2,780 m), whereas Indo-west Pacific *Porphyrocrinus* occur at depths of 218–616 m (Bourseau *et al.* 1991; Roux *et al.* 2002; Messing 2007; Tunnicliffe *et al.* 2015). *Phrynocrinus nudus* has been recorded from Japan and New Zealand at 1,000–1,200 m (Clark 1907; McKnight 1979). Améziane & Roux (2001) mentioned *P. nudus* and an undescribed species of *Porphyrocrinus* from seamounts south of Tasmania.

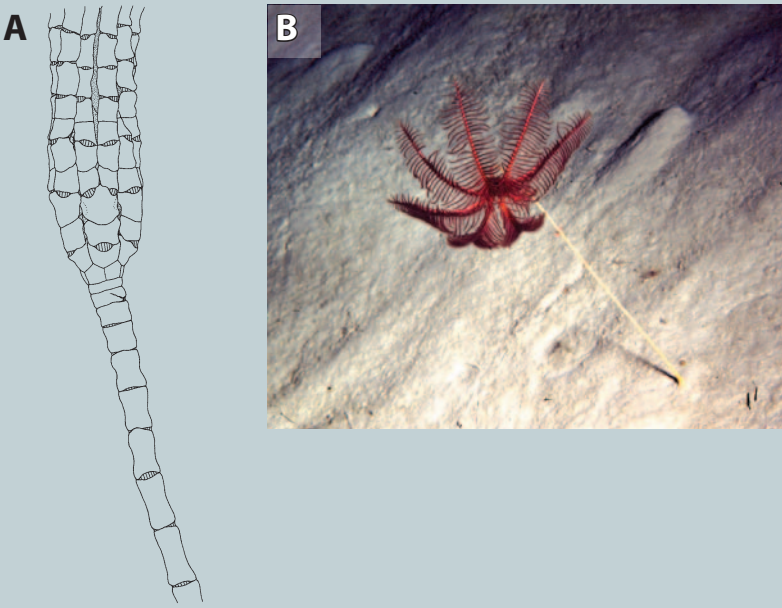


Figure 7.39 Family Septocrinidae.
A, base of crown and proximal end of stalk of ***Zeuctocrinus spiculifer*** from off southern Japan at a depth of 6,780–6,785 m.
B, ***Rouxicrinus vestitus***, from the Bahamas at a depth of 887 m.
[A, from Mironov 2000; B, Smithsonian Institution/ Harbor Branch Oceanographic Institute]

Family Septocrinidae

Figure 7.39

The calyx is conical with five basals and five radials of almost equal heights (**Fig. 7.39A**). The five rays divide once at primibrachial 2 to produce 10 arms. Primibrachs 1–2 and secundibrachs 1–2 and 3–4 are united by synostoses that occur more distally at variable intervals. The tegmen is incompletely covered by primibrachs 1 and 2. The first pinnule is usually on brachial 10, but sometimes on brachial 6 to 12. Pinnulars are semi-circular in cross-section and lack both covering and lateral plates. The ambulacra bear large, rod-like spicules. The stalk anchors by means of a radix in *Septocrinus*, while the attachment in *Zeuctocrinus* is unknown. The family includes five species in three genera: *Septocrinus* (2), *Rouxicrinus* (1) and *Zeuctocrinus* (2).

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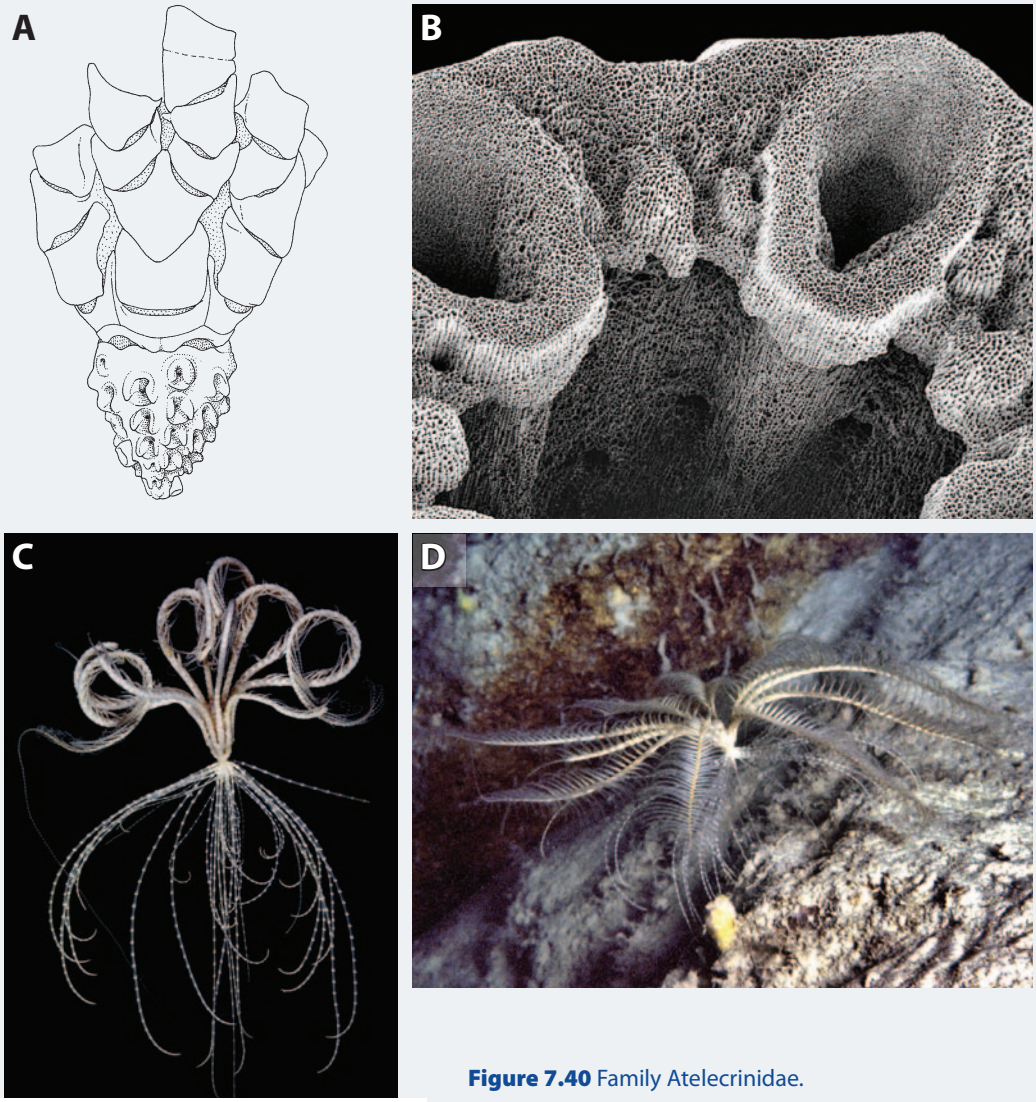


Figure 7.40 Family Atelecrinidae.

A, **B**, ***Paratelecrinus wyvillii***.
A, centrodorsal, narrow basal ring, and bases of three rays of the holotype collected at Challenger sta. 174C, Fiji. (specimen NHM 88.11.9.2)
B, scanning electron micrograph of a portion of the oral rim of the centrodorsal showing deep interradial pits.

C, **D**, ***Paratelecrinus cubensis***.
C, specimen from San Salvador Island, Bahamas, collected at a depth of 876 m.
D, animal *in situ* off New Providence Island, Bahamas, at a depth of 705 m.

[A,B, C.G.Messing; C,D, Smithsonian Institution/ Harbor Branch Oceanographic Institute]

Septocrinus disjunctus and *Rouxicrinus vestitus* (**Fig. 7.39B**) are known only from the western Atlantic Ocean. The two species of *Zeuctocrinus* are known only from the north-eastern Atlantic in 2,000–2,432 m and central western Pacific in 6,780–6,785 m (Roux 1977; Mironov 2000; Mironov & Pawson 2010).

Family Atelecrinidae

Figure 7.40

This small group of deepsea feather stars exhibits a series of unusual features that has complicated its phylogenetic placement: the proximal pinnules are absent; the basal

circlet is unmetamorphosed, and the cirrus sockets have paired lateral tubercles (Clark & Clark 1967; Rasmussen 1978; Simms 1988; Simms *et al*. 1993; Hess & Messing 2011c; **Fig. 7.40A**). Messing (2003b) added additional characters: interradial concavities or deep pits in the oral rim of the centrodorsal (**Fig. 7.40B**), a pair of elongate ridged processes of unknown function that face each other on two adjacent IBr axils and project into the visceral mass, and, along the proximal and middle portions of the arms, pairs of modified ambulacral lappets that resemble sessile pedicellariae. However, Mironov & Pawson (2010) described similar elongated ridged or knobby processes on the interior IBr surfaces of several bathycrinid genera and the bourgueticrinid *Democrinus conifer*. Sequence data subsequently reinforced the connection between the two groups: Hemery *et al*. (2013) returned two atelecrinids as a clade sister to two Bathycrinidae and nested within an otherwise entirely stalked clade of former Bourgueticrinina (Bathycrinidae, Bourgueticrinidae, Phrynocrinidae), indicating that members of Comatulida have repeatedly lost and regained the stalk.

Rasmussen (1978) included extant *Atelecrinus*, *Sibogacrinus* and *Atopocrinus*, and Upper Cretaceous *Jaekelometra* in the family, but the latter two have since been removed (Hess & Messing 2011c). The single known specimen of *Sibogacrinus anomalus* has thick, wedge-shaped basals similar to those of Atelecrinidae rather than the thin plate-like basals of *Jaekelometra* (Messing 2013). The cirrus sockets of *S. anomalus* also bear weak triangular fulcral processes, although its centrodorsal cavity is much less spacious than in the other atelecrinids. By contrast, Atelecrinidae and *Atopocrinus* share only a conical centrodorsal with uniquely modified cirrus sockets, while the latter shares with *Pentametrocrinus* unbranched rays, the first syzygy uniquely at br4+5, and similarly modified distal brachial articulations (Messing 2003b).

Messing (2013) divided *Atelecrinus* into three genera based primarily on the structure of basal ossicles and the nature of marginal depressions or pits in the adoral rim of the centrodorsal: *Atelecrinus* (2 Atlantic species); *Adelatelecrinus* (2 East Indian species), and *Paratelecrinus* (7 species ranging from Hawaii to Madagascar and the tropical western Atlantic; **Fig. 7.40C,D**).

Atelecrinids occur at depths ranging from 180 to over 3,500 m (Messing 2013). None has been recorded from Australian waters, but several have been collected in waters surrounding the Solomon Islands (*Adelatelecrinus sulcatus*, *Ad. vallatus*, *P. wyvillii* and *P. conifer*) and may be expected to occur within Australian waters in the Coral Sea.

Family Guillecrinidae

Figure 7.41

The three species in two genera all occur in the deep Indo-western Pacific (**Fig. 7.41**). The adult stalk consists of numerous similar columnals (homeomorphic), lacks synarthries and terminates in an attachment disc. Proximal columnals usually articulate by means of symplexies with grouped crenulae, while distal facets have radial crenulae resembling those of syzygies. The calyx is small and low, the basals are usually swollen, and the radials and following brachials are of similar dimensions. Non-muscular arm articulations are syzygies or cryptosyzygies. The pinnules are small, fragile and highly flexible, with pinnulars crescentic in cross-section; the first pinnule arises from primibrachs 2 or 3. The disc extends well out onto the proximal brachials. *Guillecrinus* differs from *Vityazicrinus* in having deep ligamentary pits separating columnal facet crenulae; five rather than three basals; arms undivided rather than dividing at brachial 7; five deep interradial holes in the tegmen, and no anal papilla. *Vityazicrinus* also exhibits a pseudo-synarthry, a unique mesistele stalk articulation that differs from a synarthry in lacking a hinge-like fulcral ridge; instead, it bears two additional ligamentary fossae bordered by prominent crescentic ridges lying at opposite ends of the bilateral symmetry axis (Eléaume *et al*. 2014b).

Roux (1985b) and Bourseau *et al*. (1991) considered the first-discovered species, *Guillecrinus reunionensis*, a survivor of the Palaeozoic Inadunata based on the apparent presence of infrabasal ossicles. However, Améziane & Roux (2005) determined that these ossicles were absent; they discussed possible affinities with Hyocrinidae and Bourgueticrinina but considered placement uncertain. Mironov & Sorokina (1998) erected Guillecrinidae for the two species of

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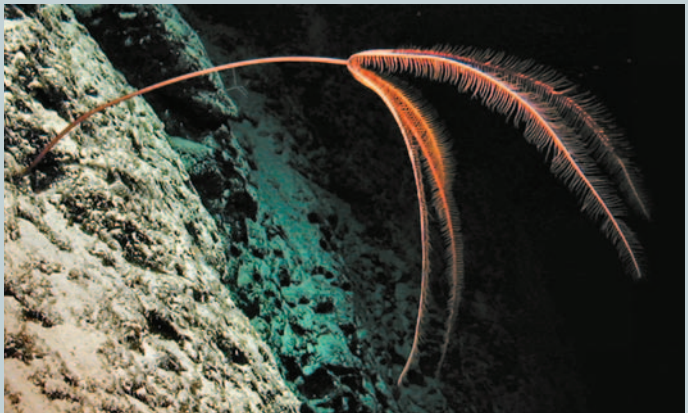


Figure 7.41 Family Guillecrinidae.
Guillecrinus neocaledonicus attached to a rocky slope in the SW Pacific Ocean.
[NOAA HURL Archives]

Guillecrinus and Vityazicrinidae for *Vityazicrinus* and placed both in suborder Guillecrinina within Hyocrinida. However, because Améziane & Roux (2005) found substantial differences between juvenile and adult stalks in *Guillecrinus*, and, because *Vityazicrinus* was based on a single, possibly juvenile specimen, Hess (2011g) tentatively included both genera in a single family. He also tentatively assigned the suborder to Comatulida based on molecular evidence in Cohen *et al.* (2004). Rouse *et al.* (2013) consistently returned *Pentametrocrinus* as sister to a clade consisting of *Vityazicrinus* and *Guillecrinus* and formally reduced Guillecrinina to family status.

Guillecrinus reunionensis is known only from the south-western Indian Ocean at depths of 1,300–2,000 m, while *G. neocaledonicus* is known from Indonesia in 1,244 to at least 1,892 m, and around New Caledonia and the Norfolk Ridge in ~1,100–1,500 m. *Vityazicrinus petrachenkoi* is known only from the central Pacific Ocean south of the Hawaiian Islands at depths of 4,100–4,400 m (Roux 1985b; Bourseau *et al.* 1991; Mironov & Sorokina 1998; Tunnicliffe *et al.* 2015).

Incertae sedis

Family Caledonicrinidae

Figure 7.42

The swollen calyx of the single included species, *Caledonicrinus vaubani*, known only from New Caledonian waters, consists of tall basals covered by large bulging radials (**Fig. 7.42**). Rays divide at primibrachials 2 to produce ten robust arms. The first pinnule is on secundibrachials 4 or 5. The proximal columnals articulate by a flat synostosis, and the middle and distal columnals by synarthries lacking deep ligament fossae. Mesistele columnals are cylindrical or barrel-shaped, not elongate. The stalk anchors via an expanded terminal plate.

Caledonicrinus vaubani was first placed in Bathycrinidae (Améziane-Cominardi *et al.* 1990), and subsequently in its own subfamily Caledonicrininae (Mironov 2000; Hess 2011f) and family (Mironov 2008). Heinzeller (1998) and Bohn & Heinzeller (1999) reported that its unique nervous system differed from that of other 'bourgueticrinines' as well as the other crinoids examined. Cohen *et al.*'s (2004) molecular data placed *Caledonicrinus* among cyrtocrinids. Subsequently, Rouse *et al.* (2013) placed it as sister to Comatulida, although it returned with weak support as sister to an Isocrinida/Hyocrinida+Cyrtocrinida clade in their MP analysis, the same arrangement as in Hemery *et al.* (2013). Here, we treat it as belonging to a monophyletic family, order *incertae sedis*.



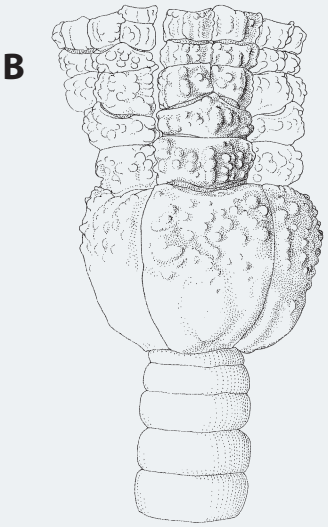


Figure 7.42 Family Caledonicrinidae.
Caledonicrinus vaubani.
A, complete specimen collected from south of Grand Terre, New Caledonia, at a depth between 410 and 440 m. (specimen MNHN IE-2013-10026)
B, upper stalk, calyx and ray bases.
[A, N.Améziane; B, C.G.Messing]

Although Oji & Kitazawa (2008) maintained *Naumachocrinus hawaiiensis* in Bathycrinidae, Mironov (2008) suggested that it shared a series of features with *C. vaubani*: a cryptic basal ring; radial ring with convex sides; more proximal position of P1 (on brachials 4 and 5), mesistele columnals cylindrical or barrel-shaped (not with a constricted waist), and expanded attachment disc rather than a rootlike radix. Nevertheless, he questioned this placement and suggested that the cryptic basal ring might be convergent in the two.

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Figure 8.1 Australian seas are a rich environment occupied by over 300 species of seastars like ***Fromia polypora*** (Goniasteridae). This brightly coloured yellow, orange or red seastar is a conspicuous member of the southwest Pacific Ocean fauna including the southern waters of Australia and Norfolk Island down to depths of 160 m. This seastar is often seen with a black speckling on the abactinal surface due to the presence of black papulae, extended small respiratory structures. It grows up to 120 mm in width.

[G.Bell]

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8: Class ASTEROIDEA

Maria Byrne, Frank W.E. Rowe, Loisette M. Marsh and Christopher L. Mah

General introduction

Echinoderms of the class Asteroidea are popularly referred to as seastars or starfish, and are among the most familiar marine invertebrates (**Figs 1.1C, 1.2D,E, 8.1, 8.2**). Comprehensive reviews of asteroid biology include general accounts (see Hyman 1955; Clark 1977; Lawrence 2013a) and reviews of functional morphology (Blake 1989; Lawrence 2013a), histology and ultrastructure (Chia & Koss 1994; Gale 2011), feeding and nutrition (Sloan 1980; Jangoux 1982; Lawrence 2013a; Martinez *et al*. 2017), life histories (Byrne 1999, 2013; McEdward & Miner 2001; McEdward *et al*. 2002), reproduction (Mercier & Hamel 2013), evolution (Mooi & David 2000) and diversity (Marsh 1974, 1976, 1978). The history of phylogenetic assessments of extant Asteroidea and considerations of fossil species have also been reviewed (Mah & Blake 2012). In recent years insight into the taxonomic relationships between living asteroid groups have derived from molecular phylogenetic studies (Mah & Foltz 2011a, 2011b; Mah & Blake 2012; Feuda & Smith 2015). The monotypic Xyloplacidae shows a highly divergent morphology and this has led to a highly contentious discussion over its classification (Mah 2006a; Mah & Blake 2012; **Box 6.2**, see below). The family phylogeny adopted here follows Mah & Blake (2012; see also **Table 8.1**). **Figures 8.3–8.7** show some of the morphological structures that characterise the Asteroidea and which are used in classification, as detailed below for the families.

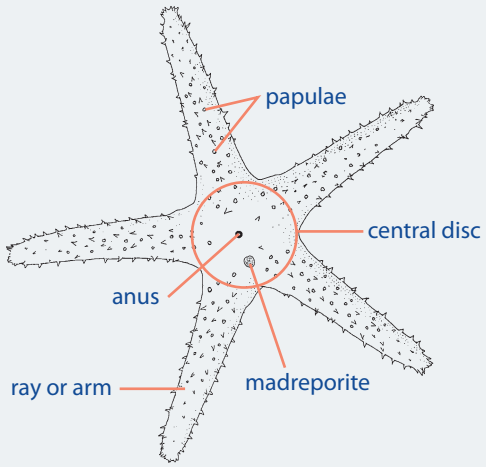
Asteroids are free-moving, dorsoventrally flattened, stellate echinoderms with five or more arms (rays) projecting from a central disc (**Figs 1.1C, 1.2D–F, 8.1, 8.2**). Body profile varies depending on the number and size of the arms and the shape of the disc. Most taxa have five arms, but some, particularly in the families Solasteridae and Asteriidae and the order Brisingida, have multiple arms — between six and 20 (**Fig. 8.43**). Some forcipulate taxa, such as *Labidiaster*, can have up to 50 arms sharply offset from the disc (**Fig. 8.40**). Asteroids with a stellate profile, such as *Echinaster*,



Figure 8.2 ***Nectria macrobrachia*** (Goniasteridae), is one of over 100 seastars known only from Australian waters. It is also one of eight species belonging to the Australian endemic genus ***Nectria***, all of which are found in the waters of temperate southern Australia. This particular species reaches a maximum of 160 mm in width.

[K.Gowlett-Holmes]

A Abactinal view



B Actinal view

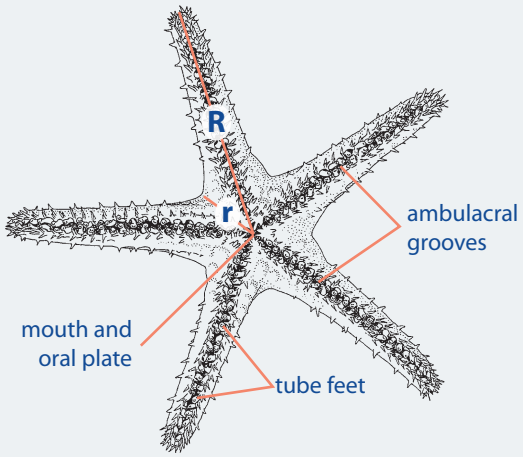


Figure 8.3 Major external anatomical features of Asteroidea.

A, abactinal (aboral) view.

B, actinal (oral) view. The major measurements radius (**R**) and disc interradius (**r**) are indicated.
R = the radius, the major ambulacral axis, the length from the centre of disc to the tip of the arm.
r = the minor axis, the length of the interambulacrum from the centre of the disc to the edge of the interim. The ratio **R/r** is taxonomically important for some species.

[courtesy C.G.Messing]

have elongate arms and a small disc (**Fig. 8.38**), while pentagonal species such as *Culcita* (**Fig. 8.28**), have very short arms and a large disc. The bizarre Podosphaerasteridae are almost completely spherical (**Fig. 8.31**), whereas some members of the Asterinidae (for example, *Anseropoda*) are so dorsoventrally flattened as to appear leaf-like. Size varies from the tiny fissiparous asterinids, *Aquilonastra anomala* and *Ailsastra heteractis* and the stichasterid *Allostichaster palmula* only a few millimetres wide (O'Loughlin & Rowe 2005, 2006; Benavides-Serrato *et al.* 2007; **Figs 3.7B, 8.41C–E**), to the large *Thromidia catalai* (**Fig. 2.14**) that can reach nearly a metre in diameter. In addition to *T. catalai*, *Coscinasterias muricata*, *Astrostole scabra* and *Luidia australiae* are among the largest Australian asteroids.

Although the fundamental asteroid body plan is conservative, there is considerable variation in the expression of the skeleton. The skeleton can vary from poor to absent, as seen in the families Pterasteridae and Poraniidae, to heavily calcified and strongly developed in members of the Oreasteridae and Ophidiasteridae.

The asteroid disc comprises the digestive system and body coelom, and encloses the mouth frame (**Fig. 8.3B**). Continuity between disc and arms varies among modern asteroids (Neoasteroidea) (Gale 1987; Blake & Hagdorn 2003). In some groups, the arms are sharply offset from the disc (Asteriidae), whereas in others the arms and disc are fully contiguous (Goniasteridae). Abactinal plating (**Fig. 8.4**) and disc and arm ornamentation are generally similar.

The primary carinal plates on the disc are the first to develop after metamorphosis and are more prominent in some taxa (Goniasteridae) than in others (Pterasteridae). The primary radial (or carinal) ossicle series proceeds along the arm between the terminal plate and the primary carinal plate. The body wall comprises articulated ossicles arranged in various patterns including, but not limited to, reticulated networks (Asteriidae), abutting or imbricate mosaics (Goniasteridae and Asterinidae) that occur within a layer of dermal tissue.

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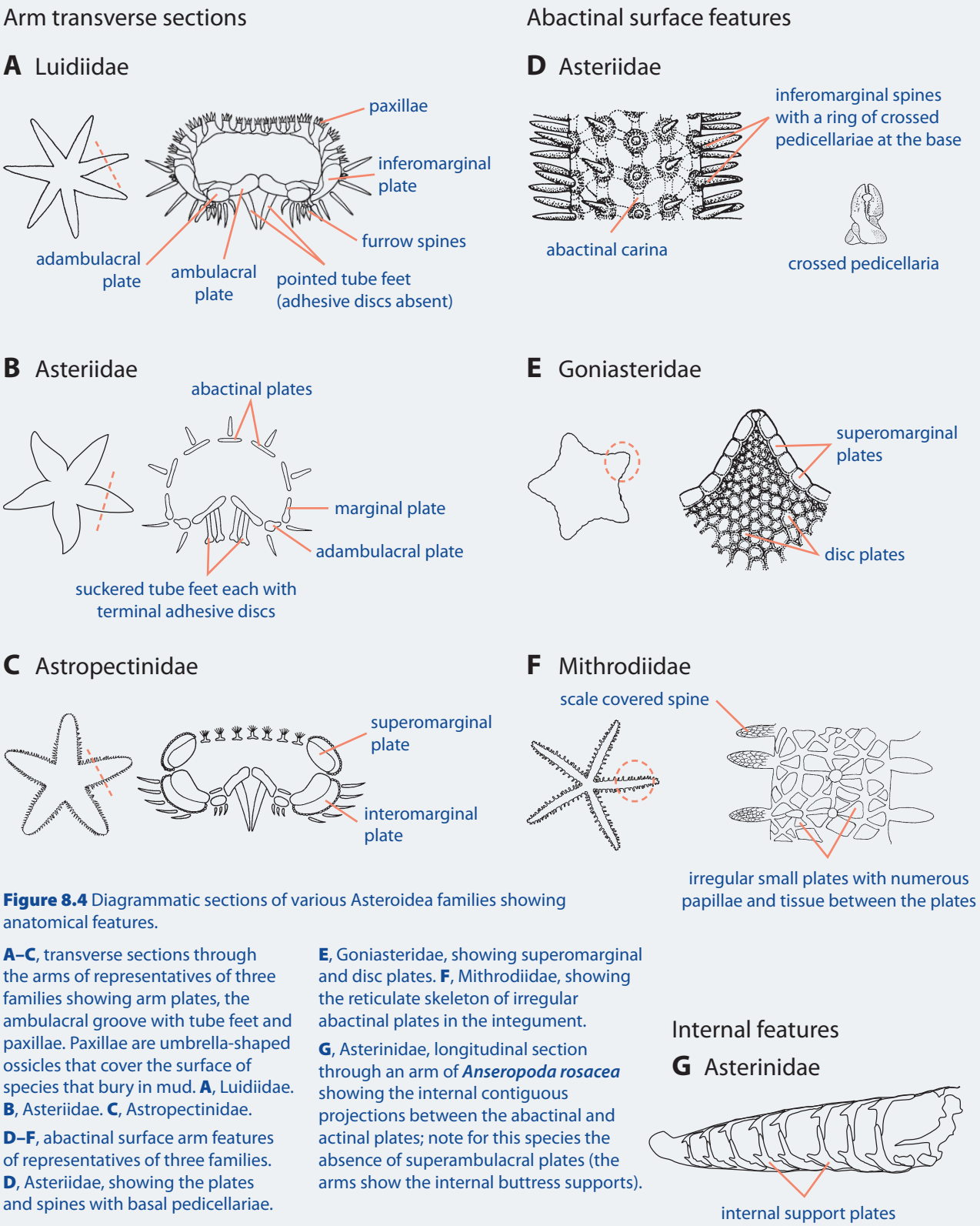


Figure 8.4 Diagrammatic sections of various Asteroidea families showing anatomical features.

A–C, transverse sections through the arms of representatives of three families showing arm plates, the ambulacral groove with tube feet and paxillae. Paxillae are umbrella-shaped ossicles that cover the surface of species that bury in mud. **A**, Luidiidae. **B**, Asteriidae. **C**, Astropectinidae.

D–F, abactinal surface arm features of representatives of three families. **D**, Asteriidae, showing the plates and spines with basal pedicellariae. **E**, Goniasteridae, showing superomarginal and disc plates. **F**, Mithrodiidae, showing the reticulate skeleton of irregular abactinal plates in the integument.

G, Asterinidae, longitudinal section through an arm of ***Anseropoda rosacea*** showing the internal contiguous projections between the abactinal and actinal plates; note for this species the absence of superambulacral plates (the arms show the internal buttress supports).

[A–F, Museum Victoria; G, after O'Loughlin & Waters 2004]

The abactinal (aboral) surface is demarcated by the marginal ossicle series (**Fig. 8.4**). These ossicles can occur in a single row (Zoroasteridae) or double row (in most other families). Marginals have been used in asteroid classification since the nineteenth century (Sladen 1889; Perrier 1894), but the formal morphological definition of the marginal ossicle series was established more recently (Blake 1987). The marginal ossicle series track from the terminal plate to the primary plates on the disc, varying in size and shape, as well as having a range of accessories and other ornamentation such as granules, spines and tubercles. These are informative features for classification and phylogenetic reconstruction. Marginal ossicles (**Fig. 8.4**) can be distinct from the abactinal and actinal ossicle series, as they are in the Paxillosida and the Valvatida, or they can be similar to them, as in the Forcipulatida and the Spinulosida. Most members of the Velatida (Korethrasteridae, Pterasteridae, Myxasteridae) do not show clearly distinguishable marginal ossicle series.

The actinal (oral) surface has the central mouth and the ambulacral grooves (also referred to as tube foot grooves) bearing the tube feet (**Fig. 8.3B**). The actinal intermediate ossicles are often arranged into interradial fields, expressed differently across a variety of taxa. For example, they comprise a chevron-like arrangement in the Valvatida, but are minimal in the Forcipulatida. These ossicles occur interradially between the marginal ossicle and the adambulacral ossicle and the tube foot furrow (**Fig. 8.4A**). Actinal intermediate ossicles vary in size and shape and, like the marginal and abactinal ossicles, are often adorned with accessories and/or ornamentation. The presence of an actinal ossicle series (or field) is a synapomorphy for the Neoasteroidea (Blake & Hotchkiss 2004).

Paired ambulacral ossicles form a tent-like boundary between which the tube feet project into the ambulacral groove (**Fig. 8.4A**). These articulate with the adambulacral plates (**Fig. 8.4A,B**). Adambulacral plates are almost always adorned with several series of granules, spines, or spinelets that project into the tube foot furrow (**Fig. 8.4A**). Adambulacral and ambulacral ossicles converge at the mouth where several enlarged oral plates project into the oral opening. Neoasteroids have two or four rows of muscular and often highly distendable tube feet, traditionally classified as suckered (Asteriidae) or pointed (Paxillosida). However, work by Vickery & McClintock (2000) and Santos *et al.* (2005) revealed a third type of tube foot with a simple disc rather than a sucker or a pointed tip. This implies that the historical dichotomy of asteroid classification based on tube foot morphology is not as straightforward as previously thought.

Pedicellariae, jaw- or valve-shaped structures, are taxonomically useful structures on the surface of nearly all asteroid groups, except the Velatida and the Spinulosida (**Figs 1.5G, 8.6**). They are prominent stalked structures with three-piece blades in the



Figure 8.5 Seastars like the stichasterid ***Uniophora granifera*** are voracious consumers of bivalves such as oysters, mussels and clams. Using their tube feet they grip the shells and, by applying pressure to both valves, pry open the bivalve. Once open even a fraction, the seastar extends its stomach between the valves and begins digestion of the soft tissue.

[K.Gowlett-Holmes]

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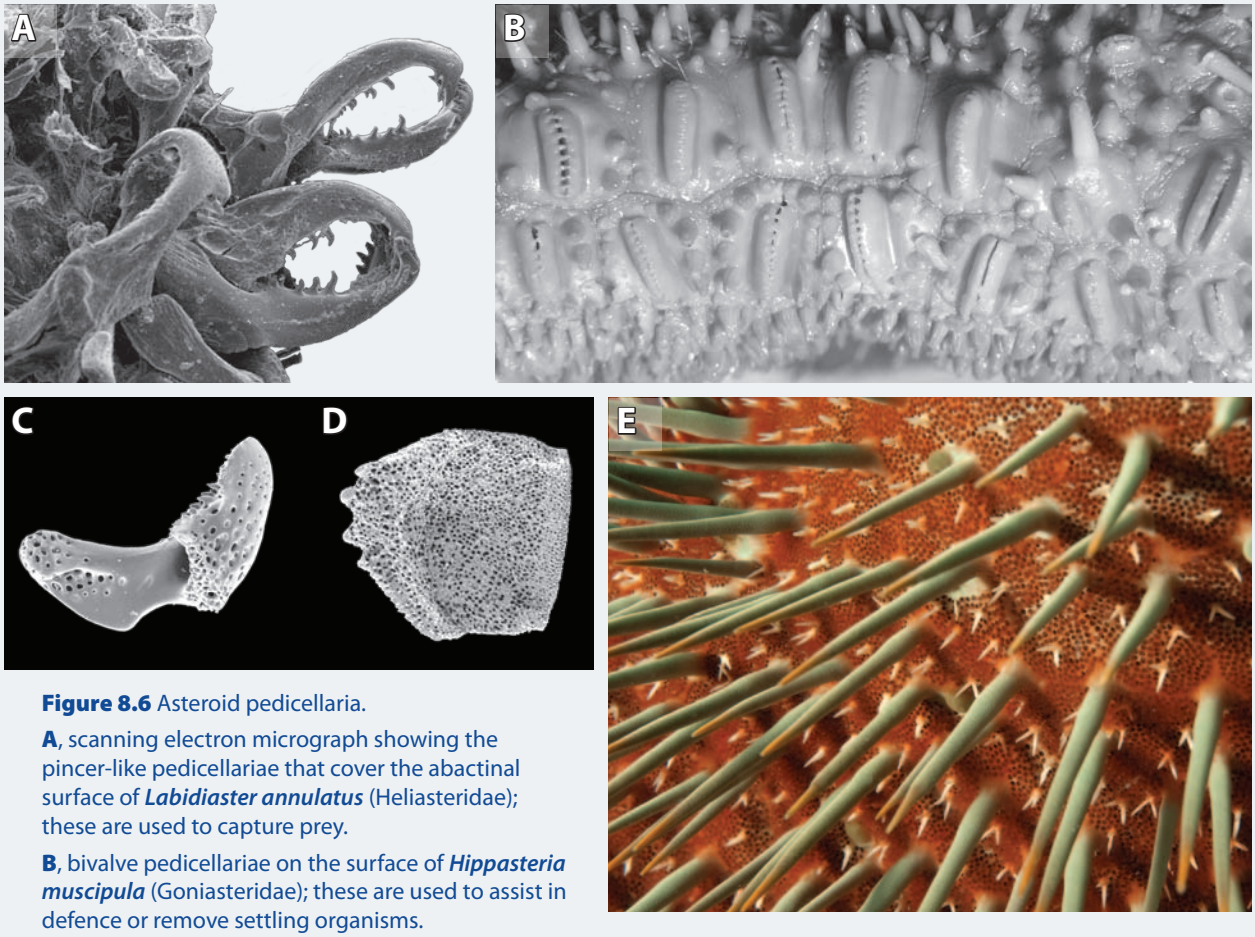


Figure 8.6 Asteroid pedicellaria.

A, scanning electron micrograph showing the pincer-like pedicellariae that cover the abactinal surface of ***Labidiaster annulatus*** (Heliasteridae); these are used to capture prey.

B, bivalve pedicellariae on the surface of ***Hippasteria muscipula*** (Goniasteridae); these are used to assist in defence or remove settling organisms.

C, **D**, scanning electron micrographs of ossicles from pedicellariae: **C**, an ossicle from an asteroid pincer-like pedicellaria. **D**, a single ossicle of a bivalve pedicellaria from ***Hippasteria phrygiana*** (Goniasteridae).

E, pincer-like pedicellariae are scattered among the spines of crown-of-thorns, ***Acanthaster planci*** (Acanthasteridae).

[A,B, B.Ford; C,D, M.Byrne; E, J.Freund]

Forcipulatida (**Fig. 8.6A**) or sessile bivalve or spoon-shaped two-piece structures in the Valvatida and Paxillosida (Jangoux & Lambert 1988; **Fig. 8.6B,D,E**). Several asteroids use their pedicellariae for feeding or defence (Dearborn 1977; Lambert *et al*. 1984; Dearborn *et al*. 1991). The surface of many species are covered by papulae, fluid-filled finger-like extensions of the coelom, which function in respiration (**Figs 1.24, 8.7A**). These structures are also important in asteroid taxonomy.

The asteroid mouth opens into a stomach that connects to the pyloric caeca, enzyme-secreting and nutrient storage glands. Extrusion of the stomach for feeding varies among taxa (Jangoux 1982; Lawrence 2013a). Asteroid skeletal anatomy and the orientation of the mouth and tube foot grooves are closely associated with feeding mode (Blake 1990). For example, the well-developed extrusable stomach, the wide ambulacral grooves with four rows of tube feet, and the adoral carina (abutted oral adambulacrals) in forcipulates (**Fig. 8.4B**; **Box 4.3**) are associated with feeding on bivalves and other molluscan prey (**Figs 1.8B, 8.5**). Some invertebrates have developed mechanisms for avoiding predation by seastars (**Fig. 8.8**).

Most species reproduce sexually (Byrne 2013; Mercier & Hamel 2013), their gonads located in the disc and

arms, depending on the taxon (**Fig. 3.3B; Box 3.2**). Some species are also fissiparous (**Fig. 3.7B; Box 1.3**). *Ailsastra* species (**Fig. 3.7B**) do not appear to produce gonads, at least in the fissiparous form (M.Byrne, unpublished observations). Brooding of young also occurs as seen in the viviparous asterinids (**Boxes 3.1, 4.5**) and the biscuit star *Tosia neossia* (**Box 8.1**).

The earliest known animals identifiable as asteroids appeared in the Ordovician. These fossils show a diversity of body forms indicating life modes similar to living asteroids (see Mah & Blake 2012 for overview). All living asteroids are members of a monophyletic clade, and are morphologically distinct from those observed in the Palaeozoic (Blake 1987; Gale 1987). Modern Asteroidea are thought to be consistent with an extinction-diversification pattern observed in all Echinodermata showing an extinction bottleneck in the late Palaeozoic, narrowing surviving taxa, followed by recovery in the Early Triassic (Twitchett & Oji 2005). Among the oldest living modern asteroids are the Triassic *Noriaster barberoi*, a member of the extant Poraniidae (Valvatacea) (Blake *et al.* 2000), and *Trichasteropsis*, identified as a member of the extant Forcipulatacea (Blake & Hagdorn 2003; Blake *et al.* 2006). Asteroids preserve poorly in the fossil record, making inference about the diversification and evolution of modern taxa difficult. However, nearly all major clades, including Velatida, Forcipulatacea (includes Forcipulatida and Brisingida), Valvatida, and Paxillosida, are present by the Jurassic.

The Asteroidea is the second largest echinoderm class, with over 1,900 species in 37 families (although some families appear to be paraphyletic — for example, Pedicellasteridae), assigned to seven orders (Clark & Rowe 1971; Clark & Downey 1992; Mah & Blake 2012). Australian Asteroidea include 309 species and 121 genera in 27 families (O'Hara 2012). The Valvatida, particularly the Asterinidae, Goniasteridae, Oreasteridae and Ophidiasteridae, are especially diverse in the Australian and Indo-Pacific regions (Blake 1990; Rowe & Gates 1995; O'Loughlin & Waters 2004; O'Loughlin & Rowe 2005, 2006). The current understanding of Asteroidea classification based on Mah & Blake (2012) is shown in **Table 8.1**.

The basis of modern asteroid classification is that of Blake (1987), whose morphology-based phylogenetic treatment has become the basis for most taxonomic accounts (for example, Clark 1989, 1993, 1996; Clark & Downey 1992; Clark & Mah 2001). Our treatment also follows Blake (1987) with subsequent modifications by Fujita & Rowe (2002) and from the molecular work of Mah & Foltz (2011a, 2011b). Comprehensive taxonomic accounts are available from the World Asteroidea Database (Mah 2014).

Molecular (Wada *et al.* 1996; Knott & Wray 2000; Matsubara *et al.* 2004, 2005) and combined molecular and morphological studies (Lafay *et al.* 1995; Janies 2001) over recent years have formed an active area

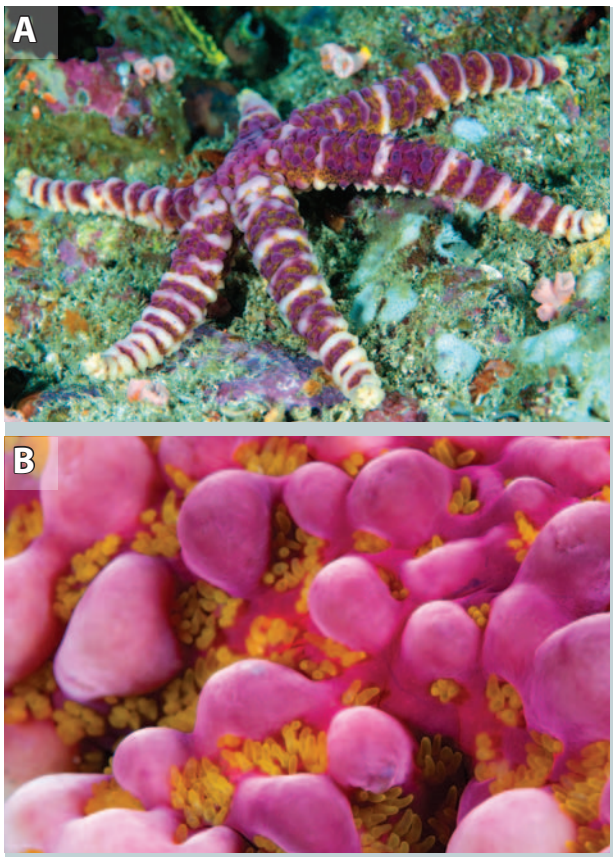


Figure 8.7 ***Echinaster callosus*** (Echinasteridae).
A, adult; species are found across the Indo-west Pacific including tropical waters off northern Queensland.
B, details of the central disc displaying small, yellow finger-like structures called respiratory papulae. The papulae extend through openings in the skeletal plates into the surrounding seawater to undertake gas exchange.
[G.Bell]

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Table 8.1 Classification of the Asteroidea following Mah & Blake (2012). Only those groups recorded from the Australian region are included here. The sequence in which the orders are presented here do not reflect current understanding of asteroid phylogeny (see introductory section).

* Not confirmed for Australia

** Recent research indicates that the Poraniidae is a sister clade to the Valvatacea (Paxillosida + Valvatida) (Mah & Foltz 2011a)

Class Asteroidea	
Order Paxillosida	Order Velatida
Family Astropectinidae	Family Caymanostellidae
Family Benthopectinidae	Family Korethrasteridae
Family Ctenodiscididae	Family Myxasteridae
Family Goniopectinidae	Family Pterasteridae
Family Luidiidae	Order Spinulosida
Family Porcellanasteridae	Family Echinasteridae
Family Pseudarchasteridae	Order Forcipulatida
Family Radiasteridae	Family Asteriidae
Order Valvatida	Family Heliasteridae
Family Acanthasteridae	Family Pedicellasteridae *
Family Archasteridae	Family Stichasteridae
Family Asterinidae	Family Zoroasteridae
Family Asterodiscididae	Order Brisingida
Family Asteropseidae	Family Brisingidae
Family Chaetasteridae	Family Freyellidae
Family Ganeriidae	*Incertae sedis*
Family Goniasteridae	Family Xyloplacidae *
Family Mithrodiidae	
Family Odontasteridae	
Family Ophidiasteridae	
Family Oreasteridae	
Family Podosphaerasteridae *	
Family Poraniidae **	
Family Solasteridae	

of study. The most recent molecular accounts with comprehensive taxon sampling and greater numbers of genetic markers (Janies *et al*. 2011; Mah & Foltz 2011a, 2011b) have contributed significantly to our understanding of asteroid classification. These treatments have isolated the Velatida as potentially a basal taxon and have positioned the Paxillosida, Solasteridae, and Asterinidae among the Valvatacea. Janies *et al*. (2011) demonstrated that the enigmatic *Xyloplax* nests among the Velatida. Mah & Foltz's (2011b) molecular treatment of the Forcipulatacea re-established the previously synonymised Stichasteridae and recognised the phylogenetic importance of the Poraniidae as a clade basal to the clade containing the Valvatida+Paxillosida.

Australian asteroids were documented by H.L.Clark (1909, 1914, 1916, 1921, 1938, 1946). The most recent summary of Australian asteroid taxa is provided by the Australian Faunal Directory (O'Hara 2012). Local photographic guides include those of N.Coleman



Figure 8.8 In Antarctic waters the dorid nudibranch, ***Tritoniella belli***, uses chemical defence to protect itself from predation by the seastar ***Odontaster validus*** (Odontasteridae). [N.Wu]

(1994, 2007) and Edgar (2001). Clark & Rowe (1971) provided keys to tropical, shallow-water Australian taxa, and temperate taxa were documented by Zeidler & Shepherd (1982). O'Hara (1999a) summarised asteroids from Macquarie Island. Australian, deep-water asteroids were described by Clark (1909, 1916). The taxonomic reviews and surveys of Asteroidea in New Zealand waters (H.E.S.Clark 1962, 1970; Clark & McKnight 2000, 2001; McKnight 2006) include many species also known in Australian waters.

Order PAXILLOSIDA

The Paxillosida has been the focus of one of the most enduring questions in higher-level asteroid classification: 'Which is the most ancestral group [plesiotypic] of extant Asteroidea?' Based on the absence of the brachiolaria larva, the inability to extrude the stomach, the absence of an anus, and the presence of pointed tube feet (except for the Radiasteridae), Mortensen (1922) and Gale (1987, 2011) supported the Paxillosida as the most stemward living Asteroidea. The contrary position, that these features were derived, adaptations to a habitat of unconsolidated and soft sediment, was first advanced by MacBride (1921, 1923) and later supported by Blake (1987). There have been many exchanges on this topic in the literature (see Bather 1921; MacBride 1921, 1923; Mortensen 1922), and summaries of the conflicting views are presented by Blake (1989) and Gale (2013). Early molecular data did little to elucidate the phylogenetic position of the Paxillosida (see Lafay *et al*. 1995; Knott & Wray 2000; Matsubara *et al*. 2005). However, more recent molecular phylogenetic treatments of the Asteroidea (Janies *et al*. 2011; Mah & Foltz 2011a), involving more

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comprehensive taxon sampling and genetic data, have shown the Paxillosida as relatively derived within the Valvatacea and provided alternative candidates for potential basal asteroid clades (for example, Velatida). Further molecular work has also added the Pseudarchasteridae and the Benthopectinidae to the Paxillosida clade, broadening the suite of recognised morphological features associated with the group. The Paxillosida is still argued to be ancestral based on developmental and morphological evidence (Gale 2013), but this is likely to be an oversimplification and obscured by poor taxon sampling (Mah & Blake 2012; Blake & Mah 2014).

The most recent classification of the Paxillosida recognises eight families (**Table 8.1**), all of which have representatives in Australian waters. The order is diverse and ubiquitous. Paxillosidans are common in sandy and muddy sediments and many are infaunal. Species that have pointed tube feet use them to displace sediment and often bury themselves completely. Many paxillosidans spend much of their time immediately beneath or near the sediment surface, including groups such as the Pseudarchasteridae which have suckered tube feet.

Most paxillosidans have five arms (**Fig. 8.9**), but some luidiids have as many as 11 (**Fig. 8.13**). Paxillosidans have a well-defined disc with long, straight-sided arms that taper to pointed tips. The abactinal, marginal and actinal plates are distinct and can carry spines, granules and sometimes pedicellariae. Luidiids have superomarginals that are indistinguishable from paxillae. Pedicellariae are generally of the 2-valve type, borne on one ossicle. The abactinals are almost exclusively in the form of paxillae or simplified ossicles that are apparently based on paxillae. The madreporite is large, conspicuous and located near the marginals. Papulae are restricted to, and widely distributed over, the abactinal surface, and are concealed by paxillae in astropectinids, goniopectinids, luidiids, pseudarchasterids, and radiasterids. The marginal plates form a distinct, even and conspicuous edge to the disc, and the arms and inferomarginals often bear enlarged spines. Intermarginal plates are absent. Fascioles or cribriform organs of ciliated, geometrically arranged spinules are often located between the marginal plates. The ambulacral plates overlap and the tube foot furrow is broad and angular and has two rows of tube feet. The oral plates are obvious, as they project above surrounding plates and are noticeably keeled below. Superambulacral plates can sometimes occur internally along the arms. The interbrachial septa are membranous. Some paxillosids (other than the Luidiidae) have a blind-ending, epiproctal cone occupying the normal position of the anus in other asteroids. Tube feet are pointed in some taxa.

Family Astropectinidae

Figure 8.9

The Astropectinidae is a widespread family with 26 genera and 243 species, present in tropical to temperate waters (Mah & Blake 2012). Of these, 24 species are known from Australian waters (O'Hara 2012). Astropectinids occur at depths ranging from shallow water — *Astropecten* species, to deep waters — see the collection of *Dytaster spinosus* from Bass Strait (Museum Victoria OZCAM). In Australia, *Astropecten polyacanthus* and *A. vappa* (**Fig. 8.9**) are widely distributed, occurring in temperate and tropical waters. *Bollonaster pectinatus*, from



Figure 8.9 Family Astropectinidae.

Astropecten vappa occurs throughout the eastern Indo-west Pacific region. It is circum-Australian in waters down to 130 m, and can be common in nearshore sandy habitats.

[W.Boyle]

temperate Australia, is a small (R = 50 mm) colourful astropectinid often confined to deep water (Edgar 2001). *Tethyaster* species (R = 160–280 mm) are among the largest astropectinids (Clark & Downey 1992); the one species, *T. tangaroae*, recorded from Australian waters is found off Norfolk Island in waters at depths of 390–430 m. Two species of *Psilaster* are known from Australian waters — *Psilaster charcoti* from off Macquarie Island at depths of 25 m to 3,248 m (O'Hara 1998), and *P. acuminatus*, a similar species, widespread from New South Wales, around southern Australia to Western Australia (O'Hara 2012).

Astropectinids are characterised by having five arms that taper to a round tip with a knob-like terminal plate. Internally they have double tube foot ampullae. The disc is usually large and distinct. A central epiproctal cone is sometimes present and is used for respiration, especially when the seastar is buried (Christensen 1970). The madreporite can be obscured by paxillae, and the abactinal plates are small and crowded. Marginal plates are block-like, form a distinct edge to the body, often bear a formidable array of large spines and are usually covered by granules. Superomarginal and inferomarginal plates generally correspond to each other and are separated laterally by distinct spaces between plates (called fasciolar grooves) lined by fine spines. The abactinal paxillae are small and crowded, and the actinal areas are small and include very few actinal plates. The most prominent plates seen from the actinal surface are the broad, regularly arranged inferomarginal plates and spine-bearing subambulacral plates lining the tube foot furrow. Pedicellariae are simple.

Astropectinids are carnivores and take a range of prey, primarily molluscs as well as crustaceans and other *Astropecten* species (Sloan 1980; Schmid & Schaerer 1981; Freeman *et al.* 2001). The ecology and general biology of *Astropecten* are reviewed by Ventura (2013). *Astropecten* species have a strong influence on the density of their infaunal prey and usually engulf their prey whole (Christensen 1970; Franz & Worley 1982; Ventura *et al.* 2001). They are commonly found either partially or completely buried, and shallow-water species often emerge at dusk and at dawn to forage (Nojima 1981; Beddingfield & McClintock 1993).

The diets of *Astropecten sumbawanus*, *A. zebra* and *A. velitaris* are dominated by bivalve and gastropod molluscs; these food items constitute 90% and 75% of their intake respectively (Lemmens *et al.* 1995; Wells & Lalli 2003). *Astropecten velitaris* also complements its diet with crustaceans (Lemmens *et al.* 1995). The Antarctic species *Psilaster charcoti* appears to utilise a range of feeding modes from predation to detritus-feeding; the stomach contents have been found to include mud, fish, polychaetes and ascidians (Dearborn 1977; McClintock 1994). *Dytaster grandis*, from the abyssal North Atlantic, is a predator and an omnivorous scavenger (Gage *et al.* 1983).

A study of the Atlantic *Astropecten irregularis* revealed a seasonal distribution pattern (Freeman *et al.* 2001). This species reaches high densities in shallow water during the summer spawning season and returns to deeper water in winter. This winter migration is thought to be a strategy to avoid unfavourable conditions such as storm surges (Nojima 1983; Freeman *et al.* 2001). The distribution of *Astropecten* species is also influenced by the organic content of the substrate (Ventura & Fernandes 1995).

Astropecten species in temperate and tropical regions have been reported to spawn large numbers of small eggs (*ca.* 115 µm diameter) in spring and summer (Nojima 1983; Grant & Tyler 1986; Emlet *et al.* 1987; Marion *et al.* 1998; Ventura *et al.* 1998), and the development of several species has been described (Oguro *et al.* 1976; Komatsu & Nojima 1985; Chia *et al.* 1993). *Astropecten* species with small eggs (100–120 µm diameter) develop through a bipinnaria larva, and those that spawn large eggs (300–460 µm diameter) have a simple, barrel-shaped, lecithotrophic larva (Chia *et al.* 1993). The deep-water astropectinids from the north-eastern Atlantic Ocean, *Plutonaster bifrons* and *Dytaster insignis*, have small eggs and planktotrophic development, while *Psilaster andromeda* and *Bathybiaster vexillifer*, from the same region, have large eggs (950 µm and 1,000 µm diameter, respectively) and probably some form of benthic development (Tyler & Pain 1982b; Gage *et al.* 1983). *Psilaster charcoti* has large eggs (770–950 µm diameter) and develops though a non-feeding yolky larva (Pearse & Bosch 1994).

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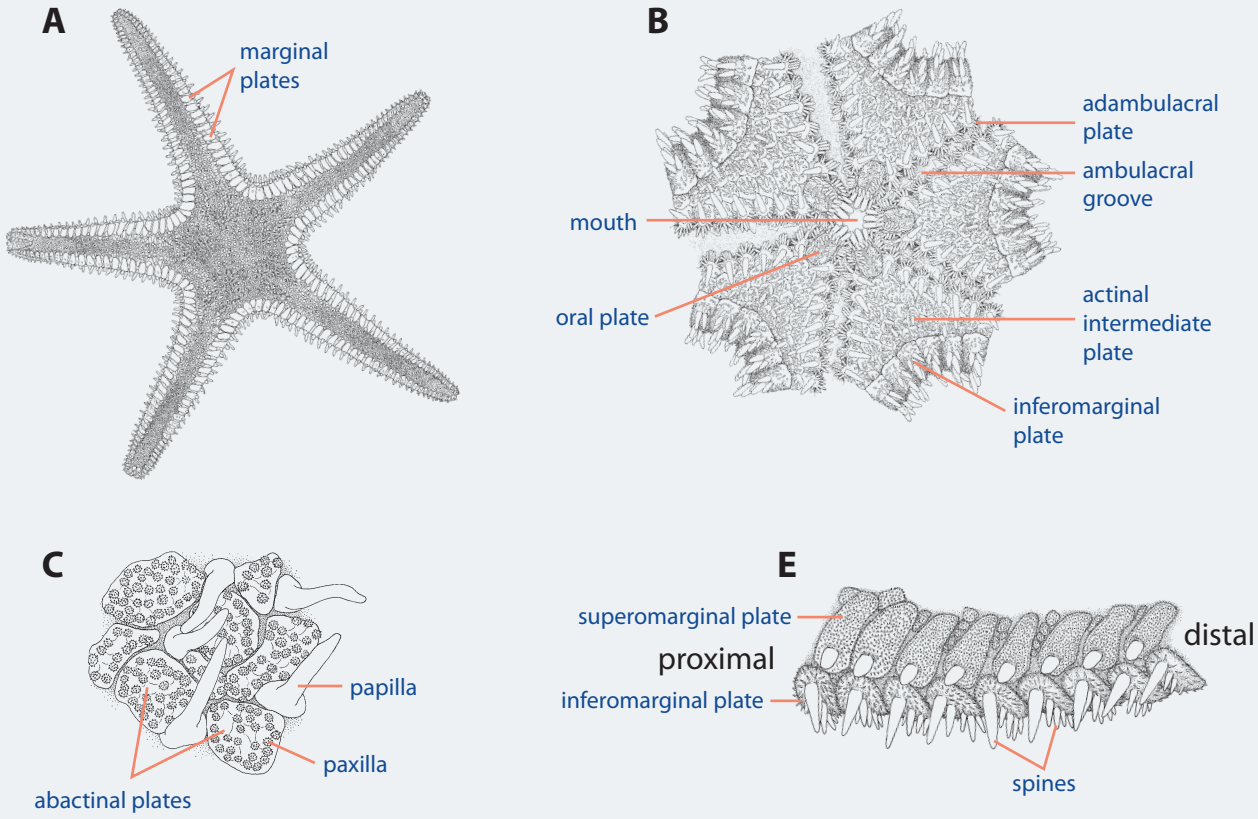


Figure 8.10 Family Benthopectinidae.

Cheiraster subtuberculatus is found in deep waters off Sydney, New South Wales:

A, abactinal view of whole animal.
B, actinal view of mouth region.
C, part of the abactinal surface near the base of a ray, showing abactinal paxillar plates and papillae; dorsal view.
D, a single abactinal paxillar plate.
E, lateral view of part of a ray showing the alternation in position of the inferomarginal and superomarginal plates.
(specimen AMJ9207)

[A.Murray]

Family Benthopectinidae

Figure 8.10

The cosmopolitan Benthopectinidae includes eight genera and 69 species, six of which have been recorded from Australia (O'Hara 2012). Benthopectinids are generally found below 200 m (Blake 1990).

The disc is small with long, tapering arms that are thin and strap-like (**Fig. 8.10A**). The terminal plate is robust with a distinctive U-shaped cleft on the plate tip, and the madreporite is large and conspicuous. Internally, the dorsal arm muscles are well developed, paired and attach near the arm base. Generally, the interradial arcs are angular, and the abactinal plates are thin and scale-like. Marginal, abactinal and actinal plates are distinct, although the abactinal plates are occasionally reduced and embedded in dermal tissue. Occasionally, plates are isolated, particularly on the arms, and abactinal plates can bear a close cover of paxillae, especially on the disc (**Fig. 8.10C,D**). Some central paxillar spines are enlarged, and papulae are restricted to proximal patches (papularia) at the base of

the rays or on the disc. The papularia are oval, bi-lobed or occasionally horseshoe-shaped. The anus, situated near the disc centre, is usually obvious. Marginal plates tend to alternate, most obviously interradially where the unpaired superomarginal plate sometimes bears a long, slender, conspicuous spine (**Fig. 8.10E**). Smaller spines (spinules) are generally present on both sets of plates. Large spines and spinelets are occasionally present, especially on the inferomarginals. Actinal areas are small and generally restricted to the vicinity of the disc where actinal plates are variable in size and arrangement. The adambulacral plates are angular or rounded with a well-developed fringe of spines. At least one subambulacral spine is conspicuous. Pedicellariae are simple with two valves, or complex with many blades. They can incorporate spinelets from several plates. The suckered tube feet are biserial, and superambulacrals are absent.

Little is known about benthopectinid biology. The stomach contents indicate an omnivorous or predatory lifestyle, but suspension feeding also has been suggested (Blake 1990). *Cheiraster gerlachei*, from Antarctic waters, is an active predator on ophiuroids (Dearborn 1977; McClintock 1994). *Benthopecten simplex* is relatively abundant in parts of the Atlantic Ocean, where specimens of a range of sizes have been hauled from soft muddy sediments at 2,000 m (Gage *et al.* 1983). This species and *Pectinaster filholi*, also from the North Atlantic, have large eggs (950 µm and 850 µm diameter, respectively), indicating lecithotrophic development (Pain & Tyler 1982; Gage *et al.* 1983). Juvenile development and early skeletal plate formation in these benthopectinids are described by Sumida *et al.* (2001).

Family Ctenodiscididae

Figure 8.11

The Ctenodiscididae includes only one extant genus and is closely related to the Goniopectinidae. The family includes five species, one of which, *Ctenodiscus orientalis*, occurs in Australian waters (O'Hara 2012). This species is found in deep water (436–546 m) off Tasmania (Dartnall 1971b) and has also been collected from north-western Australia. *Ctenodiscus* has a circumpolar distribution in both hemispheres (Dartnall 1971b). Ctenodiscididae includes one fossil genus.



Figure 8.11 Family Ctenodiscididae.
Ctenodiscus crispatus is an abundant circumboreal species. Its features are similar to those of ***C. orientalis***, the only Australian representative of the genus; it is found in deep water (400–500 m) off Tasmania and north-western Australia. These asteroids live in burrows in the upper layer of muddy sediment habitat, and feed on fauna in whole sediments. The epiproctal cone is indicated by a white arrow. In life this structure extends to the surface and appears to be used to facilitate gas exchange.

[C.L.Mah]

Ctenodiscids have five arms and are characterised by the presence of an epiproctal cone, cribriform organs present along the arms, angular marginals, and three to six furrow spines. There are no studies of the Australian species but the biology of *Ctenodiscus crispatus* (**Fig. 8.11**), a locally abundant circumboreal species, has been described in detail in a series of papers (Shick 1976; Shick *et al.* 1981a, 1981b). Ctenodiscids are particulate suspension and non-selective deposit feeders (Jangoux 1982; Blake 1990) living in temporary burrows in the uppermost layer of the sediment. The aboral surface is thin, and its epiproctal cone connects with the surface while the seastar is buried. This cone is highly extensible and it seeks out the surface in response to anoxic conditions (Shick 1976). The epiproctal cone keeps the burrow open to the overlying

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water. Ctenodiscids ingest large quantities of mud, and their highly expandable stomach can contain a wide range of objects, including sponge spicules, gastropods, bryozoan fragments and worms (Fisher 1940). Stable isotope analysis also indicates that *Ctenodiscus* feed on bulk sediment and molluscs (Gale *et al*. 2013). As there is no anus, the waste from ingested material is extruded through the mouth (Shick *et al*. 1981b). The ciliated lamellae of the cribriform organs generate strong currents that are important in keeping water circulating through the burrow (Shick *et al*. 1981b). Water is pumped through the organs, and particles drawn into the burrow by these currents are trapped in mucus that is then ingested. Excurrent channels are excavated hydraulically from the arm tips to the sediment surface.

Ctenodiscus crispatus spawns large, positively buoyant eggs (*ca*. 400 µm diameter) indicating development through a planktonic lecithotrophic larva (Shick *et al*. 1981a). The aseasonal reproductive pattern of this species may be due to the presence of a continuously available food source (Shick *et al*. 1981a).



Figure 8.12 Family Goniopectinidae.
Prionaster megaloplax is one of four species in the genus ***Prionaster***. They occur throughout the central Indo-Pacific in deep water (400–500 m).
[C.L.Mah]

Family Goniopectinidae

Figure 8.12

The family Goniopectinidae includes three genera and 10 species, one of which is reported from Australian waters (O'Hara 2012). The genus *Prionaster* (**Fig. 8.12**) has been found at 400–500 m off north-western Australia.

Goniopectinids usually have five arms, the tips of which are protected by conspicuous terminal plates bearing two or three slender spines. The disc is well defined and bears an epiproctal cone, and the abactinal plates are paxilliform. Papulae are widespread on the abactinal surface, but absent from the midline of the rms. The marginal plates are well developed, and the superomarginals correspond with inferomarginals. The cribriform organs are simple and are present between some or all of the marginal plates. Pedicellariae are absent. The actinal plates run in a double series from adambulacrals to inferomarginals, the double series of plates being separated from each other by distinct channels. The adambulacral plates are conspicuous, and the furrow spines are webbed basally. Subambulacral spines are also present. The oral plates are conspicuous, and there can be one or two enlarged spines projecting over the mouth. No information is available on the biology of the Goniopectinidae.

Family Luidiidae

Figure 8.13

The Luidiidae is a widely occurring monogeneric family present in tropical to temperate waters (Clark 1989). Seven of the 49 known species of *Luidia* have been reported from Australian waters (O'Hara 2012). They are common in shallow waters. The Australian taxa include *L. hardwicki* from Cape Leeuwin, Western Australia, to Jervis Bay, New South Wales, and *L. prionota* and *L. hexactis* from northern waters. *Luidia maculata* is a widespread tropical species found in waters of northern Western Australia, Elizabeth Reef, Lord Howe Island and Norfolk Island. *Luidia avicularia* also occurs at Elizabeth Reef and Norfolk Island. *Luidia neozelanica* is found in south-eastern Australia and *L. australiae* (**Fig. 8.13**) has a widespread temperate distribution in Australian waters.

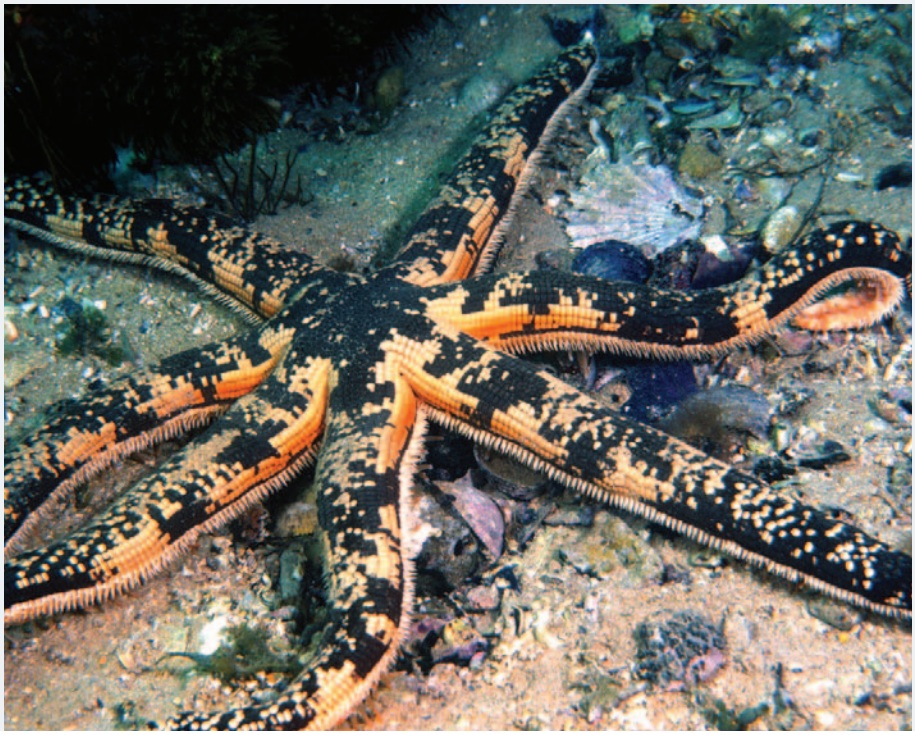


Figure 8.13 Family Luidiidae. ***Luidia australiae*** is a large predatory seastar endemic to the southern waters of Australia down to depths of 150 m. It is found in seagrass beds and sandy and silt areas often semi-buried in the sediments. Typically, it has seven flexible arms and may reach 400 mm in width. [W.Boyle]

Luidia includes 5-armed species, and others with as many as 11 arms (**Fig. 8.13**). The arms are strap-like and taper gradually to an inconspicuous terminal plate, and the disc is small and flattened. These asteroids are often brightly coloured, and the abactinal paxillae are striking, often having fine, thorny spines in regular longitudinal and transverse rows, especially laterally. On the midline of the arms and on the disc centre the arrangement is less regular. The large inferomarginals are distinct and band-like and generally bear some enlarged spines. They occupy most of the arm margin and are separated laterally by distinct fasciolar grooves lined by fine spines. The superomarginals are small and differ little from neighbouring abactinal paxillae. Papulae are widespread and extend to the arm tip; they are unusual in being branched. The lower surface has few actinal plates, and these are often located only between adambulacral plates and the inferomarginals. Pedicellariae can be large and distinct, sessile or stalked, and generally with two, but occasionally three, blades. The madreporite is interradial and is often large and conspicuous. Superambulacral plates are often seen when the arms are broken.

Little is known of the biology of Australian *Luidia* species, but they are well studied elsewhere in the world (see the review by Lawrence 2013b). Luidiids are primarily carnivores although there are some reports of detrital feeding (Fenchel 1965; Sloan 1980; Jangoux 1982). They are active and agile predators preying on epifauna (primarily other asteroids and gastropods) and infauna (holothuroids, ophiuroids and bivalves) (Lawrence 2013b). *Luidia maculata* engulfs and consumes heart urchins (*Breynia*) in Shark Bay, Western Australia (L.M.Marsh, personal observations). *Luidia clathrata*, from the western Atlantic and Caribbean, changes behaviour, and prey species and prey size, depending on availability. This asteroid also feeds on detritus, but small prey, including bivalves and echinoderms, are preferred and are engulfed whole. *Luidia clathrata* retreats below the sediment to digest prey. Luidiids are well known for their ability to autotomise their arms. Unlike other asteroids where autotomy occurs at the base of the arms, *Luidia* species can break off parts of their arms at various points along their length.

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Species of *Luidia* spawn large numbers of small eggs (120–170 μm diameter) (Emlet *et al*. 1987). The bipinnaria larvae are very large (3–7 mm long) and are readily identified in plankton samples (Mortensen 1938; McEdward *et al*. 2002). They metamorphose in the plankton, and the larval body carries the juvenile that eventually settles to the benthos and attaches with the juvenile tube feet. The juvenile is large and well developed by settlement. *Luidia* bipinnariae undergo an unusual form of asexual reproduction during larval life (Bosch *et al*. 1989; Vickery *et al*. 2002); they bud off portions of the larval body and each of these develops into a new larva.

Family Porcellanasteridae

The Porcellanasteridae includes 12 genera and 30 species (Mah & Blake 2012) with most species inhabiting lower bathyal to abyssal depths on soft to muddy bottoms. Madsen (1961a; 1961b) provided a detailed treatment of the Porcellanasteridae. One species, *Porcellanaster ceruleus*, occurs in Australian waters (O'Hara 2012).

Porcellanasterids often occur in large numbers and exhibit a broad range of sizes. *Porcellanaster ceruleus*, a small (R = 3.6 mm), almost cosmopolitan species, lives on soft deepsea ooze and has been recorded from south-eastern Australia at depths of 1,160–6,040 m (Rowe & Gates 1995). Sampling off Western Australia has revealed the presence of two further genera, *Sidonaster* at 700 m and *Styracaster* at 1,600 m (L.M.Marsh, unpublished observations).

The five arms of porcellanasterids are distinct from the disc, and the arm tips are protected by a conspicuous terminal plate that often carries 1–3 distinct spines. The abactinal surface is covered by plates that can bear spines or paxillae. Papulae are either absent or inconspicuous. Marginal plates form a distinct edge to the body, are often very thin, and occasionally carry spines. Superomarginal plates from each side of the arm can meet part way along arms. Cribriform organs are lamelliform or papilliform covered patches that are located in distinct depressions between the marginal plates. These regions are composed of grooves with sheets of tissue and well-developed ciliary tracts which serve to enhance particulate feeding and respiration. Slightly larger spinelets mark a periphery around each cribriform region. The madreporite is interradial and located near the superomarginal plates. The actinal plates are flat, often arranged in a regular series parallel to the marginals and are sometimes covered by a thick skin. Often distinct channels are seen between the adambulacral and inferomarginal plates. The adambulacral plates are large, have a recurved margin and two or three furrow spines, while the oral plates are large and conspicuous.

Porcellanasterids are thought to be particulate suspension and deposit feeders, depending on phytodetritus and ingesting heterotrophic bacteria (Sloan 1980; Jangoux 1982; Blake 1990; Howell *et al*. 2002). They can also scavenge on animal remains (Clark & Downey 1992). These burrowing animals live well below the surface, and the epiproctal cone, an extension from the abactinal surface, can be the only connection with the overlying water. Specimens are often collected with the disc greatly distended by ingested mud. They are likely to feed in a manner similar to the better-studied *Ctenodiscus* (see Ctenodiscididae). The cribriform organs create water currents to enhance particulate feeding and respiration. Food particles trapped in strings of mucus are conveyed to the mouth. *Hyphalaster inermis* and *Styracaster chuni* from the North Atlantic produce large eggs (650 μm diameter) indicating lecithotrophic development (Ramirez-Llodra *et al*. 2002). Juvenile development and early skeletal plate formation in these species and other porcellanasterids are described by Sumida *et al*. (2001).

Family Pseudarchasteridae

The Pseudarchasteridae, which includes *Pseudarchaster* and related genera, such as *Paragonaster* and *Perissogonaster*, were referred by Mah & Foltz (2011a) to the Paxillosida. This family comprises four genera and 29 species (Mah & Blake 2012). Five species of *Pseudarchaster* occur in Australian waters (O'Hara 2012).

Pseudarchasterids are morphologically intermediate between goniasterids (Valvatida) and the Paxillosida, appearing superficially similar to the Astropectinidae. They are characterised by paxillate abactinal plates, extensive fasciolar channels, poorly defined carinal rows, elongate marginal plates and superambulacral plates. However, historical classifications have placed strong emphasis on the importance of tube foot morphology, which in *Pseudarchaster* is not pointed as it is in other Paxillosida.

The biology of pseudarchasterids is poorly understood. Gut contents of species of *Pseudarchaster* and *Paragonaster* have included sediment, detritus and the remains of other invertebrates. The habitat of *Pseudarchaster* includes soft bottoms, and different species occur at depths ranging from shallow (*P. parelii*) to abyssal (for example, *Pseudarchaster jordani*). *Pseudarchaster parelii* and *Paragonaster subtilis*, from deep water in the North Atlantic Ocean, have very large eggs (~1.0 mm diameter) (Tyler & Pain 1982a), indicating lecithotrophic development.

Family Radiasteridae

Figure 8.14

The Radiasteridae is a monogeneric family with five species (Mah & Blake 2012). One species occurs in Australia, *Radiaster gracilis* at depths from 90–2,377 m in the south-eastern region (O'Hara 2012).

Radiasterids are characterised by their suckered tube feet and large anus ringed by six or seven very distinct plates. They have a large disc, and the five arms taper evenly to a conspicuous terminal plate (**Fig. 8.14**). The abactinal plates are paxilliform with, usually, four to six short basal lobes that can overlap. The plates bear a central rounded trunk crowned by a tuft of very fine, slender, hyaline spinelets that gives the abactinal surface a 'hairy' appearance. The interradial madreporite is large and obscured by paxillae. The abactinal plates are arranged in very regular rows. The marginal plates are often stacked on one another and define the body margin. Papulae are present over the entire abactinal surface; occasionally one or two papulae are present in the membranous areas

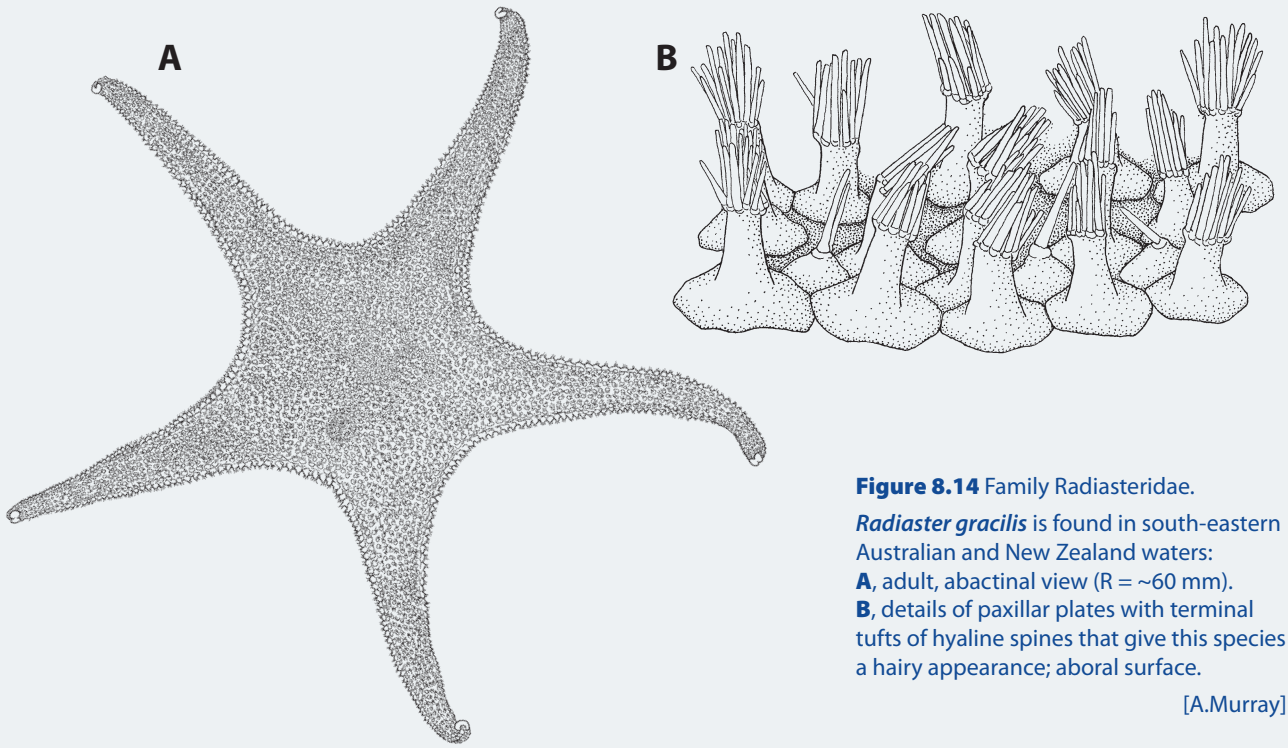


Figure 8.14 Family Radiasteridae.
Radiaster gracilis is found in south-eastern Australian and New Zealand waters:
A, adult, abactinal view (R = ~60 mm).
B, details of paxillar plates with terminal tufts of hyaline spines that give this species a hairy appearance; aboral surface.
[A.Murray]

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between the plates. The actinal plates are paxilliform, compact and regularly arranged, and separated by very distinct, naked grooves. These paxillae form regular rows that extend between the adambulacral plates and the inferomarginals. The adambulacrals are regularly arranged and have conspicuous hyaline spines. The furrow spines are sturdy. The oral plates are raised and also have a conspicuous array of slender hyaline spines. There are no pedicellariae. Internally, the interradial septa are membranous and the gonads possibly open actinally on each side of the interradial septum. This could indicate an egg-laying mode of reproduction. No information is available on the biology of these deep-water asteroids.

Order VALVATIDA

The most recent classification of the Valvatida recognises 17 families, 15 from the Australian region (**Table 8.1**). Valvatidans are among the most frequently encountered and ecologically important asteroids, particularly the Asterinidae, Acanthasteridae, Goniasteridae and Oreasteridae. They are a diverse assemblage of seastars ranging from tropical to polar seas and are often dominant in shallow tropical waters (Clark & Rowe 1971; Yamaguchi 1975). In the Indo-Pacific valvatidans are the most diverse of the asteroids (Clark & Rowe 1971; Blake 1983; O'Loughlin & Waters 2004). They vary in shape from the flat cushions and large discs typical of many asterinids (*Parvulastra*) to the high-domed cushion shape of the oreasterids (*Culcita*), the stellate ophidiasterids (*Linckia*) and the small discs of odontasterids (*Odontaster*).

A molecular phylogenetic overview of the Valvatacea, the larger group containing the Valvatida and Paxillosida, by Mah & Foltz (2011a) has shown the Poraniidae as emerging stemward relative to other valvatidans and paxillosidans (= the Valvatacea). This study clarified the position of the Asterinidae and Solasteridae as members of the Valvatida. *Pseudarchaster* and its allies, historically placed within the Goniasteridae, have been shown by molecular evidence to be members of the Paxillosida (Mah & Foltz 2011a). The enigmatic Leilasteridae was shown to be embedded within the Asterinidae. The Poraniidae is included herein for convenience until further work defines its relationship within the broader Valvatacea.

Much of the following account of the diagnostic characters of valvatidans follows Blake (1987) and Clark & Downey (1992). All species use adambulacral and jaw ossicles to close over their tube foot furrows and oral region. The body skeleton is often stout, and the marginal, abactinal and actinal skeletal elements are highly variable. They include tabulate, regularly bulbous or thin to thick polygonal shapes. The ossicles are usually closely arranged, typically abutting or weakly overlapping. The body surface bears granules, spinelets, stout or slender spines or tubercles. Pedicellariae are numerous to few or absent, and they are generally bivalved. Pedicellaria valves vary in morphology, being sessile or alveolar, and they are borne on one ossicle. The madreporite is small and generally located near the centre of the disc. Abactinals can be tabulate, flattened, more or less irregular and bulbous; paxillate abactinals are uncommon. Valvatida have well-defined and distinctive central plates at the base of radial and interradial axes on the disc. Developmentally, these are the oldest plates, and they are also termed the primary circlet, or calycinals. The terminals are small and the marginals are generally well defined, although in some species these can be obscured by a covering of dermis. The marginals of the two series are similar, and intermarginals are rare. The longest actinal row is that adjacent to the adambulacrals, except in the Poranidae. The oral plates are triangular, and the adambulacrals are upright and weakly overlapping. The furrow spines are arranged longitudinally. Internally, superambulacrals occur in some taxa, and the interbrachial septa can have ossicles. Papulae are widely distributed over the abactinal surface, and can occur intermarginally and actinally. Tube feet are generally in two rows, rarely in four, and have suckers. Valvatidans vary in size from the minute *Parvulastra parvivipara* (R = 5 mm) to the large *Acanthaster planci* (R = up to approximately 200 mm).

Family Acanthasteridae

Family 8.15

The Acanthasteridae comprises one genus, *Acanthaster*. Currently, two species are recognised, *A. planci* and *A. brevispinus* (**Box 4.4**); both species have an Indo-Pacific distribution that includes tropical Australian waters (see **Chapter 4**). However, recent molecular data indicates that *A. planci* is a species complex of four species that can be identified by colour pattern (Vogler *et al.* 2012). The crown-of-thorns seastar, *A. planci*, is a well-known specialist corallivore found in all Australian coral reef habitats from the far north-east and north-west to Lord Howe Island. In contrast, *A. brevispinus* occurs in tropical Queensland and off Ningaloo Reef in north-western Australia where it inhabits sandy inter-reefal areas to 20 m depth and feeds on bivalves, but never on coral.

Acanthaster species are multi-rayed seastars with 8–21 arms (**Fig. 8.15; Box 4.4**). They have a reduced articulated aboral skeleton bearing articulated spines, and a soft skin, with fine, well-spaced granules, that covers the skeleton and spines. There are numerous madreporites, and two-jawed pedicellariae also provide protection for the aboral surface (**Fig. 8.6E**). *Acanthaster* species have well-developed interbrachial septa and double ampullae.

Acanthaster planci is a large seastar (diameter up to 400 mm, rarely to 700 mm) (Moran 1986). It is usually a rare (0.06 per hectare) species, but large 'outbreak' populations (50–100 per hectare) occur sporadically, causing widespread coral mortality (**Fig. 4.9A,B**). The causes of these outbreaks have been the subject of extensive research and debate (see reviews by Uthicke *et al.* 2009; Fabricius 2013; Pratchett *et al.* 2014; and **Chapter 4**). *Acanthaster planci* feeds on corals by extruding its large gastric sac over the prey and releasing enzymes that digest the coral tissue, leaving behind the white coral skeleton (**Fig. 4.9**). The spines covering the surface of *A. planci* contain a toxin that deters predators; the spines can cause painful injury to humans. The eggs contain a high concentration of saponin, a chemical toxic to fish and presumed to protect the eggs and embryos from predation (Lucas *et al.* 1979). The toxins and array of spines possessed by *A. planci* are likely to have evolved as defensive features in response to predation in its evolutionary past. Today, aside from a few specialist snails (for example, *Charonia tritonis*; **Figs 2.12, 4.10**), a shrimp, a pufferfish and the Maori Wrasse that occasionally prey on *A. planci*, populations of this seastar are more or less invulnerable (Ormond *et al.* 1990; Pratchett *et al.* 2014).

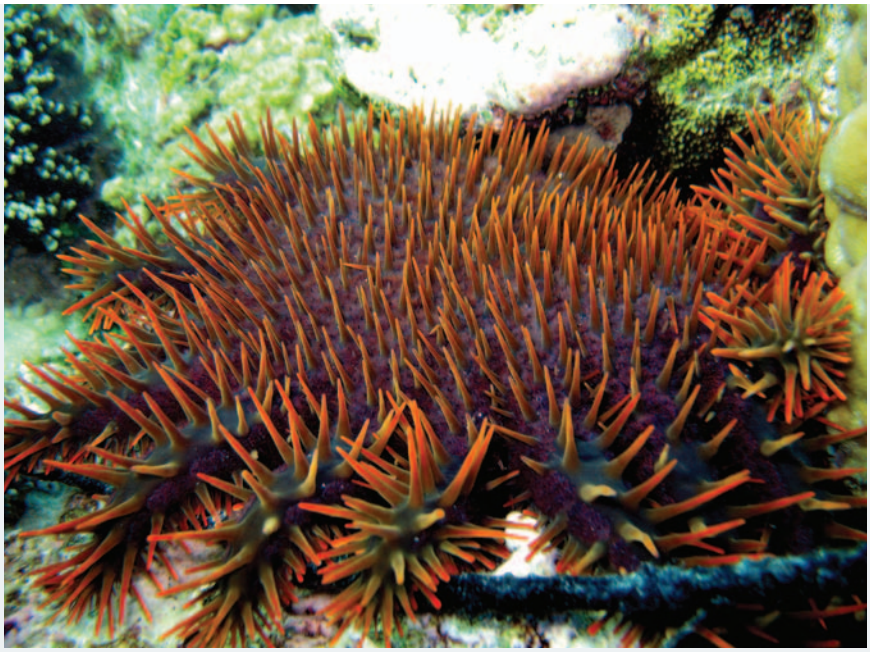


Figure 8.15 Family Acanthasteridae. ***Acanthaster planci***, commonly known as the crown-of-thorns, is found throughout the Indian and Pacific Oceans including Australia's tropical reefs where it preys on live coral (see **Box 4.4**). This large seastar is covered in toxic spines up to 50 mm long.

[S.Uthicke]

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Due to extensive research, the biology of *A. planci* is comparatively well understood (Moran 1986; Brodie *et al.* 2005; Fabricius 2013; Pratchett *et al.* 2014). Sexual maturity is reached at 1.5–2.0 years, and the seastar is dioecious with a massive input into reproduction by males and females. Females are highly fecund, releasing about 60 million eggs (Babcock *et al.* 1994). Larval development extends through plankton-feeding bipinnaria and brachiolaria larvae (**Fig. 3.11A,B**), as is typical of most asteroids (Lucas 1982; Kamya *et al.* 2014; Wolfe 2015a, 2015b). The juveniles first feed on crustose coralline algae and then switch to a coral polyp diet after several months, at a size of R = ~4 mm (Yamaguchi 1973; Johansson *et al.* 2016; Kamya *et al.* 2016).

Family Archasteridae

Figure 8.16

The Archasteridae is a monogeneric family with two species, *Archaster typicus* and *A. angulatus* (**Fig. 8.16**). Both species are distributed throughout the Indo-Pacific, usually in shallow, sheltered habitats and occasionally in deeper water (50–60 m). In Australia, *A. typicus* and *A. angulatus* are found in tropical waters, the latter also extending into temperate latitudes (O'Hara 2012).

The disc is small and gives rise to five elongate arms that are flattened and pointed (**Fig. 8.16**). Due to several convergent features, such as paxilliform abactinal plates, flattened, spade-shaped spines on the inferomarginals and a reduced actinal intermediate region, archasterids superficially resemble astropectinid seastars. However, archasterids have suckered rather than pointed tube feet. They also have a very distinctive carinal (radial) plate series. The carinal plates are large in comparison to the adjacent adradial plates. Aboral ossicles are tabulate and paxilliform, and adradial plates are arranged in oblique transverse rows. When viewed from the (internal) coelomic side, the plates appear as narrow bar-shaped imbricate ridges. When present, the alveolar pedicellariae are located on adambulacral plates.

Archaster species live in soft sediment habitats and are predators of sediment-dwelling invertebrates (Mukai *et al.* 1986; Lawrence *et al.* 2010; Keesing *et al.* 2011a).

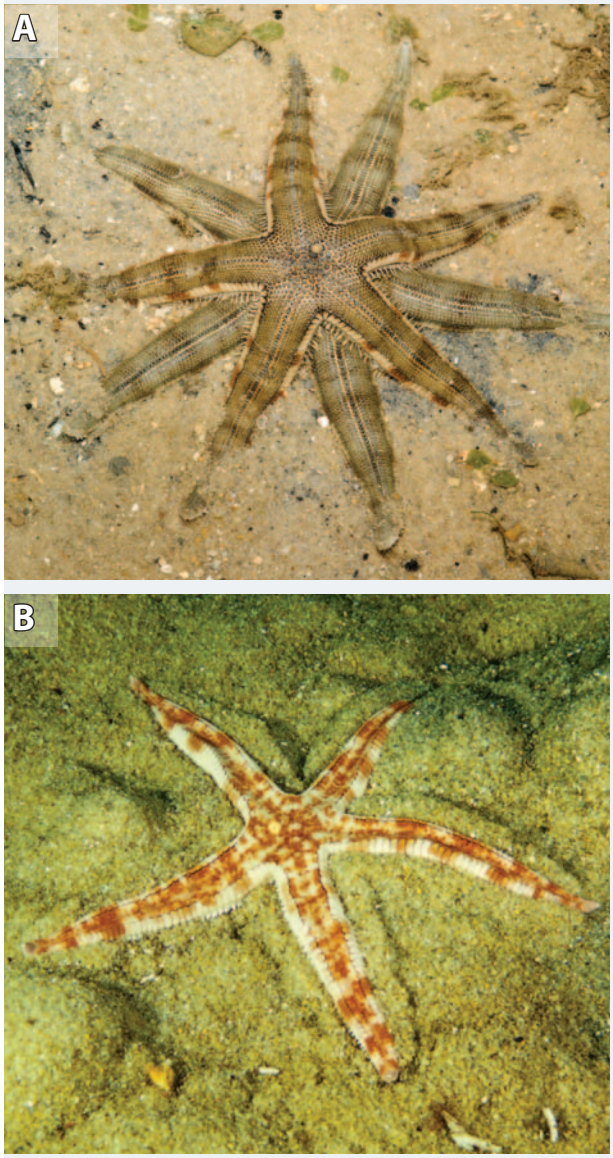


Figure 8.16 Family Archasteridae.

Only two seastars, ***Archaster typicus*** (**A**) and ***A. angulatus*** (**B**), undergo male-on-female pairing during the breeding season. Seastars begin to aggregate several months before spawning. The male positions itself on top of the female and may remain in that position for up to two months; all the while the female is active and feeding. During this time they synchronise their gonad growth and when the female releases her eggs the male releases his sperm almost simultaneously. This increases the chance of successful fertilisation.

[A, R.Tan; B, C.Bryce]

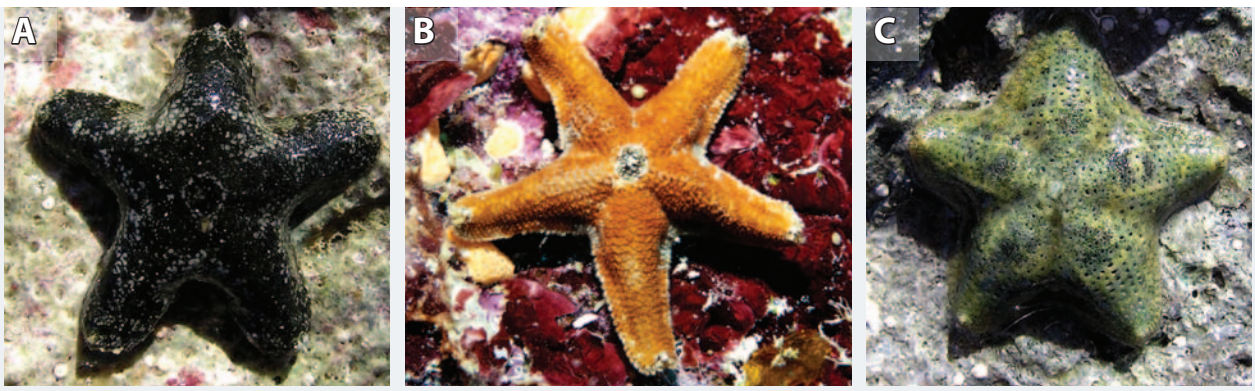
Archaster typicus lives on muddy sand, whereas *A. angulatus* lives on coarser sand. Both species are widespread and abundant throughout the Indo-Pacific (Clark & Rowe 1971; Mukai *et al.* 1986). *Archaster* species are the only asteroids to have pairing of males and females during spawning (Run *et al.* 1988; Keesing *et al.* 2011a; Bos *et al.* 2013). As the breeding season approaches, *A. typicus* displays increased mobility. The male climbs on the female's aboral surface and the arms of the two stars overlap as gametes are released (**Fig. 8.16A**). This pairing behaviour, a form of pseudocopulation, undoubtedly enhances the success of fertilisation. Development through the planktotrophic bipinnaria and brachiolaria larval stages takes approximately two weeks (Yamaguchi 1977a; Komatsu 1983).

Family Asterinidae

Figure 8.17

The Asterinidae is a large, widely distributed family (O'Loughlin & Waters 2004; O'Loughlin & Rowe 2005) that is likely to be paraphyletic (Mah & Blake 2012). The family comprises 25 genera and 147 species, of which 42 occur in Australian waters (O'Hara 2012). These asteroids are common around the coast of Australia (**Figs 1.9, 8.17**). Taxonomically, the Asterinidae is a challenging family due to the similar morphology of many species and difficulties with traditional taxonomic characters (Clark 1983; Clark & Downey 1992; O'Loughlin & Waters 2004). It has undergone numerous major revisions (Verrill 1913; Clark 1983; O'Loughlin & Waters 2004; O'Loughlin & Rowe 2005, 2006; O'Loughlin & MacKenzie 2013). Cryptic species (new species recognised from within an otherwise widely distributed taxon) have been identified from molecular data, life history traits and new morphological features, including internal plate arrangement (**Fig. 8.4G**) (Clark & Downey 1992; Hart *et al.* 1997; Dartnall *et al.* 2003; O'Loughlin *et al.* 2003; O'Loughlin & Waters 2004; Waters *et al.* 2004). The 5-armed *Parvulastra parvivipara* (R = 5 mm) is one of the smallest known asteroids, whereas the multi-rayed *Anseropoda rosacea* (R = 130 mm) is among the largest of Australian asterinids.

A high degree of endemicity exists among Australian Asterinidae, and several species have very narrow ranges. *Parvulastra vivipara* (**Box 3.1**) and *P. parvivipara* occur in south-eastern Tasmania and the west coast of the Eyre Peninsula, South Australia, respectively (Dartnall 1971a; Keough & Dartnall 1978). *Cryptasterina hystera* (**Fig. 8.17C**) has a range of about 100 km along the central Queensland coast (Byrne *et al.* 2003; Dartnall *et al.* 2003), and *Aquilonastra byrneae* (**Fig. 8.17A**) is known only from the southern Great Barrier Reef (Byrne & Walker 2007). Three tropical Australian species of *Tegulaster* are endemic: two species, *T. emburyi* and *T. praesignis* from Queensland waters, and one, *T. alba*, from Lord Howe Island (O'Loughlin & Waters 2004). One of the two species of *Disasterina* known from Australia, *D. longispina*, is endemic to south-western Australia. Three species of *Pseudonepanthia* occur in Australia (O'Loughlin & Waters 2004). *Pseudonepanthia nigrobrunnea* is found on the central eastern coast while *P. troughtoni* is known from the southern and south-western coasts (O'Loughlin & Waters 2004). *Nepanthia crassa* is endemic to the central western coast, *Paranepanthia*



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grandis (**Fig. 8.17E**) is endemic to southern Australia and *Aquilonastra rosea* is confined to the south-west (O'Loughlin & Waters 2004).

Many species formerly in *Patiriella* were removed to new genera, among them *Meridiastra*, *Parvulastra* and *Cryptasterina* (Dartnall *et al*. 2003; O'Loughlin & Waters 2004). Multi-rayed (with six or more arms) endemic *Meridiastra* species are prominent among Australia's shallow-water southern fauna (**Figs 2.2, 8.17F; Box 3.1**). They include *Meridiastra gunnii*, *M. calcar* (**Fig. 8.17F**), *M. oriens*, *M. medius*, *M. nigranota* and *M. occidens* (O'Loughlin *et al*. 2003; O'Loughlin & Waters 2004; Waters *et al*. 2004). The distributions of *M. medius*, *M. oriens* and *M. occidens* overlap in southern Australia (O'Loughlin *et al*. 2003). The ease with which some of these species can be hybridised in the laboratory, and apparently also in the field (Byrne & Anderson 1994), can make identification difficult where they overlap.

The small cushion star *Parvulastra exigua* (R = 12 mm) has a broad distribution across the southern hemisphere from Africa to Australia where it is found in midintertidal rocky shores (**Fig. 1.9; Box 3.1**) and also on sandy and muddy substrata (Dawson & Pillay 2011; Shepherd & Edgar 2013). Its broad distribution in the southern hemisphere is suggested to be achieved by floating on seaweed assisted by the West Wind Drift, the clock-wise pattern of water circulation in the Southern Ocean (Mortensen 1933b; Fell 1962c; Waters & Roy 2004; Hart *et al*. 2006). However, some



Figure 8.17 Family Asterinidae.

A, ***Aquilonastra byrneae*** in life is mottled green, brown and red, with cream or white; it is found in rocky shallows on the southern Great Barrier Reef, Queensland; a specimen from Guam has been tentatively identified as this species. R = up to 15 mm.

B, ***Aquilonastra cepheus*** has an Indo-west Pacific distribution including the northern tropical waters of Australia where it is found down to 70 m. Its live colour varies greatly with mottled colours of pink, mauve-red, grey, tan to brown, black flecking, green, cream and white, and the disc frequently has a broken white border; sometimes the colour is uniform.

C, ***Cryptasterina hystera*** is one of several viviparous seastars endemic to Australian waters. It has a narrow distribution, in the intertidal zone of mid-state Queensland waters.

D, ***Disasterina longispina***, endemic to south-western Australia, is found in the intertidal zone to 2 m.

E, ***Paranepanthia grandis*** is found in southern Australian waters from northern New South Wales to Tasmania and west to Perth, Western Australia; it occurs at depths of 0–40 m.

F, ***Meridiastra calcar***, like the other seven Australian representatives in ***Meridiastra***, is found on inshore rocky habitats in southern Australian waters.

[A,C, M.Byrne; B,D, C.Bryce; E,F, K.Gowlett-Holmes]

specimens identified as *Parvulastra exigua* could represent new species or new genera (for example, *Cryptasterina*, see Dartnall *et al*. 2003). Molecular and morphological analyses will be required in any revision of this complex (Hart *et al*. 2006).

Many asterinids have a flat, cushion-shaped profile and a pentagonal or stellate shape, and some have a thin leaf-like body (**Fig. 8.17; Boxes 3.1, 4.2, 4.5**). Asterinidae have an abactinal skeleton that comprises many small flattened and imbricate ossicles embedded in dermal tissue, resulting in a body wall that is both highly flexible and tough. The abactinal skeleton bears spinelets or granules, singly or in groups or tufts. Minute marginal plates define the ambitus, and marginal armament is similar to that of the abactinal plates or slightly coarser. Imbricate actinal intermediate plates occur in regular transverse or longitudinal series and bear a few spinelets or granules; sometimes the spinelets form combs. The inferomarginals are wedge-shaped and, internally, the body is buttressed by support plates, the superambulacrals (**Fig. 8.4G**). These were distinguished by O'Loughlin & Waters (2004) as being of three distinct types: 1) an internal plate articulating between the actinal end of the ambulacral plate, and actinal or marginal or abactinal plate; 2) the superactinal plate, an internal interradial plate articulating between abactinal, and actinal or other superactinal or superambulacral plates; and 3) transactinal plates, internal plates in transverse series across rays above the actinal plates. The plates in the papular areas appear more or less crescent-shaped except for those of the midradial row, which, if developed, have a double proximal notch for two papulae. The papulae are usually single, sometimes in small clusters, and they are restricted to the adradial areas. Superomarginal plates are often distinguished from the adjacent abactinal plates only by their position above (or alternating with) the inferomarginals. Pedicellariae, if present, are usually simple with two or four curved spiniform valves.

Asterinids are among the most familiar of Australia's seastars and often occur in large numbers in temperate and tropical regions on rocky shores and under boulders in shallow water. They are adapted to a broad range of habitats. Some asterinids are found in upper and mid-shore levels (*Cryptasterina hystera* and *Parvulastra exigua*), while others occur in the lower mid-shore (*Meridiastra calcar* and *M. occidens*) or in the nearby shallow subtidal (*M. oriens* and *M. gunnii*). Other species occupy subtidal reefs and rubble fields down to depths of 500 m or more. Most asterinids browse the epifauna and flora and, therefore, are usually restricted to hard substrates. These seastars also feed on molluscs, sponges and algae and some also scavenge on dead animals (Shepherd 1968; Keough & Butler 1979; Shepherd & Edgar 2013). *Pseudonepanthia troughtoni* and *Paranepanthia grandis*, from southern Australia, prey on compound ascidians as well as sponges and small gastropods (Shepherd & Edgar 2013). *Meridiastra* species are omnivores and scavengers, eating a variety of animals and plants (Shepherd & Edgar 2013). *Parvulastra* and *Cryptasterina* species have diurnal feeding patterns, hiding under boulders during the day, adhering to the surface with their flat ventral surface, and emerging at night to feed.

Despite the diversity and abundance of asterinids in Australia, their ecology is poorly documented. Many of the small cushion stars (*Parvulastra* and *Cryptasterina* species) feed on microalgal biofilms (Branch & Branch 1980; Jackson *et al*. 2009; Pillay *et al*. 2010; Martinez *et al*. 2013, 2017). They extend their stomach over rock surfaces and can remove up to 60% of the algae from the area beneath their stomach in one feeding event (~20 minutes) (Jackson *et al*. 2009). Thus they can have significant impacts on algal distribution (Branch & Branch 1980; Jackson *et al*. 2009). On many eastern and south-eastern Australian rocky shores, *Parvulastra exigua* occurs just above *M. calcar*. Where the two species co-occur this distribution appears to be controlled by predation. *Meridiastra calcar* preys on *P. exigua* and elicits strong avoidance behaviour by this species (Stevenson 1992). The North Pacific asterinid *Patiria miniata* preys on sea urchins and influences their local distribution (Schroeter *et al*. 1983).

The propensity for life history evolution in the Asterinidae over short evolutionary time scales has been a major influence in speciation in the family (**Box 3.1**), and vicariance events have influenced speciation within clades (Waters *et al*. 2004). A recent study indicates that the two *Cryptasterina* species along the Queensland coast may have diverged as recently as 6,000 years ago (Puritz *et al*. 2012).

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The variety of life histories seen among Asterinidae spans that of echinoderms in general (**Figs 3.3B, 3.6D,E, 3.7B, 3.10, 3.11; Box 3.1**). Species with planktonic development are dioecious, while those with benthic development are occasionally (*P. exigua*) or always (*P. vivipara*, *P. parvivipara* and *C. hystera*) simultaneous hermaphrodites. The viviparous, live-birth mode of propagation, the most highly derived life history mode known in the Asteroidea, is found in only six asteroid species, all of which are asterinids, including Australian endemics *P. vivipara*, *P. parvivipara* and *C. hystera* (Byrne 2005; **Boxes 3.1, 4.5)**. As might be expected from their limited capacity for dispersal, the viviparous species have highly restricted distributions. Some are found only along 50–100 km stretches of the coast or on offshore islands (Dartnall *et al*. 2003; Byrne 2006). This life history strategy is also associated with highly reduced genetic diversity (Puritz *et al*. 2012; Keever *et al*. 2013).

Several asterinids reproduce asexually by fission of the disc (**Fig. 3.7B**), including *Meridiastra fissura*, *Aquilonastra anomala*, *Ailsastra heteractis* and *Nepanthia belcheri* (Ottesen & Lucas 1982; O'Loughlin & Rowe 2005, 2006; O'Loughlin & MacKenzie 2013). *Nepanthia belcheri* also reproduces sexually and is a hermaphrodite (Ottesen & Lucas 1982). The occurrence of pentamerous sexually reproducing populations and hexamerous fissiparous populations of *Aquilonastra burtoni* from across the Indo-Pacific, including forms in Australia, was a puzzle for some time (Achituv & Sher 1991; Karako *et al*. 2002). It is now understood that specimens previously attributed to this taxon included a number of cryptic species, many of which have been described recently; these include fissiparous and non-fissiparous species (O'Loughlin & Rowe 2006; O'Loughlin & MacKenzie 2013).

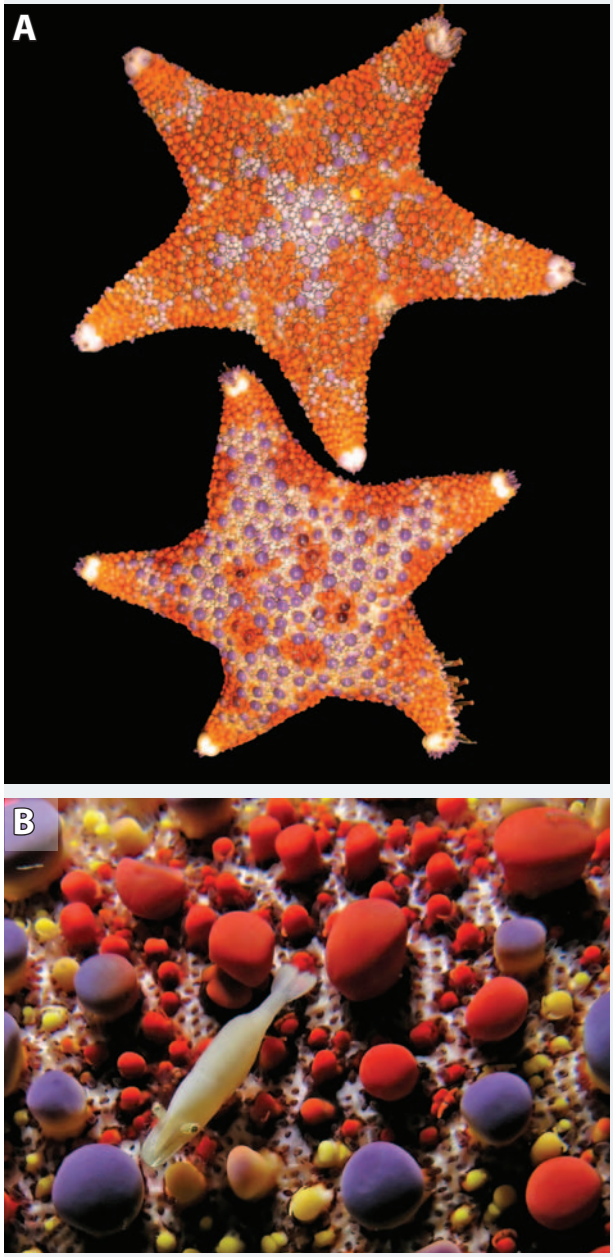


Figure 8.18 Family Asterodiscididae.

Asterodiscides truncatus, commonly called the fire brick seastar, is found in the South Pacific, including eastern and southern Australian waters, West Norfolk Ridge and the Kermadec Islands, New Zealand:
A, seastars collected from 120 m at Wanganella Bank, West Norfolk Ridge, eastern Australia, 120 m.
B, details of surface tubercles, and an associated, but unidentified, shrimp.

[A, K.Gowlett-Holmes, CSIRO; B, D.Harasti]

Family Asterodiscididae

Figure 8.18

The family Asterodiscididae is known from four genera and 20 species in the tropical Indo-Pacific. One genus, *Asterodiscides*, and seven species are known from Australian waters, and several of these are endemic (O'Hara 2012). Rowe (1985b) discussed the origin and

distribution of *Asterodiscides* species. A large species, *A. truncatus* (R = 166 mm) (**Fig. 8.18**), occurs from Western Australia to New South Wales. It lives on rocky reefs in deep water off southern Australia where it is collected by dredging (Zeidler & Shepherd 1982); it is also common on shallow subtidal rocky reefs in New South Wales. *Asterodiscides truncatus* is a striking species covered with purple and orange tubercles.

Asterodiscides species are stellate to pentagonal and have five arms. The abactinal skeleton is reticulate with a group of papulae between the plates. The marginals are few, widely spaced, and unusually inconspicuous, but the terminal superomarginal plate is often massive. Papulae are only abactinal, and the interbrachial septum is membranous. The tube feet have suckers and lack spicules. Nothing is known of the biology of asterodiscidids.

Family Asteropseidae

Figure 8.19

The Asteropseidae comprises five genera and six species (Mah & Blake 2012). Three species occur in Australian waters: *Asteropsis carinifera*, *Petricia vernicina* (**Fig. 8.19**) and *Valvaster striatus* (O'Hara 2012). They are moderate-sized asteroids (R = 60–104 mm). *Asteropsis carinifera* is a shallow-water (0–15 m) tropical seastar, while *P. vernicina* is a temperate species that occurs in southern Australia, Lord Howe Island and Norfolk Island and has a soft rubbery appearance. *Petricia vernicina* is found in the intertidal on sheltered or moderately exposed coasts where it usually occurs under ledges with encrusting sponges; it has also been recorded to depths of 70 m (Marsh 1991). *Valvaster striatus*, another tropical species, lives on the margins of coral reefs down to depths of 25 m.

Asteropseids have a 5-rayed stellate profile as adults and pentagonal as juveniles (**Fig. 8.19**); juveniles are triangular in cross-section and have a median keel. The body is flat below and convex or carinate above, with a distinct ventro-lateral angle. It is covered in a thick skin that gives it a rubbery texture and obscures the skeleton. The abactinal plates are flat and pavement-like in juveniles, and the contact faces of the plates extend during growth to link with the secondary plates, leaving papular areas enclosed by a more-or-less reticulate skeleton. Single or numerous conical spines can be present on each plate. The marginal plates are well developed, and the inferomarginals are thick and cuneate, usually projecting to form a ventrolateral angle. Asteropseids have variable surface skeletal features: *Poraniella* has a fringe of marginal spines, *Valvaster* has spines and conspicuous pedicellariae,

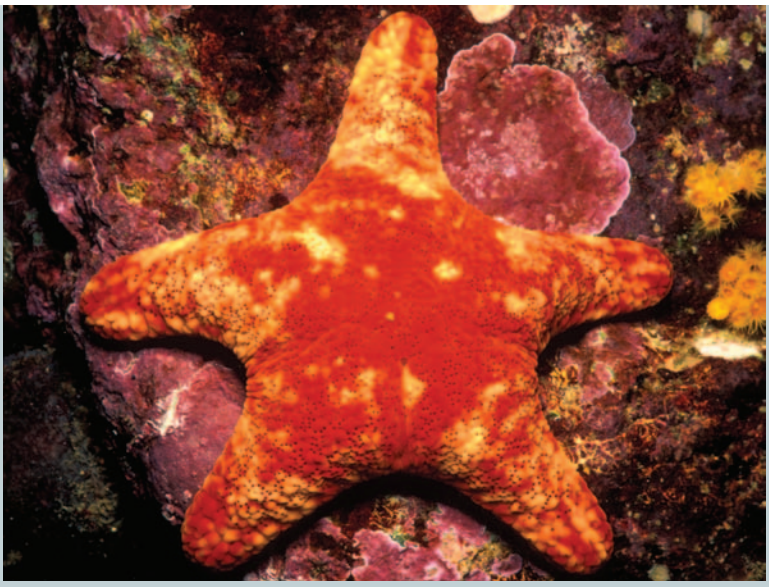


Figure 8.19 Family Asteropseidae.
Petricia vernicina, commonly known as the velvet seastar, feeds on sponges, bryozoans and ascidians across the south-west Pacific including Australia's southern waters — southern Queensland to Western Australia, including Tasmania, Norfolk Island and Lord Howe Island. It grows to a diameter of 200 mm.
[K.Gowlett-Holmes]

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Petricia has a few spines distally, and *Asteropsis* has a spine on each inferomarginal plate and often on the carinal plates along the mid-line of the aboral surface. Actinal plates occur in longitudinal series parallel to the ambulacra. The interbrachial septum is reinforced by a proximal, vertical, calcified column. The pedicellariae are elongate and bivalved, granuliform or elongate and tong-shaped.

The biology of asteropseids is not well known. *Asteropsis carinifera* is thought to be a scavenger (Yamaguchi 1975). *Petricia vernicina* occurs among rocky substrates in sheltered and exposed reefs and is a generalist browser on encrusting animals, particularly sponges, ascidians and bryozoans (Shepherd 1968; Keough & Butler 1979). *Asteropsis carinifera* has small eggs (200 µm diameter) and develops through planktotrophic larval stages lasting about four weeks (Mortensen 1937).

Family Chaetasteridae

Figure 8.20

The Chaetasteridae is a monogeneric family present in temperate and tropical waters and includes four species (Mah & Blake 2012). One species, *Chaetaster moorei*, occurs in Australian waters (O'Hara 2012; **Fig. 8.20**). This is a robust seastar with five distinct arms and is known from Lord Howe Island, Middleton Reef and the northern Tasman Sea, from the continental shelf at depths of 20–72 m (Rowe & Gates 1995). In New Caledonia it occurs on outer reef slopes on hard substrates.

Chaetaster moorei has five long, slender, tapering, rounded arms and a small central disc. The conspicuous terminal arm plates are large and bare, and are often slightly upturned. The abactinal plates are very regular in their arrangement, being stellate or lobed basally, with a thick column that expands along the arms into an oval or oblong spinelet-bearing head. Near the superomarginals the plates are more rounded, and a distinct carinal series of plates can be present along the mid-line of the arms. Paxillae are obvious along the arms and on the disc. Centrally, there are small spines that appear almost granular. These are fringed by longer, well-spaced spines. The fringing spines are unusual in that they often taper to a pointed tip, and can be flattened and hyaline for most of their length. Papulae are solitary between the plate lobes, usually six around each plate, and while they are present to the arm tips they are absent from the actinal and marginal areas. Marginal plates are small with an odd interradial marginal in each series. The madreporite, interradial near the disc centre, is sunken, round, strongly dissected and surrounded by paxillae. The adambulacral plates

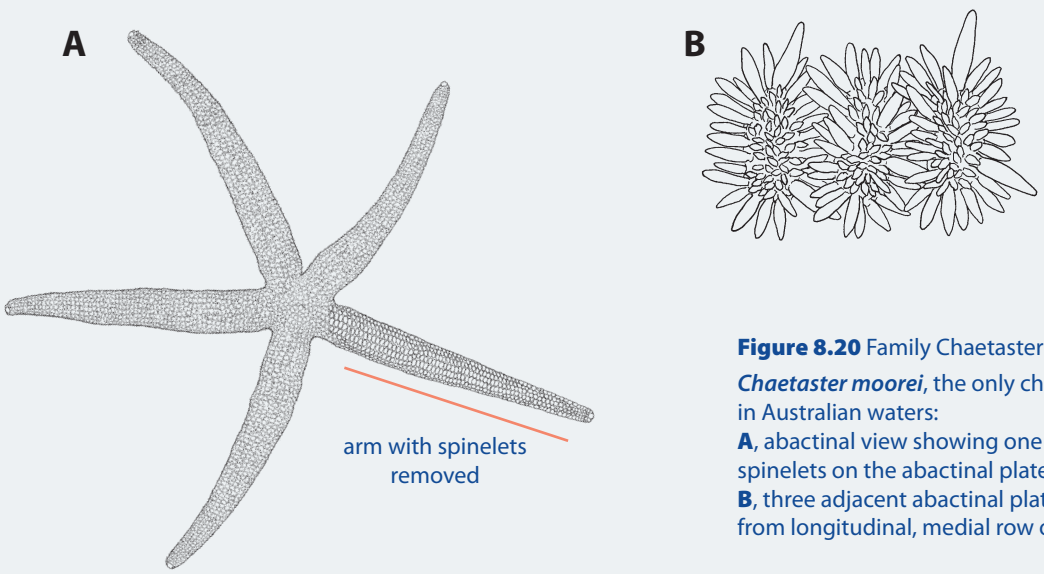


Figure 8.20 Family Chaetasteridae.
Chaetaster moorei, the only chaetasterid found in Australian waters:
A, abactinal view showing one arm without spinelets on the abactinal plates.
B, three adjacent abactinal plates with spinelets from longitudinal, medial row on radius.
[A.Murray]

are very regular, each bearing five or six furrow spines, and the subambulacral armature is dense, conspicuous and in several rows. The most anterior spines meet, or almost meet, with spines from opposite plates. Tube feet, where visible, are short and compact with a well-developed sucker. Centrally, the oral plates are crowded with enlarged suboral spines that are hyaline for part of their length. The ampullae are large, sac-like and single. The ambulacral plates are compact and broad with a flat top. There is no evidence of internal superambulacral plates, nor are there obvious connecting plates between the abactinal plates. The gonads are unusual in that they occur as a series of small structures attached near the marginal plates and are present almost to the arm tips. The biology of chaetasterids is poorly understood.

Family Ganeriidae

Figure 8.21

The Ganeriidae includes nine genera and 21 species (Mah & Blake 2012) with three species in Australian waters (O'Hara 2012). This family is largely an Antarctic and subantarctic group, living at depths of 10–350 m. *Perknaster fuscus fuscus* and *P. fuscus antarcticus* (**Fig. 8.21A**) are known from Heard Island and Antarctica, respectively. Several species of *Cycethra* are also known from southern waters. *Cycethra frigida* (**Fig. 8.21B**) is common in shallow waters (0.5–2 m) and occurs at depths to 20 m around Macquarie Island (O'Hara 1999a). Ganeriids range in radius from 15 to 90 mm (Clark & Downey 1992).

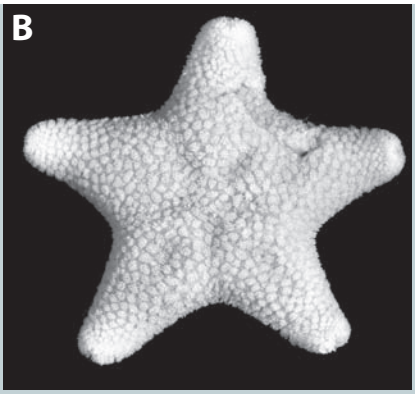




Figure 8.21 Family Ganeriidae.

A, ***Perknaster fuscus antarcticus*** and aggregations of the nemerteans ***Parborlasia corrugatus*** gathered around a food source in Antarctic waters.

B, a museum specimen of ***Cycethra frigida***; it is found in subantarctic waters including those of Macquarie Island.

[A, N.Wu; B, C.Rowley]

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Ganeriids have five short arms with a round profile, and poorly developed endoskeletons. They have block-like marginals and the marginal plates can be obscured by dermal tissue (Clark 1983). The abactinal plates can be imbricate, paxilliform or tabulate, and these plates often carry clusters of granule-like spinelets. Papulae are confined to the abactinal surface and are usually present in groups between plates. Marginal plates are either distinct and block-like, or they can be inconspicuous. Groups or combs of spines are occasionally present. In some ganeriids the skeleton is reduced, and a layer of dermal tissue protects the aboral surface. On the actinal surface, plates are obvious, form distinct rows and often bear well-defined groups of spines. In *Vemaster* actinal plates are not distinct. Along the tube foot grooves, the adambulacral plates are small with one or two furrow spines and generally two subambulacral spines that form rows (generally) parallel to the tube foot grooves. Pedicellariae are absent, although occasionally several spinelets form a simple fascicle. The tube feet are suckered, biserial and have two internal ampullae. There are no superambulacral plates, and a conspicuous interradial column of plates supports the abactinal surface.

Ganeriids usually live on soft or sandy substrates. *Perknaster fuscus antarcticus* and *P. fuscus fuscus* are spongivores (particularly on *Mycale*) and may also feed on ciliary mucus (Dearborn 1977; McClintock 1994). *Cycethra frigida* is found mostly in kelp beds on rocky substrates in association with sponges, hydroids and red algae (O'Hara 1999a). This species is dioecious and has very large eggs (*ca*. 800 µm diameter), indicating that it is a direct developer that can lay benthic egg masses (Simpson 1982). *Perknaster fuscus antarcticus* is occasionally caught in baited traps, indicating that it also eats carrion (Dearborn 1977). Historically, *Perknaster fuscus antarcticus* was thought to be a ciliary-mucus feeder (Dearborn 1977), but this species has been observed preying on stalked crinoids (Bowden *et al*. 2011; **Fig. 7.14B**). It also has been recorded as a detritivore/scavenger, and has been reported to feed on small bottom particles such as sponge and bryozoan fragments. *Perknaster fuscus antarcticus* has a large egg and planktonic brachiolaria larva, and the eggs contain a chemical that can deter predatory fish (McClintock & Vernon 1990).

Family Goniasteridae

Figure 8.22 & Box 8.1

The Goniasteridae is the most diverse family of seastars, comprising 65 genera and 256 species (Mah & Blake 2012); 48 species are found in Australian waters (O'Hara 2012). These seastars are common and conspicuous (**Fig. 8.22**). At least four genera, *Styphlaster* from north-western Australia, *Pseudogoniodiscaster* from Queensland, and *Tosia* and *Nectria* from southern Australia, and approximately a dozen species, including *Styphlaster notabilis* and *Pseudogoniodiscaster wardi*, *Tosia australis*, *Nectria macrobrachia* and *Stellaster inspinosus*, are endemic. The eight endemic species included in *Nectria*, based on cladistic analysis of morphological characters and because they are related to *Mediaster* (C.L.Mah, unpublished data), are included here in the Goniasterideae. Most *Nectria* species occur in shallow water rocky habitats (**Fig. 8.22F,G**), but *N. humilis* is found at 500 m. *Nectria ocellata* occurs in soft sand-muddy habitats (**Fig. 2.8**). Two genera, *Fromia* and *Neoferdina*, were recently moved to the Goniasteridae from Ophidiasteridae (Mah & Foltz 2011a).

Among the most familiar goniasterids in Australia is *Tosia australis* (**Box 8.1**), one of the little biscuit stars, that is common in shallow water (0–40 m depth) on reefs, jetty piles and in boulder fields and seagrass beds (Rowe & Gates 1995). *Tosia australis* shows a broad range of morphological variation, from a stellate to a more pentagonal form (Marsh 1991). This taxon is a complex of species with one new species, *Tosia neossia*, recently identified (**Box 8.1**). The third endemic *Tosia* species, *T. magnifica*, is the largest of the biscuit stars, growing to a maximum size of 160 mm (**Figs 3.2A, 8.22C**). The related *Pentagonaster duebeni* (**Figs 1.2D, 8.22B)** also varies from stellate to pentagonal body forms (Clark 1953a). The *Tosia-Pentagonaster* group was reviewed by Mah (2007b), resulting in transfer of tropical *Tosia queenslandensis* to the new genus *Anchitosia*, thus restricting *Tosia* itself to Australia. *Tosia neossia* is the only goniasterid known to brood its young (Naughton & O'Hara 2009). It is unusual in caring for its young below the body surface and having a benthic non-motile larva (**Box 8.1**).



The temperate *Fromia polypora* (Fig. 8.1), known from southern Australia, occurs on algae-covered rocks where it grazes encrusting organisms; it is also known from deeper water (to 160 m) (Shepherd 1968). *Fromia indica* and *F. monilis* (Figs 3.2B, 8.22D,E) are conspicuous on many Indo-Pacific reefs, including reefs in tropical Australia.

Ceramaster patagonicus is a wide-ranging species which, in the Australian region, occurs on mud and rock off Macquarie Island at depths of 105–148 m (O'Hara 1999a).

Goniasterids occur in all of the world's oceans from the intertidal to depths of more than 1,000 m (Clark 1993), with most species occurring in deeper water on continental shelves. Occurrences of deep water goniasterid genera, including *Glyphodiscus* and *Iconaster* (Fig. 8.22A) which occur in Australian waters, were reviewed by Mah (2005, 2006b).

Figure 8.22 Family Goniasteridae.

A, ***Iconaster longimanus*** is a large seastar (diameter to 300 mm) native to the tropical west and central Indo-Pacific including northern Australia.

B, ***Pentagonaster duebeni***, known as the vermillion seastar, is only found in the southern waters of Australia. Growing to 130 mm in diameter it inhabits reefs to depths of 200 m, and feeds on encrusting invertebrates.

C, ***Tosia magnifica*** grows to 160 mm in width, but is rarely seen across its distribution range of south-eastern Australia. It inhabits rocky bottoms and soft sediments down to 200 m.

D, ***Fromia monilis*** lives in shallow water in rocky environments across the Indo-west-central Pacific including northern Australia.

E, ***Fromia indica***, common across the Indo-west-central Pacific, is also found in the tropical northern waters of Australia. Young seastars are often bright red with black tips.

F, ***Nectria multispina*** is an Australian endemic found in shallow waters to 20 m in southern Australia, from Victoria to Western Australia, but not Tasmania.

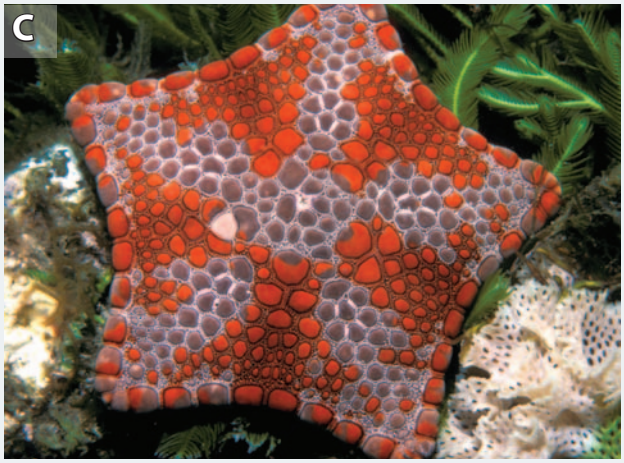
G, ***Nectria wilsoni***, one of eight species of an Australian endemic genus, occurs along the southern waters of Australia from Victoria to Western Australia.

H, ***Nectria ocellata***, a section of the abactinal surface of the disc showing the enlarged tabulae.

[A,B,C,G, K.Gowlett-Holmes; D, D.Harasti; E, C.Bryce; F, W.Boyle; H, B.Patullo]

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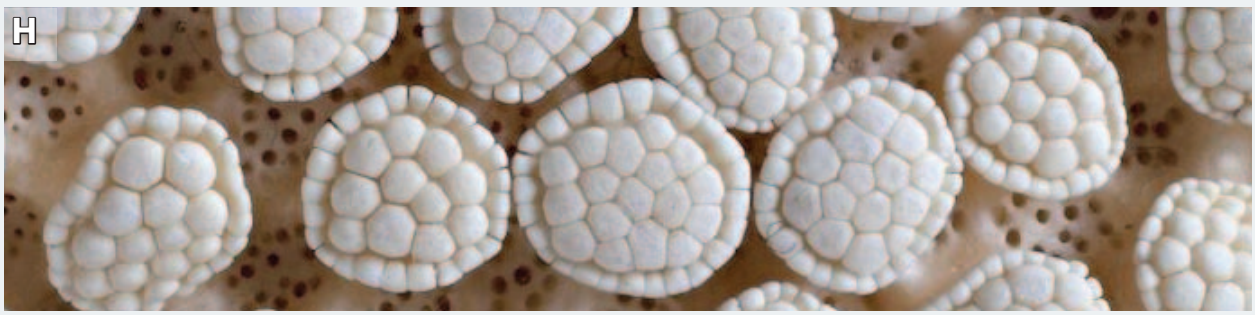

C


D


E


F


G


H

Box 8.1

Two common, but easily confused, little biscuit stars

Kate Naughton

Two species that are very common in shallow, subtidal waters, rocky reef communities and under piers are *Tosia australis* and *T. neossia*. Due to their striking and attractive appearance, they are frequently observed and photographed by divers and snorkellers on the southern coast of Australia. While both are very similar in appearance, they differ markedly in their life histories. One conforms with most others in the family, but the other is very curious.

Features The two species, previously known as little biscuit stars, *Tosia australis* and *Tosia neossia*, are smooth, thick-bodied, heavily calcified animals, ranging in shape from small, flat and pentagonal to larger and more stellate in appearance (**Figs a, b**). Both are brightly coloured, eye-catching species. The more recently discovered species, *T. neossia*, is smaller and flatter than *T. australis,* which often has more rounded or expanded plates.

The distinctive colour patterns of *T. neossia* are illustrated in **Figure b**. This species shows alternating, radiating bands consisting of two of the following colours: brown, cream, red/orange or black. **Figure a** shows *T. australis*, which exhibits a much wider range of colours and patterns. Thus the two species can be distinguished by their different colours.

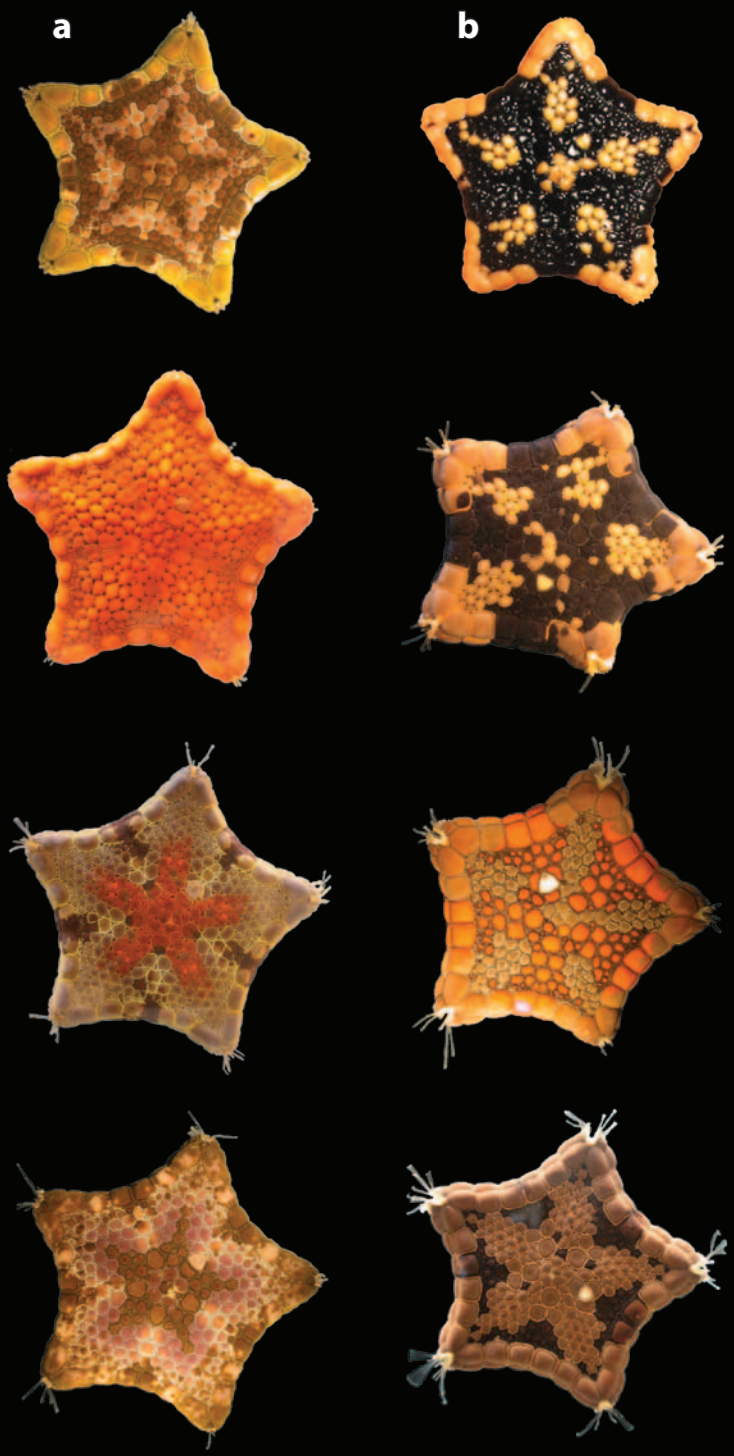
Distribution *Tosia australis* is widely distributed in southern Australia and is found in Western Australia, South Australia, Victoria and Tasmania, although its presence to the east of Wilsons Promontory, Victoria, is unconfirmed. By contrast, *T. neossia* has a more restricted distribution. It is found in Tasmania and Victoria, but, like *T. australis*, it is not found east of Wilsons Promontory. It is also found in South Australia but has only been reported east of the Coorong region, where it is found at localities along the Limestone Coast such as Robe and Port Macdonnell.

Way of life Curiosity was raised concerning reproduction in *T. australis* when Neville Coleman in 1994 published a photograph that showed adult seastars in position above a brood of tiny juveniles. Previously, the family Goniasteridae was thought not to be able to brood larvae externally due to their heavy calcified body, which would make it difficult for them to bend and form a brood space. However, brooding was confirmed. A molecular investigation by Naughton & O'Hara (2009) revealed that there are in fact two *Tosia* species: one that is a free spawner with a planktonic larva, *T. australis*, and one that is a brooder, the new species, *T. neossia*, thus providing evidence of cryptic species. *Tosia neossia* releases gametes from the oral surface and these develop into non-swimming benthic larvae that complete development to the juvenile stage on the substratum (**Fig. c**).

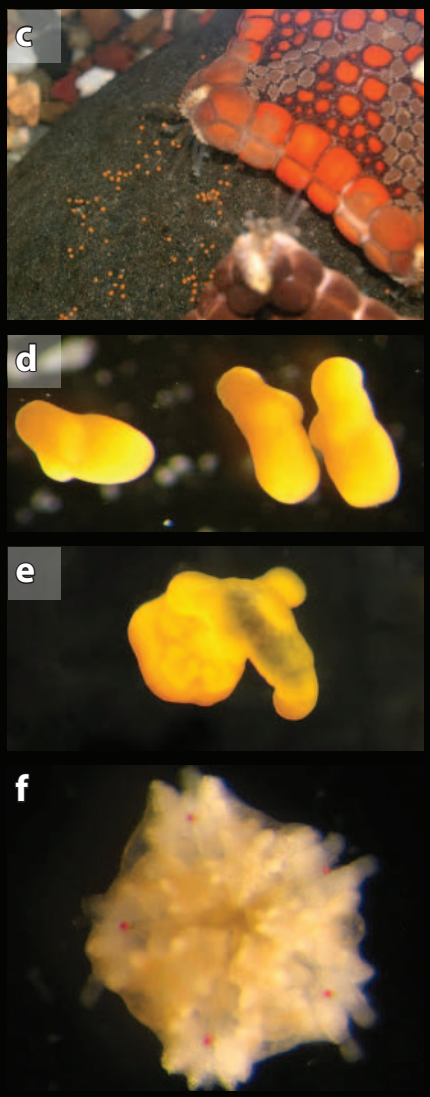
Order Valvatida
Family Goniasteridae
Species *Tosia australis* Gray, 1840
Tosia neossia Naughton & O'Hara, 2009

Further reading Coleman 1994; Naughton & O'Hara 2009

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Figures a–b Different colours and patterns on the abactinal surfaces of ***Tosia*** species:
a, ***Tosia australis***.
b, ***Tosia neossia***.



Figures c–f The lecithotrophic larvae of ***Tosia neossia*** are negatively buoyant; once the eggs are released they sink and rest on the substrate where they are fertilised and the embryos develop:
c, adults and the amber-orange larvae seen as dots on the surface of the rock.
d, benthic early brachiolaria larvae; they do not swim.
e, 'tripod phase' metamorphosing larva with the developing juvenile evident.
f, juvenile, actinal view; red-pigmented sensory cells ('eyespots') are visible at the tips of the developing arms.

[a,b, from Naughton & O'Hara 2009; c–f, courtesy of K.M.Naughton & T.D.O'Hara]

Goniasterids typically have five rays and range from pentagonal to deeply stellate with very distinct and elongate rays (**Fig. 8.22; Box 8.1**). Most species have a prominent series of marginal plates forming a well-defined periphery to the body. Typically they have a heavily calcified endoskeleton, and often have very robust bodies. Disc and arm plate series are often very prominent and can form distinctive patterns as in the tessellated surface of *Tosia*; they show great variability (**Box 8.1**). Disc plates can be tablet- to shaft-like in shape, and although they are often decorated with accessories such as granules or spinelets, they can also be smooth and bare (as in *Tosia*). Some goniasterids, such as *Mediaster*, *Nectria* and *Nymphaster*, have paxilla-like tabulae (**Fig. 8.22F,H**). Goniasterids vary greatly in size, with small species, such as *Anchitosia queenslandensis* at R = ~20 mm and larger species, such as *Stellaster princeps* at R = ~150 mm. Most range from R = 25 to R = 70 mm. Pedicellariae, when present, can be bivalved or tong-like in shape, and are often in sunken pits on the plate.

Feeding biology in goniasterids is highly variable (Shepherd & Edgar 2013). *Nectria* species, *Tosia australis*, *Fromia polypora* and *Pentagonaster duebeni* feed on sponges, bryozoans and compound ascidians (Shepherd 1968; Keough & Butler 1979; Shepherd & Edgar 2013). Prey items (and trophic types) can vary among species of the same genus. Thus, *Mediaster australiensis* off Tasmania preys on the ophiuroid *Ophiacantha fidelis* (Blaber *et al.* 1987), whereas *M. aequalis* on the west coast of North America is a detrital/deposit feeder and an opportunistic predator (Jangoux 1982). *Hippasteria spinosa* has been observed preying on the gorgonian *Primnoa* sp. in the Gulf of Alaska, where it consumed up to 45% of the polyps at the sites studied (Kreiger & Wing 2002); other species of this genus have been reported throughout the Atlantic and Pacific, primarily in cold-water or deepsea settings, feeding on octocorals (Mah *et al.* 2014). *Nectria* has been recorded feeding on bryozoans, sponges and other rock-encrusting organisms (Shepherd 1967).

Most goniasterids are dioecious and free-spawning (**Fig. 3.2A**). They release large eggs and have planktonic lecithotrophic brachiolaria larvae (Marsh 1988; Naughton & O'Hara 2009). The 1.0–1.2 mm diameter eggs of the Indo-Pacific *Iconaster longimanus* and the North Pacific *Mediaster aequalis* are particularly large (Birkeland *et al.* 1971; Lane & Hu 1994). The yolky brachiolaria larvae of *I. longimanus* settle after 10 days (Lane & Hu 1994). The reproductive cycle of these asteroids is not well studied, although *Hippasteria spinosa* from the deep sea has well-synchronised seasonal spawning (Baillon *et al.* 2011).

Family Mithrodiidae

Figure 8.23

The Mithrodiidae is a poorly known family of tropical asteroids comprising two genera and seven species (Mah & Blake 2012). Three species are reported from Australian waters (O'Hara 2012): *Mithrodia clavigera*, *Thromidia catalai* and the endemic *T. brycei* (**Figs 2.14, 8.23**). *Mithrodia clavigera* has long slender arms (R = 185 mm) (**Fig. 8.23B**). This Indo-Pacific species occurs from north-eastern Australia to Lord Howe Island, and inhabits intertidal reef flats to a depth of 80 m. *Thromidia catalai* is very large (R = 350 mm) with a small disc and stout arms; it is one of the heaviest asteroids, up to 5.9 kg. *Thromidia catalai* is rare in the Indo-Pacific, including on the Great Barrier Reef where it occurs in coral reef lagoons and slopes and the inner continental shelf (10–105 m depth). *Thromidia brycei* (**Fig. 8.23A**) is a recently described species endemic to Western Australia (Marsh 2009). It is found on the inner continental shelf from the Houtman Abrolhos to Broome.

Mithrodiid discs are small and the (usually) five arms are elongate (**Figs 2.14, 8.23**). In *M. clavigera* the arms are slightly constricted at the base where they are liable to break (Clark 1967a). Specimens with autotomised arms are often encountered. Mithrodiid seastars have an open or compact reticulate skeleton bearing irregular blunt spines. The abactinal and marginal skeleton consists of relatively few large-lobed (usually hexagonal) primary plates, well spaced from each other and linked by secondary plates. The whole surface, including spines, is overlain by a thick skin bearing rough granules, tubercles or spinelets. Numerous papulae are present, but interbrachial septa are absent. Ambulacral plates have a prominent fan of slender webbed furrow spines. The ampullae are double, and the pedicellariae are elongate and multi-valved.

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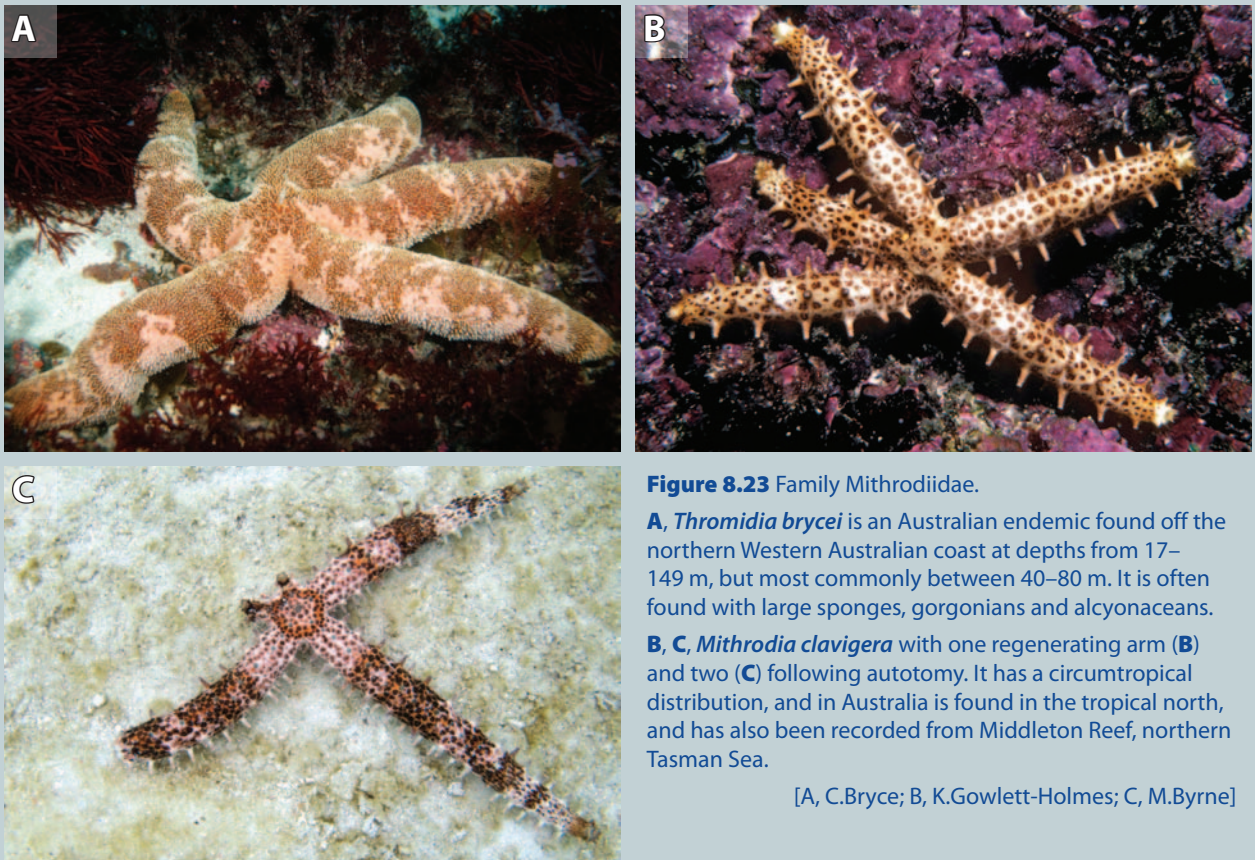


Figure 8.23 Family Mithrodiidae.

A, ***Thromidia brycei*** is an Australian endemic found off the northern Western Australian coast at depths from 17–149 m, but most commonly between 40–80 m. It is often found with large sponges, gorgonians and alcyonaceans.

B, **C**, ***Mithrodia clavigera*** with one regenerating arm (**B**) and two (**C**) following autotomy. It has a circumtropical distribution, and in Australia is found in the tropical north, and has also been recorded from Middleton Reef, northern Tasman Sea.

[A, C.Bryce; B, K.Gowlett-Holmes; C, M.Byrne]

There is a paucity of data on the biology and ecology of mithrodiids. *Thromidia catalai* has been observed feeding on encrusting organisms (Pope & Rowe 1977). *Mithrodia clavigera* readily autotomises its arms (M.Byrne, personal observation), and thus often has an irregular profile (**Fig. 8.23C**). *Mithrodia clavigera* is known to have small eggs and a plankton-feeding larva (Yamaguchi 1975).

Family Odontasteridae

Figure 8.24 & Box 8.2

The Odontasteridae includes six genera and 28 species (Mah & Blake 2012) with four species known from Australian waters. *Odontaster benhami* occurs in deep water (550 m) off the New South Wales coast, and *O. penicillatus* occurs in deep water (370 m) near Macquarie Island (O'Hara 1998). *Odontaster validus*, an ecologically important seastar in the Southern Ocean, is a well-studied, circumpolar Antarctic species that is found from the intertidal to 940 m (Pearse 1969b; **Figs 1.8A, 8.8, 8.24; Box 8.2**). The evolutionary history of *Odontaster* is reviewed in Janosik *et al.* (2011). *Hoplaster* is a deep-water genus usually found at depths of 1,800–3,300 m. *Hoplaster kupe* occurs on the seamounts south of Tasmania (T.D.O'Hara, unpublished data). Most odontasterids are known from the lower shelf and upper bathyal.

Because odontasterids usually have five rays that are clearly delineated from the disc, they often exhibit a strongly stellate profile (**Fig. 8.24**). Abactinal plates are usually paxilliform, although there is a tendency for the plates to be tabulate. The plates, generally lobed, are rather regularly arranged. Papulae are widespread abactinally, occurring in the meshes between the plates. The marginal plates form two regular series, with an odd pair of these plates located interradially. Abactinal and marginal plates have a dense cover of small spines. Actinal areas are broad, with the plates often occurring in regular rows, some with enlarged spines. Generally, there is one large, sturdy, recurved, hyaline-tipped spine on each of the two oral plates. Pedicellariae, when present, are small, simple and often fasciculate. Internally, there are no superambulacral plates, and the interradial septa are membranous.

Box 8.2 *Odontaster validus*, the Antarctic seastar

Odontaster validus is a well-studied, circumpolar Antarctic species that occurs in conspicuous aggregations. Around Antarctica this species plays an important ecological role as a benthic predator and scavenger.

Features *Odontaster validus* has five rays clearly delineated from the disc and so has a stellate profile. It has a distinct red upper surface and is pale below. It is not well calcified and as a result has a soft texture. The upper surface is covered by paxillae, and papillae are abundant.

Distribution This seastar is circumpolar and occurs from the Antarctic north to South Georgia, and from the intertidal to 940 m in depth.

Way of life *Odontaster validus* occurs on soft sediment and hard substrates. It is an opportunistic omnivorous feeder on gastropods, crustaceans, sponges, echinoids and asteroids. Working in groups it can overwhelm larger prey such as the large seastar *Acodontaster hodgsoni* (**Fig. a**). Large aggregations of *O. validus* gather to feed on seal faeces (**Fig. b**). Predation by this species is important in the regulation of sponge populations.

As a cold water species *O. validus* grows very slowly, with most of the southern Antarctic population estimated to be 20 years old, the larger individuals possibly exceeding 100 years in age. It is dioecious, spawning small eggs (140 µm diameter) in winter and has feeding planktonic bipinnaria and brachiolaria larvae. Development is slow in the cold water and it can take up to six months before the larvae reach settlement stage.

Similar species Two other species of *Odontaster* occur in Australian waters. *Odontaster benhami* occurs in deep water (550 m) off New South Wales and New Zealand, and *O. penicillatus* occurs in deep water (370 m) near Macquarie Island. *Odontaster aucklandensis* occurs off northern New Zealand at depths of 55–350 m.

Order Valvatida
Family Odontasteridae
Species *Odontaster validus* Koehler, 1906

Further reading Pearse 1965, 1966, 2013; Dayton *et al*. 1974; Dearborn 1977; Pearse & Bosch 1986, 2002; McClintock 1994; Janosik *et al*. 2011



Figure a A group of ***Odontaster validus*** attack and feed on another odontasterid seastar, ***Acodontaster hodgsoni***. [N.Wu]

Figure b ***Odontaster validus*** feeding on seal faeces under the Antarctic ice. [N.Wu]

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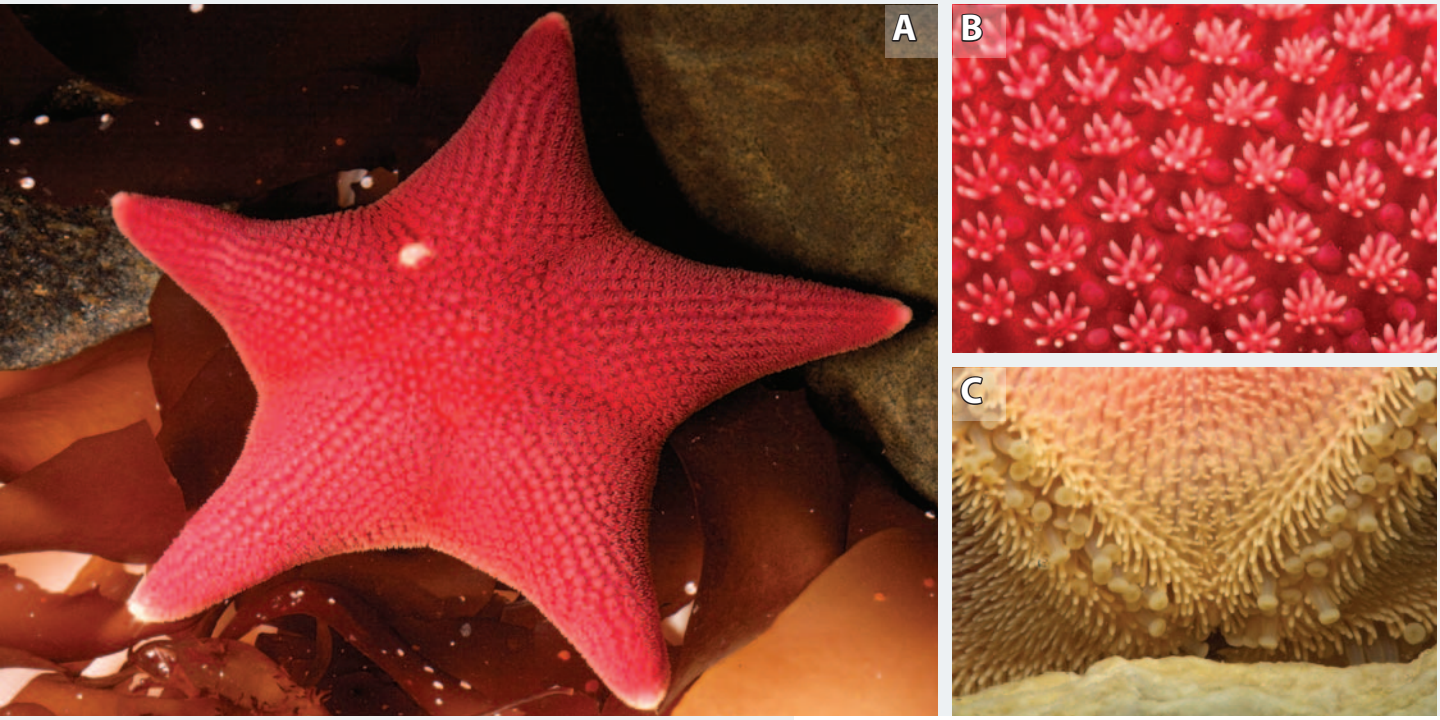


Figure 8.24 Family Odontasteridae.

Odontaster validus, growing to 40 mm in diameter, is one of the most common and ecologically important seastars found in Antarctic waters.
A, adult perched on macroalgae. The white spot in the upper left is the madreporite, the opening to the water vascular system.
B, abactinal surface covered with paxillae, and with papulae interspersed between the paxillae.
C, the pale pink actinal surface showing two of the five ambulacral grooves with tube feet meeting in the oral region.

[A.D.Miskelly]

Family Ophidiasteridae

Figures 8.25 & 8.26

The Ophidiasteridae is an important family of tropical seastars, comprising 27 genera and 106 species, with 49 species known from Australian waters (O'Hara 2012; **Figs 1.1C, 8.25**). Most ophidiasterids are pentamerous, but some are multi-rayed. They are small to medium sized, ranging from the minute *Bunaster uniserialis* (R = 10 mm) to the comparatively large *Leiaster leachi* (R = 400 mm). Molecular revision of the Ophidiasteridae moved three goniasterid-like genera, *Celerina*, *Fromia* and *Neoferdina* to the Goniasteridae (Mah & Foltz 2011a). Although not all goniasterid-like genera were tested, this suggests that similar-appearing ophidiasterids such as *Ferdina*, *Paraferdina* and *Sinoferdina* should also be tested as possible members of the Goniasteridae.

Ophidiasterids are predominantly shallow-water and shelf species, often associated with coral reefs (Clark 1967b), like the conspicuous cobalt blue *Linckia laevigata* (**Fig. 8.25A**) and the less brightly coloured *L. guildingi* (**Fig. 8.25B**). Found across the Indo-Pacific including Australia, *Linckia laevigata* is common on reef flats and patch reefs, whereas *L. guildingi*, a tropical cosmopolitan species, occurs on reef terraces (Yamaguchi 1977b). Genetic studies have confirmed that *L. laevigata* and *L. multifora* (**Figs 3.7C, 8.26**) cannot be distinguished using mitochondrial DNA, which suggests either that they represent a single species, or they have evolved so recently that their mitochondrial DNA has not had time to diverge (Williams 2000). The morphological and life history disparity between these two species (sexual and asexual reproduction, respectively) indicate that more data are needed (Rowe

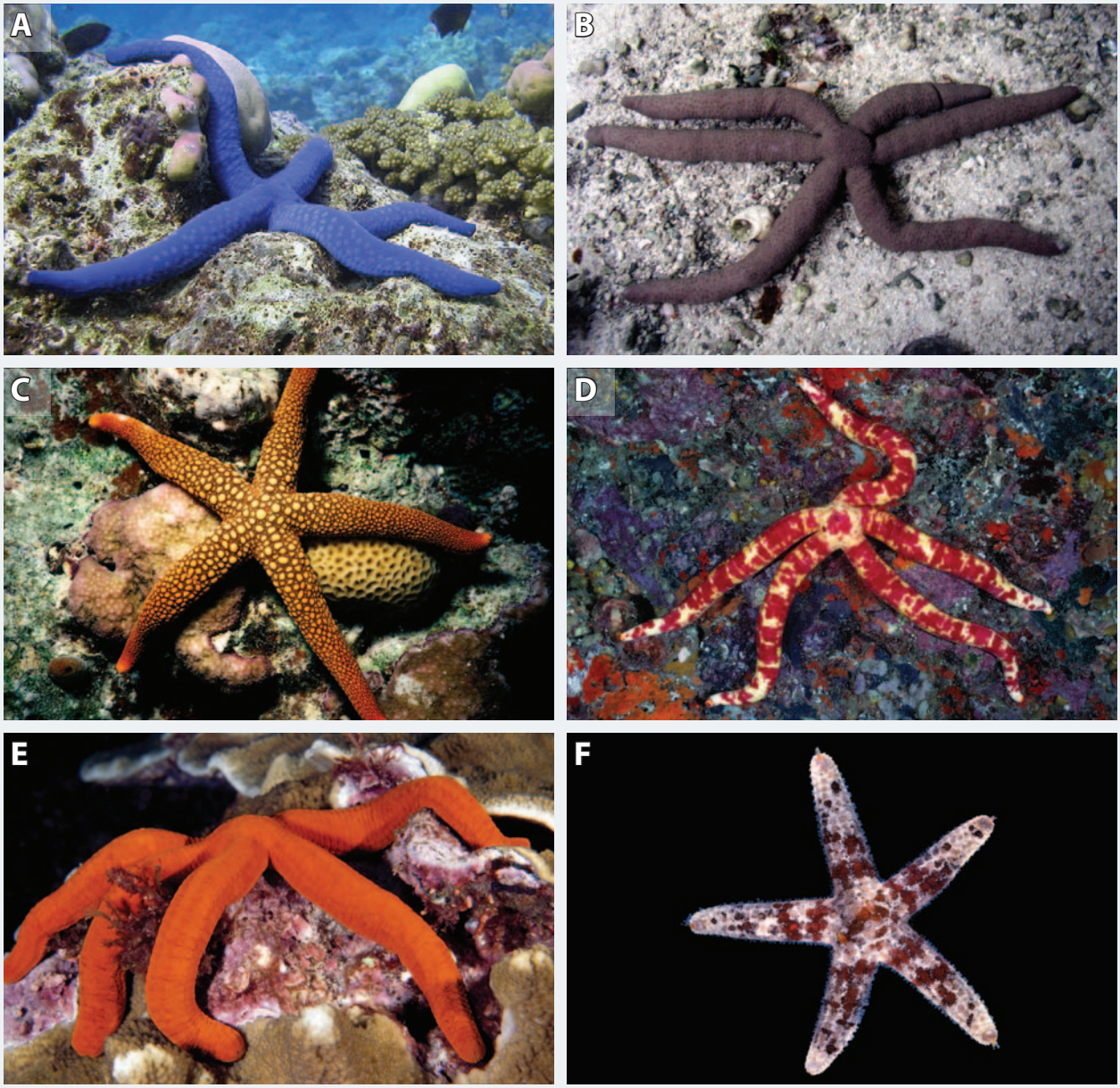


Figure 8.25 Family Ophidiasteridae.

A, ***Linckia laevigata***, commonly known as the blue Linckia or the blue star, is common throughout the tropical Indo-Pacific region, including the northern waters of Australia where it inhabits coral reefs and seagrass beds. This species is herbivorous, feeding on biofilm.

B, ***Linckia guildingi*** is found mostly in shallow tropical waters around the world including northern Australia. It is often green in colour, but may be in shades of brown, blue and dull red.

C, ***Nardoa novaecaledoniae*** lives on coral reefs in the shallow tropical waters of the central-west Pacific region; it is common on the Great Barrier Reef.

D, ***Leiaster leachi*** is found in the tropical waters of northern Australia and throughout the Indo-Pacific at depths down to 180 m.

E, ***Ophidiaster confertus*** inhabits shallow water to 50 m across the south-west Pacific as well as the east coast of Australia and Norfolk and Lord Howe islands.

F, ***Ophidiaster granifer*** lives on coral reefs in shallow waters of the Indo-west-central Pacific Ocean, including the tropical waters of northern Australia.

[A, D.Harasti; D,E, G.Bell; B,F, M.Byrne; C, J.Keesing]

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& Richmond 2004). *Nardoa novaecaledoniae* (**Fig. 8.25C**) is common on Queensland's coral reefs. In contrast, the secretive coral reef species *Ophidiaster granifer* (**Fig. 8.25F**) is rarely seen.

Ophidiasterids are characterised by having a small disc and long, slender, cylindrical arms (**Fig. 8.25**). The skeleton is tessellate, with the plates arranged in longitudinal series with large or small papular areas. Papulae occasionally occur on the actinal surface (**Fig. 1.24A**). The marginals are small to prominent and are arranged in two series. Small internal superambulacral plates are usually present, and intermarginal plates are found in a few species. The body is normally covered by a granulose membrane (bare in *Leiaster*, with a few spines in *Cistina*). Pedicellariae, when present, are foraminate or excavate, and furrow spines are recessed and small.



Figure 8.26 Family Ophidiasteridae.
Linckia multifora with a gastropod parasite causing a gall-like swelling of the arm. This parasite prevents arm autotomy, thus preserving its habitat.
[M.Byrne]

Ophidiasterids feed mainly on hard substrates such as coral rubble or reef, and mostly eat sponges and microscopic organisms (Yamaguchi 1977a; Jangoux 1982). The tropical *Cistina columbiae* is a substrate film feeder (Yamaguchi 1975), while the three *Linckia* species are also substrate feeders, consuming detritus and micro-organisms, and *L. guildingi* is also a scavenger (Yamaguchi 1975; Thomassin 1976; Rideout 1978). *Nardoa* species are substrate feeders and also consume coral mucus (Thomassin 1976).

Ophidiasterids reproduce by sexual or asexual means. *Linckia* species are dioecious, spawn small eggs (150 µm diameter) and develop by means of planktotrophic bipinnaria and brachiolaria larvae (Pearse 1968; Yamaguchi 1973, 1977b). Juveniles attain an arm radius of 14 mm in just over a year, and can join the adult population within two years of settlement (Yamaguchi 1977b). Free-spawning and the planktotrophic development life history pattern are also reported for *Ophidiaster hemprichi* and *Leiaster leachi* (Chia *et al*. 1993). *Ophidiaster granifer* has a large egg (600 µm diameter) and develops through a lecithotrophic brachiolaria (Yamaguchi & Lucas 1984). Because no males are present, Yamaguchi & Lucas (1984) suggested that the larvae are produced parthenogenetically, although this requires confirmation by histological examination of the gonads for microhermaphroditism. Several Australian ophidiasterids reproduce by arm autotomy followed by regeneration of an entire individual from an arm fragment, including *Linckia multifora*, *L. guildingi* and *Ophidiaster cribrarius* (Rideout 1978; Marsh 1994). *Linckia multifora* has an impressive capacity to propagate asexually. Whole seastars can regenerate from a single autotomised arm or part of an arm, forming a comet-like profile (**Fig. 3.7C**). An array of profiles with arms at different stages of regeneration is a peculiar feature of *L. multifora*. Its arms often have local swellings that contain encysted gastropods that appear to inhibit autotomy of the infected arm (Davis 1967) (**Fig. 8.26**). The eulimid gastropod *Thyca crystallina* (**Fig. 2.21**), found on *Linckia laevigata*, is blue, matching the host body colour (Wilson 1993).

Family Oreasteridae

Figures 8.27–8.30

The Oreasteridae is a well-known asteroid family with representatives in tropical and temperate habitats (**Figs 2.4, 8.27–8.30**). The family includes 20 genera and 74 species with 44 species known from Australian waters (O'Hara 2012). These are large (R = 50–350 mm), predominantly shallow-water and continental shelf species; 11 of the 15 Australian genera extend from low tide to the continental shelf. Aggregations of *Protoreaster* species occur on the Great Barrier Reef

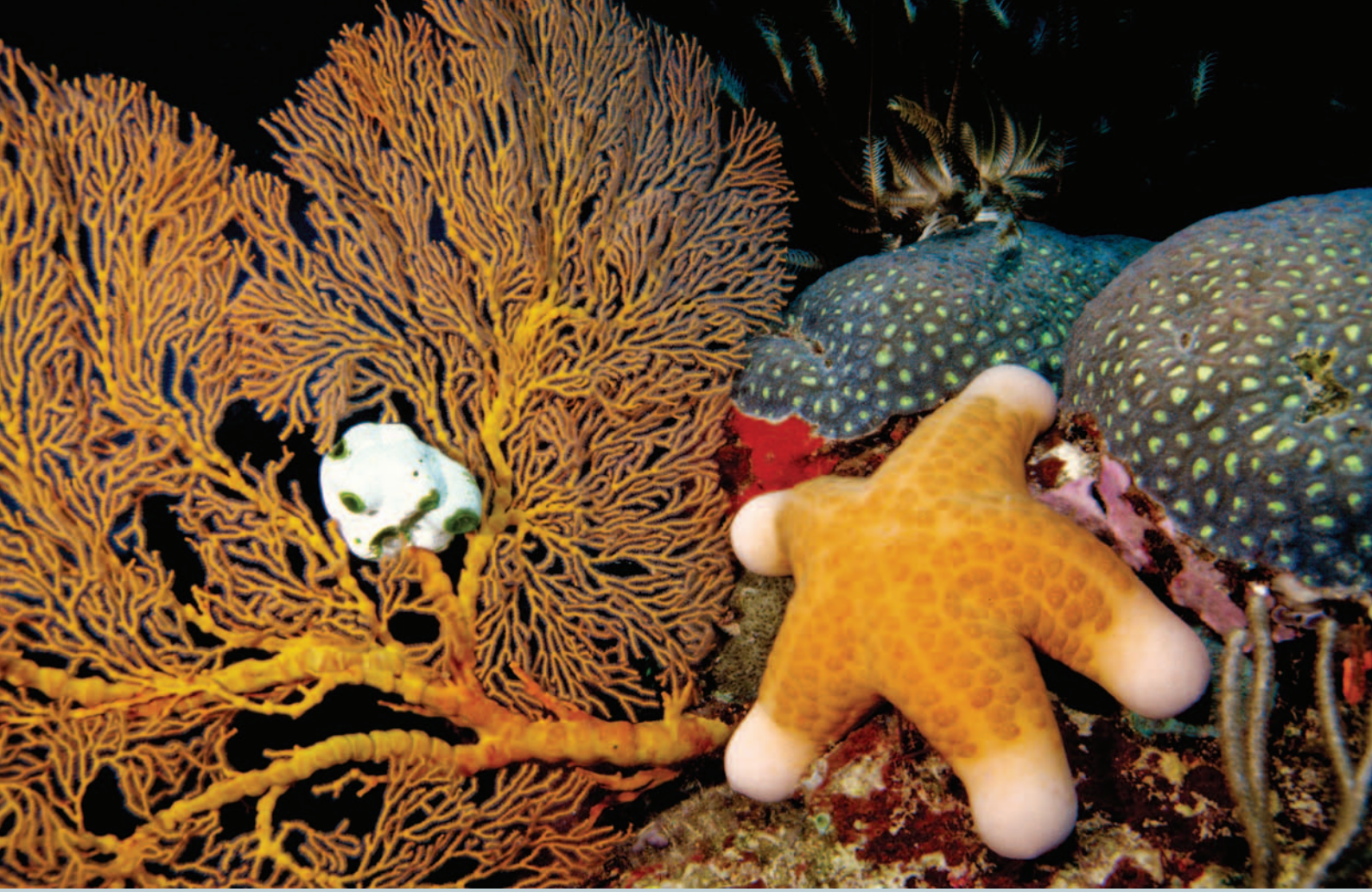


Figure 8.27 Family Oreasteridae.

Commonly known as the cushion or granulated seastar, ***Choriaster granulatus*** lives throughout the shallow tropical waters of the Indo-west Pacific including reef environments of Queensland and Western Australia in Australia. It feeds on small invertebrates, coral polyps, algae, detritus and dead animals, and grows to 270 mm in diameter.

[C.Bryce]

(Fig. 8.29). The pincushion star *Culcita novaeguineae* (Fig. 8.28) occurs on reef flats, patch reefs, lagoon sand and on outer reef slopes to 20 m depth. Four genera, *Anthaster*, *Gymnanthenea* and *Pseudoreaster*, each with one species, are endemic to Australia. A single species of *Acheronaster*, *Acheronaster tumidus*, occurs on the south-east coast at depth ranges 110–146 m (O'Hara 2012). *Anthenea sidneyensis* and *Anthaster valvulatus* are common in sheltered habitats (0–40 m depth) on sand, mud, algae-covered reefs and among rocks in the waters of eastern Australia (Fig. 8.30C). *Anthaster valvulatus* occurs in South Australia and Western Australia. *Anthenea conjungens* (Fig. 8.30A) occurs in Western Australia. *Protoreaster* is a common tropical genus: *P. nodosus* (Fig. 8.29A) is common throughout the Indo-Pacific, including northern and eastern Australia, whereas *Protoreaster nodulosus* (Figs 2.4, 8.29B) is an Australian endemic restricted to Western Australia. A very large cushion-shaped oreasterid, *Halityle regularis* (R = 60 mm), has been found in shelf waters of north-western Australia and Queensland. This spectacular species is found from East Africa to Fiji (L.M.Marsh, personal observation).

Oreasterids are cushion-shaped to stellate asteroids with a large disc that often has an inflated, high-domed appearance. This morphology is extreme in adult *Culcita* with its pentagonal pillow-like profile

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(**Fig. 8.28C**). Juvenile *Culcita*, however, are stellate (**Fig. 8.28A,B**) and look superficially like *Tosia* (Goniasteridae); they bear little resemblance to the adult form. Unbalanced marginal plate growth and arm length increase can be responsible for the change from the stellate to the pentagonal form (Kano *et al.* 1991). On the abactinal surface oreasterids have a reticulate skeleton composed of stellate plates linked by secondary ossicles leaving conspicuous papular areas. The marginal plates are well developed but not always conspicuous, and intermarginal plates can be present. The skeleton is covered by a thick skin that bears granules and tubercles. *Pentaceraster* has its aboral surface covered with tubercles. In contrast to the tuberculose species, *Choriaster granulatus* (**Fig. 8.27**) has a soft texture and is completely covered with a granulated layer of smooth dermal tissue. There are no papulae on the actinal surface, and the interbrachial septa are calcareous. The tube feet have spicules in their walls and a terminal disc. Pedicellariae are sunken and bivalved, forcipulate or resemble split granules.

In temperate Australia, *Anthaster* occurs on rocky reefs where it browses on encrusting fauna such as bryozoans, sponges, compound ascidians and, occasionally, algae (Shepherd 1968). Oreasterids are common in tropical areas where they are usually found in sandy and seagrass-dominated habitats and on coral reefs. *Choriaster granulatus*, from tropical waters, feeds on surface films and scavenges, and *Culcita novaeguineae* feeds on corals, echinoids, bryozoans, algae, sponges and benthic films (Yamaguchi 1975; Glynn & Krupp 1986). Coral mortality caused by individual *Culcita* species is about one-fifth of that caused by acanthasterid individuals (*Acanthaster* species), but its selective feeding habits can influence the relative abundance of some coral species (Glynn & Krupp 1986). *Protoreaster nodosus*, a substrate film feeder (Yamaguchi 1975), is common in sand and seagrass-dominated habitats (Bos *et al.* 2008). This species is collected for ornamental purposes by the curio trade (see **Fig. 4.14**) and has disappeared from some locations within its Indo-Pacific distribution (Bos *et al.* 2008); the closely related *Oreaster reticulatus* from the Caribbean is now locally extinct (Scheibling & Metaxas 2001).

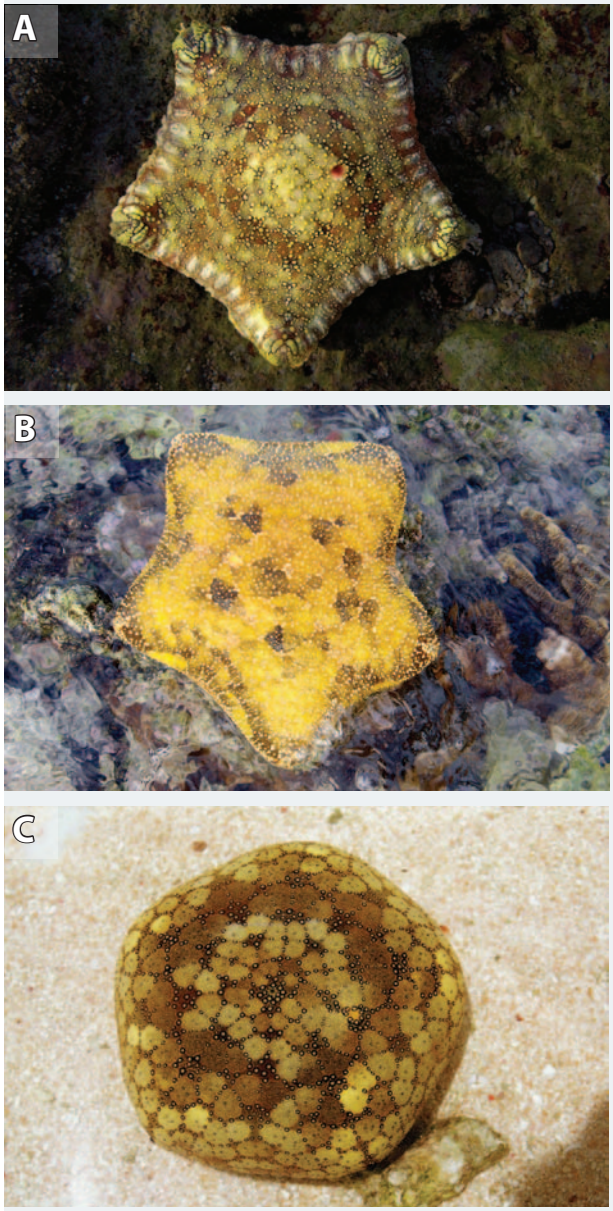


Figure 8.28 Family Oreasteridae.
Growth series of the pincushion seastar ***Culcita novaeguineae***. These seastars are stellate as juveniles and as they grow to the adult they change to the cushion star shape:
A, juvenile.
B, subadult.
C, adult.
[A, S.Walker; B,C, M.Byrne]





Figure 8.29 Family Oreasteridae.

The genus ***Protoreaster*** comprises three species — ***P. lincki***, ***P. nodulosus*** and ***P. nodosus*** — all of which occur in the tropical waters of Australia; ***P. lincki*** occurs in the Indian Ocean and in Australia is found on the north-west coast of Western Australia:

A, ***Protoreaster nodosus***, commonly known as the rhinoceros seastar or the chocolate chip seastar, is found on sandy to sandy-muddy bottoms of the Indo-west-central Pacific including northern Australia from Queensland to Western Australia.

B, ***Protoreaster nodulosus*** is found only along the coast of Western Australia from the Houtman Abrolhos to the Kimberley region (Cape Voltaire).

[A, D.Harasti; B, C.Bryce]

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Only limited data are available on the biology and ecology of *Protoreaster nodosus*, but detailed information is available for *Oreaster reticulatus*, a species from the western Atlantic Ocean and the Caribbean Sea (Metaxas *et al*. 2002; Scheibling 2013). *Oreaster reticulatus* is a microphagous substrate grazer, eating meiofauna, microalgae and detrital films, and has a major impact on chlorophyll content of the sediment (Scheibling 1980, 2013; Scheibling & Lawrence 1982; Guzmán & Guevara 2002). It is an opportunistic feeder, sometimes ingesting sponges (selecting for particular sponge species), and can prevent local colonisation by reef sponges (Wulff 1995, 2006); also it will prey on sea urchins (Scheibling 2013). *Oreaster reticulatus* typically occurs in low densities and occasionally forms aggregations in sand patches surrounded by seagrass (Scheibling 1980).

Culcita novaeguineae, *Protoreaster nodosus* and *Choriaster* are dioecious, spawn small eggs and have plankton-feeding bipinnaria and brachiolaria larvae (Yamaguchi 1973, 1977a). In the Philippines, *Protoreaster nodosus* spawns in the warm months (Bos *et al*. 2008). Development of *Culcita novaeguineae* and *Protoreaster nodosus* at 28°C takes 2–3 weeks (Yamaguchi 1973, 1977a). It takes two years for juvenile *C. novaeguineae* to change from the stellate juvenile form into the cushion-shaped adult (**Fig. 8.28**). Shallow seagrass beds, and coral or mangrove habitats appear to be recruitment and nursery habitats for *Protoreaster nodosus* and *Oreaster reticulatus* (Scheibling 1980, 2013; Scheibling & Metaxas 2001; Bos *et al*. 2008). These species migrate to the sandy habitat of adults and then develop their conspicuous colour.

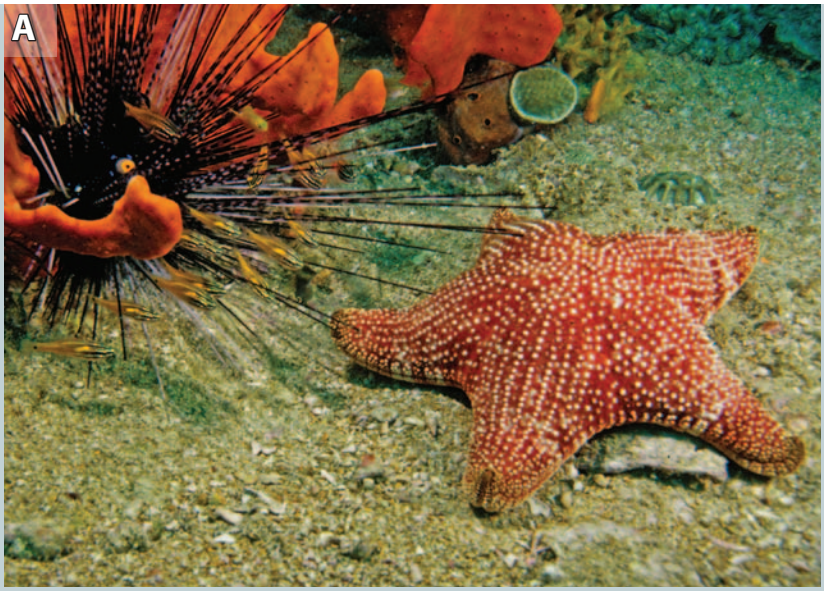






Figure 8.30 Family Oreasteridae.

A, ***Anthenea conjungens*** found only in tropical Australian waters from Shark Bay, Western Australia, to Darwin, Northern Territory, at depths ranging from 20 to 76 m.

B, ***Anthenea obesa*** has a very restricted distribution along the Western Australian coast between Lancelin, north of Perth, to Kalbarri, at depths of 53–137 m.

C, ***Anthenea sidneyensis***, living in silty sediment, is found at depths of 0–72 m along the east coast of Australia from mid-Queensland to Tasmania, and around Manus Island, New Guinea. It is common in Sydney Harbour.

[A,B, C.Bryce; C, G.Edgar]

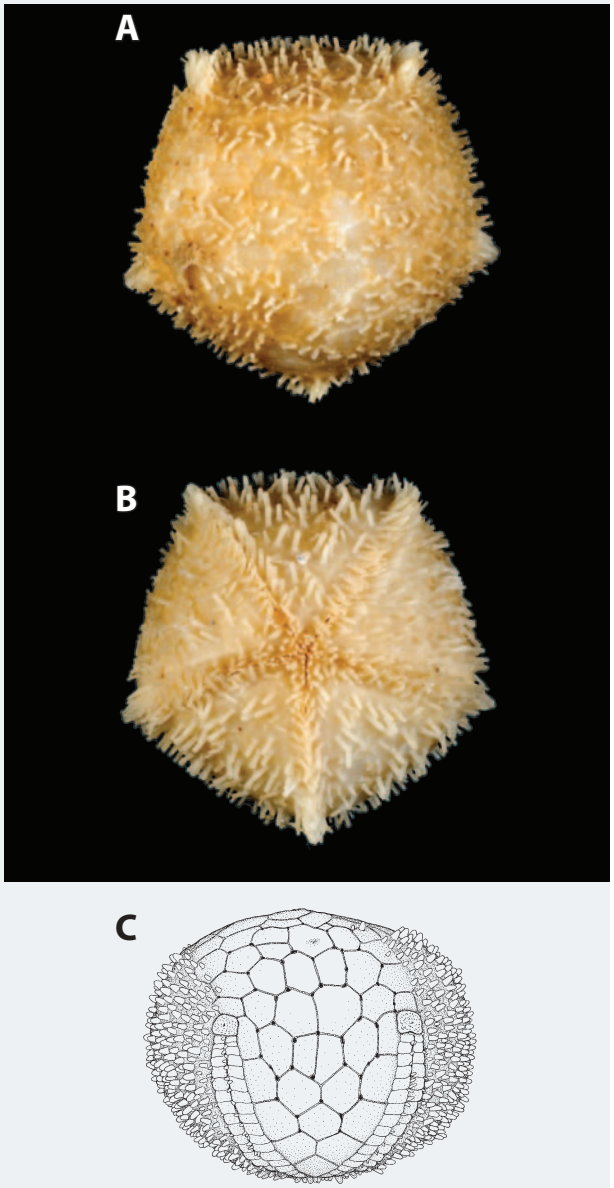


Figure 8.31 Family Podosphaerasteridae.

The unusual spherical seastar ***Podosphaeraster somnambulator*** was originally described from a specimen collected from near Chatham Rise, central New Zealand.

A, **B**, a specimen collected from Wanganella Bank, West Norfolk Ridge, 1,360 km east of Australia:

A, abactinal view.

B, actinal view.

C, detail of skeleton showing the polygonal plates; height ~7.8 mm.

[A,B, B.Patullo; C, A.Murray]

Family Podosphaerasteridae

Figure 8.31

The Podosphaerasteridae includes one genus, *Podosphaeraster*, and six species found in the North Atlantic and Pacific oceans. They have not been found in Australian waters, but do occur nearby in New Zealand (McKnight 2006) and the Arafura Sea to the north of Australia (Rowe & Nichols 1980). These asteroids were once included in the fossil family Sphaerasteridae, but Blake (1984) questioned this, leading to the description of a new family Podosphaerasteridae by Fujita & Rowe (2002).

Podosphaerasterids are unique among asteroids in that they have evolved a semi-rigid dome-like body (**Fig. 8.31**). They are comparatively small (R <20 mm), deep-water (151–170 m) asteroids (Fujita & Rowe 2002). The skeleton consists of thick polygonal plates firmly sutured together as in an echinoid test. The abactinal ossicles form an armless dome abutted and articulated by means of soft tissue along thin lateral ossicular edges. The plates bear spaced blunt granules or short spinelets and are notched at the corners for papulae. The robust, inflexible skeleton gives these asteroids an echinoid appearance. Marginal plates are not evident, although structures thus interpreted were recognised by Fujita & Rowe (2002). The ambulacra are defined by rectangular adambulacrals, no ambital margin is apparent, and each interradius is reinforced internally by a calcareous ridge below the ambitus (Fujita & Rowe 2002).

The digestive system of *Podosphaeraster* is highly specialised with the cardiac stomach reduced (Fujita & Rowe 2002). Little is known about the biology of these unusual asteroids. However, they appear to be associated with sponges, and Fujita & Rowe (2002) suggested that they occupy a cryptic habitat.

Family Poraniidae

Figure 8.32

The Poraniidae comprises 10 genera and 22 species; two species are reported from Australian waters, *Marginaster littoralis* and *Glabraster* (formerly *Porania*) *antarctica* (O'Hara 2012). Poranids are small to moderately large-sized asteroids (R = up

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Figure 8.32 Family Poraniidae.

Glabraster antarctica has a domed appearance and five short arms, and is very variable in colour — off white to yellowish or bluish white, and various hues of red, pink, orange, purple and grey. It lives on soft sediments on the seafloor in Antarctic and subantarctic waters. Here it is seen with the brittle star ***Ophionotus victoriae*** (Ophiuridae) and scallops.

[S.Harper]

to approximately 120 mm). *Marginaster littoralis* (**Fig. 4.12**) was found in south-eastern Tasmania in the 1960s (Dartnall 1970), but has not been seen since. It is not clear if this small 5-armed seastar was native or a short-lived introduced species (see **Chapter 4**). The genus *Marginaster* is an artificial assemblage that has historically included juvenile forms of *Porania* (Clark 1984, 1993), a genus typically found only in cold or deep waters. The identity of the Tasmanian specimens needs to be re-assessed. The circumpolar *Glabraster antarctica* (**Fig. 8.32**) occurs in Australian Antarctic waters and at Macquarie Island over a broad range of depths (12–1,300 m) (O'Hara 1999a). A recent review of the family (Mah & Foltz 2014) using molecular data separates '*Porania*' *antarctica* from the Arctic '*Porania*', *P. pulvillus*, and reinstates *Glabraster*.

Poraniids usually have five short arms, and the disc has a thick and convex aboral surface and a flat or gently concave oral surface (**Fig. 8.32**). The skeleton is often reduced, and the abactinal surface is protected by a layer of dermal tissue that conceals the abactinal plates. The latter form a distinct reticulum, and there is often a carinal series along the midline of the arms. Some plates carry spines, spicules or granules, while in larger specimens the abactinal plates are greatly reduced and sometimes can be lost. Papulae can be solitary or grouped between plates, and they can also be present near the superomarginal plates. The marginal plates can be well developed, forming a distinct edge to the body. Occasionally, the two plate series alternate, or occasionally the superomarginals are more or less vertical and the inferomarginals are almost horizontal.

The marginals can be greatly reduced, with the thick, enveloping dermis hiding the contours of the abactinal plates, sometimes also enveloping the actinal and marginal plates. The dermal covering is often especially conspicuous on the abactinal surface, which can be traversed by distinct, spaced, fasciolar grooves extending to the margins. Actinal plates are absent occasionally, but when well developed the actinals show a regular arrangement, forming a series of arcs parallel to the margin and sometimes bearing coarse granules or spinelets. Ambulacral and subambulacral spines are few (1–3) and are covered by skin. There are no pedicellariae, and tube feet are generally biserial with distinct suckers. Internally, there are no superambulacral plates. The interbrachial septa are occasionally partly calcified, especially if the abactinal skeleton is well developed.

Recent observations have shown active predation and/or possible scavenging by several poraniid species (Mah & Foltz 2014). *Bathyporania* appears to be a predator on antipatharians (Mah & Foltz 2014). *Porania* is known to prey on octocorals, ascidians and brachiopods (Mah & Foltz 2014).

Glabraster antarctica spawns large eggs (550 µm diameter) that develop through yolky bipinnaria and brachiolaria larvae (Bosch 1989; Bosch & Pearse 1990; Pearse & Bosch 1994). These unusual larvae are facultative planktotrophs, an example of a larval form intermediate between the obligate planktotrophic and lecithotrophic extremes (Bosch 1989). The gonads of *G. antarctica* are attached to the interradial septa with an abactinal gonopore, and its eggs appear to be protected chemically from fish predators (McClintock & Vernon 1990).

Family Solasteridae

Figure 8.33

The Solasteridae is a large cosmopolitan family of nine genera and 51 species (Mah & Blake 2012), with six species recorded from Australian waters — *Crossaster multispinus*, *C. campbellicus*, *Rhipidaster vannipes*, *Solaster notophrynus* (**Fig. 8.33B**), *S. torulatus* and two subspecies of *Solaster regularis, S. r. subarcuatus* and *S. r. regularis* (O'Hara 2012; **Fig. 8.33A**).

Solasterids generally have a large disc and 5–15 short arms that are round in cross-section and taper to a narrow tip (**Fig. 8.33**). They are large-sized asteroids (R = up to approximately 200 mm) and occur from the shallow subtidal to deeper water (600 m). The abactinal plates are often lobed and form an irregular reticulate skeleton. The plates are simply paxillate or have a tuft of spines or spinelets. Papulae, where present, occur singly or in groups in membranous areas between plates on the abactinal surface. Marginal plates can be present, with both series well developed or, occasionally, with the superomarginals considerably smaller. On the actinal surface the plates are generally restricted to the disc and sometimes almost to the arm tips. The adambulacral plates bear two combs of spines, one parallel to the tube foot furrow, the other with the subambulacral spines extending at right angles across the plate.

Solasterids are active predators on a range of invertebrates, including other echinoderms (Sloan 1980). With their capacious disc and large sturdy ambulacra they can seize and subdue their prey (Mauzey *et al*. 1968; Van Veldhuizen & Oakes 1981). They have a tough flexible body and a strong ambulacral construction. *Solaster* occurs primarily in the northern hemisphere. Solasterids are common in temperate areas living on rocky reefs and soft sediment habitats. The biology of several species is well documented. *Solaster dawsoni* from the north-eastern Pacific is a specialist asteroid predator and also eats holothuroids (Birkeland *et al*. 1982; Byrne 1985a). This asteroid induces an escape response in the large predatory seastar *Pycnopodia helianthoides*, causing it to autotomise its arms; it also induces evisceration in some dendrochirotid sea cucumbers (Mauzey *et al*. 1968; Byrne 1985a). *Solaster endeca*, also from the north-eastern Pacific, induces swimming responses in the aspidochirotid sea cucumber *Apostichopus californicus* to evade predation (Margolin 1976). *Crossaster papposus*, from around the northern temperate region, is one of the best studied solasterids (Sloan 1980; Jangoux 1982). This species has a broad diet that includes molluscs, asteroids, holothuroids and bryozoans.

All solasterids that have been studied produce large eggs (800–1,000 µm diameter) and lecithotrophic development through a planktonic brachiolaria larva (Emlet *et al*. 1987; Strathmann 1987; McEdward & Miner 2001).

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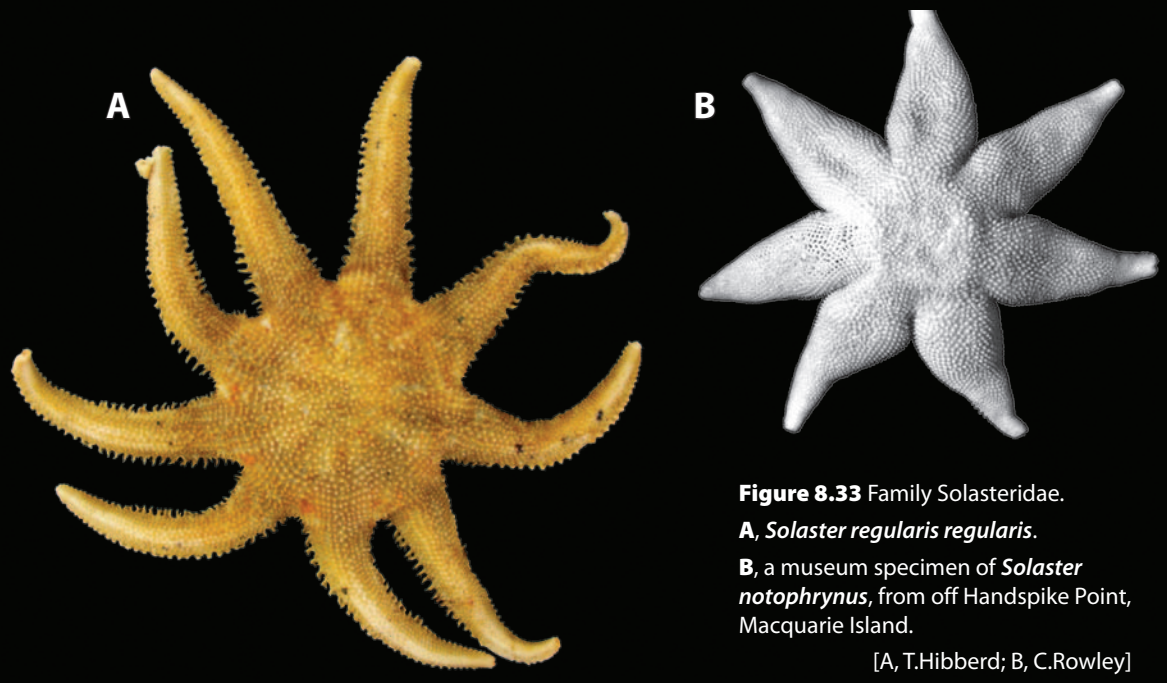


Figure 8.33 Family Solasteridae.
A, ***Solaster regularis regularis***.
B, a museum specimen of ***Solaster notophrynus***, from off Handspike Point, Macquarie Island.
[A, T.Hibberd; B, C.Rowley]

Order VELATIDA

The recent classification of the Velatida recognises 14 families worldwide, four from the Australian region (**Table 8.1**). Velatidans commonly show a poorly developed endoskeleton. Most known species occur in cold and temperate waters or deepsea environments (Mah & Blake 2012). Molecular phylogenetic work (Mah & Foltz 2011a, 2011b; Janies *et al*. 2011) places velatidans in a basal position within the Asteroidea, according new relevance to these formerly obscure taxa.

The Velatida includes 5-armed and multi-rayed species often with a large disc. The marginal, abactinal and actinal (if present) plates are often small and sometimes paxilliform. The aboral skeleton is normally open and irregularly reticulate with paxillate plates. Some plates bear slender, delicate spinelets. The marginal plates are inconspicuous with (as in the Asterinidae) the inferomarginals bearing spines. The madreporite is usually small, except in the Pterasteridae, and papulae are widespread abactinally and can be found marginally. The oral plates are prominent and often distinctly keeled. The adambulacral and subambulacral spines occasionally are webbed. Pedicellariae are absent and suckered tube feet occur in two or four rows.

Family Caymanostellidae

Figure 8.34

Caymanostellidae have been collected from lower bathyal to abyssal depths in the Atlantic, Pacific, and Indian oceans, primarily from sunken wood. Two genera and six species are known (Mah & Blake 2012), and one species of each genus, *Caymanostella phorcynis* and *Belyaevostella hispida*, is present in Australian waters, in New South Wales and Queensland, respectively (Rowe 1989a; O'Hara 2012). These were placed within the Velatida by Blake (1987) and Clark (1996). Morphology suggests affinities with the Valvatida but until a more definite case can be made, they remain within the Velatida.

This is a family of minute (R <20 mm) deep-water asteroids with thin flexible bodies (**Fig. 8.34**). The arms, generally five, are very short and scarcely distinguished from the broad, arched disc. Abactinally, thick, scale-like, overlapping plates form a close skeleton, and there is generally a mid-radial series of more obvious carinal plates. The abactinal plates are covered with very short, uniform, well-spaced spinelets, and the superomarginal

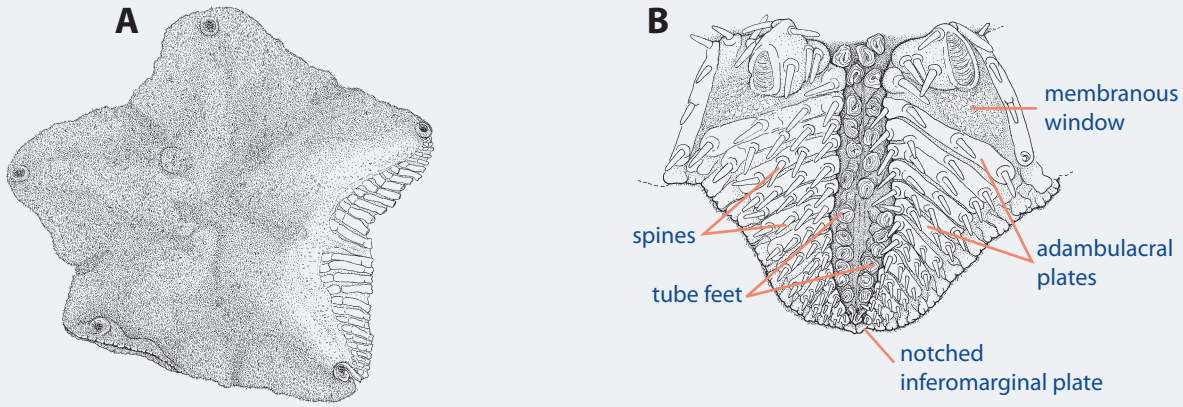
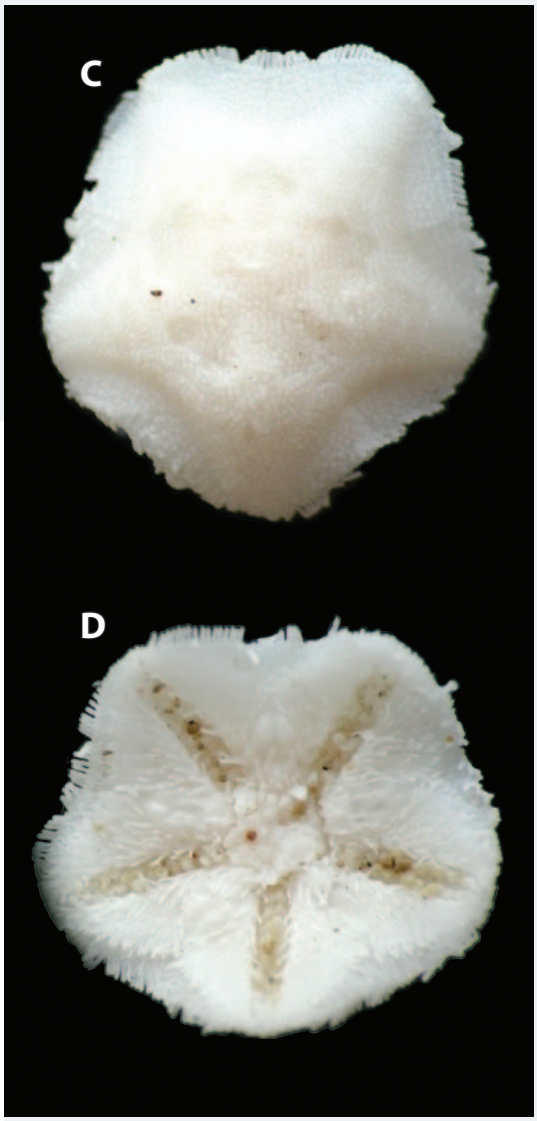


Figure 8.34 Family Caymanostellidae.

A, **B**, ***Belyaevostella hispida***, in Australian waters, is found at bathyal depths off the north-east coast of Queensland:
A, abactinal view of adult. The cut away on the right side shows the marginal plates.
B, actinal view of an arm showing enlarged adambulacral plates, actinal membranous 'windows' covering the gonads, two rows of tube feet in the ambulacral groove, three to four spines on each adambulacral plate and the notched terminal inferomarginal plate.

C, **D**, ***Caymanostella*** sp., a specimen collected from the Solomon Islands at a depth of 414–456 m:
C, abactinal view.
D, actinal view.

[A,B, A.Murray; C,D, C.L.Mah]



plates are long and narrow and confined to the abactinal surface. The innermost superomarginal in each series is either notched or pierced by a hole, the opening of the genital duct. Numerous small papulae are present in *Belyaevostella* but absent from *Caymanostella*. Inferomarginal plates are narrow and wedge-shaped and carry a distinct fringe of small, well-spaced, round-headed spines. The arm tips are protected by a quite conspicuous plate and pore.

Actinal areas are dominated by elongate adambulacral plates extending between the tube foot furrow and inferomarginal plates. There is also a characteristic clear membranous window-like area, bordered by the oral and first adambulacral plates. The gonads are visible through this 'window'. The first adambulacral plate near the oral plates is very short, the second and third are the longest. These long adambulacral plates are well separated by shallow, trench-like membranous areas and usually have rows of conspicuous slender spines. There can be one to three furrow spines, and there are two rows of squat, well-spaced tube feet.

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Family Korethrasteridae

Figure 8.35

The Korethrasteridae, comprising three genera and seven species (Mah & Blake 2012), have been collected primarily from cold-water environments, in polar and subpolar regions as well as in the deep sea. Koehler (1920) described *Peribolaster macleani* from off Adélie Land, Antarctica, in 276 m. Undetermined *Peribolaster* specimens have been collected off seamounts south of Tasmania (T.D.O'Hara, unpublished data).

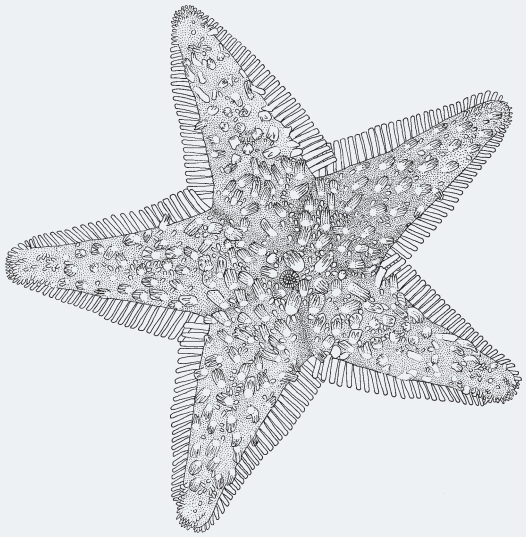


Figure 8.35 Family Korethrasteridae.
Peribolaster macleani is known from Antarctic waters.
[K.Nolan]

Korethrasterids are small (R <~40 mm), cushion-shaped and plump with five short arms (**Fig. 8.35**). Abactinal plates are rounded or sometimes lobed, and slender connecting ossicles can be present. The plates bear a raised boss crowned by fine spines and joined by a membrane, and papulae are sometimes present in membranous areas between plates. The marginal plates are rather indeterminate, and the inferomarginals form a single unwebbed series. The oral plates are broad and conspicuous, but the spines are never webbed. Tube feet are in two or four rows.

Family Myxasteridae

Figure 8.36

Myxasteridae occur worldwide and include three genera and nine species (Mah & Blake 2012). A few specimens, probably of unnamed species, have been found in the Tasman Sea (C.L.Mah, personal observation). Myxasterids are rarely collected, and they live predominantly in deep water at depths of 1,184–3,676 m (Clark & Downey 1992).

Myxasterids have 5–10 long flexible arms with small delicate plates (**Fig. 8.36**). The plates can be isolated or united and bear fascicles of delicate, webbed spinelets. The central osculum is surrounded by primary radial plates that bear webbed spines. Distinct interradial sulci are present, and the madreporites are conspicuous. The spines on the adambulacral and oral plates are webbed.

Little is known of the biology of this family.



Figure 8.36 Family Myxasteridae.
Asthenactis papyraceus from the Hawaiian Islands.
[NOAA HURL Archives]

Family Pterasteridae

Figure 8.37

The cosmopolitan Pterasteridae comprises eight genera and 116 species (Mah & Blake 2012); eight species are found in Australian waters (O'Hara 2012) — *Euretaster insignis*, *Pteraster obesus*, *P. affinis*, *P. tetracanthus*, *Hymenaster carnosus*, *H. coriaceus*, *H. platyacanthus* and *H. pudicus*.

Euretaster insignis (**Fig. 8.37**) is a mainly tropical species extending from south-western Australia to Queensland; it is found on sand, rock or muddy rubble substrates at depths down to 150 m. Pterasterids occur in cold-temperate areas at depths down to 4,900 m (Gage *et al.* 1983). *Hymenaster* species can occur from depths greater than 3,000 m in subantarctic waters (A.M.Clark 1962). In the North Atlantic Ocean species in this genus are most abundant at 2,550–2,650 m (Gage *et al.* 1983; Howell *et al.* 2002).

Pterasterids have 5–8 arms and a stellate or pentagonal body (**Figs 8.37**). An unusual supradorsal membrane is present above the aboral surface, supported by groups of spinelets from the paxillate aboral plates. This arrangement creates a space above the aboral surface (the supradorsal cavity) and is used by some species as a brood chamber for the developing young. The middle of the supradorsal membrane has a contractile aperture (osculum) that opens and closes regularly to vent the chamber (**Fig. 8.37B**). The subambulacral spines on the adambulacrals either support the actinal web or merge in the actinal surface. Actinal intermediate plates are absent. The mouth angle plates are broad and plough shaped. Interradial septa are membranous, and the tube feet are in two or four rows.

The biology of several species of *Pteraster* from the northern hemisphere has been documented. These are commonly seen with their stomachs everted over encrusting sponges, bryozoans, hydroids and ascidians (Sloan 1980). When disturbed, they secrete a mass of chemically rich mucus which is thought to deter predators (Nance & Braithwaite 1981). At Macquarie Island, *P. affinis* was found on boulders in a kelp bed (O'Hara 1998). *Diplopteraster multipes* from northern polar regions feeds on ophiuroids and sediment (Jangoux 1982), and *Hymenaster* species prey on molluscs, echinoderms and crustaceans and also feed on sediment. *Hymenaster membranaceus* from the North Atlantic Ocean was thought to live partially buried in sediment; however, photographic evidence indicates that it lives on the surface (Gage *et al.* 1983).

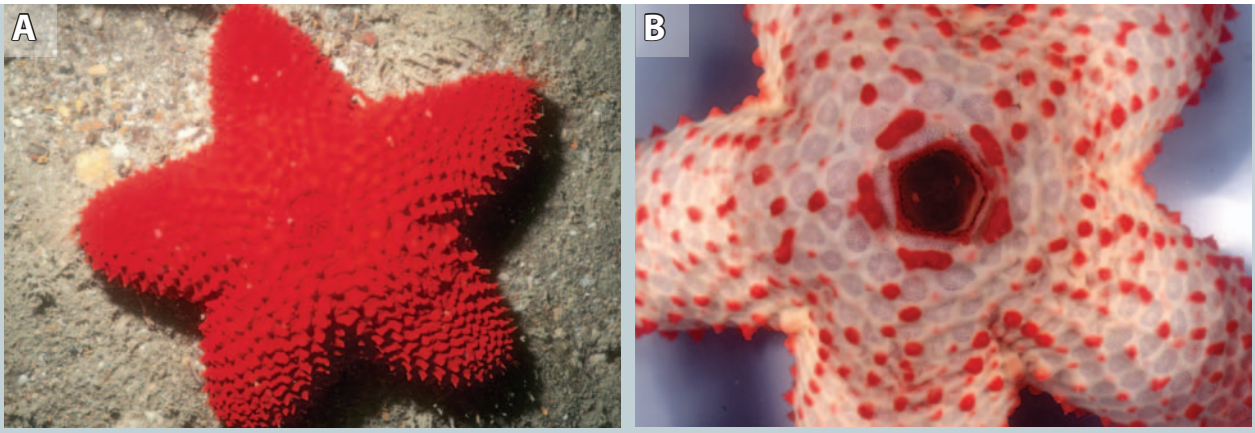


Figure 8.37 Family Pterasteridae.

Euretaster insignis is found in the west-central Pacific region including the tropical waters of Australia. These unusual asteroids brood their young in a specialised supradorsal cavity which is vented by the opening and closing of the osculum.
A, abactinal view with the osculum closed.
B, abactinal view with the osculum open.

[D.Lane]

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Reproduction in several species of *Pteraster* involves production of large eggs (~1.5 mm diameter) and lecithotrophic larvae (McClary & Mladenov 1988, 1989; McEdward 1992, 1995). Most species investigated brood their young in the supradorsal cavity, including *P. stellifer* from Macquarie Island (O'Hara 1998; McEdward & Miner 2001). The eggs are spawned into the cavity, fertilisation occurs there, and the juveniles emerge thorough the aperture. *Pteraster militaris* appears capable of both brooding and broadcasting, releasing some larvae and keeping others in the chamber to the juvenile stage (McClary & Mladenov 1988). This species has seasonal reproduction, releasing eggs into the supradorsal cavity in spring (McClary & Mladenov 1989). *Hymenaster* species from the North Atlantic Ocean have large eggs (1.1 mm diameter) and continuous reproduction (Paine *et al.* 1982). The embryology and larval development of *P. tesselatus* has been well studied; this species has large eggs (up to 1.5 mm diameter) and a highly unusual ovoid larva that bears no resemblance to those of other lecithotrophic asteroids (McEdward *et al.* 2002) and gives rise directly to the juvenile form (McEdward 1992; McEdward *et al.* 2002).

Order SPINULOSIDA

In the past the classification of the order Spinulosida has varied considerably; now only one family, the Echinasteridae, is recognised (see **Table 8.1**). Consequently, the taxonomic treatments of the order and family are combined.

Family Echinasteridae

Figure 8.38

The Echinasteridae includes eight genera and 133 species (Mah & Blake 2012) with 16 species in Australian waters (O'Hara 2012). These seastars are widely distributed and are most common in shallow water and on continental shelves. Two echinasterid genera, *Echinaster* and *Henricia* (**Figs 8.7, 8.38A–D,F**), are highly speciose and form species complexes that often exhibit only minor morphological variation across their range. Differences between the two genera were summarised by Clark & Downey (1992). Although species of *Echinaster* occur largely in circumtropical shallow water, *E. arcystatus* and *E. glomeratus* are endemic to southern Australia. *Echinaster colemani* is endemic to southern Queensland and New South Wales. *Echinaster arcystatus* (**Fig. 8.38A**) inhabits rocky reefs (0–46 m) — a dense covering of papulae give this asteroid a slippery texture when handled (Zeidler & Shepherd 1982). *Echinaster glomeratus* also occurs on rocky bottoms (0–64 m) (Rowe & Gates 1995), and *E. luzonicus* (**Fig. 8.38B,F**) from the Great Barrier Reef, displays a broad Indo-Pacific distribution. *Henricia* (**Fig. 8.38D**) is cosmopolitan in distribution, occurring primarily in cold-water environments, including polar and deep-water habitats. *Henricia compacta*, *H. kapalae* and *H. obesa* are known from the continental shelf and slope of Australian and adjacent waters and *Henricia studeri* is known from cool southern waters including Macquarie Island (Rowe & Gates 1995; O'Hara 1999a). *Henricia obesa* is especially widespread, occurring from New South Wales to Bass Strait, to Macquarie Island and elsewhere in the Southern Ocean (O'Hara 1999a). *Plectaster decanus*, a striking echinasterid with a mosaic-like surface (**Fig. 8.38E**), is common on southern Australian temperate, shallow, rocky reefs, from New South Wales to Western Australia.

The widespread genus *Odontohenricia*, which includes eight species, is interesting as it shares with the Southern Ocean family Odontasteridae a single, recurved, hyaline spine at the apex of the paired oral plates. One species, *O. endeavouri*, occurs along the south-eastern coasts of Australia, and another, *O. anarea*, off Macquarie Island (Rowe & Albertson 1988; O'Hara 1999a).

The echinasterid body is thickened, with a small disc and long slender arms that are often cylindrical (**Fig. 8.38**). Marginals, abactinals and actinals are similar and either pseudopaxilliform with stout bases,

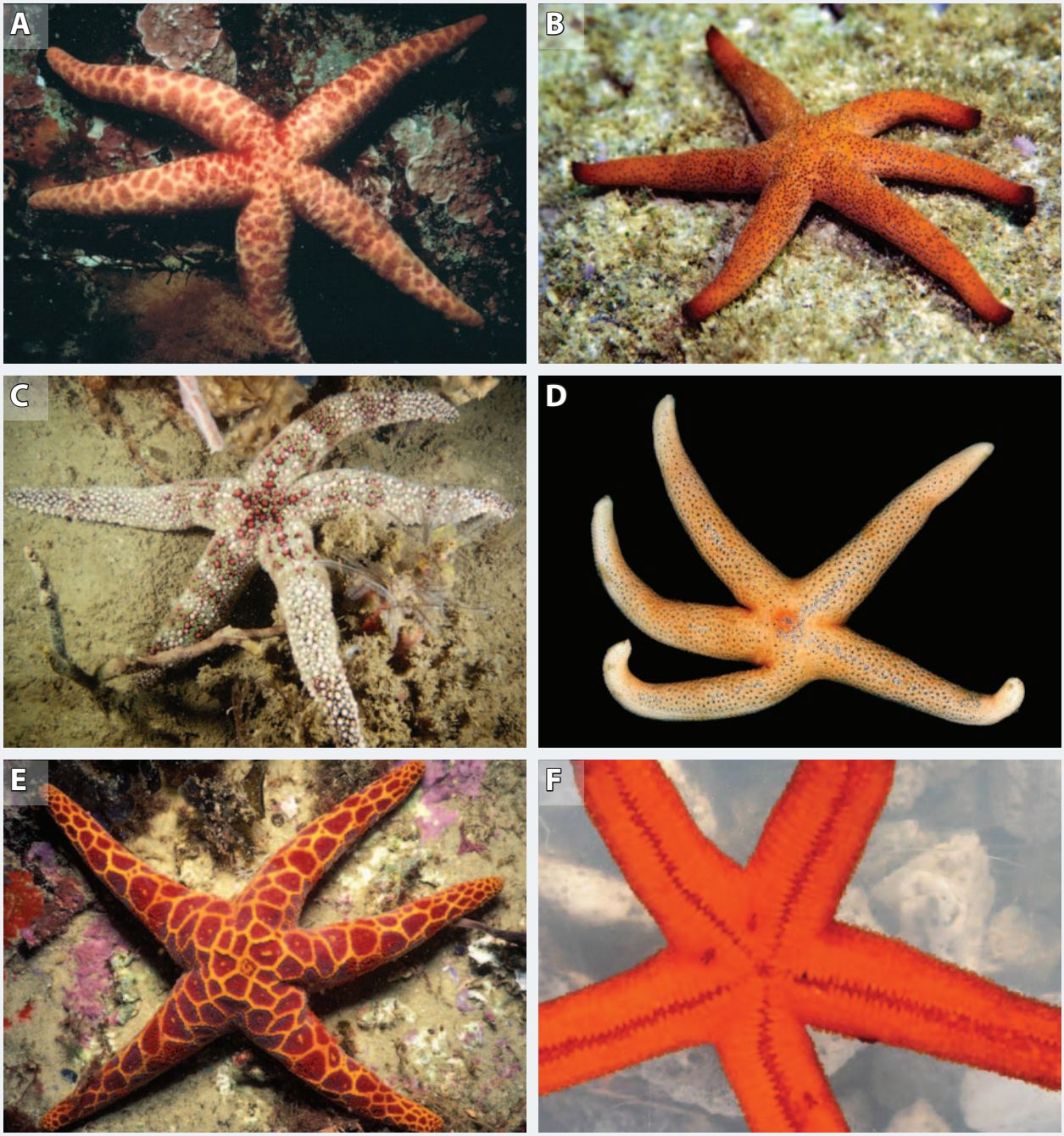


Figure 8.38 Family Echinasteridae.

A, ***Echinaster arcystatus***, an Australian endemic seastar, is found inshore in southern waters from New South Wales to Western Australia.

B, ***Echinaster luzonicus*** is a common seastar throughout the Indo-Pacific including tropical Australia.

C, ***Echinaster superbus*** is found only in the tropical waters of north-western Australia.

D, ***Henricia compacta*** collected from the outer continental shelf off south-eastern Tasmania at depths between 180 and 237 m.

E, ***Plectaster decanus*** is restricted to the southern waters of Australia to depths of 200 m.

F, ***Echinaster luzonicus*** with commensal copepods.

[A, J.Keesing; B,C, C.Bryce; D, CSIRO; E, K Gowlett-Holmes; F, M.Byrne]

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or flattened and rounded. The ossicles form a reticulate skeleton, and the papular area can extend to the actinal surface. Abactinals are paxilliform or flattened, and marginals are slightly enlarged. Intermarginals are often present; the inferomarginals therefore extend to the actinal surface of the disc. Actinals are few, and, if more than one row is present, the longest row is adjacent to the adambulacrals. The oral plates are triangular and fit closely, and podial pores are small. The adambulacrals are short, inclined and moderately overlapping. Adambulacral plates are angular, with furrow spines typically projecting into the tube foot furrow. In *Plectaster* the furrow spines form a transverse fan-shaped series on the adambulacral plates and, consequently, the inclusion of the genus in this family has been questioned (Rowe & Gates 1995). The subambulacral spinelets are transversely aligned or reduced, and the interbrachial septum has a calcified keel near the disc margin. Pedicellariae are absent.

Echinasterids are epifaunal on hard to particulate substrates, including rock, shell, sand and mixed sand and mud (Blake 1990). The biology and ecology of *Echinaster* are reviewed by Turner (2013). Echinasterids graze on encrusting invertebrates (Sloan 1980). In Australia, *Echinaster glomeratus*, *E. arcystatus* and *Plectaster decanus* feed on sponges, ascidians, molluscs and detritus (Shepherd & Edgar 2013) and *E. luzonicus* feeds on algae and micro-organisms in the substrate film (Yamaguchi 1975). *Echinaster luzonicus*, a conspicuous often bright orange seastar on the Great Barrier Reef, is often a host for commensal crustaceans such as copepods, that are the same colour as the host (**Fig. 8.38F**), and the emperor shrimp *Periclimenes imperator* (Fransen & Hoeksema 2014). *Henricia* species feed on encrusting animals, and are also scavengers. The review by Chia & Koss (1994) provided considerable detail on the histology and ultrastructure of *Henricia*. *Echinaster* species also use ciliary currents to ingest microscopic organisms and detritus (Turner 2013). *Henricia* is a suspension feeder (Ferguson & Walker 1993).

Echinasterids are dioecious, spawn large eggs (0.5–3.5 mm diameter) and have development through lecithotrophic brachiolaria larvae (Emlet *et al*. 1987; McEdward & Miner 2001; Turner 2013). Some species have a planktonic brachiolaria, and others brood their young in a brood chamber formed by the proximal portion of the arms (Atwood 1973; Chia & Walker 1991). *Henricia* from the north-eastern Pacific Ocean is a complex of species, some of which can be distinguished by differences in life history — larger individuals are free spawners and the small individuals are brooders. The brooders were recently described as a new species (Eernisse *et al*. 2010). Similarly, two sympatric morphospecies of *Echinaster* from the western Atlantic Ocean have different life histories, with the small species laying benthic egg masses and the larger having planktonic larvae (Scheibling & Lawrence 1982). *Henricia obesa* from Macquarie Island produces a few large eggs (1.2 mm diameter), but nothing is known of their development (O'Hara 1999a).

Echinaster luzonicus is well known for its ability to autotomise arms and regenerate from one arm, a form of asexual reproduction. Thus, the body profile of this tropical species is usually irregular (Yamaguchi 1975).

Order FORCIPULATIDA

The Forcipulatida (commonly referred to as forcipulates) are among the most frequently encountered and common asteroid species in temperate and cold-water habitats, including polar and deepsea environments. The most recent classification of the Forcipulatida recognises six families worldwide, five from Australia including Pedicellasteridae from Antarctic waters (**Table 8.1**). Forcipulates rarely occur at tropical latitudes, except in deep water. They are exceptionally diverse and include familiar species such as *Asterias amurensis*, *A. rubens*, *Coscinasterias muricata* and *Pisaster ochraceus*, which are important ecological species and widely used for experimental biology (Paine 1966; Ross *et al*. 2002, 2004; Barker 2013; Byrne *et al*. 2013a).

Pedicellariae in some forcipulate asteroids are composed of three elements: two are crossed at the base, and articulate with the third, basal element. The

valves of these pedicellariae are often ornamented with teeth or other distinctive features (Chia & Amerongen 1975). Pedicellariae can occur in dense rosettes or individually around the bases of the spines (**Fig. 1.5G**), or they can be distributed across the body surface. Pedicellariae are used to capture mobile prey and for defence against predators (Van Veldhuizen & Oakes 1981; Dearborn *et al*. 1991). Arm number varies from five in *Asterias* to more than 50 in the Antarctic *Labidiaster*. Many forcipulates are predatory (Sloan 1980; Jangoux 1982), and their taste for molluscs often puts them in conflict with commercial aquaculture and fisheries (**Box 4.3**). Forcipulates range in size from tiny species such as the Australian *Allostichaster palmula* (R = 5 mm) (**Fig. 8.41C–E**) to the very large northern Pacific species *Pycnopodia helianthoides* (R = 400 mm).

Mah & Foltz (2011b) provided a 3-gene molecular phylogenetic revision of the Forcipulatacea, including all nominal forcipulate groups. Their work supported and clarified relationships within the largest family, the Asteriidae, and found several region-related clades (for example, Boreal, Tropical, Antarctic). Some forcipulate deepsea groups, such as the Brisingidae and the Zoroasteridae, were supported as monophyletic, whereas the Pedicellasteridae was shown to be paraphyletic. Relationships within the Heliasteridae were clarified and the previously synonymised Stichasteridae was supported as monophyletic and reinstated.

Forcipulates generally have a relatively small but well-defined disc and a distinct, reticulate, open-meshed skeleton. The abactinal plates are never paxillate, and the marginal plates are inconspicuous. Spines or tubercles are usually scattered over the body surface, and the madreporite is generally quite small and inconspicuous, lying near the centre of the disc. Papulae are widely distributed over the body surface and extend to the ambulacral row. Actinally, the oral plates are small, while the most proximal ambulacral plates are much larger and more obvious. The ambulacral plates are numerous, short and compressed, and while they are sometimes staggered, they rarely overlap. Most forcipulates have four rows of suckered tube feet along the tube foot furrow, but some groups have only two. Superambulacrals are present or lacking, the oral region is sunken, and the jaw elements are reduced, allowing a flexible but strong jaw frame, a key feature in the predatory existence of these asteroids (Blake 1990). Forcipulates generally have a thick body, and the long, flexible arms are usually round or elliptical in cross-section. Occasionally, the arms are distinctly constricted near the disc, the point at which arm autotomy commonly occurs. These asteroids readily shed their arms in response to disturbance by predators (**Box 1.3**).

Family Asteriidae

Figure 8.39

The Asteriidae is the largest of the forcipulate families in Australia. This family comprises 35 genera and 178 species (Mah & Blake 2012), with 15 species found in Australian waters (O'Hara 2012). The species are distributed primarily in cold to temperate waters with the greatest diversity of asteriids in the polar and subpolar regions. Familiar genera include *Coscinasterias* and *Astrostole* (**Figs 2.6B, 4.7; 8.39; Box 1.3**). *Coronaster halicepus* and *C. volsellatus* occur in deep water (100–500 m) (Rowe & Gates 1995). These have also been collected in deep water (100–400 m) off north-western Australia. *Astrostole scabra* (**Fig. 4.7**), a 7-armed species (R = 220 mm), is superficially similar to *Coscinasterias muricata*. This New Zealand native is common on reefs along the east coast of Tasmania. The introduction of *Asterias amurensis* to southern Australia has resulted in marked changes to local ecosystems (see **Chapter 4**) and concerns about changes to the Southern Ocean and Antarctic fauna if this species spreads south from Australia (Byrne *et al*. 2016b).

Asteriids include five-rayed (for example, *Asterias*) and multi-armed (for example, *Coscinasterias*) genera with up to 15 arms. Some species possess well-ordered, longitudinal and transverse rows of plates in the abactinal skeleton. A carinate series of plates can also be observed. Abactinal plates can bear solitary or clustered spines of different shapes and sizes. Superomarginal plates are not conspicuous, but the inferomarginals are obvious, and the latter can bear two or three enlarged spines, often forming an oblique row. Actinal plates can be few, form only a partial series, and bear spines. The adambulacral plates are short and compact, generally with two spines along the margin

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Figure 8.39 Family Asteriidae.
The carnivorous eleven-armed seastar ***Coscinasterias muricata*** is one of the largest seastars in southern Australian waters, growing to 500 mm in diameter. It lives in sheltered rocky and sandy areas to a depth of 150 m. The body is coloured orange, mottled with blue, grey, green, cream, red/brown, mauve and white.
[P. Watson]

of the tube foot furrow. Centrally, the oral plates are distinct and narrow, and an obvious adoral carina is present consisting of one or more pairs of contiguous adambulacral plates. The oral spines are similar to the furrow spines. Tube feet occur proximally in four rows.

Asteriids are a major group of predatory seastars that are common in intertidal and shallow subtidal rocky reef and soft sediment habitats. They utilise a range of prey types including molluscs, annelids and crustaceans, and they also scavenge on dead animals. *Asterias* and *Coscinasterias* species often exhibit a preference for bivalve prey (**Fig. 1.8B; Box 4.3**) and increases in populations of the seastars are often followed by a decline in mollusc numbers. The biology and ecology of *Asterias* and *Coscinasterias* were recently reviewed (Barker 2013; Byrne *et al*. 2013a.

Coscinasterias muricata is the largest asteroid in temperate Australian waters (R = 250 mm) and is one of the most common species in the region (**Fig. 8.39**). This species is an important predator that feeds predominantly on mussels and other molluscs on subtidal rocky reefs (Keough & Butler 1979; Zeidler & Shepherd 1982; Day *et al*. 1995). It rarely feeds on abalone; these molluscs release an effective chemical deterrent to predators (Day *et al*. 1995). Attempts by *C. muricata* to prey on urchins (*Heliocidaris erythrogramma*) were also unsuccessful, the seastar being deterred by the pedicellariae (Day *et al*. 1995). In addition to molluscs, they also eat other species such as crabs (**Fig. 1.8C**) and are scavengers (Lamare *et al*. 2009; Barker 2013; Byrne *et al*. 2013a).

Asterias species can exhibit population fluctuations, with large numbers appearing sporadically (Uthicke *et al*. 2009). These are often reported as feeding fronts in intertidal areas: in the north-eastern Atlantic Ocean juvenile *A. rubens* sometimes appear in large numbers (for example, 89 individuals per square metre) in the *Mytilus* zone or in aggregations on subtidal bivalve beds (Brun 1968; Sloan 1980).

Most asteriids are highly fecund broadcast spawners with small eggs (110–175 µm diameter) (**Box 3.2**) and develop through planktotrophic bipinnaria and brachiolaria larvae (Emlet *et al*. 1987; Chia *et al*. 1993; McEdward & Miner 2001; Byrne 2013; **Fig. 3.6A,B**). Development of asteriids with planktotrophic larvae is well understood (see Barker 2013). Others have large eggs (0.7–4 mm diameter) and non-feeding larvae; *Leptasterias* species from the north-east Pacific lay benthic egg masses (Chia 1968; Emlet *et al*. 1987; Bosch & Pearse 1990). The Antarctic species *Diplasterias brucei* and *Notasterias armata* have particularly large eggs (2.8–3.5 mm diameter) (Bosch & Pearse 1990). *Anasterias directa* and *A. mawsoni* from Macquarie Island also have large eggs; these species brood their young under the disc (Simpson 1982; Pearse & Bosch 1994; O'Hara 1998).

Reproduction is initiated by environmental factors, with day length having a major influence on the timing of gametogenesis (Pearse & Walker 1986; see **Chapter 4**). *Coscinasterias muricata* has a prolonged breeding cycle, spawning small eggs (120–140 µm diameter) for up to six months of the year, depending on location, in spring and summer (Barker 1977, 2013; Georgiades *et al*. 2006). *Astrostole scabra* has a similar reproductive pattern (Town 1980). Development and early juvenile ecology of *C. muricata* are described by Barker (1978, 2013). The larvae settle in shallow, coralline algal habitats.

Asteriids are well known for their ability to regenerate arms lost by autotomy (**Box 1.3**); this is also a mechanism for asexual reproduction by fission in multi-armed species including *Coscinasterias muricata* (Emson 1978; Crump & Barker 1985; Johnson & Threlfall 1987; O'Loughlin 1991). When an individual splits in half, a narrow region of softening body wall is formed across the disc allowing the two halves to move away from one another followed by regeneration of each part (**Box 1.3**). Small *C. muricata* tend to be asexual, while larger seastars are more likely to reproduce sexually (Crump & Barker 1985; Sköld *et al*. 2002). Habitat also seems to be influential, with populations in more environmentally challenging intertidal or food-poor areas propagating by fission (Crump & Barker 1985; Sköld *et al*. 2002). Genetic studies indicate that small fissiparous and large sexually reproductive *C. muricata* at the same location are indeed the same species (Johnson & Threlfall 1987). Molecular studies of *C. muricata* in New Zealand and Australia suggest that this species might be a species complex (Waters &

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Roy 2003). *Stolasterias calamaria* is superficially very similar to *C. muricata*, with which it was previously confused (clarified by Clark & Downey 1992).

Family Heliasteridae

Figure 8.40

The Heliasteridae includes two genera and five species (Mah & Blake 2012) with a single species present in Australian waters (O'Hara 2012). These medium to large multi-rayed asteroids occur in shallow tropical-temperate as well as in deeper, cold-water habitats (Mah & Blake 2012). *Labidiaster annulatus* (**Fig. 8.40**), primarily an Antarctic species, has been collected from Heard Island at depths of 140–275 m (Fisher 1940). *Heliaster* is known only from the temperate/tropical East Pacific and South America.

Heliasterid arms, numbering 9–50 or more, are long and slender (**Fig. 8.40**). The abactinal skeleton is either an open meshwork of delicate plates, or the plates can be isolated and scattered. There is a single enlarged inferomarginal spine bearing a conspicuous wreath of crossed pedicellariae. The gonopores are lateral and there are no actinal plates. The suckered tube feet are biserial, quadriserial or a mixture of both.

Labidiaster annulatus is a remarkable large asteroid (R = 370 mm) with the largest number of arms (at least 50 or more) known for any species (**Fig. 8.40**). *Labidiaster* and *Heliaster* are voracious predators. *Labidiaster annulatus* has a broad diet, consuming up to 50 types of prey including bivalves, ophiuroids, isopods, euphausids, gastropods and fishes (Dearborn 1977; Dearborn *et al.* 1991). In Antarctica, the locally abundant *L. annulatus* is a major predator in the benthic ecosystem. It captures fish by waving its flexible arms through the water; prey are ensnared by the tips of the arms. The arms are banded with annuli bearing batteries of large, crossed pedicellariae. Prey are captured and manipulated by the pedicellariae and podia. Euphausids form the bulk of its diet, but it also feeds on sponges and scavenges (McClintock 1994). *Labidiaster* species are parasitised by large myzostomes (*Asteromyzostomum*) that attach between the arms (Grygier 1985).



Figure 8.40 Family Heliasteridae.
Labidiaster annulatus, a common Antarctic seastar, may reach a diameter of 740 mm and have as many as 50 or more arms radiating from the slightly inflated disc. It lives on the seafloor among rocks, and on sand, mud and gravel.
[B.Baker]

The ecology and biology of *Heliaster* are reviewed by Castilla *et al.* (2013). *Heliaster helianthus* is a keystone predator on South American shores, consuming a broad range of prey including bivalves, barnacles, gastropods and limpets (Castilla *et al.* 2013). This species is dioecious and free spawns, releasing small eggs. Its planktotrophic larvae are long-lived, taking two to three months to achieve the juvenile stage (Castilla *et al.* 2013). The juveniles occur in the intertidal and are often found in protected habitats such as under boulders and within crevices.

Family Pedicellasteridae

The Pedicellasteridae is considered to be paraphyletic (Mah & Blake 2012). The family includes seven genera and 32 species. Although no species have been recorded from Australian waters, *Pedicellaster* and *Anteliaster* have been collected from Antarctica and nearby subantarctic regions (A.M.Clark 1962).

Pedicellasterids have a greatly reduced to non-existent adoral carina and endoskeleton, as well as other features that suggest an intermediate position between forcipulates and non-forcipulate asteroids. Four genera, *Pedicellaster*, *Peranaster*, *Anteliaster* and *Hydrasterias*, have biserial tube feet, whereas *Tarsaster* has quadriserial tube feet proximally and biserial ones distally, and *Ampheraster* species have a mixed arrangement (Clark & Downey 1992). They have five or six arms. Pedicellasterids are found over a broad bathymetric range (100–4,260 m), with most in deep water.

Family Stichasteridae

Figure 8.41

Mah & Foltz (2011b) presented a 3-gene molecular phylogenetic revision of the Forcipulatacea, reinstating the previously synonymised Stichasteridae as a

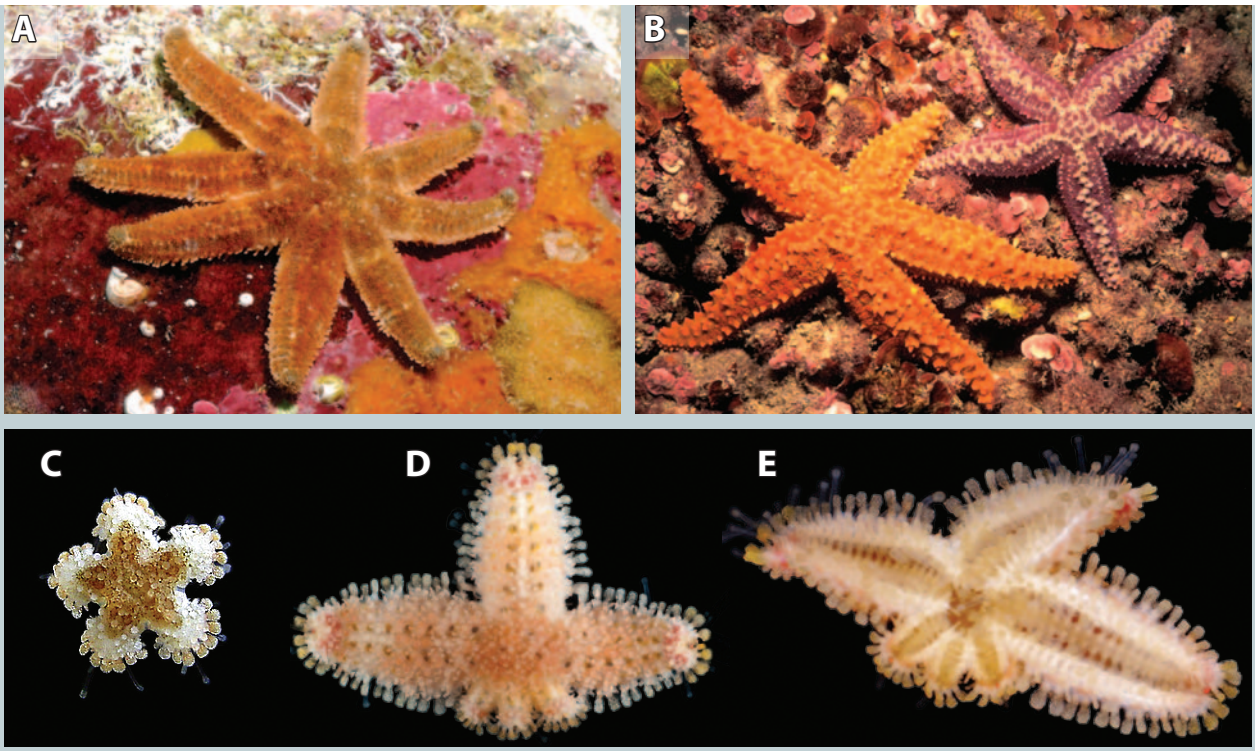


Figure 8.41 Family Stichasteridae.

A, ***Allostichaster polyplax*** is found in the south-west Pacific in the waters of southern Australia and New Zealand from the intertidal to depths of 240 m.

B, ***Uniophora granifera*** is one of three species belonging to the endemic genus ***Uniophora***. ***Uniophora granifera*** occurs in south-eastern Australia living in rocky and sandy areas to a depth of about 140 m.

C–E, ***Allostichaster palmula***, known only from Victoria, south-eastern Australia, is one of the smallest known seastars in the world with adults measuring only up to 10 mm across. It is a fissiparous seastar wherein the central disc divides in two and each half regenerates, forming a new seastar (**D**, **E**).

C, adult (R = 5 mm).
D, abactinal view of a regenerating individual developing three new arms after division; the paddle-shaped spines can also be seen.
E, actinal view of regenerating individual showing the ambulacral grooves and tube feet.

[A, G.Edgar; B, K.Gowlett-Holmes; C, T.McMurrich; D,E, L.Altoff]

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Box 8.3 The black and white seastar

Timothy D. O'Hara

In the coastal seas of south-eastern Australia you can find the black and white seastar, *Smilasterias multipara*, a fascinating seastar with very strange reproductive habits. Unfortunately the accessible intertidal habitat makes this species potentially vulnerable to a range of human activities and to climate change (O'Hara 2002).

Features *Smilasterias multipara* has a small central disc and subcylindrical arms to 23 mm long. The upper surface is covered by minute sharp spinelets that form obvious transverse rows across the arms. Each adambulacral plate bears four longitudinal rows of tube feet protected by two spines.

The distinctive colour pattern consists of grey or black markings on a pale background; the dark colour can form irregular bands on the arms. Newly released juveniles are pink.

Distribution The species is found off the south-eastern Australian coast from Cape Bridgewater to Walkerville in Victoria, the Bass Strait islands and the north and east coasts of Tasmania, at depths down to 3 m. It appears to be restricted largely to basalt rock platforms where it occurs in shallow pools, often under rocks.

Way of life The reproductive habit of this species is particularly interesting: it is one of only four seastars known to brood its young in the stomach. The males initiate reproduction in mid-August (winter) by releasing sperm, and the females respond by shedding eggs through a duct on the side of the arms near the disc. After the eggs are fertilised, the females use their tube feet to transfer the eggs along the arm to the mouth. They then brood up to 300 embryos in the cardiac (lower) stomach



Figure a The gastric brooding black and white seastar, ***Smilasterias multipara***, is found on the undersurface of boulders, usually basalt, to depths of 3 m.

[M.Norman]

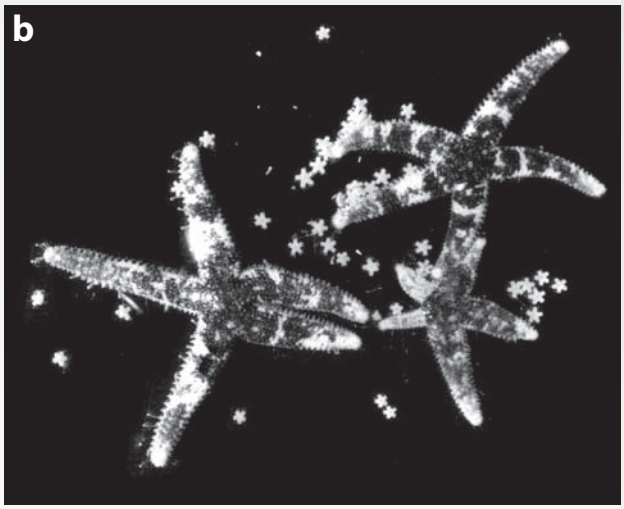


Figure b Adult ***Smilasterias multipara*** with recently emerged juveniles. The juveniles emerge from the mouth at about 3 mm in diameter.

[P.M.O'Loughlin]

for at least 35 days during which the eggs develop and metamorphose into juvenile seastars. The females appear not to eat during this period. The juveniles emerge from the mouth of the female at a size of ~ 3 mm in late October and early November, when thousands of tiny stars can be found in the shallow rock pools at locations such as Flinders in Victoria.

Like many discoveries, the gastric-brooding behaviour of this species was first observed entirely by accident. When a new species of asteroid is described, it is important to note details of the underlying skeleton. Typically, asteroid skeletons are examined by placing a museum specimen in bleach, which dissolves the skin and removes any covering of spines. In this case the specimen was accidentally left in bleach for far too long, and when he returned to examine it, Mark O'Loughlin could see through the disarticulated skeleton to the masses of juveniles in the stomach.

Similar species Two other species of *Smilasterias* occur in south-eastern Australia, *viz*. the red and white *S. irregularis*, which also tends to be subtidal, and the chocolate-brown *S. tasmaniae*, which has a very restricted intertidal distribution around Bruny Island in south-eastern Tasmania. Other 5-armed stichasterid species include *Uniophora granifera*.

Order Forcipulatida
Family Stichasteridae
Species *Smilasterias multipara* (O'Loughlin & O'Hara, 1990)

Further reading O'Loughlin & O'Hara 1990; Komatsu *et al*. 2006

primarily southern hemisphere and deepsea, cold-water clade. The Stichasteridae comprises nine genera and 28 species (Mah & Blake 2012) with nine species occurring in Australian waters (O'Hara 2012), including familiar *Stichaster* and *Allostichaster* species (**Fig. 8.41**). Although it was not included in Mah & Foltz's analysis, *Uniophora* (**Figs 8.5, 8.41B**) should be included within the Stichasteridae. *Uniophora* is an endemic southern Australian genus of three species (O'Hara 2012).

Most stichasterids are identified by the ordered, linear papular rows along the arms, the blunt, short spines, the presence of pedicellariae on the body surface rather than in clusters on spines, and the strongly developed endoskeleton relative to asteriids.

Information on the biology of stichasterids is scattered, partly because as a group, the Stichasteridae has been recognised only recently. Stichasterids appear to occupy important ecological niches in the southern hemisphere, the equivalent of which are occupied by the Asteriidae in the northern hemisphere. The multi-armed New Zealand species *Stichaster australis* is ecologically important in New Zealand intertidal communities (Menge *et al*. 1999). *Cosmasterias lurida* from South America is abundant and is importance ecologically for kelp forest communites (Castilla 1985).

The development and early juvenile ecology of *Stichaster australis* are described by Barker (1978). The larvae settle in shallow, coralline algal habitats. *Allostichaster polyplax* reproduces by asexual and sexual reproduction (Emson 1978; Crump & Barker 1985; Johnson & Threlfall 1987; O'Loughlin & O'Hara 1992) and so the body profiles are often irregular (**Fig. 8.41A**). Recently, a minute fissiparous species, *Allostichaster palmula* (maximum R = 5 mm) (**Fig. 8.41C–E**), was described from southern Australia, possibly the world's smallest seastar (Benavides-Serrato *et al*. 2007). The southern temperate *Smilasterias multipara* broods its young in pouches in the cardiac stomach (**Box 8.3**).

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Family Zoroasteridae

Figure 8.42

The Zoroasteridae comprises seven genera and 36 species (Mah & Blake 2012) with five species known from Australian waters (O'Hara 2012). The family inhabits deep-water environments (200–6,000 m), especially in the Indo-Pacific (Clark & Downey 1992). This group was reviewed by Mah (2007a).

Zoroasterids have a small disc, and both the disc and arms have a regular arrangement of plates (**Fig. 8.42A,B**). Arms are usually five; they taper, and bear a well-defined carinal series of plates; other plates form regular transverse and longitudinal series. Primary radial, interradial and centrodorsal plates are conspicuous on the disc. Zoroasterids are distinctive in that only a single marginal plate series is present (Blake 1987, 1990). Actinally, the adambulacral plates are distinctive and either carinal, with a shoulder, ridge and crest, that project into the tube foot furrow, or non-carinate plates that do not project forwards (**Fig. 8.42C**). The pedicellariae include large duck-billed types (**Fig. 8.42D**) with rounded edges to the blades and with one blade larger than the other. Straight pedicellariae are also present. Tube feet near the mouth have a large disc and occur in four rows; they are shorter and in two rows near the tips of the arms. Superambulacral plates are most obvious proximally, but these are greatly reduced in *Zoroaster*.

Most of our understanding of these deep-water seastars is derived from the research of Gage and Tyler and their colleagues on the echinoderms of the abyssal north-

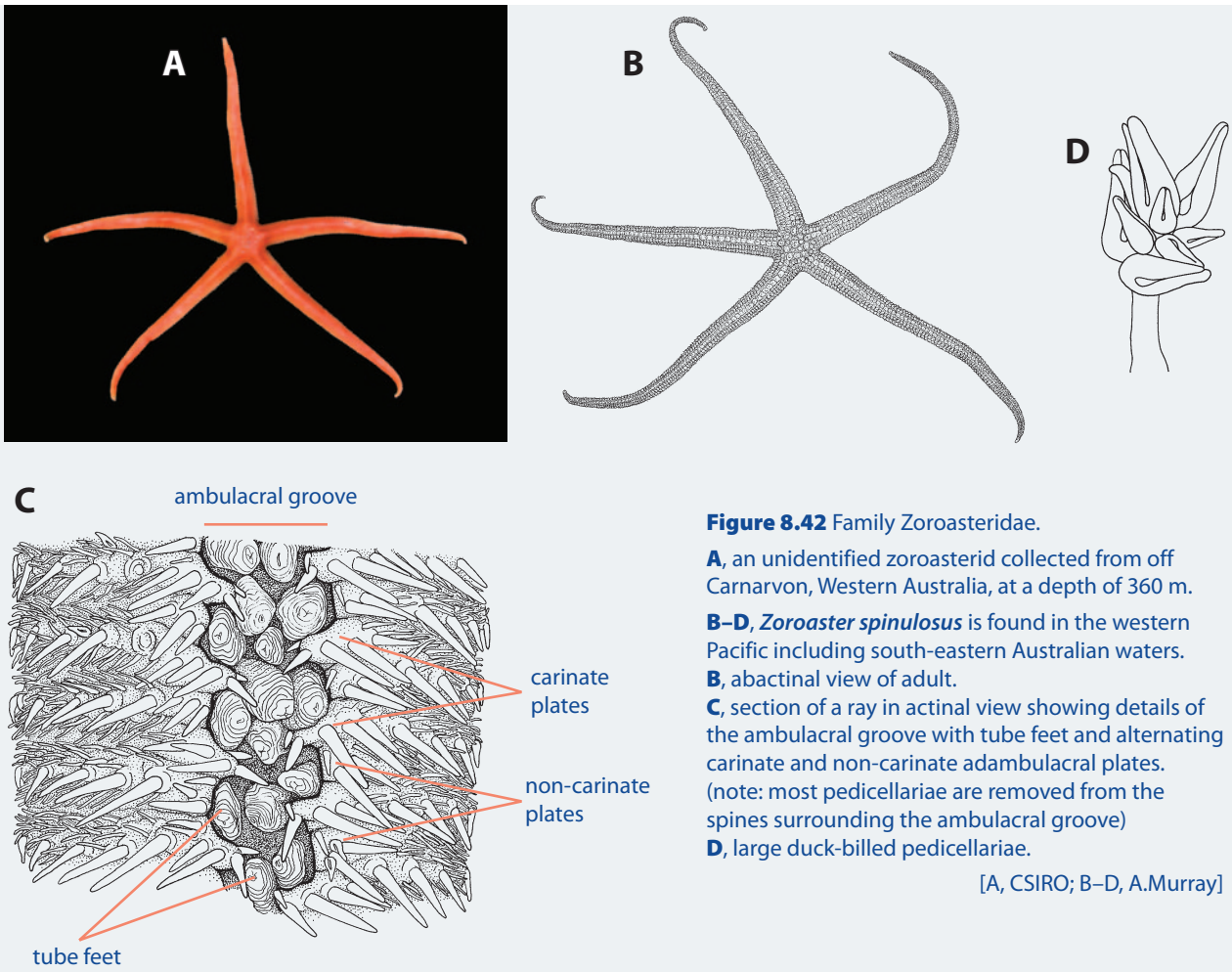


Figure 8.42 Family Zoroasteridae.

A, an unidentified zoroasterid collected from off Carnarvon, Western Australia, at a depth of 360 m.

B–D, ***Zoroaster spinulosus*** is found in the western Pacific including south-eastern Australian waters.
B, abactinal view of adult.
C, section of a ray in actinal view showing details of the ambulacral groove with tube feet and alternating carinate and non-carinate adambulacral plates. (note: most pedicellariae are removed from the spines surrounding the ambulacral groove)
D, large duck-billed pedicellariae.

[A, CSIRO; B–D, A.Murray]

eastern Atlantic Ocean (Gage *et al*. 1983; Tyler *et al*. 1984; Howell *et al*. 2002). A study of two *Zoroaster* species indicated that they are most common at depths of 1,500–3,700 m. Howell *et al*. (2003) observed benthic echinoderms and crustaceans in the stomach contents of *Z. longicauda* (= *Z. fulgens*), but they also found evidence from fatty acid biomarkers that they derived additional nutrition by suspension feeding. In Australia, *Z. macracantha* occurs off the Great Australian Bight at depths of 457–1,006 m (Rowe & Gates 1995), and *Pholidaster squamatus* occurs from Western Australia to the Philippines (Marsh 1976). Fossils of *Zoroaster aff. fulgens* have been collected in large numbers from the Eocene La Meseta formation on Seymour Island, Antarctic Peninsula (Blake & Zinsmeister 1979, 1988). *Zoroaster fulgens* is a generalist infaunal predator (Gale *et al*. 2013).

Zoroasteriids have large eggs. *Zoroaster fulgens* has eggs with a diameter of 950 µm, and can have seasonal reproduction, an unusual pattern for deep-water asteroids (Tyler *et al*. 1984). Juvenile development and early skeletal plate formation in this species are described by Sumida *et al*. (2001). A molecular study revealed the presence of three morphotypes of *Zoroaster fulgens*, stratified by depth, indicating the presence of cryptic species (Howell *et al*. 2004). Grygier (1985) reported that *Z. carinatus* from 350–450 m off north-western Australia carried cysts of ascothoracidian barnacles.

Order BRISINGIDA

The order Brisingida comprises multi-armed, suspension-feeding, deep-water asteroids that inhabit the continental shelf to hadal depths (100–7,000 m). The most recent classification of the Brisingida recognises two families (**Table 8.1**). Several alternative taxonomic treatments are given for the Brisingida (Fisher 1917, 1928, 1940; Galkin & Korovchinsky 1984; Downey 1986; Clark & Downey 1992). Downey (1986) described two families within the order based on different abactinal plate morphologies: the Brisingidae and the Freyellidae. Mah (1998b, 1999) and Clark & Mah (2001) presented several family level groupings (for example, Odinellidae, Novodiniidae) that reflect clades in Mah's morphology-based revision (1998b, 1999). These arrangements await further clarification and definition.

Brisingids have a small, sharply delimited disc with many elongate arms, 60–190 mm in length (**Figs 2.10, 8.43**), but they can have arm spans of up to 600 mm (in *Midgardia xandaros*). The brisingid disc consists of several tightly fused ossicles that form an oral ring. The oral ring is closely articulated with the arms, which are composed of vertebra-shaped ambulacral ossicles and hourglass-shaped adambulacral ossicles. Marginal plates are greatly reduced to an incomplete series occurring in close association with the oral ring and the adambulacral plate series. Long acicular spines occur commonly on the adambulacrals, but also on other plates, and have an ensacculate covering of dense and abundant, crossed 3-element pedicellariae. Papulae are greatly reduced or absent in most derived taxa, but they can be abundant on the disc and arms in basal genera (*Brisingaster*, *Novodinia* and *Odinella*) (Mah 1998b). Tube foot furrows are wide and have two rows of suckered tube feet.

A phylogeny of the Brisingida supports an onshore-offshore pattern of evolution within the group. Stemward genera, such as *Odinella*, *Brisingaster* and *Novodinia*, occur in shallower continental shelf habitats, in contrast to the derived Freyellidae which inhabit deeper lower-bathyal, abyssal and even hadal depths, often on soft bottoms.

Family Brisingidae

Figure 8.43

The family Brisingidae includes 10 genera and 63 species in the Atlantic, Indian and Southern Oceans (Mah & Blake 2012). Three species are known to occur in Australian waters: *Brisingaster robillardi* from near Norfolk Island, Wanganella Bank, as well as Mauritius, Japan, and New Caledonia (Mah 1999); *Brisingenes anchista* from subantarctic waters (4,755 m); and *Novodinia australis* (**Figs 2.10, 8.43**) from the

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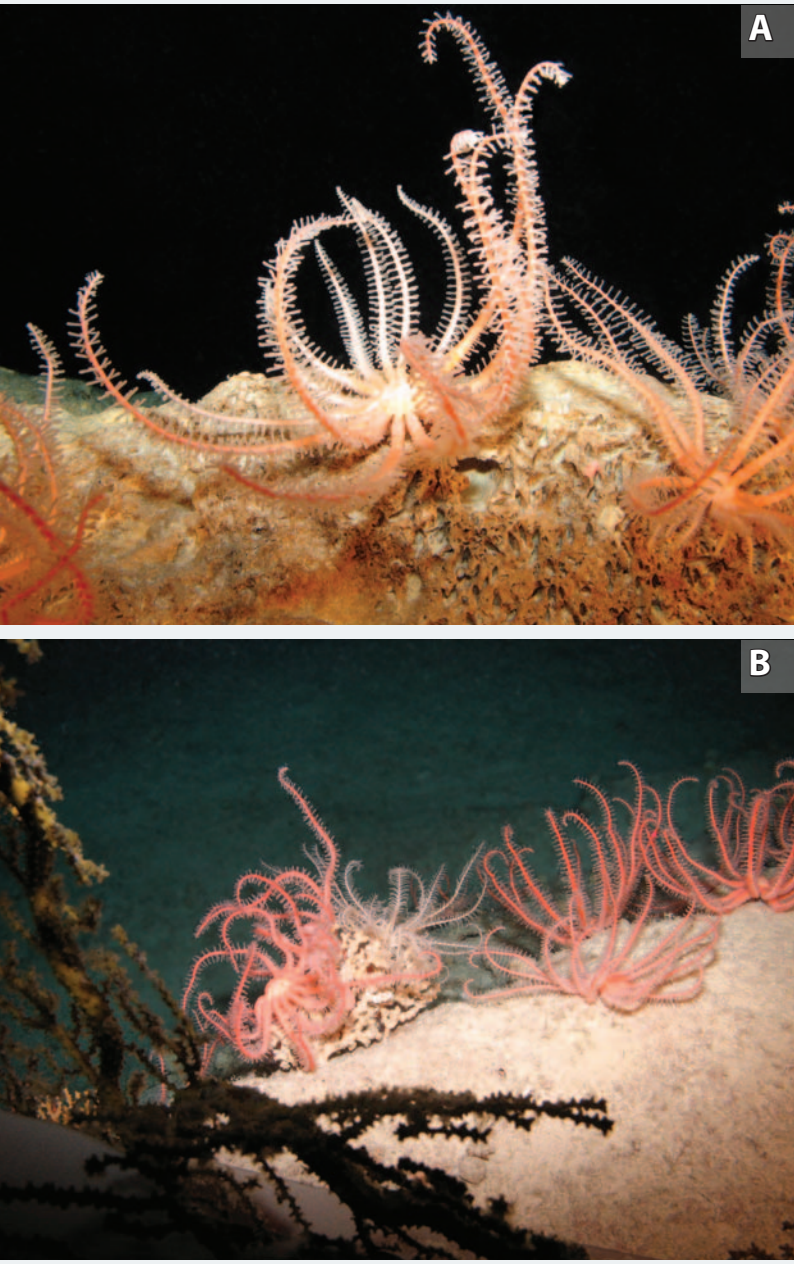


Figure 8.43 Family Brisingidae.

Brisingids extend their arms into the water column to catch planktonic prey with the pedicellaria.

A, ***Novodinia*** sp. from Bougainville Reef, Queensland, at a depth of about 400 m.

B, ***Novodinia*** sp. from Osprey Reef, Queensland, at a depth of 600 m.

[A,B, courtesy of J.Reitner]

continental shelf off Victoria and New South Wales (360–569 m) (O'Hara 2012). Several undescribed taxa have been identified among Tasmanian seamount faunas (Mah 1998a), *Astrostephane* cf. *moluccana* has been found at 450 m off north-western Australia, and species of *Novodinia* and *Brisinga* have also been collected from the north-west slope.

Based on work by Downey (1986), genera within the Brisingidae are distinguished by the presence of distinct rib-like series of abactinal plates across the abactinal surface. The Brisingidae also exhibit non-muscular fusion of the adambulacral and marginal plates. Basal members of the Brisingida show significant differences in plate arrangement and papular distribution. Abactinal arm plates in *Novodinia* are fenestrate and form an essentially solid mosaic through which the papulae emerge. However, in the basal *Brisingaster* there is an open reticulated mesh. Full character state comparisons between these two genera were provided by Mah (1998b).

Suspension-feeding behaviour in brisingids was first documented by Pawson (1976) from *in situ* observations. Feeding biology of *Novodinia antillensis* was described by Emson & Young (1994a). Brisingids sit with their arms extended into the water, allowing water currents to carry small prey and other organic matter to the extensive arrays of pedicellariae-covered spines and abactinal surface ossicles. The fused oral ring has been interpreted as an attachment structure for the arms held above the substrate during suspension feeding (Blake 1987). Food or prey are caught by the pedicellariae, moved by means of the tube feet down to the mouth and ingested. Howell *et al.* (2003) reported on prey items, and by using fatty acid biomarkers in three North Atlantic species, were able to confirm those brisingid species as specialist predators on benthopelagic copepods. Stable isotope analysis also indicates that *Novodinia* are specialist predators on benthopelagic crustaceans (Gale *et al.* 2013).

Brisingids for which observations are available have large eggs and thus are likely to have lecithotrophic development (Tyler *et al.* 1984) — ~1.2 mm diameter for *Brisinga endecacnemos* and *Hymenodiscus coronata*. Juvenile development and early skeletal plate formation in *Brisingella coronata* are described by Sumida *et al.* (2001).

Brisingids are hosts to a variety of parasites and commensal organisms, including polynoid polychaetes (Pettibone 1990; Rice & Miller 1991), ascothoracidan barnacles (Grygier 1983, 1987, 1990) and eulimid gastropods (Warén & Lewis 1991).

Family Freyellidae

The family Freyellidae includes seven genera and 47 species (Clark & Downey 1992; Mah & Blake 2012). One species, *Freyella dimorpha*, occurs in the Torres Strait (2560 m), while several undescribed freyellids have been collected from the Tasmanian seamounts (Mah 1998a). Freyellidae is supported by preliminary phylogenetic analysis as a monophyletic group (Mah 1998b).

Abactinal plates in the Freyellidae form a mosaic of abutting plates, resulting in a continuous surface between the disc and arms. With the exception of *Freyellaster*, they lack an articulated (that is, non-muscular) interradial fusion between the proximal adambulacral and marginal plates. Papulae are absent, except in the problematic genus *Colpaster*.

As indicated above, freyellids occur at much greater depths than other brisingids. Differences in their proximal arm articulation and abactinal plate morphology suggest a significant difference in feeding ecology from that observed in other brisingids. The feeding biology of *Freyella* is described by Galkin & Korovchinsky (1984).

Incertae sedis

Family Xyloplacidae

Figure 8.44

The Xyloplacidae comprises one genus and three species: *Xyloplax medusiformis* (New Zealand), *X. janetae* (north Pacific) and *X. turnerae* (Bahamas) (Mah & Blake 2012). *Xyloplax* generated considerable interest when it was first discovered living on sunken wood at abyssal depths (Baker *et al.* 1986). These minute discoid asteroids (1–8 mm diameter) have a distinctive internal and skeletal morphology compared with other echinoderms (**Fig. 8.44; Box 6.2**). They were originally thought to represent a new class of Echinodermata (Baker *et al.* 1986; Rowe *et al.* 1988, 1994). This generated great debate, but the weight of evidence now points to *Xyloplax* species being aberrant asteroids (Janies & McEdward 1994; Pearse & Pearse 1994; Janies & Mooi 1999; Janies 2001). Although Janies *et al.* (2011) currently recognise Xyloplacidae as a family within the order Velatida, the placement is not settled and so we have elected to classify the family as *'Incertae sedis'* until the matter is resolved.

Among the most significant diagnostic features of *Xyloplax* are the absence of the actinal plate surface, the peripheral ring of tube feet, and the remarkable spermatozoa (Rowe *et al.* 1988, 1994). Based on external morphology, Mah (2006a) described a recently discovered third species of *Xyloplax* and provided an overview of these asteroids. The substantial morphological differences between *Xyloplax* and other Asteroidea are considered to be associated with post-Palaeozoic diversification rather than a secondary derivation from an established and conservative morphology. The following revised diagnosis is based on Mah (2006a).

The body of *Xyloplax* is dorsoventrally flattened, and the discoid body is divided into five discrete regions, each of which is subdivided interradially. Each region has an identical number of tube feet and adambulacral spines. The abactinal plates are flattened, irregularly rounded, overlapping and variable in size, the largest plates being approximately five times the size of the smallest ones. The centrodorsal plate is overlapped by 5–7 smaller plates. Abactinal spines are present. Terminal plates are flattened, rounded and have a pronounced, distal-facing, medial cleft corresponding to the position of the terminal tube foot. Terminal plates are enlarged relative to the adjacent adambulacral and disc plates. Adambulacrals are flattened, overlapping and form the periphery of the body. They are oblique and are positioned adjacent to the adambulacral plates and podial pores. The terminal tube foot is flanked on either

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side by an equal number of podial pores. The tube feet have a bulbous tip. Adambulacrals in individual series are not paired; rather, they are arranged around the periphery of the body between the adambulacral and oral plates. The oldest ambulacrals and adambulacrals are adjacent interradially. Adambulacral spines form a continuous series around the periphery of the body. The oral plates are curved and tusk-shaped. Narrow tips of adjacent oral plates abut interradially. An odontophore is present interradially, between narrow tips of adjacent oral plates. Otherwise, the oral plates form the innermost series of plates (as observed actinally). A stomach is present in adults of the single Caribbean species, but absent in those of the two Pacific taxa (although a vestigial stomach develops and is then lost in developmental stages of the brooded juveniles). Sexual dimorphism is evident, the males having paired cygnoid interradial spinelets.

Little is known of the biology of these abyssal asteroids apart from the fact that they appear to be associated with sunken wood. Detritus, foraminiferans and shell fragments have been found in the stomach of *X. turnerae*, but it has been postulated that, at least for *X. medusiformis*, direct absorption of dissolved organic material is the norm (Rowe *et al*. 1988). The males may use the cygnoid spinelets (**Fig. 8.44B**) to support the penial projection to aid sperm transfer. If this is true, these are the only echinoderms to have a copulatory device. The females are also larger than the males (Rowe *et al*. 1988; Mah 2006a). Two of the three known *Xyloplax* species are intra-ovarian brooders and care for their young in the oral region. In *X. janetae* the juveniles were found tucked inward in tissue infolds (Mah 2006a). In contrast, the Caribbean species *X. turnerae* (**Fig. 8.44A; Box 6.2**) does not appear to brood its young.

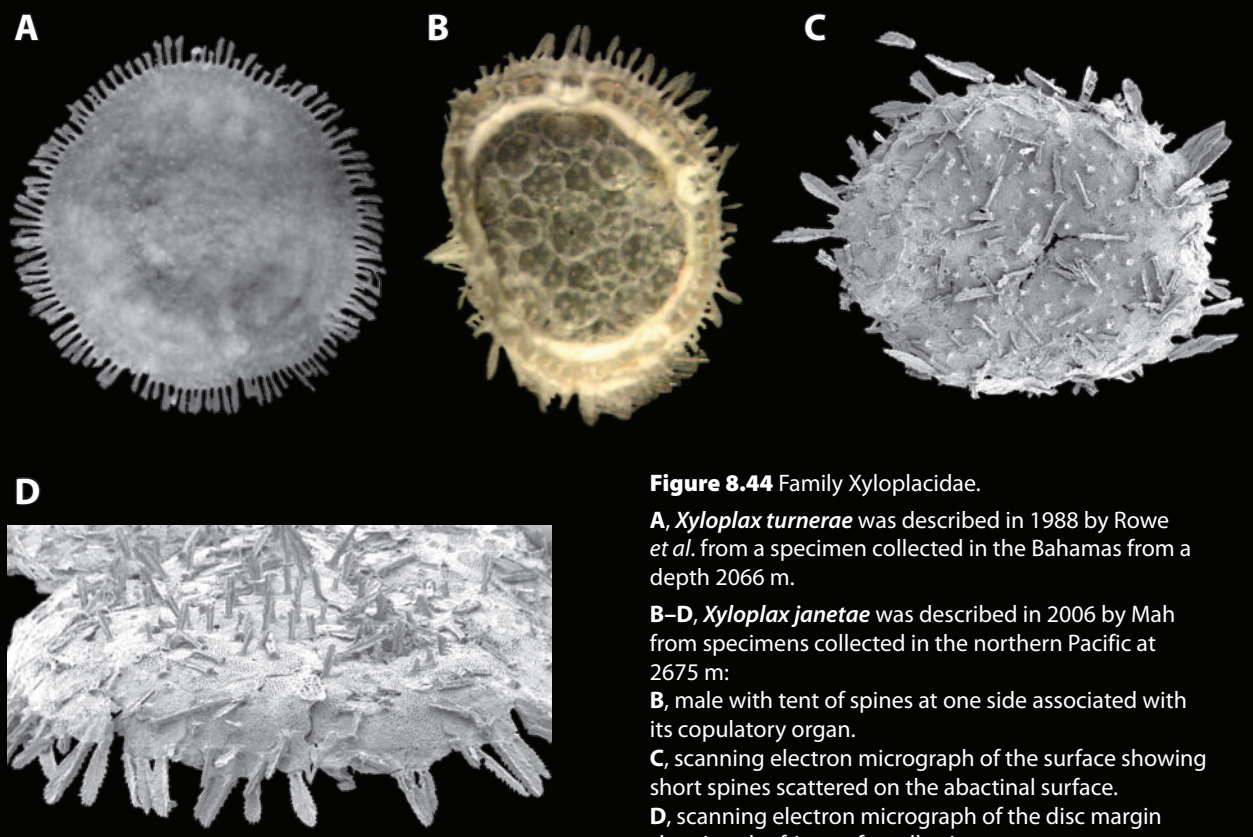


Figure 8.44 Family Xyloplacidae.

A, ***Xyloplax turnerae*** was described in 1988 by Rowe *et al*. from a specimen collected in the Bahamas from a depth 2066 m.

B–D, ***Xyloplax janetae*** was described in 2006 by Mah from specimens collected in the northern Pacific at 2675 m:
B, male with tent of spines at one side associated with its copulatory organ.
C, scanning electron micrograph of the surface showing short spines scattered on the abactinal surface.
D, scanning electron micrograph of the disc margin showing the fringe of small spines.

[A, from Rowe *et al*. 1994; B–D, C.L.Mah]



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9: Class OPHIUROIDEA

Timothy D. O'Hara

General description

Ophiuroids have a round central disc and slender flexible arms that enable the animal to move. The arms can be simple (brittle stars or snake stars) or branched (basket stars) (**Figs 1.1B, 1.2A–C**). Usually there are five arms, although fissiparous (self-dividing) species have six (**Fig. 3.7A**), or rarely more. The Antarctic gorgonocephalid *Astrochlamys sol* has 9 to 10 arms arising directly from the disc. The arms of the basket stars also branch repeatedly to the arm tips (**Figs 1.2A, 1.12**). The flexibility of the ophiuroid arm derives from its segmented structure (**Fig. 1.6D**). Apart from the branching of the arms, ophiuroids exhibit little variation in form. The maximum diameter of the disc in adults varies from about 2 to 65 mm. The arm-length to disc-diameter ratio varies from less than one in *Astrophiura permira* to 33.3 in *Asteroschema tenue* (Fell 1966b; Lawrence 1987).

Comprehensive reviews of ophuroid biology include general accounts (see Hyman 1955) and reviews of functional morphology, histology and ultrastructure (Byrne 1994), feeding and nutrition (Warner 1982), reproduction and life histories (Hendler 1991; McEdward & Miner 2001; Byrne & Selvakumaraswamy 2002) and global diversity (Stöhr *et al.* 2012, 2014). The most recent inventory of Australian ophiuroid taxa is provided by the Australian Faunal Directory (O'Hara 2012).

In modern ophiuroids, each arm segment consists of a vertebral ossicle surrounded by a series of external arm plates (**Fig. 1.6A,B**). The vertebrae are composed of fused halves, homologous with the paired ambulacral plates of the modern asteroids. The ventral arm plates completely enclose the radial canal and nerves and so ophiuroids have a closed ambulacral system (see **Chapter 1**). In contrast, the ambulacral groove in asteroids and many Palaeozoic ophiuroids are not covered over and so have an open ambulacral system. The lateral arm plates bear a series of spines (**Fig. 1.6B,D**). The tube feet are small, and have no ampullae or terminal sucker (**Fig. 1.23**). A tube foot emerges on each side of the ventral arm plate on arm segments. The tube foot pore typically is protected by one or more flattened or rounded spines called tentacle scales (**Fig. 1.23**).

The ophiuroid disc is covered by thick skin or plates, often with spines (Byrne 1994; Irimura 1998). The first plates to develop after metamorphosis are the central plate (the centrodorsal) and five primary radial plates (Selvakumaraswamy & Byrne 2004; Stöhr 2005; Falkner & Byrne 2006). These can be seen on the adults of many species as slightly larger plates near the centre of the disc. A pair of enlarged plates (radial shields) is present near the arm bases (**Fig. 9.3E**).

Figure 9.1 The basket star ***Conocladus australis***, perched on a finger-shaped sponge, extending some arms to feed. This species is endemic to southern Australia, occurring on the continental shelf from south Queensland across to Jurien Bay, Western Australia. It has a slightly different form and colour across its long range that may be indicative of separate cryptic species or just regional variation.

[F. Bavendam]

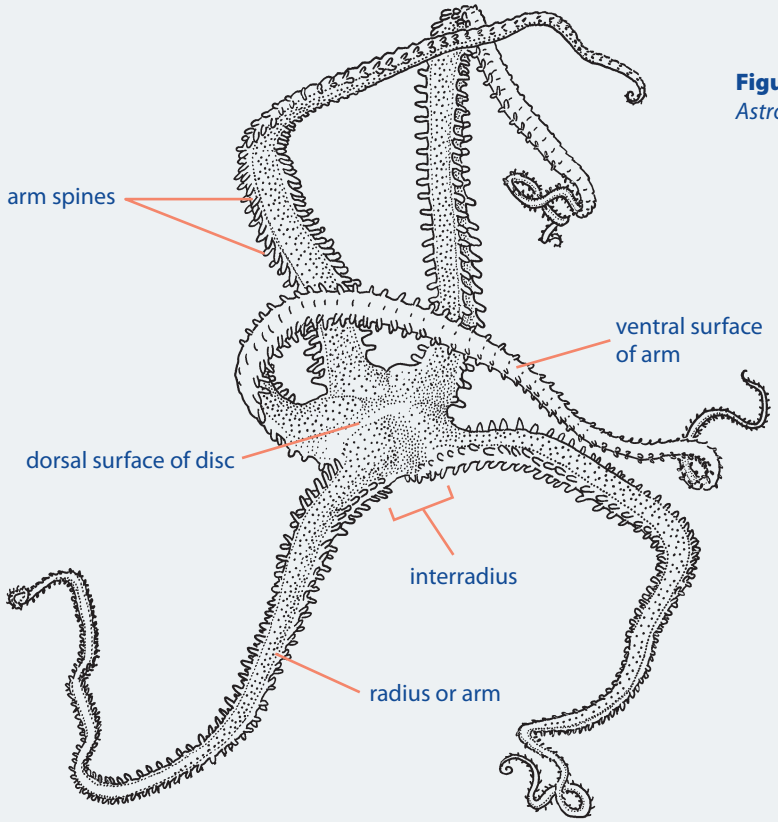


Figure 9.2 Gross anatomical features of ophiuroids. *Astrogymnotes catasticta* (Ophiolepididae). [K.Nolan]

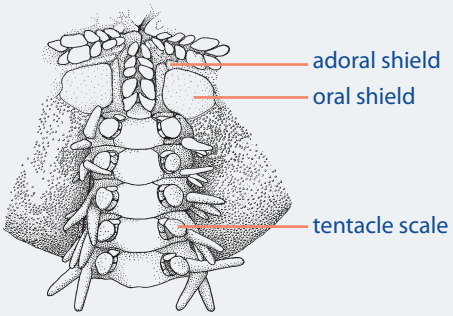
On the ventral surface, the arms continue inwards towards the central mouth. In most species, the arms are bordered on either side by the bursal or genital slits (**Figs 1.10B, 1.25**), the openings of the internal bursal sacs which have a respiratory and reproductive function. The sides of the bursal slit are bordered by the narrow genital plates that extend around the disc margin and articulate internally with the radial shields. The interradial ventral surface is covered by disc scales or skin, similar to the dorsal surface of the disc. The mouth is star-shaped and is bordered by five wedge-like jaws that form the oral frame (**Fig. 9.14B**). The side of each jaw, the oral plate, is actually composed of two pieces that fuse together during early growth. In addition there is usually a narrow plate bearing the teeth at the apex of each jaw. A series of small papillae is present in some groups along the jaw sides (oral papillae) or at their tip (dental or infradental papillae). At the posterior side of the oral plates is a round oral (or buccal) shield, bordered on each side by smaller adoral shields. One (or rarely more) of the oral shields functions as the inlet (madreporite) for the water vascular system (see **Chapter 1**). Internally there are small plates, the peristomial plates that can only be seen if you remove the disc from the oral frame (Hyman 1955; Nichols 1966; Lawrence 1987).

The plates of the oral frame are considered to be two modified arm segments that are split down the middle by the jaw slit (Ludwig 1878; Hendler 1978). Two tube feet (the oral tentacles) emerge from each side of the jaw, sometimes protected by tentacle scales (**Fig. 1.10A**). The inner and outer pieces of the oral plate are ambulacral plates, homologous with the vertebrae, and the adoral shields are adambulacral plates, homologous with the lateral arm plates. However, while the ambulacrals and adambulacrals are homologous with the similar plates in asteroids, the radial shields, genital plates and oral shields appear to be ophiuroid specialisations (Hendler 1978). The homology of the various oral papillae is unclear as they move considerably during early growth from their point of origin (Hendler 1978, 1988).

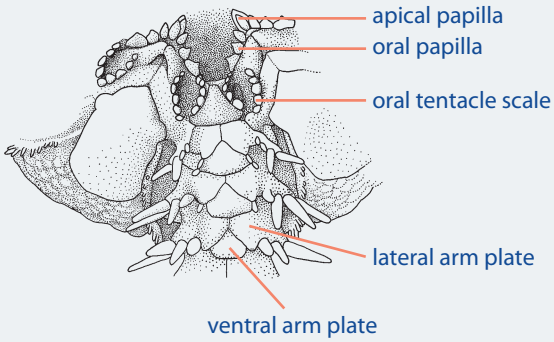
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Ventral characters

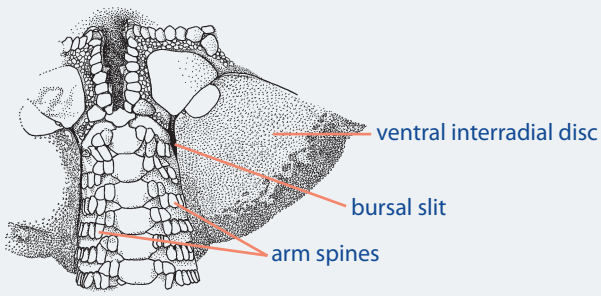
A Ophionereididae



B Ophiuridae

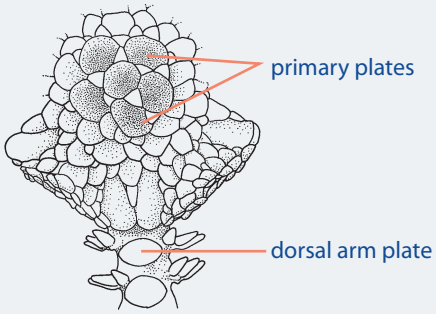


C Ophiodermatidae

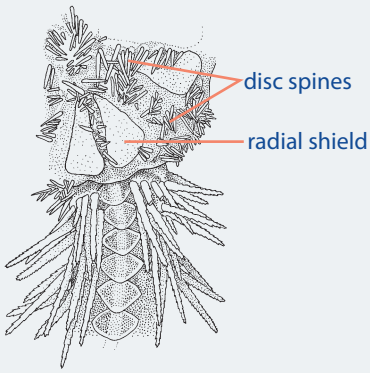


Dorsal characters

D Amphiuridae



E Ophiotrichidae



F Ophiocomidae

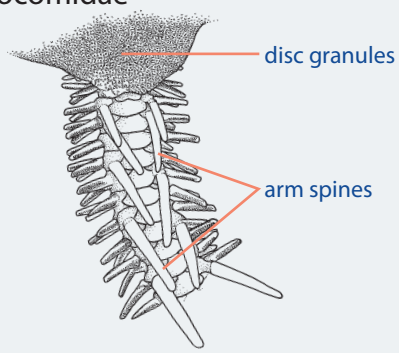


Figure 9.3 External anatomical features of the central disc and arms of ophiuroids.

A–**C**, ventral features.
A, ***Ophioplax lamellosa*** (Ophionereididae).
B, ***Ophiura kinbergi*** (Ophiuridae).
C, ***Ophiarachnella ramsayi*** (Ophiodermatidae).

D–**F**, dorsal features.
D, ***Amphiura constricta*** (Amphiuridae).
E, ***Ophiothrix aristulata*** (Ophiotrichidae).
F, ***Ophiocoma occidentalis*** (Ophiocomidae).

[K.Nolan]

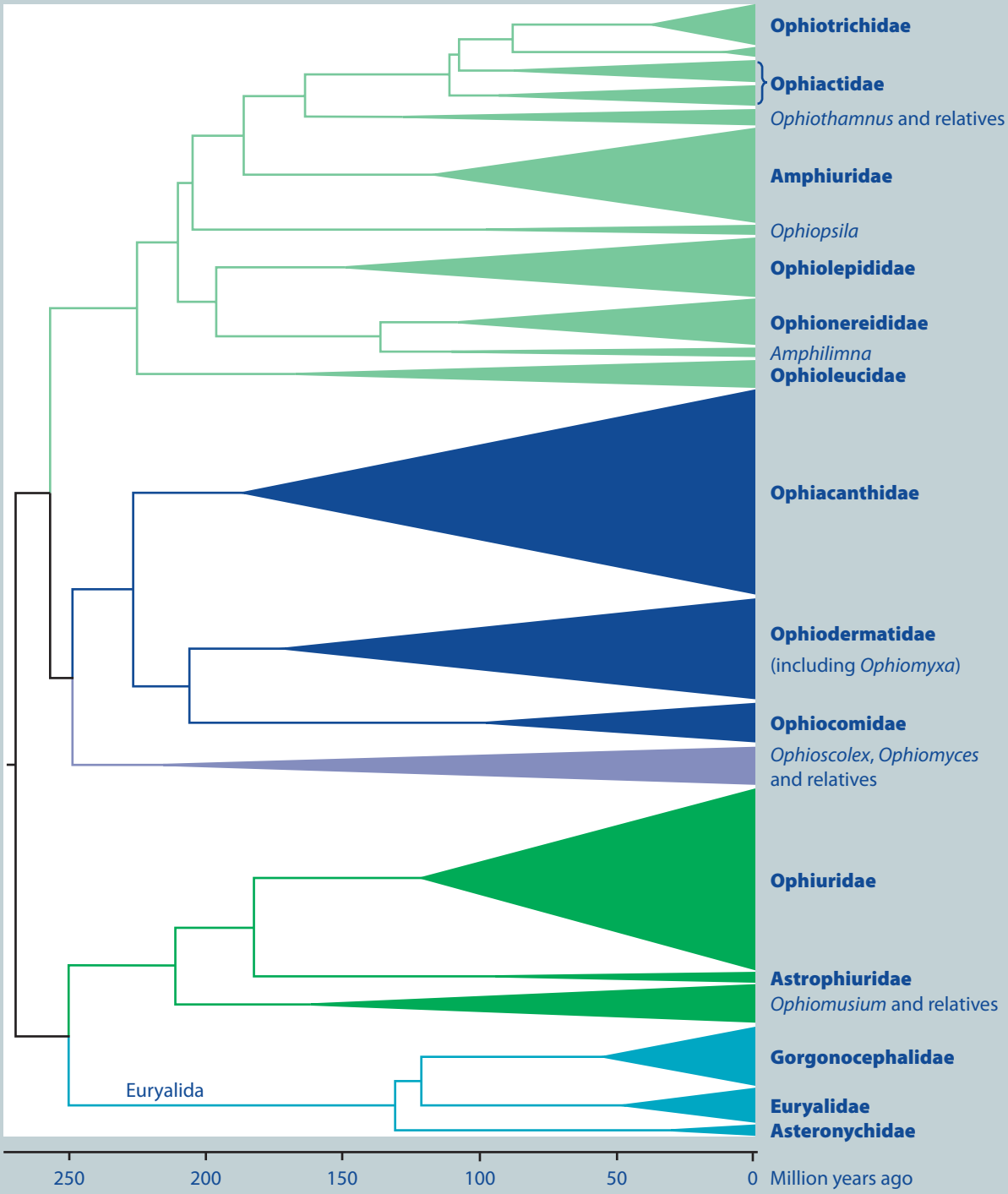


Figure 9.4 Schematic of a fossil-calibrated molecular phylogeny of the Ophiuroidea showing the relationships of the groups described in the text. These groups form five major lineages (separately coloured); only one has an existing name, the order Euryalida.

[derived from Hugall *et al.* 2015]

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Table 9.1 A comparison of the Ophiuroidea classification used in this work, following Hugall *et al*. 2015, with the 'traditional' classification.

† the only lineage with an existing name

This work	'Traditional' classification
Clade 1	**Order Euryalida**
Euryalida †	Family Asteronychidae
Family Euryalidae	Family Gorgonocephalidae
Family Gorgonocephalidae	Family Euryalidae
Family Asteronychidae	Subfamily Euryalinae
	Subfamily Astrocharinae
Other families & groups	Subfamily Asteroschematinae
Families Ophiuridae and Astrophiuridae	**Order Ophiurida**
Ophiomusium and relatives	Suborder Ophiomyxina
	Family Ophiomyxidae
Clade 2	Subfamily Ophiomyxinae
Other families & groups	Subfamily Ophiobyrsinae
Ophioscolex, *Ophiomyces* and relatives	Suborder Ophiurina
Family Ophiacanthidae	Family Ophiacanthidae
Family Ophiocomidae	Infraorder Hemieuryalina
Family Ophiodermatidae (including *Ophiomyxa*)	Family Hemieuryalidae
Family Ophioleucidae	Infraorder Gnathophiurina
Family Ophionereididae	Superfamily Amphilepididea
Ophiopsila	Family Amphilepididae
Amphilimna	Superfamily Gnathophiuridea
Family Ophiolepididae	Family Amphiuridae
Family Amphiuridae	Family Ophiotrichidae
Family Ophiactidae, *Ophiothamnus* and relatives	Family Ophiactidae
Family Ophiotrichidae	Superfamily Ophiocomidea
	Family Ophionereididae
	Family Ophiocomidae
	Subfamily Ophiocominae
	Subfamily Ophiopsilinae
	Infraorder Chilophiurina
	Family Ophiuridae
	Family Ophioleucidae
	Infraorder Ophiodermatina
	Family Ophiochitonidae
	Family Ophiodermatidae
	Subfamily Ophiodermatinae
	Subfamily Ophiarachninae
	Infraorder Ophiolepidina
	Family Ophiolepididae

The mouth opens into a small stomach and there is no intestine or anus (**Fig. 1.10B**). Gonads are confined to the disc in most ophiuroids (**Fig. 1.10B**) with the exception of some basket stars and snake stars and oddities like *Ophiocanops* (Byrne 1994; Pearse *et al*. 1998). The gonads usually open into the bursal sacs and the gametes emerge through the bursal slits. Characteristic calcareous ossicles occur in the walls of the bursae, gonads and stomach (Irimura 1988, 1991).

The Ophiuroidea is the second largest echinoderm class, after the Asteroidea, with approximately 2100 extant species in approximately 273 genera (Stöhr *et al*. 2014). They occur in most of the world's marine waters, from the tropics to the poles and from the intertidal zone to the abyssal depths. They are important ecologically, and some species occur in large numbers and can dominate their local faunal assemblages, forming extensive aggregations (Warner 1979; Metaxas & Giffin 2004; Kogure 2010). This is seen in the abundance of *Ophiocamax applicatus* on the seamounts (**Fig. 9.11G**). Australia and its offshore territories, including the Australian Antarctic Territory, have particularly rich ophiuroid faunas.

Many ophiuroid families have long fossil histories (Simms *et al*. 1993) and, with minor exceptions, all living families are widely distributed (Fell 1982). There are no recognised endemic families in the Australian or Antarctic regions.

Since the beginning of the nineteenth century living ophiuroids have usually been divided into two groups, the Euryalae (basket stars, snake stars and their relatives) and the Ophiurae (brittle stars). Euryalae were characterised by the presence of thick skin covering the disc and arms, the absence of, or rudimentary, dorsal arm plates, and the position of the subventral or ventral arm spines. Their arm vertebrae articulate with broad 'hourglass-shaped' surfaces (streptospondylous articulation), allowing the arms to coil. This group included genera with either branched or unbranched arms. Ophiurae were unbranched forms, most with dorsal and ventral arm plates, radial shields, oral shields and genital plates. Their vertebrae usually articulate with 'ball and socket' joints (zygospondylous articulation) that restrict most movement to the horizontal plane (Byrne 1994; Stöhr *et al*. 2012). The division between Euryalae and Ophiurae was variously implemented at the level of genus, family, suborder and order. Many authors persisted with this simple classification until the early 1960s (Hyman 1955; Fell 1960). Most Palaeozoic ophiuroids, not directly related to modern forms, were placed in the ill-defined Auluroidea.

These early classifications were not satisfactory. The form of the vertebral articulation has been found to vary within some families, particularly the Ophiomyxidae and Ophiacanthidae, and it can be related to function as well as phylogeny (LeClair 1994; Litvinova 1994; Irimura 2003). The Auluroidea was found to include somasteroids as well as true ophiuroids.

Early in the twentieth century, the ophiuroids were split into four orders based on internal skeletal characters (Matsumoto 1915). These were Phrynophiurida (the euryalids and the family Ophiomyxidae), Laemophiurida (Ophiacanthidae and Hemieuryalidae), Chilophiurida (Ophiuridae, Ophioleucidae, Ophiocomidae, Ophionereididae and Ophiodermatidae) and Gnathophiurida (Amphiuridae, Ophiactidae, Amphilepididae and Ophiotrichidae). A separate subclass, the Oegophiuroida, was created for the Palaeozoic ophiuroids, distinct from the Myophiuroida, or 'true' ophiuroids (Matsumoto 1915). The crown-group or extant ophiuroids were termed the Metophiurida (Matsumoto 1929).

Matsumoto's (1915) ordinal classification was criticised on two grounds: 1) that the Phrynophiurida is an unnatural grouping, and 2) that the other orders are poorly characterised (Mortensen 1927; Hyman 1955). Succeeding monographs recognised four ophiuroid orders: Stenurida, Oegophiurida, Phrynophiurida and Ophiurida (Spencer & Wright 1966; Fell 1982), with the Laemophiurina, Gnathophiurina and Chilophiurina treated as suborders of the Ophiurida. The only attempt at an Ophiuroidea-wide morphological phylogeny supported the earlier view that the Euryalida formed a clade distinct from the Ophiurida (including the Ophiomyxidae) (Smith *et al*. 1995).

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A large molecular study using transcriptomic data for 425 genes (102,143 amino acids) indicates that a new classification of the Ophiuroidea is required (O'Hara *et al*. 2014b). Convergent evolution (where a feature evolves more than once in different lineages) is common within the Ophiuroidea and has confused earlier attempts at classification. Many accepted families and genera are not true evolutionary units but mixed assemblages of convergent species. While, the aforementioned phylogenies are insufficiently resolved for development of a comprehensive new taxonomic scheme, there is enough data and adequate resolution (O'Hara *et al*. 2014b; Hugall *et al*. 2015) to be able to identify some of the larger groups.

At the highest level the phylogenetic analysis derives two clades (O'Hara *et al*. 2014b; **Fig. 9.4**; **Table 9.1**). The first contains the Ophiuridae, the *Ophiomusium*-complex (formerly in the Ophiolepididae), and the Euryalina (basket stars and snake stars; Asteronychidae, Euryalidae, Gorgonocephalidae). The second clade contains all remaining families. This separation was first suggested by Martynov (2010b) who noted that the euryalids and ophiurids have similar arm spine articulation morphologies and that all other families 'form a compact group with numerous intermediate taxa'. The suprising inclusion of both ophiurins and euryalins in the same clade has some fossil support: the Triassic species *Aspiduriella streichani* has the external appearance of the Ophiuridae but has euryalin hourglass articulation surfaces on the arm vertebrae (Hess & Meyer 2008). This is the classification that will be adopted in this chapter.

Fossil ophiuroids are still generally assigned to two groups, the Stenuroidea and Oegophiuroida. The Stenuroida was erected for certain primitive Palaeozoic ophiuroids (Spencer 1951). These fossils have some ophiuroid characters such as a clearly demarcated disc or internal gills. However, instead of having modern ophiuroid arm vertebrae, they have paired ambulacral plates running down the centre of each arm, typical of asteroids and somasteroids. The ambulacral plates are either alternate, as in asteroids or somasteroids, or opposite, as in modern ophiuroids. These plates lie at the top of an open ambulacral furrow which contains the radial vessel of the water vascular system. There are no ventral or dorsal arm plates. Adambulacral plates, or laterals, sometimes function as lateral arm plates. The basin of each tube foot is spread over two adjacent plates. Blake (2013) recognises the Stenuroidea as a separate class of echinoderms.

The Oegophiurida, also predominantly Palaeozoic, are closer to modern ophiuroids in having the basins of the tube feet restricted to a single ambulacral plate. The ambulacrals are either alternate or opposite. In some later forms, the opposite plates fuse to become primitive vertebrae. Oegophiurida lack ventral arm plates and the ambulacral groove remains open. The aberrant Indonesian ophiuroid *Ophiocanops fugiens* has been classified as a living oegophiurid (Fell 1962a; Smith *et al*. 1995). It has paired serial gonads extending along the proximal part of the arm, the gut extends into the arm, and soft tissue is present in the relictual ambulacral groove (Pearse *et al*. 1998). However, other classifications place *O. fugiens* near the Ophiomyxidae as, unlike fossil oegophiurids, it has oral shields, adoral plates and a first ventral arm plate (Hotchkiss 1977; Janies 2001; Stöhr *et al*. 2008). The latest genetic data places *Ophiocanops felli* within the Ophiacanthidae (Hugall *et al*. 2015).

The classification of fossil ophiuroids outlined here is still regarded by some palaeontologists as unsatisfactory because it is based on grades of organisation rather than phylogenetic relationships (Hotchkiss 1976; Simms *et al*. 1993). The Palaeozoic taxa, in particular, are probably polyphyletic or paraphyletic, with some forms likely to be part of the stem group of true ophiuroids and related echinoderms (Simms *et al*. 1993). The form of the ancestor of modern ophiuroids has also been debated. Hotchkiss & Haude (2004) observe a continuum between the Devonian *Stephanoura*, Carboniferous *Aganaster* and modern *Ophiomusium*; while Martynov (2010b) notes similaritites between the Devonian *Eugasterella* and the modern *Ophioscolex* and *Ophioplexa*.

The oldest ophiuroid fossils known belong to the stenurid genus *Pradesura*, and were found in Early Ordovician rocks from Europe (Dean Shackleton 2005). The first recognisable oegophiurids, *Hallaster*, are from slightly later Ordovician rocks of Europe and North America while the first modern ophiuroids are from the Late Silurian period (Simms *et al*. 1993).

Table 9.2. Fossil ophiuroids recorded from Australia (nomenclature updated).

† states and territories of Australia: NSW, New South Wales; NT, Northern Territory; QLD, Queensland; TAS, Tasmania, VIC, Victoria; WA, Western Australia.

Species	Reference(s)	Modern Classification	Geological Period and Location (State) †
Stuertzura brisingoides	Withers & Keble 1934b	Somasteroid	Silurian-Devonian, VIC
Taeniactis yeringae	Withers & Keble 1934b	Asteroid	Silurian-Devonian, VIC
Stuertzaster ?mitchelli	Withers & Keble 1934b	Stenuroidea, Pradesuridae	Silurian-Devonian, VIC, NSW
Stenaster obtusus	Jell & Baillie 1984	Stenuroidea, Stenasteridae	Silurian, TAS
Crepidosoma kinglakensis	Withers & Keble 1934b	Oegophiurida, Encrinasteridae	Silurian-Devonian, VIC
Urosoma glabridiscus	Talent 1965	Oegophiurida, Encrinasteridae	Silurian-Devonian, VIC
?Urosoma parvus	Withers & Keble 1934b; Spencer 1950	Oegophiurida, Encrinasteridae	Silurian-Devonian, VIC
?Urosoma bakeri	Withers & Keble 1934b; Spencer 1950	Oegophiurida, Encrinasteridae	Silurian-Devonian, VIC
Mausoleaster sugarloafensis	Jell & Holloway 1983	Oegophiurida, Encrinasteridae	Silurian-Devonian, VIC
Lapworthura miltoni	Withers & Keble 1934b; Talent 1965	Oegophiurida, Lapworthuridae	Silurian-Devonian, VIC
Lapworthura pulcherrima	Withers & Keble 1934b	Oegophiurida, Lapworthuridae	Silurian-Devonian, VIC
Furcaster kilmorensis	Withers & Keble 1934b	Oegophiurida, Furcasteridae	Silurian-Devonian, VIC
Furcaster leptosomoides	Withers & Keble 1934b	Oegophiurida, Furcasteridae	Silurian-Devonian, VIC

Many Palaeozoic ophiuroids are broadly similar in form to living species, and may have occupied similar ecological niches (Fell 1966b). The Stenurida and Oegophiurida became extinct in the Palaeozoic (Devonian and Permian respectively). Within the Metophiurida, several lineages persisted through the Permian-Triassic mass extinction event (O'Hara *et al.* 2014b), although all genera were replaced (Chen & McNamara 2006). Post-extinction event recovery was rapid, and the Metophiurida radiated extensively in the Early Triassic (Chen & McNamara 2006).

Australian fossil record

The documented ophiuroid fossil record in Australia is very scant, comprising only 23 named species (**Table 9.2**). The majority were described or recorded early last century from a few, often poorly preserved, specimens; their status requires a modern reappraisal. Several authors have already cast doubt on some of the original identifications (Clark 1946; Spencer 1950; Spencer & Wright 1966). Two species are no longer considered ophiuroids.

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Species	Reference(s)	Modern Classification	Geological Period and Location (State) †
Furcaster spryi	Withers & Keble 1934b; Spencer & Wright 1966	Oegophiurida, Furcasteridae	Silurian-Devonian, VIC
Eospondylus tenuis	Withers & Keble 1934b	Oegophiurida, Furcasteridae	Silurian-Devonian, VIC
?Aganaster gregarius	Withers & Keble 1934b; Clark 1946	Myophiuroida, Aganasteridae	Carboniferous, VIC
Ophioflabellum cristatum	Kristan-Tollman & Gramann 1992	Metophiurida, Ophiuridae	Triassic, WA
Aplocoma sp.	Runnegar 1969; Chen & McNamara 2006	Metophiurida, Aplocomidae	Triassic, QLD
Ophioderma ?cf. *waliabadensis*	Kristan-Tollman & Gramann 1992	Metophiurida, Ophiodermatidae	Triassic, WA
Ophioglyphoida fosteri	Chapman 1934; Clark 1946	Metophiurida, Ophiacanthidae	Lower Cretaceous, QLD
Ophiacantha ?cf. *binitorulosa*	Kristan-Tollman & Gramann 1992	Metophiurida, Ophiacanthidae	Triassic, WA
Ophiacantha ?cf. *subtilirugosa*	Kristan-Tollman & Gramann 1992	Metophiurida, Ophiacanthidae	Triassic, WA
?Sigsbeia sp.	Hall 1902; Spencer & Wright 1966	Metophiurida, Hemieuryalidae	Miocene-Pliocene, VIC
Amphiura felli	Skwarko 1963	Metophiurida, Amphiuridae	Upper Cretaceous, NT

The majority of Australian ophiuroid fossils have been found in Palaeozoic rocks, with only seven post-Palaeozoic species. Most of the Palaeozoic specimens were collected from Silurian or Early Devonian sandstone and mudstone of central Victoria.

The Australian fossils can be used to illustrate the evolution of modern ophiuroid characters. *Stuertzaster* is a Late Silurian genus of the oldest known ophiuroid family, the Pradesuridae. *Stuertzaster* species have short blunt arms, a large bulbous disc and the aboral disc surface covered by a sparse network of fine ossicles. These species show the primitive condition of alternating ambulacrals, with the base of each tube foot being shared over two adjacent ossicles. They are assumed to have been sessile forms, but not burrowers (Spencer & Wright 1966). *Stenaster obtusus*, an Early Silurian fossil from the United Kingdom, North America, Kazakhstan and Tasmania, also has short blunt arms, a swollen aboral disc surface and the base of each tube foot shared between two neighbouring ambulacrals. However it differs from *Stuertzaster* in having the ambulacral plates opposite. The lateral plates are very large and could be moved ventrally to close the ambulacral groove. It is asteroid-like, but this is likely to be a secondary adaptation to a

deposit-feeding mode of life similar to that of modern paxillosidan seastars (Dean 1999). This apparently widespread species is known from Ordovician rocks of North America, British Isles and Kazakhstan, as well as the Early Silurian of Tasmania (Jell & Baillie 1984).

Lapworthura miltoni has been recorded twice from Australia, however it is better known from Britain where it was found in Late Ordovician to Late Silurian rocks (Spencer 1925). It has long arms, a star-shaped disc, and the dorsal disc surface is covered by overlapping scales, although there are no radial shields. The paired ambulacral ossicles have some of the characteristics of modern ophiuroid vertebrae. They are opposite in position, articulate with dorsal and ventral ball and socket joints, and the basin of the tube foot is restricted to a single ossicle. However, they still differ from modern forms in not being fused into a single vertebra. The radial canal of the water vascular system is also completely enclosed in a channel between the ambulacral plates. There is no ventral arm plate and the dorsal arm surface is weakly calcified. The lateral arm plates are slender, but they can still be moved downwards to protect the ambulacral groove, which is further protected by groove spines. The oral plates are similar to those of modern ophiuroids, but the teeth are long and slender as in asteroids. The jaws could be opened widely and possibly functioned like a trap rather than a masticating structure. While there are no oral plates, the thick madreporite is oral in position.

More recent Palaeozoic to Tertiary fossil ophiuroids from Australia are inadequately known. The euryalid-like *Eospondylus tenuis*, from the extinct Furcasteridae, was described from one poorly preserved specimen. The specimens of *Aganaster gregarius* are poorly preserved juveniles, and their identity has been questioned (Clark 1946). The *Sigsbeia* record is based on one disarticulated vertebra, and the systematic positions of *Ophioglyphoida fosteri* and *Amphiura felli* are doubtful, given that important diagnostic features of their jaw and aboral disc surface are unknown. *Amphiura felli* is sometimes recorded as the earliest known amphiurid fossil (Simms *et al*. 1993). Four other ophiuroid species have been identified from fragments found in sediments dredged from the Exmouth Plateau off Western Australia (Kristan-Tollman & Gramann 1992). Three of these taxa had widespread Tethyan distributions during the Triassic.

EURYALIDA

The Euryalida includes the basket stars and the snake stars (**Figs 1.2A, 1.12A, 9.5–9.7**). The most obvious feature of basket stars is their complexly branching arms that can be held up to catch plankton. The snake stars are also filter feeders, holding several of their five arms out into the current, often in a sinusoidal pose. Most species live in deep water on the continental shelf and slope (McKnight 2000; Frensel *et al*. 2010). Little is known of their biology, although species that occur in shallow water are comparatively well studied (Hendler 1982a; Stewart & Mladenov 1995, 1997; Stewart 1998). Many Euryalida appear to live semi-permanently in a mutualistic relationship with black corals, sea whips or gorgonians, presumably improving their access to food (Hendler & Miller 1984b; Fujita 2001). Some individuals have been seen on the same perch for years (Stewart 1998).

Basket stars and snake stars are covered in a thick skin armed with calcareous tubercles; the tubercles of some species are so dense that they form a continuous coat over the animal and obscure the skin (Byrne 1994; McKnight 2000). The anatomy of the arms is different from that of regular brittle stars. The arm vertebrae articulate with each other by broad hourglass-shaped surfaces (streptospondylous articulation) (Martynov 2010a, 2010b) which permit the coiling of the arm in three dimensions. The dorsal arm plates are rudimentary or absent, the lateral arm plates and arm spines are subventral in position, and the ventral arm plates are also rudimentary (**Figs 1.6C, 3.6C**). The arm spines are often modified into hooklets, particularly at the tip of the arm (**Fig. 1.12B**). Tentacle scales are usually absent, but they may be replaced by a 'barrel' of calcareous plates that surround each tube foot. Large bursal or

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genital slits are usually present ventrally on each side of the arm. These slits open into bursal sacs that are used for respiration; in some species the bursae are fused into a single ring-like sac. Eggs and sperm are also shed into the surrounding water through the bursal slits.

Many species lack tentacle scales, arm plates and radial shields, and in branched specimens it is often very difficult to measure the arm length. Useful diagnostic characters include the armament of the disc and arm surface, the number and position of madreporites, the presence or absence of ventral arm plates, the number of arm segments before the first branch, and features of the arm spines and girdle hooks (Baker 1980).

The Euryalida comprises three families. The Euryalidae and Gorgonocephalidae have species with branched and unbranched arms. The Gorgonocephalidae is characterised by bands of girdle hooks on the dorsal arm surface. The Euryalidae is characterised by gonads that extend into the arms (**Fig. 3.6C**). The Asteronychidae have unbranched arms. The Asteroschematidae is sometimes accorded subfamily status (Okanishi *et al.* 2011a), sometimes family (Okanishi & Fujita 2013). An expanded Euryalidae, incorporating the Asteroschematinae, is accepted here as recent phylogenomic data indicates that it has a level of genetic diversity similar to other families such as the Gorgonocephalidae.

Family Euryalidae

Figure 9.5

This family comprises species with simple or branched arms that can be coiled dorso-ventrally. The teeth are large and stout, forming a single ventral row on the dental plate, the oral papillae are pavement-like and cover the side of the jaws, the basal portions of the arms are widened in mature specimens due to the extension of the gonads from the disc, and the first tentacle pore has two, rarely three arm spines (Okanishi *et al.* 2011a). The family was revised recently and is now considered to contain three subfamilies: Euryalinae, Astrocharinae and Asteroschematinae (Okanishi *et al.* 2011a). The Euryalinae differs from the other subfamilies in having lateral arm plates that are separated ventrally throughout the arm, either by ventral arm plates (*Astrobrachion*) or by a specialised 'bridge' on the arm vertebrae that spans the two ventrolateral spurs and encloses the radial canal and nerve (*Asteromorpha*, *Asterostegus*, *Astroceras*, *Euryale*, *Sthenocephalus* and *Trichaster*). The radial shields are made out of a single layer of calcite in the Astrocharinae (*Astrocharis* and *Squamophis*) and multiple overlapping layers of calcite in the Asteroschematinae (*Asteroschema* and *Ophiocreas*).

The family comprises 11 genera and 78 species that occur on the continental shelves and slopes of tropical and temperate regions. *Ophiocreas abyssicola*, recorded from the abyssal plain in the north-eastern Pacific Ocean, is now placed in the genus *Astrodia* in the Asteronychidae (Okanishi & Fujita 2014). The Euryalinae and Astrocharinae are restricted to the Indian and Pacific Oceans, whereas the Asteroschematinae also occur in the Atlantic Ocean. Ten euryaline, one astrocharine and seven astroschematine species occur in Australian waters (Rowe & Gates 1995; O'Hara 2012).

Three branched species are known from Australia (O'Hara 2012) *Euryale aspera* (**Fig. 9.5A**), originally described by Lamarck (1816a) from Indonesia, can attain a disc diameter of 50 mm, and the arms can branch up to 22 times. It has distinctive spines on the radial shields and dorsal surfaces of the arm joints. This species has now been found on reefs throughout the Indo-Pacific region, and in Australia from the south-west of the Great Australian Bight across northern Australia and south to New South Wales. *Trichaster elegans* occurs throughout the eastern Indo-west Pacific region and has recently been recorded from the Arafura Sea, off northern Australia (O'Hara 2012). *Sthenocephalus indicus* was discovered at 400 m off Barrow Island, north-western Australia (O'Hara 2012).

The Australian unbranched euryalins all live epizoically on gorgonians and other deepsea corals. *Astroceras* differs from *Asteromorpha* in having prominent tubercules along the dorsal surface of the arm (Baker 1980). *Astroceras elegans*, with five arms, ranges throughout the south-western Pacific Ocean and has been found off Norfolk Island. *Astroceras pergamena* and *A. compar* were found recently off north-western Australia (O'Hara 2012). The other three species are fissiparous, with up to seven arms; several arms are

considerably larger than the others. *Astroceras pleiades* is known from New South Wales to New Caledonia at depths of 100–500 m. *Asteromorpha tenax*, known from a few specimens collected off Moreton Bay, Queensland (Baker 1980) and the east coast of New Caledonia (Okanishi *et al*. 2013), has several large irregularly placed dome-like tubercles on the disc. *Asteromorpha koehleri* has been found off the south-west coast of Australia (Okanishi *et al*. 2013). It is likely that several other species currently known from Indonesia and New Caledonia (for example, *Astroceras mammosum* and *A. nodosum*) will also be found in Australian waters. *Squamophis albozosteres* is known only from its type locality off north-western Australia at a depth of 96 m (Okanishi *et al*. 2011b). It is the only Australian member of the Astrocharinae (Okanishi & Fujita 2013).

Astrobrachion is an Australasian genus with two species and is characterised by having a small ventral plate separating the lateral arm plates with a well-developed dermal tissue layer providing support (**Fig. 1.6C; Box 9.1**). The mainly tropical *A. adhaerens* ranges from Albany, Western Australia, around the northern Australian coast to New South Wales; it also occurs at Lord Howe Island and the Kermadec Islands. The temperate *A. constrictum* is found off south-eastern Australia and across the Tasman Sea to New Zealand. Populations of this species occur at SCUBA diving depths in New Zealand fiords, facilitating access for research. The ecology and reproduction of these populations has been investigated in several studies (Grange 1991; Stewart & Mladenov 1995, 1997; Stewart 1998). *Astrobrachion constrictum* uncurls its arms after sunset to start feeding. Some arms are held out into the water column for feeding while others brush along the branches of the host colony (Stewart 1998). The gut contents of *A. constrictum* included detrital material and mucus from the host (Stewart 1998). It is suggested they keep the host colony free from epizoic organisms (Stewart 1998). Tagging individual animals indicates that initial growth to 15 mm disc diameter occurs within 2.5 years and is then followed by slower growth to maximum size of 23 mm disc diameter by around eight years of age (Stewart & Mladenov 1997). *Astrobrachion constrictum* has a large egg and reproduction is continuous with peak maturity in April–June (Stewart & Mladenov 1995).

Astrobrachion constrictum and *A. adhaerens* are allopatric except at Lord Howe Island. They can be distinguished by colour pattern, size and features of the lateral arm plates (Baker 1980). The larger *A. constrictum* has transverse colour banding on the arms, while *A. adhaerens* has longitudinal stripes. The actual colour of both species can vary considerably, from red to yellowish-white (Baker 1980). Both species are found almost exclusively on black corals (Stewart & Mladenov 1997; McKnight 2000).

Ophiocreas sibogae, one of the better known euryalid species, is red and pink in colour with distinctive spoke-like radial shields on the disc (**Fig. 9.5B**). It can grow up to 28 mm in disc diameter, with arms to 640 mm long, and is usually found with its arms tightly coiled around the branchlets of gorgonians or antipatharians (Baker 1982a). *Ophiocreas sibogae* is distributed around southern Australia, New Zealand and Indonesia on the upper continental slope. *Ophiocreas oedipus*, from the Indo-Pacific region and the south Atlantic Ocean, differs in having swollen basal arm segments (Baker 1980). *Ophiocreas* species have a thick fleshy dermis that covers their reduced skeleton (Byrne 1994). Three western Pacific species of *Asteroschema*, *A. igloo*, *A. tubiferum* and *A. salix*, have been collected on continental slopes in the Tasman Sea. *Asteroschema* differs from *Ophiocreas* in having conspicuous granulation on the disc and arms.

The behaviour of the Caribbean species *Asteroschema tenue* was studied from a submersible (Emson & Woodley 1987). Found with its very long arms coiled around the stalk of a particular gorgonian, it appears to feed only at night, and unusually for a snake star, it is a microphagous suspension feeder. During feeding the arms are uncoiled slightly to expose the tube feet to the current. The arm spines are used for locomotion, not feeding. The eggs are large, which suggests abbreviated development. An earlier report (Warner 1982) of an asteroschematine moving its long arms sinuously through the water has been discounted (Emson & Woodley 1987). Kroh (2004) reported a fossil from the family Euryalidae from the middle Miocene of the central Mediterranean.

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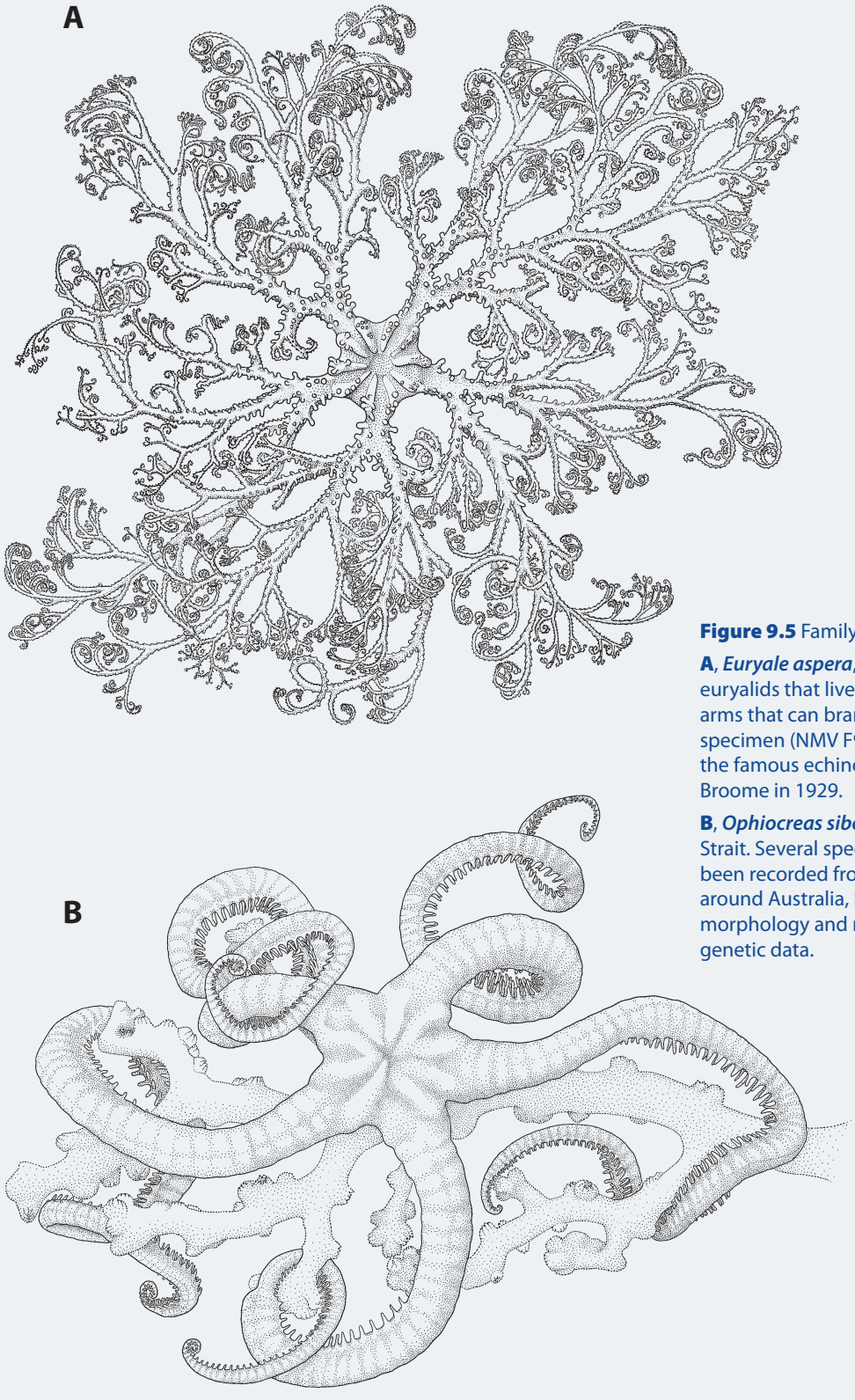


Figure 9.5 Family Euryalidae.

A, ***Euryale aspera***, one of the three branched euryalids that lives in Australian waters, has arms that can branch up to 22 times. This specimen (NMV F92149) was collected by the famous echinodermologist H.L.Clark off Broome in 1929.

B, ***Ophiocreas sibogae*** from eastern Bass Strait. Several species of ***Ophiocreas*** have been recorded from the continental slopes around Australia, but they all have a similar morphology and need to be reassessed with genetic data.

[K.Nolan]

Box 9.1 The grasping snake star, *Astrobrachion constrictum*

Features *Astrobrachion constrictum* has a round disc of up to 23 mm in diameter and very long arms that can have a span up to 20 times the diameter of the disc. The upper surfaces of the disc and arms are covered in a soft smooth skin. Two pairs of small spines are located on the ventral side of each arm segment. The sides of the jaws are smooth or bear a few low granules.

Males and females are outwardly similar. The gonads occur under the skin along the upper side of the arm and empty into a bursal sac that runs internally around the disc. The eggs or sperm are released from this sac via the conspicuous bursal slits that lie adjacent to the base of each arm.



The grasping snake star can be coloured yellow, red or have transverse banding on the arms, but is always found on black coral trees, which it uses as a perch to feed.

[K.Gowlett-Holmes]

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There are several colour varieties, including uniformly red or yellow, or variegated. Some individuals have transverse black stripes. However, this snake star never has longitudinal stripes along the arms.

Distribution *Astrobrachion constrictum* is found off the eastern and south-eastern coasts of Australia from Heron Island in Queensland to Maria Island in Tasmania. It also occurs at Lord Howe Island, off New Caledonia and all around New Zealand. It is well known to divers who have visited the fiords of southern New Zealand, where it is common on black coral trees in relatively shallow water (10–30 m). Elsewhere it is known from depths of 18–540 m.

Way of life The grasping snake star lives only on black coral trees. In the fiords of New Zealand, it appears to have a mutually beneficial relationship with its host black coral tree, *Antipathes fiordensis*. The snake star feeds on the mixture of mucus and food captured by the coral, without harming the coral polyps. The large branching coral trees are more efficient than the snake star at capturing plankton. In addition, *Astrobrachion* keeps the coral tree free of debris from landslides that are common in the fiords.

The snake star can also catch food directly from the plankton. It extends two or three arms into the current, catching microscopic prey with its tube feet and then impaling them on the hook-like arm spines. The food is then passed from one tube foot to another down to the mouth.

Grasping snake stars probably breed all year round with a peak spawning period in autumn (April to June). The eggs are relatively large and yolky, suggesting that the larvae probably do not stay in the water for very long before metamorphosing into juveniles. The absence of juveniles on coral trees suggests that the larvae settle onto rocks and hide in crevices for their first year before seeking a suitable coral tree. Initial growth is rapid, particularly in spring and summer. They reach a disc diameter of approximately 23 mm at eight years of age. They move to the ends of the coral branches as they age, presumably when their size makes them less vulnerable to being eaten by predators. Coral trees that are 2 m tall can support up to 80 snake stars.

Interaction with humans These snake stars are a favourite of scuba divers, some of whom have mistaken them for coils of insulated electric wire. The black coral trees on which they live are slow growing deep-water animals that are vulnerable to a number of human activities — observers on fishing boats regularly report broken corals being brought up by fishing trawlers in nets in the early days of a fishery. Divers also have been known to accidentally damage black coral trees that are living in relatively shallow water.

Similar species A second species of *Astrobrachion*, *A. adhaerens*, the clinging snake star, lives across tropical Australia from south-western Australia to New South Wales and the northern Tasman Sea. It can be distinguished from *A. constrictum* by the longitudinal markings on the arms.

Family Euryalidae
Species *Astrobrachion constrictum* (Farquhar, 1900)

Further reading Stewart & Mladenov 1995, 1997; Stewart 1996, 1998

Family Gorgonocephalidae

Figures 9.1 & 9.6

The arms of gorgonocephalids are simple or branched and, like other basket stars and snake stars, they can be coiled in the vertical plane. However, unlike Euryalidae which also have branched arms, the radial canal and nerve lie in an open ventral depression of the vertebrae throughout the arm, and there are rows of girdle hooks across the dorsal arm surface (**Fig. 9.6C**). There can be one to five madreporites (Fell 1982; Rowe & Gates 1995). Gorgonocephalidae are the most diverse and best known of all Euryalida with 35 genera and 99 species (Stöhr *et al*. 2014). They range from tropical to polar regions at all depths (Fell 1982). Eleven genera are represented in Australia, with 26 species (O'Hara 2012). Three additional species from two genera are known from eastern Antarctica and one from the subantarctic, including near Australia's Heard Island (T.D.O'Hara, unpublished data).

The characteristic southern Australian species is *Conocladus australis* (**Fig. 9.1**). This basket star can grow up to 55 mm in disc diameter, and is common in subtidal waters from south-west of Western Australia to southern Queensland. It is usually found on sponges and gorgonians, and feeds actively at night by spreading its branched arms into the current (O'Toole & Turner 1990). This species is variably coloured from pale grey to dark brown, and the arms are sometimes distinctly banded (Baker 1982a). *Conocladus* is a monotypic genus, but east-west clinal variation in the development of tubercles on the arms and disc has been interpreted as incipient speciation (Baker 1980), although this requires confirmation from molecular studies. *Astrosierra* includes three distinct species: *A. densus* occurs from southern Queensland to the central coast of New South Wales, *A. amblyconus* from northern New South Wales to northern Tasmania, and *A. microconus* from Geraldton, Western Australia, south to the Great Australian Bight (Rowe & Gates 1995).

Several other species also occur in deep water off the New South Wales coast, occasionally extending into Bass Strait and Tasmania. These include the branched species *Gorgonocephalus pustulatum* and *G. dolichodactylus*, and the unbranched species *Asteroporpa australiensis* (**Fig. 9.6A**), *Astrothrombus rugosus* and *Astrothorax waitei* (**Fig. 1.25**). All five species are also known from New Zealand (McKnight 2000). *Gorgonocephalus pustulatum* and *A. waitei* have also been recorded from South Africa, and both *Gorgonocephalus* species occur in south-east Asia. *Astrothorax waitei* is hermaphroditic and a brooder. One to three small juveniles may be present in the bursae, and larger juveniles cling to the



Figure 9.6 Family Gorgonocephalidae.

A, several unbranched ***Asteroporpa australiensis*** on a primoid coral, from 250 m water depth on the Wanganella Bank, north-east of New Zealand. This species is not host-specific and lives on a variety of deepsea gorgonians.

B, this densely-branched ***Astroboa ernae*** was collected in Backstairs Passage, South Australia, by the pioneering marine consultant Jan Watson in 1974.

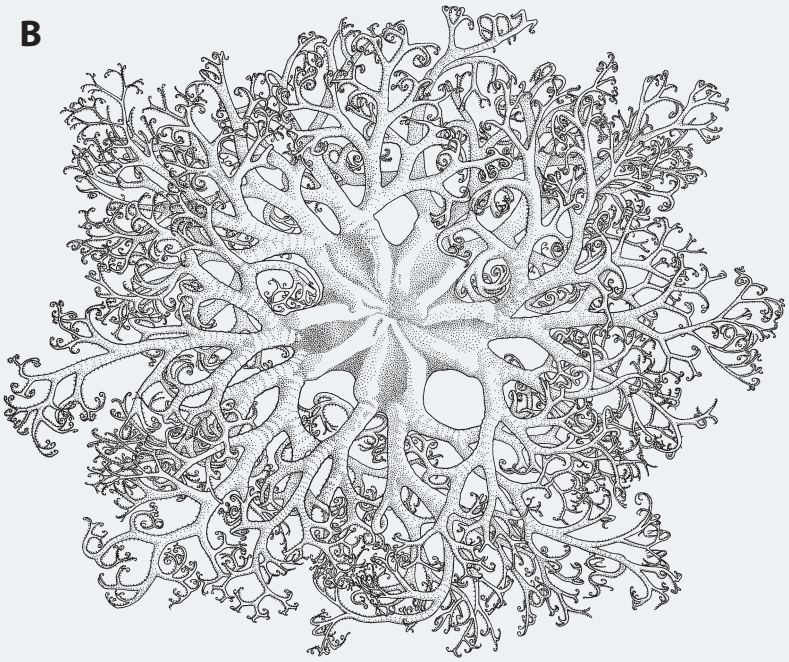
C, the arms of ***Gorgonocephalus chilensis***, from off Heard Island, showing the girdles of hooklets (arrows) on the upper side of the arms.

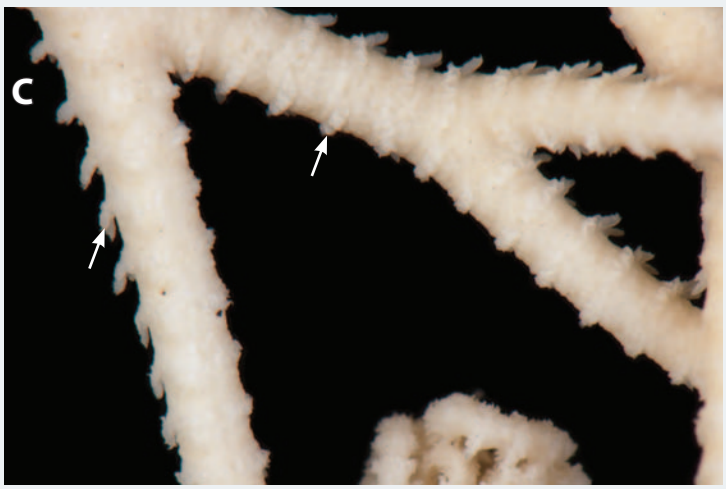
[A, K.Gowlett-Holmes; B, K.Nolan; C, B.Patullo]

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external ventral and dorsal disc surfaces (Baker 1980). *Gorgonocephalus* is common on muddy or sandy seabeds (McKnight 2000).

At least 14 gorgonocephalid species are known from tropical Australian waters and most of these are widespread on continental shelves throughout the Indo-Pacific (Rowe & Gates 1995; O'Hara 2012). Interestingly, in Australia most of the branched species have been observed only on the north-western and/or the northern coasts. They include *Astroboa clavata*, *A. nigrofurcata*, *A. tuberculosa*, *Astrochalcis tuberculosus*, *Astrocladus exiguus*, *A. ludwigi*, *Astroclon suensoni* and *Astroglymma sculptum*. Only two branched species are known from the Great Barrier Reef: *Astroboa granulatus* and *A. nuda*. The orange-red or pink coloured *Astroboa ernae* (**Fig. 9.6B**) ranges widely along the Australian coast from the Gulf of Carpentaria, around Western Australian and southern waters, where it lives on rocks and sponges in shallow water to a depth of 50 m (Baker 1980). Of the unbranched tropical species, *Asteroporpa indicus*, originally described from north-west coast between Point Cloates and Port Hedland, has since been collected from the Arafura Sea and northern Tasman Sea. Two other unbranched species, *Asteroporpa reticulata* and *Astrothrombus vecors*, occur on seamounts on the Norfolk Ridge; the latter is also known from Malaysian waters. A large species, *Astrotoma manilense*, has been recorded from the continental slope of the Great Australian Bight and off New South Wales (O'Hara & Harding 2014). Unbranched species are often found clinging to deep-water corals or other sessile invertebrates.





Gorgonocephalids are the only Euryalida to occur in the Southern Ocean. Three unbranched species have been recorded from the Australian Antarctic Territory: *Astrotoma agassizii*, *Astrochlamys bruneus* and *A. sol*; all brood their young. *Astrotoma agassizii* is common throughout the Antarctic in depths of 75–1,000 m, but is probably a species complex with different reproduction strategies (Hunter & Halanych 2008; Heimeier *et al*. 2010). *Astrochlamys bruneus* is sexually dimorphic, with one or two small males generally found clinging

to the dorsal disc surface of the female. It is a bursal brooder and can have up to 200 embryos in the bursae (Mortensen 1936). *Astrochlamys sol* differs from the five-armed *A. bruneus* by having nine or ten arms. It is associated with coral-like bryozoans, and is an intra-ovarian brooder (Madsen 1967).

Only one branched species, *Gorgonocephalus chilensis* (**Figs 1.2A, 9.6C**), occurs in the Southern Ocean and is known from the Antarctic Peninsula near South America, as well as various subantarctic islands and New Zealand (McKnight 2000). It has been collected near Heard Island, but not from Macquarie Island or the Australian Antarctic Territory (T.D.O'Hara, unpublished observations). This species does not brood young in the bursae, but juveniles are often found clinging to the external body surface of adults.

The feeding biology of these animals has been studied in detail through use of observations on SCUBA and in submersibles (Fell 1961; Davis 1966; Patent 1970; Dearborn 1977; Hendler 1982a; Hendler & Miller 1984b; Emson *et al*. 1991). The unbranched *Astrotoma agassizii* and *Asteroporpa annulata*, from the Antarctic and Carribean respectively, adopt various feeding postures. Some species are epizoic on colonial cnidarians and sponges (Dearborn 1977; Hendler & Miller 1984b). *Asteroporpa annulata* uncurls its arms at dusk and is a nocturnal feeder (Hendler & Miller 1984b). These species extend three to four of their very long and flexible arms into the water currents to feed while the other arms maintain their grasp on the substrate. The arm tips coil around captured prey and the disc can be twisted so that the mouth is turned towards the feeding arms. Batteries of moveable hooks on the arms are used to ensnare prey (Hendler & Miller 1984b). Food, mainly copepods, other crustaceans, mollusc veliger larvae and larval fishes, is placed in the mouth by drawing the arms across the jaws. *Asteroporpa annulata* are host to siphonostome copepods that attach to the stomach wall (Hendler & Miller 1984b).

Branched species typically use their arms to form a parabolic fan that can filter large amounts of water (Hendler 1982a). *Astroboa nuda* (**Fig. 1.12A**), with an arm fan area of 0.75 square metres, can filter 86 cubic metres of seawater over eight hours in a 40 mm/s current (Fricke 1966). *Astrophyton muricatum* is the most common gorgonocephalid in the Caribbean and its feeding behaviour is well documented (Hendler 1982a; Wolfe 1982). During the day it hides among coral, sponges or gorgonians, but at night it climbs to a prominent point in the water current and spreads its arms to feed. The arms tips wave from side to side, increasing the efficiency of the otherwise wide-meshed filtration posture (Hendler 1982a; Wolfe 1982). The tips of the arm branches bear rows of tube feet and girdle hooklets. Prey, mostly crustacean larvae 1–50 mm long, are captured in an arm loop and impaled on the hooks (Davis 1966). The tube feet probably play a sensory role only (Wolfe 1982). When sufficient food has been captured, the arm is coiled towards the mouth (Wolfe 1982). Juveniles with as few as three branchlets also feed in this manner (Davis 1966). The branchlets near the mouth are not modified for feeding and either grasp the substratum or cover the disc (Davis 1966). Some species have shorter arms with limited branching, and these appear to be specialised for capturing larger prey (Emson *et al*. 1991). Some euryaline species also use mucus to aid capture of prey (Patent 1970). Overall reproduction in gorgonocephalids involves production of large eggs, and many species are brooders (Hendler 1991).

A single species of commensal marine shrimp, *Lipkemenes lanipes* (**Fig. 2.29A**), is associated with basket stars including *Astroboa nuda* and *Astroglymma sculptum*. In one case up to 56 specimens of *L. lanipes* were found on a single *Astroboa nuda*, taking advantage of the relatively large size of the basket star. Several copepods are also associated with *A. nuda*, often in the stomach (Humes 1986).

Family Asteronychidae

Figure 9.7

Asteronychidae are characterised by the unbranched slender arms that are distinctly offset from the disc. Thick naked skin covers the disc and arms (Byrne 1994), and the vertebrae have a ventral depression. There are at least three arm spines, and distal spines are sometimes modified into hooklets. The gonads are restricted to the disc, and the genital slits are small. A single madreporite is present (Fell 1982).

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The family includes three genera and nine species (Stöhr *et al*. 2014) and these are distributed on continental slopes from tropical to boreal regions (Fell 1982). One *Astrodia* and one *Asteronyx* species occur in Australian waters and both have broad geographical and bathymetric distributions (Rowe & Gates 1995; O'Hara 2012).

Asteronyx loveni has been found throughout the Atlantic Ocean, northern and south-western Pacific Ocean, eastern Indian Ocean and the Southern Ocean, at depths of 100–4,721 m (Baker 1980; Smirnov 1994; McKnight 2000; **Fig. 9.7A**). In Australian waters, it has been collected along the southern coast (O'Hara 2012). This species has a soft disc (to 33 mm in diameter) with obvious radial shields near the base of each arm. The arms are long (to 10 times the disc diameter) and they bear up to nine hook-shaped arm spines on the large subventral lateral plates (Baker 1980).

The ecology of Japanese and Indonesian populations of *Asteronyx loveni* has been described from deep-sea photographs and observation from submersibles (Fujita & Ohta 1988; Fujita 2001). In those populations *A. loveni* lives epizoically on whip-like gorgonians and pennatulids and is a suspension feeder. Two (rarely three) of the arms, on opposite sides of the disc, are thickened in adult animals and appear to be adapted for attachment. The other arms and the distal portion of the thickened arms are stretched out into the current, sometimes in a sinusoidal posture, presumably increasing feeding efficiency. The diet of Japanese specimens consists of resuspended detrital material. These animals are usually found between 200 and 350 mm above the seafloor, the optimal height for collecting resuspended detritus. In contrast, the juveniles appear to feed directly on detritus on the seafloor and do not develop the specialised arms until after they move up onto their host. In the Atlantic Ocean this species has been reported to feed on zooplankton, mainly copepods, which it catches with an arm loop (Warner 1982). Reports of them grazing on pennatulids and gorgonians have been dismissed as a research artefact (Warner 1982). Off southern Australia, *A. loveni* is often found on the alcyonacean *Anthomastus* (T.D.O'Hara, personal observation).

Astrodia tenuispina (**Fig. 9.7B**) is widespread along the lower continental slopes (510–3,720 m) of the Pacific, Atlantic and Indian oceans. In Australia, it has been recorded from off Kangaroo Island, South Australia, to Sydney, New South Wales, at 1,000–3,240 m (Baker 1980; O'Hara 2012). *Astrodia tenuispina* can be distinguished from *A. loveni* by the smaller number of arm spines (two to four) that are not modified into hooks.

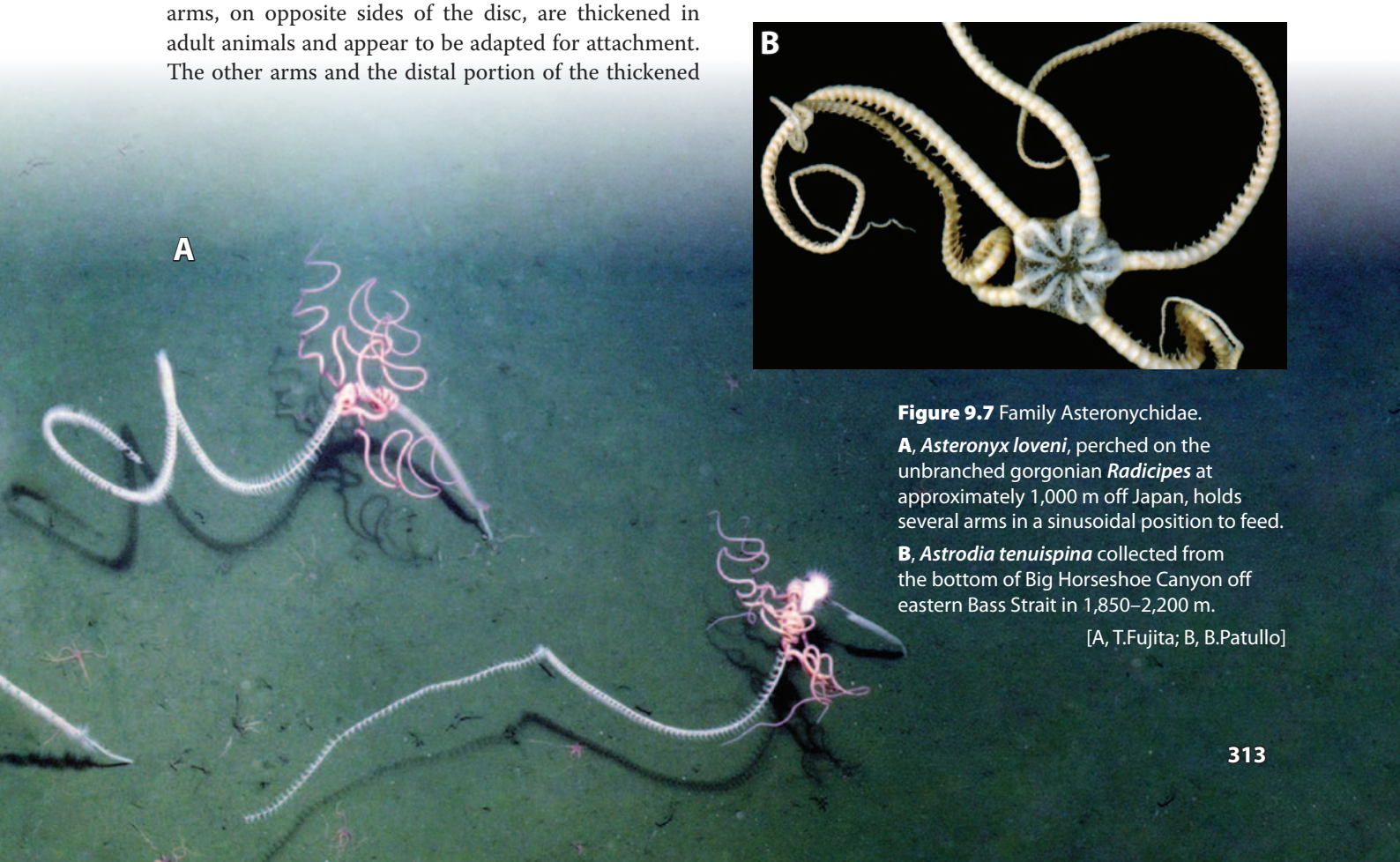


Figure 9.7 Family Asteronychidae.

A, ***Asteronyx loveni***, perched on the unbranched gorgonian ***Radicipes*** at approximately 1,000 m off Japan, holds several arms in a sinusoidal position to feed.

B, ***Astrodia tenuispina*** collected from the bottom of Big Horseshoe Canyon off eastern Bass Strait in 1,850–2,200 m.

[A, T.Fujita; B, B.Patullo]

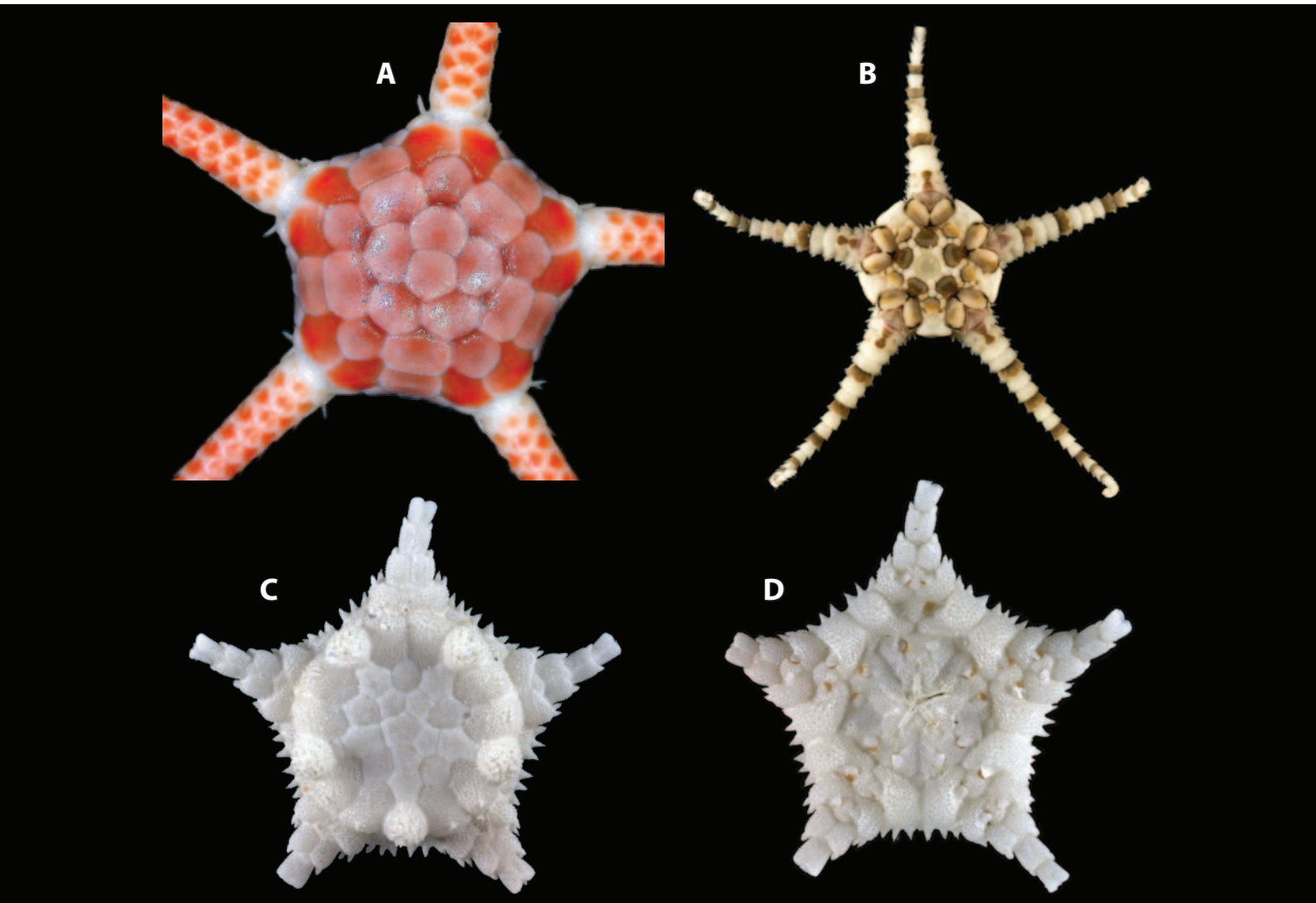
Other families

Families Ophiuridae and Astrophiuridae

Figure 9.8

The arms are fused laterally with the disc, and the disc is usually covered in thick plates, only very rarely bearing granules or spines. There is an unpaired infradental papilla at the end of each jaw, and a series of oral papillae along the side of the jaw (**Fig. 9.3B**), although occasionally these are fused together. The arms are usually long and stout, have well-developed arm plates, and bear short adpressed arm spines (Fell 1982). The tentacle pores are often largest near the disc, and sometimes surrounded by numerous small tentacle scales. The pores are often reduced in size on the distal section of the arm. Many species have an 'arm comb', a distinctive series of spines or papillae on the genital plate at the dorsolateral base of the arm, adjacent to the radial shields (Stöhr 2011). In many species these merge ventrally into a series of papillae along the bursal slit. Sometimes there is an opposing row of spines on the dorsal arm plates (for example in *Dictenophiura*).

Recent genetic data (O'Hara *et al.* 2014b; Hugall *et al.* 2015) suggest that small species with widened



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basal lateral arm plates are best placed in a separate family, the Astrophiuridae. Australian species include *Astrophiura permira*, reported from off the Northern Territory (Rowe & Gates 1995), which has a large thin pentagonal disc that includes most of the arms. The short and slender free portion of the arm has no ventral or dorsal arm plates, or tentacle pores. The animal was once believed to be an intermediate between ophiuroids and asteroids (Hyman 1955). *Ophiomisidium flabellum* from Bass Strait is star-shaped, the arms are widened distally, and the marginal interradial disc plate is produced into a tubercle (**Fig. 9.8C,D**).

The Ophiuridae comprises 35 genera and approximately 320 named species, distributed worldwide from the intertidal to hadal depths (Stöhr *et al.* 2014). Genetic data (Hugall *et al.* 2015) indicates that several of the large genera (for example, *Ophiura*, *Amphiophiura* (**Fig. 9.8A**), and *Ophiocten*) each comprises several unrelated lineages. However, pending a formal reclassification of these taxa, the existing names are used here.

The family is particularly characteristic of the deep sea and polar regions. *Perlophiura profundissima* from the Bougainville Trench at 8,135 m is the deepest known ophiuroid (Belyaev & Litvinova 1972).

Most Ophiuridae are active carnivores, scavengers or deposit feeders, and due to their abundance are ecologically important (Warner 1982; Stancyk *et al.* 1998; Kogure 2010). A deepsea species from the north Pacific, *Ophiura sarsii*, has been observed capturing live fish, squid and krill, either by trapping them in an arm loop or by several individual ophiuroids jumping together onto larger prey animals (Stancyk *et al.* 1998). The robust arms of ophiurids, which can coil only in the horizontal plane, and the short adpressed arm spines, are adaptations to these methods of feeding. *Ophioplinthus gelida* is an epifaunal detritus feeder, living on soft substrates. It has been photographed moving surface sediments into small mounds that it then eats (Dearborn 1977). Bands on the arm skeleton have been used to age deepsea populations (Gage 1990). Ophiuridae have a range of reproductive strategies, from the production of large numbers of planktotrophic larvae to intra-ovarian viviparity (Mortensen 1936; Hendler 1975; Tyler & Gage 1980; Strathmann 1987; Tyler & Fenaux 1994).

Twelve genera and 65 species have been reported from Australia (O'Hara 2012); most are found on the continental slope. A few species venture into shallow waters (<20 m, for example, *Ophiura kinbergi*, *Dictenophiura ctenophora* and *Ophiocrossota multispina*). The discovery of additional species

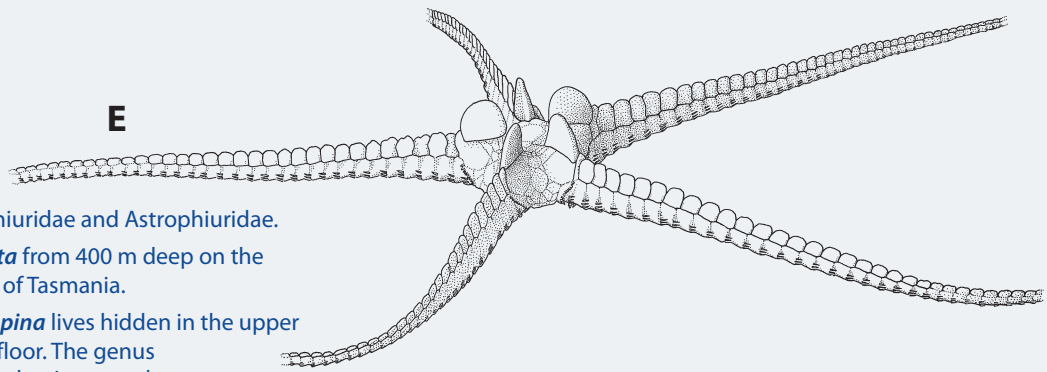


Figure 9.8 Families Ophiuridae and Astrophiuridae.

A, ***Amphiophiura laudata*** from 400 m deep on the continental slope south of Tasmania.

B, ***Ophiocrossota multispina*** lives hidden in the upper layer of sand on the seafloor. The genus ***Ophiocrossota*** is now endemic to southern Australia but fossils are known from the Americas.

C, D, ***Ophiomisidium flabellum*** is a small species that lives on soft sediments on the outer continental shelf of south-east Australia. It belongs to a group of genera where the enlarged first lateral arm plates form the margin of the disc on the ventral surface. Unfortunately most museum specimens, including the one photographed, have lost the slender tips of the arms.
C, dorsal surface.
D, ventral surface.

E, the Antarctic ***Ophiosteira debitor*** with a large keel-like process between the radial shields. Their function is uncertain but may help in controlling the flow of water across the animal.

[A, CSIRO; B, L.Altoff; C,D, C.Harding; E, K.Nolan]

is expected to result from further sampling of the continental slope around Australia.

The tropical ophiurid fauna of Australia is imperfectly known. Widespread continental shelf and upper slope species found off northern Australia or in the Tasman Sea include *Amphiophiura insolita* and *Ophiura micracantha*. *Ophiura kinbergi* (**Fig. 9.3B**) is very common on coarse sediments throughout the Indo-Pacific, including all coasts of Australia from 1 to 500 m. It is one of the most common of the Bass Strait ophiuroids.

A number of endemic species occur in the Tasman and Coral seas, including *Dictenophiura ctenophora*, *D. squamosa* and *D. platyacantha*. The small species *Haplophiura gymnopora* (<5 mm disc diameter) from the south-eastern coast is unusual within the Ophiurinae for having low granules on the ventral and lateral surfaces of the disc. This species is common in fine sands or mud. *Ophiocrossota multispina* lives on coarse sediments from the Houtman Abrolhos in Western Australia to New South Wales, but not in Tasmania. It has a distinctive triangular plate with a papillate margin at the distal edge of the radial shields (**Fig. 9.8B**). This plate can be seen in a series of fossils from North and South America, among which several species are now recognised from the Eocene to Miocene (Blake & Allison 1970; Blake 1975; Caviglia *et al*. 2007).

Many ophiurids occur on the continental slope of south-eastern Australia and most of these are widespread in the Indo-west Pacific region, including *Ophiura ooplax*, *Amphiophiura urbana* and *Ophiomastus tugulitius* (Baker 1979; O'Hara 1990). *Ophiura flagellata* occurs throughout most of the Indian and Pacific oceans, and Japanese animals have been photographed swimming (Ohta 1983). *Ophiura* (*Ophiuroglypha*) *jejuna* is also known from the South Atlantic Ocean, and *Ophiocten hastatum* is probably cosmopolitan in the deep sea. *Ophiura jejuna* and other members of *Ophiura* subgenus *Ophiuroglypha* have modified hook-like distal arm spines. Their function has never been demonstrated, but presumably they are used to grip objects (Fell 1961), at least in the juvenile stage.

More than half the ophiuroid species known from the Australian Antarctic Territory belong to the Ophiuridae (44 species). Characteristic genera include *Ophioplinthus* (with synonyms *Ophiurolepis* and *Theodoria*, 10 species) and *Ophiosteira* (4), but the widespread genera *Ophiura* (7) and *Ophiocten* (11) are also diverse in the region. *Ophioplinthus gelida* is often easily recognised by the dense covering of an epizoic sponge, *Iophon radiatum* (Fell 1961; Dearborn 1977), particularly those living on bryozoan-sponge mats (Dearborn *et al*. 1973). The more solid skeleton of other species, such as *Ophioplinthus brevirima* and *O. mordax*, appears to be able to resist most infestations (Fell 1961; Dearborn 1977). Local increases in *Ophiocten hastatum* are suggested to be associated with fallout of phytodetritus on which it feeds (Iken *et al*. 2001; Gage *et al*. 2004). North Atlantic populations of *Ophiocten hastatum* and *O. gracilis*, cosmopolitan abyssal and bathyal species, have an annual reproduction, spawning small eggs and developing through planktotrophic ophiopluteus larvae (Sumida *et al*. 2000; Gage *et al*. 2004). Postlarval development of the skeleton of *Ophiocten* and *Ophiura* is described in Sumida *et al*. (1998).

Ophiosteira species, in particular *O. debitor* (**Fig. 9.8E**), have the disc and arms ornamented strikingly. Large radial plates, separating each pair of radial shields, have a keel-like crest with a spongy open texture (Fell 1961). The arms are laterally compressed and have keel-like dorsal extensions. This ornamentation is coloured white, in sharp contrast to the deep purplish brown of the rest of the living animal. The genus is restricted to Antarctic waters (Fell 1961).

Several other genera are found only in the Southern Ocean, including *Ophioperla*, *Ophiogona* and *Ophionotus* (Fell 1961; Madsen 1967). The circumpolar *Ophioperla koehleri* is bright red or reddish-orange in colour and has distinctive long blunt arm comb papillae. It apparently feeds on euphausiid shrimps that can be much longer than the ophiuroid's disc diameter (Dearborn 1977). Whether *Ophioperla koehleri* can capture live shrimps, or whether it feeds on carrion that has fallen from the surface, has yet to be determined (Dearborn 1977). *Ophiogona doederleini* has a granulated disc surface and lacks an arm comb.

Ophionotus species have fragmented dorsal arm plates, with a large central plate and a mosaic of platelets on

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either side. *Ophionotus victoriae* inhabits circumpolar Antarctic waters and is a large five-armed species with a disc diameter up to 40 mm (Fell 1961, Dearborn 1977). This species often occurs in high densities and its ecology and reproduction are well studied (Dearborn 1977; Fratt & Dearborn 1984; Manjón-Cabeza & Ramos 2003; Grange *et al*. 2004). *Ophionotus victoriae* is an active carnivore feeding on a variety of foods, including euphausiid shrimps, copepods, sponges and polychaetes, and is even cannibalistic on juveniles of its own species (Dearborn 1977; Fratt & Dearborn 1984). It is dioecious releasing small eggs in summer, although the timing varies, and is likely to have an ophiopluteus larva (Grange *et al*. 2004). Growth rings on the vertebral ossicles of *O. victoriae* indicate asymptotic growth after 20 years (Dahm & Brey 1998). The congener *O. hexactis* has six arms and occurs in subantarctic localities, including waters around Heard Island. It is a hermaphrodite that broods its young in the ovaries. There is an average of 25 young per animal, occupying most of the disc cavity (Turner & Dearborn 1979). The two *Ophionotus* species only occur together at South Georgia in the South Atlantic Ocean (Mortensen 1936).

The Antarctic species *Ophiosparte gigas*, formerly considered to be an ophiacanthid (Koehler 1922) or ophiomyxid (Dearborn *et al.* 1996) has recently been reassigned to the Ophiuridae (Martynov 2010b). It is one of the largest ophiuroids, with a disc that can reach 50 mm in diameter (Fell 1961). It occurs in muddy sediments, where it actively hunts sponges, ophiuroids, bivalves, polychaetes and crustaceans, which it often consumes whole. The large conical tube feet and spatulate arm spines could be used as 'paddles' when the animal is moving through the soft substratum (Fell 1961), although it is also likely that they play a chemosensory role in capturing prey (Warner 1982).

Fossil *Ophiura* specimens have been found at various localities outside Australia. The extant Japanese species *Ophiura sarsii* has been recorded from middle Miocene strata (Ishida & Fujita 1999). *Ophiura paragraysonensis* is known from the early Cretaceous of Alexander Island and *O. hendleri* from the Eocene of Seymour Island, both off the Antarctic Peninsula (Taylor 1966; Blake & Aronson 1998).

Ophiomusium and relatives

Figure 9.9

Traditionally *Ophiomusium* has been placed in the Ophiolepidinae (Matsumoto 1915), a subfamily of the Ophiuridae (Spencer & Wright 1966). Genetic evidence, however, indicates that *Ophiolepis*, and the related genera *Ophioplocus* and *Ophiozonella*, are not closely related to Ophiuridae but rather to Ophionereididae (O'Hara *et al*. 2014b). This leaves *Ophiomusium* and related genera *Ophiosphalma* and *Ophiolipus* in an unnamed clade that is sister to the Ophiuridae.

These genera are characterised by the reduction of visible tentacle pores to a few basal segments. They generally have long heavily calcified arms fused laterally into the disc, and bearing short adpressed arm spines. The middle arm spine is often hook-shaped, especially near the arm tip. The dorsal and, particularly, the ventral arm plates are reduced in size and often absent after the first few. The disc is covered with thick plates or occasionally skin or spinules. There is an unpaired, infradental papilla at the end of each jaw, and a series of oral papillae along the side of the jaw, although these can be fused. The second oral tentacle pore opens on the sides of the jaw inside the oral slit and is often not visible from the ventral side.

Ophiomusium generally has zero to two pairs of visible tentacle pores (**Fig. 9.9A**), whereas *Ophiosphalma* has three to four (**Fig. 9.9C**). *Ophiolipus* is similar to *Ophiosphalma* except that it has thick skin covering the disc. *Ophiosphalma* also has small ventral arm plates that continue down the arm and often has spinules on the disc near the base of the arms. Electron microscopy indicates that tiny tube feet are present on distal segments of both *Ophiomusium lymani* and *Ophiosphalma jolliense*, but they emerge from a microscopic pore at the edge of the lateral arm plate (Hendler 1988). Several *Ophiomusium* species are reported to lack tentacle pores (Baker 1979). However, pores can be seen on juvenile specimens of one of these — *O. incertum* (O'Hara 1990). *Ophiomusium*, the largest genus, has almost 60 species (Fell 1982) while *Ophiosphalma* includes 28 species and *Ophiolipus* three.

The cosmopolitan deepsea species *Ophiomusium lymani* (**Fig. 9.9D–F**) has been reported off southern Australia and in the Tasman Sea (O'Hara 2012), although evidence from mitochondrial DNA suggests that it could be a complex of species (T.D.O'Hara, personal observation). This species can dominate megafaunal seafloor assemblages between 1,000 and 3,000 m, where it holds up its arm tips and filter feeds from the water column (Tyler 1980). The age structure of populations of these species is examined in several detailed studies using growth bands on the vertebral ossicles (Gage 1982, 1990). *Ophiomusium lymani* has a large egg (420 µm diameter), and is likely to have a yolky (non-feeding) pelagic larva (Gage & Tyler 1982). Although it has advanced eggs throughout the year, it appears that spawning, larval development and settlement may be synchronous and that the cycle is entrained by seasonal pulses of sinking organic matter from the surface. Juveniles grow to 12 mm disc diameter in the first year and another 13 mm over the next two years until they reach sexual maturity.

Another widespread species, *Ophiosphalma armigerum* (**Fig. 9.9C**), was first collected from Australian waters (as *Ophiomusium planum*) by the Australian Antarctic Expedition in 1914 off Kangaroo Island in depths of 3,400 m (Koehler 1922). Tropical Indo-Pacific species such as *Ophiomusium scalare*, *O. simplex*, *O. facundum* and *Ophiosphalma properum* and *O. elegans* occur on the continental slopes around the north of Australia and across the Coral Sea. *Ophiomusium scalare* (**Fig. 9.9A,B**) extends around south-western Australia to the Great Australian Bight, where it was previously named *O. aporum* (O'Hara & Harding 2014); *O. anisacanthum* and *O. australe* are endemic to southern Australia up to the western side of Bass Strait. *Ophiomusium incertum* appears to be endemic to Tasmania and southern New South Wales.

Several fossil species show similarities with *Ophiomusium* in the abrupt cessation of ventral arm plates and visible tentacle pores, including the Late Devonian *Stephanoura belgica* and Early Carboniferous *Aganaster gregarius* (Hotchkiss & Haude 2004). This suggests that the most recent common ancestor of all living ophiuroids was *Ophiomusium*-like in appearance. The type species of *Aganaster*, *A. gregarius*, is dubiously recorded from Carboniferous rock in Queensland (Withers & Keble 1934b). These genera are generally placed in a separate family, the Aganasteridae.

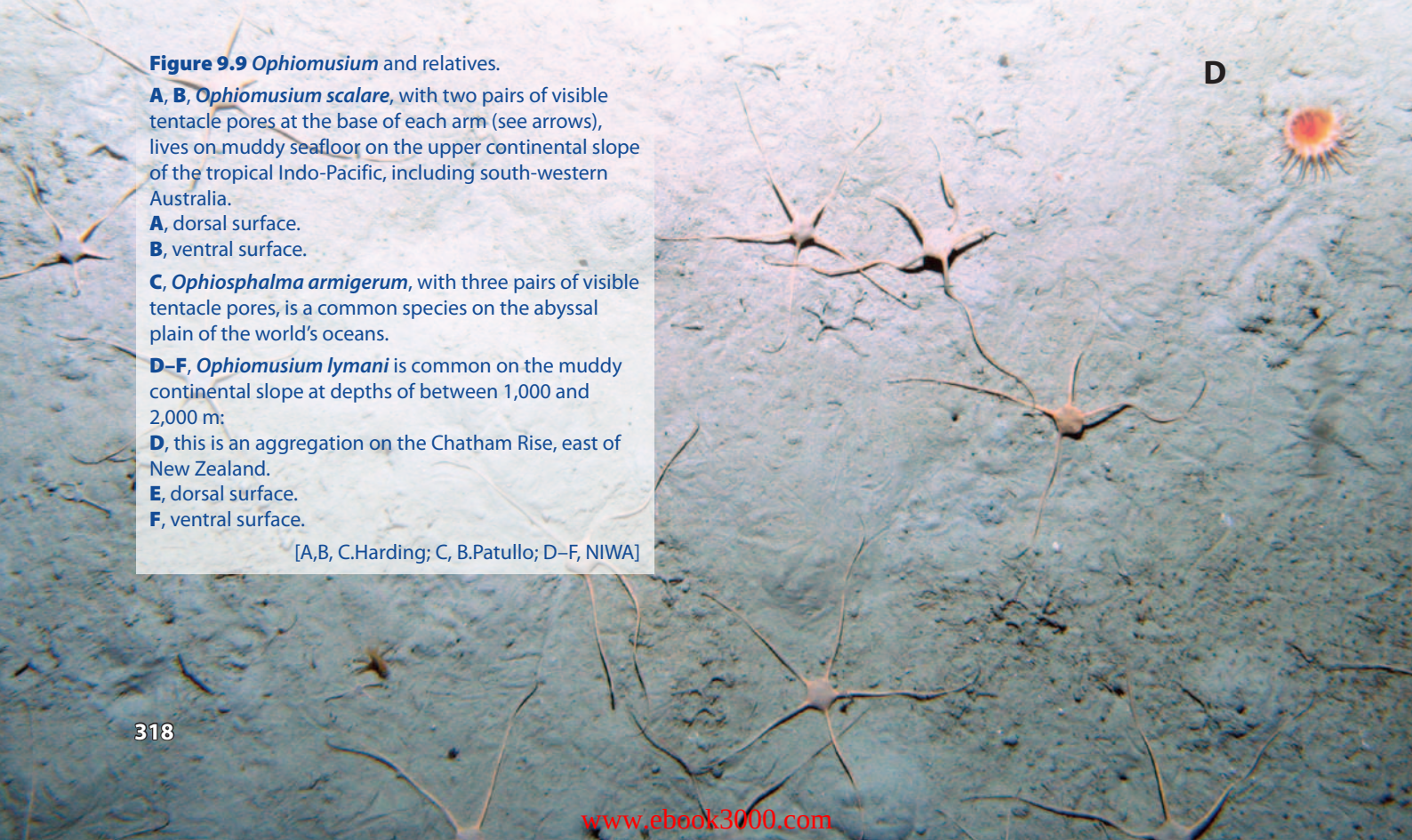


Figure 9.9 ***Ophiomusium*** and relatives.

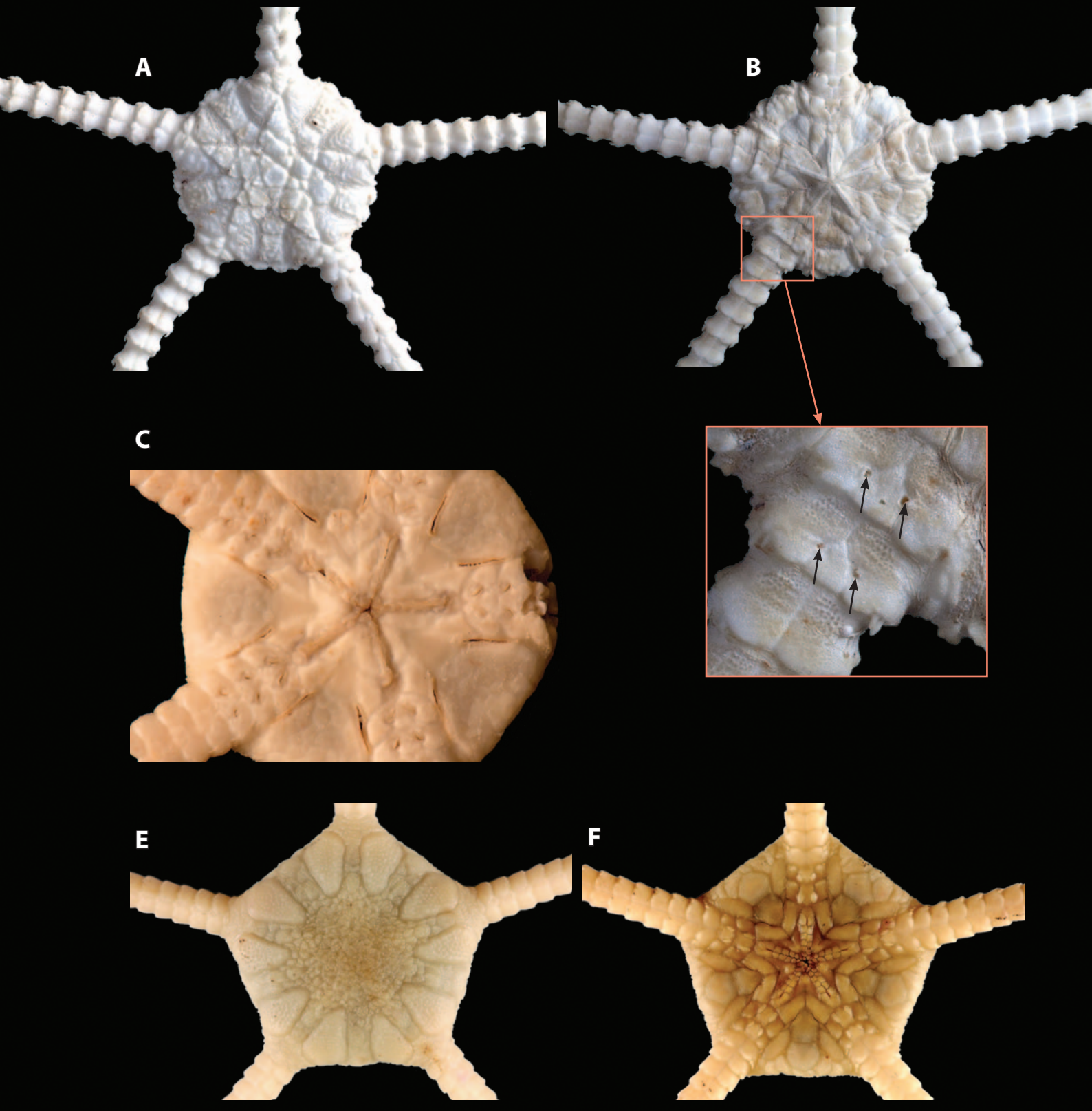
A, **B**, ***Ophiomusium scalare***, with two pairs of visible tentacle pores at the base of each arm (see arrows), lives on muddy seafloor on the upper continental slope of the tropical Indo-Pacific, including south-western Australia.
A, dorsal surface.
B, ventral surface.

C, ***Ophiosphalma armigerum***, with three pairs of visible tentacle pores, is a common species on the abyssal plain of the world's oceans.

D–F, ***Ophiomusium lymani*** is common on the muddy continental slope at depths of between 1,000 and 2,000 m:
D, this is an aggregation on the Chatham Rise, east of New Zealand.
E, dorsal surface.
F, ventral surface.

[A,B, C.Harding; C, B.Patullo; D–F, NIWA]

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A
B
C
E
F

Ophioscolex, Ophiomyces and relatives

Figure 9.10

Molecular phylogenetic analyses by Hugall *et al.* (2015) show that there is a clade that is sister to the ophiacanthids, ophiocomids and ophiodermatids, that includes genera that were formerly considered 'primitive' ophiomyxids (Martynov 2010b) plus others from the ophiacanthid subfamily Ophiohelinae. This ancient group is probably deserving of an order-level taxonomic rank; it comprises four subgroups that could be regarded as separate families, one of which would be the Ophiohelidae. Because of the uncertain nature of the classification, they are grouped together here.

The 'primitive ophiomyxids' include the genera *Ophioscolex*, *Ophiolycus*, *Ophiologimus*, *Ophiophrura* (**Fig. 9.10A**), *Ophioplexa* and the species '*Ophiotoma*' *tertium* (but not *Ophiotoma alberti* and *O. assimilis* which are ophiacanthids). These genera are characterised by the disc covering, usually of thin plates or skin, the rudimentary radial shields, and the thin or fragmented dorsal arm plates (Martynov 2010b). *Ophiolycus* and *Ophiologimus* have hook-shaped dorsal arm spines on distal segments. *Ophioscolex glacialis* has a spine on the adoral shield, which is usually present only on ophiuroid postlarvae (Martynov 2010b). These genera are poorly represented in Australia and its territorial waters, with only four genera and 14 species (five undescribed) recorded. An *Ophioscolex* species, very similar to the North Atlantic species *O. glacialis* (Clark 1946), is known from southern Australia. A few specimens of *Ophiolycus* have been found around Heard Island, Macquarie Island and off south-western Australia (T.D.O'Hara, personal observation). Some of the south-western Australian specimens have six arms and are bioluminescent. *Ophiolycus* differs from *Ophioscolex* in having hook-like upper arm spines. *Ophioplexa condita* is an abyssal species known from around Antarctica.

These genera are not at all related to others that were formerly placed in the Ophiomyxidae (Hugall *et al.* 2015). The genera *Ophiomyxa* and *Neoplax* appear to be derived ophiodermatids, distantly related to *Ophioconis* and *Ophiarachna*; *Astrogymnotes* is related to *Ophiozonella* (Ophiolepididae); and *Ophiocanops* to the ophiacanthids. The large Antarctic species *Ophiosparte gigas*, formerly considered to be an ophiomyxid (Dearborn *et al.* 1996), has been reassigned to the Ophiuridae (Martynov 2010b).

The position of *Ophiobyrsa* is uncertain. *Ophiobyrsa rudis* is endemic to south-eastern Australia from the Great Australian Bight, through Bass Strait to Merimbula, New South Wales, at depths of 50–585 m (O'Hara 2012). It is predominantly brown with yellow spots around the disc and arm spines and it has an unusual hook-like tentacle scale or lower arm spine projecting inwards over the tentacle pore.

The Ophiohelidae are characterised by soft sac-like discs, absent or hidden radial shields, numerous flattened oral papillae in several rows, large tentacle pores, and simple arm spine articulation tubercles on the lateral arm plates. The sac-like disc and absence of radial shields allow the arms to stand erect over the aboral disc surface, and many preserved specimens have that posture. Ophiohelids have been grouped with ophiacanthids by some authors (H.L.Clark 1915; Paterson 1985) and assigned to a separate family by others (Verrill 1899; Thuy & Meyer 2013). However, Martynov (2010b) suggested that they have greater affinity with Ophiactidae. The genetic data suggests that they are related to *Ophioscolex* and relatives. The name Ophiomycetidae (Thuy & Meyer 2013) has sometimes been used for this family, however, Ophiohelidae is the older name.

Four genera are known: *Ophiomyces*, *Ophiotholia*, *Ophiohelus* and *Ophiothauma*. *Ophiohelus* and *Ophiotholia* (**Fig. 9.10B**) have tiny, but very distinctive parasol-like hooklets on distal arm segments (Fujita *et al.* 2010). Similar structures have been found on fossils dating back to the Middle Jurassic, 160 mya (Thuy & Meyer 2013). *Ophiomyces* and *Ophiotholia* have flattened, spatulate to comma-shaped oral papillae.

Four species are known from Australia (O'Hara 2012). *Ophiomyces delata* has been found on the continental slope in the Tasman Sea (Baker 1979; O'Hara & Stöhr 2006). *Ophiomyces grandis* occurs in abyssal waters off eastern Bass Strait as well as in the Atlantic Ocean (O'Hara 1990), *Ophiotholia spathifer* near Norfolk Island (McKnight 1968), and the unusual, seven-armed

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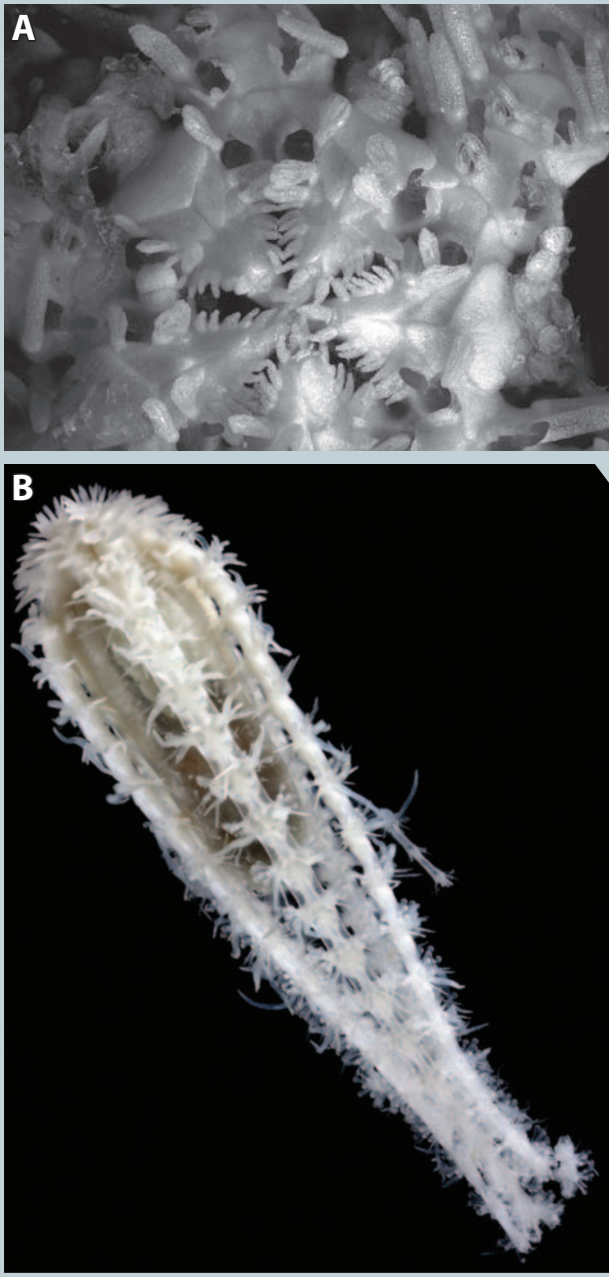


Figure 9.10 ***Ophiophiura*** and ***Ophiotholia***.

A, the ventral disc surface of ***Ophiophiura liodisca*** collected from the northern Norfolk Ridge in the Coral Sea. It one of several delicate ophioscolecids that occur in the south-western Pacific Ocean.

B, ***Ophiotholia supplicans*** collected from the seafloor at 4,200 m in the Clarion-Clipperton manganese nodule zone in the northern Pacific Ocean. The bizarre ***Ophiotholia*** has an elongated disc, upturned arms and minute umbrella-like spines along the arm.

[A, T.D.O'Hara; B, C.Harding]

Ophiothauma heptactis is known only from the coast of the Cobourg Peninsula, Northern Territory (Rowe & Gates 1995). It is possibly commensal with the ophiotrichid ophiuroid *Macrophiothrix paucispina* (erroneously referred to *M. belli* by Clark 1938, see Hoggett 1991).

Family Ophiacanthidae

Figure 9.11

The Ophiacanthidae is characterised as having a single to a cluster of apical papillae at the jaw tip and several oral papillae on each side of the jaw. The arms are usually long and often constricted at the proximal end of each segment (particularly in juveniles) and the ventral and dorsal arm plates are small. The arm spines are long, glassy, often serrated and erect, with volute-shaped articulation surfaces (Martynov 2010b). Some species have streptospondylous vertebral articulation and can coil their arms orally. The disc is often covered with skin, spines or tubercles (Fell 1982; **Fig. 9.11C–F**).

The large and diverse Ophiacanthidae have been a taxonomic problem (Paterson 1985). Four subfamilies have been described, based on characteristics of the disc scales and radial shields, the form and arrangement of the jaw, oral papillae and tentacles, and on the type of arm spine articulation (Paterson 1985). However, Martynov (2010a, 2010b) revised the family based on internal characters such as the form of their arm spine articulation, dental and oral plates. He transferred most of the genera of one subfamily, the Ophiotominae, to the Ophiomyxidae (treated here as the Ophioscolicidae), suggested that Ophiohelinae are related to the Ophiactidae, and concluded that the remaining two subfamilies, Ophiacanthinae and Ophioplinthacinae are too poorly differentiated to be supported at present.

Genetic data suggests an alternative arrangement (Hugall *et al*. 2015). Firstly, the genus *Ophiocamax* (**Fig. 9.11G**) is sister to all other ophiacanthids. *Ophiocopa*, *Ophiotoma*, *Ophiomitra*, *Ophiotreta*, *Ophiopristis* and *Ophiocomina* form a second clade. *Clarkcoma* and *Ophiopteris*, formerly in the Ophiocomidae, form a third and fourth group. Finally a fifth group comprises *Ophiacantha*, *Ophiolebes*, *Ophiomitrella*, *Ophialcaea*,

Ophioplinthaca, *Ophiurothamnus* and *Ophiomoeris*. This last group also includes the enigmatic *Ophiocanops* (see below). These groups have not been predicted by morphological studies and more work is required to define their status and prepare diagnoses.

The genera *Ophiomoeris* and *Ophiochondrus* were transferred recently from the Hemieuryalidae to the Ophiacanthidae (Martynov 2010b). The Hemieuryalidae were characterised by heavy plating on the disc and arms, stout vertebrae that allow coiling of the arm in the vertical plane, and reduced dorsal and ventral arm plates (Matsumoto 1915; Rowe & Gates 1995). However, these characters are linked to their epizoic habit and are not necessarily indicative of a phylogenetic relationship (Martynov 2010b). Detailed examination of the lateral arm plates showed that these two genera have typical ophiacanthid arm-spine articulation surfaces (Martynov 2010b). The remaining taxa in the Hemieuryalidae appear to be related to the ophiolepids (see below).

The Indonesian species *Ophiocanops fugiens*, formerly placed in its own family (Ophiocanopidae) or the Ophiomyxidae (Stöhr *et al*. 2008), is now considered to be an ophiacanthid (Hugall *et al*. 2015). Two more species are now known from the genus, *O. multispina* from Reunion Island in the western Indian Ocean and *O. felli* (formerly *Renetheo*) from the south-western Pacific Ocean (McKnight 2003; O'Hara 2012). These animals have a greatly reduced disc, and sometimes the gonads extend into the long arms that, in turn, wrap around black corals (Pearse *et al* 1998).

The extended family includes at least 29 genera (Martynov 2010b; Hugall *et al*. 2015), most of which occur in Australia and its territories. *Ophiacantha* is the largest genus with over 130 species but again genetic data suggest this taxon is not monophyletic (Hugall *et al*. 2015).

With the exception of a few littoral *Ophiacantha* species, all extant Australian species occur on the continental slope or on the abyssal plain (O'Hara 2012). Some are very widespread and a few could be considered cosmopolitan. In overall terms, there appears to be a single tropical ophiacanthid fauna on the upper to middle continental slope (200–2500 m) across the Indo-west Pacific from Africa to the Hawaiian Islands, with limited east–west differentiation (O'Hara & Stöhr 2006). This fauna grades into distinct temperate bathyal faunas near South Africa, China and Japan, and Australia and New Zealand, with an almost complete changeover of species by 45° in both northern and southern hemispheres. Less than 10% of the deepsea ophiacanthid fauna around New Caledonia (16–26°S) is shared with southern Australia and 15% with New Zealand (34–48°S).

Many ophiacanthid species are suspension feeders, using their long arm spines to catch prey and form dense aggregations (Fell 1982; Metaxas & Giffin 2004; **Fig. 9.11B,G**). Some are epiphytic or epizoic and climb sessile animals to reach higher water currents, while others are predators or scavengers (Warner 1982). A number of species are viviparous, including *Ophiomitrella conferta* from the Southern Ocean (O'Hara 1990), *Ophiacantha vilis* from Macquarie Island (O'Hara 1998) and the *O. vivipara* complex from the southern Tasmania seamounts and throughout the Southern Ocean (Mortensen 1936; O'Hara *et al*. 2008). *Ophioplinthaca plicata* was reported to be sexually dimorphic, with one specimen having what was interpreted to be a dwarf male clinging to the aboral disc surface of the female (Baker & Devaney 1981). However, this observation has never been repeated despite the numerous specimens now available (T.D.O'Hara, personal observation).

Ophiacantha species are represented in tropical Australia by two common shallow-water species, *O. dallasii* and *O. indica*, and by many more on the continental slope, particularly in the Tasman Sea (O'Hara & Stöhr 2006). *Ophiacantha alternata* (**Fig. 9.11A**) is a characteristic southern Australian species with a vertical range from the intertidal, where it occurs on algae and seagrass, to 127 m. *Ophiacantha clavigera* and *O. heterotyla* are south-western and eastern Australian species respectively, with ranges extending into Bass Strait (O'Hara 1990). *Ophiacantha shepherdi* is restricted to the South Australian and Victorian coasts between Encounter Bay and Harmers Haven (O'Hara 1990), and *O. brachygnatha*, *O. fidelis* and *O. rosea* are common on the continental slope off south-eastern Australia. *Ophiacantha fidelis* occurs

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in large dense aggregations (Blaber *et al*. 1987) and forms an important component of the diets of several fish and a seastar (*Mediaster australiensis*) that feed on epibenthic invertebrates (Blaber & Bulman 1987; Blaber *et al*. 1987). Numerous undescribed species occur on seamounts to the south of Tasmania (T.D.O'Hara, personal observation).

Seven *Ophiacantha* species are recorded from the Australian Antarctic Territory, including the well known *O. vivipara*, *O. pentactis* and *O. antarctica*. *Ophiacantha vivipara* usually has six or more arms, but it does not appear to be fissiparous. It is a bursal brooder, but parents can also be found with juveniles clinging to the external disc surface (Mortensen 1936). *Ophiacantha pentactis* is five-armed and occurs at more southerly latitudes than *O. vivipara* (Fell 1961). DNA evidence shows that five- and six-armed specimens from Antarctica are very closely related and possibly represent a single species (O'Hara *et al*. 2013); conversely, six-armed specimens from off Australia and New Zealand appear to be a distinct undescribed species (O'Hara *et al*. 2014a). Another six- to seven-armed species (possibly the true *O. vivipara*) occurs in subantarctic and Patagonian waters (O'Hara *et al*. 2013; Brogger & O'Hara 2015). *Ophiacantha antarctica* can be one of the most common animals on the Antarctic seabed where it can constitute up to one-third of the total biomass (Fell 1961). The viviparous *O. vilis* occurs at Macquarie Island, where it is the only ophiuroid in waters less than 20 m deep (O'Hara 1998).

The abyssal species *Ophiacantha cosmica*, *O. sollicita*, *O. pacifica* and *O. bathybia* are all very similar and species limits are unclear. The name *O. sollicita* is used for specimens around Australia and New Zealand.

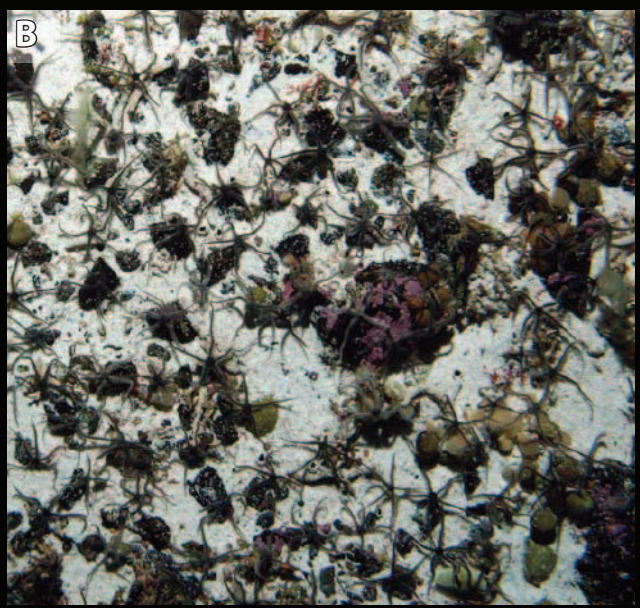
Ophiotreta species occur on the continental slopes, particularly in tropical regions (O'Hara & Stöhr 2006). They differ from *Ophiacantha* in having an elongate jaw and numerous (five or more) oral papillae, the distal ones often larger and spatulate. Most species have slender, thorny disc spines and a single tentacle scale on most pores, except *Ophiotreta valenciennesi* (**Fig. 9.11I**), which has disc granules and two tentacle scales and bears a resemblance to an ophiocomid species.

Ophiopristis axiologus is a rare species, known from only three specimens from the continental shelf off south-eastern Australia (O'Hara 1990). An *Ophiolimna* species on the southern continental slope and seamounts appears to be similar to a species previously known as *Toporkovia antarctica* from the Southern Ocean. The latter was once thought to be a member of the Ophiodermatidae with an unusual bipolar distribution (Baker 1977); however, it is a widespread species of Ophiacanthidae (O'Hara & Stöhr 2006). Another large Antarctic species, *Ophiosparte gigas*, is now considered to be an ophiurid (Martynov 2010b).

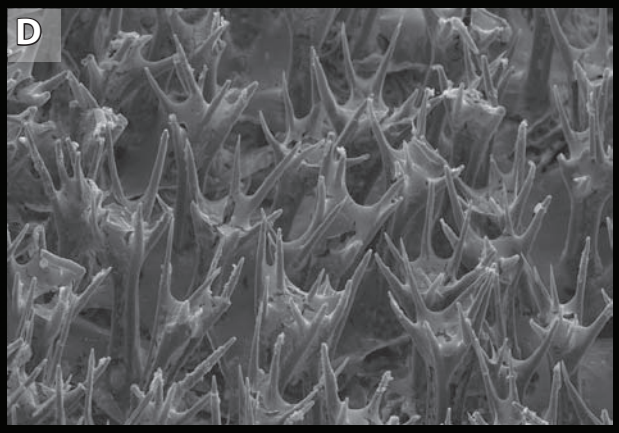
Deep-water species of *Ophioplinthaca*, *Ophiocamax* and *Ophiomitrella* occur off Australia and its territories (Madsen 1967; Rowe & Gates 1995; O'Hara & Stöhr 2006). *Ophiomitrella conferta* exhibits 'polar emergence', occurring at littoral depths in the Antarctic (O'Hara 1990), although Australian and Antarctic forms may be separate cryptic species (O'Hara *et al*. 2013). *Ophiomoeris obstricta* (**Fig. 9.11J**) is known from Australian waters around Lord Howe Island and Norfolk Island in the south Pacific Ocean (O'Hara & Stöhr 2006). It appears to live epizoically on corals. The record of *Ophiomoeris nodosa* from the Norfolk Ridge (Rowe 1989b) is based on a misidentification (T.D.O'Hara, personal observation).

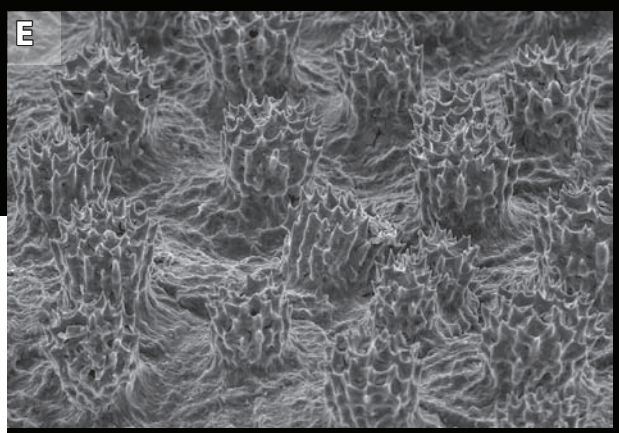
Clarkcoma is a genus of southern Australian and New Zealand species that are characteristic of subtidal (0–30 m) rocky reefs. *Clarkcoma canaliculata* (**Fig. 9.11H**) appears to consist of multiple species that have subtly different colour schemes dominated by brownish red, purple or orange (Naughton *et al*. 2014a). Some arm spines have thickened epithelial coverings that are orange-red on living animals (Rowe 1985c). The function of these fleshy covered (paddle) spines is unknown as histological investigation did not reveal specialised glandular structures (M.Byrne, personal observation). *Clarkcoma bollonsi* has been reported from the continental shelves of southern Australia and New Zealand (Rowe 1985c); genetic evidence, however, suggests that separate species occur in each country (Naughton *et al*. 2014a). *Clarkcoma pulchra* has decorative variegated colouring (**Fig. 3.1**). Its distribution is disjunct: it is common in waters of Western Australia, South Australia and New South

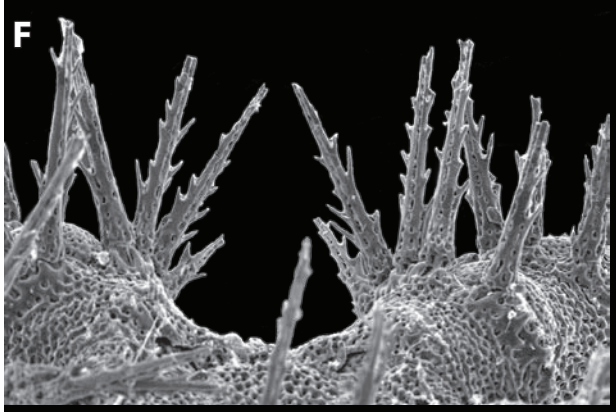












Wales, but unknown in Victoria and Tasmania. *Clarkcoma australis*, until recently considered an *Ophiocomina*, appears to be restricted to *Posidonia* seagrass beds in South Australia and Victoria (O'Hara 2012). The black colour of this species provides a perfect camouflage against the dark rotting seagrass fronds that accumulate on the seafloor (T.D.O'Hara, personal observation). Genetic evidence indicates that *Clarkcoma*, *Ophiopteris* and *Ophiocomina nigra* are related only distantly. There has been considerable debate about the placement of *Ophiocomina*, with Wilkie (1980) placing it in the Ophiacanthidae and Baker & Devaney (1981) next to *Clarkcoma*. The genetic evidence suggests *O. nigra*'s true relationship is with *Ophiotreta valenciennesi* from which it differs only in having a small cluster of dental papillae.

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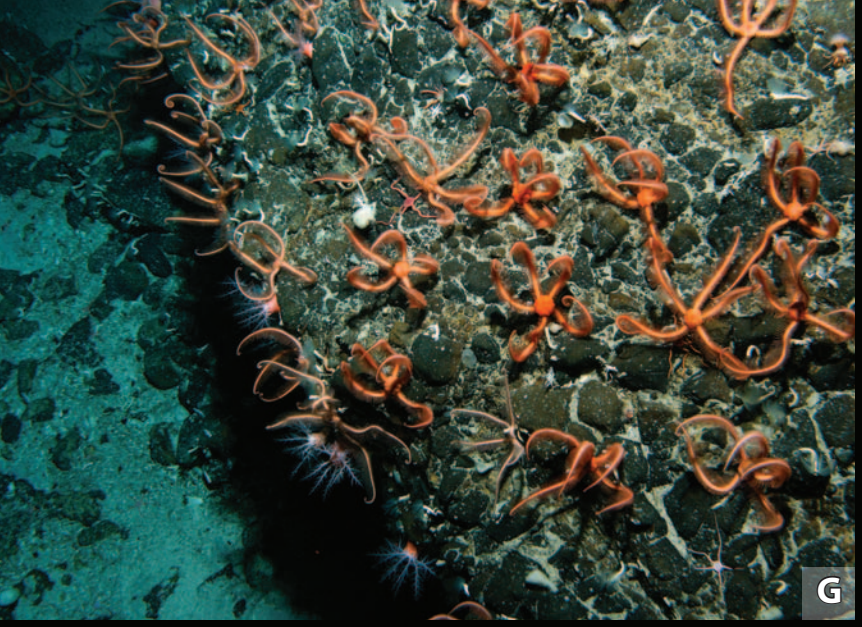








Figure 9.11 Family Ophiacanthidae.

A, the tiny ***Ophiacantha alternata*** is typically found on seagrass or in algal turf along southern Australia.

B, ***Ophiacantha otagoensisis*** is common along the top of the northern Macquarie Ridge south of New Zealand.

C–**F**, scanning electron microscope images of disc spines (**C**–**E**) and arm spines (**F**) of undescribed ophiacanthid species from southern Australia.
C, ***Ophiolebes***.
D, ***Ophiacantha***.
E, ***Ophiomitrella***.
F, ***Ophiocamax***.

G, the arms of ***Ophiocamax applicatus*** held high into the water to capture planktonic food on the mucus-covered arm spines and tube feet. This aggregation at 500 m depth on an unnamed seamount along the North Macquarie Ridge was popularised as 'brittle-star city' in press reports of the voyage of the Tangaroa in 2008.

H, ***Clarkcoma canaliculata*** is commonly found under rocks across southern Australia.

I, like many cosmopoliton taxa, ***Ophiotreta valenciennesi*** is probably a complex of closely related species. This animal was collected in 2015 off the Galapagos Islands.

J, the morphologically variable ***Ophiomoeris obstricta*** is epiphytic on branching cnidarians.

[A, L.Altoff; B,G, NIWA; C–F, J.Clark & B.Patullo; H, K.Gowlett-Holmes; I, C.Harding; J, B.Patullo]

Clarkcoma pulchra and *C. canaliculata* spawn moderate-sized eggs (300 µm diameter; Fig. 3.1) and develop through a non-feeding vitellaria larva (Selvakumaraswamy & Byrne 2000a; Cisternas *et al.* 2004; Falkner *et al.* 2013). Post-larval development of the juvenile skeleton of *Ophiacantha* species from the north Altantic is described in Sumida *et al.* (1998).

Ophiacanthidae have a diverse fossil record, particularly single plate microfossils. *Europacantha paciphila*, known from lateral arm plates from the Middle Triassic (245 mya), is the earliest known ophiacanthid fossil (Thuy 2013). Complete specimens of the Late Triassic ophiacanthid *Leadagmara gracilispina* are known from Japan (Thuy *et al.* 2013). A Cretaceous fossil species from Queensland, known only from its oral surface, has been placed in its own genus, *Ophioglyphoida* (Clark 1946).

Family Ophiocomidae

Figure 9.12

This family is characterised by a clump of dental papillae at the jaw apex, and series of oral papillae along the side of each jaw, short adoral shields which are positioned to the side of the oral shields, stout arms that are usually broadest at some distance from the base and inserted ventrally under the disc, and long erect arm spines (**Figs 9.3F, 9.12D**). The teeth have a hyaline edge, and the disc is usually covered in granules and/or spines or may be naked (Fell 1982; Rowe & Gates 1995).

A restricted definition of the family is adopted here, as recent genetic data (Hugall *et al*. 2015) indicates that some genera formerly assigned to the Ophiocomidae are better placed in other families. *Ophiopsila*, with its extended bioluminescent arms and long, crossed tentacle scales, is more closely related to the Ophionereididae. *Clarkcoma*, *Ophiocomina* and *Ophiopteris*, with long adoral shields that meet in front of the oral shield, fall within the Ophiacanthidae. The phylogeny suggests that a cluster of papillae at the jaw apex has evolved several times independently throughout the Ophiuroidea.

The family Ophiocomidae, as thus restricted, comprises *Ophiocoma* (23 species), *Ophiomastix* (15), *Ophiarthrum* (3) and *Ophiocomella* (4), all with distributions in tropical and subtropical littoral waters (Stöhr *et al*. 2014). Species of the genus *Ophiocoma* can dominate the coral reef cryptofauna (Sloan *et al*. 1979; Byrne *et al*. 2004a). All four genera occur in Australian waters (O'Hara 2012). Three species are endemic: *Ophiocoma occidentalis* (**Fig. 9.3F**) in south-western Australia; *O. endeani* from the mid-eastern coast; and *Ophiomastix corallicola*, known only from the type specimens, from the Great Barrier Reef, Queensland. The other species have Indo-west Pacific distributions, although several are known in Australia only from northern Queensland (Rowe & Gates 1995).

Many *Ophiocoma* species are sympatric, and numerous taxa can occur at the same location, although they may prefer different microhabitats (Sloan *et al*. 1979; Chartock 1983; Byrne *et al*. 2004b). *Ophiocoma scolopendrina* is commonly found in intertidal rock pools and under boulders throughout the Indo-Pacific. This species appears to be well adapted to harsh conditions, tolerating temperatures up to 40°C and wide variations in salinity (Magnus 1964; Oak & Scheibling 2006). *Ophiocoma dentata* (**Fig. 9.12B**), *O. doederleini* and *O. pusilla* prefer cryptic shallow-water habitats (1–10 m), whereas *O. erinaceus* and *O. pica* (**Fig. 9.12C**) are often found in deeper water in coral heads (Sloan *et al*. 1979). *Ophiomastix* species (**Fig. 9.12A,D**) are also typically subtidal (Devaney 1978; Byrne *et al*. 2004b). Many *Ophiocoma* species actively compete for shelter, occasionally aggressively (Sides 1985).

Ophiocomids are primarily suspension- or deposit-feeders and often use mucus-covered spines to trap food (Warner 1982; Chartock 1983; Oak & Scheibling 2006; Tamura & Tsuchiya 2010). They also use other methods such as arm-loop capture of larger prey, scavenging or browsing (Warner 1982). *Ophiocoma scolopendrina* is commonly seen feeding on the water surface layer at low tide raking the surface scum (**Fig. 2.3**). Its primary food source is suspended particulate matter and bacteria attached to sediment (Tamura & Tsuchiya 2010). With the presence of hundreds of thousands of *Ophiocoma scolopendrina* in expansive populations, this species is important in coral reef trophodynamics as a link between decomposers, primary producers and higher level consumers (Tamura & Tsuchiya 2010; **Fig. 2.3**).

Some *Ophiocoma* species change colour from day to night (Hendler 1984b; O'Hara *et al*. 2004), including *Ophiocoma erinaceus* (**Box 1.4**), a species common on the Great Barrier Reef. The Caribbean species *Ophiocoma wendtii* has special lens-like structures on the dorsal arm plates which form a rudimentary vision system that transmits incoming light to the underlying neurons (Hendler & Byrne 1987; Aizenberg *et al*. 2001). At dusk the pigment cells start to migrate, changing the colour of the ophiuroid and thereby exposing sensory structures. *Ophiocoma* species are hosts to numerous associates, including scale worms, crabs and sea-spiders (Sloan *et al*. 1979). *Ophiomastix* species babysit the juveniles of other ophiocomids in their bursae and on their body surface (Fourgon *et al*. 2007; **Fig. 2.27**).

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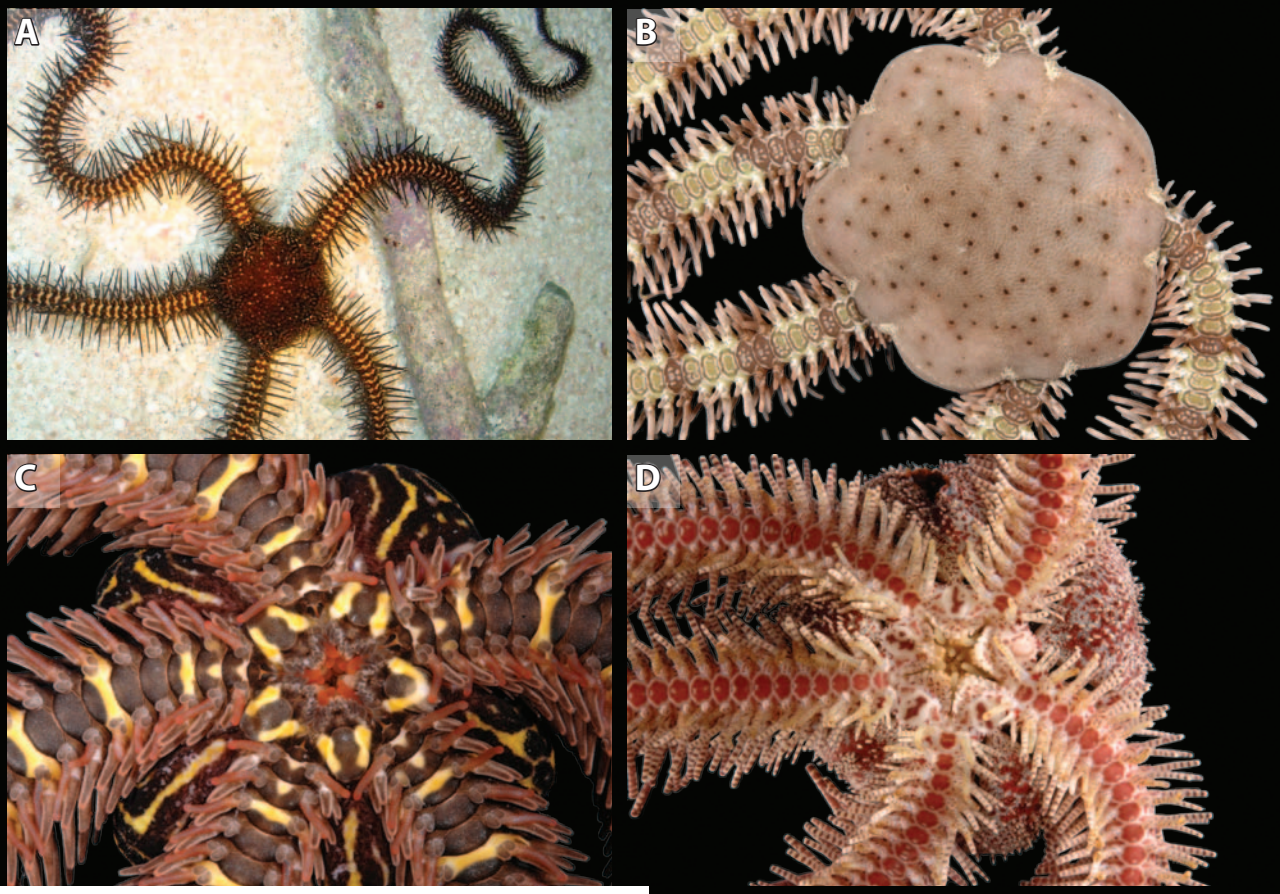


Figure 9.12 Family Ophiocomidae.

A, the spiny ***Ophiomastix janualis*** is a colourful inhabitant of coral reefs, from which it extends its arms to feed. This animal was from Raine at the north end of the Great Barrier Reef, Queensland.

B, ***Ophiocoma dentata*** from Ningaloo Reef, Western Australia, has a disc covered in small round granules.

C, the colourful ***Ophiocoma pica***, from Ningaloo Reef, is normally found buried deep in coral heads.

D, the oral side of ***Ophiomastix annulosa*** from the Ningaloo Reef off Western Australia, showing the tall annulated disc spines.

[A, M.Byrne; B–D, F.Michonneau]

Ophiocoma species have been separated into four informal groups based on features of the arm spines and disc granules (Devaney 1970). *Ophiomastix*, which occurs only in the Indo-west Pacific, is characterised by having a combination of spines and granules on the disc, alternating arm spines, and a modified uppermost arm spine. The modified upper arm spine can be enlarged, swollen or forked, and is covered with a thickened glandular epithelium (Devaney 1978). Some of these characters are shared by the 'scolopendrina group' of *Ophiocoma* species and the two groups may not be distinct.

Ophiarthrum species are characterised by the disc surface covered in naked skin with no granules or spines. *Ophiarthrum pictum* is beautifully patterned yellow, white and grey; *O. elegans* is pale red with a dark central patch on the disc. *Ophiocomella sexradia* (**Fig. 3.7A**) is a diminutive Indo-Pacific species, in Australia ranging from Rottnest Island, Western

Australia, to Lord Howe Island (Rowe & Gates 1995). It has five to seven arms (usually six) and is fissiparous. Suggestions that *Ophiocomella* species (**Fig. 3.7A**) are merely 6-armed juveniles of *Ophiocoma* species (Clark 1946) were rejected by more recent researchers on the basis of morphological and biogeographical differences (Clark 1967a; Devaney 1970), although others have suggested that they could be congeneric (Mladenov & Emson 1990).

Ophiocomids have diverse life history modes (Cisternas *et al*. 2004; Falkner *et al*. 2013). All known *Ophiocoma* species spawn small eggs and have an ophiopluteus larva, with the exception of *O. endeani*, which has a large egg and some form of lecithotrophic development (McEdward & Miner 1991; Cisternas *et al*. 2004; Soong *et al*. 2009; Falkner *et al*. 2013). Species of *Ophiomastix* and *Ophiarthrum* have large eggs and a vitellaria larva (Fell 1982; Cisternas *et al*. 2004; Fourgon *et al*. 2005; Delroisse *et al*. 2013).

Family Ophiodermatidae (including *Ophiomyxa*)

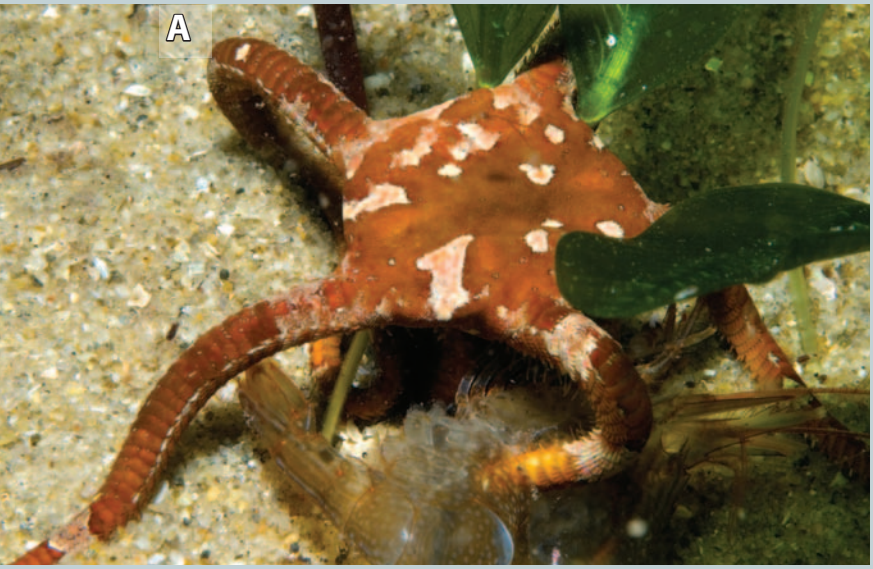
Figures 9.13 & 9.14

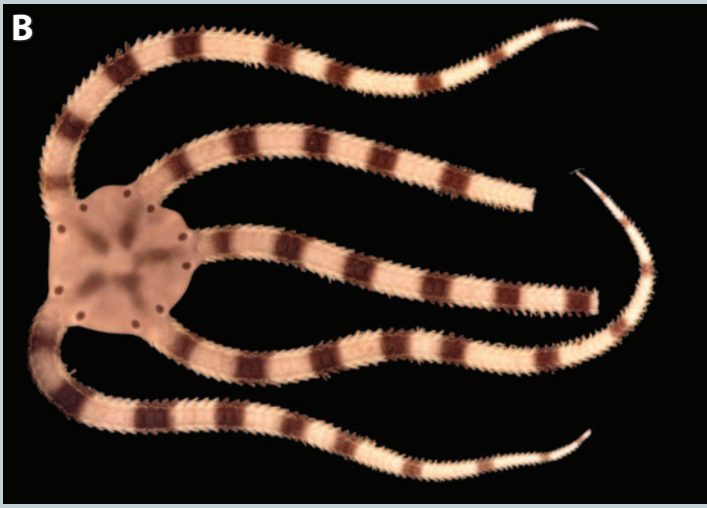
Genetic data indicates that the ophiodermatids fall into at least three major groups, all of which probably warrant family status (T.D.O'Hara & A.F.Hugall, unpublished observation). The first consists of *Ophiopeza* plus several *Ophiarachnella* species, including *O. infernalis*, *O. similis* and *O. sphenisci*, which have characteristic patterns of naked and granule-covered coarse disc plates. The second group consists of the old subfamily Ophiarachninae (*Ophiarachna*, *Ophiurochaeta*, *Ophioconis*) with relatively long arm spines and partially separated arm vertebral halves, *Ophiarachnella septemspinosa* (**Fig. 9.13B**) and relatives with small circular naked radial shields, and the morphologically divergent genus *Ophiomyxa*, which has a thick skin covering the disc and arms, obscuring the thin fragmented dorsal arm plates, and enclosing the skeletal arm spines, a barrel-shaped protective cover for the tube feet instead of the usual tentacle scale (Byrne 1994) and denticulate oral papillae. This relationship between *Ophiomyxa* and the ophiodermatids was not deduced from previous morphological studies. However, the fragmented dental plate and serrated teeth are similar in *Ophioconis* and *Ophiomyxa*. The third group includes the bulk of traditional ophiodermatids, including *Ophioderma*, *Ophiopsammus*, *Cryptopelta*, *Ophiochasma* and *Bathypectinura*, all with short, adpressed arm spines and a dense covering of granules on both sides of the disc (**Fig. 9.3C**). Characters of generic importance include the form and extent of the granulation, the number and form of the tentacle scales and arm spines, and the structure of the genital slit, which in some species is divided into two (*Ophioderma*). The earlier widespread use of the generic name *Pectinura* for species with granules covering the radial shields was abandoned because of the uncertain nature of the type species. Instead, these species are now referred to as *Ophiopeza* and *Ophiopsammus*. *Ophiopsammus* is distinguished from *Ophiopeza* by the smaller, more numerous disc scales (Vail & Rowe 1989).

Ophiodermatids are mostly active carnivores, although microphagous surface-deposit feeding has been reported (Hendler 1982b; Warner 1982). *Ophiopsammus maculata* from New Zealand captures prey with a dorso-ventral arm loop (Pentreath 1970); the disc is raised by the proximal portion of the arm, and the food is passed underneath to the mouth. This species has very small tube feet and, consequently, it uses its arm spines to assist in locomotion. The arm spines are raised on contact with the substratum, giving the moving animal extra leverage. The feeding behaviour of the Carribbean Sea species *Ophioderma brevispina* is affected by temperature (Hendler 1982b). In warm water this primarily tropical species is an active carnivore, feeding mainly on amphipods. When the water temperature falls below 5°C, the animals become sluggish. They aggregate and deposit-feed, using their tube feet; there appears to be no cessation of feeding during the spawning period. By rapidly twisting its legs, the large tropical species *Ophiarachna incrassata* can catch small fish that swim beneath its raised disc (**Box 1.2**).

Ophiodermatids spawn large eggs and develop through a non-feeding vitellaria larva as seen in *Ophiarachnella gorgonia*, a species found on the Great Barrier Reef (McEdward & Miner 2001; Byrne & Selvakumaraswamy 2002; Cisternas & Byrne 2005; Cisternas *et al*. 2004). *Ophiopeza spinosa*, a hermaphroditic brooder, also

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found on the Great Barrier Reef, keeps its vitellaria larvae in the bursae (Byrne *et al*. 2008c). These larvae are similar to the planktonic form. Fissiparity has not been verified for ophiodermatids (Emson & Wilkie 1980), although the six-armed *Ophioclastus hataii* can appear asymmetrical, with three arms developed more than the others (Guille *et al*. 1986).

The traditional Ophiodermatidae includes 108 described species in 20 genera (Stöhr *et al*. 2014) with a further 24 species when *Ophiomyxa* is added. Most occur in shallow tropical waters while a few are temperate or abyssal (Fell 1982). A species recorded from polar regions, *Toporkovia antarctica*, has been sometimes considered an ophiodermatid (Fell 1961), but it has been shown to be congeneric with the ophiacanthid genus *Ophiolimna* (O'Hara & Stöhr 2006).

Figure 9.13 Ophiodermatidae.

A, ***Ophiopsammus assimilis*** feeding on a carid shrimp at midnight under Busselton Pier, Western Australia.

B, the little known ***Ophiarachnella macracantha*** was first described from the Caroline Islands.

C, ***Ophiarachnella gorgonia***.

D, the oral side of ***Ophiarachna megacantha*** from One Tree Island, Queensland. This species has characteristic chisel-like lowermost arm spines.

[A, J.Finn; B,C, G.Paulay; D, M.Byrne]

Thirty-two ophiodermatid species in 10 genera have been recorded from the waters around Australia (Vail & Rowe 1989; Rowe & Gates 1995; O'Hara 2012). Most are tropical, and, with a few exceptions (*Ophiopsammus aequalis*, *Ophioconis cupida* and *Ophiarachna quinquespinosa*), live in shallow waters. Endemics are few (*Ophiarachna megacantha*, **Fig. 9.13D**, and *Ophiodyscrita acosmeta*), most species having broad Indo-west Pacific distributions. *Ophiarachna incrassata,* one of the larger ophiuroid species, has a disc diameter that can exceed 55 mm and arms that can grow to 200 mm in length. The disc is a vivid bright green with black and white spots, and the arms are banded white and black (**Box 1.2**). It is common under large rocks and coral rubble in shallow water. *Ophiarachnella gorgonia* (**Fig. 9.13C**) is another common green species, but is smaller (to 25 mm disc diameter) and has adpressed arm spines. This taxon is likely to be a species complex (Hoareau *et al*. 2013). *Ophiopeza spinosa* is notable in having numerous short sharp arm spines, typically 9–12 on each side of an arm segment (Vail & Rowe 1989). Another species, *Ophiopeza exilis*, described from Indonesia but also present on the outer continental shelf of north-western Australia, with its erect arm spines would be more appropriately referred to *Ophiurochaeta*, a relative of *Ophioconis* (T.D.O'Hara, personal observation).

In the coastal zone off southern Australia, *Ophiopsammus assimilis* (**Fig. 9.13A**) and *Ophiarachnella ramsayi* are known from Western Australia to northern New South Wales or southern Queensland, but are absent or rare from the cool temperate coast around Tasmania and western Victoria. *Ophiarachnella ramsayi* (**Fig. 9.3C**) is a notable member of the rocky shore fauna where it occurs. *Ophiopsammus assimilis* has also been collected in New Zealand. Two other species are known from Bass Strait. *Ophiopeza cylindrica* (formerly *O. arenosa*) is common in muddy/shelly sediments on the continental shelf as far as northern New South Wales and in New Zealand. *Ophiopsammus angusta* is present in slightly deeper water on each side of Bass Strait and down the east coast of Tasmania. *Ophioconis opacum* is an endemic south-western species, occurring in sheltered coastal habitats from Shark Bay, Western Australia, to Gulf St Vincent, South Australia.

The very large orange and cosmopolitan (Madsen 1973) species *Bathypectinura heros* has been recorded from the continental slope off southern Australia and in the Tasman Sea (Rowe & Gates 1995). Specimens from the Caribbean Sea are known to swim (Hendler & Miller 1991). Juveniles have enlarged basal lateral arm plates (Madsen 1973) and have been described as a separate species, *Ophiomidas aurum* (T.D.O'Hara, personal observation).

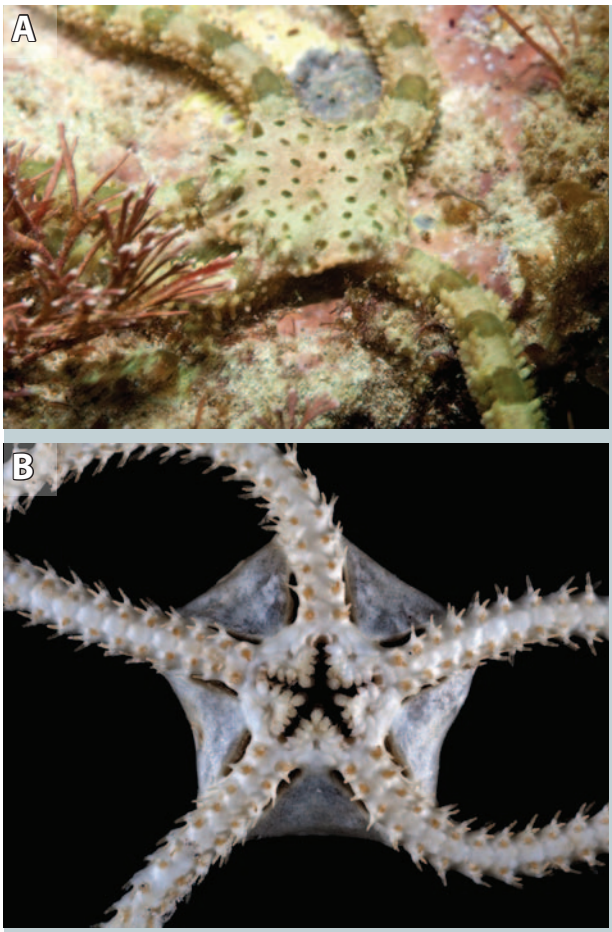


Figure 9.14 ***Ophiomyxa***.

A, the widespread ***Ophiomyxa australis*** occurs in a large number of colours and patterns.

B, the characteristic ***Ophiomyxa*** oral frame with denticulate glassy oral papillae lining the jaw. This specimen of ***O. vivipara*** was collected from depths of 500 m around Amsterdam Island in the southern Indian Ocean.

[A, J.Finn; B, C.Harding]

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Ophiomyxa australis (**Figs 2.6A, 9.14A**) is a widespread Indo-Pacific taxon that ranges from the intertidal zone to 400 m (deeper water records are likely to be of other species). It occurs throughout Australian waters, except in the Gulf of Carpentaria (Rowe & Gates 1995); in southern Australia it is one of the largest (disc to 35 mm diameter) and best known species from rocky subtidal reefs (Phillips *et al*. 1984). It is variously coloured, usually red or green in combination with yellow, grey and brown, with the disc often spotted and the arms banded (Baker 1982a). *Ophiomyxa* species have teeth and oral papillae that are flat and glassy with a serrated edge (**Fig. 9.14B**). The eggs of *O. australis* measure 250 µm in diameter, and it seems probable that the species has separate sexes, lecithotrophic larvae, and does not brood its young (Mortensen 1924). In contrast, *O. brevirima* from New Zealand and *O. vivipara* from southern South America brood their young in the bursae (Mortensen 1936; Garrett *et al*. 1997). A common *Ophiomyxa* species that occurs on the continental slope of southern Australia and New Zealand is very similar to *O. vivipara* (**Fig. 9.14B**), both genetically and morphologically, although brood juveniles are rarely found (O'Hara *et al*. 2014a).

The feeding habits of *O. australis* are unknown, but some details are available for *O. brevirima* from New Zealand (Pentreath 1970), which is predominantly a carnivore, its gut contents dominated by small ophiuroids, amphipods and algal fragments. Food is picked up by the tube feet and transferred to the mouth by an arm coil. The tube feet are protected by a 'barrel' consisting of two calcareous ossicles embedded in the thick skin and only the terminal knob of the tube foot protrudes from the barrel. However, there is enough flexibility for the tube feet to be used in locomotion. The gut contents of another species, the northern Atlantic *O. serpentaria*, have been found to be mainly crustaceans, sponge spicules and foraminiferans (Warner 1982). The skin of *Ophiomyxa* species produces mucus and is slimy to touch, and while the arms lack the armour-like skeleton characteristic of other ophiuroids, instead they have a reduced skeleton and layers of connective tissue that can stiffen the arm in a defensive response when it is touched (Byrne & Hendler 1988).

Family Ophioleucidae

Figure 9.15

This family is characterised by the continuous series of oral papillae along the jaw edge, the second tentacle scale opening within the oral slit, long adoral shields and arms inserted ventrally to the disc; the disc is covered in granules, dorsal arm plates are contiguous and there are few tentacle scales on pores distal to the disc (Madsen 1983).

Ophioleucids sometimes have been treated as a subfamily of the Ophiuridae (Madsen 1983; Smith *et al*. 1995). Several genera that were included in the family, such as *Ophiotrochus* and *Ophioperla*, have been transferred progressively to the Ophiuridae (Fell 1961; Paterson 1980) and the character states of the remaining genera overlap those of ophiurid genera (Madsen 1983). However, genetic data places them unequivocally as sister to a clade with the Ophionereididae, Ophiolepididae, Amphiuridae, Ophiactidae and Ophiotrichidae (Hugall *et al*. 2015). *Ophiernus* is sufficiently divergent from the others to warrant its own family.

The family includes five extant genera: *Ophioleuce*, *Ophiernus*, *Ophiopallas*, *Ophiopyren* and *Ophiostriatus* (Madsen 1983), of which four genera and five species occur in Australian and Antarctic waters (Fell *et al*. 1969; Rowe & Gates 1995). *Ophiernus vallincola* (**Fig. 9.15**), a widespread abyssal species, has a specialised row of bristle-like spines on the lateral arm plate, dorsal to the usual arm spines (Madsen 1977). Similar spines have been observed to be swimming organs in a closely related species, *Ophiernus adspersus*, from the Caribbean (Hendler & Miller 1991). In the living animal they are feather-like, and are erected and withdrawn in sequence, assisting the swimming animal's propulsion through the water.

Most species are fragile, deep-water animals with long slender arms, a few adpressed arm spines and large oral shields (Fell 1982). Some authorities consider the family archaic (Hertz 1927b), others neotenous (Matsumoto 1917). Accessory arm spines such as used in extant species for swimming have been reported from a Jurassic fossil species, *Ophiopinna elegans* (Hendler & Miller 1991). The first appearance of

Ophioleucidae in the fossil record is that of *Eirenura kohli* from the early Jurassic (Thuy 2005).

Ophiopallas paradoxa, *Ophiostriatus bispinosus*, *Ophioleuce seminudum* and *O. brevispinum* are Indo-Pacific species; they are reported from the upper continental slope in the Tasman Sea (Baker 1979; O'Hara 1990; 2012). *Ophiostriatus* species have notable transverse striations on the arm plates and unusual large hollow semi-cylindrical tentacle scales. *Ophiostriatus bispinosus*, a rare species, was reported previously to have two scales (Baker 1979), but these represent the inner and outer surfaces of a single hollow scale (T.D.O'Hara, personal observation). *Ophiopallas valens* has been found on carbonate mounds on the Sahul Banks in the Timor Sea, although the latest genetic data suggests that it is a species of Ophiodermatidae rather than Ophioleucidae (T.D.O'Hara, personal observation).

Ophioleuce regulare is a widespread species in the Southern Ocean, and has also been found on the continental slope off south-eastern Australia (O'Hara 1990). It has a flattened disc that is concave ventrally and fringed by elongate granules. It is possible that the concave disc assists the animal to adhere to hard surfaces (Mortensen 1936; Fell 1961), while the large proximal tentacle scales could be used to sweep food under the disc.

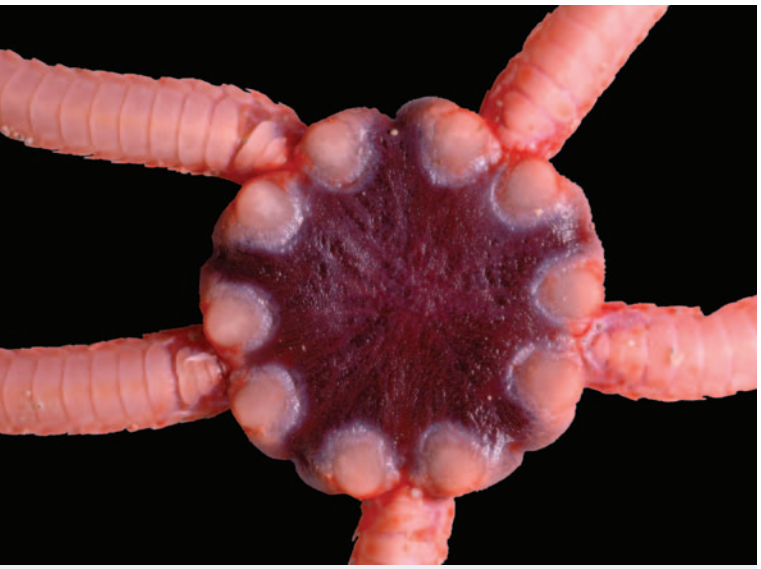


Figure 9.15 Family Ophioleucidae.
The deepsea ***Ophiernus vallincola*** has specially modified upper arm spines that probably assist it to swim for short distances. This specimen was collected from the Challenger Plateau, west of New Zealand.
[NIWA]

Family Ophionereididae

Figure 9.16

The ophionereid disc is large, flat and covered with small overlapping scales. The scales can be obscured by skin or occasionally by small spines on the ventral surface. Granules are present on the ventral disc surface of one genus, *Ophioplax* (**Fig. 9.3A**). A series of papillae occurs along the genital slit in some species; on *Ophiodoris* such papillae have increased in length to become spines that continue around the margin of the disc. The arms are typically robust, widest at some distance from the disc, sometimes keeled ventrally, and inserted beneath the disc. The arm spines are often long and erect and the tentacle scales are usually large and leaf-like (**Fig. 1.23**). Supplementary plates (**Figs 1.6D, 9.16C**) are present on either side of the dorsal arm plates in *Ophionereis*. There is one blunt papilla at the jaw apex, and a short series of oral papillae on both sides (**Fig. 9.3A**). The teeth are stout and can be triangular to quadrangular. Many species are brightly coloured. (H.B.Fell 1960; F.J.Fell 1982; Rowe & Gates 1995; Smith *et al*. 1995)

This family is regarded here as having four genera: *Ophionereis* (29 species), *Ophiochiton* (10), *Ophioplax* (8) and *Ophiodoris* (4). Of the other genera variously attributed to this family, *Ophiotriton*, *Ophiocrasis* and *Ophiodesmus* are synonyms of *Ophionereis* (the name *Ophiodesmus* is also invalid, having been used previously for a millipede genus) (Clark 1953b; Hendler 2002).

Ophionereis has been placed in its own subfamily, the Ophionereidinae (Matsumoto 1915), distinguished from the Ophiochitoninae (*Ophiochiton*, *Ophioplax* and *Ophiodoris*) by internal skeletal characters, including well-developed lateral wings on the oral plates and V-shaped dorsal projections on the vertebrae. Some authors have considered the similarity of the two families to be convergent and have placed them in separate higher taxonomic categories (Smith

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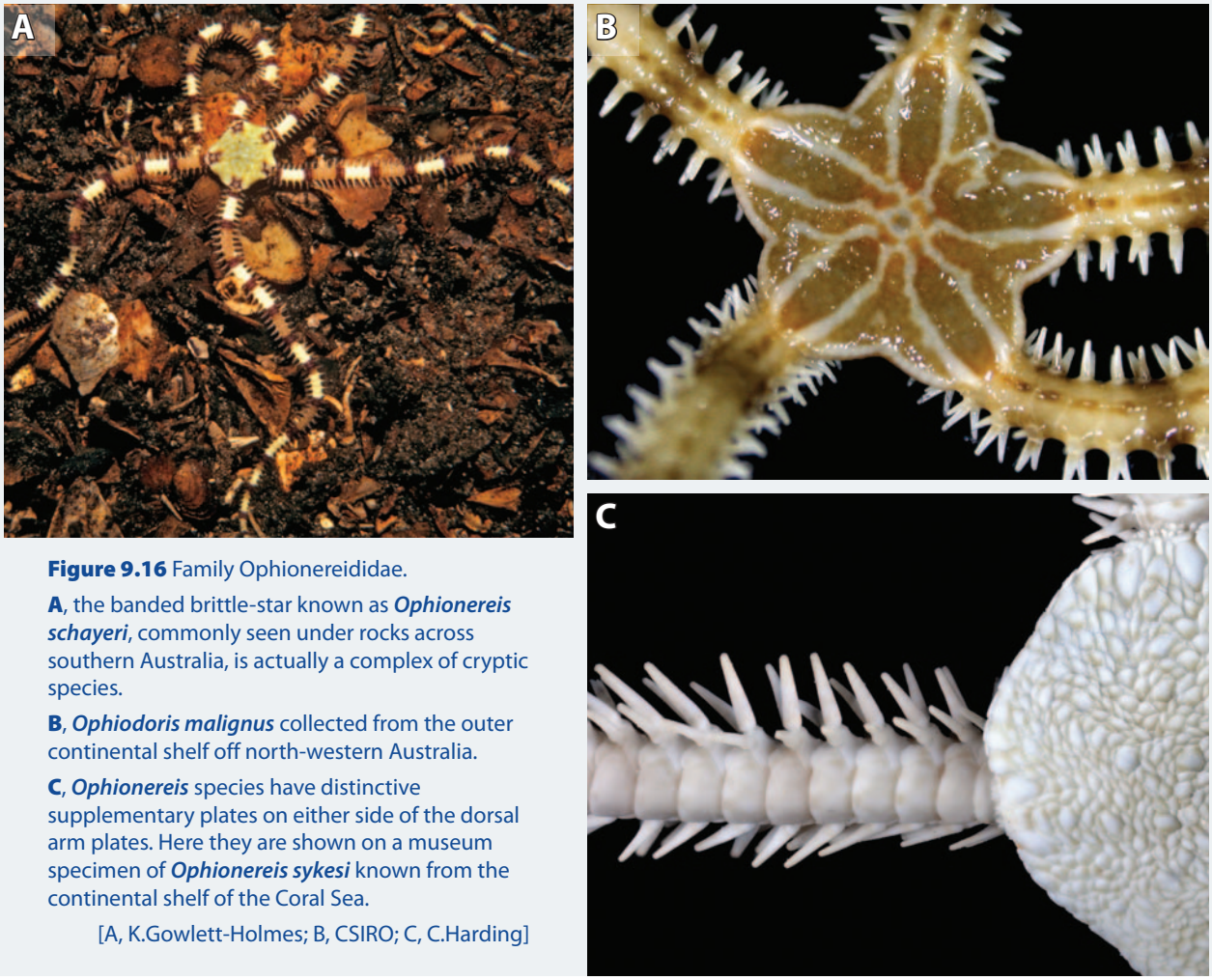


Figure 9.16 Family Ophionereididae.

A, the banded brittle-star known as ***Ophionereis schayeri***, commonly seen under rocks across southern Australia, is actually a complex of cryptic species.

B, ***Ophiodoris malignus*** collected from the outer continental shelf off north-western Australia.

C, ***Ophionereis*** species have distinctive supplementary plates on either side of the dorsal arm plates. Here they are shown on a museum specimen of ***Ophionereis sykesi*** known from the continental shelf of the Coral Sea.

[A, K.Gowlett-Holmes; B, CSIRO; C, C.Harding]

et al. 1995). However, genetic data indicates that *Ophionereis* clusters with the other genera (Hugall *et al*. 2015). A morphological transition can be seen between *Ophiochiton lentus*, with no supplementary arm plates, through *Ophionereis triphylax* and *O. australis*, with a few basally, to *Ophionereis schayeri* with well-developed supplementary plates along the length of the arm (**Fig. 1.6D**).

Ophionereis occurs in tropical and temperate regions, but most species are found in shallow tropical waters (Clark 1953b). Nine species of *Ophionereis* have been reported from tropical Australia (O'Hara 2012). *Ophionereis dubia* is a complex of closely related species, including two that have been named, *O. amoyensis* from China and *O. andamanensis* from India. Also similar are two six-armed Indo-west Pacific species, *O. hexactis* with V-shaped markings over the concealed radial shields and *O. thryptica* with a reticulate-patterned disc and visible radial shields (Clark 1946; Guille & Wolff 1984). Although both species have six arms they show no evidence of fission. *Ophionereis porrecta* is another species complex (Hoareau *et al*. 2013). *Ophionereis semoni* has a widespread Australian distribution, extending around the south-western coast as far as Investigator Strait in South Australia. Several other Indo-west Pacific species, including *O. fusca*, *O. variegata* and *O. intermedia*, have been recorded rarely from Australia's north (Rowe & Gates 1995). There are two endemic species, *O. tigris* and *O. lineata*, from northern Queensland.

Ophionereis schayeri (**Fig. 9.16A**) is very common on rocky subtidal reefs from the Houtman Abrolhos in Western Australia to southern Queensland. The disc is a pale grey, and the arms are characteristically banded black, grey, white and green. Genetic evidence shows that *O. schayeri* comprises a number of cryptic lineages, including an outer shelf species, a species from the Kermadec Islands, and several shallow water Australian species with overlapping distributions (K.M.Naughton & T.D.O'Hara, personal observation). *Ophionereis novaezelandiae* also occurs in south-eastern Australia and northern New Zealand on the outer continental shelf and upper slope (Mills & O'Hara 2013). Several undescribed species, similar to *O. australis* from South Africa, with supplementary plates restricted to a few basal segments, have been found on the continental shelf around Australia (Rowe & Gates 1995; T.D.O'Hara, personal observation).

Ophiochiton, *Ophioplax* and *Ophiodoris* occur on continental slopes in tropical and temperate regions. Almost nothing is known of their biology, although many species are likely to live on soft sediments (T.D.O'Hara, personal observation). Four species have been found off Australia. *Ophiochiton lentus*, *O. fastigatus* and *Ophioplax lamellosa* (**Fig. 9.3A**) have been collected from the continental slope adjacent to Bass Strait (Rowe & Gates 1995; O'Hara 2012). *Ophiodoris malignus* (**Fig. 9.16B**) has been found down the Western Australia coast into the Great Australian Bight (O'Hara 2012).

Ophionereis species are microphagous feeders. The New Zealand species *Ophionereis fasciata* extends several of its arms from its shelter into the water current at a slight angle to the horizontal (Pentreath 1970). The tube feet spread mucus threads between the arm spines and continually stroke the spines; the accumulated food particles are then scraped off onto the large tentacle scale. Pairs of tube feet later roll the accumulated food into a bolus which is passed to the mouth. *Ophionereis reticulata* from the Caribbean and *O. schayeri* from southern Australia adopt similar feeding postures (Sides 1985; O'Hara 1995b). The former species can alter the shape of the crevice in which it shelters, preferring a small narrow space and opening. This manipulation of the crevice acts as a competitive mechanism, rendering the shelter unsuitable for other ophiuroid species (Sides 1985). *Ophionereis schayeri* is a nocturnal feeder, extending its arms from the daytime hiding place to suspension and deposit feed (M.Byrne, personal observation). This species is often seen associated with the polychaetes scale worm *Lepidonotus melanogrammus* perched on its disc (**Fig. 2.25B**). *Ophionereis schayeri* and *O. fasciata* are bioluminescent (Mallefet *et al* 2004; **Box 2.2**).

The Ophionereididae include species with the full range of life histories seen in the Ophiuroidea from development through planktotrophic larvae to brooded development in the bursa (Byrne 1991; Hendler 1991; Selvakumaraswamy & Byrne 2000a). Four brooding species are known, from the subantarctic, Caribbean and Californian coasts, and are hermaphrodites (Byrne 1991; Hendler 2002). Other species, such as *O. fasciata* from New Zealand, have small eggs (100 µm) and planktotrophic larvae (Falkner *et al*. 2006). *Ophionereis schayeri* has comparatively small eggs (240 µm diameter) for a species with lecithotrophic development (Selvakumaraswamy & Byrne 2000b; Falkner *et al*. 2006). Spawning in this species mainly occurs during the summer with low-intensity gamete release occuring under favourable conditions until August (Selvakumaraswamy & Byrne 1995; Falkner *et al*. 2006). This species develops through reduced ophiopluteal and vitellaria stages before settling after 6–7 days (Selvakumaraswamy & Byrne 2000a, 2004). The West African *O. sexradia* and the small Japanese specimens named '*O. dictydisca*' are fissiparous (Clark 1967a).

Ophiopsila

Figure 9.17

Ophiopsila, which is distinguished by the presence of unequal tentacle scales, has the inner scales much longer than the outer ones and which cross over the opposite one from the other side of the segment (**Fig. 9.17C**). *Ophiopsila* species also have a cluster of dental papillae at the jaw apex, long narrow radial shields and numerous arm spines. The genus was grouped with ophiocomids on the basis that they shared a cluster of dental papillae at the jaw apex (Matsumoto 1915). However, Martynov

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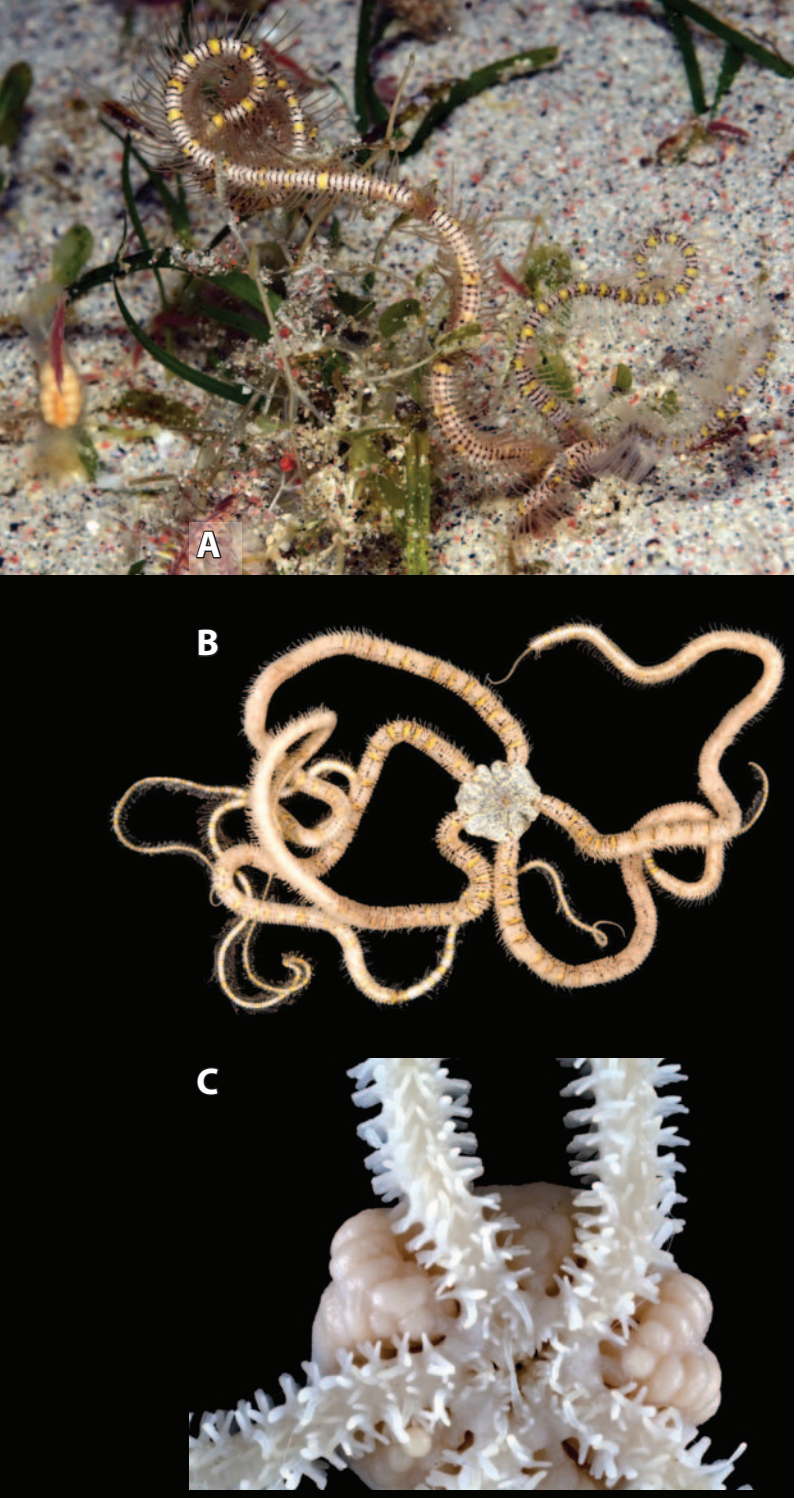


Figure 9.17 *Ophiopsila*.

A, ***Ophiopsila polyacantha*** from the Philippines extends its arms to feed from a burrow in the sediment.

B, the same animal of ***Ophiopsila polyacantha*** as **A**.

C, ventral view of an ***Ophiopsila*** individual collected at 100 m off Carnarvon, Western Australia, showing the long crossed tentacle scales.

[A,B, G.Paulay; C, C.Harding]

(2010b) suggested on the basis of several internal skeletal characters that this genus is more appropriately placed near the Amphiuridae. Available genetic data indicate that it forms a divergent clade deserving of family-level status. Like amphiurids and ophionereids, ophiopsilids have long arms that are used to filter feed (**Figs 2.19B, 9.17A,B**) and are brightly bioluminescent (**Box 2.2**). Around Australia, most specimens have been identified as *Ophiopsila pantherina*, which has a colourful green patterned disc and banded arms, however numerous species have been described from around Indonesia and the Philippines in 10–300 m and at least some of these are likely to be found in Australian waters. *Ophiopsila pantherina* has been found in dense aggregations on the leeward side of subtidal dunes (65–70 m) in the central Great Barrier Reef region (Woolsey *et al*. 2013; **Fig. 2.19B**). When touched, this species emits a bright green flash that presumably distracts predators.

Amphilimna

Figure 9.18

Amphilimna is characterised by having arm spines under the disc that are fused into moveable flanges (**Fig. 9.18B**). The included species also have spines or granules on the disc; small, sunken, parallel radial shields; long arms; a pair of papillae at each jaw apex; and, several oral papillae on each side (Thomas 1966). The genus can be divided up into two groups characterised by ovoid or spiniform inner tentacle scales. There has been much confusion over the systematic position of *Amphilimna*. Originally considered to be amphiurids, Thomas (1975b) transferred the genus to the Ophiacanthidae. Liao (1983) erected a new genus, *Sinophiura*, in Ophiuridae, for one species, *A. multispina*. However, Martynov (2010b) after examining many internal and miscroscopic features re-established their amphiurid affinity. In contrast, the genetic data indicates that *Amphilimna multispina* is related most closely to ophionereids, possibly deserving of family status.

Several species have been discovered in Australia on the north-western outer continental shelf and upper slope (100–400 m). These include *Amphilimna multispina*, *A. tanyodes* (**Fig. 9.18A**), *A. transacta* (**Fig. 9.18B**) and *A. granulosa* (O'Hara 2012), all previously known from Indonesia, southern China or the south-west Pacific Ocean.

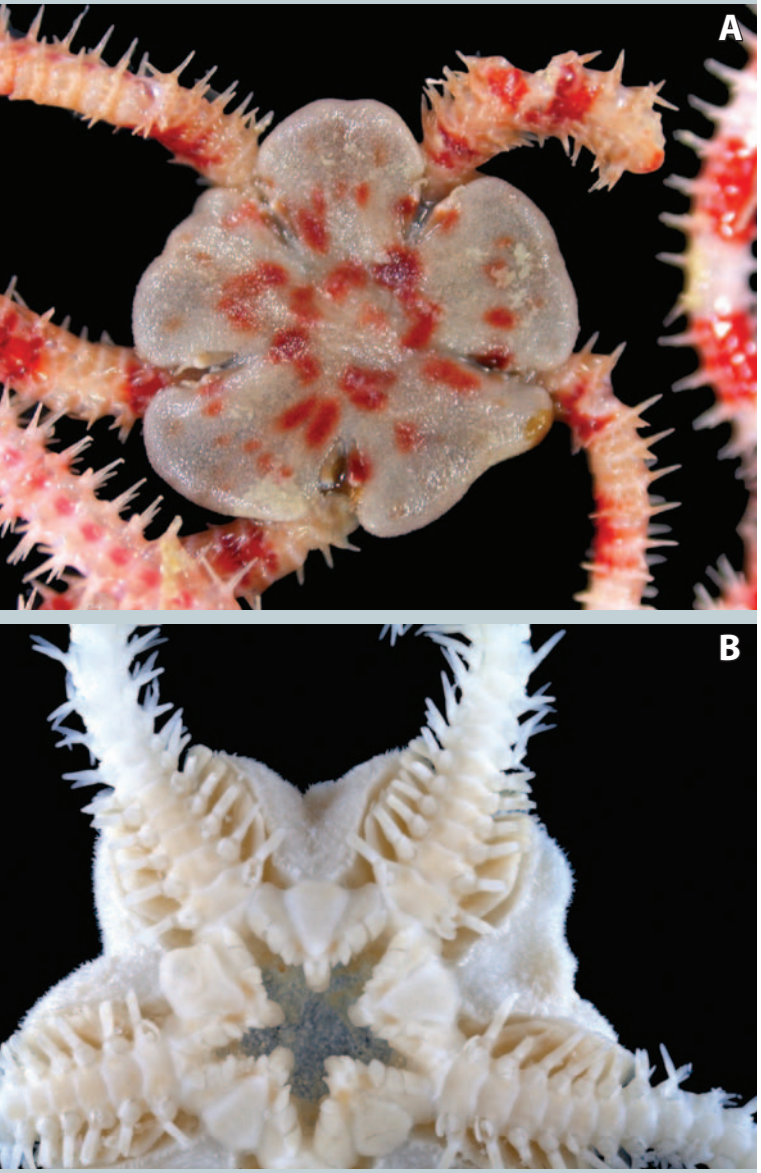


Figure 9.18 *Amphilimna*.

A, ***Amphilimna tanyodes*** collected at 415 m from off Kalbarri, Western Australia.

B, ventral view of ***Amphilimna transacta*** showing the flange-like fused basal arm spines under the disc.

[A, CSIRO; B, C.Harding]

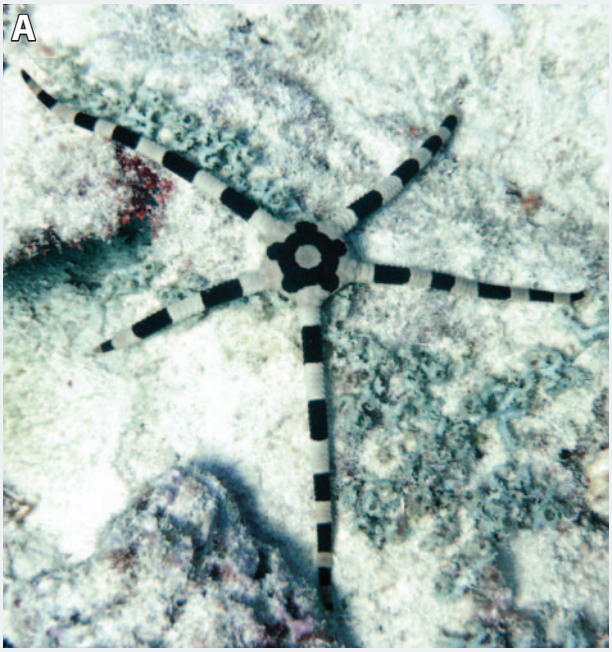
Family Ophiolepididae

Figure 9.19

The arms of ophiolepidids are long and stout, fused laterally into the disc, and bear short adpressed arm spines. The dorsal arm plates are fragmented or augmented by supplementary plates in several genera, and the disc is usually covered with thick plates. Tentacle pores are usually well developed throughout the arm and are protected by one to several scales. There is an unpaired, infradental papilla at the end of each jaw, and a series of oral papillae along the side of the jaw, although occasionally these are fused. The second oral tentacle pore opens on the sides of the jaw inside the oral slit and is often not visible from the ventral side (H.B.Fell 1960; F.J.Fell 1982). The classification of ophiolepids has been problematic, mostly because, traditionally, it has included both *Ophiolepis* and *Ophiomusium*-like species, which is no longer considered related (O'Hara *et al*. 2014b). Consequently, ophiolepids were frequently grouped with the Ophiuridae (Matsumoto 1915; Spencer & Wright 1966). *Ophiomusium*, *Ophiosphalma* and *Ophiolipus* are now considered to belong to a separate family (see above).

Ophiolepididae are known from the intertidal to the mid-continental slope depths (2,500 m). Important genera include *Ophiozonella* (28 species), *Ophiolepis* (23) and *Ophioplocus* (11). Seven genera with 22 species have been recorded from Australia (O'Hara 2012), and ophiolepidids can often be a notable component of the tropical littoral fauna. *Ophiolepis* species occur in sandy habitats, and five Indo-Pacific species have been recorded from Australia (Rowe & Gates 1995). These are sluggish animals (Clark 1946), and at least one species is readily displaced from its shelter under rocks by more aggressive *Ophiocoma* species (Sides 1985). The strikingly patterned *Ophiolepis superba* (**Fig. 9.19A,D**) is found as far south as Sydney, New South Wales, and *Ophioplocus imbricatus* (**Fig. 9.19E**) is very common in shallow waters across tropical Australia and throughout the Indo-Pacific from Zanzibar to Japan. Small *Ophiolepis* species are hermaphroditic brooders (Byrne 1989). *Ophioplocus* species have characteristic fragmented dorsal arm plates. The two Australian species of the aberrant genus

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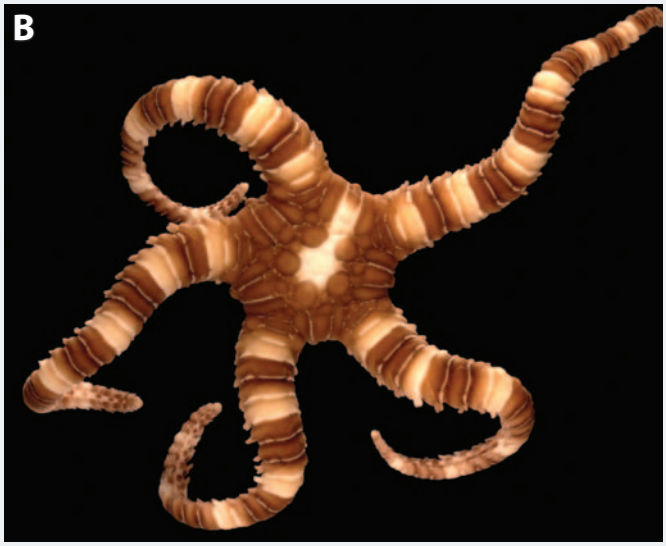




Figure 9.19 Family Ophiolepididae.

A, the rigid black-white ***Ophiolepis superba*** from One Tree Island, Queensland.

B, ***Sigsbeia oloughlini*** is a recently described species, found off Esperance in Western Australia.

C, ***Astrogymnotes*** species have colourful ventral surfaces suggesting that they face outward from their perches on black coral trees. This image is of ***A. hamishia*** found off New Caledonia. (specimen MNHN EcOs 22298)

D, ventral surface of ***Ophiolepis superba*** from Heron Island off Queensland.

E, ***Ophioplocus imbricatus*** is composed of a complex of similar species that occur across shallow water tropical Indo-west Pacific habitats. This image of an animal from Heron Island, Queensland, shows the fragmented dorsal arm plates.

[A, J.Reifell; B,C, C.Harding; D,E, F.Michonneau]





Ophioteichus are only known from a few specimens, *O. parvispinum* is known only from the type specimen found on Lord Howe Island. The marginal plates on the disc are swollen, forming a rampart like structure (Pineda-Enriquez *et al*. 2014). The tropical deepsea ophiolepidid fauna is imperfectly known, with several species known only from single localities, including *Ophiozonoida innominata* from off north-western Australia (Rowe & Gates 1995).

Ophioplocus bispinosus, a brooding species, is common on rocky shores of south-eastern Australia, but it appears to have quite a limited distribution from Encounter Bay, South Australia, to Harmers Haven in Victoria, including the north and east coasts of Tasmania (O'Hara 2012). *Ophioplocus incipiens* is the only species found in Antarctic and subantarctic waters, south of Australia, including off Macquarie Island (O'Hara 1998). It is closely related to *O. bispinosus* from southern Australia and two other species from New Zealand that were all formerly assigned to the genus *Ophioceres* (Thomas 1975a). *Ophioplocus incipiens* is suspected to be an aprotandric hermaphrodite that broods its young in bursae (Mortensen 1936). *Ophioplocus januarii* has a vitellaria larva (Komatsu & Tomoko 1993). *Ophioplocus januarii* from Patagonia has large eggs (400 µm diameter) in a continuous reproductive cycle through the year with lecithotrophic development and a likely vitellaria larva (Brogger *et al*. 2013). *Ophiozonella* species are restricted largely to the upper continental slope, predominantly in tropical waters. Two species, *O. bispinosa* and *O. depressa*, persist into southern Australia (O'Hara 2012), and the New Zealand species *O. stellata* occurs on the Macquarie Ridge (O'Hara *et al*. 2013).

Our genetic evidence suggests that the ophiomyxid genus *Astrogymnotes*, and a group of similar genera formerly assigned to the Hemieuryalidae, are more appropriately referred to the Ophiolepididae. *Astrogymnotes catasticta* (**Fig. 9.2**) has been found off south-western Australia at depths of 51–183 m (Marsh 1991) as well as off Jolo in the Philippines (Mortensen 1932). It has six, rarely seven, arms, divides by fission (Clark 1946), and has been found on black antipatharian corals (Mortensen 1932), occasionally also associated with the asteroschematid ophiuroid *Astrobrachion adhaerens* (Marsh 1991). It lies with the dorsal side of its disc against the coral, and is most brightly coloured on its exposed ventral surface (Mortensen 1932). The three species of *Astrogymnotes* from around the Kermadec Islands, New Caledonia (**Fig. 9.19C**) and Japan are also found on black corals in a similar feeding position (Baker *et al*. 2001).

Four similar genera, *Hemieuryale*, *Sigsbeia*, *Ophioholcus*, and *Ophioplus*, grouped together as the Hemieuryalinae, are known largely from the Caribbean and the tropical eastern Pacific Ocean. However, a new species of *Sigsbeia* (**Fig. 9.19B**) was discovered recently off Esperance in the Great Australian Bight (O'Hara & Harding 2014). *Sigsbeia* species have previously been found on stylasterids, coral-like hydroids (Byrne 1994), although this is unknown for the Australian species. Some *Sigsbeia* species are brooders (Byrne 1991). A single stout disarticulated vertebra from Miocene or Pliocene rocks in Victoria has been referred to *Sigsbeia* (Hall 1902), although this needs modern reappraisal.

Family Amphiuridae

Figure 9.20

The amphiurid disc is either naked or covered with thin imbricate scales, occasionally with small spines or tubercles. The arms tend to be long and slender, and inserted ventrally under the disc. The lateral arm plates are often reduced, neighbouring plates being separated by ligaments that allow considerable horizontal flexibility of the arm. The development of the upper condyle on the proximal side of each vertebra allows aboral flexion of the arm in at least one species (*Amphipholis squamata*). Arm spines are short and stout, but not adpressed, and, occasionally, the tips of one or more arm spines are modified as specialised digging organs. A pair of infradental papillae, usually block-like in shape, is situated at each jaw apex, and within the mouth slit there are two pairs of oral tube feet, the first of which can be protected by a buccal scale. Two to four oral papillae occur on each side of the jaws, and the teeth are broad and blunt (Emson & Wilkie 1982; Fell 1982; Rowe & Gates 1995). The family is the largest in the Ophiuroidea with 36 genera and over 511 species (Stöhr *et al*. 2014). While 202 of these species belong to a single genus (*Amphiura*), many of the other genera contain only a few species.

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The number and arrangement of oral papillae and buccal scales are fundamental in amphiurid taxonomy (A.M.Clark 1970). The principal patterns are typified by the four largest genera, *Amphiura*, *Amphiodia*, *Amphipholis* and *Amphioplus*. In *Amphiura* there is a gap along the side of the jaw between the apical papillae and the oral papilla; the oral papilla is placed well back on the edge of the adoral shield, and a buccal scale lies between the apical and oral papilla at a deeper level in the oral slit. *Amphiodia* and *Amphipholis* have two oral papillae on the side of each jaw immediately adjacent to the apical pair (**Fig. 9.20C**). In *Amphipholis* the distal papilla is often considerably widened. *Amphioplus* has a continuous series of three oral papillae on the side of each jaw. The papillae in these genera are not homologous, however, and they arise on different plates at different ontological stages (Hendler 1978, 1988). For example, the buccal scale is a significant ossicle in many juvenile amphiurids. It is transformed into the second oral papilla in *Amphioplus* and resorbed completely in *Amphipholis* and *Amphiodia*.

Some species have unusual oral arrangements and the size and shape of the oral papillae and scales can vary widely. For example, *Amphiura bidentata* from the northern Australian coast has two distal oral papillae. In morphology, many aberrant species of *Amphioplus* occupy intermediate positions between *Amphioplus sensu stricto* and other genera (A.M.Clark 1970). The genetic data indicate that *Amphioplus* is a polyphyletic taxon.

A few genera have disc spines or tubercles. *Ophiocentrus* has an *Amphiura*-type oral arrangement and minute disc spines, *Dougaloplus* has an *Amphioplus*-type jaw and disc spines, and *Amphistigma* has an *Amphipholis*-type jaw with tubercles on the dorsal disc surface (**Fig. 9.20A**). Some *Amphiura* species can have swellings on the disc scales.

Taxonomy of Amphiuridae is unstable. Several attempts have been made to subdivide the larger genera based on the number of tentacle scales and extent of disc scaling (Fell 1962b), internal skeletal characters (Thomas 1966) or a combination of disc and arm characters (A.M.Clark 1970). This has caused some confusion in the taxonomic and ecological literature. A.M.Clark's (1970) taxonomic scheme has been followed in the Australian context (Rowe & Gates 1995).

The Amphilepididae is sometime considered a subfamily of the Amphiuridae (A.M.Clark 1970), a decision not accepted by all authors (Wilkie 1980; Smith *et al*. 1995). *Amphilepis* has a flattened jaw with narrow teeth, and a series of papillae on the sides of the jaw. The proximal papillae can sometimes be infradental in position. No *Amphilepis* species are recorded for Australia. *Amphilepis gymnopora* was described from the Australian Antarctic Territory (Hertz 1927a); however the type specimens are probably juvenile *Amphiura belgicae* (Madsen 1967). Several other *Amphilepis* species are also juvenile *Amphioplus* (Brogger & O'Hara 2015). *Amphilepis neozelandica* is known from New Zealand (Mills & O'Hara 2010). Development of the juvenile skeleton of *Amphilepis ingolfiana* is detailed in Sumida *et al*. (1998).

The fossil history of the Amphiuridae is not extensive. The earliest recorded amphiurid fossil, recorded from Switzerland, is *Xanthamphiura hauteriviensis* from the Early Cretaceous (Hess 1970) although its relationships are also unclear (B.Thuy, personal observation). The systematic position of *Amphiura felli*, from the Late Cretaceous of Queensland (**Table 9.2**), requires confirmation, given that the structure of the jaw and the aboral disc surface are unknown.

Amphiurids are common in all seas, from the intertidal to abyssal depths (**Fig. 9.20E**). They can be very abundant in soft sediments, and they often characterise local faunal assemblages in forming dense aggregations (Fell 1966b; O'Connor *et al*. 1983; Munday & Keegan 1992). They live buried with their disc in a shallow burrow and several arms extended aborally to feed on the surface (Fell 1966b). Microhabitat preferences often vary between sympatric species. For example, in south-eastern Australia *Amphiura constricta* (**Fig. 9.3D**), *A. poecila* and *Amphipholis squamata* live under rocks and among shellgrit or algal turf (Kelaher 2002; Falkner & Byrne 2006; T.D.O'Hara, personal observation). *Amphiura* (*Ophiopeltis*) *parviscutata* lives in sandy sediments, and *A. elandiformis* occurs in the thick mud (T.D.O'Hara, personal observation). *Amphiura trisacantha* occurs in seagrass beds, and *Ophiocentrus pilosus* is a common infaunal species in soft sediments throughout southern Australia.

On the Great Barrier Reef some species inhabit coral heads (Austin *et al*. 1980). *Amphiura belgicae*, from deep water off Antarctica, occurs on polyzoan masses (Fell 1961), and the viviparous subantarctic species *A. magellanica* is both epiphytic and epizoic, using its elongated ventral arm spines to climb the substratum (Mortensen 1924). The ubiquitous *Amphipholis squamata* is reported to be the most widespread of all brittle stars, occurring in most seas and in a large variety of habitats, from the intertidal to at least 1,350 m (Gage *et al*. 1983), however, it is likely to be a suite of cryptic species (Sponer *et al*. 2001; Sponer & Roy 2002; Le Gac *et al* 2004; Boissin *et al*. 2008).

Although amphiurids are primarily microphagous, larger prey can occasionally be caught by an arm loop (Warner 1982). Suspension- and deposit-feeding are widely practised; the latter can take place at the surface (**Figs 1.11, 9.20D**) or in the sub-surface. Sub-surface feeding has been demonstrated for the New Zealand species *Amphiura aster* (Pentreath 1970) and an *Amphipholis* species from South Carolina (Gielazyn *et al*. 1999). The animal lies buried in sand, 50–100 mm beneath the surface. One arm is held near the disc, maintaining the burrow, while the others maintain channels to the surface, with only the arm tip protruding. The tube feet secrete mucus to support the channel walls. Food particles are passed to the mouth and ingested. The animal moves under the surface by thrusting the subterranean arm forward. *Amphipholis squamata* can employ either deposit- or suspension-feeding (Warner 1982), the latter being prevalent when there is water movement. Several arms are raised stiffly into the current, the arm spines become covered with mucus, and trapped food particles are removed by the tube feet (Pentreath 1970; O'Hara 1995b). This is a bioluminescent species (Deheyn *et al*. 2000).

Partial predation by fish on exposed arms is common, while autotomy of the dorsal disc can also occur, possibly as a means of predator avoidance (Clements 1985) or to dislodge parasites (Radar 1982). The disc can regenerate within several days. Dredging can also cause disc autotomy, and thus creates difficulties for the identification of specimens. Several Australian amphiurids appear to lose their disc readily, among them the southern Australian species *Amphiura elandiformis* (T.D.O'Hara, personal observation).

Reproductive strategies in amphiurids range from planktotrophic larvae to brooding (Byrne 1991; Hendler 1991; Byrne & Selvakumaraswamy 2002). There are many studies of the brooding biology of the cosmopolitan species *Amphipholis squamata* (Fell 1946; Walker & Lesser 1989; Byrne 1994). This species is a simultaneous hermaphrodite with an ovary and testis on both sides of each bursal sac (Hyman 1955). Gametogenesis is non-seasonal, and 2–7 eggs and embryos can be found in a specimen at any one time (Rumrill & Pearse 1985). Embryos are brooded in the bursae before the relatively large juveniles (almost half the size of the adult) are released (**Fig. 3.5 A–C**). Juveniles can take three to four hours to emerge (Hendler 1991). This reproductive strategy supports opportunistic recruitment and rapid colonisation (Rumrill & Pearse 1985), abilities that have probably enabled this species to achieve its very widespread, although patchy, distribution (Hendler 1991). Other brooding species include *Amphiura constricta* and *Amphistigma minuta* (**Fig. 9.20A**) from southern Australia (O'Loughlin 1991; Falkner & Byrne 2006) and several *Amphiura* species from the Southern Ocean (Mortensen 1936). *Amphiura constricta* is a simultaneous hermaphrodite with the unusual arrangement of having both ovaries and testes on the interradial side of the bursa (Hyman 1955). Skeleton development of juvenile *A. constricta* is described in Falkner & Byrne (2006). Fissiparity, the other reproductive strategy typical of small species, is not common in the Amphiuridae. Several fissiparous species have been recorded, including the Indo-Pacific *Amphiura velox*, the northern Atlantic *Amphipholis torelli*, *Amphioplus hexabrachiatus* and the western Atlantic *Ophiostigma siva* (Emson & Wilkie 1980; Hendler 1995; Stöhr 2003). Another fissiparous species, *Amphiodia dividua*, is now considered conspecific with the ophiocomid *Ophiocomella sexradia* (A.M.Clark 1970).

The genera *Ophiodaphne* and *Ophiosphaera* have been transferred recently from the Ophiactidae to the Amphiuridae on the basis of their patterns of oral papillae and arm-spine articulations (Martynov 2010b). Both are unusual in that they are sexually dimorphic, females are often found carrying dwarf males over the mouth; they are associated with echinoids (Mortensen 1933a). *Ophiodaphne formata* usually

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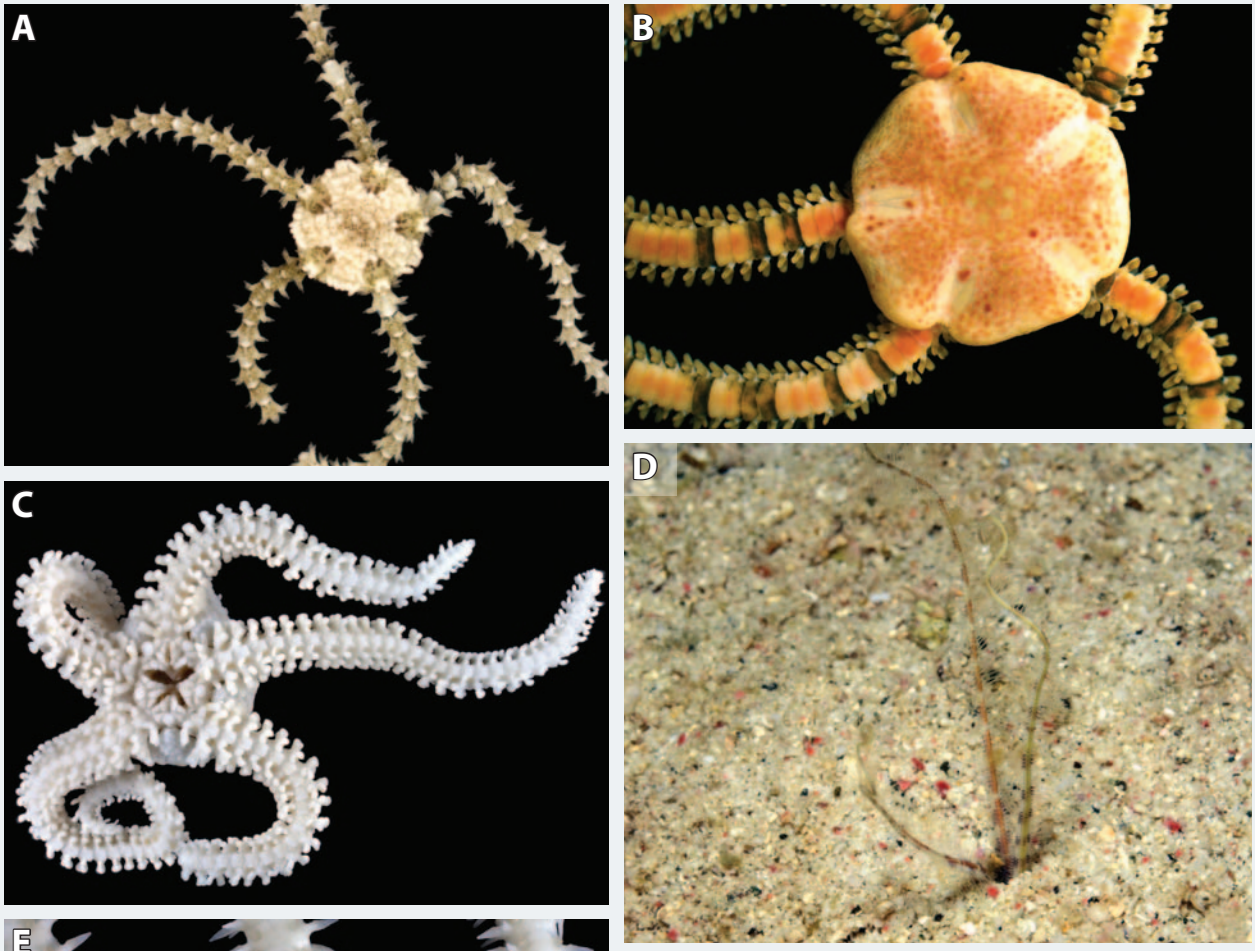


Figure 9.20 Family Amphiuridae.

A, the tiny brooding ***Amphistigma minuta*** lives among seaweeds in rockpools across southern Australia.

B, ***Amphioplus ochroleuca*** is a tropical shallow water amphiurid that also occurs in bays across southern Australia.

C, ***Amphipholis linopneusti*** is usually found on the underside of heart urchins on the continental shelves of the south-west Pacific Ocean, where it presumably steals the host's food.

D, amphiurid species frequently extend their arms from a burrow to feed. The tube feet are extended horizontally and covered in mucus to capture small prey.

E, ***Amphioplus daleus*** occurs on the abyssal plains of the world's oceans. ***Amphioplus*** differs from most other amphiurid genera in having a continuous row of oral papillae along the jaws.

[A, L.Altoff; B, M.Byrne; C,E, C.Harding; D, G.Paulay]

Box 9.2 The brooding brittle star, *Amphipholis squamata*

Features *Amphipholis squamata* is a small brittle star, usually with a disc diameter of 1–3 mm, very rarely up to 5 mm. Arm lengths are 3–5 times the disc diameter. The disc is covered with tiny plates, and has no spines or tubercles. The jaw has two rectangular papillae at the apex and a square inner and broad, rectangular, distal papilla on each side. Two tentacle scales guard each tube foot pore, and four erect arm spines occur on each side of the arm segments. Specialist cells (photocytes) along the arms become bioluminescent when the animal is touched.

This species is a hermaphrodite and broods its young (**Fig. 3.5A–C**). Male and female gonads empty sperm and eggs into the bursal sac. Embryos are retained in the bursal sac, where they can grow up to a disc diameter of 900 µm before they emerge.

Amphipholis squamata exhibits many colour varieties, including grey, orange, black and several spotted variations. In southern Australia, the disc is often pale grey, the radial shields are white distally and darker towards the disc centre, and the arms are white.

Cancerilla copepod parasites can often be seen on the ventral or marginal surface of the body.

Distribution The brooding brittle star occurs in all but polar regions, from the subtidal to 1,350 m. Around Australia it has been found along most coastlines, including Macquarie Island, at depths to 841 m.

Way of life This species is enigmatic insofar as it is the most widespread of any shallow-water echinoderm and yet it broods its young, generally an indication of limited dispersal capabilities. Moreover, while molecular studies have found considerable genetic variability between populations, all appear to be morphologically indistinguishable. The many colour variants do not correspond with the major clades that have been defined genetically. Different populations and colour forms can reproduce at different times.

Recent research points to the probability of *Amphipholis squamata* being an ancient complex of cryptic species, many of which have achieved a worldwide distribution. Each of these 'species' has multiple colour forms, some of which are similar to colour forms in other 'species'. The different colour forms could be adapted to local environmental conditions, enabling the animal to hide from predators in seaweeds of different colour or habit. Within each 'species' distant populations appear to be genetically distinct, which suggests that long distance dispersal is infrequent (although *Amphipholis* can survive for up to 6 months in detached seaweed). There is also evidence of self-fertilisation and perhaps even parthenogenesis (asexual reproduction) which would greatly enhance the tendency of this species to split into separate genetic clades.

As a defence from predators, these brittle stars are able to autotomise arms that then wriggle about, thus distracting the predator and allowing the brittle star to escape. Bioluminescence could accentuate this process, as a flashing arm could be more attractive to a predator.

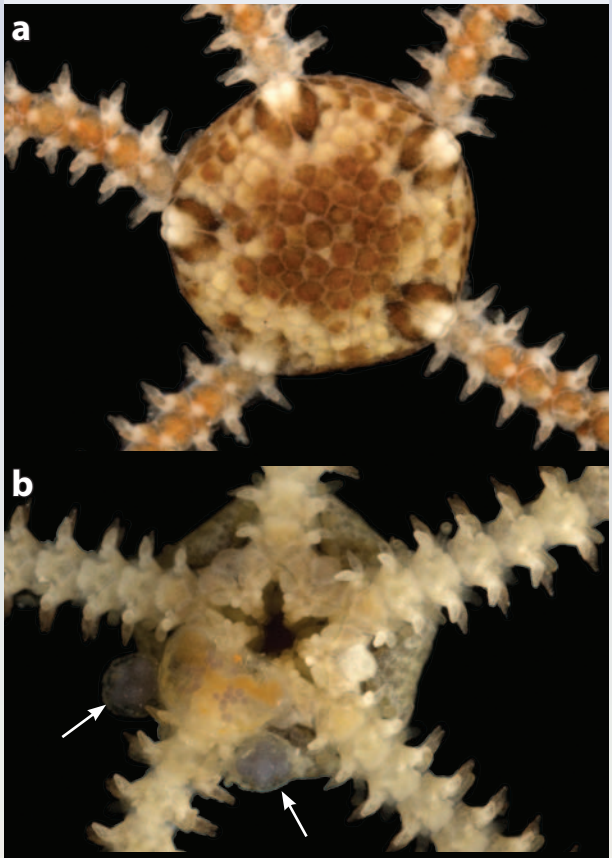
Interaction with humans This brittle star is common in algal turf on rocky shores, but it is rarely noticed due to its small size.

Similar species *Amphipholis* species known from the tropical Indo-Pacific have either much longer arms (*A. misera*) or enlarged lowermost arm spines

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near the disc (*A. linopneusti*). *Amphipholis loripes* with one tentacle scale has been recently transferred to *Amphiodia* (Stöhr 2011). *Amphistigma*, another genus of minute brittle stars restricted to Australia, has similar mouth parts, but can be distinguished microscopically by the presence of tubercles around the edge of the disc.

Family Amphiuridae
Species *Amphipholis squamata* (Della Chiaje, 1828)



Figures a, **b** ***Amphipholis squamata***.
a, these brooding brittle stars are a common animal in shallow water under stones and in algal turfs across the globe.
b, they are frequently parasitised by ***Cancerilla*** copepods (arrows).
[L.Altoff]

occurs on the oral surface of sand dollars, such as *Astriclypeus mannii*, *Clypeaster reticularus* and *C. japonicus* in Japan (Tominaga *et al*. 2004), and *C. tumidus* in the Coral Sea (McKnight 1989). The brittle star's mouth is usually turned away from the sand dollar, suggesting that it does not feed directly from the sand dollar's radial food track but uses its host as a convenient breeding site to increase fertilisation success (Tominaga *et al*. 2004). *Ophiosphaera insignis* has been found associated with *Tripneustes gratilla* in Madagascar (Cherbonnier & Guille 1978).

Eight amphiurid genera and 70 species have been recorded from around Australia: *Amphiura* (39 species), *Amphioplus* (14), *Ophiocentrus* (8), *Amphistigma* (2), *Amphiodia* (1), *Amphipholis* (3), *Dougaloplus* (1), *Ophiodaphne* (1) and *Ophiosphaera* (1) (Rowe & Gates 1995; O'Hara 2012). In addition, numerous species in collections await description. The large genera *Amphiodia* and *Amphipholis* are comparatively poorly represented in Australia. Approximately 10 amphiurid species, belonging to the genera *Amphiura*, *Amphioplus* and *Amphipholis*, are present near the Australian Antarctic Territory and the subantarctic islands.

The majority of Australian amphiurids are found in the tropics, including most Australian species of *Amphiura*, *Amphioplus*, *Ophiocentrus*, *Amphiodia*, *Amphipholis* and *Dougaloplus*. Most of these have also been collected at other Indo-west Pacific localities; only 12 are listed as endemic (Rowe & Gates 1995). The southern amphiurid fauna is less diverse but the family is still the most species-rich in the region and its representation will increase as many deep-water amphiurids cannot be assigned to named species (T.D.O'Hara, personal

observation). The southern Australian amphiurid fauna includes the endemic genus *Amphistigma*, and many endemic species. Several species are restricted to the south-western (for example *Amphiura nannodes*) or south-eastern coasts (*Amphiura elandiformis* and *A. parviscutata*). Two southern species are distributed outside Australia, *viz. Amphioplus ochroleuca* (Indo-Pacific) (**Fig. 9.20B**) and *Amphipholis squamata* (cosmopolitan) (**Box 9.2**).

Family Ophiactidae, *Ophiothamnus* and relatives

Figure 9.21

The Ophiactidae are characterised by the disc usually bearing small spines or granules (**Fig. 9.21A**), broad square-tipped teeth, a single papilla at the apex of the jaw, and a separate group of one or two (rarely three) oral papillae on the sides of each jaw (Fell 1982; Rowe & Gates 1995; **Figs 1.10, 9.21C**). The arm vertebrae articulate by a large dorsal condyle, allowing the flexibility of movement and fine control required for fissiparous division and rheotaxis (Emson & Wilkie 1980).

Originally described as a subfamily of the Amphiuridae (Matsumoto 1915), ophiactids are now referred to a separate family, and along with Amphiuridae and Ophiotrichidae are often placed in the superfamily Gnathophiuridea (Smith *et al.* 1995). The family generally includes five genera: *Ophiactis*, *Ophiopus*, *Ophiopholis*, *Hemipholis* and *Histampica* (formerly *Amphiactis*) (Stöhr *et al.* 2014). *Ophiopus* and *Ophiopholis* are restricted to the northern hemisphere (Clark 1911) and *Hemipholis* to the Pacific and Atlantic coasts of North and South America (Hendler 2011). *Hemipholis* is an aberrant genus that lacks bursal sacs and slits, gametes being released during spawning from protuberant genital papillae near the arm bases (Heatwole & Stancyk 1982). The position of other genera has been contentious. *Ophiodaphne* and *Ophiosphaera* have been recently transferred to the Amphiuridae from the Ophiactidae on the basis of their patterns of oral papillae and arm-spine articulations (Martynov 2010b). *Ophiothamnus* have been also sometimes considered to be close to ophiactids (Martynov 2010b). Our genetic data shed some light on these relationships (Hugall *et al.* 2015): *Ophiodaphne* is an amphiurid, whereas *Hemipholis* is a derived ophiactid. *Ophiopholis* is intermediate between the Ophiactidae and Ophiotrichidae, which explains the tendency for the presence of multiple dental papillae at the jaw apex of some species. Ophiactids form two clades that appear to be defined by the number of distal oral papillae. Species with one papilla include *Ophiactis definita* and *Hemipholis*. Species with two include *Ophiactis savignyi* and *O. abyssicola*. These two groups do not even cluster together on some phylogenetic trees and may represent two family-level lineages (**Fig. 9.4**). *Ophiothamnus* and *Histampica* form an isolated clade, sister to all ophiactids and ophiotrichids, deserving of family-level status.

Seventeen species of *Ophiactis* occur in Australian waters, with most species found in the tropics (O'Hara 2012). Several have very widespread distributions; *O. savignyi* (**Fig. 9.21D**) occurs throughout the Indo-Pacific and on both the east and west coasts of tropical America (Caspers 1985); molecular research suggests the presence of several cryptic taxa (Roy & Sponer 2001, 2002). *Ophiactis macrolepidota* may also be found to have a pantropical distribution, once all the relevant synonyms are included (Rowe & Gates 1995). Two species are typical of southern Australia, *O. resiliens* and *O. tricolor*, with the former also found off Lord Howe Island, Elizabeth and Middleton reefs, and New Zealand. *Ophiactis brevis*, from north-western Australia, resembles a darker *O. resiliens*.

Ophiactis abyssicola (**Fig. 9.21B,C**) occurs in deep water around southern Australia and New Zealand (O'Hara *et al.* 2014a). A related population or subspecies occurs in the south-western Indian and Atlantic oceans. Lower bathyal animals (>1,650 m) belong to a separate species, *Ophiactis amator*. Depth-stratified cryptic species are common on the continental slope. At lower latitudes these species are replaced by the *Ophiactis definita* complex which also includes multiple depth-stratified species (O'Hara *et al.* 2014a). *Ophiactis profundi* and *O. hirta* are two small fissiparous species complexes that also occur on continental slopes and seamounts around Australia and New Zealand.

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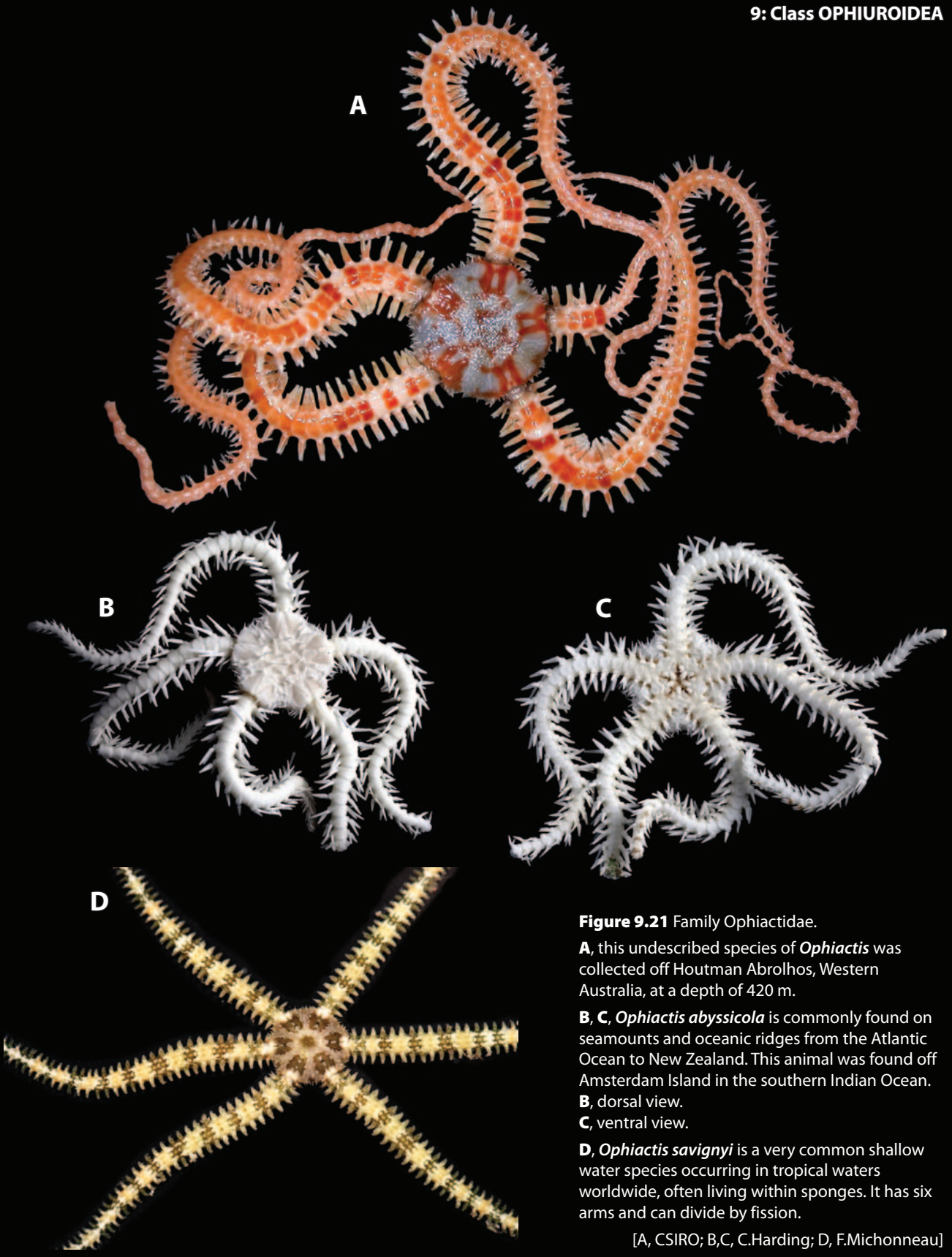


Figure 9.21 Family Ophiactidae.

A, this undescribed species of ***Ophiactis*** was collected off Houtman Abrolhos, Western Australia, at a depth of 420 m.

B, **C**, ***Ophiactis abyssicola*** is commonly found on seamounts and oceanic ridges from the Atlantic Ocean to New Zealand. This animal was found off Amsterdam Island in the southern Indian Ocean.
B, dorsal view.
C, ventral view.

D, ***Ophiactis savignyi*** is a very common shallow water species occurring in tropical waters worldwide, often living within sponges. It has six arms and can divide by fission.

[A, CSIRO; B,C, C.Harding; D, F.Michonneau]

Many *Ophiactis* species have six (rarely seven) arms and some reproduce asexually by fissiparity. Fifteen species have been recorded as fissiparous (Emson & Wilkie 1980), although this could be reduced to as few as 10 when all the synonyms have been suppressed. In Australian waters the following species are fissiparous: *O. savignyi*, *O. hirta*, *O. profundi*, *O. macrolepidota* and, possibly, *O. luteomaculata*. These are commonly found in the process of regeneration with three large and three small arms. *Ophiactis savignyi* is one of the most extensively studied: the percentage of animals in a population showing a sign of fission varies from 6% to 82% (Emson & Wilkie 1980; Chao & Tsai 1995), with fewer dividing in winter. Males are more likely to divide than females, possibly because females are more likely to lose reproductive capacity after fission (McGovern 2002). Fissiparity appears to be a reliable method of local recruitment (Lawrence 1987) and has been invoked to explain the broad distribution of this species (Hyman 1955). Sexual reproduction also occurs, even in regenerating animals, and it provides a mechanism for dispersal (Lawrence 1987). The occurrence of fission in the deepsea species *O. profundi* and *O. hirta* is noteworthy, given the view that fissiparity is usually linked to intertidal distributions (Emson & Wilkie 1980). Individuals of some fissiparous species can occasionally be found with five equal arms. Conversely, some non-fissiparous five-armed species, such as *O. abyssicola*, can, on rare occasions, be found with six equal arms (T.D.O'Hara, personal observation).

Other five-armed *Ophiactis* species are non fissiparous. *Ophiactis resiliens* populations near Sydney, New South Wales, have an annual reproductive cycle with the most intense spawning period in May and June (Falkner & Byrne 2003). After three months in the plankton as an ophiopluteus (**Fig. 3.11E**), larvae settle between August and January, with small juveniles (0.5 mm disc diameter) observed in the wild from February to May (Selvakumaraswamy & Byrne 2000a; Byrne & Selvakumaraswamy 2002; Falkner & Byrne 2003, 2006). Local increase in density of this species occurs around the breeding season (Falkner & Byrne 2004). Skeleton development of juvenile *O. resiliens* and *O. abyssicola* have been described by Sumida *et al*. 1998; Falkner & Byrne 2006.

Ophiactis savignyi is commonly found between the branches of coral, among algal fronds, and in sponges (Caspers 1985; Mladenov & Emson 1990). Off the Hawaiian Islands, it frequently occurs on the sponge *Damiriana hawaiiana*, with as many as 20 animals forming one or two tangled clumps within the canal system of the host (Caspers 1985). The ophiactids are almost immobilised by the thick slimy secretions of the sponge and it is not known how they feed. However, once they have become established, it appears that the *Ophiactis* populations are maintained by asexual fissiparous reproduction, as most of the inhabitants of a single sponge are clones (Mladenov & Emson 1990). Populations living in sponges are genetically distinct from those in algae in the Caribbean Sea, and could represent sibling species (Mladenov & Emson 1990).

Ophiactis resiliens is a suspension feeder (Pentreath 1970; O'Hara 1995b). Individuals tend to bury their discs in coarse sediments, under rocks, or in rock crevices, with 1–4 arms extended vertically into the current. The arms alter their orientation according to the current flow (rheotaxis), and the tube feet are widely spread laterally. Particles of food are caught on the papillate tube feet, less commonly on the arm spines, and. are transferred to the mouth in a 'collapsing wave' of tube feet. Each tube foot in turn collapses and thereby rubs any trapped particles on to its proximal neighbour. Near the arm base the food is compressed into a bolus that is passed to the mouth in a fashion similar to that illustrated in **Figure 1.11B–C**. Ingested food consists mainly of diatoms (Pentreath 1970).

Ophiactis plana is host to eulimid gastropod parasites. The snail *Ophieulima fuscoapicata* was described from a specimen off the Kermadec Islands (Warén 1981), and south-eastern Australian specimens have been found with similar parasites (T.D.O'Hara, personal observation).

Recognisable *Ophiactis* fossils have been found back to the mid Cretaceous (111 million years ago) in Mexico (Martin-Medrano *et al*. 2008).

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Family Ophiotrichidae

Figure 9.22

Ophiotrichids are well differentiated from other ophiuroids by their distinctive jaw structure (**Fig. 9.3E**). The family is unique in lacking oral papillae and in having a cluster of small dental papillae on the ventral end of the dental plate. Ophiotrichid species vary enormously in size, from the minute *Ophiothela danae* (**Fig. 9.22F**) with a disc diameter of only about 2 mm and arms of 5–10 mm long, to the much larger *Macrophiothrix* (**Fig. 9.22C**). A specimen of *Macrophiothrix paucispina* from Broome, Western Australia, had a disc diameter of 28 mm and arms 750 mm long, which is perhaps the longest arm length recorded for any brittle star (Hoggett 1991). Useful taxonomic characters include disc armament, relative size and shape of arm plates, arm spine ornamentation, arm and oral tentacle ornamentation, and the position of the longest arm spine in the dorso-ventral series (Hoggett 1990). The family was originally described by Ljungman (1867) under the name Ophiothricidae (an incorrect Latin formation of the name), based on the genus *Ophiothrix*. His description included jaw characters, and these are still regarded as the primary diagnostic features of the family.

Worldwide, the family comprises 16 genera of which 11 occur in Australia. The most speciose genus, *Ophiothrix*, has five subgenera, all of which occur in Australia. The Australian ophiotrichid fauna comprises 75 species with 41 belonging to *Ophiothrix* (O'Hara 2012). Ophiotrichids are found throughout Australian waters and are often abundant in the shallow-water fauna of both tropical and temperate areas.

Although most species live in waters less than 100 m deep, the Indo-Pacific *Ophiothrix aristulata* (**Fig. 9.3E**) is common on the upper continental slope (O'Hara *et al*. 2014a) and *O. albostriata* has been found at 1,000 m in the Great Australian Bight (O'Hara & Harding 2014). A surprisingly large number of tropical ophiotrichids (12) appear to be endemic to certain sections of northern Australia, and others are found only in northern Australia and nearby sections of the Indo-Malay Archipelago (O'Hara 2012). The remaining species with tropical affinities are more-or-less widely distributed in the Indo-west Pacific. Eleven ophiotrichid species are restricted to temperate waters in Australia, and most of these are endemic (O'Hara 2012). There is a broad zone of overlap between the tropical and temperate ophiotrichid faunas on both the eastern and western coasts (Rowe & Gates 1995).

The only comprehensive hypothesis of relationships within the family is based on morphological and electrophoretic data (Hoggett 1990). Four genera (*Ophiomaza*, *Ophiocnemis*, *Gymnolophus* and *Ophiolophus*) with relatively smooth arm spines, which are round in cross-section, are considered to have diverged from the rest of the family early in its evolution. The remaining genera share the specialised flattened and thorny arm spines. Within this larger group, it appears that at least four of the five nominal subgenera of *Ophiothrix* (*Ophiothrix*, *Acanthophiothrix*, *Placophiothrix* and *Keystonea*) are not monophyletic. Species referred to the last two subgenera are more closely related to *Macrophiothrix* species (**Fig. 9.22D**), and are perhaps referable to that genus (Hoggett 1990).

Little is known of the biology and ecology of Australian ophiotrichids. Many species extend their arms into the water to feed on plankton (Warner 1982). Some species are epizoic, coiling their arms more-or-less tightly around corals (for example, *Ophiothrix* (*Acanthophiothrix*) *purpurea* (**Fig. 9.22A**) and *Ophiothrix martensi* (**Fig. 9.22E**), gorgonians (for example, *Ophiothela danae*, **Fig. 9.22F**), or crinoids (for example, *Ophiomaza cacaotica*), and others shelter within non-branching hosts such as sponges (for example, *Ophiothrix ciliaris*, *O. caespitosa*, *O. aristulata*). *Ophiothrix caespitosa* is the most common ophiuroid on the continental shelf within Bass Strait. Despite its name, *Macrophiothrix spongicola* (**Fig. 9.22B**) is usually found under rocks or within *Ecklonia* holdfasts (T.D.O'Hara, personal observation), while *Ophiocnemis marmorata* and most members of *Macrophiothrix* live in soft sediments.

Macrophiothrix exhibits a variety of reproductive strategies, with a range of egg sizes (150–400 µm diameter), and both feeding and non-feeding reduced ophioplutei (Hart & Podolsky 2005; Allen

& Podolsky 2007). *Ophiothrix caespitosa* and *M. spongicola* (**Fig. 9.22B**) have small eggs (100–130 µm diameter) that develop into eight-armed ophiopluteus larvae (Selvakumaraswamy & Byrne 2000a, 2006; Byrne & Selvakumaraswamy 2002; **Fig. 3.11D**). *Ophiothrix caespitosa* spawns mainly from March to June and *M. spongicola* in July (Selvakumaraswamy & Byrne 2000a). There is a high degree of species specificity in the behaviour of sperm towards egg extracts of various Australian *Macrophiothrix* species, compared to other genera and families of brittle stars, and compared to holothuroids (Miller 1997).

The ecology of the European species *O. fragilis* has been studied in detail (Warner 1971, 1982; Warner & Woodley 1975; Turon *et al.* 2000; Morgan & Jangoux 2004). At some localities juveniles settle preferentially on sponges, presumably taking advantage of the inhalant currents of the sponge (Turon *et al.* 2000), whereas elsewhere they can settle on adult *O. fragilis* (Morgan & Jangoux 2004). This perhaps reflects the presence of cryptic species or ecotypes within this taxon (Baric & Sturmbauer 1999). *Ophiothrix fragilis* forms large persistent aggregations that can be maintained for at least 50 years (Broom 1975; Warner 1982). The benefits of aggregation include an increased chance of reproductive success, protection against predation, stability in fast-flowing currents, and increased deposition of suspended food particles through disturbance of the benthic water currents (Warner 1982). *Ophiothrix aristulata* has been found in large aggregations off Tasmania (Madsen 1967).

Some species have interesting dispersal mechanisms. *Ophiocnemis marmorata* has been observed on the bell of swimming rhizostome jellyfish at several localities, including off north-western Australia (Marsh 1998; **Box 1.5**). Presumably it settles directly on the jellyfish and lives by sweeping its surface for food. In the Caribbean, juveniles of the coral reef species *Ophiothrix orstedii* and *O. angulata* can re-enter the plankton after settlement, enabling movement to more suitable habitat (Hendler *et al.* 1999b).



Figure 9.22 Family Ophiotrichidae.

A, ***Ophiothrix (Acanthophiothrix) purpurea*** wrapped around a coral on the Great Barrier Reef, Queensland.

B, ***Macrophiothrix spongicola*** from south-east and south-west Australia is one of the few ophiotrichids that have colonised temperate Australian waters. It is frequently found within the holdfast of the large brown alga ***Ecklonia radiata***.

C, ***Macrophiothrix belli*** is one of the few ***Macrophiothrix*** species with a characteristic colour pattern. This animal was found off Heron Island, Great Barrier Reef, Queensland.

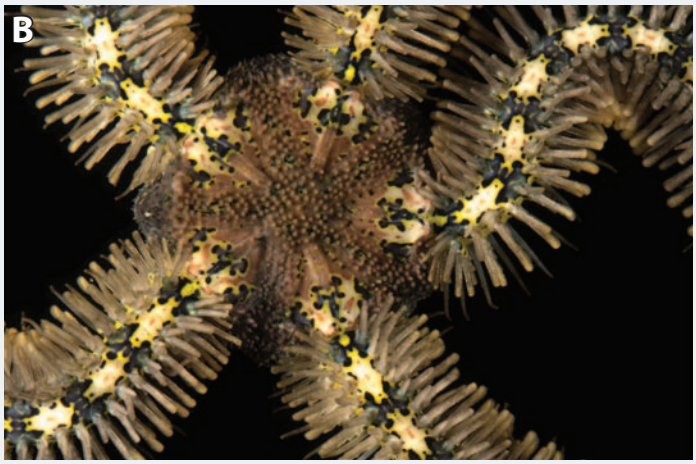
D, the striking ***Macrophiothrix nereidina*** is characterised by the banded colour pattern and absence of spines from the centre of the disc.

E, ***Ophiothrix martensi*** clings closely onto its coral home, the colour of the brittle star blending into the background.

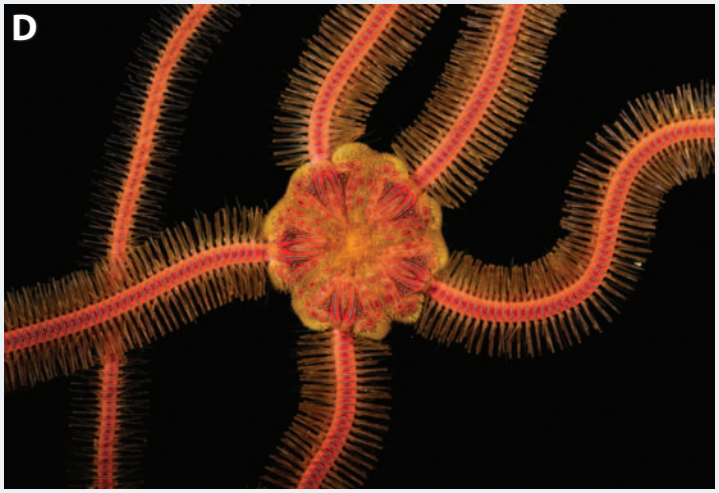
F, the multi-coloured six-armed ***Ophiothela danae*** is fissiparous, dividing into two 3-armed halves as a form of asexual reproduction.

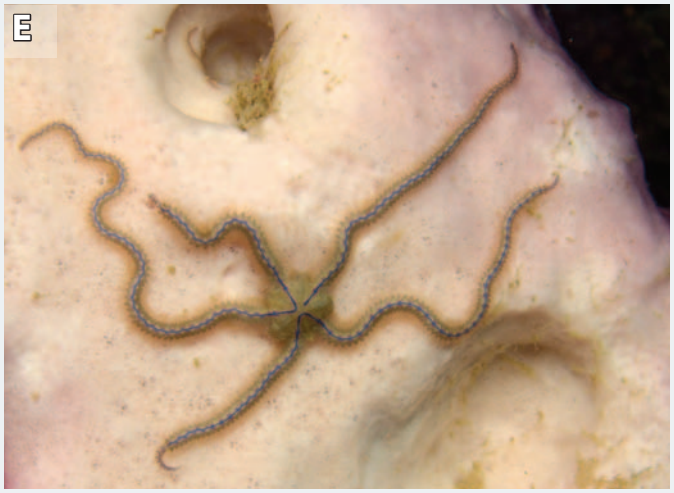
[A, J.Finn; B, L.Altoff; C, F.Michonneau; D–F, G.Paulay]

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B


C


D


E


F



Figure 10.1 The regular sea urchin ***Salmacis belli*** (Temnopleuridae) is often solitary, grazing on algae and seaweeds across the west Pacific including Australian waters from Western Australia across the north and south to New South Wales down to 125 m. It occurs mostly on loose sediments where it can use the spatulate spines on its oral surface to facilitate movement.

[A.D.Miskelly]

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10: Class ECHINOIDEA

Kenneth J. McNamara, David L. Pawson, Ashley D. Miskelly and Maria Byrne

General introduction

Members of the class Echinoidea are among the most familiar echinoderms (**Figs 10.1, 10.2**). Depending on their shape, they are popularly referred to as sea urchins, sand dollars, sea biscuits or heart urchins (**Figs 1.1E, 1.2J–L, 1.4, 1.14B**). Comprehensive reviews of echinoid biology and ecology include general accounts (Hyman 1955; Birkeland 1989a; Lawrence 2013c) and reviews of functional morphology, histology and ultrastructure (Cavey & Märkel 1994; Ziegler *et al*. 2008a, 2008b, 2010, 2012), feeding and nutrition (De Ridder & Jangoux 1982; De Ridder & Lawrence 1982; Lawrence & Sammarco 1982; Holland 2013; Watts *et al*. 2013), life histories and reproduction (Pearse & Cameron 1991; Emlet *et al*. 2002; McEdward & Miner 2001; Lawrence 2013d; Metaxas 2013), diseases (Wang *et al*. 2013), regional biodiversity (Mortensen 1930; McKnight 1974; David *et al*. 2005a), evolution (Wray 1992; Lessios 2010; Smith & Kroh 2011) and phylogeny (Kroh & Smith 2010; Smith & Kroh 2013). The monumental monographic series by T.Mortensen (1928, 1935, 1940, 1943a, 1943b, 1948a, 1948b, 1950, 1951) provided the basis for the morphological classification of the Echinoidea.

Echinoids are free-moving and are characterised by their rigid theca or test (**Fig. 1.4, 2.13**). The test comprises a series of interlocking plates arranged in rows from the apex to the mouth on the oral (ventral) surface (**Fig. 10.3**). Regular sea urchins have radial, pentameral symmetry, whereas irregular echinoids (for example, sand dollars, sea biscuits and heart urchins) are bilaterally symmetrical. However, regular sea urchins with symmetries other than pentameral are also occasionally encountered (**Box 10.1**). Most regular sea urchins are spherical to ovoid in shape (for example, *Salmacis sphaeroides*, **Fig. 1.2L**), although the oral surface can be somewhat flattened. Irregular sea urchins display a great variety of shapes. The more basal orders within the Neognathostomata have essentially spherical tests (for example, *Echinolampas ovata*) albeit with bilateral rather than radial symmetry, while



Figure 10.2 The Australian endemic echinoid fauna is dominated by heart urchins (Spatangoida) and sand dollars (Clypeasteroida). Most of the endemic fauna is found in southern Australia like the heart urchin ***Spatagobrissus incus*** (Maretiidae) which has a restricted distribution from eastern Victoria to northern Tasmania. Currently, 69 echinoid species are known only from Australian waters.

[A.D.Miskelly]

Box 10.1 Tetramerous and hexamerous symmetry in regular sea urchins

Ashley D. Miskelly

The overwhelming majority of regular sea urchins show pentamerous symmetry, in which the body is divided into five parts, each radiating from a central axis. Occasionally, individuals may have tetramerous or rarely hexamerous radial symmetry where all morphological features such as ambulacra, interambulacra, ocular plates, genital plates, teeth and auricles number four or six. The cause of this is unknown. Tetramerous symmetry may also develop in sea urchins that have sustained an injury to the plates in the apical system that produce the ambulacra and interambulacra. In these cases, the test is obviously misshapen, but nonetheless the abnormal body plan of four-fold symmetry is retained. Sea urchins with tetramerous or hexamerous symmetry are difficult to identify live in the field, unless the tube feet are fully extended.

In Australia, species with tetramerous (four-fold) and hexamerous (six-fold) symmetry have been recorded for a number of families including Temnopleuridae, Echinometridae and Toxopneustidae. In Temnopleuridae, tetramerous symmetry is known for a number of species including *Amblypneustes pallidus*, *Amblypneustes ovum*, *Holopneustes inflatus*, *Microcyphus compsus* and *Mespilia globulus*. For specimens of *Holopneustes inflatus* examined from around Botany Bay, Sydney, an estimated one in every 300 to 400 individuals is tetramerous. This value is based on examination of beach washed specimens over 25 years. Interestingly, however, there are only two known records of *H. inflatus* displaying hexamerous symmetry despite years of examination of beach washed specimens. One example was collected recently from Kurnell, Sydney, New South Wales (**Fig. a**), the other was figured in 1943 by Mortensen in *A Monograph of the Recent Echinoidea III (2). Camarodonta.*

The echinometrid *Heliocidaris erythrogramma* is another species that displays tetramerous symmetry, but this is more prevalent in the white test form that occurs in south-eastern South Australia (**Fig. b**). These tetramerous sea urchins rarely grow larger than 37 mm test diameter, and occur at the rate of approximately 1% of the population, which is comparatively high when compared to other species. The olive/grey form from the eastern states rarely shows tetramerous symmetry — only two specimens are known, both from Botany Bay, Sydney, New South Wales (**Fig. c**).

Tetramerous symmetry in toxopneustid sea urchins is rare. The only record is of a single specimen of *Pseudoboletia maculata*, with a test diameter of 60 mm, collected in 1989 from Shoal Bay, New South Wales (**Fig. d**). Due to the brown markings on the test of *Pseudoboletia maculata* the tetramerous symmetry is more obvious than that seen in *Heliocidaris* and *Holopneustes*.

Further reading Mortensen 1943a

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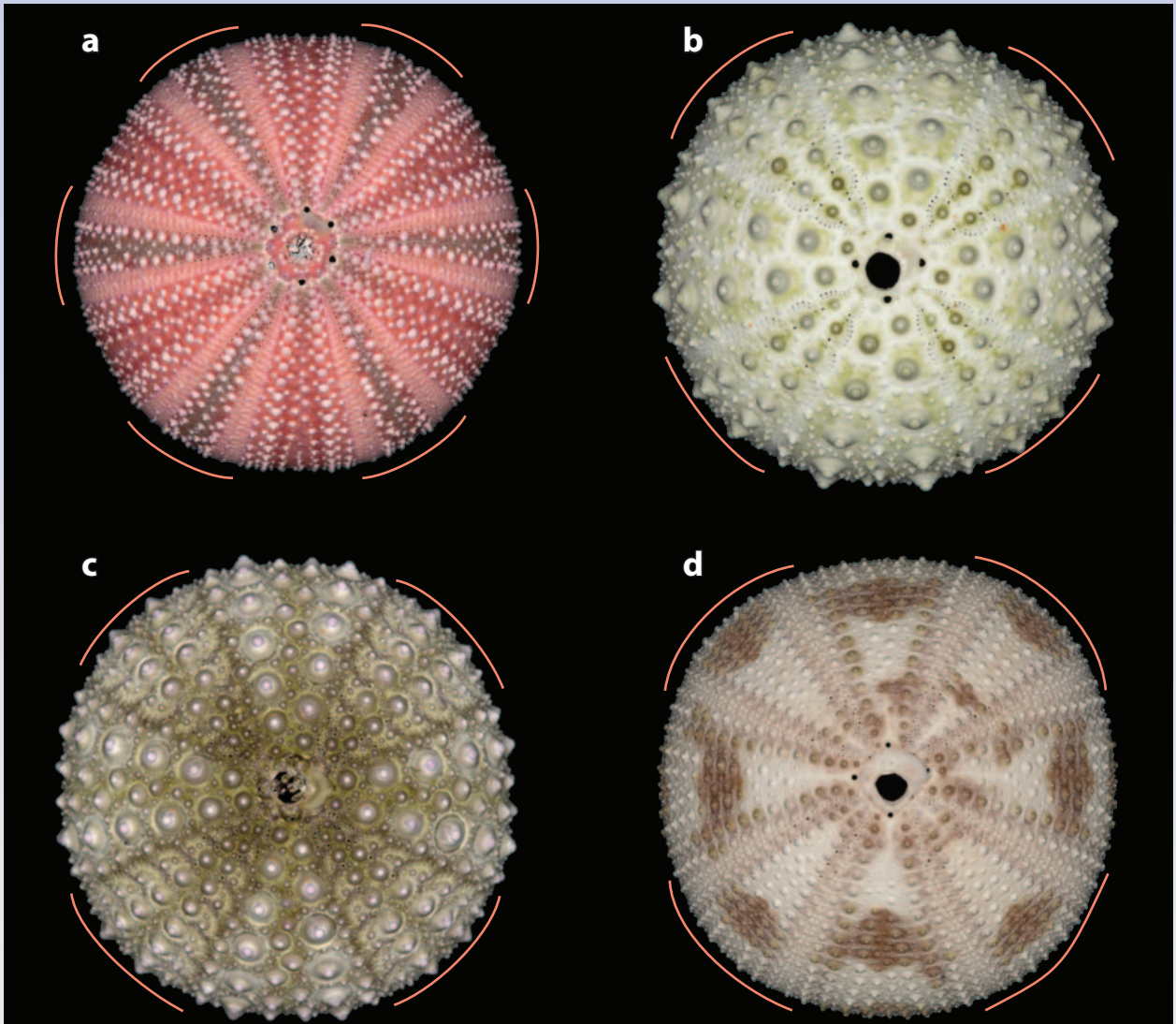


Figure a–d sea urchins with tetramerous and hexamerous symmetry.

a, hexamerous symmetry, ***Holopneustes inflatus*** (Temnopleuridae) test; specimen from Kurnell, Sydney, New South Wales. Test diameter 29 mm.

b, tetramerous symmetry, ***Heliocidaris erythrogramma*** (Echinometridae), the white test form; specimen from Port MacDonnell, South Australia. Test diameter 32 mm.

c, tetramerous symmetry, ***Heliocidaris erythrogramma***, the olive/green test form; specimen from Botany Bay, Sydney, New South Wales. Test diameter 46 mm.

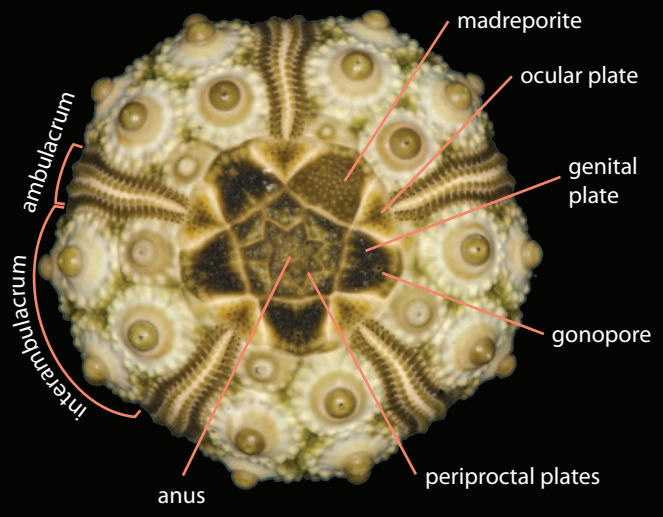
d, tetramerous symmetry ***Pseudoboletia maculata*** (Toxopneustidae); specimen from Shoal Bay, New South Wales. Test diameter 59 mm.

(ambulacra indicated with orange lines)

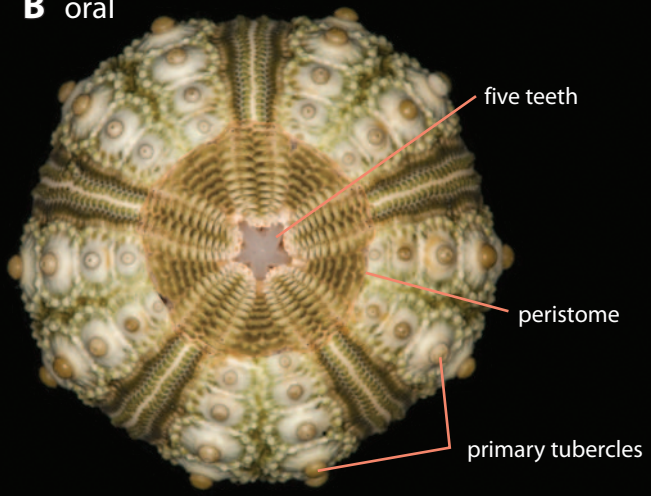
[A.D.Miskelly]

Regular echinoids

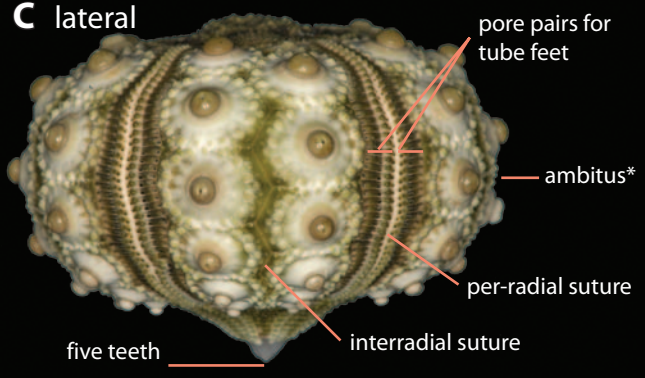
A aboral



B oral

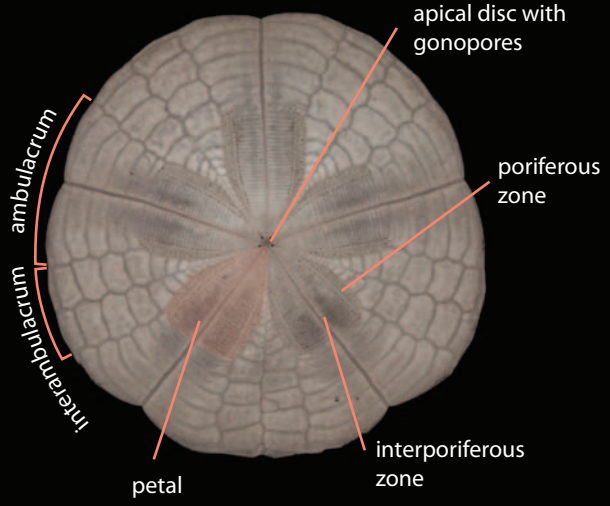


C lateral

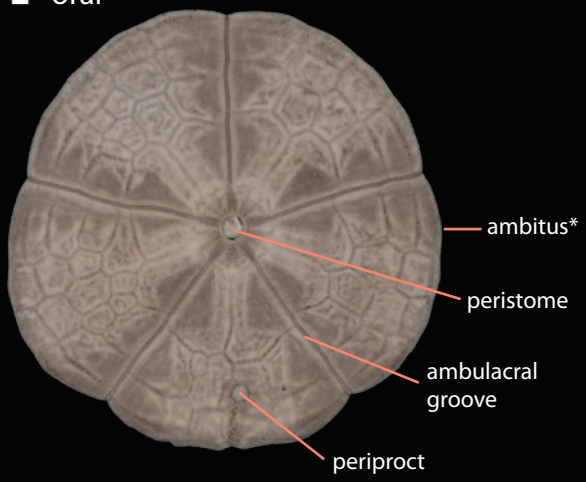


Sand dollars

D aboral



E oral



F lateral



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Heart urchins

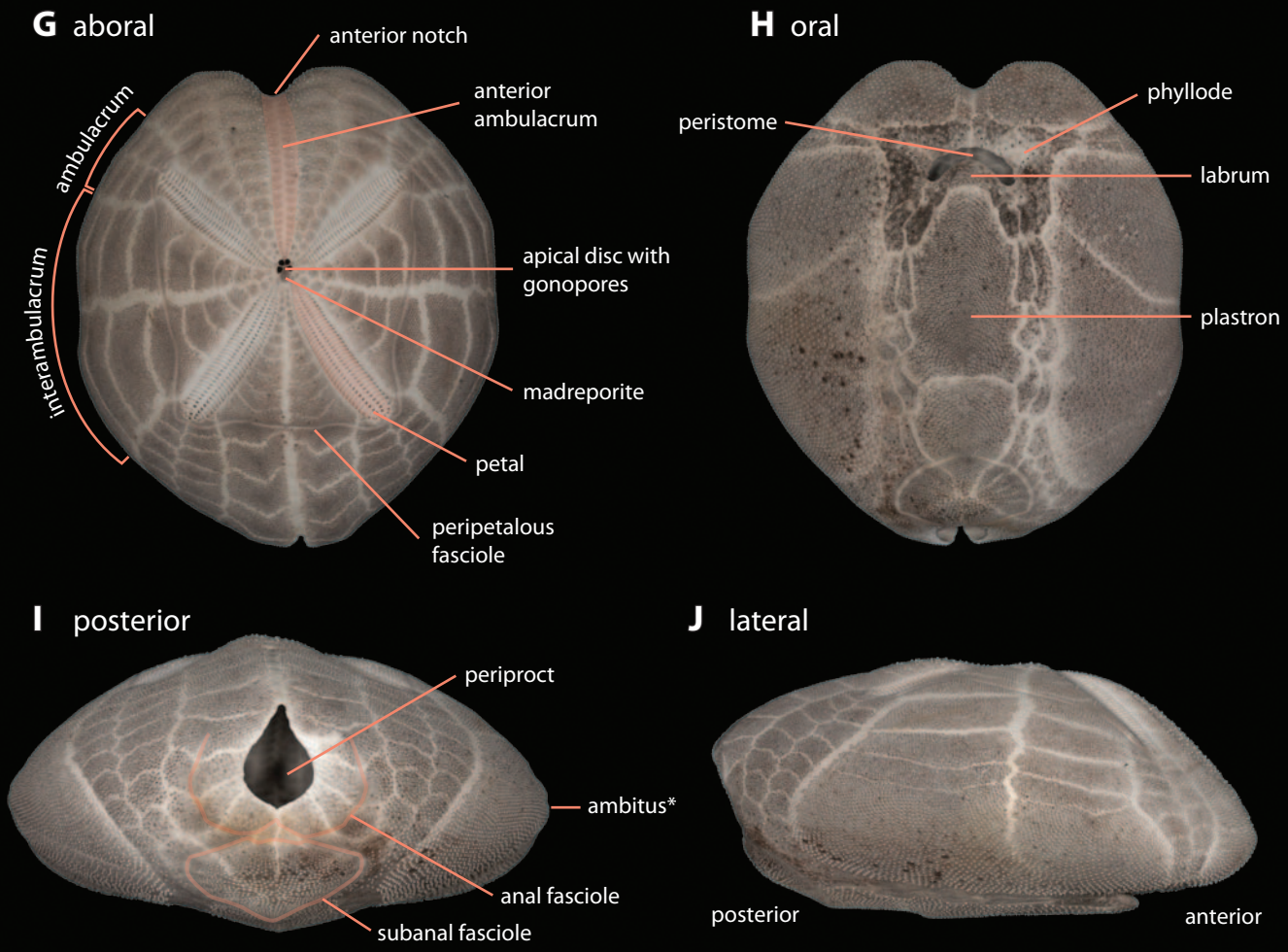


Figure 10.3 Skeletal morphology of echinoids. Typically all tests are formed from closely fitting plates which are arranged in 10 double columns, five ambulacral columns and five interambulacral columns.

A–C, test of ***Plococidaris verticillata*** (Cidaridae), a regular echinoid. Regular sea urchins usually have globular, but somewhat depressed, tests that have pentaradial symmetry. The peristome houses the mouth and the periproct houses the anus.
A, aboral view.
B, oral view.
C, lateral view.

D–F, test of ***Ammotrophus cyclius*** (Clypeasteridae), a sand dollar. Sand dollars and their relatives have a bilaterally symmetrical test that is typically flat and may be round, oval or sometimes polygonal in shape. All the ambulacra are mostly identical and display a distinctive petal-like pattern consisting of the pore-pairs through which tube feet project for respiration.
D, aboral view.
E, oral view.
F, lateral view.

G–J, test of ***Metalia angustus*** (Brissidae), a heart urchin. Heart urchins (Spatangoida) have a bilaterally symmetrical test that is oval or heart-shaped. The ambulacra support variously developed specialised zones called petals which are comprised of enlarged pore pairs. Heart urchins typically have four distinct petals which support pore-pairs through which respiratory tube feet project, and a fifth, somewhat rudimentary petal, the anterior ambulacrum, at the anterior end, that supports tube feet responsible for construction of a respiratory tunnel in burrowing species.
G, aboral view.
H, oral view.
I, posterior view.
J, lateral view.

[A.D.Miskelly]

* ambitus is the point of widest circumference on the test; ambital refers to at or towards the ambitus.

the Spatangoida range from heart-shaped and inflated (*Schizaster compactus*, *Protenaster australis*, **Fig. 1.2K**) to flattened (for example, *Maretia planulata*). Some Holasteroida have a highly elongate, flask-shaped test (species of *Pourtalesia*), while Clypeasteroida are typically very flattened (for example, *Arachnoides placenta*, **Fig. 1.14B**). The largest living echinoid is probably the asthenosomid *Hygrosoma hoplacantha*, which can have a diameter exceeding 300 mm (Lawrence 1987). The Australian fibulariid *Fibularia nutriens* and the Atlantic trigonocidarid *Genocidaris maculata* are among the smallest extant echinoids, at only 4 mm and 5 mm in diameter respectively.

In living echinoids, the interlocking plates form alternating double columns of ambulacra and interambulacra, making a total of 20 columns (**Fig. 1.4B**). Ambulacral plates have pore pairs through which the tube feet extend (**Fig. 1.4B**). On the aboral surface in the Spatangoida some tube feet are larger and confined to a discrete number of ambulacral plates and are known as petals (**Fig. 10.3G**). These may be flush with the surface of the test or sunken. Echinoids have a closed ambulacral system, the radial water vessels and other radial structures being internal to the skeleton (see **Chapter 1**). The ambulacral plates can be simple (one pore pair per plate), bigeminate (two pore pairs per plate), trigeminate (three per plate) or compound (many pores per plate). In the Atelostomata (Holasteroida and Spatangoida) the interambulacral plates on the oral surface between the peristome and periproct are known as sternal plates. In spatangoids the anterior-most pair are often very enlarged and constitute the plastron (**Fig 10.3H**). Between the sternal plates and the anteriorly positioned peristome in atelostomates is a single plate called the labrum (**Fig. 10.3H**). This may protrude partially across the peristome.

The test plates bear tubercles that support either movable spines (**Fig. 10.3B**) or pedicellariae, small, pincer-like structures on stalks (**Figs 1.5F, 2.15**). Pedicellariae are defensive structures and their morphological diversity in echinoids is suggested to reflect an evolutionary 'arms race' against pests and parasites (review Coppard *et al*. 2012). These can be globiferous (with long valves ending in sharp points, **Fig. 2.15**), tridentate (three large, pointed valves, **Fig. 1.5F**), triphyllous (very small, flattened valves) or ophicephalous (blunt-ended valves with serrated edges). Spines are usually large and few in number in regular echinoids (**Figs 1.1E, 10.7A, 10.8A–D, 10.15**), but much more numerous and far smaller in irregular echinoids (**Figs 1.2J,K, 10.2, 10.43**). In spatangoids, spines attached to the plastron are used for burrowing in the sediment (**Fig. 2.36**). All skeletal elements consist of a three-dimensional calcite meshwork known as stereom (Smith 1980).

The apical system on the aboral surface consists of a ring of five genital plates alternating with five ocular plates (**Fig. 10.3A**). Some or all of the genital plates are pierced by single pores (gonopores) through which the gametes are released (**Figs 3.2C, 3.4E**). The ocular plates are terminal ambulacral plates and each has a minute pore through which the end of the radial water vessel projects as the terminal tube foot. The apical system can be monocyclic (genital and ocular plates in a single ring around the periproct), dicyclic (genital and ocular plates in two circles and only the genitals in contact with the edge of the periproct), monobasal (apparently fused genital plates) or tetrabasal (only four separate genital plates). In regular sea urchins, the apical system encircles the periproct which consists of a series of flexible plates through which the anus passes (**Fig. 10.3A**). In irregular sea urchins, the periproct is situated outside the apical system in a posterior position (**Fig. 10.3I**).

The peristome, containing the mouth, is situated on the oral surface and has a connective tissue support surrounding the mouth (**Fig. 1.13C**). Like the periproct, the peristome is covered by a series of flexible plates. The plates closest to the peristome are the first formed in development and are known as basicoronal plates. The enlarged, crowded ambulacral pores grouped around the peristome are called phyllodes, and the swollen interambulacra around the peristome are termed bourrelets. Together, the phyllodes and bourrelets constitute the floscelle. In regular echinoids the edge of the peristome has ten interambulacral notches (buccal slits) that are adjacent to the ambulacral plates (**Fig. 10.21B**)

Set inside the test, in the oral region of most echinoid orders, is a dental apparatus called the Aristotle's lantern (**Fig. 1.13A,B**). This is a defining feature of regular

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Table 10.1 Classification of echinoid families in Australian waters, after Smith & Kroh (2011).

Class Echinoidea		
Cidaroidea		
Order Cidaroida		cidaroids
Family Histocidaridae		
Family Cidaridae		
Family Psychocidaridae		
Euechinoidea		
Order Echinothurioida		echinothurioids
Family Phormosomatidae		
Family Echinothuriidae		
Order Micropygoida		diadematoids and pedinoids
Family Micropygidae		
Order Aspidodiadematoida		
Family Aspidodiadematidae		
Order Diadematoida		
Family Diadematidae		
Order Pedinoida		
Family Pedinidae		
Order Stomopneustoida		stirodonts
Family Stomopneustidae		
Order Arbacioida		
Family Arbaciidae		
Order Salenioida		
Family Saleniidae		
Order Camarodonta		camarodonts
Family Temnopleuridae		
Family Trigonocidaridae		
Family Echinidae		
Family Toxopneustidae		
Family Echinometridae		
Irregularia		
Order Echinoneoida		
Family Echinoneidae		
Neognathostomata		
Family Apatopygidae		neognathostomates
Order Cassiduloida		
Family Cassidulidae		
Family Neolampadidae		
Order Echinolampadoida		
Family Echinolampadidae		
Order Clypeasteroida		
Family Clypeasteridae		
Family Arachnoididae		
Family Fibulariidae		
Family Echinocyamidae		
Family Laganidae		
Family Astriclypeidae		
Atelostomata		
Order Holasteroida		atelostomates
Family Corystusidae		
Order Spatangoida		
Family Micrasteridae		
Family Hemiasteridae		
Family Schizasteridae		
Family Pericosmidae		
Family Brissidae		
Family Asterostomatidae		
Family Spatangidae		
Family Eupatagidae		
Family Maretiidae		
Family Loveniidae		

echinoids and is used in grazing the surface and feeding in these epifaunal species. In some orders the lantern is absent, reflecting quite a different style of feeding — deposit-feeding, as seen in infaunal irregular echinoids.

The entire skeleton, apart from some spines in cidaroid sea urchins and the tips of the teeth (**Figs 1.13B,C, 2.26**), is covered by epithelium and so is a true endoskeleton. The inside of the test is filled with coelomic fluid along with organs including the digestive tract and gonads (**Fig. 3.3A**). Five gonads are present in regular echinoids (**Fig. 3.3A**), but this number can be reduced in some irregular forms (**Fig. 3.4**) and can even vary within species. Gonads are situated in an interradial position and are connected to the exterior through the gonopores (**Figs 3.3A, 3.4E, 10.3A**).

Echinoids have a tubular gut that runs around the circumference inside the test. The digestive system includes the pharynx, oesophagus, intestine, rectum and anus (De Ridder & Lawrence 1982; Cavey & Märkel 1994; Holland 2013). The pharynx is situated within the lantern, and when the lantern is absent as in the spatangoids, so too is the pharynx (De Ridder & Jangoux 1993). A broad caecum, a diverticulum connecting to the oesophagus, is present in most sea urchins except cidaroids (Ziegler *et al.* 2010). In sand dollars this structure is often filled with sand, serving as a weight belt to reduce dislocation in wave-swept environments (Mooi & Chen 1996; Ziegler *et al.* 2016). In the heart urchin *Echinocardium cordatum*, symbiotic bacteria thrive in the intestinal caecum and appear to play a key role in digestion of sediment ingested by this deposit feeding species (Temara *et al.* 1993). The digestive system of *E. cordatum* is described in detail by De Ridder & Jangoux (1993). Echinoids also have a siphon or siphonal groove that originates near the junction of the oesophagsus and the stomach and runs parallel to the stomach and rejoins the digestive tract near the intestine (Holland 2013). A long oesophagus leads into a double U-shaped, looped intestine. Stewart's organs are internal coelomic pouches associated with the Aristotle's lantern; they act as fluid reservoirs.

Some regular echinoids have buccal slits around the peristome (**Fig. 10.21B**) that accommodate expansion sacs called 'gills', although these structures do not serve a respiratory function. Gas exchange occurs through the tube feet (Shick 1983). In some groups, such as the Spatangoida and Clypeasteroidea, specialised tube feet are used exclusively for respiration (Nichols 1959a, 1959b).

The echinoid water vascular system consists of an oral water ring around the oesophagus above the lantern and five radial water vessels that run inside the test along the ambulacra. The stone canal leads from the ring vessel up to the madreporite, a modified perforated genital plate that functions as the external opening of the water vascular system (**Fig. 1.21B**). The radial water vessels supply the tube feet and associated ampullae, water-filled reservoirs that allow the tube feet to function as independent units. Echinoid tube feet function in respiration, sensation, feeding and funnel construction. They are most diverse in form and function in heart urchins (**Fig. 1.15A–C**).

Echinoids have a simple nervous system that closely follows the course of the water vascular system (Cavey & Märkel 1994). A nerve ring surrounds the oesophagus, and from it five radial nerves arise. Branches from the radial nerves extend to each ambulacral pore, through which they pass to the exterior of the test and innervate the tube feet (Cavey & Märkel 1994). Echinoids have a diffuse network beneath the epidermis, a sensory nerve plexus innervating spines and pedicellariae.

Echinoids occur from coastal waters to the deep sea with just over 1,000 extant species (Kroh & Mooi 2014). In Australian waters 39 families, 97 genera and up to 280 species have been reported (Rowe & Gates 1995; McNamara 1998; O'Hara 2012; A.D.Miskelly, unpublished data); most species are known from the continental shelf. Three-quarters of the species are found only at tropical and subtropical latitudes, while the remaining 25% are known from southern Australia. In terms of families, of the 39 known from Australian waters (**Table 10.1**), 30 occur in the north, and 12 of these are endemic to this area. Twenty-one families occur in the south, of which only three are endemic. It is likely that the fauna of cooler southern waters has its origins in the northern, tropical fauna (Rowe & Vail 1982). This is borne out by the fossil record (McNamara 1999).

Some regular sea urchins that live subtidally burrow in loose, soft sediments. The spatulate spines on the oral surface aid in digging, and push substrate aside while the urchin gradually sinks into the sediment. Once this is achieved, long ambital spines anchor the sea urchin in position (A.D.Miskelly, unpublished data). Many urchins that live in unconsolidated habitats transport large debris such as shells and rubble to the aboral surface by their tube feet potentially to act as camouflage and to reduce the intensity of incident light (Pawson & Pawson

Figure 10.4 The sand dollar ***Arachnoides tenuis*** (Arachnoididae) lives on sand flats in tropical climates. It buries itself rapidly in the fine sand when it becomes exposed at low tide, an ability that may be important to avoid heat stress. The numerous fine spines on the oral surface facilitate this action effectively. On this occasion it took nine minutes for the exposed sand dollar to completely bury itself. Test diameter 41 mm.

[A.D.Miskelly]

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A
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Figure 10.5 Sea urchins have a number of predators including molluscs, crabs, fishes and birds, and other echinoderms such as seastars. Here the sea urchin ***Tripneustes gratilla*** (Toxopneustidae) is being attacked and eaten by the gastropod mollusc ***Cassis cornuta*** (Cassidae).

[B.Halstead]

2013). Covering is also seen in deepsea echinoids where neither camouflage nor light provides a rationale for this behaviour. It is suggested that covering behaviour may simply be a tactile reflex action in some regular echinoids (Pawson & Pawson 2013), but a recent study by Brothers *et al*. (2016b) on the covering behaviour in *Sterechinus* species indicates that covering may be a response to the presence of predatory king crabs. Burrowing is most evident in Temnopleuridae, in particular *Salmaciella oligopora* and *S. dussumieri* which become hardly visible once the burrowing process is complete, and *Temnopleurus toreumaticus*, which although it has fewer spatulate oral spines and longer ambital spines than *Salmaciella*, is an effective burrower. These sea urchins, however, do not completely bury themselves.

In heart urchins, deep burrowing is achieved by a combination of specially modified spines, tube feet and fascioles (**Fig. 2.36; Box 10.6**). Special inhalent/exhalent channels are constructed to ensure freshly oxygenated water is available for respiration, as well as to expel waste. Some heart urchins erect rows of spines on the aboral surface to produce a channel for water intake. As the heart urchin sinks deeper, mucus is secreted and used to cement sand grains together to prevent the channels from collapsing, thus allowing respiration and feeding without difficulty.

Sand dollars mostly plough through surface sediment in a forward anterior direction (**Figs 2.37, 10.4, 10.30, 10.31**). Burrowing is achieved by the digging action of numerous short spines, while tube feet grasp and transfer larger particles to the aboral surface as in many *Clypeaster* species. Some species, such as *Arachnoides placenta* (**Fig. 10.4**), spin on a circular axis (A.D.Miskelly, unpublished data) when the temperature is very hot, and thus bury themselves very quickly.

Both regular and irregular sea urchins are susceptible to predatory attack by gastropod molluscs. Predation from helmet shells (Cassidae; **Fig. 10.5**) and triton shells (Ranellidae) are the most frequently encountered, with the evidence of predation being a denuded test with a hole bored through it.

Echinoids have been a culinary delicacy in the Mediterranean region since Roman times (Sloan 1985), and they have been harvested in Brittany since the Iron Age (1000 B.C.) (Allain 1972). They are still fished today, including in Australia, and also with a focus on aquaculture (Keesing & Hall 1998; Andrew *et al*. 2002; Lawrence 2013c). There are several sea urchin fisheries in Australia based on *Heliocidaris erythrogramma* and *Centrostephanus rodgersii* (**Fig. 4.5; Chapter 4**).

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Fossils

Although Mesozoic echinoids are very rare in Australia (McNamara 1986, 1987b), there is a very rich Cenozoic fossil record (Holmes 1993). Cidaroids and their ancestors, with their strong skeletons, are well known as fossils. Irregular echinoids have the best fossil record, a consequence of living in soft substrates where active sedimentation can occur, in contrast to the sea urchins that tend to live on rocky substrates (Philip 1963b; Rowe 1969; Kier 1977; Smith 1984b).

The Palaeocene fauna of the Carnarvon Basin is dominated by holasteroids (Foster & Philip 1978) and spatangoids (McNamara & Philip 1980a). This is more reminiscent of a Late Mesozoic fauna than a Cenozoic one. The succeeding Late Eocene faunas that occur in southern and western parts of Australia indicate a strong decline in holasteroids and a marked increase in spatangoid (**Fig. 10.6D**) and neognathostomate (**Fig. 10.6A,B**) diversity (McNamara & Philip 1980a, 1980c, 1984; McNamara 1985a; McNamara *et al*. 1986; McKinney *et al*. 1992). The rich Oligocene and Miocene echinoid assemblages of southern Australia in particular show the appearance of many genera that are still extant in Australian waters, such as *Lovenia* (**Fig.10.6D**), *Eupatagus* and *Clypeaster* (McNamara & Philip 1980a, 1980c, 1984; McNamara 1985a, 1985b, 1987a, 1993; McNamara *et al*. 1986; McNamara & Ah Yee 1989; McNamara & Barrie 1993). At the ordinal level there is a marked increase in diversity of the clypeasteroids (**Fig. 10.6C**) in conjunction with a marked decline in the other neognathostomate orders, mirroring the pattern found in other parts of the world (McKinney *et al*. 1992). Following the onset of the circum-Antarctic current in the Late Oligocene, and the decline in Southern Ocean water temperatures in the later Miocene and into the Pliocene, there was a marked change in the composition of the southern fauna, resulting in the development of distinct northern tropical and southern temperate echinoid provinces (see **Chapter 5**).

Many of the echinoid genera found in Australia's tropical province have long fossil histories, particularly in southern Australia where they no longer occur. Before the Pliocene, the Cenozoic sediments of southern Australia, principally in the Eucla, St Vincent, Otway and Murray basins, contain echinoid faunas that show many parallels with the present day tropical province. Common elements of the Miocene include *Lovenia*, *Schizaster*, *Echinolampas*, *Pericosmus* and *Brissopsis* (McNamara & Philip 1980a, 1980c, 1984; McNamara *et al*. 1986). Some of these, *Schizaster*, *Echinolampas*, *Pericosmus* (McNamara & Philip 1984) and *Brissopsis*, were also present in the Early Miocene in north-western Australia (McNamara & Kendrick 1994). Today, these genera are confined to the tropical north. Other genera present in the southern province with a long fossil record, such as *Apatopygus*, *Protenaster*, *Eupatagus*, *Granobrissoides*, *Spatagobrissus* and *Goniocidaris*, are presumably more tolerant of a broader range of water temperature.

A number of cosmopolitan echinoid genera show their earliest appearance in the Mediterranean, and then appear to spread into the north-western Indian Ocean followed by an eastward dispersal towards Australasia (Foster & Philip 1978; McNamara 1999). This pattern is evident in spatangoids (for example, *Eupatagus*, *Breynia*, *Brissus*, *Meoma*, *Opissaster* and *Cyclaster*), clypeasteroids (for example, *Echinocyamus* and *Sismondia*), for the camarodont *Ortholophus* and for holasteroids (Foster & Philip 1978; McNamara 1999). A number of other echinoid genera that appear to have originated in the north-western Indian Ocean also spread eastwards through India to Australasia (McKinney *et al*. 1992).

This eastward trend was not confined to the Indian Ocean. Some elements of the Mediterranean fauna dispersed eastwards into the Indo-Pacific province (McKinney *et al*. 1992). The Tethyan seaway may have provided a route for such dispersal during the Late Palaeogene. For instance, *Brissopsis* and *Lovenia*, both relatively common elements in the Australasian region during the Oligocene, first appeared in the Mediterranean during the Eocene (McKinney *et al*. 1992).

The stratigraphic record of the widespread tropical genus *Echinometra* (**Box 10.3**) suggests that it too underwent an easterly spread across the Indian Ocean during the Neogene, first appearing in the Mediterranean region during the Early Miocene and possibly reaching south-western Australia via the Red Sea and Indian Ocean during the Pleistocene (McNamara 1992). This would have probably been



Figure 10. 6 Fossil echinoids.

A, cassiduloid ***Eurhodia*** sp. nov., Middle Eocene, Nanarup, Western Australia; aboral surface. Test length 30 mm.

B, cassiduloid ***Australanthus longianus***, Middle Eocene, Nanarup, Western Australia; oral surface. Test length 30 mm.

C, clyperasteroid ***Monostychia australis***, Early Miocene, Murray River, South Australia; aboral surface. Test length 43 mm.

D, spatangoid ***Lovenia forbesii***, Early Miocene, Murray River, South Australia; aboral surface. Test length 32 mm.

[A,B, K.J.McNamara; C,D, K.Brimmell]

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influenced by the initiation of the warm north to south flowing Leeuwin Current (McNamara 1992, 1999). A similar pattern occurs in eastern Australia, in that the tropical echinoid fauna around Lord Howe Island and Norfolk Island have spread from the east coast of the mainland, presumably by means of larval dispersal from the Great Barrier Reef, Queensland, in the East Australian Current (McNamara 1999).

While the dispersal of echinoids in the Early Cenozoic occurred when Australia was at much higher latitudes than it is today (**Fig. 5.7**), that of the Middle to Late Cenozoic took place during the northward passage of the continent through about 25 degrees of latitude (**Fig. 5.7**). This had a profound impact on the nature of the marine fauna as a whole, dramatically reducing the diversity of marsupiate (brooding) echinoids (McNamara 1994a). Today, only one such echinoid is known from Australian waters, *Fibularia nutriens*. However, the Australian Cenozoic fossil record includes a rich assemblage of marsupiates. Currently, these echinoids are largely confined to the seas around Antarctica (**Fig. 3.4; Box 10.5**). Although it has been inferred that their presence in the fossil record is indicative of low ocean temperatures, no such relationship can be confirmed (McNamara 1994a).

Marsupiates disappeared from Australia during the Pliocene. As these echinoids including *Abatus* species (**Box 10.5**) now live in stable environments as seen today in their Antarctic distribution, the decrease in marsupiate diversity from southern Australia may be due to the increase in environmental instability (McNamara 1994a). Temporal changes in the diversity of marsupiate echinoids in southern Australia during the Cenozoic indicate that their spatial and temporal distribution may be more closely correlated with their life history strategy, limited dispersal ability and environmental stability than with low temperature (McNamara 1994a). The present day southern Australian coastal echinoid fauna is dominated by species with pelagic lecithotrophic larvae (**Fig. 3.11H**; **Box 10.4**), including species in the genera *Microcyphus*, *Phyllacanthus* and *Amblypneustes*.

CIDAROIDS

Cidaroids are distinctive sea urchins with thick, strong tests and comparatively few large primary spines (**Figs 2.26, 10.7–10.9**). The biology and ecology of cidaroids is reviewed in Lawrence & Jangoux (2013). The cidaroid test is rigid in extant forms (**Figs 10.3A–C, 10.7B,C, 10.8E–G, 10.9C**), flexible in some fossils, approximately spherical, and circular in outline. The ambulacra are significantly narrower than the interambulacra. Each ambulacral plate has a single pore-pair, and the plates are never compounded, while each interambulacral plate has a large, conspicuous primary tubercle that is usually perforate, non-crenulate, and with a large areole. The teeth are not keeled. The peristome is covered with overlapping plates. The large primary spines are a conspicuous feature of most cidaroids. Characteristically, the shafts of primary and secondary spines, when mature, lack an epidermis; spines of all other sea urchins are coated with an epidermal layer. Cidaroid spines are also unusual in having an outer polycrystalline cortical layer, and this layer is harder than the underlying monocrystalline skeleton (Märkel *et al*., 1971; David *et al*. 2009). The microstructure of cidaroid spines is described in detail by David *et al*. (2009). The outer cortical layer protects the spines from dissolution in some deep-water low pH environments (David *et al*. 2009; Dery *et al*. 2014; Dubois 2014). The spines are often heavily colonised by ectosymbionts (**Fig. 2.26**). Globiferous and tridentate pedicellariae are present in cidaroids (Coppard *et al*. 2012).

Echinoids almost became extinct during the Permo-Triassic extinction event. The cidaroids were the only surviving sea urchins, with a fossil record that dates back to the Palaeozoic era; they are considered to be ancestral to all post-Palaeozoic echinoids (Kroh & Smith 2010). The Permian-Jurassic *Miocidaris* is the only known echinoid genus to cross the Palaeozoic-Mesozoic boundary. Cidaroids differ from all other modern echinoids in lacking a complete perignathic girdle (they have only interambulacral apophyses) and in lacking gills and gill slits (Jensen 1981; Smith 1984b).

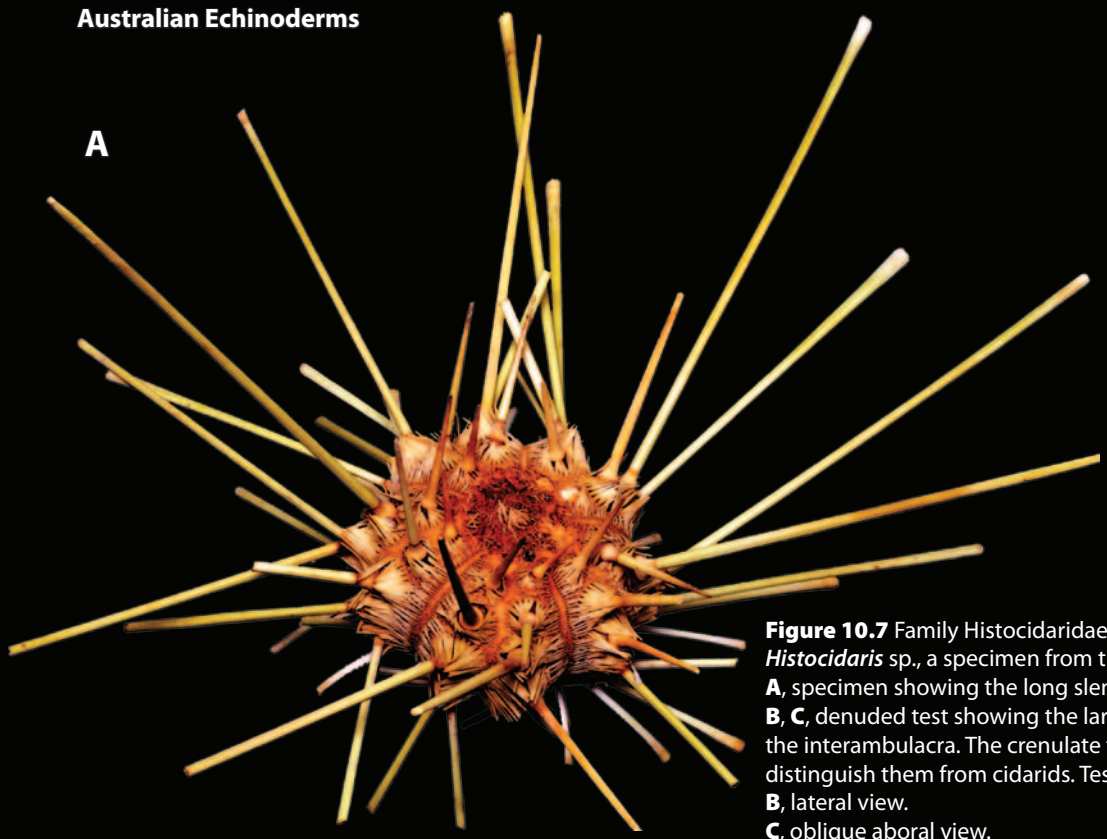


Figure 10.7 Family Histocidaridae.
Histocidaris sp., a specimen from the Philippines:
A, specimen showing the long slender primary spines.
B, **C**, denuded test showing the large crenulate tubercles of the interambulacra. The crenulate tubercles of histocidarids distinguish them from cidarids. Test diameter 100 mm.
B, lateral view.
C, oblique aboral view.

[A.D.Miskelly]

Taxonomically, cidaroids are considered to be a subclass (Cidaroidea) with a single extant order (Cidaroida) and ten families, six of which include only extinct taxa (Kroh & Smith 2010; Kroh & Mooi 2014). The Psychocidaridae is represented today by a single tropical species, *Psychocidaris ohshimai*, and the Histocidaridae has one genus, *Histocidaris*, with at least 16 species, three of which occur in Australia (Smith & Kroh 2011; O'Hara 2012). The majority of living cidaroids, approximately 108 species and 26 genera or subgenera, are referable to the family Cidaridae (Smith & Kroh 2011). The Antarctic ctenocidarids (David *et al*. 2005a, 2005b) are sometimes regarded as a separate family (Kroh & Smith 2010; Kroh & Mooi 2014).

Family Histocidaridae

Figure 10.7

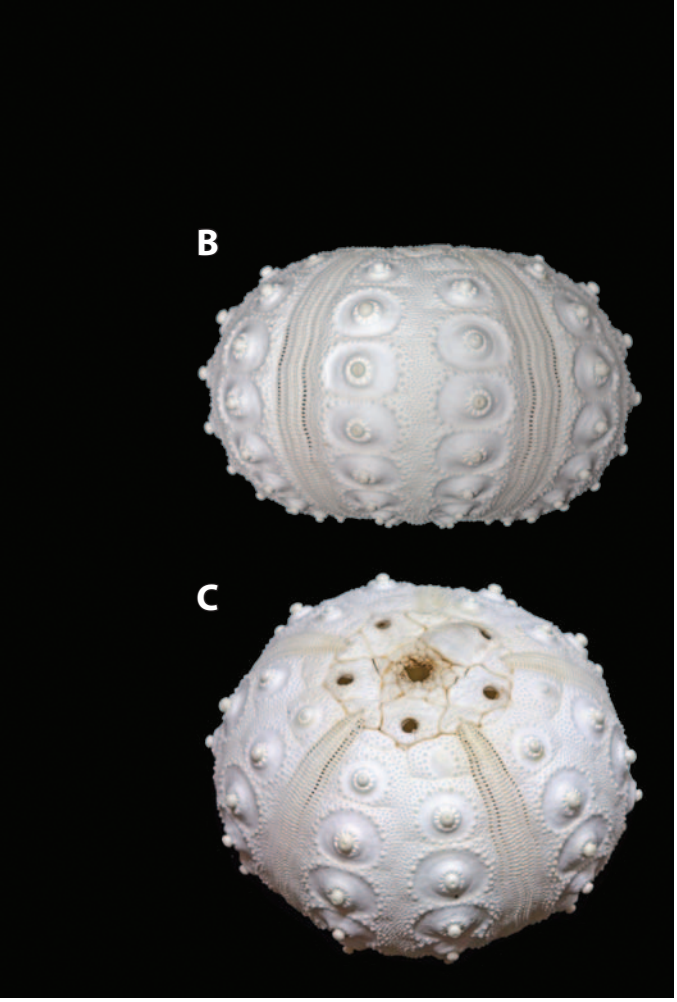
Histocidaris, the only genus in the family (**Fig. 10.7**), includes 16 nominal species (Kroh & Mooi 2014) mostly restricted to bathyal depths (Mortensen 1928). Many are known from only very few specimens, and several could be conspecific (Rowe & Hoggett 1986). Fossil species are known from as far back as the Late Triassic (Smith & Kroh 2011); however, no fossil specimens have been collected from Australia (Irwin 2001). Members of the Histocidaridae have tests with tessellate sutures, perforate and strongly crenulate primary tubercles that are confluent adorally and ambitally, straight ambulacra, long cylindrical primary spines with simple unbranched cortical hairs, and slender unflattened secondary spines (Smith & Kroh 2011).

Three species of *Histocidaris* are known from Australia: the Indo-Pacific *H. elegans* extends into southern Australia, *H. australiae* is endemic to the upper slope of south-eastern Australia, from New South Wales to Tasmania, and *H. crassispina*, known only from the type specimen, may be an aberrant specimen of *H. elegans* (Rowe & Hoggett 1986).

Gut contents of *H. elegans* from Australia include bottom foramiferous sediment, and that of *H. australiae* bryozoan/hydroid material and crushed bivalves and gastropods (De Ridder & Lawrence 1982).

Both *H. elegans* and *H. australiae* are inferred to have pelagic non-feeding larvae (Emlet 1995a).

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Family Cidaridae

Figure 10.8

The cidarid test is always rigid, and the primary tubercles are invariably perforate (**Figs 10.3A–C, 10.8E–G**). Cidarids are known to range as far back as the Late Silurian, some 400 million years ago. In Australia, fossil cidarids are quite conspicuous; 22 species are known, most from the Tertiary (Philip 1964b; Holmes 1987). Some genera, well-known as fossils, flourish in the present day, for example *Eucidaris* (McNamara & Kendrick 1994).

The living Australian cidarid fauna includes 25 species in 10 genera: *Phyllacanthus* (6 species), *Prionocidaris* (5), *Goniocidaris* (3), *Stylocidaris* (4), *Stereocidaris* (2), and the single representatives *Chondrocidaris brevispina*, *Eucidaris metularia*, *Acanthocidaris maculicollis*, *Plococidaris verticillata* and *Rhopalocidaris gracilis* (Rowe & Hoggett 1986; Hoggett & Rowe 1986b; O'Hara 2012). *Aporocidaris antarctica* has also been recorded from Australian Antarctic waters; it is sometimes placed in the family Ctenocidaridae. Currently, four endemic species are known from Australian waters: *Phyllacanthus longispinus*, *Phyllacanthus magnificus*, *Goniocidaris tubaria* (**Fig. 10.8C**) and *Goniocidaris impressa*. Diversity around Australia is high, with 35% of the world's genera and 21% of species occurring in Australian waters.

Cidarids are widely distributed in the world's oceans, but they are most diverse in the tropical Indo-west Pacific and around Antarctica (Mortensen 1928; David *et al*. 2005a). A few species in the tropics are conspicuous members of the littoral fauna, but most cidarids live offshore most commonly in shelf and bathyal depths; only three species extend to depths below 3,000 m. Species of *Phyllacanthus* are common in shallow waters around the entire coast where suitable rocky habitats can be found (**Figs 2.26, 10.8A,B**). *Prionocidaris* species tend to inhabit less exposed habitats, usually at depths of more than 10 m (**Fig. 10.8D**).

A few very large and conspicuous species, such as *Phyllacanthus imperialis* (**Fig. 10.8A**), occur around the Australian coast. They can reach a diameter, including spines, in excess of 300 mm. Despite their usually drab brownish colouration they are imposing sights to the SCUBA diver. Rocky substrates are the preferred shallow water habitats, and individuals are often found wedged into crevices or attached to the undersides of rock ledges (Baker 1982b; Marsh 1991; Marsh & Pawson 1993). The primary spines are used to anchor these urchins to the substrate (McPherson 1968).

The diet of cidarids varies, depending on where they live (Lawrence & Jangoux 2013). They are flexible omnivorous species. Species that live on soft bottoms tend to ingest a mixture of benthic material, mostly fragments of shell, bryozoans, foraminiferans, and sponges (De Ridder & Jangoux 1982). Deep-sea cidaroids eat seagrass and animal detritus originating from surface waters (Young *et al*. 1993). *Phyllacanthus irregularis* (**Fig. 10.8B**) from south-western Australia eats a greater amount of animal material than algae (Vanderklift *et al*. 2006). Some tropical cidarids that live on hard substrates consume sponges, and also graze the hard surfaces eating algae, encrusting organisms and coral (Glynn *et al*. 1979; Santos *et al*. 2002).

Because they lack an epithelial cover, the spines of cidarids are often colonised by ectosymbionts that attach to the outer cortex of the spines (David *et al*. 2009). These typically include colonial organisms such as bryozoans, sponges and hydroids (Hétérier *et al*. 2004; **Fig. 2.26**). In some areas cidarids provide the primary hard substrate for a diversity of species, especially in soft substrate habitat (Hétérier *et al*. 2004; Linsea *et al*. 2008).

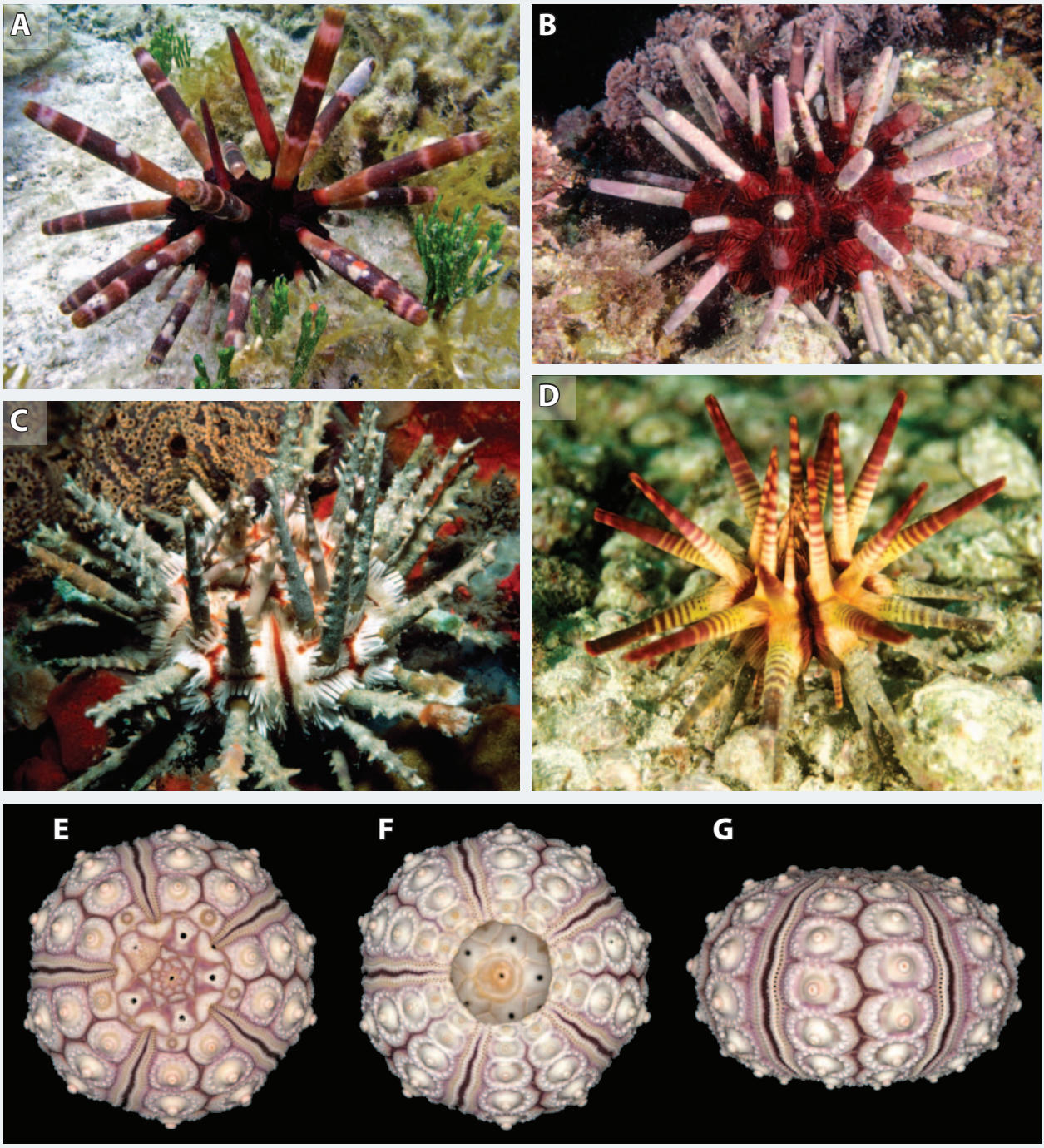


Figure 10.8 Family Cidaridae.

A, ***Phyllacanthus imperialis***, a common pencil urchin found throughout the Indo-Pacific, is a conspicuous member of the nocturnal reef fauna around the coast of Australia.

B, ***Phyllacanthus irregularis*** is found in Australia's southern waters from Port Willunga, South Australia, to Houtman Abrolhos, Western Australia.

C, endemic to southern Australian waters, the thorny sea urchin, ***Goniocidaris tubaria***, lives in the open on shellgrit and coarse rubble to over 600 m.

D, ***Prionocidaris baculosa*** found in Western Australia and throughout the Indo-west Pacific.

E–G, test of ***Goniocidaris tubaria***, diameter 42 mm.
E, aboral view.
F, oral view, peristomial plates absent.
G, lateral view.

[A, E–G, A.D.Miskelly; B,D, C.Bryce; C, K.Gowlett-Holmes]

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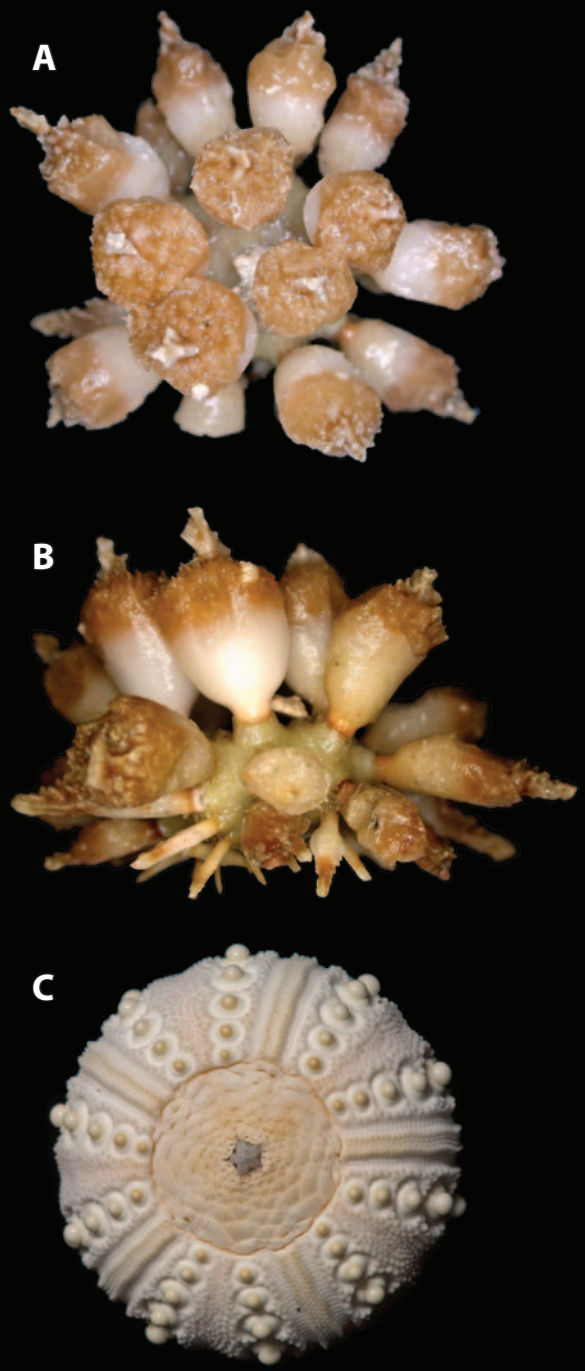


Figure 10.9 Family Psychocidaridae.
Psychocidaris ohshimai is a small sea urchin with a test diameter up to 35 mm.
A, aboral view of animal showing the glandiform spines.
B, lateral view showing the oral and glandiform spines.
C, oral surface of test with the peristomial plates intact.
The imperforate primary tubercles on the interambulacra distinguish the Psychocidaridae from the Cidaridae.
[A,B, CSIRO; C, A.D.Miskelly]

Reproduction in many cidarids is reported to have an annual cycle (Lawrence & Jangoux 2013), including *Phyllacanthus parvispinus* from eastern Australia (O'Connor *et al*. 1976). In the Caribbean species *Stylocidaris lineata* pairing between individuals occurs during the spawning period; this is suggested to indicate pheromonal attraction (Young *et al*. 1992). Cidarids with lecithotrophic larvae can have very large eggs (>1,000 µm diameter) (Emlet *et al*. 1987; Tyler & Gage 1984a). Development usually involves either a free-swimming larval stage that includes species with small eggs and feeding echinopluteus larvae, or others with large eggs and non-feeding lecithotrophic larvae (Emlet *et al*. 2002). Echinoplutei are common in the genus *Prionocidaris*, whereas lecithotrophic larvae are common in species of *Phyllacanthus* and *Goniocidaris* (Emlet *et al*. 1987; Emlet 1990, 1995a). The larva of *Phyllacanthus parvispinus* is highly modified, lacking the characters typical of echinoid plutei (Parks *et al*. 1989). The larva of *Phyllacanthus imperialis* is a lecithotrophic reduced pluteus with four arms, and appears to be transitional between feeding and non-feeding echinoid larvae (Olson *et al*. 1993). Many cidarids, especially Antarctic species, brood their young; *Notocidaris remigera* and *Ctenocidaris geliberti* brood their young in sunken peristome cavities (Lockhart *et al*. 1994). *Goniocidaris umbraculum*, from New Zealand, broods its young among its spines (Barker 1985).

Family Psychocidaridae

Figure 10.9

This family, with the single species *Psychocidaris ohshimai* (**Fig. 10.9**), is characterised by having glandiform aboral spines and oral spines with longitudinal flanges (Smith & Kroh 2011). Psychocidarids are unlike cidarids in that the primary tubercles are imperforate. In Australia, *P. ohshimai* is known from the tropical Arafura Sea at a depth of 174 m (O'Hara 2012). Although few Australian specimens are known, this species occurs in very large numbers at similar depths in the Philippines (A.D.Miskelly, unpublished data); it also has been recorded from the Ogasawara Islands (Bonin Islands), south-east of Japan (Schultz 2015).

ECHINOTHURIOIDS

Echinothurioids are readily recognisable by their flexible, fragile tests that tend to collapse into a 'pancake' shape when they are collected or preserved (**Fig. 10.10**). The test is low, hemispherical to spherical and circular in outline. The component plates overlap at the edges, or they have membranous junctions, making the test comparatively flexible. The ambulacra and interambulacra extend across the peristome, and the tubercles are non-crenulate. The apical system is monocyclic in adults, gills and gill slits are inconspicuous or absent, and the spines are usually hollow.

These rather delicate echinoids have a poor fossil record. Kroh & Smith (2010) recognise three families, the extant Kamptosomatidae, Phormosomatidae and Echinothuriidae, within the order Echinothurioida. Eleven of the 13 reported genera of echinothurioids are extant, and while fossil species are known back to the Middle Jurassic of Europe, none has been reported from Australia. The relationships of the echinothurioids and their systematic position have been disputed for some years. Mortensen (1935) and Philip (1965a) believed that the presence of ambulacral plates on the peristome (shared with cidaroids) and overlapping test plates (shared with numerous fossils) tended to align the echinothurioids with more primitive echinoids. However, Jensen (1981), Smith (1984b) and Smith & Wright (1990) have regarded the echinothurioids as being more advanced, as they have perignathic girdles and gills. The presence of ambulacral plates on the peristome is possibly convergent with the cidaroid condition.

Echinothurioids have a worldwide distribution in modern seas. Two families (Echinothuriidae and Phormosomatidae) and 12 of the approximately 50 extant species are known from Australian waters (Mooi *et al.* 2004; O'Hara 2012). The two species in the Kamptosomatidae (*Kamptosoma asterias* and *K. abyssale*) occur in abyssal depths in the Pacific and Southern oceans (Mooi *et al.* 2004). Echinothurioids are best represented in the Indo-west Pacific, and only nine species are known from the Atlantic Ocean. Most echinothurioids have a bathyal or abyssal distribution, reaching depths of almost 5,000 m. Some of the best work on echinothurioids comes from deepsea research in the Atlantic (see Grassle *et al.* 1975; Tyler & Gage 1984a; Emson & Young 1998).

Family Phormosomatidae

Figure 10.10

Phormosomatids are characterised by polyporous ambulacra, club-shaped primary spines on the oral surface, the absence of terminal hooves on the spines and the presence of pointed teeth.

The Phormosomatidae include three extant genera, and no fossil forms are known. *Hemiphormosoma* and *Paraphormosoma* are known from Indonesia, and so may occur in northern Australia. *Phormosoma* is a very widespread genus in the Pacific and Atlantic oceans (**Fig. 10.10**), from shelf to abyssal depths. One species is known from Australia, *Phormosoma bursarium* (**Fig. 10.10A,C,D**). It is an Indo-west-central Pacific species that has been recorded from the east and west coasts of Australia and Lord Howe Island (as *P. rigidum*). *Phormosoma rigidum* was recently synonymised with *P. bursarium* by Anderson (2016).

The primary oral spines of species of *Phormosoma* are equipped with venom sacs on their tip (Halstead 1965). *Phormosoma* species ingest surface sediments, they form the sediment into small balls bound with mucus, and these can fill the intestine (Mortensen 1935, 1938; Pawson 1982b).

Observations from submersibles indicate that *Phormosoma* can move rapidly across soft substrates by active and coordinated stepping of its blunt primary spines on the oral surface (Emson & Young 1998). Some species of *Phormosoma* carry 10–20 soft fleshy sacs on their aboral spines that look like elongate balloons (Grassle *et al.* 1975; Emson & Young 1994b, 1998; **Fig. 10.10A,B**). It was initially thought that these sacs provided buoyancy enabling the animals to 'tip-toe' easily across the soft substrate on their sharp oral spines, but this is not the case, for the sacs are not buoyant (Emson & Young 1998). These sacs

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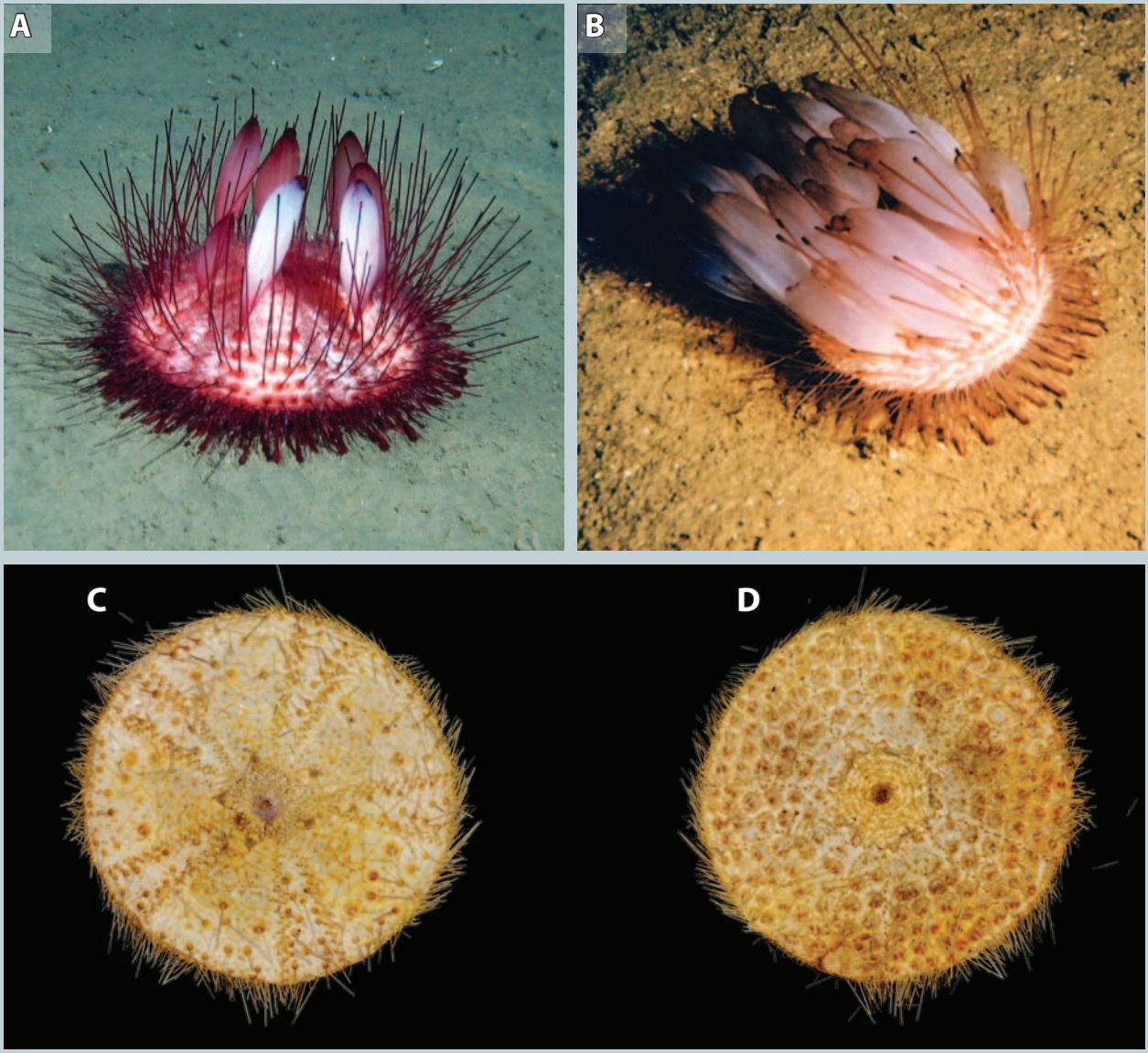


Figure 10.10 Family Phormosomatidae.

A, ***Phormosoma bursarium*** uses its club-shaped oral spines to move across the muddy seafloor, Sagami Bay, Japan. The aboral spines are erect, some covered by a leaf-like, fleshy sac.

B, ***Phormosoma placenta*** on the seafloor in the Bahamas. It has few spines on the aboral surface, and up to 20 of those may be each enclosed in a large membranous sac.

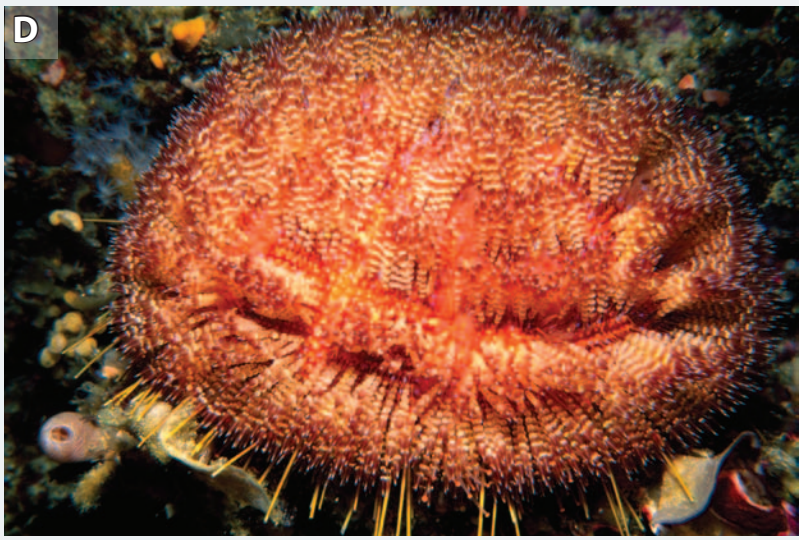
C, **D**, a specimen of ***Phormosoma bursarium*** from the Indo-Pacific; animals removed from the sea become flattened, and spines are often lost including the aboral membranous sacs enclosing the spines. Test diameter 74 mm.
C, aboral view.
D, oral view.

[A, JAMSTEC; B, D.L.Pawson; C,D, A.D.Miskelly]









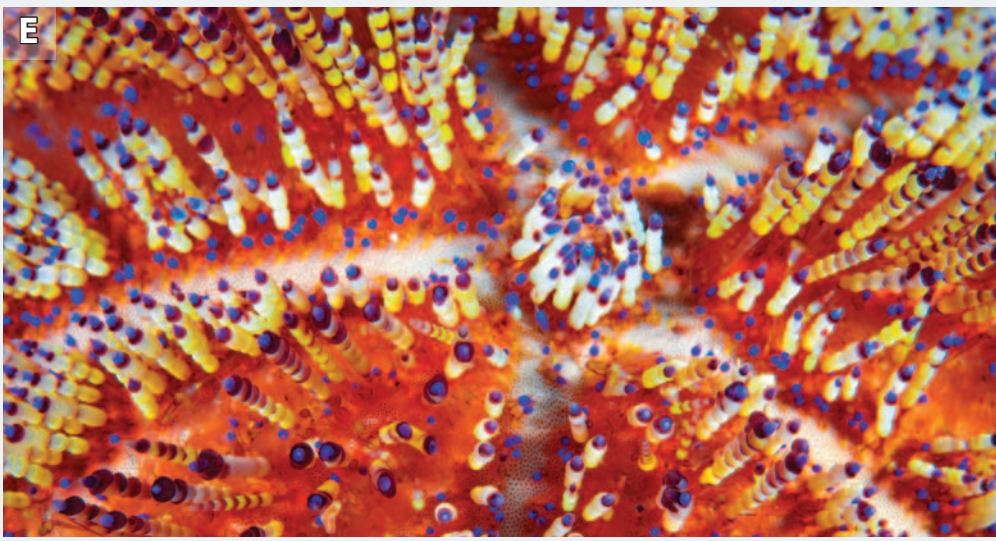


Figure 10.11 Family Echinothuriidae.

Species of ***Asthenosoma*** are known as fire urchins. They are brightly coloured and may inflict a painful venomous sting.

A, **B**, ***Asthenosoma ijimai***.

C, **D**, ***Asthenosoma varium***.

E, venomous spines on the aboral surface of ***Asthenosoma varium***.

[A,B,E, G.Bell; C, C.Bryce; D, L.Newman & A.Flowers]

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move passively in water currents and are composed of an outer epithelium and an inner layer of diffuse connective tissue and cells (Emson & Young 1998). The sacs are suggested to have a defensive function (Emson & Young 1998). When these animals are collected in dredges and trawls, the sacs become detached from the spines, leaving almost no trace.

The Atlantic species *Phormosoma placenta* has seasonal reproduction and spawns large (1,100 µm diameter) positively buoyant eggs and the lecithotrophic larvae are thought to be able to reach surface waters in two days from depths of 600–800 m (Tyler & Gage 1984a; Young & Cameron 1987; Baillon *et al*. 2011).

Family Echinothuriidae

Figure 10.11

Echinothuriids tend to be quite large, often reaching diameters of 300 mm (**Fig. 10.11**). The ambulacra are trigeminate, the primary spines on the oral surface have terminal hooves, and the teeth have rounded tips.

This family comprises nine genera and ranges from the Late Cretaceous to the Recent. Five genera have no fossil record (Smith & Kroh 2011), while *Echinothuria* is known only from the Late Cretaceous and *Retzneiosoma* from the Miocene of Austria (Smith & Kroh 2011). Eight genera and 20 species have been reported from Australia: *Araeosoma* (8 species), *Asthenosoma* (4), *Hygrosoma* (2), *Sperosoma* (2), and the single representatives *Tromikosoma australe*, *Kamptosoma asterias*, *Calveriosoma gracile* and *Hapalosoma pulchrum* (O'Hara 2012; Anderson 2016; A.D.Miskelly, unpublished data). Little is known of their biology. With few exceptions, echinothuriids are shelf and slope dwellers, only a few species being accessible in shallow water. Species of *Asthenosoma* (**Fig. 10.11**) are known from comparatively shallow waters in northern Australia, while the remaining Australian species inhabit the continental shelf and slope, and they can be expected to have wide distributions around the coast (O'Hara 2012). Members of the deep-water echinothuriid genera are distributed across the Tasman Sea to New Zealand where they are strongly associated with seamount type habitats (Anderson 2013).

The secondary aboral spines of *Asthenosoma* (**Fig. 10.11E**) and *Araeosoma* are highly venomous and have a venom sac covering the tip of the spine (Mortensen 1935; Cavey & Märkel 1994; Emson & Young 1994b, 1998). These venom organs are best developed in *Asthenosoma*. Puncture wounds from these spines can be extremely painful (Endean 1964), and even life-threatening under some circumstances (Mortensen 1935). Other authors report that they cause a 'nettle-like' sting of short duration (Emson & Young 1998). Observations from submersibles show that echinothuriids can move rapidly across soft substrates by active and coordinated movement of spines that have hoof-like tips (Pawson 1982b; Emson & Young 1998). The hoof-like tips may help in preventing the spines from sinking into the substrate (Pawson 1982b). Some of the spines on the upper and lateral surface of *Araeosoma belli* have fleshy tips that may have a toxic-predator deterrant function or function to support the fragile tip of the spine (Emson & Young 1998).

Some deepsea echinothuriids are highly selective feeders, appearing to subsist on virtually exclusive diets of leaves, seagrasses or seaweeds that have drifted down from terrestrial or near-shore environments (Mortensen 1935, 1938; Wolff 1979). Studies in the Caribbean show that at least one echinothuriid species preferentially ingests seagrass (*Thalassia* sp.) and seaweed (*Sargassum* sp.) fragments on a year-round basis (Pawson 1982b; D.L.Pawson, unpublished data). Caribbean echinothuriids can have a 'clumped' distribution seemingly independent of the distribution of plant fragments; such clumping may enhance reproductive potential (Pawson 1976; Young *et al*. 1992; D.L.Pawson, unpublished data).

Species of *Araeosoma* and *Asthenosoma* have large buoyant eggs (~1,300 µm diameter) indicating lecithotrophic development (Amemiya & Tsuchiya 1979; Tyler & Gage 1984a; Cameron *et al*. 1988). The development of *Asthenosoma ijimai* from shallow rocky reefs (20–30 m) in Japan is well studied (Amemiya & Emlet 1992). This species has a buoyant larva with vestigial pluteal features (Amemiya & Emlet 1992; Emlet *et al*. 2002).

DIADEMATOIDS and PEDINOIDS

Regular echinoids, apart from the cidaroids and echinothurioids, form a phylogenetic group that is currently termed the infraclass Acroechinoidea (Kroh & Smith 2010; Kroh & Mooi 2014). The diadematoids and pedinoids are basal members of this group, characterised by grooved teeth, simple ambulacral plate arrangements and semi-rigid coronas (Kroh & Smith 2010; Kroh & Mooi 2014). These animals have sometimes been classified together as the Aulonta or Diadematacea (Fell 1966c). However, recent phylogenetic work has shown that this is not a natural group but a primitive 'grade' of organisation (paraphyletic with respect to other regular echinoids); all of the included families have long evolutionary histories and should be considered as separate orders in their own right (Smith 1981; Emlet 1988; Kroh & Smith 2010; Smith & Kroh 2011; Kroh & Mooi 2014). Nonetheless, these families share other primitive features. Vestigial Stewart's organs are present in *Caenopedina* and in two species of diadematoid, which provides a link with the cidaroids and echinothurioids in which these organs are well developed (Smith 1981).

The families currently recognised are the Micropygidae, Aspidodiadematidae, Diadematidae and Pedinidae. The genus *Lissodiadema* was formerly assigned its own family (Fell 1966c), but is now included in the Diadematidae (Kroh & Mooi 2014).

The fossil history of this order is complicated by the poor preservation of many early Mesozoic fossils, probably due to the tendency of the test to break apart soon after death (Kier 1977). Some fossil genera, previously thought to be basal diadematoids, have recently been discovered to have keeled rather than grooved teeth (Smith & Kroh 2011). The extant families extend back to the late Triassic (Pedinidae), Early Jurassic (Aspidodiadematidae), Middle Jurassic (Diadematidae) and Early Eocene (Micropygidae) (Smith & Kroh 2011). Because of their strong tests, pedinoids are well known as fossils, and in some horizons, for example the Early Jurassic of Europe, they can be very abundant.

Most of the 50 or so extant species of diadematoids and pedinoids live in shallow waters down to 100 m (Smith & Kroh 2011; Byrne & Andrew 2013; Muthiga & McClanahan 2013). The Pedinidae occupy the upper contintental slopes (to 2,000 m) and some Aspidodiadematidae can reach abyssal depths. These families are well represented in the Indo-Pacific, and only six species are known to occur in the Atlantic Ocean. Many appear to be primarily herbivorous grazers (De Ridder & Lawrence 1982; Byrne & Andrew 2013; Muthiga & McClanahan (2013).

Family Micropygidae

Figure 10.12

The micropygid test is large, up to 140 mm in diameter, flexible, hemispherical, and flattened on the oral surface. The mouth and apical system are central on opposite surfaces of the test, and the apical system is monocyclic. The ambulacral plates are compound and trigeminate. Deep gill slits are present and the primary tubercles are perforate and non-crenulate. The spines are of moderate length and equipped with thorns. Tube feet of the outer series are transformed into large, umbrella-shaped organs of unknown function. They contain anchor-shaped ossicles.

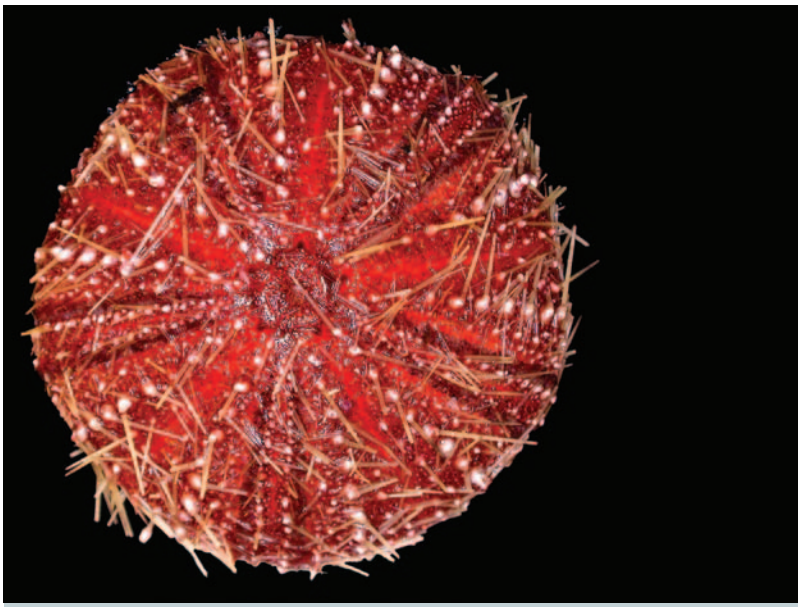


Figure 10.12 Family Micropygidae.
Aboral view of ***Micropyga tuberculata*** collected from near Mermaid Reef, Rowley Shoals, north-west Western Australia, at a depth of 430 m.
[CSIRO]

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The Micropygidae are represented by one modern genus, *Micropyga*, and two species, *M. violacea* and *M. tuberculata*, which range from East Africa to the western Pacific. One fossil genus, *Kierechinus*, from the Eocene of Somalia, is known (Smith & Kroh 2011). The only species found in Australian waters, *M. tuberculata*, lives in bathyal depths and is known from Queensland and north-west Western Australia (**Fig. 10.12**), and elsewhere in the Indo-west Pacific (Clark 1946; O'Hara 2012).

Species of *Micropyga* ingest plant material and form it into balls in the intestine (Mortensen 1938, 1940). This plant material can include land plant debris as well as algae that have sunk to the deep seafloor. *Micropyga* species are thought to have planktotrophic larvae. (Emlet 1995b).

Family Aspidodiadematidae

Figure 10.13

In the Aspidodiadematidae, the test is small, spherical to ovoid and fragile (**Fig. 10.13C**). The primary tubercles are crenulate, and the apical system is monocyclic. Spines are verticillate, and the longer spines are conspicuously curved downwards. The central cavity of the spines is divided by delicate perforated plates that are connected by strands of calcite.

The family comprises four genera, two of which are known only as fossils from the Late Jurassic and Late Cretaceous of Europe and Africa. The extant genera *Aspidodiadema* (Indo-Pacific and Caribbean; **Fig. 10.13A**) and *Plesiodiadema* (Indo-Pacific and Atlantic; **Fig. 10.13B**) are each represented in Australia by a single species: *Aspidodiadema tonsum* from the Norfolk Island Ridge, and *Plesiodiadema indicum* from off Queensland and New South Wales (O'Hara 2012).

Aspidodiadematids are typically slope and abyssal dwellers, with a depth range of approximately 70–5,000 m. They are widely

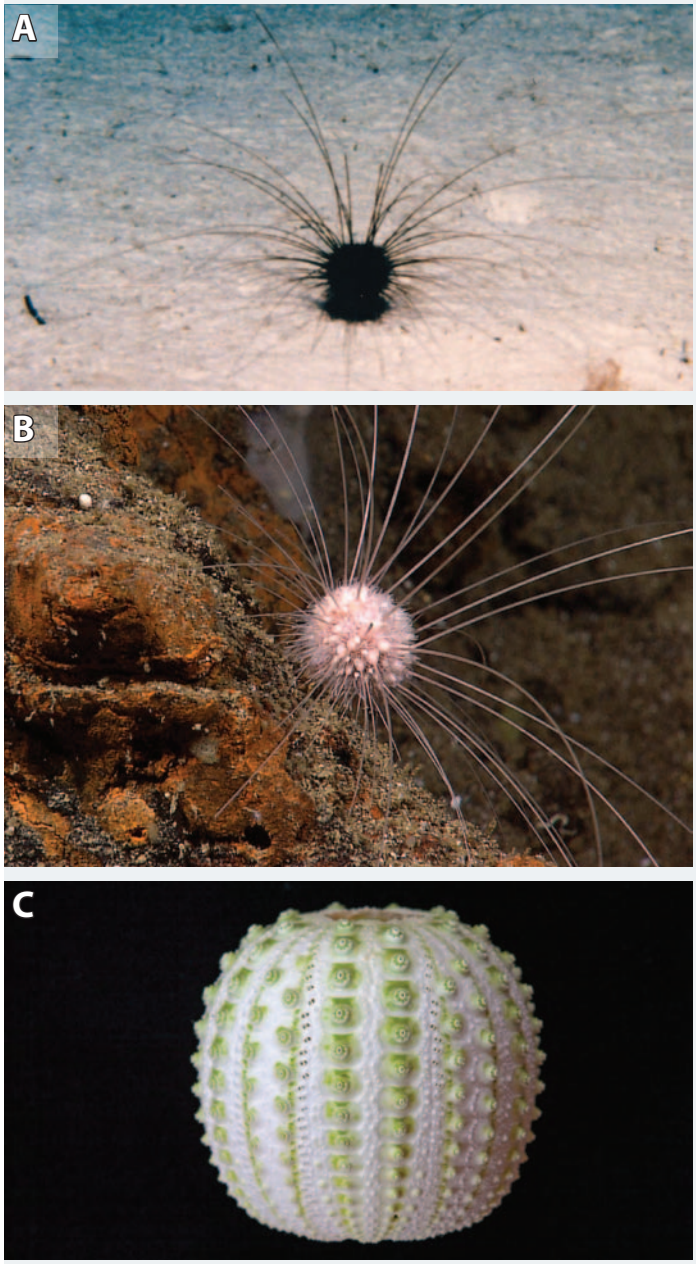


Figure 10.13 Family Aspidodiadematidae.

Aspidodiadematids have long recurved spines which hold the small central body off the substrate. They move rapidly across the substrate, tip-toeing on their spines.

A, ***Aspidodiadema jacobyi*** is found at depths over 1,000 m in the Caribbean Sea and Gulf of Mexico; this urchin is from the Bahamas.

B, ***Plesiodiadema*** sp. from deep water off the Bahamas.

C, fragile test of ***Aspidodiadema*** species from deep water off Norfolk Ridge with greenish perforate tubercles, showing the characteristic barrel shape. Test height 34 mm.

[A, D.L.Pawson; B, NOAA Okeanos Explorer Program, INDEX-SATAL 2010; C, A.D.Miskelly]

distributed in the Indo-Pacific and Atlantic oceans. At least nine species are thought to have pelagic feeding echinopluteus larvae (Emlet 1988, 1995b). The larva of the Caribbean species *Aspidodiadema jacobyi* can survive for about eight weeks, apparently on yolk material, before it becomes an obligate planktotroph, suggesting that this flexibility could be a response to the patchy availability of food in the deep sea as well as enhancing the ability of the larvae to disperse (Young *et al*. 1989). These larvae develop for at least five months and grow five pairs of larval arms including posterolateral arms; they also have an unpaired posterior process, in this respect resembling spatangoid larvae (Young & George 2000; Emlet *et al*. 2002). The fully developed larva differs from the two-armed larvae of other diatematoids (Young & George 2000; Emlet *et al*. 2002).

Australian species are herbivores like their shallow-water relatives, although some ingest mud balls (Mortensen 1940). In their preferred habitat of soft deepsea sediments, aspidodiadematids have been observed to move quite rapidly across the seabed on the tips of their long, curved primary spines, with the test held up off the seafloor (D.L.Pawson, unpublished data).

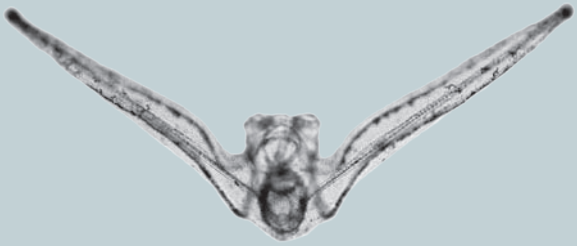


Figure 10.14 The two-armed diadematid echinopluteus of ***Centrostephanus rodgersii***.The larva develops long postoral arms as a potential adaptation to facilitate long distance dispersal. The other arms as seen in more typical echinoplutei show reduced or no development. The arms grow to 1.5 mm in length. In this specimen the arms are 300 µm long.

[N.Soars]

Family Diadematidae

Figures 10.14 & 10.15

Diadematidae have a test that is moderate to large in size and is usually somewhat flattened and flexible (**Fig. 10.15C**). The apical system is dicyclic or monocyclic, the primary tubercles are crenulate, and the spines are verticillate and not divided internally by transverse septa. Four of the 13 genera are extinct, and two others, *Diadema* and *Centrostephanus*, have fossil records that extend back to the Early Tertiary.

Seven of the nine extant diadematid genera are represented in Australia by 13 species: *Centrostephanus* (2 species), *Chaetodiadema* (3), *Diadema* (3), *Echinothrix* (2) and *Astropyga radiata*, *Eremopyga denudata* and *Lissodiadema lorioli* (O'Hara 2012; **Fig. 10.15**). The biology and ecology of *Diadema* is reviewed in Muthiga & McClanahan (2013) and that of *Centrostephanus* is reviewed in Byrne & Andrew (2013).

Long black spines characterise many diadematids (**Figs 2.11, 10.15**). *Diadema savignyi* and *D. setosum* can be difficult to tell apart and this is complicated by hybridisation and introgression (Lessios & Pearse 1996). These two species often occur in mixed populations, which may include hybrids (Pearse 1998). In addition, the pigment patterns on these species can differ between night and day (Coppard & Campbell 2005). Comparison of apical system, spine and tridentate pedicellaria morphology shows characteristics that can be used to facilitate identification of these *Diadema* species (Coppard & Campbell 2006a, 2006b). The biogeography of *Diadema* species is summarised in Lessios *et al*. (2001).

Diadematids are highly conspicuous on coral reefs worldwide, and in Australia the genera *Diadema* and *Echinothrix* (**Fig. 10.15A–E**) are common in these habitats (Pearse 1998). *Diadema* is also occasionally found in warm temperate locations in eastern Australia (Miskelly 2002). The two *Centrostephanus* species found in Australia are temperate and occur in eastern (*C. rodgersii*, **Box 2.1**) and western Australia (*C. tenuispinus*). One (*Lissodiadema lorioli*) of the two species of *Lissodiadema* occurs throughout the tropical western Pacific, including Australia; the other is known only from the Hawaiian Islands. *Astropyga* (**Fig. 10.15F**), *Eremopyga* and *Chaetodiadema* tend to inhabit sheltered offshore waters in the tropics. *Diadema palmeri* (**Fig. 10.15D**), a distinctive red species, occurs

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in southern Australia and New Zealand (O'Hara 2012); this is the only *Diadema* species to have a monocyclic apical system (Coppard & Campbell 2006a).

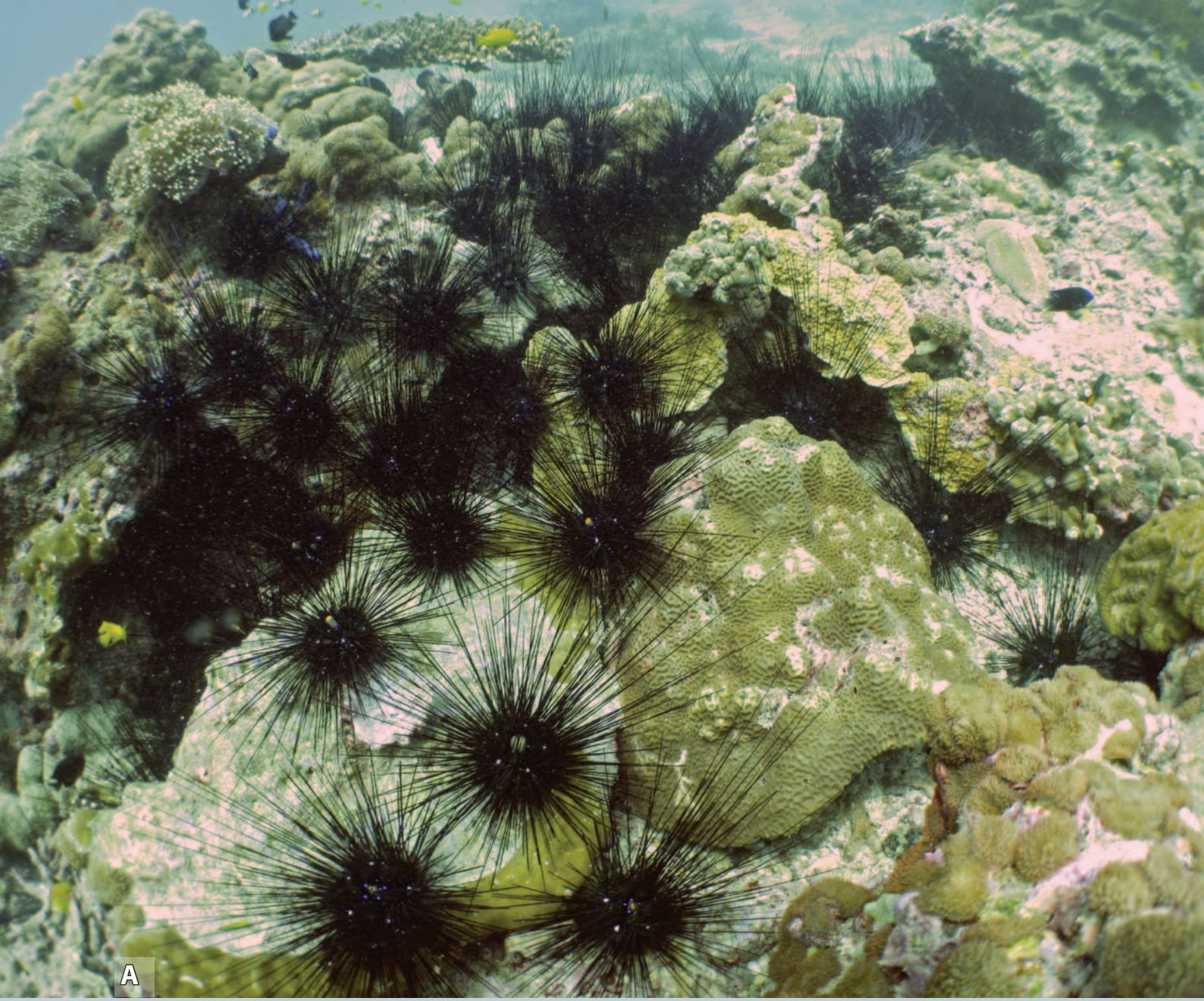
Diadematids are primarily grazers, and play an important ecological role in controlling the growth of algae (**Box 2.1**). *Diadema* species are common throughout their range in tropical reefs and are generally found in shallow water, although some are reported to occur at 70 m (Muthiga & McClanahan 2013). In tropical Australian waters several diadematids are sympatric (Young & Bellwood 2011). These species exhibit different preferences for algal species (Coppard & Campbell 2007). The role of *Diadema* species in coral reef ecology is well documented (Muthiga & McClanahan 2013). In the Caribbean a massive die-off of *Diadema antillarum* in 1983 extending along 4,000 km of coastline resulted in a rapid overgrowth of many reefs by algae (Lessios 1988). *Diadema* species can also play a role in bioerosion and this varies among locations. Bioerosion by *D. setosum* is a significant factor in the carbon cycle of Kenyan reefs where this species is abundant (Muthiga & McClanahan 2013), whereas this species has a minimal impact on Ningaloo Reef in Western Australia (Johansson *et al*. 2010).

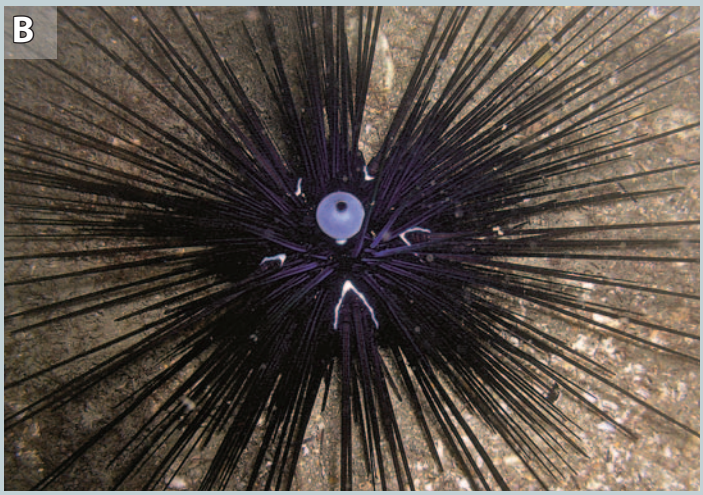
Diadema species typically seek shelter during the day, and do most of their foraging and feeding at night (Muthiga & McClanahan 2013). Diadematids are vulnerable to predation from fishes including trigger fishes (**Fig. 2.11**). Young & Bellwood (2012) report that *D. setosum* was more vulnerable to predation than the other diadematid *Echinothrix calamaris*, likely due to the antipredator morphology of the latter species (for example, larger and toxic spines). Large numbers of individuals can form 'herds' (Pearse & Arch 1969), especially on reefs that are over-fished. Experiments with the Caribbean species *D. antillarum* have shown that they exhibit an escape response when they are exposed to chemical stimuli produced by tissues of conspecifics that are crushed or broken upstream from the herd (Snyder & Snyder 1970). Despite their ecological importance tropical diadematids are not well studied in Australian waters.

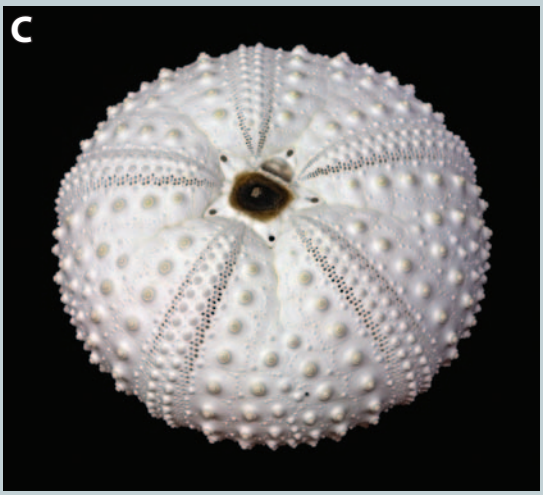
The two *Centrostephanus* species occur subtidally on Australian temperate rocky reefs: *C. rodgersii* from northern New South Wales to Tasmania (**Fig. 4.5G**), and *C. tenuispinus* along the southern coasts of South Australia and Western Australia. *Centrostephanus rodgersii* has been more extensively studied due to its ecological importance in eastern Australia, where grazing by these urchins create macroalgal-free barrens habitats. Recent colonisation of Tasmania by this species is attributed to ocean warming with major ecological consequences for the colonised environment (Andrew *et al*. 1998; Ling 2008; Ling *et al*. 2009a, 2009b; Johnson *et al*. 2011; Byrne & Andrew 2013; **Box 2.1**). Along the New South Wales coast, vast subtidal areas are covered by encrusting coralline algae, largely caused by grazing by *C. rodgersii*, limpets and turbinid gastropod molluscs (Fletcher 1987; Byrne & Andrew 2013). These echinoids are important in maintaining suitable habitats for limpet and fish species but also can displace abalone by overgrazing suitable habitats (Baker 1982b; Byrne & Andrew 2013; see **Box 2.1**). *Centrostephanus rodgersii* and *C. tenuispinus* are largely herbivorous grazers that also feed on drift algae (Vanderklift & Wernberg 2008). As in *Diadema*, *Centrostephanus* species do most of their foraging and feeding at night, avoiding daytime predators such as wrasses (**Box 2.1**), although night-time predators, such as lobsters, are important (Ling & Johnson 2012).

Diadematids are dangerous to humans because their sharp, brittle spines can easily penetrate the skin. The spines break off and, due to the reverse barbs along the shaft (Coppard & Campbell 2004) leave fragments inside the wound. Infection can result (Halstead 1965; Gillett 1968), caused by foreign matter carried into the wound, and not necessarily by venom associated with the spine.

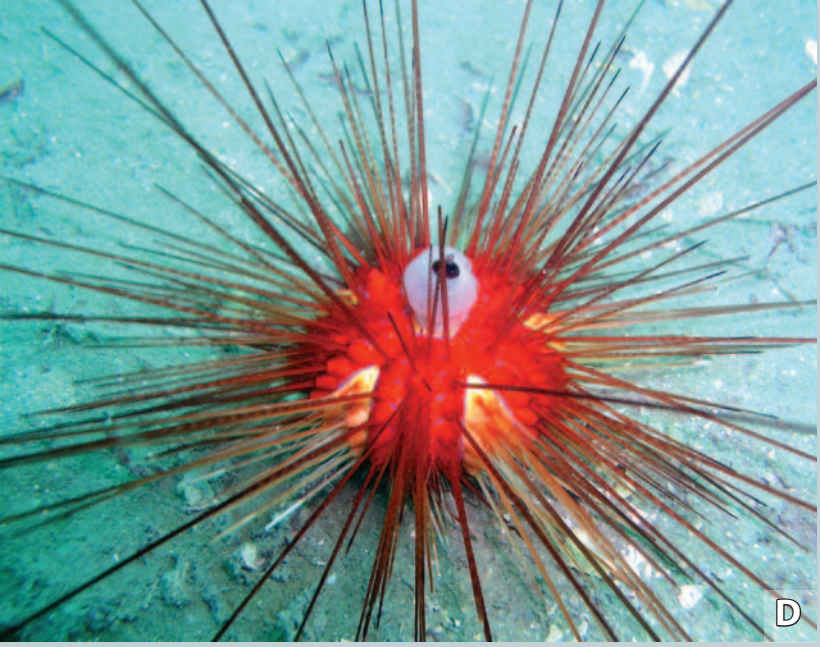
Reproduction in *Diadema* and *Echinothrix* species often has a monthly lunar cycle near to the equator with greater seasonality at higher latitudes (Pearse & Cameron 1991; Coppard & Campbell 2005). *Centrostephanus rodgersii* spawns in winter when temperatures are lowest and day lengths shortest (King *et al*. 1994; Byrne *et al*. 1998); they have a peak spawning period between July and August (King *et al*. 1994), although they can be induced to spawn from mid-May through to early October. Gamete growth and proliferation takes place from February to June, accompanied by a decline in the amount of nutritive tissue in the gonads.







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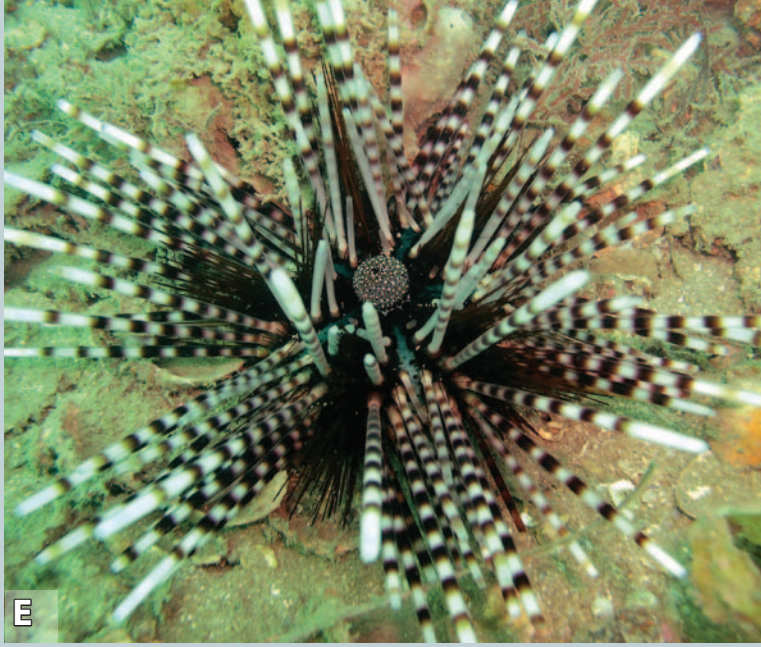






Figure 10.15 Family Diadematidae.

A, ***Diadema setosum*** is an abundant species that grazes algae in warm tropical shallow waters. It is found throughtout the Indo-west Pacific including Australia. This species has five distinctive white pigment spots.

B, **C**, ***Diadema savignyi*** is found on the tropical western and eastern coasts of Australia, occasionally as far south as Sydney Harbour, New South Wales, in the east:
B, a live urchin showing the distinctive blue v-shaped markings.
C, oblique aboral view of the fragile turberculate test. Test diameter 92 mm.

D, ***Diadema palmeri*** lives subtidally in rocky habitats along the coast of New South Wales.

E, ***Echinothrix calamaris*** is a tropical species with banded primary spines and needle-sharp darker secondary spines that can inflict painful wounds.

F, ***Astropyga radiata***, an exclusively tropical species, is brightly coloured with lines of blue spots (iridophores) on the aboral surface.

G, ***Centrostephanus rodgersii*** in its favoured habitat during daylight hours partially concealed in rock crevices at the base of large boulders.

[A, M.J.Kingsford; B–E, A.D.Miskelly; F, G.Bell; G, N.Soars]

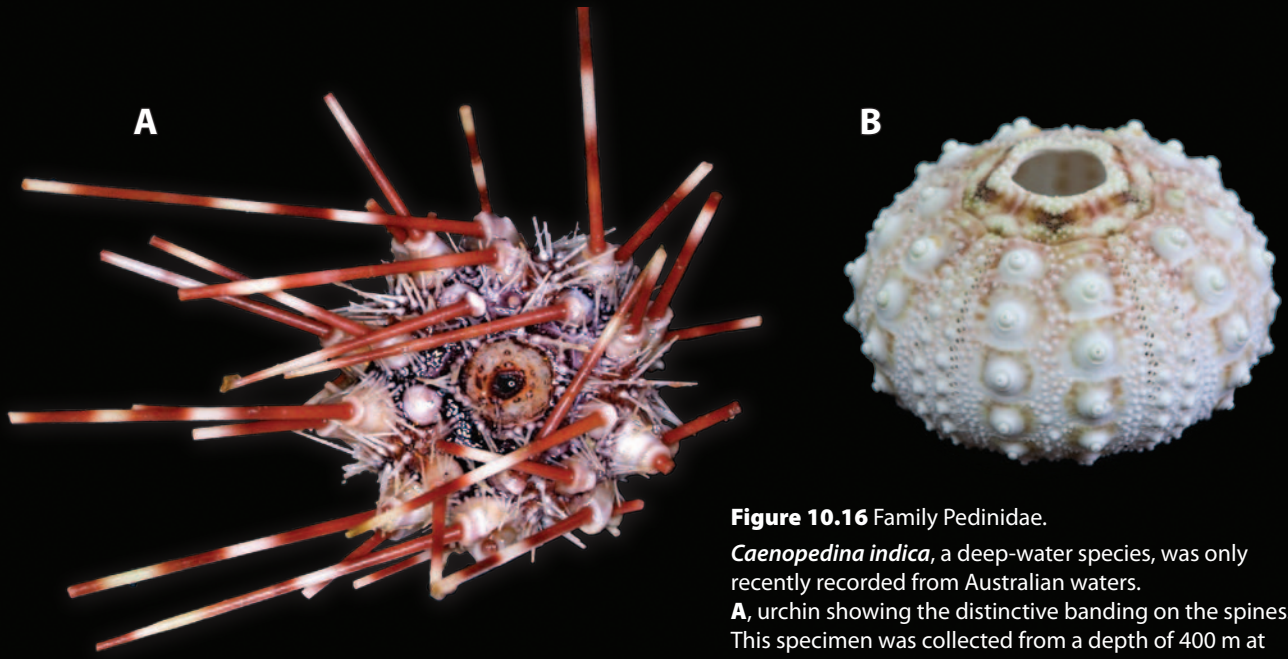


Figure 10.16 Family Pedinidae.
Caenopedina indica, a deep-water species, was only recently recorded from Australian waters.
A, urchin showing the distinctive banding on the spines. This specimen was collected from a depth of 400 m at Ashmore Reef, north-west Western Australia.
B, test in oblique view; test diameter 27 mm.
[A, CSIRO; B, A.D.Miskelly]

Diadematid larvae are unusual in only developing a single pair of arms (Fig. 10.14) which grow much longer (up to 1.5 mm) than the arms of other echinoplutei (Fig. 3.11C) (Huggett *et al.* 2005; Soars *et al.* 2009, Soars & Byrne 2015). This two-armed condition is a result of evolutionary loss or reduction in growth of the other pairs of arms, and may have evolved for long distance dispersal (Soars & Byrne 2015). The recent colonisation of Tasmania by *C. rodgersii* was likely to have been through larval transport as evidenced by the thermal biology of larval development in this species (Pecorino *et al.* 2013a, 2003b; Hardy *et al.* 2014). *Centrostephanus rodgersii* is commercially exploited in south-east Australia (see Chapter 4).

Family Pedinidae

Figure 10.16

The pedinid test (Fig. 10.16B) is of moderate size, only rarely exceeding 40 mm in diameter, subspherical, depressed-hemispherical or spherical, rigid, with the component plates not overlapping. The ambulacral plates are of the simple or compound diadematoid type, and the primary tubercles are perforate and non-crenulate. Gills are present, the gill slits notching the margin of the peristome. The apical system is dicyclic. The spines are striate, with thorns; primary spines are solid, and the secondaries are hollow. Pore series in the ambulacra are uniserial throughout, or are uniserial only adapically.

The Pedinidae includes one extant genus, *Caenopedina*, which has 12 living species mostly spread across the continental slopes of the Indo-Pacific. Only one species is known from the Atlantic Ocean, *Caenopedina cubensis*. Species of *Caenopedina* are very distinctive, with their long banded spines (Pawson 1964; Anderson 2009). The genus is more or less circumtropical, and it inhabits the shelf and slope at depths of 100–2,000 m (Mortensen 1940). Extant pedinid species appear to be rather rare, being known from few specimens, in contrast to some fossil taxa that are very abundant. Eight species are known from Australia (O'Hara 2012; A.D.Miskelly, unpublished data) — *C. mirabilis* ranges from Japan to tropical Australia, *C. novaezealandiae* is known from New Zealand, Norfolk Island and New South Wales, *C. alanbakeri* occurs only near Norfolk Island, and *C. indica* is found at Ashmore Reef in the Indian Ocean (Fig. 10.16), *C. pulchella*

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is known from Wanganella Bank, south of Norfolk Island, *C. hawaiiensis* is recorded from South Norfolk Ridge, and *C. otagoensis* is from Cape 'U' seamount, Tasmania. A giant (100 mm test diameter) recently discovered purple species *C. porphyrogigas* occurs on seamounts from Tasmania to the Louisville Ridge, east of New Zealand, and sub-Antarctic areas in depths of 350–1200 m (Anderson 2009). *Caenopedina mirabilis* ingests seafloor detritus including foraminiferans and shells (Mortensen 1940).

Two species of *Caenopedina*, from Japan and the western Atlantic, have planktotrophic larval stages (Emlet 1995a).

STIRODONTS

The orders Salenioida, Stomopneustoida and Arbacioida, and some fossil forms, were traditionally grouped as the Stirodonta (Smith & Kroh 2011). However, cladistic analyses have shown that this is a paraphyletic group, defined by the absence of features characterising the more recently evolved Camarodonta (Kroh & Smith 2010).

Family Stomopneustidae

Figure 10.17

The stomopneustid test is very large, sometimes exceeding 100 mm in diameter. The pore series in the ambulacra are arranged in horizontal arcs of three (**Fig. 10.17B**). The peristome is large with deep gill slits, and the primary tubercles are imperforate. Oculars I and V insert in the apical system. The spines are very robust and pointed.

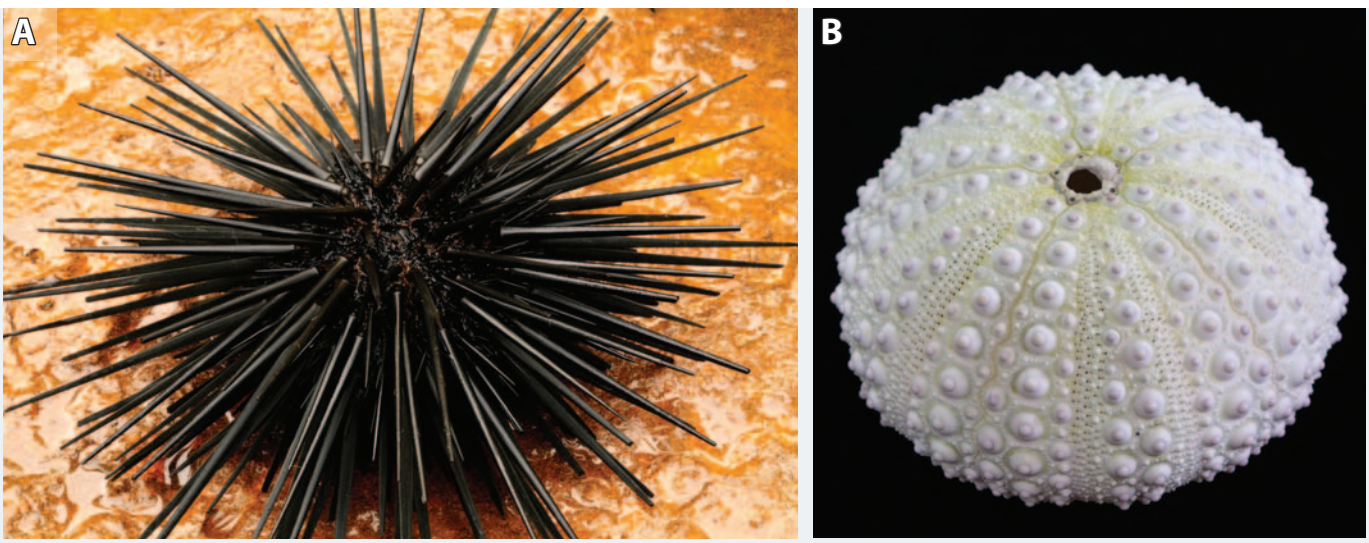


Figure 10.17 Family Stomopneustidae.

Stomopneustes variolaris is a predominantly tropical intertidal species that lives in high energy habitats on hard substrates. Test diameter 73 mm.
A, live example showing the long sharp spines.
B, oblique aboral view of test.

[A.D.Miskelly]

The Stomopneustidae is one of two extant families within the order Stromopneustoida. The single extant species, *Stomopneustes variolaris* (**Fig. 10.17**), is a strictly littoral Indo-Pacific form that lives in crevices in tropical rocky shore and coral reef habitats (Drummond 1991). In Australia it is found in northern tropical waters from Queensland to Western Australia (O'Hara 2012).

The other family, the Glyptocidaridae, also has only one extant species, *Glyptocidaris crenularis* from the north-western Pacific Ocean. This was once considered the only extant species of the Phymosomatoida but the ambulacral plates and apical disc structure better resemble the stomopneustids (Kroh & Smith 2010). Fossil stomopneustoids range from the Early Jurassic onwards.

The preferred foods of *S. variolaris* include brown, red, and green algae, calcareous algae, foraminifera, bryozoans and diatoms (Herring 1972). This species has an annual reproductive cycle and spawns small eggs (120 µm diameter) (Drummond 1991). It has a planktotrophic larva with unusual bilateral asymmetry (Yanagisawa 2004; Emlet 2009).

Family Arbaciidae

Figure 10.18

The Arbaciidae are comparatively small urchins (**Fig. 10.18**), up to 50–60 mm in diameter, with imperforate, non-crenulate tuberculation and primary tubercles well developed orally but reduced, absent or confined to adradial margins adapically (Smith & Wright 1993). Most genera have a distinctive interradial naked zone. The epistroma is conspicuous on the test, and the apical system is dicyclic, lacking tubercles.

Arbaciidae, with eight genera, is considered to be the only extant family within the order Arbacioida. Arbaciidae includes all 24 extant species of the order, and only *Arbacia* (Pliocene–Recent) and *Coelopleurus* (Eocene–Recent) are known to have a fossil record. Two other fossil families are recognised, the Acropeltidae (two fossil genera, *Goniopygus* and *Acropeltis*) and the Glyphopneustidae (fossil genera *Glyphopneustes* and *Arbia*). Fossil arbacioids date to the Early Jurassic (Smith & Wright 1993).

With a few notable exceptions, such as the much-studied shallow water *Arbacia* species (Gianguzza & Bonaviri (2013), arbaciids occur offshore, tending to inhabit the shelf and continental slope, and most species appear to have restricted distributions. Only six species, all *Arbacia*, are commonly found in rocky intertidal and shallow water habitats, four of them on the west coasts of Central and South America, one in the Mediterranean and one along the east coast of North America (Gianguzza & Bonaviri 2013). These shallow water species are common in a range of habitats from rocky reef to seagrass beds (Gianguzza & Bonaviri (2013).

Two species occur in Australian waters; both are found in deep water on the continental shelf (O'Hara 2012): *Coelopleurus australis* only from the eastern shelf off Tasmania, and *Coelopleurus maculatus* from Norfolk Island and off Cape Leveque, northern Western Australia, and throughout Asia.

The biology and ecology of *Arbacia* is reviewed in Gianguzza & Bonaviri (2013). The biology of the species in North America, *Arbacia punctulata*, is well studied, particularly its reproduction and development (Harvey 1956).

The test of *Arbacia* is rather stout and orally flattened and ranges in size from 15–50 mm diameter (Mortensen 1943a; Gianguzza & Bonaviri 2013). The spines are of moderate length and those near the mouth have flattened tips. There are usually conspicuous naked areas in the apical region of the interambulacrae (Gianguzza & Bonaviri 2013).

Coelopleurus is distinctive in having very long spines that can be three to four times the diameter of the test (**Fig. 10.18**); the spines are triangular in cross-section, and curve upwards. In other arbaciids, the spines seldom exceed the diameter of the test. Their long spines and strikingly brilliant colouration make *Coelopleurus* species very attractive. This genus does not seem to be 'very closely connected' with other recent forms in this family, suggesting that it could be derived from the Late Jurassic to Eocene genus *Codiopsis* (Mortensen 1935).

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A fossil species, originally assigned by Gregory (1890) to *Coelopleurus*, *C. paucituberculatus*, was considered by Philip (1965b) to be sufficiently distinct to warrant placement in its own genus, *Murravechinus*. The species was recorded from Miocene rocks at Morgan, South Australia (Gregory 1890).



Figure 10.18 Family Arbaciidae.
The primary spines of ***Coelopleurus maculatus*** are banded in red and greenish white. It is found in the seas off Japan, the Philippines, the Indo-Malayan Region and Norfolk Island at depths of 60–360 m.
[A.D.Miskelly]

Arbacia species are opportunistic omnivorous feeders (Cobb & Lawrence 2005; Gianguzza & Bonaviri 2013). They have a strong tendency to carnivory, grazing the surface of hard substrates and consuming calcareous polychaetes, barnacles, bryozoans and other epifauna (Gianguzza & Bonaviri 2013). Thus they use their teeth for durophagous feeding. Most populations of *Coelopleurus* occur in the deep aphotic zone, so food is most likely to be algae falling to the depths or locally generated detritus. Little is known about the biology of *Coelopleurus*.

Arbacia species have seasonal reproduction and their development through a planktotrophic echinopluteus larva is well characterised (Harvey 1956; Emlet 1995b; Gianguzza & Bonaviri 2013). *Coelopleurus maculatus* is also thought to have an echinopluteus larva (Emlet 1995b).

Family Saleniidae

Figure 10.19

The saleniid test is usually small, only rarely reaching 45 mm in diameter (**Fig 10.19C**). The primary tubercles are imperforate, the ambulacral tubercles are non-crenulate, and the interambulacral tubercles are usually crenulate. The ambulacral plates are of the simple type, or bigeminate or trigeminate. The apical system has a single large suranal plate that gives the apical system its very distinctive appearance. In addition, the apical system is very large, occupying almost the entire upper surface of the test, and it is usually conspicuously ridged and pitted.

The fossil record of this family dates back to the Early Cretaceous. In Australia the oldest species is *Pleurosalenia tertiaria* from the Middle Eocene of southern Australia.

The three extant genera are rather widespread in the Indian and Pacific oceans (Pawson 1965; Rowe 1989b). *Salenia* has five species, none reported from Australian waters, with relatively restricted distributions at depths of 102–540 m (O'Hara 2012). The eight species of *Salenocidaris* have broader distributions, probably due to their tendency to live at greater depths (370–3,120 m). *Salenocidaris hastigera* is known from Norfolk Island and several other localities in the Indian and Pacific oceans (Pawson 1965; Rowe 1989b; **Fig. 10.19B,C**). The five species of *Bathysalenia* are found in deep water from 90 to 500 m, mostly throughout the Indo-Pacific; one species, *Bathysalenia goesiana*, is restricted to the Atlantic Ocean. In Australia, *Bathysalenia cincta* is known from a single specimen collected at a depth of 200 m off the north-west coast of Western Australia (O'Hara 2012; **Fig. 10.19A**).

The primary spines of saleniids have a distinct downwards curve, so that when the animal is moving about on soft muddy substrates, it appears to 'walk' on the tips of its spines, with the test suspended above the sediment (D.L.Pawson, unpublished data). Species of *Salenia* and *Salenocidaris* ingest fine-grained bottom material, including sand and foraminiferans (Mortensen 1935). Two species each of *Salenia* and *Salenocidaris* are inferred to have pelagic, planktotrophic larval stages (Emlet 1995b). Little is known of the biology of these echinoids.

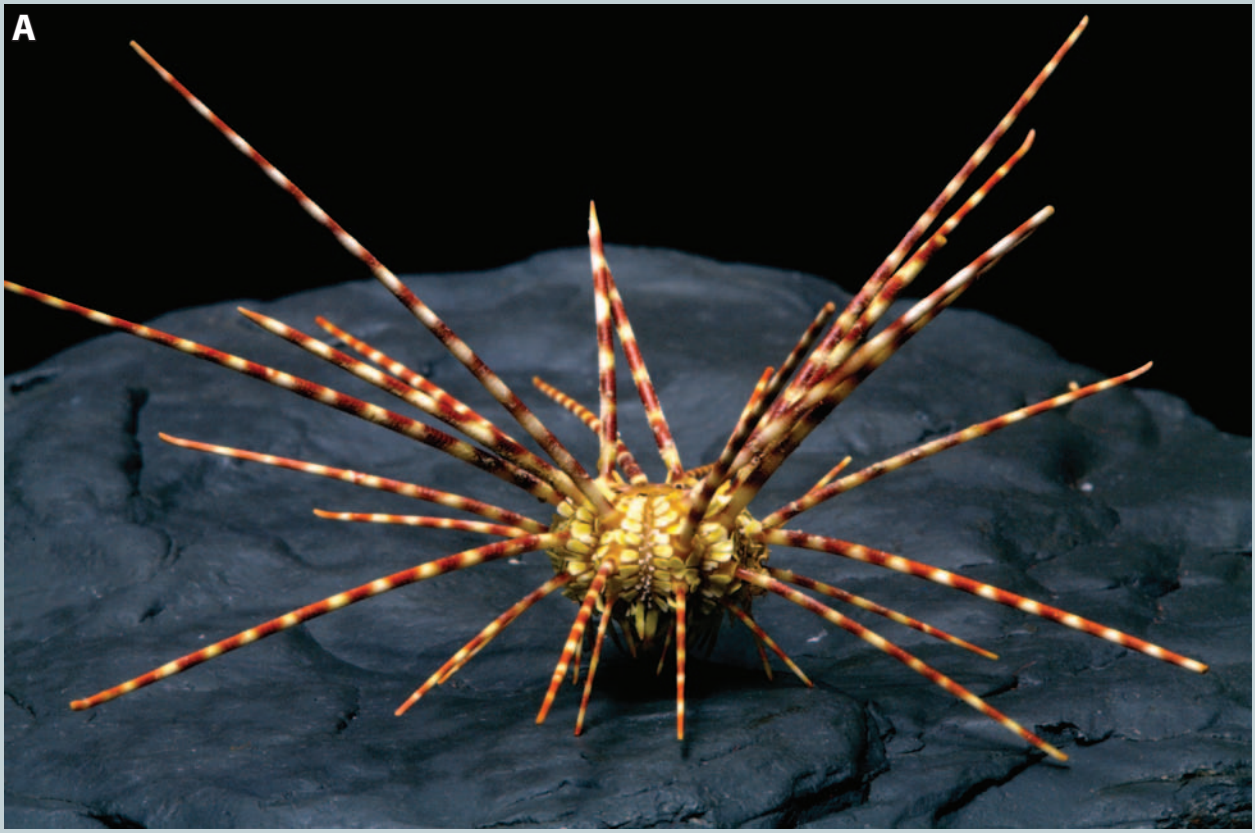


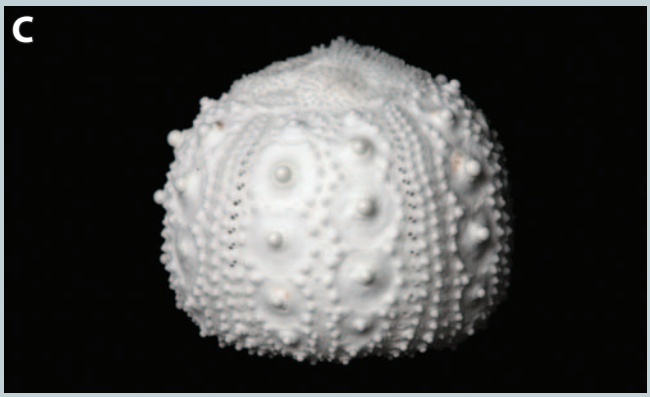


Figure 10.19 Family Saleniidae.

A, ***Bathysalenia cincta***, a deep-water species, grows to a test diameter of 10 mm. It has been reported from Japan, the Malay Archipelago and northern Australia.

B,**C**, ***Salenocidaris hastigera***, a widespread deep-water Indo-Pacific species, occurs in great numbers where habitat is suitable. Test diameter 20 mm.
B, specimen with spines attached.
C, the fragile white test after removal of soft tissues and spines.

[A.D.Miskelly]



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CAMARODONTS

The camarodonts are the largest monophyletic group of living regular echinoids. They have a characteristic lantern, which is strengthened by the fusion of 'epiphyses' (aboral lantern ossicles) above the 'pyramid' ossicles (Kroh & Smith 2010). Kroh & Smith (2010) currently treat the Camarodonta as an order, with two infraorders, the Temnopleuridea (with extant families Temnopleuridae and Trigonocidaridae) and the Echinidea (Echinidae, Parechinidae, Strongylocentrotidae, Toxopneustidae and Echinometridae). The genus *Parasalenia* has been treated as being in the Echinometridae (Rowe & Gates 1995) or in its own family, Parasaleniidae (Kroh & Smith 2010), of uncertain placement within the order. The Parechinidae and Strongylocentrotidae are not represented in the Australian fauna.

The infraorder includes 38 genera, of which three are extinct, and approximately 96 extant species (Smith & Kroh 2011). These echinoids are well known from the Late Cretaceous onwards with 50 fossil species (Kier 1977). Today, the order has a worldwide distribution, with most species living on continental shelves or slopes. Individual species, particularly shallow-water taxa, appear to have quite restricted depth ranges.

Family Temnopleuridae

Figure 10.20 & Box 10.2

The family Temnopleuridae (**Fig. 10.20; Box 10.2**) comprises 15 genera with sutural depressions or pits. Currently, 12 extant genera are known, including 67 living species. This family flourishes in the Indo-Pacific, with just one species in the southern Atlantic Ocean. Most species live on continental shelves at depths of less than 100 m; the remainder inhabit the slopes. The Australian temnopleurid fauna is conspicuous and diverse, with nine of the 12 extant genera represented, and 31 of the 67 species: *Amblypneustes* (6 species), *Holopneustes* (4), *Microcyphus* (6); *Pseudechinus* (2), *Salmaciella* (2), *Salmacis* (2), *Temnopleurus* (3) and *Temnotrema* (5), and *Mespilia globulus* (O'Hara 2012; A.D.Miskelly, unpublished data). Many are common around the southern part of Australia, and are ecologically important in inshore habitats where algal growth is prolific. Some temnopleurids, such as *Mespilia globulus*, *Microcyphus compsus* and *Salmacis belli* (**Fig. 10.1**), are strikingly beautiful.

Temnopleuridae are characterised by a rigid test that is circular in outline and usually ornamented with ridges (epistroma) and/or sutural depressions. The ambulacra are compounded in the echinoid manner, always trigeminate. Gill slits are present, but shallow. The tubercles are imperforate and crenulate, although the crenulations can be indistinct. The lantern is camarodont, the spines are solid, and the apical system is dicyclic.

The degree of tubercular crenulation can vary considerably between genera, while in *Pseudechinus* crenulation is essentially absent. Moreover, the degree of sculpturing of the test can vary, so that many species have angular pores or pits and more or less well-developed sutural depressions, while in *Pseudechinus* ornamentation can take the form of a rudimentary epistroma (superficial ornamentation; some authors would restrict the use of the term epistroma to the ridges on the test of arbacioid echinoids), or there can be no trace of an epistroma. In larger temnopleuroids (such as *Salmacis* and *Amblypneustes*) the test is usually delicate and fragile, while in smaller forms (for example *Microcyphus* and *Temnotrema*) it is thick and strong (Mortensen 1943a). In the tropical *Temnotrema* the sculpturing is the deepest of all temnopleurids. Most species of *Temnotrema* are comparatively small, and deep sculpturing possibly strengthens the test, thus reducing its susceptibility to predation.

The Temnopleuridae also contains the fossil families Glyphocyphidae and Zeuglopleuridae. Fossil zeuglopleurids have North Atlantic distributions. Temnopleurids are known since the Late Cretaceous (Cenomanian), and they are an important component of the echinoid fossil record, with about 71 fossil species having been described from the Miocene alone (Kier 1977). The position of *Pseudechinus*, with its anomalous morphology (see above), is uncertain. However, molecular evidence suggests that it is sister to the Temnopleuridae (Jeffery *et al.* 2003). Fossil

Box 10.2 Canopy dwelling sea urchins

Ashley D. Miskelly

A group of predominantly southern Australian temnopleurids, principally belonging to the genus *Holopneustes* and commonly called canopy dwelling sea urchins, have adapted to a habitat suspended in kelp, seagrass and other seaweeds and their morphology reflects this. The evolutionary change from living on hard substrates such as rocky reefs and loose sediment to a suspended 'canopy dwelling' existence is associated with several morphological changes and specialisations. The first feature concerns the almost spherical test. Rather than being somewhat flattened or low-dome shaped like many other temnopleurids, the spherical test provides better resistance to drag in sea currents than a broad test. In addition to this, the sculpturing effect found in the plates that comprise the test of most temnopleurids (which is a comparatively weaker structure) is almost diminished in *Holopneustes*, resulting in a test structure that is quite robust. These improvements over their more sculptured counterparts allow a successful existence in their preferred habitat.



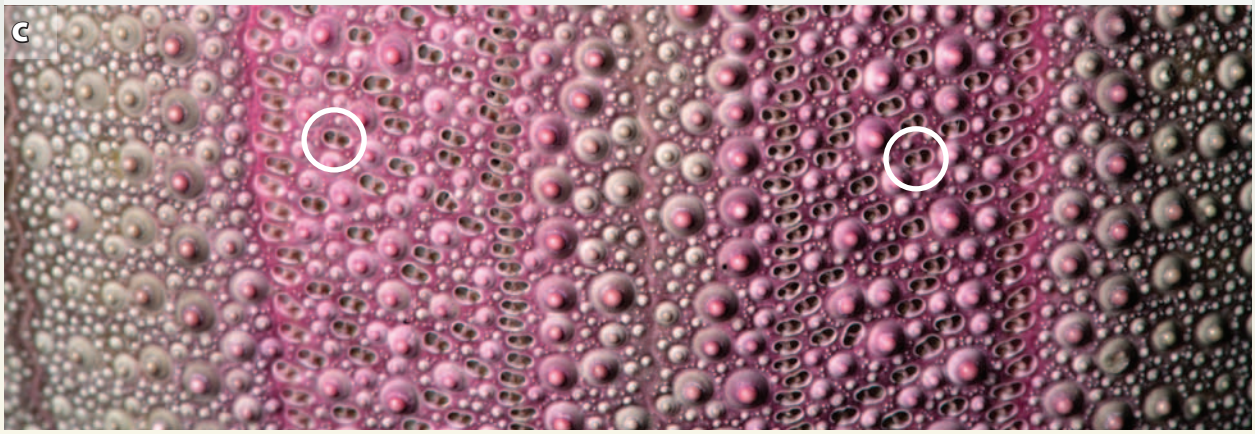
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Canopy dwelling sea urchins are subjected to increased swaying with the current and thus have adapted a more complex pore-pair arrangement for the tube feet to grasp and maintain a firm grip on the surface of an algal frond such as kelp. This is especially evident in *Holopneustes porosissimus*, where the ambulacra are much wider than the interambulacra and contain a greater surface area bearing higher concentrations of strongly suckered tube feet. In comparison, for regular sea urchins living exclusively on hard substrates, it is only necessary for oral tube feet to be strongly suckered to prevent becoming dislodged. Similarly, for those that live subtidally on loose sediment, the strength of the tube feet is less important as the current is minimal, thus the oral tube feet are not as strongly suckered and the poriferous zones are narrow in comparison.

The adaptations are further facilitated by sea urchins having short spines of equal length and tube feet that extend far beyond the spines — this enables the sea urchin to remain in close contact with the surface of the algae.

Further reading Williamson & Steinberg 2012; Bell *et al*. 2014





Figures a–c Canopy dwelling sea urchins in the family Temnopleuridae.

a, ***Holopneustes inflatus*** showing the ability of the strongly suckered tube feet to extend far beyond the short spines which are of equal length. This species is commonly found in shallow water curled up in kelp.

b, **c**, test of ***Holopneustes porosissimus***:
b, the spherical test showing the poriferous zones (indicated by two smaller white lines) of the greatly widened ambulacra. Note the absence of sculpturing typical of less advanced temnopleurids. Test diameter 74 mm.
c, a magnification of the two poriferous zones (boxed area in **b**) of an ambulacrum showing the numerous pore pairs (white circles) through which strongly suckered tube feet emerge.

[A.D.Miskelly]

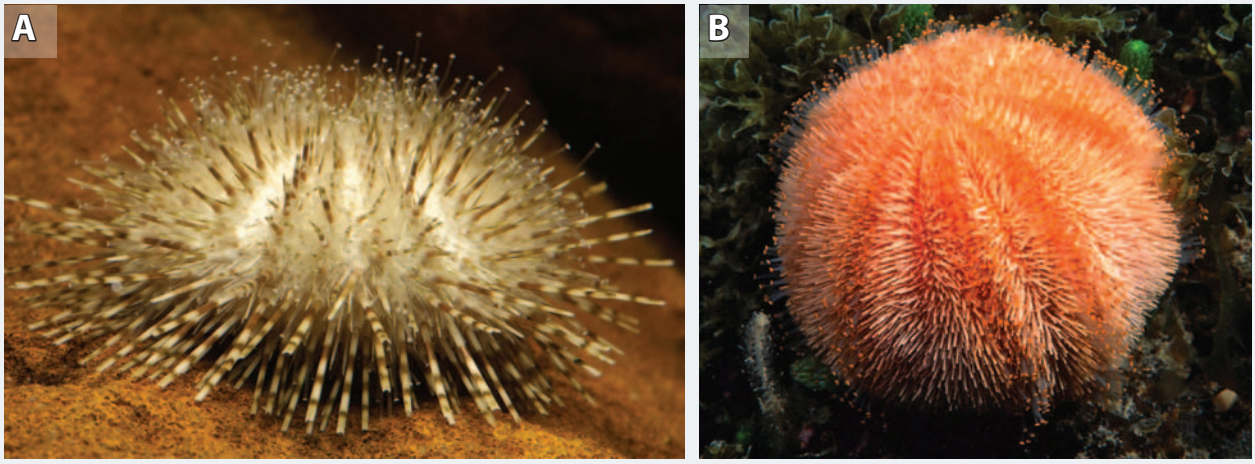


Figure 10.20 Family Temnopleuridae.

A, ***Salmaciella oligopora***, once thought to be an Australian endemic species, now also occurs in the Philippines. It has spatulate oral spines to move on loose sediment.

B, ***Holopneustes purpurascens***, a spherical canopy-dwelling species, is found commonly in the intertidal zone grazing on algae. It has short spines and tube feet with strong adhesion capability that allow this species to live in curled up algal fronds.

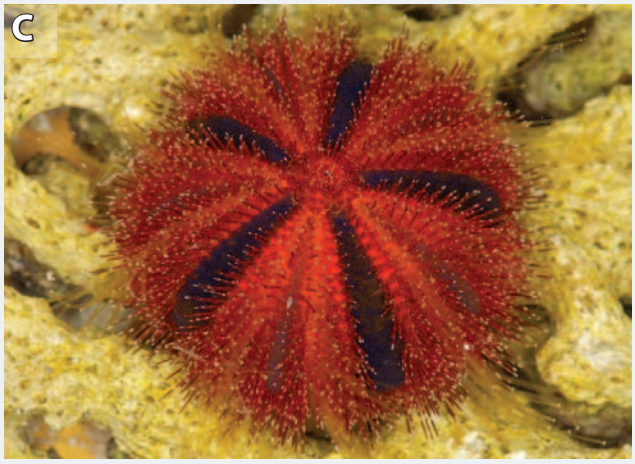
temnopleurids are very common in Eocene to Pliocene sediments in southern Australia, 19 species in nine genera having been described (Philip 1969; Philip & Foster 1971), the most speciose being *Asaphechinus*, *Orthologhus* and *Paradoxechinus*.

Temnopleurids generally ingest a mixture of bottom material and also browse on algae (De Ridder & Lawrence 1982). Unlike other living sea urchins, *Amblypneustes* and *Holopneustes* species are unusual in being 'arboreal', living attached to kelp fronds or surrounded by seagrass blades (**Figs 2.5, 2.17, 10.20B; Box 10.2**). As an adaptation to living in the canopy these urchins have very small spines and their numerous tube feet have a tenacious grip on their plant host. Their association with kelp and preferred habitat on reefs may reflect the coevolution of these genera with the kelps and also facilitates the presence of other grazers in the kelp (Bell *et al*. 2014). *Holopneustes purpurascens* consumes parts of the kelp in which it lives and in high densities can kill the host plant (Steinberg 1995; Rogers *et al*. 1998; Williamson & Steinberg 2012). Wrapped in the alga, *H. purpurascens* is protected from predation by fishes (Williamson *et al*. 2004). *Temnopleurus michaelseni* is common enough in seagrass beds at Albany, Western Australia, to have had a significant impact on their growth patterns (Marsh 1991). In South Australia, *Amblypneustes pallidus* can overgraze seagrass (Burnell *et al*. 2013).

Salmacis, *Salmaciella* and *Temnopleurus* live on coarse rubble or shellgrit substrates. They have spatulate spines on the oral surface that are used primarily for locomotion. The spines of *Salmaciella oligopora* also transfer food particles to the peristome (A.D.Miskelly, unpublished data). These three genera are always found subtidally at depths greater than 4 m and are omnivorous grazers. *Microcyphus compsus*, a small striking species, occurs predominantly in Western Australia, living among red algae at depths of about 30 m (A.D.Miskelly, unpublished data).

Despite the great diversity of temnopleurids in Australia, the reproductive biology is described for only *Holopneustes purpurascens* and *H. inflatus* (Williamson & Steinberg 2002; Swanson *et al*. 2012).

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C, ***Mespilia globulus***, a common predominantly coral reef dwelling Indo-Pacific species, is easily identified by the five bare median areas of the interambulacra.



D, ***Microcyphus elevatus*** has the distinct zigzag areas void of spines that are characteristic of the genus ***Microcyphus***. This pattern can give the sea urchin quite a striking appearance most unlike other temnopleurids. This specimen is from the Swain Reefs, Great Barrier Reef, Queensland, at a depth of 3 m.

[A,C,D A.Miskelly; B, W.Boyle]

Both species spawn from September to December, with some sporadic gamete release at other times of the year (Williamson & Steinberg 2002).

Most species of *Amblypneustes*, *Holopneustes* and *Microcyphus* have pelagic, highly reduced non-feeding (lecithotrophic) larvae (**Fig. 3.11H**), while all *Genocidaris*, *Mespilia*, *Pseudechinus*, *Salmaciella*, *Salmacis*, *Temnotrema* and *Trigonocidaris* species that have been studied have small eggs and planktotrophic echinopluteus larvae, including most Australian species (Emlet 1995b; Jeffery *et al*. 2003). Interestingly, two of the three genera with lecithotrophic larvae, *Amblypneustes* and *Microcyphus*, were present in southern Australian waters back in the Pliocene (Foster & Philip 1980). *Salmacis sphaeroides* spawns small eggs (122 µm diameter) from April to July in Malaysia and develops through a feeding echinopluteus larva with metamorphosis after 35 days (Rahman *et al*. 2012). *Pseudechinus novaezealandiae* from Macquarie Island also spawns small eggs (100 µm diameter) (Simpson 1982). Many temnopleurids in temperate Australia have large eggs and lecithotrophic development (Jeffery & Emlet 2003; Jeffery *et al*. 2003), the best studied of which is *Holopneustes purpurascens* (500 µm diameter eggs) (Morris 1995). The large larva of *H. purpurascens* is used as a model to investigate the development of echinoids with modified lecithotrophic development (Morris 1995, 2007, 2016).

Mapping larval type onto a molecular and morphological phylogeny suggests that planktotrophy is the ancestral state for the Temnopluridae (Jeffery *et al*. 2003). However, non-planktotrophic development has arisen more than once, with fossil genera in the Cenozoic having species with lecithotrophic pelagic larvae or brooded young (Jeffery & Emlet 2003). Modern species with planktotrophic larvae tend to have broader distributions than closely related species with lecithotrophic larvae, and this tendency is amply demonstrated in the Temnopleuridae (Emlet 1995a).

Marsupiate temnopleurids are remarkable common in Eocene to Miocene strata in southern Australia. Four species of *Paradoxechinus*, each with a deeply sunken apical marsupium, have been described. A single

species of *Pentechinus* has remarkable elongate aboral interambulacral marsupia. The high incidence of marsupiate echinoids in the mid-Cenozoic of Australia has been attributed to the occupation of high seasonality environments during this period (McNamara 1994a).

Family Trigonocidaridae

Figure 10.21

The Trigonocidaridae lack sutural depressions or pits. The family includes nine genera, most of which are exclusively fossil and date back to the Late Cretaceous (Turonian). Trigonocidarids have a global fossil record including the Cenozoic of southern Australia (Philip 1969, 1971; Jeffery & Emlet 2003). Extant taxa mostly occur in deeper waters (>100 m) of the Atlantic, Indian and Pacific oceans.

Four species occur in Australian waters, *Genocidaris incerta*, *Trigonocidaris micropora* at 100–500 m, *Orechinus monolini* in deeper water at 318–2,300 m, and *Desmechinus rufus* with the shallowest habitat, known only from a few specimens from the northern Great Barrier Reef at depths of about 70 m (Miskelly 2009; **Fig. 10.21**). The species of *Genocidaris* and *Trigonocidaris* that have been studied have planktotrophic larvae (Emlet 1995a).

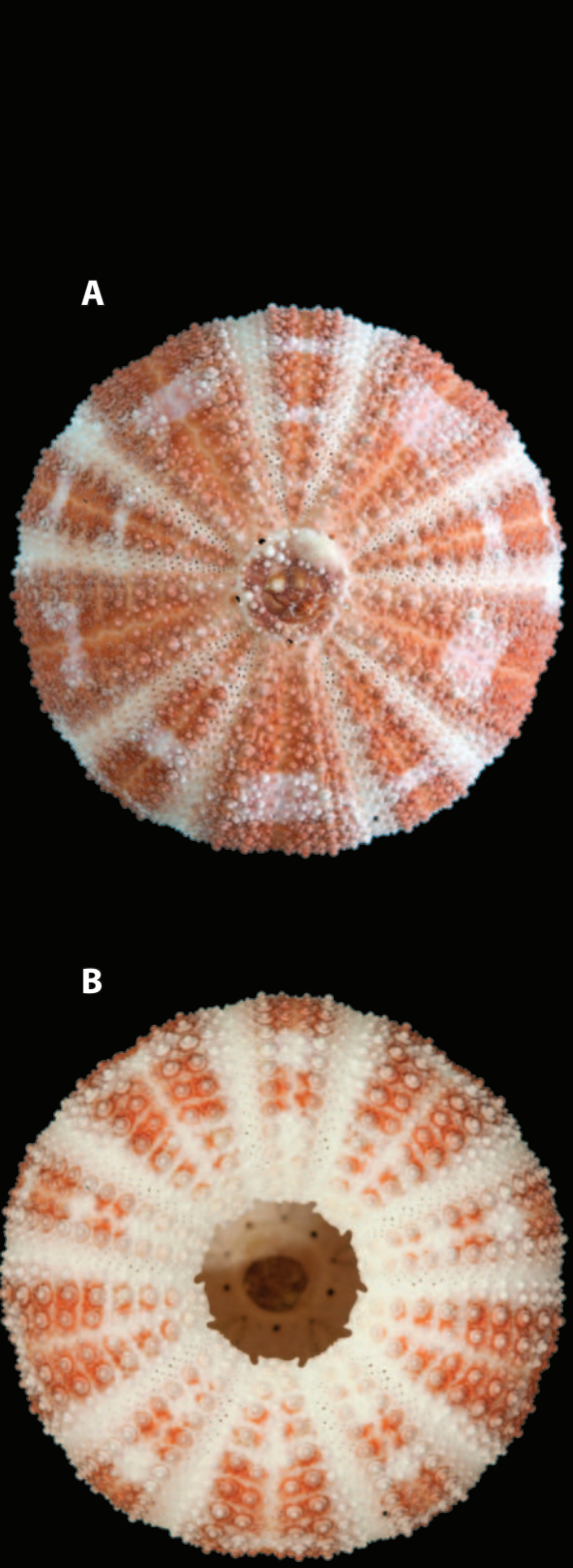


Figure 10.21 Trigonocidaridae.
A test of ***Desmechinus rufus***, a small tropical species found subtidally in the northern Great Barrier Reef, Queensland. Test diameter 25 mm.
A, aboral view.
B, oral view.

[A.D.Miskelly]

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Family Echinidae

Figure 10.22

The Echinidae have a solid test that is circular to elliptical in outline and lacks surface sculpturing and pits. They are also characterised by their globiferous pedicellariae with one or more lateral teeth on each side of the blade. The ambulacral plates are compound throughout, and the apical system is small and monocyclic or dicyclic. Gill slits are present, but shallow, and the tubercles are imperforate and non-crenulate. The lantern is camarodont, and the spines are solid.

The family comprises six genera and approximately 32 extant species (Smith & Kroh 2011). The only Australian representatives are *Dermechinus horridus* and *Gracilechinus multidentatus* (O'Hara 2012; **Fig. 10.22D–F**), both of which are common on the continental slopes of southern Australia, and *Sterechinus neumayeri*, an ecologically important echinid in Antarctica, including the Australian Territory (**Fig. 10.22A–C**). The European species *Echinus esculentus* is the archetype for the class Echinoidea, and its biology and ecology has been studied in detail (Nichols *et al*. 1985; Comely & Ansell 1988).

The striking elongate and orange-coloured *Dermechinus horridus* is an important component of the seamount benthic community south of Tasmania (Koslow *et al*. 2001; **Fig. 10.22E,F; Box 4.6**). There is nothing known about the biology of *Dermechinus* and *Gracilechinus*.

One of the best-studied echinids is the Antarctic sea urchin *Sterechinus neumayeri* (**Fig. 10.22A–C**), a circumpolar species that occurs from shallow water to 400 m (Pawson 1969; Brey & Gutt 1991). *Sterechinus neumayeri* has a central trophic role in Antarctic nearshore marine ecosystems (**Box 4.6**). This species is used as a model species for Antarctic research due to its abundance and its importance as a predator and grazer (Bosch *et al*. 1987; McClintock 1994; Brey *et al*. 1995; Byrne *et al*. 2013c). The endemism of *S. neumayeri* to this region is strongly influenced by sea surface temperature and sea ice coverage (Pierrat *et al*. 2012).

Echinids eat algae or a mixture of bottom materials (De Ridder & Lawrence 1982). Tyler *et al*. (1995b) found some evidence to support an allopatric speciation model in *Echinus* species. *Echinus affinis*, an abundant deepsea species in the North Atlantic, feeds on detritus fallout from surface material (Billett *et al*. 1983). Tyler *et al*. (1995b) investigated the distribution, diet and reproduction in *Echinus* and found that in the North Atlantic Ocean all species studied have seasonal reproduction timed to coincide with a spring phytoplankton bloom. *Sterechinus neumayeri* feeds on algae, diatoms and seal faeces and *S. antarcticus* has been observed preying on stalked crinoids (McClintock 1994; Brey *et al*. 1995; Bowden *et al*. 2011; **Fig. 7.14C**).

Echinids produce small eggs and have a feeding echinopluteus larva (MacBride 1903; Tyler & Gage 1984b; Tyler *et al*. 1995b; Byrne *et al*. 2013c). The development of *Echinus esculentus* is well described (MacBride 1903). The reproduction and development of *Sterechinus neumayeri* is also well characterised (Bosch *et al*. 1987). In the cold polar waters the echinopluteus larva of this species has a long pelagic larval duration of up to 115 days.

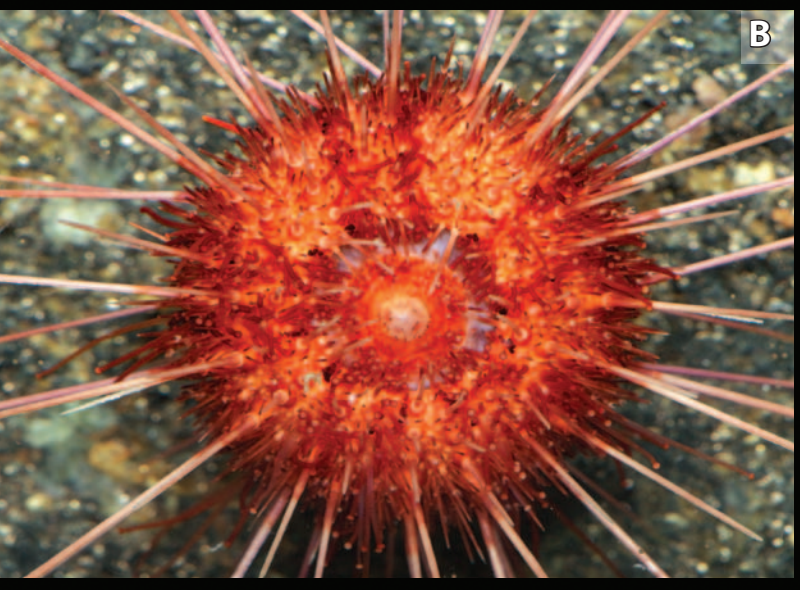
Family Toxopneustidae

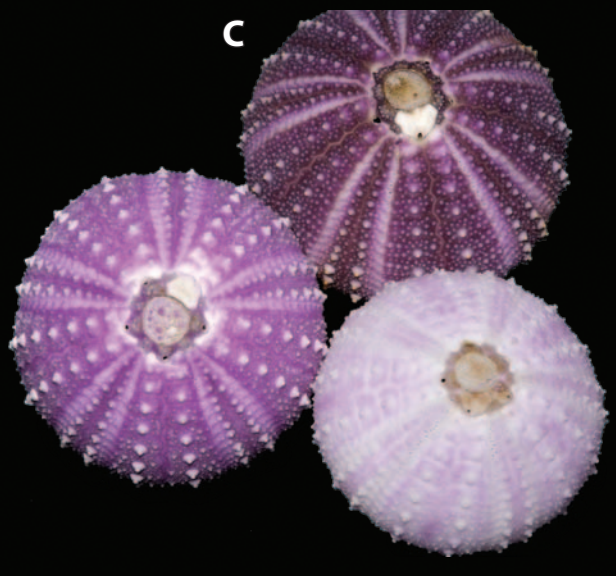
Figure 10.23

The toxopneustid test is more or less circular in outline, and the blades of the globiferous pedicellariae, reaching their greatest development in this family (Lawrence 1987; Coppard *et al*. 2012), lack lateral teeth. The pedicellariae are usually equipped with venom sacs, and with terminal teeth on the valves designed to penetrate the skin of predators to deliver venom (Coppard *et al*. 2012). Envenomation by species of *Toxopneustes*, especially *T. pileolus* (**Fig. 2.15, 10.23F**), can cause pain, faintness, generalised paralysis, respiratory distress and even death in humans (Halstead 1965). The apical system is dicyclic.

The family comprises 10 genera, two of which are extinct, and approximately 32 living species (Smith & Kroh 2011). Fossil toxopneustids are not common, and the identity of some reported specimens from the Eocene and Cretaceous is in doubt (Smith 1988b). The earliest reliable fossil was reported from the Late Oligocene of Oregon (Smith 1988b), while *Tripneustes pregratilla* was described from the Middle Miocene of Barrow Island, Western Australia (McNamara & Kendrick 1994). It is larger than the extant *T. gratilla*, with ambulacra that are more tuberculated and more regular poriferous







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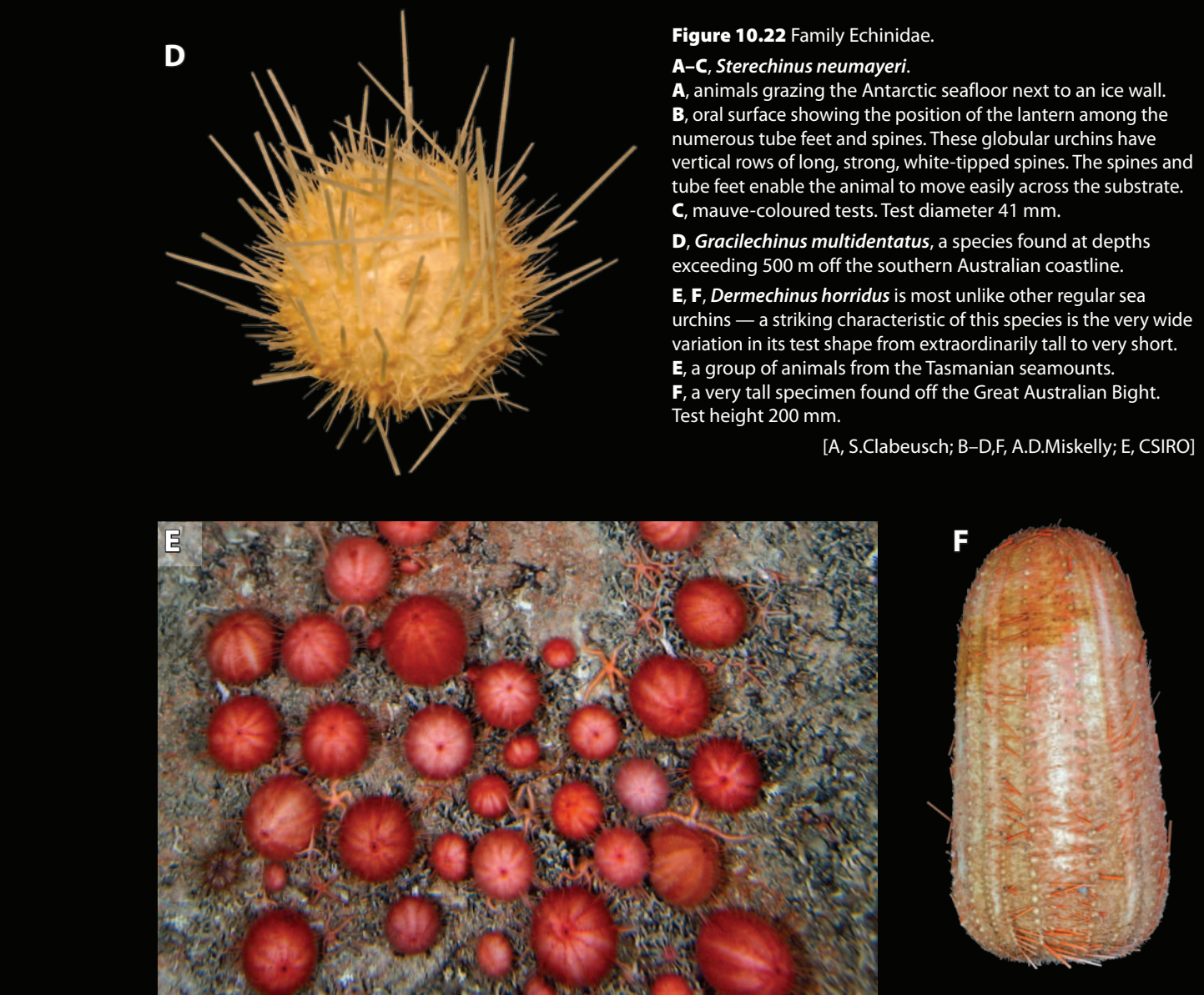


Figure 10.22 Family Echinidae.

A–C, ***Sterechinus neumayeri***.
A, animals grazing the Antarctic seafloor next to an ice wall.
B, oral surface showing the position of the lantern among the numerous tube feet and spines. These globular urchins have vertical rows of long, strong, white-tipped spines. The spines and tube feet enable the animal to move easily across the substrate.
C, mauve-coloured tests. Test diameter 41 mm.

D, ***Gracilechinus multidentatus***, a species found at depths exceeding 500 m off the southern Australian coastline.

E, **F**, ***Dermechinus horridus*** is most unlike other regular sea urchins — a striking characteristic of this species is the very wide variation in its test shape from extraordinarily tall to very short.
E, a group of animals from the Tasmanian seamounts.
F, a very tall specimen found off the Great Australian Bight. Test height 200 mm.

[A, S.Clabeusch; B–D,F, A.D.Miskelly; E, CSIRO]

columns. Six genera and 11 species of toxopneustids occur in Australian waters: *Nudechinus* (5 species) and *Pseudoboletia* (2) and the single representatives *Cyrtechinus verruculatus*, *Gymnechinus epistichus*, *Toxopneustes pileolus* and *Tripneustes gratilla* (O'Hara 2012; **Fig. 10.23**). The biology and ecology of the pan tropical genus *Tripneustes* is reviewed by Lawrence & Agatsuma (2013). The phylogeography of this genus is documented in Lessios *et al*. (2003).

Many toxopneustids, such as *Cyrtechinus*, *Gymnechinus* and *Nudechinus*, ingest small balls of bottom material, while *Tripneustes gratilla* feeds on seagrasses and algae (De Ridder & Lawrence 1982; Lawrence & Agatsuma 2013). Most toxopneustids occur below the low tide limit, with *T. gratilla* occasionally found in the intertidal zone (A.D.Miskelly, unpublished data). Approximately a dozen Australian short-spined species, including toxopneustids such as *Tripneustes gratilla*, *Toxopneustes pileolus* and *Pseudoboletia indiana*, display 'covering behaviour'. Covering usually consists of the accumulation of debris (shells, stones, drift algae) on top of the urchin's body, the debris being held in place by tube feet. Covering can provide a shade to

reduce incident light or ultraviolet radiation, or provide camouflage, or be a means of hoarding food, usually algae, and it has also been suggested that coverings may serve as ballast (Chen & Soong 2010; Lawrence & Agatsuma 2013). This complex phenomenon is also displayed in a few deepsea species (Pawson & Pawson 2013). In *Toxopneustes pileolus* individuals shed their covering items before spawning (Chen & Soong 2010).

Pseudoboletia maculata, named for its pigment spots (maculae), has a patchy distribution on the east coast of Australia and seems to prefer harbours sheltered from the open ocean. The two species of *Pseudoboletia* have a wide Indo-Pacific distribution, and in Sydney where they live in sympatry in Sydney Harbour, hybridisation and ingression occur (Ziegler *et al*. 2012). Hybrids are readily identified in the field due to having irregular pigment areas. Where the two species co-occur, *Pseudoboletia indiana* is more abundant (Ziegler *et al*. 2012).

The biology and ecology of *T. gratilla* is well studied (Lawrence & Agatsuma 2013). It is an important fishery and aquaculture species with very fast growth and has been investigated in this context in Australia (O'Connor 1976; O'Connor *et al*. 1976; Dworjanyn & Pirozzi 2008; Mos *et al*. 2011, 2015). *Tripneustes gratilla* can grow to 60 mm in five months in the Philippines (Lawrence & Agatsuma 2013). This species is cultured in Okinawa, Japan (Lawrence & Agatsuma 2013). Wild fisheries for *T. gratilla* collapsed in parts of the Philippines in the 1990s and elsewhere (Junio-Meñez *et al*. 2011; Lawrence & Agatsuma 2013).

Tripneustids tend to be limited to tropical and subtropical areas and are very common in shallow waters. They can have high local abundance with occasional outbreaks as observed in the high density of *T. gratilla* at Lord Howe Island (Valentine & Edgar 2010). The latter was attributed to an infrequent oceanographic event delivering larvae originating from northern Australia. The *T. gratilla* population created a barrens-like habitat devoid of macroalgae and dominated by crustose coralline algae, but had no effect on the corals (Valentine & Edgar 2010). Tripneustids are opportunistic feeders depending on resource availability, but many studies indicate that seagrass is an important component of the diet (Lawrence & Agatsuma 2013). *Tripneustes gratilla* can overgraze seagrass beds, but these tend to recover, especially when sea urchin numbers are modulated by predators (fish, asteroids and gastropods) (Eklöf *et al*. 2009; Lawrence & Agatsuma 2013). This species also appears to have a preference for the kelp *Ecklonia* when available (Dworjanyn *et al*. 2007).

Tripneustes species have different reproductive cycles across their broad range, from seasonal to continuous spawning (Lawrence & Agatsuma 2013). In northern New South Wales, *T. gratilla* spawns from February through April (O'Connor *et al*. 1976), while in the generally warmer waters to the north spawning can occur in spring as well as in autumn. Because the spawning season in this species appears to be linked to sea water temperature (O'Connor *et al*. 1976), the magnitude and timing of

Figure 10.23 Family Toxopneustidae.

A, **B**, two colour variants of ***Tripneustes gratilla***:
A, from Long Bay, Sydney, New South Wales, has white spines, green tube feet, and blue pedicellariae.
B, from Long Reef, Sydney, New South Wales, has orange spines, green and white tube feet and dark blue pedicellariae.

C, ***Pseudoboletia maculata*** occurs below low tide on coarse sediment, where it forages for food. It is easily distinguished from ***P. indiana*** (**D**) by its patches of brown spines among white spines.

D, ***Pseudoboletia indiana*** lives in the same habitat as ***P. maculata***, but has white spines with pink tips. It is often seen with detritus it has collected from the seafloor on its aboral surface.

E, ***Gymnechinus epistichus*** is a small species (test diameter ~25 mm) that has orange spines with white tips. It lives subtidally among filamentous algae that grow in areas of coarse sediment; it often goes unnoticed due to its capacity to camouflage itself extremely well.

F, ***Toxopneustes pileolus***. Well known for its extraordinarily large and venomous pedicellariae, this tropical species occurs as far south as Montague Island, New South Wales, in eastern Australia. Like many toxopneustids, it lives somewhat inconspicuously, camouflaged by detritus which it transfers to and maintains on the aboral surface by its tube feet.

[A,B, J.Hannan; C–F, A.D.Miskelly]

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A
B
C
D
E
F

spawning could possibly be manipulated by controlling water temperature, thereby making it a more reliable subject for aquaculture in Australia. Toxopneustids have small eggs and development through a planktotrophic echinopluteus larva (Emlet 1995a; Byrne *et al*. 2008a, 2008b; Sheppard Brennand *et al*. 2010).

Family Echinometridae

Figure 10.24, & Boxes 10.3 & 10.4

The echinometrid test is circular or elliptical at the ambitus (**Fig. 10.24C**), and the anus (periproct) is covered by many small plates. The blades of the globiferous pedicellariae either lack lateral teeth (*Parasalenia*) or they have teeth on one side only. Bilaterally symmetrical echinometrids such as *Parasalenia gratiosa* (**Fig. 1.1E**) and *P. pohlii* (**Fig. 10.24C**) have ellipsoidal tests, but unlike bilaterally symmetrical spatangoids, the test shape is not related to the possession of a locomotory 'anterior end' as they move with their short or long axis foremost with equal frequency (Grabowsky 1994). It may be associated with selection for production of elongate, groove-shaped burrows in carbonate substrates (**Box 10.3**).

The family Echinometridae dates back to the Palaeocene (Fell & Pawson 1966b). All of the 13 known genera are extant; indeed, only four genera have fossil members (Smith & Kroh 2011). One of these is *Heliocidaris*. Widespread in southern Australian waters today (**Box 10.4**), it was also present in the region in the early Miocene (Philip 1965b). The very widespread Indo-Pacific species in the *Echinometra* complex (**Fig. 2.9; Box 10.3**) have existed essentially unchanged in morphology for at least 17 million years, since the Early Miocene (Negretti *et al*. 1990). McNamara (1992) analysed the distribution of *E. mathaei* (=*Echinometra* species A; see **Box 10.3**) along the Western Australian coast following the discovery of a Pleistocene fossil specimen at Cape Burney. His study supported the opinion of others (Pearse & Phillips 1968) that the present-day distribution of *Echinometra* in Western Australia is mediated by the vagaries of the Leeuwin Current.

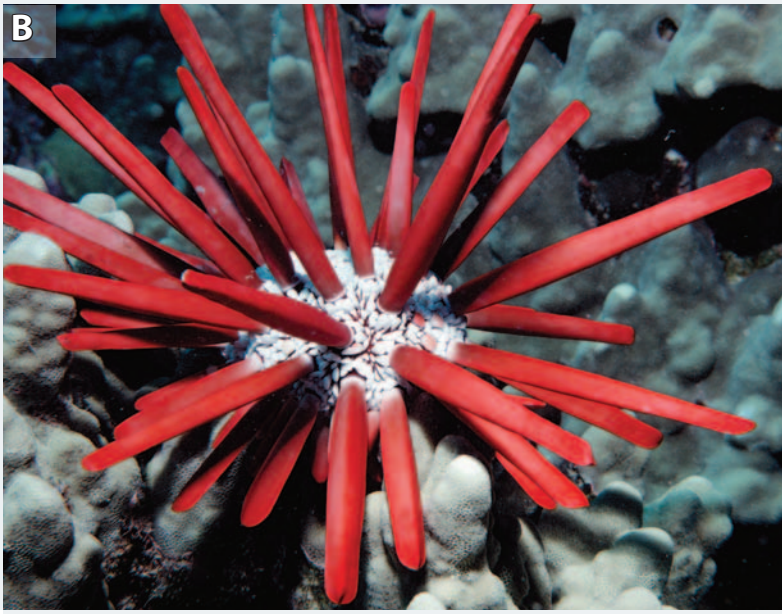
Six genera and ten species of echinometrids, including *Parasalenia*, are known from Australia: *Echinostrephus* (2 species), *Heliocidaris* (3), *Heterocentrotus* (2), *Pachechinus* (2) and *Parasalenia* (2) and the single representatives *Podophora atrata* and *Echinometra mathaei* (Hart *et al*. 2011; O'Hara 2012). However with a taxonomic revision of the *Echinometra mathaei* species complex (Uehara & Shingaki 1985; Arakaki & Uehara 1991; Arakaki *et al*. 1998; Palumbi 1996, 1999, Palumbi *et al*. 1997; Kinjo *et al*. 2004; **Box 10.3**), this number will increase. *Parasalenia* is sometimes assigned to a separate family, the Parasalenidae (Rowe & Gates 1995). The biology and ecology of *Echinometra* is reviewed in McClanahan & Muthiga (2013), that of *Heliocidaris erythrogramma* is reviewed in Keesing (2013) and that of *Heliocidaris crassispina* is reviewed in Agatsuma (2013).

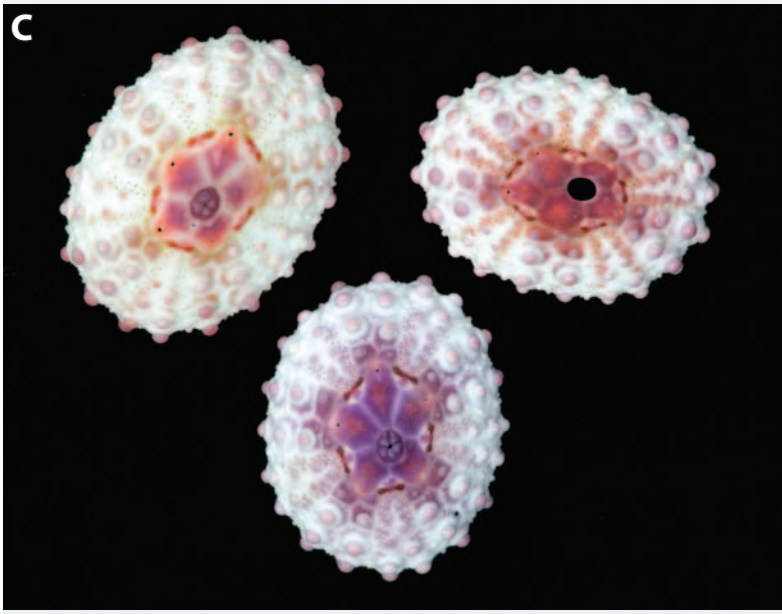
Echinometrids often live on high-energy intertidal reefs (Denny & Gaylord 1996; Asgaard & Bromley 2008) where they often occupy burrows that they create. They are active borers forming cup-shaped holes (*Heliocidaris erythrogramma*, **Figs 1.13D, 4.5E, 10.24A**), elongate grooves (*Echinometra*, **Box 10.3**) or finger-like holes (for example, *Echinostrephus*, **Fig. 1.27**) in the substrate (Asgaard & Bromley 2008). The presence of an elliptical test appears to influence the burrow profile. *Echinometra* species with an elliptical test typically make elongate burrows. The body form is suggested to be adaptive for resistance to turbulence (Lawrence 1987; Asgaard & Bromley 2008).

Echinometra species occurs in the intertidal and shallow subtidal tropical and subtropical habitats to depths of ~10 m (McClanahan & Muthiga 2013). Their diet consists mainly of algae and encrusting organisms and they tend to forage at night (De Ridder & Lawrence 1982; McClanahan & Muthiga 2013). They obtain their food by grazing the substrate and capturing drift algae and detritus (Asgaard & Bromley 2008; McClanahan & Muthiga 2013). They strip the organic material from the ingested fragments of carbonate substrate. In high insolation locations the burrows develop microalgal films and turfs and the urchins do simple gardening, harvesting these algae in a diurnal cycle with nightly feeding excursions along the burrow, cropping the day's growth (Asgaard & Bromley 2008). Species in the *Echinometra* complex occur in high densities in the intertidal zone at Rottnest Island and exposed reef edges in Ningaloo Reef, Western Australia (Black *et al*. 1982; Johansson *et al*. 2010, 2013). In these densities

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the sea urchins graze macroalgae and produce a barren habitat devoid of macroalgae. At Ningaloo Reef *Echinometra* species occur in moderate to high densities (up to ~200 individuals per 100 square metres), despite the presence of potential predators (Johansson *et al*. 2010, 2013). *Echinometra* species appear less abundant on reefs along the Great Barrier Reef (Young & Bellwood 2011). Predators of *Echinometra* species at Ningaloo Reef, the Great Barrier Reef and elsewhere in the tropics include trigger fish and wrasses (Young & Bellwood 2012; Johansson *et al*. 2013; McClanahan & Muthiga 2013). Following outbreaks of crown-of-thorns seastars the increase in dead coral habitat can lead to an increase in the density of *Echinometra*, leading to a further decline in reef habitat due to increased bioerosion by the urchins (Keesing 1993).

Growth of *Echinometra* depends on food availability and population density, with greater allocation to the size of the jaws of the Aristotle's lantern indicating food limitation as observed in the population at Rottnest Island (Black *et al*. 1982; Hart & Chia 1990). The higher density populations are typically composed of smaller adults (Muthiga & Jaccarini 2005). *Echinometra* co-occurs with an invertebrate macrofauna that exists only in the presence of the echinoids (Prince 1995).

Figure 10.24 Family Echinometridae.

A, ***Heliocidaris erythrogramma armigera*** has purple and white to brown and white banded spines. It is only found in southern Western Australia.

B, ***Heterocentrotus mammillatus***, commonly known as the slate pencil urchin, is found throughout the Indo-Pacific.

C, three spineless tests of ***Parasalenia pohlii***, a tiny species of characteristically oval shape, that lives among hard coral in the tropics. Test length 12 mm.

[A, D.Vize; B, N.Wu; C, A.D.Miskelly]

Box 10.3

The *Echinometra 'mathaei'* species complex

Maria Byrne and Sven Uthicke

Echinometra mathaei, formerly considered to be one of the world's most abundant echinoids, is now regarded as a complex of at least five species. They are currently known as *Echinometra* species A, B, C and D from across the Indo-Pacific, and *Echinometra* species E found in the Red Sea and western Indian Ocean. In some areas across the Indo-Pacific these species live in sympatry, and were considered to be colour variants of a single species, *Echinometra mathaei*. After extensive molecular phylogenetic analysis, and thorough studies of colour variation and morphological features, unidentified species were distinguished. Some of these can be identified readily by their colour and colour patterning, but there is also great variability within species. The taxonomy is further complicated by the potential for hybridisation between some of these species.

In Australian waters *Echinometra* species A and *Echinometra* species B have been identified, as well as other taxa of as yet undetermined affinity. The white-tipped spine species, currently known as *Echinometra* species A (**Figs b,c,d**), is common in warm waters, ranging from Western Australia to Queensland; it is occasionally found as far south as Sydney, New South Wales (**Fig. d**). *Echinometra* species A can be locally abundant across its range. *Echinometra* species B (**Fig. a**), which is deep pink to brown in colour, is now recognised as the 'real' *E. mathaei*; it occurs from Western Australia across the north to Queensland and south to New South Wales.

On the Great Barrier Reef, Queensland, there are at least two species of *Echinometra*: *E. mathaei*, the pink/brown species, and the white-tipped species, *Echinometra* species A. At Ningaloo Reef, Western Australia, *Echinometra* is very abundant with a number of forms present, including a conspicuous green one. All these are, at present, regarded as *Echinometra* cf. *mathaei* until their identity is confirmed by genetic analysis (**Figs e–g**). At Rottnest Island, off Perth, Western Australia, *E. mathaei* is the most common species.

Echinometra species C occurs in the tropical Pacific and may occur on the Great Barrier Reef (S.Uthicke, unpublished observations). *Echinometra* species D found at Okinawa, Japan, has been identified as *E. oblonga*.

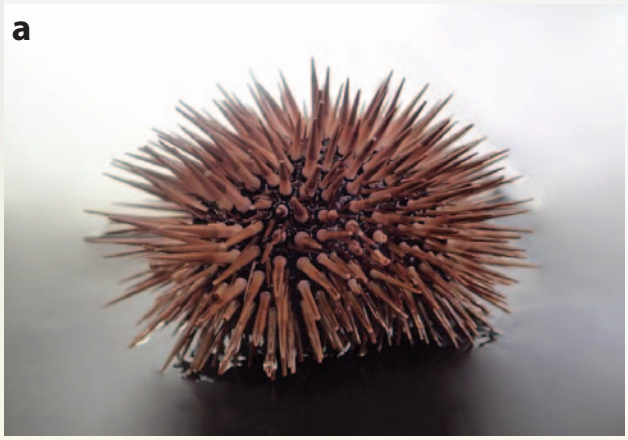


Figure a–g ***Echinometra 'mathaei'*** in Australia.

a, ***Echinometra mathaei*** (Echinometra species B) from One Tree Island, Great Barrier Reef, Queensland.

b, ***Echinometra*** species A from the Great Barrier Reef, Queensland.

c, ***Echinometra*** species A in its burrow at Lizard Island, Great Barrier Reef, Queensland.

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d, ***Echinometra*** species A from Sydney Harbour, New South Wales.

e, ***Echinometra*** **cf**. ***mathaei*** in its burrow at Ningaloo Reef, Western Australia.

f, an aggregation of ***Echinometra*** **cf**. ***mathaei*** at Ningaloo Reef, Western Australia, including the undetermined green ***Echinometra*** species.

g, ***Echinometra*** **cf**. ***mathaei*** at Ningaloo Reef in its burrow where algal growth is evident.

[a,b, M.Byrne; c, N.Soars; d, A.D.Miskelly; e–g, C.Johansson]

The total number of *Echinometra* species and species-level taxonomy remain to be clarified.

Species of *Echinometra* are ecologically important, and are among the most common sea urchins living in the tropical waters of the Indo-Pacific and Atlantic Oceans. They occur from the intertidal zone to the shallow subtidal at depths to ~10 m. They are important bioeroding species, making groove shaped burrows in coral rock habitat. During the day they hide in the reef infrastructure and at night they emerge and graze along their burrow. The burrow surface often faces towards the light, promoting algal growth during the day (**Fig. g**) which is then harvested by the sea urchin at night. Waste products from the sea urchin may fertilise the algae, facilitating their growth. Thus, in this situation *Echinometra* are like gardeners promoting growth of their food.

Order Camarodonta
Family Echinometridae
Species *Echinometra mathaei* (Blainville, 1825)

Further reading Uehara *et al*. 1990; Palumbi & Metz 1991; Palumbi 1996; Palumbi *et al*. 1997; Arakaki *et al*. 1998; Kinjo *et al*. 2004; Rahman *et al*. 2004; Bronstein & Loya 2013

Over generations species of *Echinometra* create burrows by rasping limestone and dead coral with their teeth (**Box 10.3**). *Echinometra* species are important bioeroders in coral reefs where calcium carbonate sediment is usually a large fraction of their gut contents, indicating that these echinoids play an important role in reef carbon cycles (Bak 1994; Conand *et al*. 1997; Asgaard & Bromley 2008; Dumas *et al*. 2007; McClanahan & Muthiga 2013).

Other groups of tropical echinometrids that occur in Australian waters include *Echinostrephus* and *Heterocentrotus*. *Echinostrephus* are rock-boring, deeply burrowing species that produce elongate narrow cylindrical burrows (Campbell *et al*. 1973; Asgaard & Bromley 2008). They are often abundant on reef walls, extending their spines from their burrow. They remain permanently in their burrow (**Fig. 1.27**), and are the only fully suspension feeding echinoids entirely dependent on drift material for their food. They catch passing fragments on their long aboral spines, and transfer the food to the mouth using their spines and tube feet (Campbell *et al*. 1973; Asgaard & Bromley 2008). The entrance of the burrow is often partly overgrown by surrounding biota.

Heterocentrotus species (**Fig. 10.24B**) are distinct in having very large spines that are used to lodge them in crevices in the reef infrastructure.

The Australian endemic species *Heliocidaris erythrogramma*, which is found in southern Australia from New South Wales to Geraldton, Western Australia, including Tasmania, is perhaps the most abundant and conspicuous echinoderm on the Australian coast (Dakin 1952). It comprises two subspecies: *H. e. erythrogramma* (hereafter *H. erythrogramma*) known from across the entire range and *H. e. armigera* (**Fig. 10.24A**), known only from Western Australia, from Perth south to Esperance. They are ecologically important herbivores in intertidal and shallow subtidal habitats across temperate Australia (Keesing 2013). Binks *et al*. (2011, 2012) provide a description of the difference between these subspecies in Western Australia, largely based on spine and test colour. The two subspecies have similar biology and ecology (Keesing 2013). *Heliocidaris erythrogramma* usually

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achieves a maximum ~80 mm test diameter, although very large specimens (125 mm test diameter) occur in Tasmania (Growns & Ritz 1994). *Heliocidaris erythrogramma* itself exhibits colour variation (**Fig. 4.5A–E**), particularly in the southern part of its range (Beck & Styan 2010). *Heliocidaris bajulus* (formerly *Pachycentrotus bajulus*) is endemic to eastern Tasmania in shallow subtidal rocky reef habitat with a known distribution of <500 m (Dartnall 1972; Hart *et al*. 2011, 2012).

Heliocidaris erythrogramma occurs in a range of habitats, from the intertidal to 35 m in wave-swept rich shores, sheltered bays and seagrass beds (Keesing 2013). In southern Queensland and New South Wales, *H. erythrogramma* occurs intertidally and shallow subtidally mainly on rocky reefs. Where the substrate allows, such as in sandstone reefs, *H. erythrogramma* lives in excavations that it creates by grazing. In Victoria and South Australia *H. erythrogramma* occurs in shallow subtidal habitats (Livore & Connell 2012), and in Western Australia it lives in excavations and under ledges in limestone platforms (Marsh 1991).

Like other echinometrids *H. erythrogramma* is a grazer and also consumes drift algae, especially kelp, and seagrass (Vanderklift *et al*. 2006; Vanderklift & Wernberg 2008; Livore & Connell 2012). The biomass of drift algae was much greater when *H. erythrogramma* densities were higher (Vanderklift & Kendrick 2005; Vanderklift & Wernberg 2008). These authors suggest that drift kelp, predominantly *Ecklonia*, subsidises the diet of echinoids and thereby reduces their impact on attached algae. Thus, in many areas where *H. erythrogramma* occurs it appears to be relatively stationary (Livore & Connell 2012). When it does forage this usually occurs at night. *Heliocidaris erythrogramma* provides habitat for many invertebrates and fishes which live in association with the spines or under the test, indicating the importance of this species in promoting local biodiversity. Removal of this species though fishing can adversely affect such biodiversity (Chapman & Smoothey 2014).

Removal experiments have shown that *H. erythrogramma* generally has a minimal influence on the structure of benthic algal assemblages, especially as its diet often depends on drift algae (Valentine & Johnson 2005; Vanderklift & Kendrick 2005). However, when *H. erythrogramma* occur in high densities, they can create and maintain barrens habitats, for example in Tasmania (Ling *et al*. 2010). Feeding front aggregations of *H. erythrogramma* have been observed in subtidal algal beds in New South Wales (Wright *et al*. 2005). High densities of this species are also reported to destroy seagrass beds in Western Australia (Larkum & West 1990; Langdon *et al*. 2011). A range of fish species and Port Jackson sharks prey on *H. erythrogramma* (Shepherd & Edgar 2013).

Heliocidaris tuberculata (**Fig. 4.5F; Box 10.4**), known as the red urchin, occurs in eastern Australia from southern Queensland to Montague Island, southern New South Wales, and Middleton Reef and islands in the Tasman Sea; it is abundant in Lord Howe Island. It is sympatric with *H. erythrogramma* in Queensland and along the New South Wales coast. *Heliocidaris tuberculata* grows to a larger body size (106 mm test diameter), but the relative allocation of resources to test, spines and gonads is similar in the two species (Lawrence & Byrne 1994).

Both species of *Heliocidaris* (*H. erythrogramma* and *H. tuberculata*) are harvested for food. There are particular conservation concerns for the small latitudinal range species *H. tuberculata* (see **Chapter 4**).

Echinometra at Rottnest Island in the south of Western Australia reproduces year round (Pearse & Phillips 1968), while seasonal reproduction is reported in more tropical locations (Muthiga & Jaccarini 2005; McClanahan & Muthiga 2013). The two *Echinostrephus* species reproduce seasonally (Chen & Chang 1982). *Echinometra* and *Echinostrephus* species have small eggs and feeding echinopluteus larvae (Chen & Chang 1982; Pearse 1969a; Pearse & Cameron 1991; Rahman *et al*. 2004). The echinoplutei of the Echinometridae are distinguished from those of many other echinoid families in having a robust fenestrated larval skeleton (Pearse & Cameron 1991; Kinjo *et al*. 2006, 2008)

Heliocidaris erythrogramma spawns in summer in its southern range in Tasmania and for up to six months in northern New South Wales (Dix 1977; Laegdsgaard *et al*. 1991; Byrne *et al*. 2011b). Reproduction is nearly continuous in *H. tuberculata* as gametes can be found in some populations year-round (O'Connor *et al*. 1976;

Box 10.4 A tale of two urchins: *Heliocidaris erythrogramma* and *H. tuberculata*

Maria Byrne and Mailie Gall

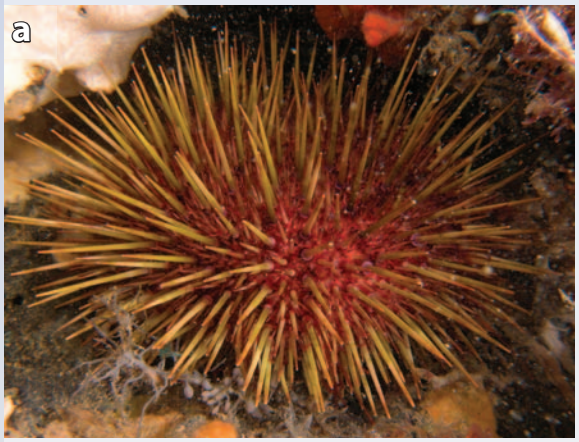


Figure a *Heliocidaris erythrogramma.* Maximum test diameter 105 mm.



Figure b *Heliocidaris tuberculata.* Maximum test diameter 115 mm.

Two *Heliocidaris* species occur in temperate Australia. The endemic species *H. erythrogramma* (*H. e. erythrogramma*, **Fig. a**) has a broad distribution from Caloundra, southern Queensland, around the southern coast to Shark Bay, Western Australia. *Heliocidaris e. armigera* occurs in Western Australia (**Fig. 10.24A**). *Heliocidaris tuberculata* (**Fig. b**) has a limited distribution from Caloundra, southern Queensland, to Montague Island, southern New South Wales; it also occurs in Lord Howe Island and Norfolk Island.

These species have contrasting modes of development. *Heliocidaris tuberculata* has the ancestral-type development for sea urchins in spawning small (95 µm diameter) eggs and having a feeding echinopluteus larva with the fenestrated (ladder-like) arm rods typical of echinometrid plutei (**Fig. d**), while *H. erythrogramma* has a derived mode of development spawning large (450 µm diameter) eggs and has a modified non-feeding larva (**Fig. f**). Depending on temperature, metamorphosis to the juvenile occurs 3–5 days post fertilisation (**Figs e,g,h**). Due to the marked differences in their development, these species have been used as a model system for comparative evolutionary developmental biology. They are intensively studied with extensive molecular resources available. Due to its rapid development, *H. erythrogramma* provides ready access to the developing juvenile sea urchin for research on development of the unusual pentameral echinoderm body plan (**Fig. h**).

The striking differences in development of the two *Heliocidaris* species appear to have arisen since they diverged less than five million years ago. Surprisingly, in contrast to the expectation that species with dispersive feeding larvae have broader distributions than those with short-lived non-feeding larvae, the trend is the opposite for these two *Heliocidaris* species. *Heliocidaris tuberculata* with the longer (~3 weeks) planktonic larval duration (PLD), has a

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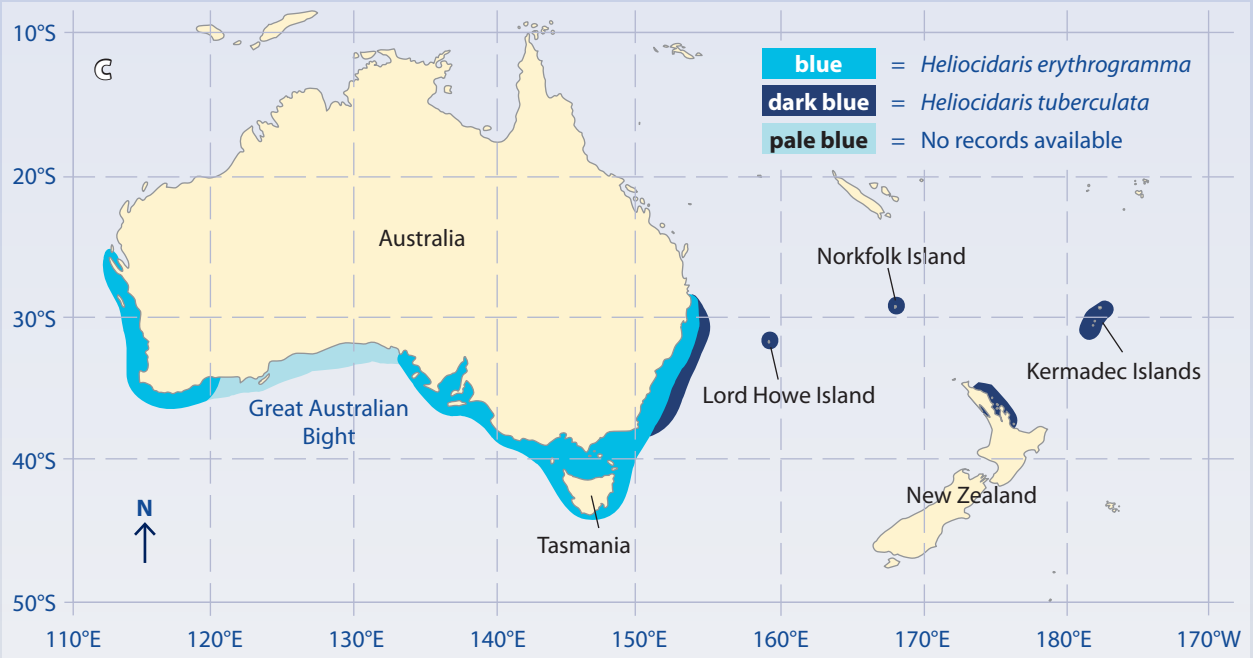
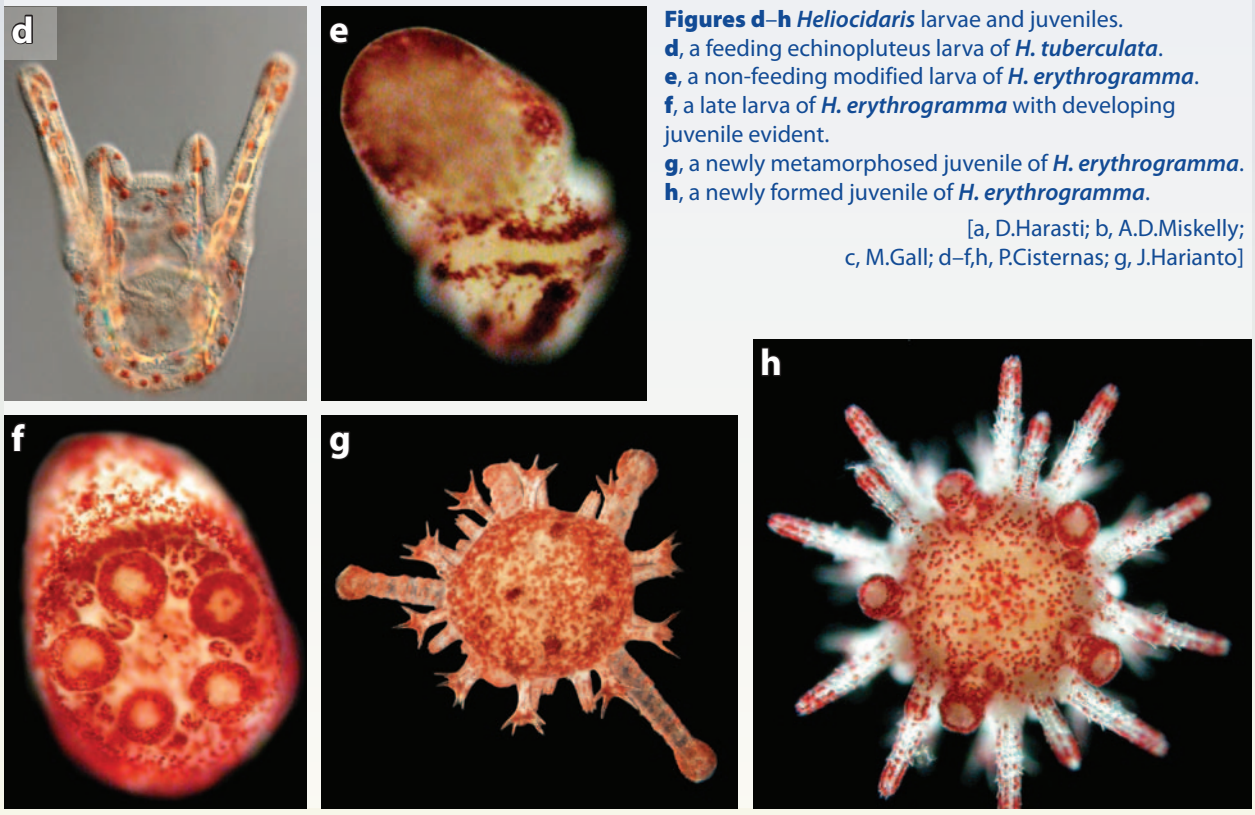


Figure c distribution of ***H. erythrogramma*** and ***H. tuberculata***.



Figures d–h *Heliocidaris* larvae and juveniles.
d, a feeding echinopluteus larva of ***H. tuberculata***.
e, a non-feeding modified larva of ***H. erythrogramma***.
f, a late larva of ***H. erythrogramma*** with developing juvenile evident.
g, a newly metamorphosed juvenile of ***H. erythrogramma***.
h, a newly formed juvenile of ***H. erythrogramma***.

[a, D.Harasti; b, A.D.Miskelly; c, M.Gall; d–f,h, P.Cisternas; g, J.Harianto]

broad trans-Tasman range spanning from Australia to the Kermadec Islands (~3,000 km) but contrastingly, has a narrow Australian range (~1,000 km). This species has one of the smallest latitudinal ranges for a sea urchin with a 'long distance' echinopluteus larva. In contrast, *H. erythrogramma* with a 3–5 day PLD displays an unexpected extensive Australian distribution (Queensland to Western Australia, ~6,000 km). The long PLD of *Heliocidaris tuberculata* facilitates a broad trans-Tasman range, but its range in Australia must be restricted by other factors such as low population size or thermal tolerance limitations of the larva. Despite having a larva in the plankton at the same time as *Centrostephanus rodgersii*, *H. tuberculata* has not extended its range (see **Box 2.1**). Due to the declining populations of *H. tuberculata* on the east coast of Australia and its use as a fishery species, there are concerns for the conservation of this species (see **Chapter 4**).

Order Camarodonta
Family Echinometridae
Species *Heliocidaris erythrogramma* (Valenciennes, 1846)
Heliocidaris tuberculata (Lamarck, 1816b)

Further reading Williams & Anderson 1975; Wray 1995; Emlet 1995a; Byrne *et al*. 2001; Zigler *et al*. 2003; Byrne & Voltzow 2004; Raff & Byrne 2006; Wygoda *et al*. 2014

Laegdsgaard *et al*. 1991). In Western Australia, *H. erythrogramma* spawns in summer and *H. e. armigera* spawns in autumn, a separation suggested to facilitate the incipient speciation of these subspecies (Binks *et al*. 2012). Comparison of the thermal tolerance of development indicated that the progeny of the populations of *H. erythrogramma* in northern New South Wales are more tolerant than those from the south, indicating a source of thermotolerant propagules in the event of global warming (Byrne *et al*. 2011a). Regional warming may go beyond the thermal tolerance of development in this species (Byrne *et al*. 2011a, 2011b; Hardy & Byrne 2014). *Heliocidaris crassispina*, a well-studied species from Japan, also has an echinopluteus larva. *Heliocidaris bajulus* broods its young tethered to pedicellaria (Dartnall 1972; Hart *et al*. 2011).

The two *Heliocidaris* species have different modes of development (**Box 10.4**). *Heliocidaris tuberculata* spawns small (95 µm diameter) negatively buoyant eggs and has the ancestral type development through a feeding echinopluteus larva with a planktonic larval duration of ~3 weeks. In contrast, *H. erythrogramma* produces large (450 µm diameter), positively buoyant lecithotrophic eggs and develops through a reduced lecithotrophic larva (Williams & Anderson 1975; Wray 1995; Emlet 1995b; Byrne *et al*. 2001; Byrne & Voltzow 2004; Morris 2011). Similarly, the diameter of the sperm head is 10 µm in *H. erythrogramma* (**Fig. 3.6B**) and only 4 µm in *H. tuberculata* (Raff *et al*. 1990). Due to its rapid development with metamorphosis in 3–5 days, *H. erythrogramma* provides ready access to the developing juvenile sea urchins (**Box 10.4**). With a comprehensive understanding of their reproductive biology, development and phylogeny, these species have been used as a model system for comparative evolutionary biology and are intensively studied (Raff & Byrne 2006), with extensive molecular resources available (Wygoda *et al*. 2014). The striking differences in development of the two *Heliocidaris* species appear to have arisen since they diverged less than five million years ago (Zigler *et al*. 2003). Surprisingly, in contrast to the expectation that species with planktotrophic larvae have broader distributions than those with lecithotrophic larvae, the trend is the opposite for two *Heliocidaris* species (**Box 10.4**).

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Order Echinoneoida

The spatangoids (heart urchins) and clypeasteroids (sand dollars) are known as irregular echinoids because they have a bilateral symmetry overlying their basic pentaradial body plan (**Figs 1.2J,K, 10.3D–J**). Thus many species are oval-shaped and the periproct opens near the posterior of the animal, almost always lying outside the apical disc plates (Smith & Kroh 2011). Spatangoids and clypeasteroids appear to form a monophyletic group (Kroh & Smith 2010; Kroh & Mooi 2014). The two main groups of irregular echinoids are the Atelostomata and Neognathostomata (see below). However, there are also several more primitive orders that do not fit into these groups. These include the extinct Holectypoida and the Echinoneoida, which contains some extant species.

The Holectypoida and Echinoneoida are a group of morphologically variable echinoids, intermediate in profile between regular and irregular echinoids. In many respects, they are the most basal of irregular echinoids, lacking, for example any modifications of the body, such as development of petals, or of spines that facilitate oxygen uptake (Lawrence 1987). The Echinoneoida have a hemispherical to globular or ovoid test; five identical ambulacra with undifferentiated double pores throughout in most forms; a tetrabasal apical system, with four genital plates, and a perignathic girdle with or without interradial ridges, varying from well developed to lacking in adults. In living forms, the girdle and lantern are present in very early juveniles, but are absent in adults. One characteristically very variable feature is the position of the periproct; it ranges from markedly supramarginal in many extinct, Jurassic forms, to submarginal and situated very close to the peristome in living forms.

Most of what we know about the Echinoneoida is based on fossil material. Only three living genera are known, *Echinoneus*, *Micropetalon* and *Koehleraster*. The more or less globose form of the living echinoneoid test can be traced back through the phylogenetic history of the group. Our entire understanding of the biology of these echinoids is based on observations of a living echinoneid, *Echinoneus cyclostomus* (Rose 1976). This is a littoral form that lives buried in coarse, often mobile sediments, frequently in association with algal or coral reefs. Living echinoneoids inhabit tropical seas, from the Caribbean through the Indian and Pacific oceans. Details of echinoneoid spines and pedicellariae come from studies of *Echinoneus cyclostomus* (Rose 1976). In these the spines are short and form a dense covering, they have a small axial cavity and terminate in a simple, rounded tip. Globiferous, tridentate, triphyllous and ophiocephalous pedicellariae are present (Coppard *et al*. 2012).

Family Echinoneidae

Figure 10.25

This family was described for the genus *Echinoneus* (Agassiz & Desor 1847; **Fig. 10.25**). Since then, two other genera have been added, the living *Micropetalon* and the Cretaceous *Paleoechinoneus*. Echinoneids are characterised by an ovate test, four genital pores, non-petaloid ambulacra with reduced plates in part or throughout, a lantern and girdle present in the young, but lost in the adult, an oblique or elongate peristome, and the periproct situated on the oral surface close to the peristome. The lantern is never used by the juveniles in feeding, as it is completely reabsorbed prior to the opening of the mouth (Lawrence 1987).

There are two extant genera, *Echinoneus* and *Micropetalon*. The latter is known only from the Hawaiian Islands (Clark 1917), whereas *Echinoneus* has a much broader distribution that includes the Caribbean Sea, East Africa, Madagascar, Australia and the South Pacific Ocean (Mortensen 1948a). *Echinoneus* can be distinguished from *Micropetalon* by its indistinct genital plates, poriferous zones not flush with the test surface, pore pairs with peripodia and perforate primary tubercles.

One of the two species of *Echinoneus*, *E. abnormalis*, is rare, being known only from near Hawaii, Mauritius and at Lizard Island, Queensland (Mortensen 1948a; A.D.Miskelly, unpublished data), while the other, *E. cyclostomus*, has an essentially pantropical distribution (**Fig. 10.25**). In Australian waters it extends from the south-east coast up the length of the east coast, across the Timor Sea to Ashmore Reef in the Indian Ocean and down the Western Australian

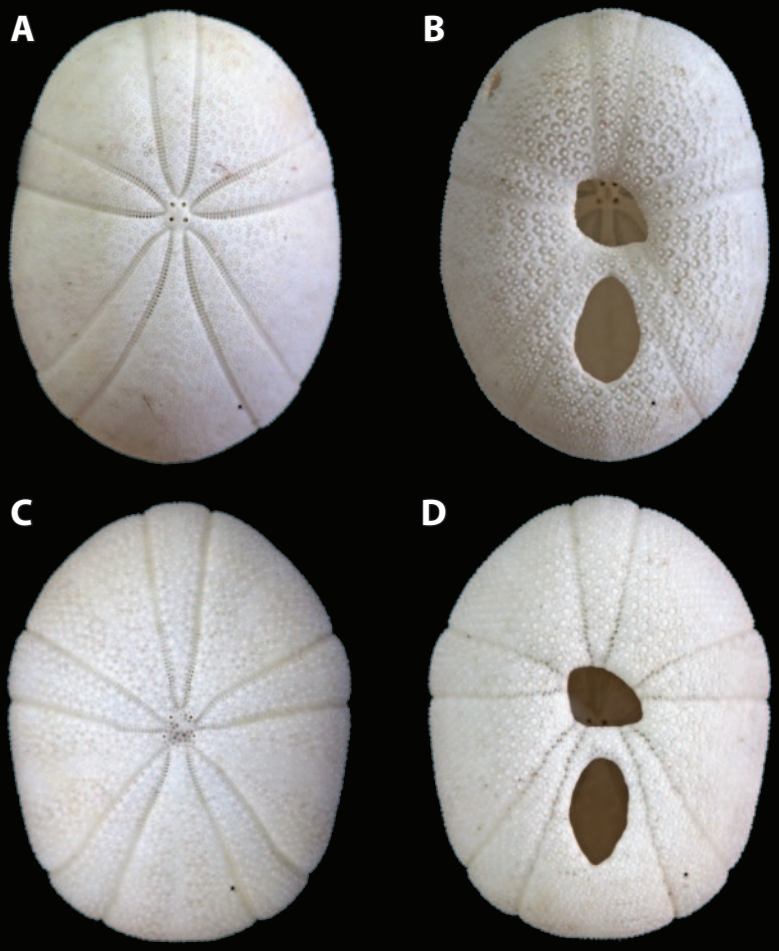


Figure 10.25 Family Echinoneidae.
Tests of ***Echinoneus abnormalis*** (**A**, **B**) and ***Echinoneus cyclostomus*** (**C**, **D**) from Lizard Island, Great Barrier Reef, Queensland. These two similar species live in coarse rubble in very shallow water in tropical coral reefs. Test length 30 mm.
A, **C**, aboral views.
B, **D**, oral views.
[A.D.Miskelly]

coast as far as North West Cape (O'Hara 2012). The genus is also known from the Early Miocene of Victoria (Hall 1907), and it has been suggested that the Miocene species *E. dennanti* is synonymous with the extant *E. cyclostomus* (Rowe & Gates 1995). However, a reassessment of that species is needed before conspecificity can be confirmed.

The depth range of echinoneids is uncertain, but *E. cyclostomus* has been found to depths of 120 m (De Meijere 1903), and *Micropetalon* to depths of 45–70 m. *Echinoneus cyclostomus* also occurs in very shallow waters, on sand flats fringing algal reefs, in sand pockets on reefs and on outer patch reefs, and in the intertidal zone (Rose 1976). This suggests that the species can tolerate shallow, turbulent waters. Thus, it is often associated with coarse substrates, especially near rocks or underneath coral slabs. This ability to inhabit a high-energy environment is reflected in its structure, *E. cyclostomus* having more extensive fusion of trabeculae across sutures than other echinoids (Telford 1985).

Echinoneus cyclostomus is more mobile at night, moving on the sediment surface, but mainly burrowing in the substrate during the day (Rose 1976). During burrowing, a process that takes about 20 minutes, the urchin uses subambital spines to move sediment away from itself, and it burrows to a depth of 20–30 mm below the sediment, leaving a crater-like depression.

Echinoneids appear to be selective feeders. Grains are passed along the ambulacra by tube feet to the mouth (Rose 1976). Spines and tube feet around the mouth hold and rotate the grains, many being passed back along the ambulacra and rejected, and with only a minority of grains pushed into the mouth by the tube feet (Rose 1976). The tube feet of *E. cyclostomus* are dark red, similar in colour to the light-sensitive tube feet of the spatangoid *Protenaster australis* (McNamara 1984b). Tube feet on the oral surface anchor the echinoid.

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NEOGNATHOSTOMATES

The Neognathostomata contains the cassiduloids, clypeasteroids, echinolampadoids and apatopygids. The Clypeasteroida is still regarded as being monophyletic. However, the traditional Cassiduloida is now recognised as being paraphyletic with respect to the other neognathostomate orders, and it contains separate, divergent lineages (Kroh & Smith 2010; Kroh & Mooi 2014).

The order Cassiduloida was described by Kier (1962) for all irregular echinoids with petals on the aboral surface, phyllodes on the oral surface (these are enlarged, crowded ambulacral pores surrounding the peristome) and bourrelets (swollen interambulacra around the peristome); the phyllodes and bourrelets together comprise the floscelle. However, such a generalised description also applies to clypeasteroids (Mooi 1990a, 1990b) if one considers the interambulacral bourrelets and reduced phyllodes with buccal and large food groove tube feet to comprise a floscelle. Mooi (1990b, 1990c) characterised cassiduloids as shallow-dwelling irregular echinoids that have a relatively vaulted test, short spines, a periproct in a posterior position and a well-developed floscelle. Considerable variability in the characters used to define cassiduloid families (such as the position of the periproct) complicates the designation of the order with any degree of assurance, and the absence of unifying characters suggests that it is not monophyletic. Kroh & Smith (2010) recognised a restricted order Cassiduloida with extant families Cassidulidae and Neolampadidae. The Apatopygidae was placed with the primitive 'stem' neognathostomatids, and the Echinolampadidae recognised as a separate order alongside the Clypeasteroida.

The Cassiduloida and Echinolampadoida, along with other stem group neognathostomates, played a dominant role in the evolutionary expansion of irregular echinoids during the Mesozoic, and even in the Eocene they represented 40% of all echinoid species (more than 500 taxa). However, they suffered a dramatic post-Eocene decline, perhaps as a direct consequence of the rise of the clypeasteroids, or as a result of increases in predation pressure during the Tertiary (McNamara 1994b). Today, the 17 living neognathostomates other than the clypeasteroids today comprise less than 2% of the 1,000 living species of echinoids. In Australia, the Cassidulidae, Neolampadidae, Apatopygidae and Echniolampadidae are represented by just six species (O'Hara 2012). Apart from the two echinolampadid species, one of which is quite common, the other families are extremely rare, being represented by less than a dozen specimens. Almost nothing is known of the biology of Australian species.

Neognathostomates are some of the earliest recorded irregular echinoids, being first known from the Bajocian in the Middle Jurassic (172–168 million years ago) (Rose & Olver 1980). All living families are thought to have evolved from the earliest neognathostomatid family, the Nucleolitidae (Suter 1994a, 1994b), the closest living relative being the Apatopygidae (Baker 1983). The cassiduloid apical system evolved from a 4-pored tetrabasal system to a 4-pored monobasal arrangement. The primitive nature of the apatopygids is further demonstrated by the retention, in *Porterpygus*, of a tetrabasal system with three genital pores, and in juvenile *Apatopygus*, a tetrabasal system.

Whereas families before 100 million years ago had pore pairs on all ambulacral plates, only single pores are present beyond the petals on subsequent taxa (Kier 1974). Neognathostomates have undergone a general relative reduction in the area of the aboral surface of the test covered by the petals. Kier (1962) suggested that this reflected an improved ability to burrow deeper in the sediment. Similarly, the trend for change from a test with an essentially circular outline to a more elongate form could be related to evolution of an improved burrowing ability. Buccal pores were absent in early neognathostomates, but they are present in Tertiary and living species.

The cassiduloid lantern is present for part of the juvenile phase, but whether or not it is functional is unclear (Gladfelter 1978). The tube feet are concentrated into a phyllode and are used in feeding, by assisting movement of sediment particles to the mouth. Swelling of the interambulacra around the mouth to form bourrelets also assists in feeding, because the small spines that cover them are used to push food particles into the mouth.

Neognathostomates occur only rarely in the Palaeocene in Australia, but they are relatively common in the Late Eocene. Indeed, in the Middle Eocene Nanarup Limestone in the Bremer Basin of Western Australia, more than 90% of individuals are of a single species of *Echinolampas* (K.J.McNamara, unpublished data). Other Middle Eocene genera are *Australanthus* and *Eurhodia* and the neolampadid *?Aphanopora bassoris* and *Pisolampas concinna* (Holmes 1995). The rich Late Oligocene to Middle Miocene deposits of southern Australia contain a less diverse neognathostomate fauna dominated by species of *Echinolampas* (McNamara & Philip 1980c). Other than clypeasteroids, no neognathostomates have been recorded from the Pliocene, an indication of their marked Late Neogene decline.

Clypeasteroids have multiple pores in each ambulacral plate and a monobasal apical system. Many forms are flattened (hence the common name 'sand dollar' or 'sea biscuit'; **Figs 1.2J, 1.14A,B**). Some, such as members of the family Arachnoididae, are very flat with a very sharp ambitus (**Figs 1.14A,B, 10.31**). Others are flattened, but with the ambitus more rounded, such as the Clypeasteridae (**Fig. 10.30**). However, species of Fibularidae (**Fig. 10.32**) have a small, strongly inflated test. Maximum test size varies greatly, from a few millimetres in some Echinocyamidae to almost 300 mm in some clypeasterids. The structure and function of clypeasteroid spines and tube feet are described in detail by Mooi (1986a, 1986b, 1986c).

The evolution of the clypeasteroid lantern is discussed by Mooi (1990b, 1990c). The clypeasteroid peristome is situated centrally on the ventral surface. The periproct is variable in position; in some forms it is on the ambitus, while in others it is either on the oral or aboral surface. The plates in the aboral petaloid ambulacra can contain alternate large and small plates, and the arrangement of pores is highly variable. Clypeasteroids are differentiated from other neognathostomates by the presence of large numbers of tube feet that pierce each ambulacral plate. The pores associated with these tube feet can be either regularly or irregularly arranged (Smith & Kroh 2011).

Neognathostomates feed by picking up individual sand grains or diatoms with their mucus-coated tube feet (Telford *et al*. 1985; Mooi 1986b; Telford & Mooi 1996), as in the spatangoids. However, it is not just the tube feet around the mouth that participate in feeding. Tube feet remote from the mouth pass the grains to adjacent feet, until the food grains reach food grooves on the oral surface, down which they are transported to the mouth (Telford *et al*. 1985). The grains are then crushed by the teeth before being ingested. In most clypeasteroids five grooves radiate from the peristome, and these can branch many times to form a complex pattern of food grooves (**Fig. 1.14**). The food grooves are lined with short tube feet that function to transport food particles to the centrally positioned peristome (Telford *et al*. 1985; Mooi 1986b; Telford & Mooi 1996). They do this in two ways. Fine particles can be swept along by ciliary currents to the mouth, or they can be caught by the sticky tube feet and transported to the mouth in strings of mucus that run along the food grooves (Mooi 1986b).

Some phylogenetically derived families of clypeasteroids have an accessory digestive tract structure called Gregory's diverticulum (Ziegler *et al*. 2016). It is most prominent in juveniles and is filled by high density sediment grains, such as magnetite, ilmenite and zircon. As the echinoid grows the structure diminishes in size and the sediment is expelled. In a few forms it is retained, paedomorphically, in the adult (Ziegler *et al*. 2016). The function of Gregory's diverticulum is not clear, although it has been suggested that it helps the juvenile to remain in place in strong currents (Wagner 1963). It is not known how the echinoids selectively gather the heavy mineral grains. Currently, no clypeasteroids from Australian waters are known to have this structure.

A number of clypeasteroids have holes or slit-like perforations (lunules) in the test (**Fig. 10.35**). The lunules can be located along the midlines of ambulacra (ambulacral lunules), or along the midline of the posterior interambulacrum, between the peristome and periproct (anal lunules). The former can develop either by resorption of the skeleton in early stages of growth, or they can begin as marginal indentations that become enclosed as growth proceeds. By contrast, anal lunules always develop by resorption (Smith & Kroh 2011). Lunules function in two ways. They can act as 'pressure drainage channels' that help prevent the animal being

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lifted out of the sediment by wave action (Telford 1983). Alternatively, they can help to process food particles more efficiently. Tube feet that project into the lunule capture large particles passing through the opening, while ciliary currents send fine particles from the dorsal surface to the food grooves on the oral surface which border the opening (Smith & Ghiold 1982).

As with regular echinoids, clypeasteroids have a lantern and a perignathic girdle. However, the lantern is more highly specialised, and while it has the same elements as in a regular echinoid, they are very low and wide and do not project from the mouth. The teeth are diamond-shaped in cross-section and steeply sloping (Smith & Kroh 2011). The lantern muscles attach to a perignathic girdle that consists of a ring of peg-like projections. Clypeasteroids have three types of pedicellariae — ophicephalous, triphyllous and tridentate (Ghiold 1984: Coppard *et al*. 2012).

Sexual dimorphism is evident in the genital papillae seen in some species, with those of the male being larger, apparently as a mechanism to facilitate dispersion of sperm above the substratum in buried species (Chia 1977; MacCord & Ventura 2004) Dimorphism is also seen in test shape as in the clypeasteroid *Echinarachnius parma* (Hamel *et al*. 1994). The oral surface is more concave in males, whereas the female has a greater overall volume, possibly due to the larger volume occupied by the ovaries compared with the testes.

Clypeasteroids are shallow burrowers and so their test lies just below the surface of the sediment. Although clypeasteroids usually inhabit more sheltered environments, some can endure rougher conditions. Their usually flattened tests can lead to some instability where currents are strong, although, as discussed above, lunules can ameliorate this. As the clypeasteroids mature, their weight and strength increase with the formation of internal buttresses and pillars of calcite that connect the upper and lower surfaces of the test. It has been argued that these also function as an anti-predation device, making it difficult for gastropods to bore through to the delicate internal organs (McNamara 1994b).

Clypeasteroids evolved in the Palaeocene, probably from a stem group neognathostomate ancestor, and they expanded rapidly from their West African origins to have a cosmopolitan distribution by the Eocene. These urchins diversified rapidly during the Palaeogene into nine families represented today by 14 genera, some of which, for example *Clypeaster* and *Echinocyamus*, are cosmopolitan (Ghiold & Hoffman 1986). Diversity decreased during the Neogene.

Most neognathostomates include species with small eggs and planktotrophic echinopluteus larvae, as seen in *Arachnoides placenta*, and species with large eggs and lecithotrophic larvae, as seen in *Cassidulus mitis* (Contins & Ventura 2011; Hardy *et al*. 2014).

Family Apatopygidae

Figure 10.26

The Apatopygidae was established by Keir (1962) for *Apatopygus recens*, which has an apical system that is clearly tetrabasal in juveniles, but appears monobasal in adults. In fact, polished adult tests also show a tetrabasal system when viewed by light shone through the apical region. Moreover, the phyllodes have unipores, and 'pyrinid' plating (demiplates enclosed between two primary plates abradially) is present in the ambulacra distal to the phyllodes, with a regular castellation of the perradial suture.

Apatopygids share several characters with the mid-Jurassic to Late Cretaceous family Nucleolitidae, including a similar test shape, straight, narrow, open petals with narrow poriferous zones, weakly developed bourrelets, and unipores in the phyllodes. Furthermore, both families have a distinct supramarginal anal sulcus (or 'ditch') from the periproct to the posterior edge of the test. These are evidently plesiomorphic features for the neognathostomates, as indicated by palaeontological and phylogenetic analyses (Suter 1994a, 1994b). Baker (1983) suggested that the Apatopygidae evolved from the Nucleolitidae in the Late Cretaceous, the earliest apatopygid occurring in the Late Palaeocene to the Early Eocene of New Zealand. Indeed, '*Apatopygus* would not have been out of place on a Middle Jurassic beach' (Hawkins 1920). There is an almost unanimous view that apatopygids are the earliest of the living neognathostomates, with nucleolitids comprising a group basal to a clade containing not only the other

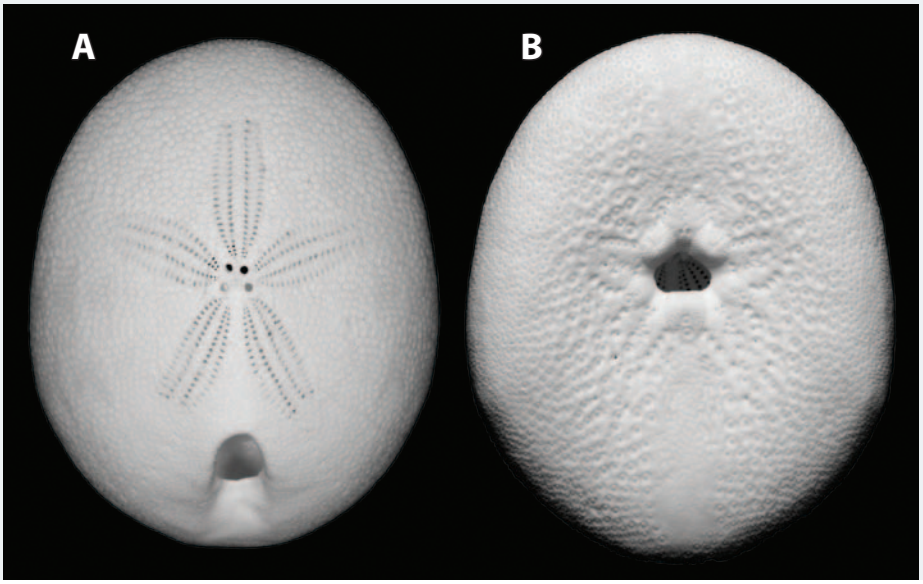


Figure 10.26 Family Apatopygidae.
A test of ***Apatopygus occidentalis*** from Mermaid Reef, Rowley Shoals, north Western Australia, at a depth of 200 m. Test length 28 mm.
A, aboral view.
B, oral view.
[A.D.Miskelly]

extant cassiduloids, but also the clypeasteroids (Mooi 1990b; Suter 1994a, 1994b). This implies that the 'cassiduloids', as originally conceived, are paraphyletic, but we prefer to retain the term here as a convenient way of grouping a large number of taxa that form a 'Hennigian comb' of successively branching clades basal to the clypeasteroids (Suter 1994a).

The Apatopygidae is known from two extant genera, *Apatopygus* and *Porterpygus*, and three species. The monotypic *Porterpygus* is found only in waters off northern New Zealand (Baker 1983), and it can be distinguished from *Apatopygus* by the presence of three rather than four gonopores. The type species, *A. recens*, is also known only from New Zealand (Mortensen 1948b), but the second species, *A. occidentalis*, was described on the basis of two tests dredged from south-western Australian waters (Clark 1938). The first specimen of this new taxon was dredged between Rottnest and Fremantle: 'As it was getting late, we hastened onward to Fremantle. Regretful at the small return for our efforts, I began looking the net over very carefully, hoping some brittle stars might have been entangled in the meshes. I found none, but to my surprise and delight I found caught between the net and the frame of the dredge, the little nucleolitid which proved the occurrence of an undescribed *Apatopygus* in Western Australian waters.' (Clark 1938). Additional specimen collections indicate that this species has a restricted geographical range, from 12 km south-west of Bunbury at about 33.5°S, north to Mermaid Reef in the Rowley Shoals (17°S) (A.D.Miskelly, unpublished data; **Fig. 10.26**). The record from Gulf St Vincent in South Australia requires confirmation (Baker 1983).

Apatopygus occidentalis has a narrower test than *A. recens*, smaller peristome and periproct, and more numerous fang-like teeth (Mooi 1990b) on the valves of the globiferous pedicellariae. At 17 mm test length, the gonopores are not yet open in *A. recens*, whereas they are in *A. occidentalis*, suggesting that the latter is a smaller species (approximately 20 mm maximum test length) (Clark 1938). *Apatopygus recens* lives buried in relatively coarse terrigenous sands (Higgins 1974a). Little is known of the biology of *A. occidentalis* except that it has been collected from depths of 18–40 m, and it lives in sand in association with *Posidonia* seagrass (Rowe & Gates 1995).

The earliest occurrence of *Apatopygus* in Australia is the Middle Eocene *A. vincentinus*, from the Eucla Basin in Western Australia and the St Vincent Basin in South Australia. This genus also occurs in the Early Miocene of the Otway Basin in Victoria and the Murray Basin in South Australia (Holmes 1999). *Porterpygus*, known only as a living species in New Zealand waters, occurs in the Midde to Late Miocene of the Murray Basin, *P. devlinensis* being the only known fossil representative of the genus (Holmes 1999).

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Family Cassidulidae

Figure 10.27

The family Cassidulidae was erected by Agassiz & Desor (1847) to accommodate those neognathostomates with a flat oral surface, a monobasal or tetrabasal apical system, broad often weakly developed petals, well-developed bourrelets and a naked zone in interambulacrum 5 adorally. Four of the nine genera assigned to the family are extant: *Cassidulus*, *Rhyncholampas*, *Eurhodia* and *Oligopodia*. The family evolved in the Early Cretaceous, and was most common in the Late Cretaceous and Early Cenozoic.

The living genera are circumtropical in their distribution, but only one, *Oligopodia*, occurs in Australian waters (O'Hara 2012). This genus is characterised by its small size (no more than 17 mm long), ovoid shape, with the posterior interambulacrum raised slightly to form a low keel that, in turn, can form a small beak above the periproct, well-developed petals that are open distally, with rounded pores of equal size, a monobasal apical system, the presence of distinct bourrelets, a rather deeply sunken and elongate peristome, and a deeply sunken periproct on the posterior margin (Mortensen 1948b).

The only living species, *O. epigonus*, is very widespread, having been recorded from off the east coast of Africa, Somalia, South Africa, Malaysia, the Philippines, Australia, Tonga and New Zealand (Mortensen 1948b; Rowe & Gates 1995). In Australia it has been found near Norfolk Island in the south Pacific Ocean (O'Hara 2012) and at Mermaid Reef, north Western Australia (A.D.Miskelly, unpublished data; **Fig. 10.27**). Beyond Australian waters specimens have been found at depths between 35 m and 141 m, whereas dead tests have been recorded at depths of 5–390 m (Mortensen 1948b). *Oligopodia epigonus* lives on coarse sands to gravelly bottoms, often in substrates with a high percentage of fragments of calcareous algae.

Once thought to be closely related to *Apatopygus*, *Oligopodia* is, in fact, quite distinct due to its monobasal apical system and so is closer to the genus *Eurhodia* (Mooi 1990a).

If the extinct *Australanthus* is considered to belong to the Cassidulidae (Suter 1994a, 1994b), then this family first appeared in Australia in the Middle Eocene, when it is represented by both *Australanthus* and *Eurhodia* species in the Nanarup Limestone in the Eucla Basin, Western Australia (K.J.McNamara, unpublished data), and in the St Vincent Basin, South Australia. *Australanthus* persisted to the Late Oligocene.

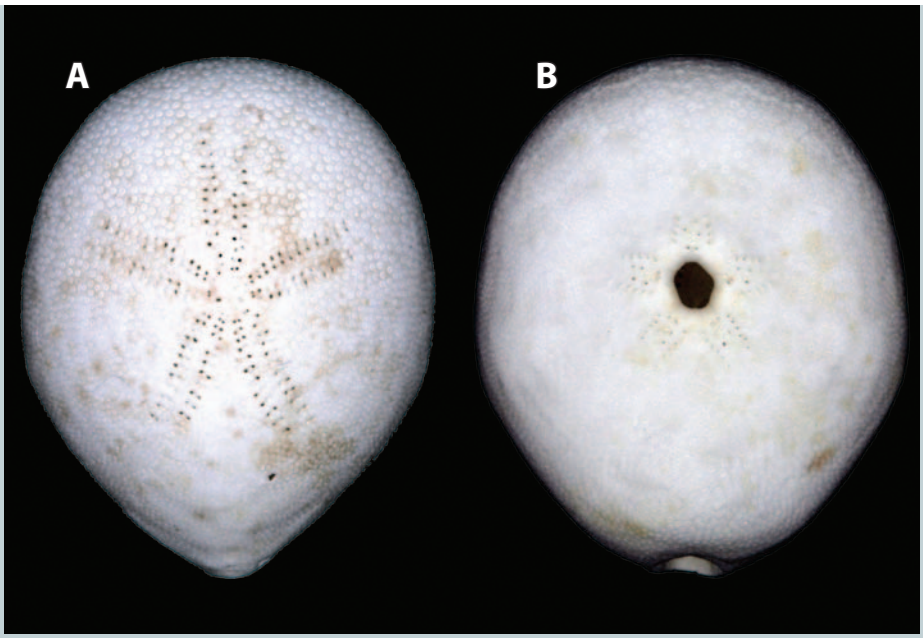


Figure 10.27 Family Cassidulidae.
A test of ***Oligopodia epigonus*** from Mermaid Reef, Rowley Shoals, north Western Australia, at a depth of 200 m. Test length 25 mm.
A, aboral view.
B, oral view.
[A.D.Miskelly]

Sexual dimorphism is evident in cases where the gonopores of the females are many times larger than those of the male (Mortensen 1948b). Dimorphism is also evident in the genital papillae seen in some species with those of the male being larger, apparently as a mechanism to facilitate dispersion of sperm above the substratum in buried species (MacCord & Ventura 2004). Reproduction and development is described in *Cassidulus mitis* from Brazil, which has large eggs and lecithotrophic larvae (MacCord & Ventura 2004; Contins & Ventura 2011).

Family Neolampadidae

Figure 10.28

The taxonomic status of the Neolampadidae has been the subject of debate, with some workers assigning it familial status within the Cassiduloida (Mortensen 1948b; Kroh & Smith 2010), others subordinal (Philip 1963a) or even ordinal (Durham & Wagner 1966) status. Much of this confusion has arisen from the paedomorphic nature of neolampadids, not only their small size, but also their greatly reduced pores on the dorsal surface, the absence of petals, and only single and very small pores on each plate. The group is also distinguished by the absence of the lantern in the adult (Mooi 1990c). Bourrelets, however, are usually well developed. The position of the periproct is quite variable, from submarginal to supramarginal (Holmes 1995).

The Neolampadidae might not be a natural group (Mortensen 1948b; Suter 1994a, 1994b; Holmes 1995). In his cladistic analysis of cassiduloids, including neolampadids, Suter (1994a, 1994b), using 'taphonomically robust' characters that are likely to be preserved in fossils and living forms, found no support for neolampadid monophyly.

Five genera are currently included in the family, of which one, *Pisolampas*, is extinct (Kroh & Mooi 2014). All four extant genera, *Aphanopora*, *Nannolampas*, *Neolampas* and *Studeria*, have tropical or subtropical

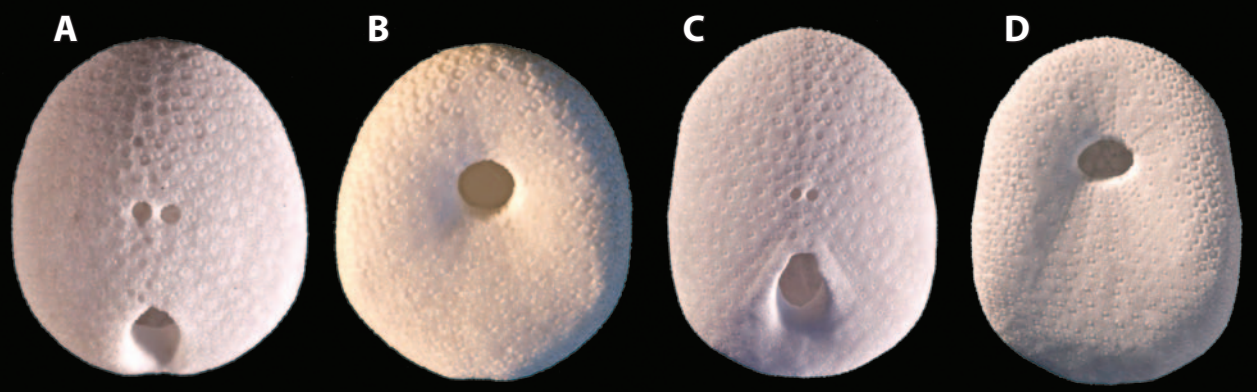


Figure 10.28 Family Neolampadidae.

A, **B**, test of ***Aphanopora echinobrissoides*** from Wanganella Bank, Tasman Sea, at a depth between 500 and 1,000 m. Test length 9 mm.
A, aboral view.
B, oral view.

C, **D**, tests of ***Aphanopora*** sp. from Mermaid Reef, Rowley Shoals, northern Western Australia, at a depth of 200 m. Test length 14.7 mm.
C, aboral view.
D, oral view.

These two species live in coarse rubble in deep water. Note the two large gonopores in these female specimens, indicating the presence of two gonads, production of large eggs, and lecithotrophic development.

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distributions. Three species, including one undescribed species, are recorded from Australia. *Studeria recens* has been reported from south-eastern New South Wales to a depth of 145 m, from the Kermadac Islands and at similar depths in the Arafura Sea (Baker & Rowe 1990). *Aphanopora echinobrissoides* is known from Wanganella Bank, Tasman Sea, the Philippines and Timor (**Fig. 10.28A,B**). An undescribed species of *Aphanopora* has been collected from northern Western Australia (**Fig. 10.28C,D**).

Aphanopora has also been recorded, albeit uncertainly, from the Late Eocene in the St Vincent Basin in South Australia (Holmes 1995).

Studeria was previously placed in a separate family, the Pliolampadidae, now regarded as synonymous with the Neolampadidae (Smith & Kroh 2011). The genus is represented by one extant species, *S. recens*, an extremely rare echinoid known from five dead tests, two of which are from Australian waters (Baker & Rowe 1990). However, six New Caledonian specimens, as well as fragments, are in the collections of the Muséum National d'Histoire Naturelle in Paris (K.J.McNamara, unpublished data). *Studeria recens* reaches a test length of 44 mm, and it has only three gonopores (the pore in interambulacrum 3 is absent). It has long, straight, open petals in which the adjacent pore pairs are widely spaced, a marginal, longitudinal periproct with a shallow subanal sulcus, and strongly developed bourrelets. Several of the New Caledonian specimens have more or less complete coverings of external appendages, yielding much additional data. The pedicellariae are similar to those of neolampadids and cassidulids and lack the oval tooth grouping typical of echinolampadids, and the peristomial membrane is populated by long, thorny, rod-like spicules (K.J.McNamara, personal observation).

Studeria recens was originally described from two tests collected in the Arafura Sea, to the north of Australia. However, it is not an exclusively tropical species, as the two Australian tests were collected off the eastern and south-eastern coasts, near Tweed Heads and Danger Point, New South Wales. A fifth specimen was collected from the Kermadec Islands, on the eastern side of the Tasman Sea. Prior to the recent discovery of the New Caledonian material, all that was known of the habits of *S. recens* were collection depths of 135–236 m (Baker & Rowe 1990). However, the Paris specimens were collected at depths 230–350 m, and the gut of one New Caledonian specimen was filled with carbonate sediment. Although the dried test weighed only 0.7 g, the gut contents weighed 1.48 g (K.J.McNamara, personal observation).

One of the two type specimens has very large gonopores (approximately 0.8 mm in diameter), whereas the other has gonopores of a more typical size (to 0.5 mm in diameter) (A.B.Smith, personal communication). Of the six New Caledonian specimens, three have small gonopores, and three have large gonopores, further suggesting that the species is sexually dimorphic, and that the females expel large eggs through their accommodatingly large gonopores. Presumably, the larvae are lecithotrophic. At a test length of 22 mm, gonopores are fully developed in the 'males', whereas 'females' with a test length of less than 25 mm have large, crater like depressions at the sites of the future gonopores, and only very small openings in the centres of these depressions. A 29 mm long 'female' has three fully formed, very large gonopores (K.J.McNamara, unpublished data).

Neolampadids have a long history in Australia. Fossils are known only from Australia, described material ranging in age from the Middle Eocene to the Late Miocene (Philip 1963a; Holmes 1993, 1995; Martin & McNamara 2004).

Family Echinolampadidae

Figure 10.29

The Echinolampadidae (**Fig. 10.29**) comprises two living genera and 14 species (Mortensen 1948b; Mooi 1990b). First seen in the Late Cretaceous (Cenomanian), and particularly common in the Tertiary, the family is characterised by the presence of long open petals in which the poriferous zones are unequal in length. Ophicephalous pedicellariae are unique among the neognathostomates in that the distal teeth on each valve are arranged in a closed oval ring (Mortensen 1948b). The periproct is inframarginal, and the bourrelets are

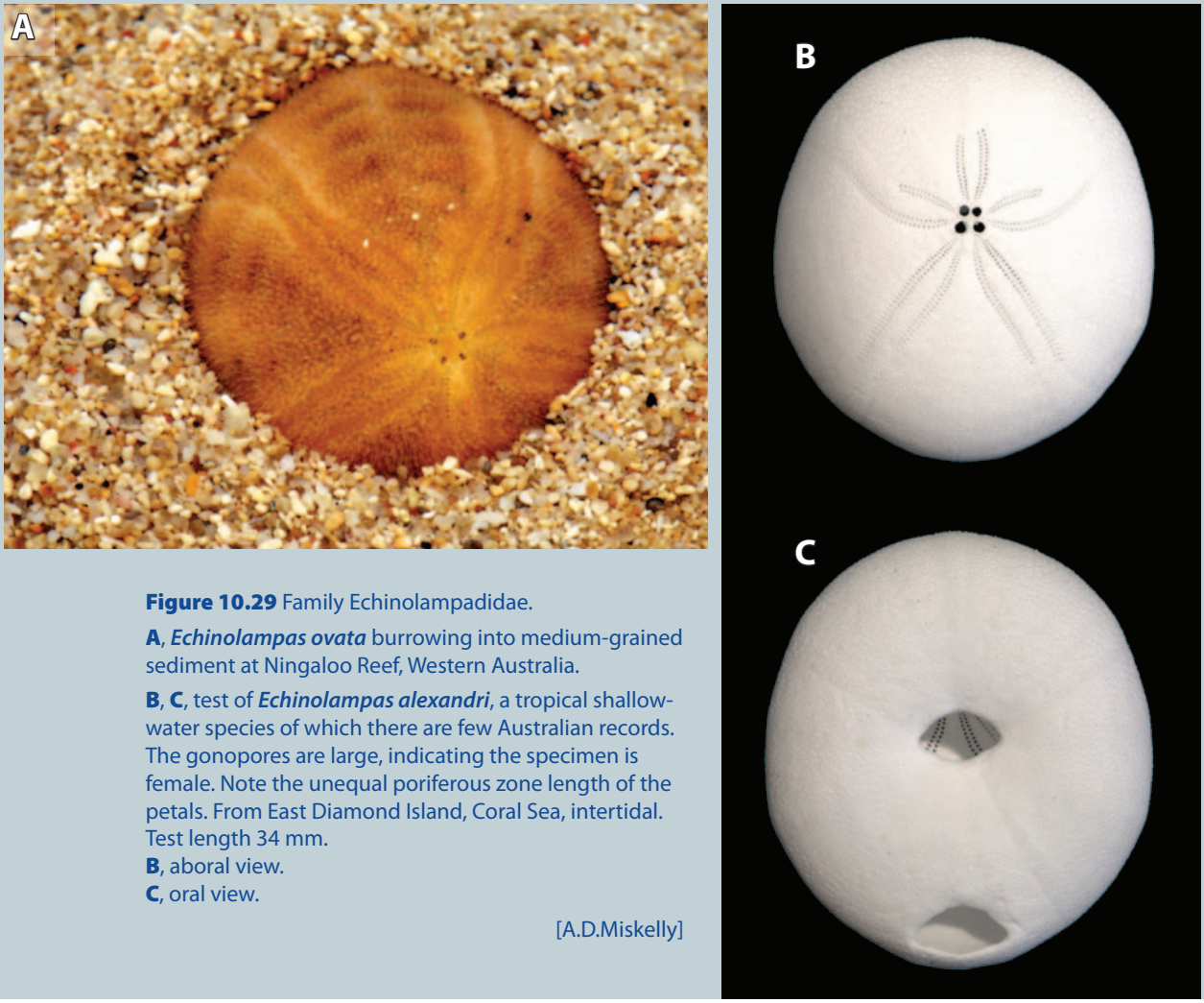


Figure 10.29 Family Echinolampadidae.

A, ***Echinolampas ovata*** burrowing into medium-grained sediment at Ningaloo Reef, Western Australia.

B, **C**, test of ***Echinolampas alexandri***, a tropical shallow-water species of which there are few Australian records. The gonopores are large, indicating the specimen is female. Note the unequal poriferous zone length of the petals. From East Diamond Island, Coral Sea, intertidal. Test length 34 mm.
B, aboral view.
C, oral view.

[A.D.Miskelly]

well developed with broad intervening phyllodes. The more widespread *Echinolampas* can be distinguished from *Conolampas* by its test having a lower and less circular outline, broader interporiferous zones in the petals, and fewer phyllopodia.

The ten living species of *Echinolampas* are widely distributed from the Indo-Pacific region to the Caribbean and the north-east Atlantic Ocean. *Conolampas*, in contrast, has a disjunct distribution with three of the four species confined to the Indo-Malay region, the other in the Caribbean.

Two widespread echinolampadid species occur in Australian waters, *Echinolampas alexandri* (**Fig. 10.29B,C**) and *E. ovata* (**Fig. 10.29A**). *Echinolampas sternopetala* lives at a depth of 200–500 m off north Norfolk Ridge, the closest record of its occurrence to Australian waters; it also occurs off Japan and New Caledonia. (A.D.Miskelly, personal observation). *Echinolampas alexandri*, a rare species, is found at Lizard Island, Great Barrier Reef, Queensland (A.D.Miskelly, unpublished data); it also occurs in the Coral Sea (Miskelly 2002), Thailand and Mauritius. *Echinolampas ovata* is a widespread Indian Ocean species recorded from the Gulf of Suez, Mauritius and Sri Lanka, as well as the west coast of Australia (Mortensen 1948b) between Ashmore Reef (12°S) and the northern end of Shark Bay (25°S). *Echinolampas ovata* is characterised by its ovoid shape, length to 70 mm, broad petals with unequally

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long poriferous zones and well-developed bourrelets and phyllodes around the peristome. Tubercles on the aboral surface are also somewhat smaller and more densely packed than in most other *Echinolampas* species. In life the colour of this echinoid varies from light to dark chestnut brown (Clark 1938).

Dollfus & Roman (1981) hinted that *E. ovata* and *E. alexandri* might be conspecific because of what they felt was a considerable overlap in the variable morphology of the two taxa. Although the analysis of more material from throughout their ranges would provide a more reliable comparison, it appears that the broader petaloids and more projecting bourrelets of *E. ovata* support its separation from *E. alexandri* (Mooi 1990b). This is also supported by the cladistic analyses of Suter (1994b), which demonstrated that the two species are not even sister taxa.

Echinolampas was far more common and widespread in Australia during the Tertiary, and seven species are recorded from Eocene to Miocene sediments in southern and north-western Australia (McNamara & Philip 1980c; McNamara & Kendrick 1994).

Little research has been carried out on the habits and behaviour of echinolampadids. At Ashmore Reef, *E. ovata* lives on fine, clean carbonate sands free of mud or silt, and at Ningaloo Reef, Western Australia, on clean medium-grained coarse sand. Ashmore Reef animals remain buried deeply during the day, but they emerge at night to plough through the sand with the top half of the test exposed (Mooi 1990b). At Ningaloo Reef this species lives in shallow waters (1–2 m) remote from the reef, but in close proximity to algal communities (A.D.Miskelly, unpublished data). It buries itself completely in the daytime to a few centimetres below the surface. If removed from their habitat, subsurface specimens will re-burrow within about 10–15 minutes. As the sea urchin commences burrowing, the anterior end sinks down into the substrate on a rather steep angle, and its surface is not covered with sand particles as it proceeds. Dead tests with algal growth on the aboral surface are common in areas where live specimens are found.

Family Clypeasteridae

Figure 10.30

In clypeasterids the test is usually circular or elongate in outline, up to 150 mm long (**Figs 10.3D–F, 10.30**). Although the oral surface is usually relatively flat, the peristome is generally sunken, and the dorsal surface can be strongly vaulted. The margin is thick and well rounded. The petals are well developed, and they are frequently swollen. The domed surface effectively raises the petals above the substrate and increases the surface area for respiration (Lawrence 1987). Every second plate in the petals is a demi-plate that does not extend across the entire ambulacral row. The apical system has five gonopores and is slightly sunken. The food grooves are simple, unbranched and poorly defined, but they almost reach the ambitus. While little is known of the method of feeding, due to the fact that food grooves lack tube feet, it is likely that particles are moved by ciliary currents to the mouth (Ghiold 1984).

Only one genus, *Clypeaster*, and eight species are known from Australian waters (O'Hara 2012; A.D.Miskelly, unpublished data). Many species, both living and fossil, have been described, and some authors have subdivided the genus into several subgenera. Australian species are referable to four of the subgenera (Rowe & Gates 1995). *Clypeaster* species are mostly inshore, shallow-water echinoids, such as *C. telurus*, which has a depth range of 5–67 m. However, deeper-water species with a broad bathymetric distribution are also known, an example being *C. virescens*, which occurs in depths of 27–630 m (O'Hara 2012).

Some Australian clypeasterids are widely distributed around the coast. For example, *C. telurus* extends from Dunsborough, Western Australia, in the south-west, along the western and northern coasts, and down the east coast to Fraser Island, Queensland. Similarly, *C. reticulatus* (**Fig. 10.30D**) is found from Houtman Abrolhos, Western Australia, north to the Timor Sea, east to Queensland and as far south as Sydney, New South Wales (A.D.Miskelly, unpublished data). *Clypeaster latissimus* has a more restricted distribution confined to the north-west coast of Australia, while *C. australasiae* extends from Bowen, Queensland, to south-eastern Victoria (**Fig. 10.30A-C**).

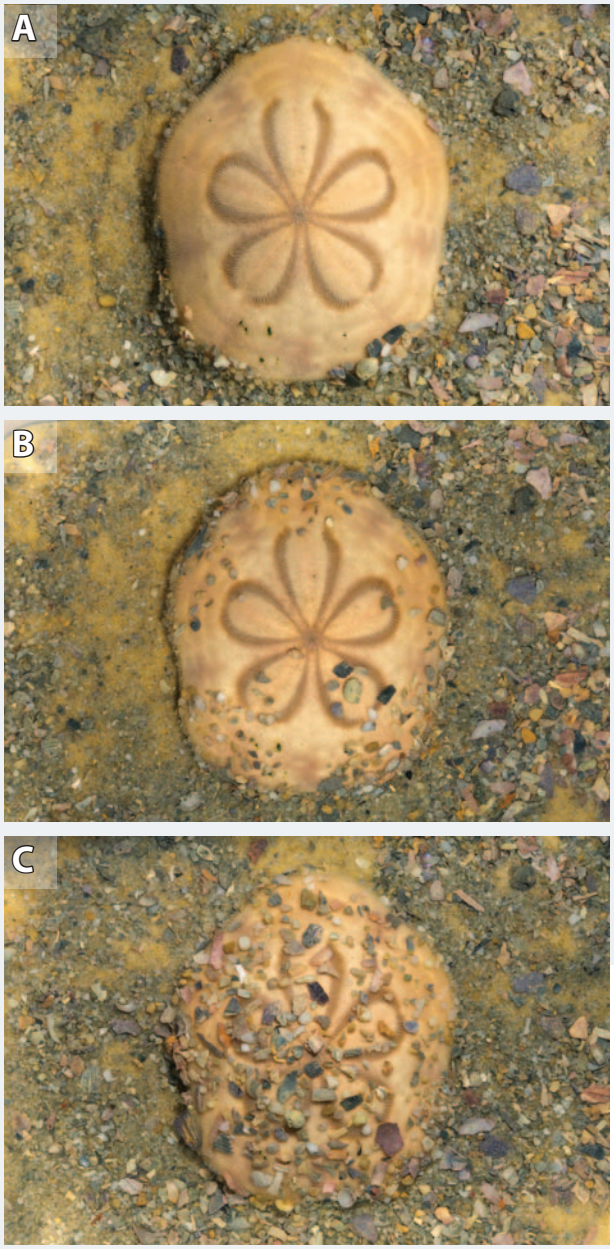




Figure 10.30 Family Clypeasteridae.

A–C, burial sequence, at 15 minute intervals, of the large sand dollar ***Clypeaster australasiae*** at a depth of 9 m in Camp Cove, Sydney Harbour, New South Wales. Coarse seafloor debris is transferred to the aboral surface by the numerous adhesive tube feet. Test length 110 mm.

D, ***Clypeaster reticulatus***, an instantly recognisable sand dollar, has an inflated test margin and pronounced plate pigmentation. These animals are from Camp Cove, Sydney Harbour, New South Wales, at a depth of 7 m. Test length 45 mm.

[A.D.Miskelly]

Clypeasterids first appeared in Australia during the Miocene, and species of *Clypeaster* are known from the Miocene of the Murray Basin in southern Australia and the Carnarvon Basin in north-western Australia (McNamara & Kendrick 1994) and the Pliocene of the Eucla Basin (McNamara 1999).

The biology of Australian clypeasterids is poorly studied. Clypeasteridae includes species with feeding echinopluteus larvae and lecithotrophic forms (Emlet 1986). *Clypeaster rosaceus* from the Caribbean is unusual in being a facultative planktotroph (Emlet 1986). The egg is large (360 µm diameter), and while the larva can complete development in the absence of exogenous food, it has a complete digestive tract and can consume phytoplankton when available. This larval form is considered to be intermediate in the evolution of non-feeding larvae (see **Chapter 3**).

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Family Arachnoididae

Figure 10.31

McNamara (1999) proposed an origin of the Arachnoididae in north-western Australia and a subsequent southerly expansion down the west coast of Australia, carried by a proto-Leeuwin Current. The family is most closely related to the Clypeasteridae, and it probably originated in the Australian region.

Members of the Arachnoididae have a very flat, rounded test with a sharp ambitus (**Figs 1.14B, 2.37, 10.4, 10.31**). The apical system has four gonopores, and the petals become very broad towards the ambitus. Also present are well-developed combed areas, alternating rows of aligned accessory pores and tubercle rows outside the petals arranged in a dense oblique series. The small peristome is situated flush on the flat oral surface. Food grooves are solitary and prominent, extending on to the dorsal surface (**Fig. 1.14B**).

The family is represented in Australia by two genera and five living species: *Arachnoides* (2 species) and *Ammotrophus* (3) (O'Hara 2012). The genera are characterised, in part, by their oral plating. *Arachnoides* has one pair of post-basicoronal interambulacral plates, and its periproct is on the sharp ambitus. In the much larger *Ammotrophus*, which can be 150 mm in diameter, the periproct is on the oral surface between the first pair of basicoronal interambulacral plates.

The extinct *Fellaster* is represented by one species, *F. incisa*. *Fellaster* has a fossil record in southern Australia, with *F. incisa* recorded from Miocene to Pleistocene deposits in Victoria (Foster & Philip 1980). Extinct genera are known from Oligocene to Miocene deposits in the St Vincent and Murray Basins, South Australia (Holmes 1993). Although only one fossil species of the extinct genus *Monostychia* has been described, there is a rich, undescribed arachnoidid fauna in Late Palaeogene and Neogene deposits in southern Australia. The earliest record is in the Carnarvon Basin, north-western Australia, where *Monostychia* occurs in Late Eocene limestones (K.J.McNamara, unpublished data).

The Arachnoididae have a broad Indo-west Pacific distribution. *Ammotrophus*, the largest genus, is restricted to coasts of South and Western Australia,

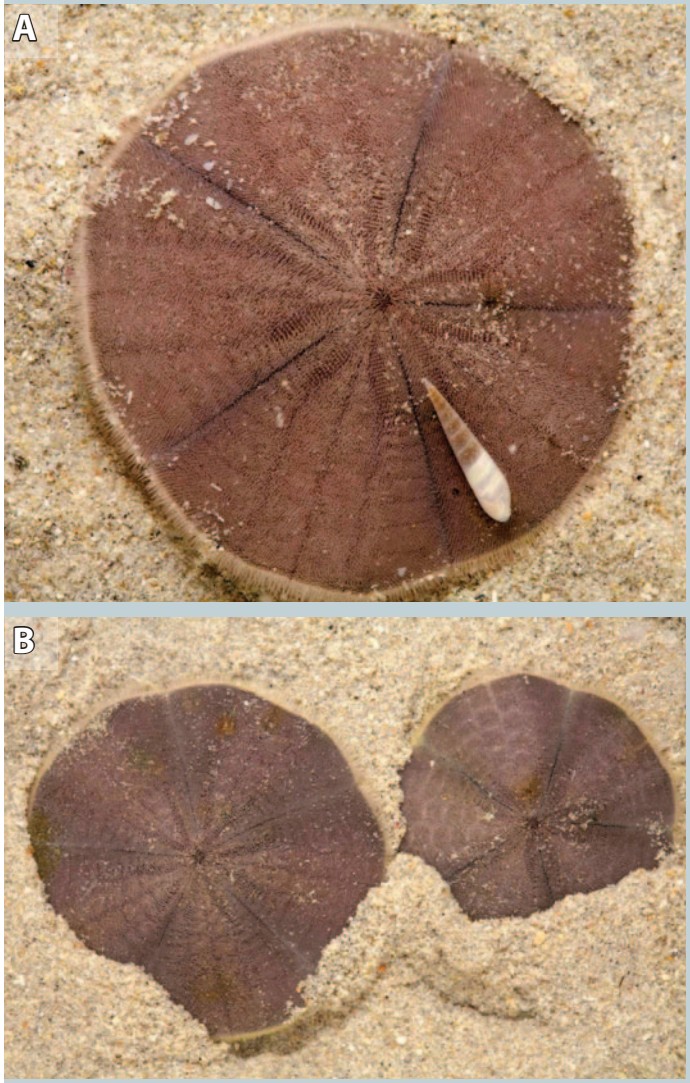


Figure 10.31 Family Arachnoididae.
Arachnoides tenuis from Wallal Downs, south of Broome, Western Australia.
A, sand dollar with an eulimid gastropod attached to the aboral surface.
B, sand dollars in the process of burial; they live under a thin veneer of sand in the low tide zone.
[A.D.Miskelly]

as far north as Jurien Bay. It inhabits shallow waters, between 20 and 45 m depth (O'Hara 2012). *Arachnoides* has a much broader Indo-west Pacific distribution. In Australia *Arachnoides tenuis* (**Fig. 10.31**) occurs off north Western Australia to as far south as Shark Bay, and *A. placenta* is found predominantly found off the north-east coast. Throughout its range *A. placenta* is common in tropical intertidal sandy beaches (Chen & Chen 1992; Haycock, 2004) where it may be superabundant (**Fig. 2.37**). Its distribution is however patchy, influenced by features of the habitat (Haycock 2004).

In north Queensland gametogenesis of *A. placenta* is seasonal, with gonad growth (December to February) followed by spawning from March to June (Haycock 2004). Sexual dimorphism is evident in *A. placenta* with the genital papillae of the male being larger (Chia 1977).

Arachnoides placenta has an echinopluteus larva (Chen & Chen 1992; Haycock 2004). This is a fast-developing species, and its comparatively large egg (*ca.* 139 μm) supports development to the advanced larval stage in the absence of feeding (M.Byrne, personal observation). Achieving metamorphosis does require access to exogenous food (M.Byrne, personal observation). As might be expected from its intertidal habitat, the larvae have a very broad thermal tolerance (Hardy *et al.* 2014) which would allow colonisation of cooler latitudes facilitated by the southerly flow of the East Australian Current (EAC), as for *Centrostephanus rodgersii* (**Box 2.1**). That this species has not extended its range suggests that the southerly range may be restricted by habitat requirements (Hardy *et al.* 2014).

Family Fibulariidae

Figure 10.32

Fibulariids (**Fig. 10.32**) have a small, oval test that is significantly longer than wide, but is rarely more than 10 mm in length. Uniquely among clypeasteroids, they lack internal buttresses and food grooves, and the centrally positioned apical system has four gonopores. Hydropores are present, but are few in number, while petals on the dorsal surface are weakly developed, each carrying only a few pore pairs. The periproct is on the oral surface close to the central peristome, and the basicoronal circlet of plates is small and unspecialised.

This family is represented in Australian waters by the genus *Fibularia* with seven species and *Fibulariella* with one species (O'Hara 2012; A.D.Miskelly, unpublished data). Bathymetric ranges of individual species can be quite broad, for example *Fibularia cribellum* occurs between 15 m and 400 m. One species, *Fibularia oblonga*, extends around most of the Australian coast, but others are either confined to the west coast (*F. japonica*, *F. cribrellum* and *F. plateia*) or to the east (*F. nutriens*, *F. ovulum* and *F. volva*) (O'Hara 2012).



Figure 10.32 Family Fibulariidae.
Live ***Fibulariella acuta*** with extended tube feet. Animals were collected from Shoal Bay, New South Wales, in 2 m of water. Test length 9 mm.
[A.D.Miskelly]

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Fibulariella acuta (**Fig. 10.32**) is known from the east and west coasts, from the shallows to depths of 90 m. Unlike many clypeasterids that can have part of the aboral test slightly raised above the sediment, this oval echinoid lives completely beneath the surface of clean, white, evenly grained sand. When it is removed live, tube feet can be seen grasping at sand grains. It lives in moderate energy environments of minimum turbulence, and population densities can reach 20 individuals per square metre (A.D.Miskelly, unpublished data).

Fibulariids are common in some Cenozoic deposits in southern Australia. Deposits of the Late Eocene Kingscote Limestone on Kangaroo Island, South Australia, contain large numbers of *Fibularia 'gregata'*. Interestingly, deposits of equivalent age in Western Australia do not contain fibulariids. Many undescribed species are known from Cenozoic deposits in Australia (Irwin 2001).

The minute fibulariid *Fibularia nutriens*, which reaches just 4 mm test length, is a direct developer. The females have a crescentic marsupium on the dorsal surface of the test for brooding the young (Clark 1909).

Family Echinocyamidae

Figure 10.33

Echinocyamids (**Fig. 10.33**) are very small clypeasteroids (usually no more than 15 mm long) with a rounded, flattened test with relatively large primary tubercles. The periproct is situated on the oral surface quite close to the peristome, and it is bounded by the first and second post-basicoronal interambulacral plates. Typically, the interambulacral zones terminate adapically in one or two small plates (Smith & Kroh 2011). Unlike other clypeasteroids, food grooves are absent in this family.

Echinocyamids feed by using the buccal and accessory tube feet to pass sand grains directly to the mouth. Teeth scrape micro-organisms from the sand grain which is then returned to the sediment (Ghiold 1984). Specialised locomotory features enable echinocyamids to burrow in fine sand and shell gravel and even climb vertically (Ghiold 1982). Rather than the spines assisting in locomotion, the tube feet carry out this role. The apical system has four gonopores and a few scattered hydropores. Although short, the petals are distinct and open distally. Internally, echinocyamids have ten radial buttresses close to the ambitus; in contrast, fibulariids lack such internal structures.



Figure 10.33 Family Echinocyamidae. Tests of ***Mortonia australis*** collected from East Diamond Island, Coral Sea, at a depth of 2 m. Test length 15 mm. [A.D.Miskelly]

Echinocyamus, the most common genus, includes 18 living species, eight of which have been recorded from Australian waters at depths between 2 and 1,886 m (O'Hara 2012; A.D.Miskelly, unpublished data); these sand dollars may grow to 9 mm test diameter. Individual species can have broad bathymetric and geographical ranges, for example *E. planissimus* occurs around most of western, northern and eastern Australia. Other species, such as *E. platytatus*, have a southern distribution.

The echinocyamid *Mortonia australis* (15 mm test length; **Fig. 10.33**) has been recorded from one remote locality in Australian waters (Coral Sea). The only other species of *Mortonia*, *M. polyporus*, is found in New Zealand and the Kermadec Islands, where it is common (McKnight 1969); its presence at Norfolk Island requires verification. The absence of all but the posterior internal buttresses distinguishes *Mortonia* from *Echinocyamus*, as does the fact that the periproct is considerably larger than the peristome and is covered in spine-bearing platelets.

Echinocyamus planissimus has an extensive geological range, from the Pliocene in south-western Australia through the Pleistocene to the present day. During this time it underwent some evolutionary change involving an increase in spine size and density, and a reduction in the number of pore pairs in the petals (McNamara 1990).

Family Laganidae

Figure 10.34

Laganids are common in Australian waters and are characterised by having lantern muscle attachment sites comprising five single pegs. Moreover, the interambulacra are narrow and continuous, terminating in a single plate towards the apex. The periproct is on the oral surface and is generally visible between the first and second paired post-basicoronal plates. Food grooves are well defined and vary in length, but they are always unbranched. The aboral ambulacra carry well-developed petals that can be open or closed distally. Internally, buttresses consist of vertical partitions running parallel to the ambitus, as well as branched radial struts.

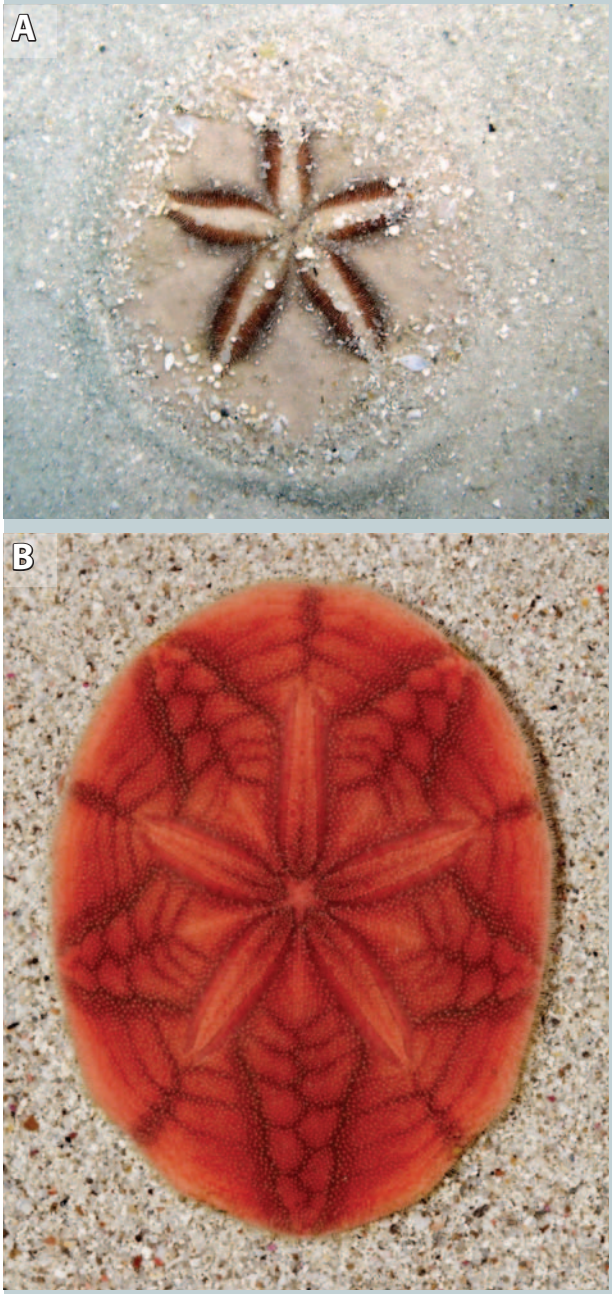


Figure 10.34 Family Laganidae.

A, ***Laganum depressum*** covering itself with coralline sand as it moves forward on the seafloor at Swains Reef, outer Great Barrier Reef, Queensland, at a depth of 5 m. Test length 70 mm.

B, ***Peronella lesueuri***, a live sand dollar, on coarse coralline sand at Jurien Bay, Western Australia, at a depth of 3 m. The plate boundaries of the ambulacra and interambulacra are very distinct.

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Two widespread genera, *Laganum* and *Peronella* (**Fig. 10.34**), are known from the Australian region (O'Hara 2012). *Laganum* has a sub-pentagonal test with a flat oral surface, and the apex is slightly raised on the aboral surface. There are five gonopores, petals are pronounced and closed towards the margin and, in many species, the periproct is located about halfway between the peristome and the posterior margin. In contrast, the periproct of *Peronella* is closer to the posterior margin and, while the genus also has straight, unbranched food grooves, there are only four gonopores rather than five. The type species, *P. peronii*, which occurs in Australian waters, has gonopores outside the apical system. Test shape is variable in *Peronella*, ranging from circular to pentagonal to ovate in outline. The margin is often thickened, petals are well developed, and either open or closed towards the margin. In *Peronella* hydropores occur over the apical disc, while in *Laganum* they are confined to a groove.

Four species of *Laganum* are widespread in inshore, tropical and subtropical Australian waters from the intertidal down to 300 m (O'Hara 2012; A.D.Miskelly, unpublished data). The common genus *Peronella* occurs on most Australian coasts and is represented by seven species. These range from small species, such as *P. peronii* (to 40 mm long), to the common *P. lesueuri* (to 180 mm) (**Fig. 10.34B**). Like *Laganum*, *Peronella* species are shallow-water echinoids, generally living in waters less than 100 m deep, although *P. peronii* occurs down to 360 m. As well as inhabiting coastal waters, *P. lesueuri* has been observed living 5 km upstream from the mouth of the Swan River, Western Australia (K.J.McNamara, unpublished data).

Peronella has an extensive fossil record during the Pliocene and Pleistocene in south-western and western Australia, and four species have been described from the Eucla, Perth and Carnarvon basins (McNamara 1996). The oldest is *P. ova* from the Pliocene Roe Calcarenite, while the living species *P. orbicularis* extends back to the Late, and possibly the Middle, Pleistocene.

The biology of *P. lesueuri* in Western Australia is well studied and the Japanese species *P. japonica* has also been investigated (Li *et al.* 2013; Yeo *et al.* 2013, 2015). *Peronella lesueuri* is locally abundant in marine and estuarine soft sediments along much of the Western Australian coastline (Keesing *et al.* 2011b). This species is the dominant macroinvertebrate where it occurs. Through locomotion and feeding *P. lesueuri* plays a major role in bioturbation (Forehead & Thompson 2010; Li *et al.* 2013; Yeo *et al.* 2013). It is estimated that populations of this sand dollar can rework the sediment in the habitats they occupy every 20 days (Li *et al.* 2013).

Peronella lesueuri has an annual reproductive cycle, spawning in summer, and it has large 210 µm diameter eggs, indicating that this species has a lecithotrophic larva (Yeo *et al.* 2015). *Peronella japonica* has a highly modified lecithotrophic larva (Tsuchimoto & Yamaguchi 2014).

Family Astriclypeidae

Figure 10.35

The family Astriclypeidae comprises three genera, *Astriclypeus*, *Amphiope* and *Echinodiscus*. Astriclypeids are flattened clypeasteroids distinguished in having a pair of posterior lunules extending to the ambitus (**Fig. 10.35**). In some species anterior ambulacral lunules can be present. The test is very thin and comparatively large, indented laterally and, in *Echinodiscus*, much broader posteriorly. The petals are well defined and as broad as the interambulacral areas. Tube feet can occur in interambulacral plates, and the periproct is located on the oral surface. Food grooves fork just beyond the primordial plates and then are finely subdivided distally; they lack tube feet. Accessory tube feet adjacent to the food grooves can assist in the transport of food to the mouth (Ghiold 1984). Internally the test possesses a complex series of buttresses close to the ambitus.

Astriclypeids are represented in Australian waters by two tropical species, *Echinodiscus auritus* (**Fig. 10.35**) and *E. tenuissimus*. They are readily recognised by the presence of a posterior pair of slit-like lunules or notches. *Echinodiscus auritus* is confined to shallow water (less than 5 m) on the north-west coast between Carnarvon and Broome, Western Australia, while on the east coast, *E. tenuissimus* has been found only near Thursday Island in the Torres Strait, Queensland, at depths to 20 m (O'Hara 2012).



Figure 10.35 Family Astriclypeidae. ***Echinodiscus auritus*** showing the distinctive posterior lunules.

[M.Claereboudt]

Echinodiscus has been reported from Oligo-Miocene to Pleistocene deposits in Japan, Taiwan, Java and from Pleistocene deposits in Egypt (Rowe & Gates 1995; Smith & Kroh 2011). However, there is no fossil record of the family in Australia.

Astriclypeids have small eggs and development through an echinopluteus larva (Emlet 1995a; Tominaga 1998). Development to metamorphosis takes about 25 days (Tominaga 1998).

ATELOSTOMATES

The Atelostomata is a monophyletic group consisting of the holasteroids, spatangoids and some primitive fossil families formerly known as disasteroids but now considered to be paraphyletic (Kroh & Smith 2010).

The Holasteroida is an unusual group of echinoids, characterised by: 1) an elongate apical system; 2) the absence of genital plate 5 in the apical system; 3) a weakly differentiated plastron; 4) petals that are not always differentiated and paired petals usually not sunken; 5) the absence of a floscelle; and 6) fascioles which may be present or absent (Durham & Melville 1957). Nine families are now recognised (Smith 2004), of which only one, the Corystusidae (**Fig. 10.36**), is present in Australia.

Holasteroids range in length from 20 to 159 mm, and some have extremely thin tests. The potential disadvantages of this are ameliorated by a more robust coelomic lining than occurs in other irregular echinoids (Mooi & David 1996). They exhibit a very wide range of test shapes, from elongate and bottle-shaped to bell-shaped, flattened or spherical. Prominent depressions or rostrum-like projections can also be present on the test.

In holasteroids, the elongate apical system ranges from a condition of contiguous plates to a condition in which there is severe disruption by a number of interambulacral plates (David & Mooi 1996). There is a reduction in the number of gonopores in some families, the Urechinidae and Calymnidae having three, or occasionally two. On the aboral surface of the Corystusidae ambulacral pores are paired throughout. The pores in ambulacrum III always differ from those of the paired ambulacra, in size, number and shape. David (1987) provides a description of plate growth in *Pourtalesia miranda* from the radially symmetrical post

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larva to the bilaterally symmetrical adult. The evolution of the extremely modified body of these holoasteroids is discussed in detail by Saucède *et al*. (2004). Based on egg size, the development in *Pourtalesia jeffreysi*, a species with continuous reproduction, is thought to include a lecithotrophic larva (Harvey & Gage 1984).

On the oral surface, the labrum can be followed by a series of alternating plates of roughly equal size which constitute the plastron. In some families only one large sternal plate is in contact with the labrum. In the Corystusidae a single plate, the rostral, occurs after a pair of plates called episternals. The plastron bears tubercles unlike those on adjoining interambulacral plates, suggesting differentiation of spines for a separate function.

The periproct varies between supramarginal, marginal and inframarginal, its position correlating approximately with small to large test size, respectively (Mooi & David 1996). Whether a fasciole (see below) is present or not, and its position when present, varies between families. Thus, in the Holasteridae there are no fascioles in some genera, but a marginal fasciole occurs in others. In the Urechinidae, the fasciole is absent or subanal, it is marginal in the Calymnidae and subanal in the Pourtalesiidae, Plexechinidae and Corystusidae.

The first holasteroids appeared in the Early Cretaceous (Valanginian) and diversified greatly in the Late Cretaceous. Their decline in the Cenozoic was as spectacular as their rise, just 3% of living species being holasteroids. In Australia, the Holasteridae were present in the Palaeocene, and the Corystusidae first appeared in the Palaeocene, disappearing in the Early Miocene, only to reappear in Recent seas.

Today, holasteroids are deep-water animals, ranging from depths of about 250 m on the middle shelf, to abyssal depths (Saucède *et al*. 2004). As a result, comparatively little is known of their habits, although females of the extraordinary Antarctic urechinid *Urechinus mortenseni* brood their young in a deeply invaginated extension of the body wall that is suspended from the interior edges of the apical plates (David & Mooi 1990; Mooi & David 1993). These brood pouches communicate with the exterior through minute openings. This type of brooding has also been described for another Antarctic holasteroid, the plexechinid *Plexechinus nordenskjoldi* (David & Mooi 1990).

Ten of the fifteen extant families of the Spatangoida (heart urchins) are known from Australian waters. Spatangoids are characterised on the basis of plating structure, in particular that of the oral surface, the presence and variety of fascioles, the nature of the apical system and the wide diversity of tube feet and spines that participate in a variety of functions. They have distinct bilateral symmetry, with the peristome anterior on the oral surface, and the periproct marginal to submarginal. The compact apical disc has ocular plates II and IV separated. There is a single interambulacral plate (the labrum) behind the peristome (**Fig. 10.3G–J**).

The Spatangoida have thin bands (fascioles) of very small, highly specialised spines (clavules) that secrete mucus (De Ridder *et al*. 1987). These can form a band around the apical system (internal), or run around the lateral and posterior margins of the test (lateroanal), extend around the entire margin or ambitus (marginal), encircle the tips of the petals (peripetalous), or form a small circle beneath the periproct (subanal) (**Fig. 10.3G,I**).

In spatangoids the labrum is situated behind the peristome, followed by a pair of sternal plates (**Fig. 10.3H**). The latter are small and asymmetrical in more primitive forms, but larger and symmetrical in more highly derived taxa. Where paired sternal plates are of very different sizes and shapes, plastronal plates can be interrupted by adjacent ambulacral plates by plate translocation (McNamara 1987a).

The spatangoid apical system is distinguished by the absence of the posterior genital plate. In the most primitive family, the Toxasteridae, the system is elongate, and the anterior and posterior pair of plates are separated from each other. However, in other families the apical system is ethmophract, a condition whereby the anterior and posterior pair are contiguous. The most advanced condition, found in groups such as the Schizasteridae and Brissidae and others, is termed ethmolytic, in which the madreporite plate extends to the rear, having translocated between the posterior pair of plates. The number of gonopores in spatangoids can vary between two and four (**Figs 10.40B, 10.41B,**

10.46C). While attempts have been made to use the number of gonopores as a generic character, it has been shown, at least in a number of Australian schizasterids, that the number can vary even within species (McNamara 1995).

Many morphological features of spatangoids have evolved in response to selection for an infaunal habit in a wide variety of sediment types (De Ridder *et al.* 1987). While some live on the sediment surface, particularly those in deep waters, most inhabit burrows (see De Ridder *et al.* 1987), from just below the sediment/water interface to depths several times the height of the animal. Spatangoids range from the intertidal zone to abyssal depths.

Spatangoids are the only echinoids capable of inhabiting fine-grained silts and muds, and they do this because of the presence of fascioles (De Ridder *et al.* 1987). The aboral fascioles produce mucus that effectively forms a barrier between the spatangoid test and the sediment. Other fascioles on the oral surface beneath the periproct are involved in the construction and effective removal of waste sediment that has passed through the animal.

The current familial classification relies heavily on the presence or absence of particular fascioles or combinations of fascioles. While this is often effective, there are many anomalies, especially where the occurrence of particular fascioles responds to ontogenetic change. However, pending a full revision of spatangoid families, these remain the most reliable diagnostic features.

A study of fascioles in spatangoids by Smith & Stockley (2005) has highlighted their importance in higher level classification within the Spatangoida. They suggest that the presence of different patterns of subanal fascioles in the Micrasteridae and Brissidae implies that they may have evolved independently. Schizasterids and hemiasterines can be subdivided into two clades on the basis of their fasciole patterns, while brissids fall into three clades on the basis of their fascioles.

Different types of spines include oar-shaped locomotory structures on the plastron, lateral spines on the adoral surface used for digging, sediment-screening spines on the aboral surface, frontal arch spines that protect the respiratory tube feet in the anterior ambulacrum, and subanal tuft spines involved in the construction of a sanitary burrow (De Ridder *et al.* 1987). The aboral concentration of tubercles increases in inverse proportion to decreasing sediment grain size (Smith 1980).

Tube feet around the mouth have mucus-secreting rosettes that pick up sediment prior to ingestion (**Fig. 1.15C**). Other mucus-secreting tube feet are present in the frontal ambulacrum on the dorsal surface. In spatangoids that burrow in relatively fine sediments, these tube feet secrete mucus to line the funnel that maintains connection with the sediment surface. In at least one genus, *Protenaster*, these same tube feet have also been shown to be light-sensitive (McNamara 1984b). Tube feet on the paired petals on the dorsal surface function in gas exchange (Smith 1984b).

A recent phylogenetic analysis of the Spatangoida (Stockley *et al.* 2005), using morphological and molecular approaches, has shown support for many traditional familial groups, such as the Loveniidae, Brissidae and Spatangidae. However, some deep-water groups, such as the Asterostomatidae, are polyphyletic, suggesting independent invasions into the deep sea.

Family Corystusidae

Figure 10.36

The Corystusidae (**Fig. 10.36**), as Corystidae, was established for three fossil genera, *Corystus*, *Cardabia* and *Huttonechinus* by Foster & Philip (1978); the spelling of Corystidae was emended to Corystusidae by the ICZN (2009). They have: 1) a modified plastron in which the first pair of episternal plates are followed by a single central rostral plate encircled by a subanal fasciole; 2) a subanal rostrum; 3) an apical system with three or four gonopores, the anterior and posterior pairs separated by juxtaposed ocular plates II and IV; 4) non-petaloid ambulacra, but with double pores; and 5) a weak or absent anterior notch.

The presence of the single rostral plate sets the Corystusidae apart from all other echinoids. The structure of the corystusid apical system is the same as in the earliest holasteroids such as *Holaster* (Mooi & David 1996), indicating that this is the ancestral condition for holasteroids.

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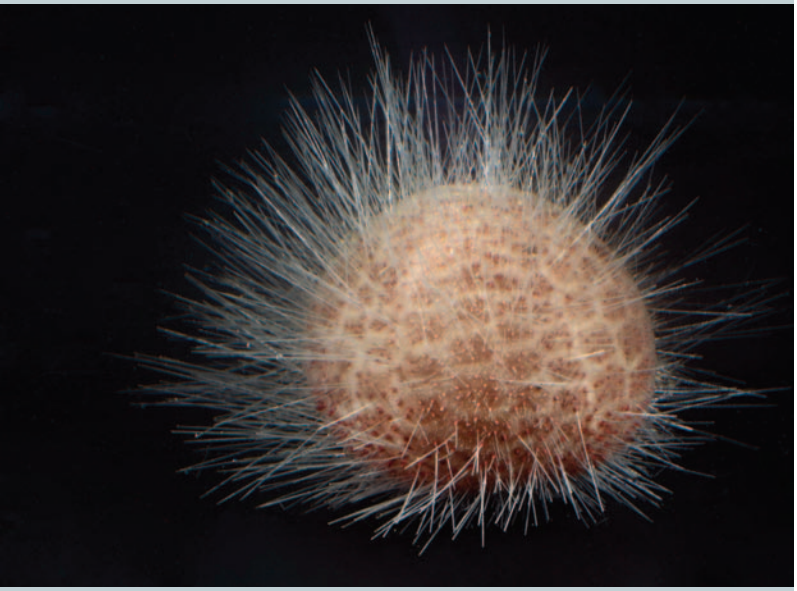


Figure 10.36 Family Corystusidae.
Corystus sp. from Tonga Trench, 2,200 m. Posterior view showing the characteristic needle-like spines and the high vaulted shape of the animal.
[O.Anderson]

Extinct members of the family are recorded only from Australia and New Zealand (Foster & Philip 1978), ranging in age from the Middle Palaeocene to the Early Miocene. A living representative of the family was recognised more recently. *Corystus relictus*, previously placed in *Stereopneustes* (Holasteridae), has a distinctive rostral plate that is characteristic of Corystusidae. Consequently, this is the only living sister taxon to the urechinid, calymnid and pourtalesiid holasteroids (Mooi & David 1996). *Stereopneustes* is now regarded as a junior synonym of the fossil form *Corystus* (Smith 2004). *Corystus* has dorsal ambulacra that are not sunken, ambulacrum III a little narrower than the paired ambulacra; pores equal in size, arranged obliquely in ambulacrum III; a poorly developed labrum; a well-developed phyllode with isopores; and a subanal fasciole.

Fourteen specimens of *Corystus relictus* were trawled from rocky and soft bottoms at depths of 390–400 m on the North West Shelf, off Western Australia (McNamara 1998). This species is quite large, reaching up to 70 mm in test length. It has also been reported from the Philippines (Sulu Sea), and from waters off Japan (Mortensen 1950).

Nothing is known of the feeding and reproductive behaviour of Corystusidae. Like other echinoids trawled off the North West Shelf in 1982 (McNamara 1984a), and which have broad geographical distributions, they are locally quite common. Their patchy distribution probably reflects settling of pelagic larvae at one site, and the growth and development of a single cohort. The absence of a frontal notch, non-petaloid ambulacra, and the presence of only a small subanal fasciole, indicates that corystusids do not burrow in the sediment. The decline in abundance of holasteroids in near-shore environments through the Tertiary, in contrast to the increase in diversity of the spatangoids, could, in part, be a consequence of this inability to burrow, making them more susceptible to predation (McNamara 1994b). There were four periods of onshore-offshore migration of corystusid genera through the Late Cretaceous and Cenozoic (Smith 2004). Unlike the living species, the Late Eocene to Early Miocene species of *Corystus* occurred in relatively coarse-grained sediments deposited in near-shore environments (Foster & Philip 1976, 1978).

Family Micrasteridae

Figure 10.37

The Micrasteridae are distinguished from other heart urchins by their ethmophract apical disc (an apical disc in which genital plate 2 is not extended posteriorly between the posterior genital plates), their alternate episternal plates and the specific pathway followed by the subanal fasciole. They are a more primitive group and appear early in the fossil record (Upper Cretaceous).

In Australia, micrasterids are represented by one extant species, *Cyclaster recens* (**Fig 10.37**) from the Keppel Bay area, Queensland, and one fossil, *C. archeri,* from the late Oligocene to early Miocene. Another extant species, *C. regalis*, is endemic to New Zealand. *Cyclaster recens* has also been recorded from Vietnam. *Cyclaster* is characterised by an ovate, inflated test with three



Figure 10.37 Family Micrasteridae.
The sole representative species for the Micrasteridae in Australia is ***Cyclaster recens***, a comparatively unspecialised heart urchin that shows no enlarged tubercles for long defensive spines, nor does it have a specialised petal structure for living in very fine sediments as do the schizasterids. Locality undetermined, but probably from Queensland. Test length 56 mm.
A, test in aboral view.
B, test in oral view.
[A.D.Miskelly]

gonopores (there is no gonopore in genital plate 2). The anterior ambulacrum is sunken adapically, with small, differentiated pore pairs. Other ambulacra form short, straight, weakly sunken petals adapically; petals extend only about half of the radial distance to the ambitus in plan view. Aboral tubercles are small and uniform and are set among fine granules. The peristome and periproct are very small. *Cyclaster recens* has three pore pairs on either side of the subanal fasciole.

Nothing is known about the biology of *C. recens*. The better-studied *C. regalis* is known to occur in deeper water (300–500 m). The finely tuberculate surface, slightly sunken petals and faintly depressed anterior notch of *Cyclaster* species suggests an unspecialised habitat where it would probably not burrow deeply (A.D.Miskelly, unpublished data).

Family Hemiasteridae

Figure 10.38

Hemiasterids are small heart urchins, and in the case of *Holanthus* grow to a maximum length of around 30 mm (**Fig. 10.38**). *Holanthus* is characterised by an inflated test, circular in outline, without an anterior notch. A peripetalous fasciole is present, and the ambulacral plates are strongly pinched immediately beneath the petals as they cross the peripetalous fasciole. The posterior petals are somewhat rounded in shape, and much reduced in length, being approximately half that of the anterior petals. There are four gonopores.

The hemiasterid fauna of Australia comprises a single genus and species, *Holanthus gibbosus* (**Fig. 10.38**), recorded from one deep-water locality north-east of Eden, New South Wales (O'Hara 2012). *Holanthus gibbosus* is also distributed along the entire coastline of New Zealand where it may be found offshore in deeper water from 512 m to 2,800 m (O.Anderson, personal communication); it also occurs in Japan and the Malayan Archipelago. Two other living species of *Holanthus* are known, *H. expergitus* from the North Atlantic to the Caribbean at depths of 950–3,200 m and *H. hickmani* from the Gulf of Oman and the Indian Ocean at depths of 1260–1520 m (Schultz 2009).

Two other extant genera in this family, *Sarsiaster* and *Palaeostoma*, are monotypic. *Sarsiaster griegii* is from the mid Atlantic from depths to 3,120 m. *Palaeostoma mirabile* is an Indo-west Pacific species from the Red Sea to Indonesia and Japan with a bathymetric range of 20–110 m. *Sarsiaster griegii* differs from *Holanthus* in having an ethmolytic apical disc with two gonopores. *Palaeostoma mirabile* only grows to 20 mm length and differs from the other two genera by its conspicuous pentagonal peristome having five triangular plates.

The hemiasterid *Bolbaster* is known from the Early Oligocene (*B. dolosus*), Middle Miocene (*B. callidus*, *B. planedeclivis*), Late Eocene (*B. subidus*) and Late Oligocene/Early Miocene (*B. verecundas*) (McNamara 1987b).

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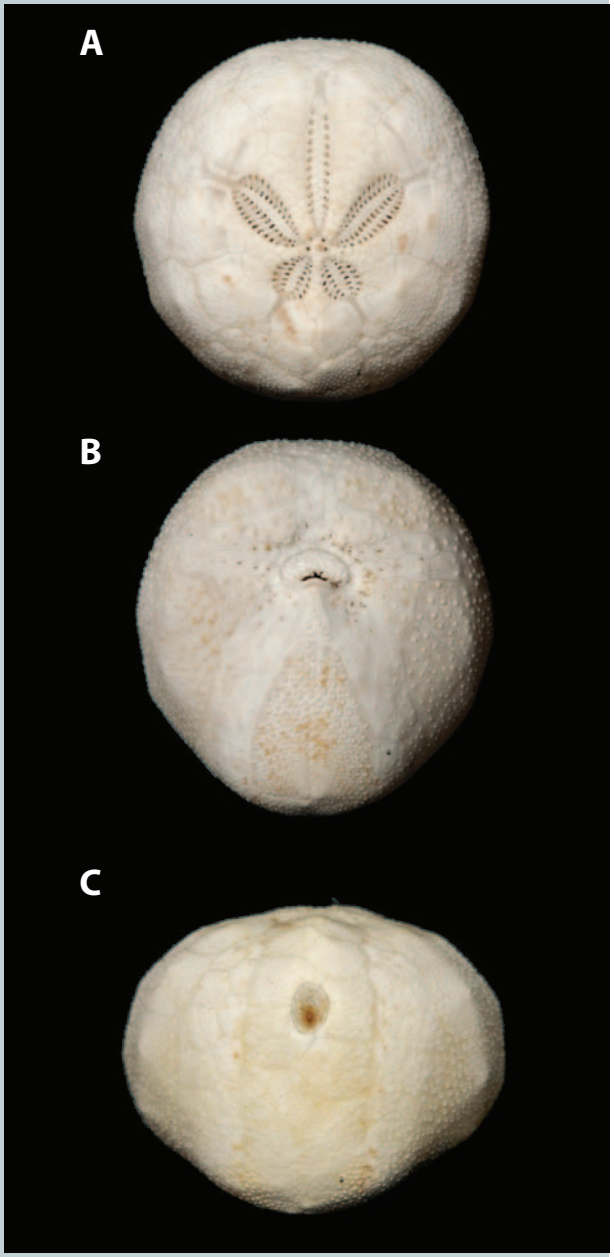


Figure 10.38 Family Hemiasteridae.

A test of ***Holanthus gibbosus*** from north-east of Eden, New South Wales, at a depth of 716 m; animals were found living in thick grey mud and hard clay. Test length 28 mm.
A, aboral view.
B, oral view.
C, posterior view.

[A.D.Miskelly]

Family Schizasteridae

Figure 10.39 & Box 10.5

The Schizasteridae established by Lambert (1905), comprises 64 extant species in 11 genera (Ghiold 1989). Among the latter are three marsupiate circum-Antarctic genera. The family originated in the Early Cretaceous, and it is characterised by the presence of a peripetalous and lateroanal fasciole, although occasionally the lateroanal fasciole can be incomplete or absent. The Schizasteridae are likely to have evolved from a hemiasterid ancestor, as the earliest schizasterid, *Periaster*, has an ethmophract apical system like most hemiasterids. This contrasts with the later schizasterids in which the apical system is ethmolytic. Moreover, apart from the presence of a lateroanal fasciole and a peripetalous fasciole, *Periaster* closely resembles such typical hemiasterids as *Hemiaster*. Other distinguishing features of the Schizasteridae include sunken petals and sunken aboral interambulacrum III, which result in the presence of a notch in most species. The test is typically heart-shaped, medium to small and relatively thin and fragile.

Schizasterids are diverse in Australia. Eight genera have been recorded from mainland waters; *Aceste* (2 species), *Ova* (2) and the single representatives *Diploporaster savignyi*, *Hypselaster jukesii*, *Moira lethe*, *Paraster gibberulus*, *Protenaster australis* (**Fig. 10.39A**), and *Schizaster lacunosus* (O'Hara 2012; A.D.Miskelly, unpublished data). Only one, genus *Protenaster*, is endemic to southern Australian waters; most of the others are cosmopolitan. Of the ten species known from mainland waters, four of them are endemic (O'Hara 2012): *Moira lethe*, *Ova portjacksonsensis*, *Protenaster australis* and *Hypselaster jukesii*.

In addition, *Brisaster antarcticus* (**Fig. 10.39B**) is known from the subantarctic Heard Island, and the marsupiate *Abatus* (**Fig. 3.4; Box 10.5**) and *Amphipneustes* from the Australian Antarctic Territory (Lockhart *et al*. 1994).

The most speciose genus, *Schizaster*, is characterised by the posterior pairs of petals being shorter than the anterior. The maximum test length is about 75 mm. The species are characterised mainly by the differences in test shape, petal depth, number of pore pairs, and the size of the labrum. Larger species, such as *S. myorensis*,

have comparatively elongate, wedge-shaped tests that narrow anteriorly, and have proportionally longer anterior petals. All petals and anterior ambulacrum III are very deep. Consequently, the anterior notch is very pronounced. Moreover, larger species have much more crowded pore pairs in the anterior ambulacrum, and the projection of the labrum across the peristome is more pronounced. The apical system is anterior. Traditionally, *Schizaster* was considered to have only two gonopores. However, studies of this character in *S. myorensis* from Queensland (McNamara & Philip 1980b) and in *S. compactus* from Western Australia (McNamara 1995) showed a range from two to four within the same population.

The morphological trends apparent among the larger species of *Schizaster* are even more pronounced in the genus *Moira*. An uncommon spatangoid, its petals are deeply sunken and are almost covered by lateral growth of the adjacent interambulacra. The test is narrow and high and well-developed keels are present on the dorsal and posterior surfaces. The only Australian species is *Moira lethe* (McNamara & Philip 1980b).

Protenaster is less extreme in its morphological characteristics. The anterior and posterior petals are more similar in length, the petals are not as deeply sunken and the apical system is more central. The uncommon *Proraster* is somewhat anomalous in that the lateroanal fasciole can be absent in some species (McNamara & Philip 1980b). *Proraster jukesii* is known from the Queensland coast, from Torres Strait south to Moreton Bay, and from around Broome in Western Australia. A few specimens of *Paraster gibberulus* have been found in shallow water off Fredericks Reef, Great Barrier Reef, Osprey Reef, and East Diamond Island in the Coral Sea (A.D.Miskelly, unpublished data).

Little is known of the behaviour and ecology of Australian schizasterids. Species of *Schizaster* have been found only in fine-grained, muddy sediments (McNamara 1995). Individuals of *S. myorensis* have been found buried to a depth of 100 mm. Specimens of *S. compactus* were recovered from inside large mud-filled pipes on the North West Shelf, off Western Australia, where they were found to be inhabiting burrows (McNamara 1995), but their depth below the sediment/water interface was unknown. There is likely to be a

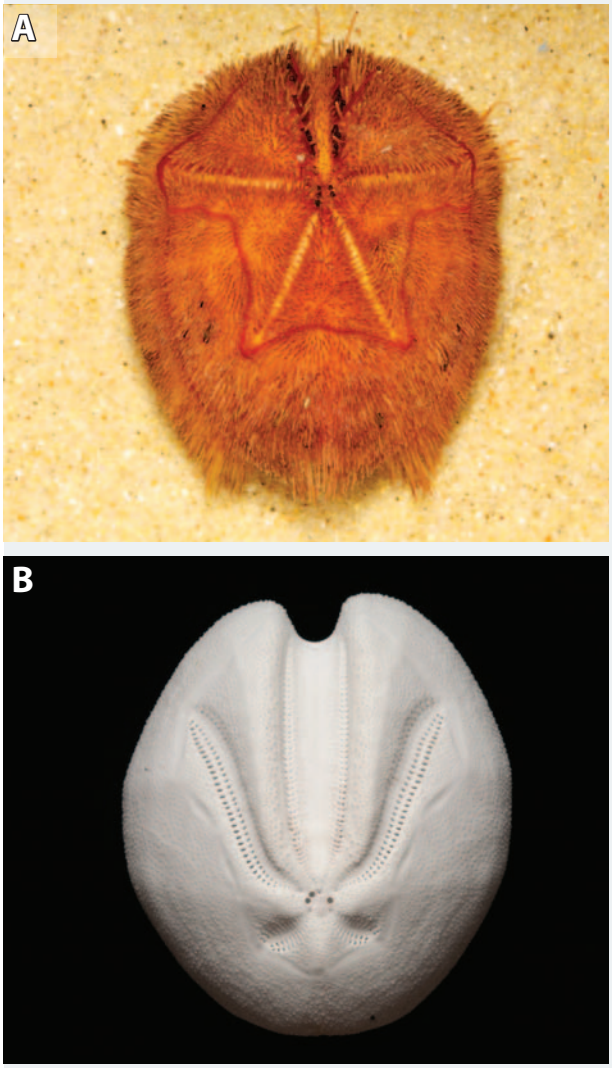


Figure 10.39 Family Schizasteridae.

A, aboral view of a live ***Protenaster australis*** found at Camp Cove, Sydney Harbour, New South Wales. These heart urchins are usually found in shallower depths than other species and often live in coarse sediment where they are undetectable when completely buried. Test length 62 mm.

B, aboral view of a test of ***Brisaster antarcticus***, a schizasterid with two very short posterior petals and two long lyre-shaped anterior petals. The tube feet and spines of the deeply sunken frontal ambulacrum aid in feeding by constructing a tunnel-like structure. Collected from 60 nm north-west of Heard Island, Southern Indian Ocean, at a depth of 430 m. Test length 48 mm.

[A.D.Miskelly]

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direct correlation between the depth of the petals, the number of pore pairs in the anterior ambulacrum, the width of the peripetalous fasciole and sediment grain size. Deeper petals, more numerous pore pairs and a wider fasciole are associated with the occupation of finer-grained sediment (McNamara & Philip 1980a).

Diploporaster savignyi has been observed at Lizard Island on the Great Barrier Reef, Queensland, where it lives buried in thick, fine-grained grey mud in depths of around 16 m (A.D.Miskelly, personal observation). This species burrows up to 100 mm deep and, from evidence of dead tests littering the seafloor and having drill holes from predatory gastropods, it occurs in large numbers.

Two species of *Aceste*, known from two specimens, are recorded from Australia. One specimen of *A. bellidifera* was collected south-west of Rottnest Island, Western Australia, at a depth of 549 m. A second, very well-preserved *Aceste* specimen, 13 mm long, has been collected from 1,087 m off Portland, Victoria (A.D.Miskelly, unpublished data).

Schizasterids occur around the entire Australian coast, although certain genera appear to have restricted distributions. Only one, *Moira lethe*, is likely to occur near all Australian coasts; it has been found off the Queensland coast from Bowen to Moreton Bay, at Botany Bay (New South Wales), Port Phillip Bay (Victoria), northern Tasmania, and at Broome (Western Australia) (O'Hara 2012). *Schizaster* and *Proraster* have northern Australian distributions, *Schizaster* extending from the New South Wales coast near Sydney to the North West Shelf near Dampier (McNamara & Philip 1980b), and *Proraster* from Moreton Bay (Queensland) to Broome (Western Australia). However, *Protenaster australis* is a southern Australian endemic, extending from Port Stephens, New South Wales, to Tasmania and in the west to as far north on the western Australian coast as Perth (McNamara & Bryce 1983; McNamara 1985b). Fossil specimens from Cape Burney at the mouth of the Greenough River (Western Australia) indicate that it extended further north during the last interglacial in the Late Pleistocene (McNamara 1985b, 1992).

The earliest *Protenaster* occurs in Late Eocene limestones in South Australia (McNamara 1985b). *Schizaster* has a fossil record extending back some 55 million years into the Palaeocene (McNamara & Philip 1980a). Species of *Schizaster* occur in Middle and Late Miocene strata in southern Australia (McNamara & Philip 1980a). However, a cooling of the Southern Ocean during the Pliocene resulted in a contraction of its range to the northern half of Australia.

Most Australian schizasterids are shallow-water species. Thus, *Schizaster myorensis* was recorded from the intertidal zone to 30 m (McNamara & Philip 1980b), *S. compactus* from 45 m (McNamara 1995), *Proraster* from tidal flats (Clark 1925; Endean 1961), and *Protenaster* from intertidal reef flats (McNamara & Bryce 1983).

Compared with other spatangoids, *Protenaster australis* (**Fig. 1.2K**) occupies a rather unusual habitat. Specimens were seen 30 m offshore from metropolitan beaches in Perth, Western Australia, buried to a depth of about 100 mm in fine-grained sands in pockets on a limestone reef at a water depth of 1.5 m (McNamara & Bryce 1983). In eastern Australia, around Port Jackson, New South Wales, *P. australis* occupies a similar habitat in shallow water (A.D.Miskelly, unpublished data).

When placed on the sediment surface *Protenaster australis* took 15 to 20 minutes to cover themselves completely with sand (K.J.McNamara, personal observation). Experiments carried out on individuals in the laboratory revealed the presence of light-sensitive tube feet in ambulacrum III (McNamara 1984b). On the east coast of Australia *P. australis* burrows in moderately coarse shellgrit in shallow water, usually less than 10 m deep, and the majority of specimens are from around 3–5 m. This species does not leave any trace of its presence by a depression in the substrate, and it is only found by random digging.

The marsupiate species from Antarctica (**Fig. 3.4; Box 10.5**) are relatively well studied due to their abundance around the continent, ecological importance as bioturbators in the sediment, and the ease of access to the developing young (Pearse & McClintock 1990; Lockhart *et al.* 1994; Thompson & Riddle 2005). Reproduction and development is described in many species and in the context of the evolution of brooding in many echinoids from the region (Poulin & Féral 1996).

Box 10.5

Abatus from the Australian Antarctic Territory

Ashley D. Miskelly

The genus *Abatus* is an exclusively Antarctic group of heart urchins comprising 11 known species. Five species occur around the coastline of Davis Station in Australian Antarctic Territory. Here they live buried or partially buried in fine silt or mud, in depths of 4 m and greater, approximately 80 m from the shoreline. Each of the five species occurs in similar abundance with the population density estimated at 30 individuals per square metre. Species of *Abatus* are not large in size. The maximum size of the largest species at Davis Station, *Abatus nimrodi*, is 45 mm. All *Abatus* species are brooders. Females have highly modified petals with deeply recessed marsupia in which young develop (**Fig. 3.4**); mature juvenile urchins leave the marsupia to live freely on the seafloor. The existence of marsupia can add to the confusion of species identification when denuded tests are examined, but in all other respects the test morphology is identical for both males and females.

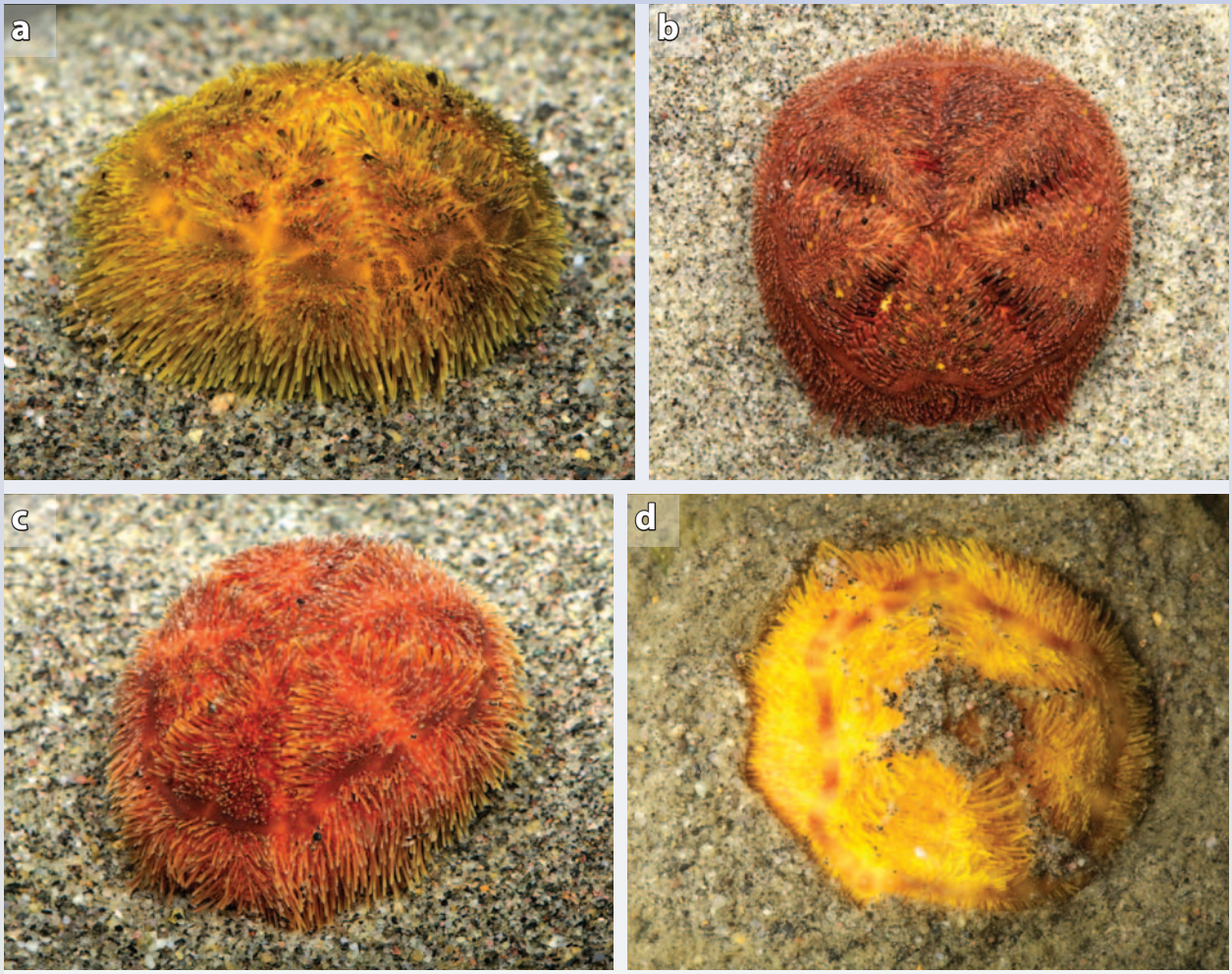
Although species of *Abatus* have a similar appearance, it is possible to determine specific identification of live urchins based on colour. However, a sufficient quantity of live specimens (of each species) is necessary for reliable identification. Urchins of different sizes also need to be examined as some *Abatus* show a higher degree of colour variation across the different growth stages than others; for example, *A. ingens* varies in colour from juvenile to adult, as opposed to *A. cavernosus* which is only ever bright yellow. Taxonomically, species are distinguished by the characteristics of the bare test.

Abatus nimrodi **(Fig. a)**. The test is elongate-oval, and an anterior notch is absent. The apical system is slightly anterior. In males petals are not deeply sunken, although some males do show a slight depression of petals which is first noticeable in specimens of 25 mm length. The petals become depressed at a distance from the ocular plates; a gap of at least six ambulacral plates is present between the apical system and petals. Large adult males of 35 mm with this feature are not to be confused with females as the size of the gonopores for these individuals is consistent with the gonopore size of specimens that do not have recessed ambulacra. They grow to a length of about 45 mm. Live colour: juveniles are pale greenish-olive, becoming darker olive at later stages of growth, finally becoming a very dark black-olive. Pedicellariae are characteristically black.

Abatus shackletoni **(Fig. b)**. The test is round, approximately as long as it is wide, and an anterior notch is absent. The apical system is slightly anterior. In males the petals are not deeply sunken. Females have four equal deeply sunken petals or marsupiae. The fasciole is generally round in outline, but it dips upwards above the periproct. The periproct is round and can be seen if viewed aborally. Occasionally, the test may be vaulted, but this is rare. The peristome is slightly depressed, the labrum is short, and the peristome is small in comparison to the other four species found at Davis Station. They grow to a maximum length of 25 mm; it is the smallest species of *Abatus* found at Davis Station. Live colour: generally dark brown, but young heart urchins are a lighter brown in colour. Pedicellariae are bright yellow.

Abatus ingens **(Fig. c)**. The test is rounded anteriorly, but tapers posteriorly. A small percentage of specimens are more or less rounded, but these

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Figures a–e The five species of ***Abatus*** found at Davis Station, Australian Antarctic Territory. The water temperature was –1.75°C at the time these animals were photographed.

a, ***Abatus nimrodi***, the largest of the ***Abatus*** species at Davis Station, has a distinctive olive colouring with black pedicellariae. The olive colour becomes darker as it grows.

b, ***Abatus shackletoni*** is brown in colour throughout its life. It has a characteristically narrow marginal fasciole just above the ambitus and is rounded in shape.

c, the colouring of ***Abatus ingens*** changes from light orange in juveniles to orange/red and red/brown in large adults.

d, ***Abatus cavernosus*** burrowing in the fine Antarctic sediment. This species is distinctly yellow at all stages of growth.

e, ***Abatus philippii*** is of similar appearance to ***A. cavernosus***, except it has flesh-pink colouring.

[A.D.Miskelly]

are an exception. The apical system is slightly anterior. In males the petals are noticeably sunken, females have deeply sunken marsupiae. Even the anterior ambulacrum is quite sunken in females, but is non-brooding. The fasciole is round and does not dip in towards the petals. The periproct is slightly oval to round, and in most cases is not able to be seen if viewed aborally. Tests that are flatter do occur, though they are rare. Taller test forms appear to be unknown. The peristome is small, especially in comparison to *A. nimrodi*. They grow to a maximum length of 40 mm. Live colour: younger specimens are yellow, progressing to orange as they grow, then orange/brown in large adults. Live urchins show some degree of plate detail.

Abatus cavernosus **(Fig. d)**. The test is rounded anteriorly, but tapers posteriorly. A slight anterior notch is present. A small percentage of specimens are more or less rounded, but these are an exception. The apical system is slightly anterior. In males the petals are noticeably sunken, females have deeply sunken marsupiae. Even the anterior ambulacrum is quite sunken in females, but is non-brooding. The fasciole is indented slightly between the anterior and posterior petals. The periproct is oval and in most cases is not able to be seen if viewed aborally. Flatter tests do occur, though they are rare. Taller test forms appear to be unknown. The peristome is fairly small. They grow to a maximum length of 35 mm. Live colour: bright yellow at all of growth stages.

Abatus philippii **(Fig. e)**. This species is morphologically similar to *A. cavernosus*. The test is rounded anteriorly and tapers posteriorly. A slight anterior notch is present. The posterior petals are shorter than those of *A. cavernosus*, being approximately half the length of the anterior petals. In females the petals are very deeply sunken; usually juveniles can be found in all four petals. The fasciole is indented slightly between the anterior and posterior petals; it is very similar to *A. cavernosus*. The periproct is oval and in most cases is not able to be seen if viewed aborally. The test is mildly inflated, certainly more so than in *A. cavernosus*. They grow to a length of 35 mm. Live colour: flesh-pink at all growth stages.

Order Spatangoida
Family Schizasteridae
Species *Abatus nimrodi* (Koehler, 1911)
Abatus shackletoni Koehler, 1911
Abatus ingens Koehler, 1926
Abatus cavernosus (Philippi, 1845)
Abatus philippii Lovén, 1871

Further reading Pearse & McClintock 1990; Lockhart *et al*. 1994; David *et al*. 2005b

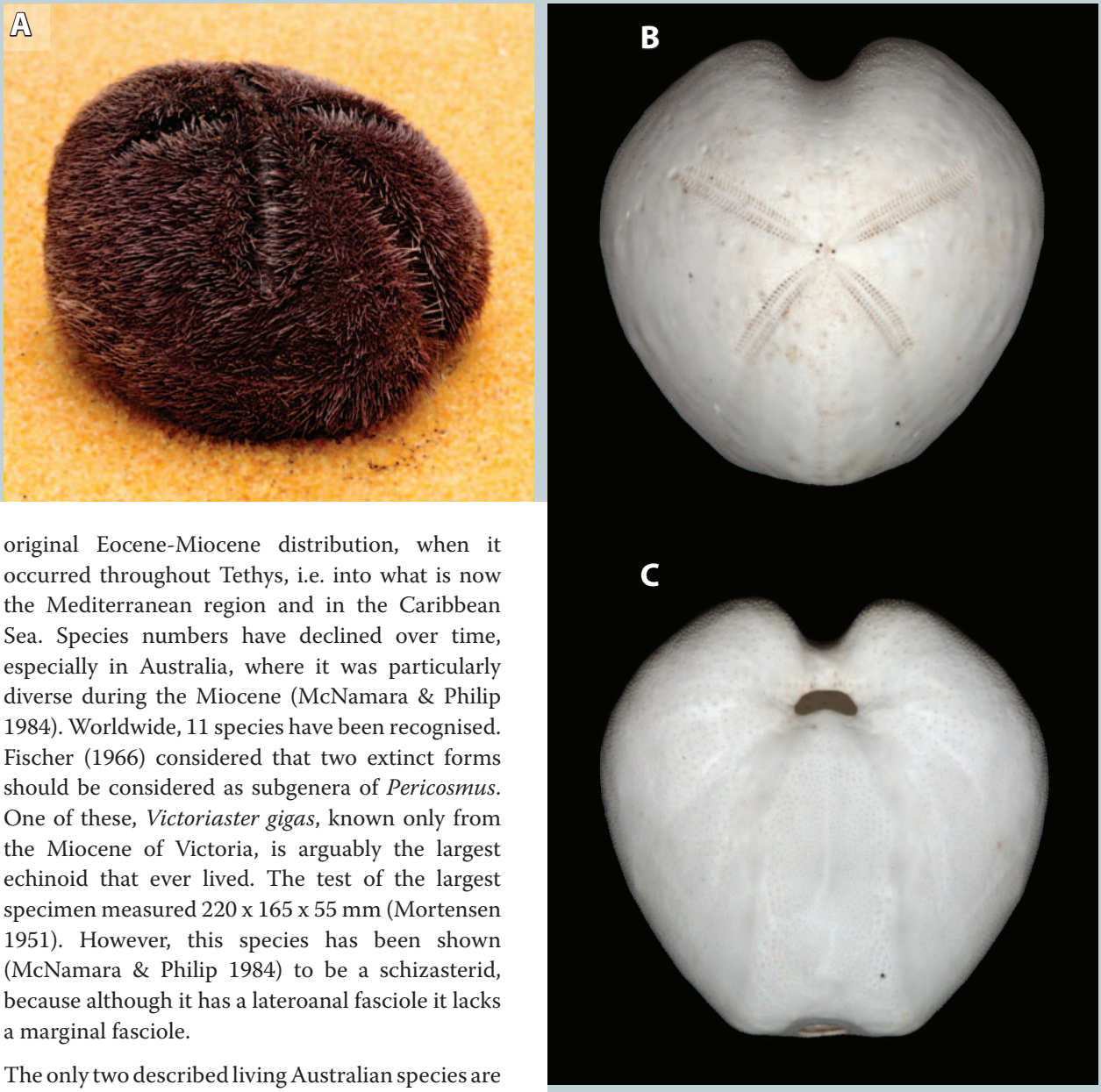
Family Pericosmidae

Figure 10.40

The Pericosmidae (**Fig. 10.40**) was established for the genus *Pericosmus*, which differs from all other spatangoids in having a marginal fasciole as well as a quite separate peripetalous fasciole (Lambert 1905); either one can degenerate anteriorly. The marginal fasciole runs around the ambitus and below the periproct. Members of this family have a distinctly heart-shaped test with three gonopores, and the petals are more or less uniformly elongate and slightly sunken.

Today, *Pericosmus* occurs in the south Pacific Ocean and in the western and eastern Indian Ocean (Ghiold 1989). This represents a contraction in its

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original Eocene-Miocene distribution, when it occurred throughout Tethys, i.e. into what is now the Mediterranean region and in the Caribbean Sea. Species numbers have declined over time, especially in Australia, where it was particularly diverse during the Miocene (McNamara & Philip 1984). Worldwide, 11 species have been recognised. Fischer (1966) considered that two extinct forms should be considered as subgenera of *Pericosmus*. One of these, *Victoriaster gigas*, known only from the Miocene of Victoria, is arguably the largest echinoid that ever lived. The test of the largest specimen measured 220 x 165 x 55 mm (Mortensen 1951). However, this species has been shown (McNamara & Philip 1984) to be a schizasterid, because although it has a lateroanal fasciole it lacks a marginal fasciole.

The only two described living Australian species are *Pericosmus porphyrocardius* (McNamara 1984a) and *Faorina chinensis*. *Pericosmus porphyrocardius* occurs in Australian waters only north of about 18°S on the western coast, and north of 26°S on the eastern coast (McNamara 1984a), extending along the North West Shelf, off Western Australia, and also off the Queensland coast at Raine Island (O'Hara 2012). It is comparatively large, the test up to 106 mm in length, and has a relatively low, broad test. Live specimens are purple in colour. Other

Figure 10.40 Family Pericosmidae.

A, ***Pericosmus macronesius*** from the Philippines. It is found in deep water between 150 and 200 m.

B, **C**, test of ***Pericosmus*** sp. collected from the Philippines at a depth of approximately 200 m. Test length 78 mm.
B, aboral view of the strongly cordiform (heart shaped) test.
C, oral view.

[A.D.Miskelly]

species are usually about half this size. Australian Miocene species were much larger, some up to 140 mm long (McNamara & Philip 1984). Undescribed species of *Pericosmus* have been found near Lizard Island and further south at 26°S, the most southerly record for the family. These forms are smaller than *P. porphyrocardius*, having a more globose test with the anterior notch less well defined. The bathymetric range of *Pericosmus* off Australia is 300–420 m, where water temperatures are 9–10°C.

Faorina chinensis, a predominantly Indo-Pacific species, occurs in northern Australian.

In attempting to interpret the palaeoecology of the Late Miocene Rutledge Marl echinoids, McNamara (1991) suggested that *Pericosmus* is a very shallow burrower. Although mucus-secreting tube feet in ambulacrum III are not extensively developed, the presence of a deep anterior notch in some species suggests limited burrowing capabilities in the fine, foraminiferan-rich mud they inhabit. The present-day tropical distribution of *Pericosmus* on the outer shelf is in contrast to the Oligocene–Miocene when it inhabited shallow water in the recently formed Southern Ocean, and in the Indian Ocean in what is now Cape Range, Western Australia (McNamara & Philip 1984). However, its presence in deeper water Rutledge Marl deposits in Victoria indicates that it had a wide bathymetric range by the Late Miocene.

Nothing is known of the behaviour, reproduction and ecology of the Pericosmidae. *Pericosmus porphyrocardius* has a patchy distribution, although the large numbers of this species trawled off the North West Shelf in 1982 (McNamara 1984a) indicate that it can be locally common.

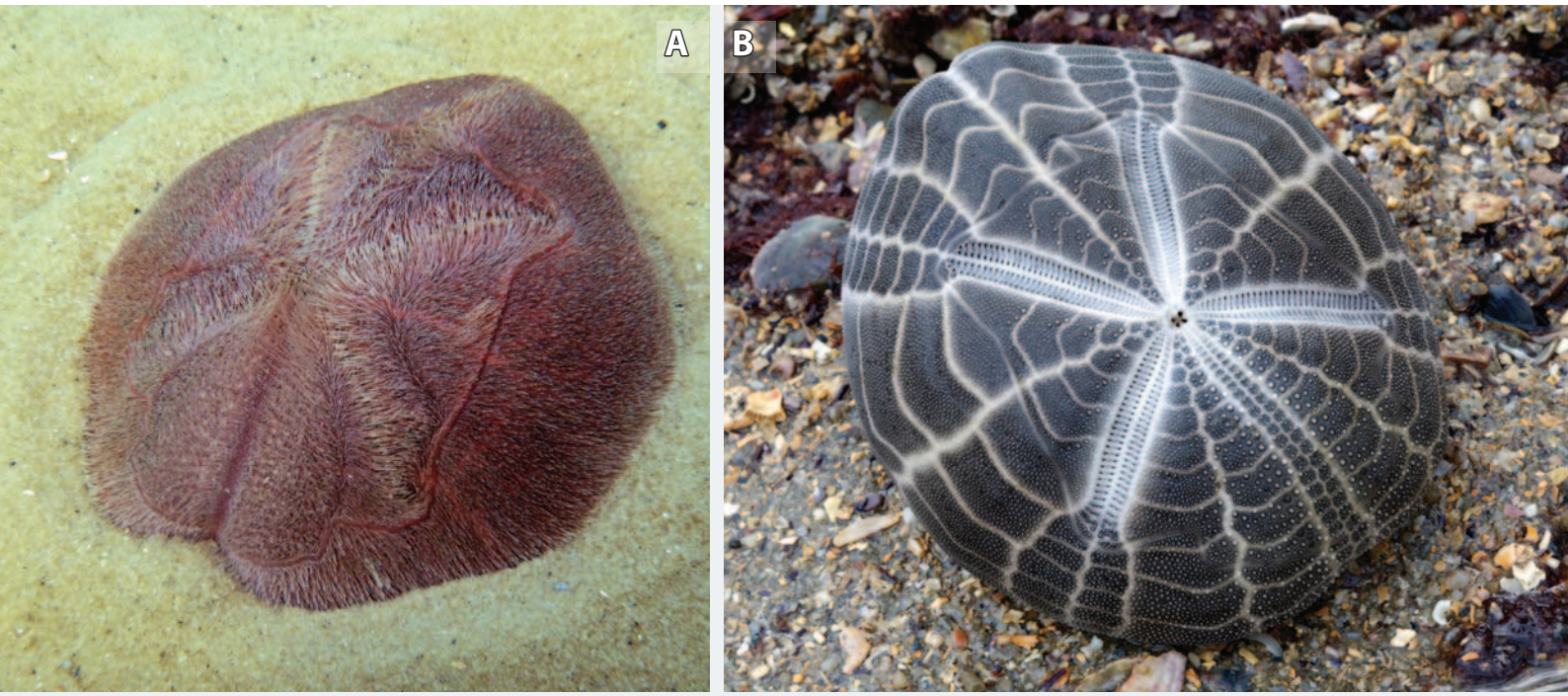


Figure 10.41 Family Brissidae.

A, ***Metalia angustus***, a large, abundant species that occurs in Sydney Harbour, New South Wales. It grows to a length of 160 mm.

B, test of ***Metalia spatagus*** found on the seafloor in Sydney Harbour, New South Wales; the highly defined plate boundaries are evident. Test length 100 mm.

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Family Brissidae

Figure 10.41

The Brissidae (**Fig. 10.41**) was established by Gray (1855), and today comprises 13 genera and 69 species (Baker & Rowe 1990; Ghiold 1989; McNamara & Henderson 1984). Interestingly, 11 of the 13 brissid genera are still living today. Four of these evolved in the Eocene, the remainder in the Miocene.

Brissids are morphologically diverse, and are characterised by having both a peripetalous and a subanal fasciole. In some genera, anal branches can also be present. It is likely that the Brissidae evolved from a micrasterid ancestor during the Late Cretaceous by the acquisition of a peripetalous fasciole. Subsequently, during the Palaeogene, genera such as *Taimanawa* evolved primary tubercles in some dorsal interambulacra, supporting large, defensive spines. Another evolutionary trend was the change from an ethmophract to an ethmolytic apical system. Petals in some genera are sunken, and some have an anterior notch. Like the Schizasteridae, gonopore number varies from two to four, and this number can also vary even within the same species.

A deep anterior notch is present in *Taimanawa* and some species of *Metalia*, whereas a shallow notch occurs in *Brissopsis*. In *Anametalia*, *Brissus* and *Rhynobrissus* an anterior notch is absent. In genera without a notch the anterior petals are transverse, or nearly so, whereas in those genera with an anterior notch the anterior petals are moderately divergent.

Brissids are relatively diverse in Australian waters, with six genera and 18 species: *Anametalia* (2 species), *Brissopsis* (2), *Brissus* (2), *Metalia* (6; **Fig. 10.41**), *Rhynobrissus* (4) and *Taimanawa* (2) (O'Hara 2012; A.D.Miskelly, personal data). Apart from *Brissus*, Australian genera tend to have either a northern or southern distribution. In general, the northern species are more widespread and abundant. The bathymetric range of the family in Australian waters is from the intertidal (*Metalia* species) to at least 1,000 m for *Brissopsis* (O'Hara 2012). The remainder are shallow-water, inner-shelf inhabitants at depths of less than 100 m, apart from *Taimanawa* which is known only from the outer shelf between 260 and 431 m (McNamara & Henderson 1984). *Brissus agassizii* occurs in tropical and temperate waters along the entire east coast of Australia, across Victoria and South Australia, to northern Western Australia.

Anametalia, *Brissopsis*, *Metalia*, *Rhynobrissus* and *Taimanawa* are tropical and subtropical, being known from North West Cape (22°S) on the west coast, across northern Australia and down the east coast to Port Jackson, New South Wales (32°S). Interestingly, *Brissus*, which has a circum-Australian distribution, has a similar distribution at the species level; *B. latecarinatus* has the same northern distribution, and *B. agassizii* is primarily a southern species. Among extant brissid genera, *Brissus* is recorded from the fossil record in Early Miocene strata of South Australia; *Brissopsis* from Early Oligocene to Middle Miocene strata in Western Australia and South Australia; and *Meoma* in the Early Oligocene of South Australia (McNamara *et al.* 1986).

Some Australian brissids are very large, *Taimanawa* reaching a test length of 150 mm (McNamara & Henderson 1984) and one species of *Metalia* 140 mm (Baker & Rowe 1990). Other brissids are much smaller. Of the nine Australian genera, one (*Taimanawa*) carries primary tubercles within the peripetalous fasciole which are densely packed and large (McNamara & Henderson 1984). Primary tuberculation in this genus typifies the situation found in many tuberculate brissids, that is tubercles are confined to only four of the eight interambulacral columns within the peripetalous fasciole, namely interambulacra 1a, 2a, 3b and 4b. Moreover, these tuberculate regions are usually set in obliquely depressed embayments.

Brissopsis burrows in very fine-grained sediments and plays a major ecological role in maintaining diversity of benthic biota (Widdicombe & Austen 1998; Widdicombe *et al.* 2000). Based on laboratory observations it takes 18 minutes to burrow completely (Chesher 1968). The deepest burrowers had their apex 28 mm from the surface of the mud. While buried, individuals moved at about 20 mm per hour, whereas on the surface they moved at 150 mm per hour. As for fine-grain inhabiting schizasterids, burrow communication with the surface is by means of a mucus-lined tunnel, constructed and maintained by anterior ambulacrum tube feet that terminate in mucus-secreting pencillate

discs. Thus, the tunnel is mainly used for ventilation of the respiratory surfaces. Posteriorly, two drainage tubes are constructed by subanal tube feet.

In contrast to its smaller size in tropical latitudes, *Brissus agassizii* grows very large in the temperate waters around Sydney, reaching a test length of 160 mm.

Most brissids live in burrows in coarse sands. The most detailed analysis of feeding and burrowing behaviour of such brissids is of *Meoma* (Chesher 1970), a genus that is not present in Australian waters. These echinoids surface shortly after sunset, perhaps in response to nocturnal reductions in oxygen levels in the sediment (Chesher 1970). The burrowing behaviour of *Metalia spatagus* from Scott Reef off Western Australia is one of a few records of behaviour for brissids inhabiting coarse sediments (L.M.Marsh & C.Bryce, personal communication). This brissid was found to have burrowed to a depth of about 100 mm below the sediment surface, similar to *Meoma* (Chesher 1970). The sediment was lime sand, with particles ranging in diameter from 0.25 to 2 mm, but mostly between 0.5 and 1 mm. Gut contents of *Metalia*, unlike those of *Brissopsis*, indicated a preference for detritus, and they contained a greater proportion of larger grains in the 1 to 2 mm size range. Many of the grains in this size range were foraminiferan shells, suggesting that these make up a substantial proportion of the diet. There is no indication of selective feeding in *Meoma* (Chesher 1970).

Examination of the stomach contents of large specimens of *Brissus agassizii* from Port Jackson, New South Wales, indicates that the species is not a selective feeder (A.D.Miskelly, unpublished data). The stomach contents consisted mainly of coarse shellgrit that was similar in consistency and content to the surrounding substrate, indicating that this species is a non-selective detritus feeder. Feeding tube feet that surround the peristome are pushed into the mud, the tube feet are then inserted into the buccal cavity and the detritus is loaded into the muscular oesophagus.

The biology of Australian Brissidae is poorly understood. The group includes species with small eggs and feeding larvae (for example *Brissopsis lyrifera*) and species with large eggs and non-feeding larvae (for example *Brisaster latifrons*) (Ferrand *et al*. 1988; Hart 1996).

Family Asterostomatidae

Figure 10.42

The Asterostomatidae was established for spatangoids characterised by the loss of petaloid structure; the frequent loss of pores in the anterior ambulacrum; the almost complete loss of fascioles (although some have peripetalous fascioles early in ontogeny, vestiges of subanal fascioles are retained by others and a few have a marginal fasciole); and, in some, the redevelopment of a superficial radial symmetry. The phyllodes and the labrum are well developed.

Although some authors considered them to be a primitive group (Mortensen 1951), it is more likely that their loss of structures is a secondary, paedomorphic effect that relates to their deep-water habitats (Fischer 1966). There is evidence (see below) that they have reversed the trends seen in many spatangoid echinoids, and 'returned' to a life on the sediment surface. It is possible that the Asterostomatidae is a polyphyletic assemblage of hemiasterids, brissids, spatangids and loveniids responding to selection for their characteristic mode of life (Fischer 1966), as suggested by molecular analyses (Stockley *et al*. 2005).

The family is usually thought to contain 15 genera (Ghiold 1989), seven of which are monotypic. The most speciose genera are *Argopatagus* (4 species), *Platybrissus* (4), *Linopneustes* (6) and *Heterobrissus* (5). Three asterostomatid genera have been recorded from Australian waters, *Heterobrissus*, *Linopneustes* and *Plesiozonus* (Baker & Rowe 1990). *Heterobrissus* (**Fig. 10.42A**) is distinguished by its lack of fascioles, and the occurrence of deep phyllodes, four gonopores and large primary tubercles and spines. *Linopneustes* (**Fig. 10.42B**) can be much larger, up to 170 mm in length, and it differs from *Heterobrissus* in having an anterior groove in the test, less prominent primary spines and, in juveniles, a marginal and subanal fasciole, the former usually retained by adults. Like *Linopneustes*, *Plesiozonus* has a marginal fasciole, but it passes beneath the periproct, not above as in *Linopneustes*. *Plesiozonus* is further characterised by the presence of only three gonopores.

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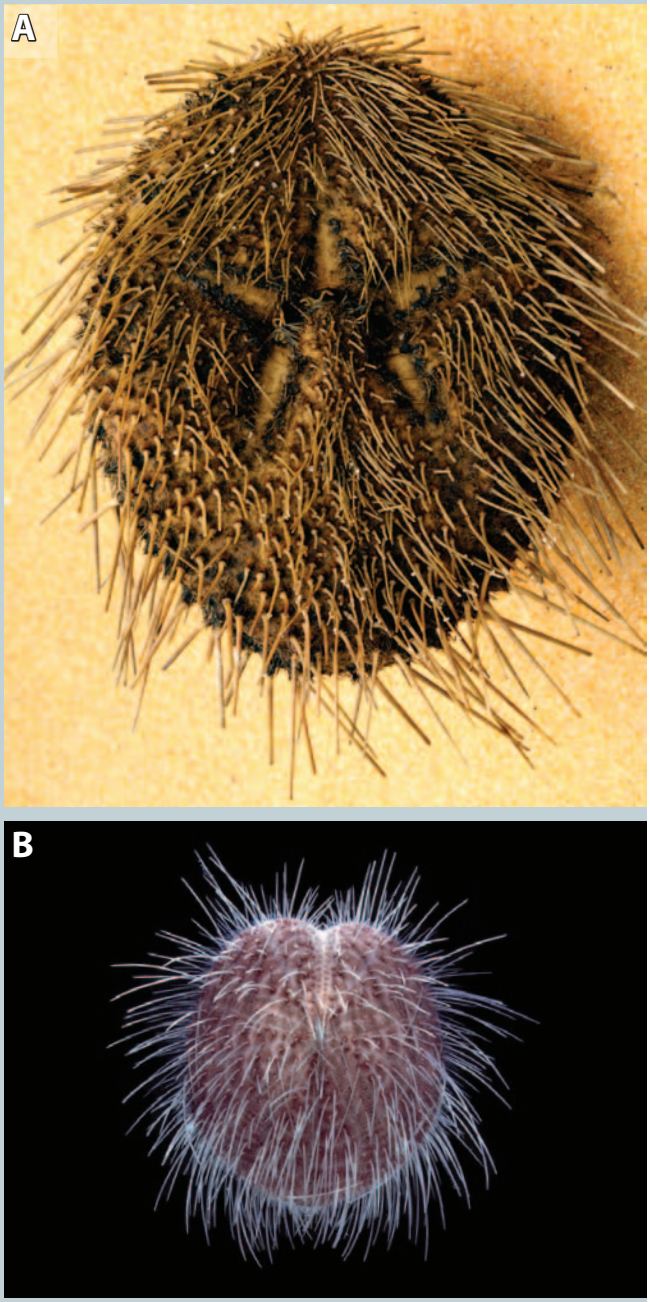


Figure 10.42 Family Asterostomatidae.

A, oral surface of ***Heterobrissus niasicus*** showing the star-shaped phyllodes; it is a widespread Indo-Pacific species, found exclusively in deep water.

B, ***Linopneustes longispinus***, from the Bahamas, lives on the surface of sandy substrates between 600 and 700 m.

[A, A.D.Miskelly; B, D.L.Pawson]

Linopneustes and *Plesiozonus* are each represented in Australian waters by single species. Two endemic species of *Heterobrissus* are known (Baker & Rowe 1990): *H. erinaceus* which has a dense concentration of short primary spines, and *H. gigas* which has fewer, longer spines, and a labrum that is broader than long. A third species, *H. niasicus*, is known from off the north-western coast of Australia. This species was previously known only from off the Andaman Islands in the Indian Ocean and between Norfolk Island and New Caledonia in the south-western Pacific.

Asterostomatids have only been recorded in the literature from south-eastern Australian waters, where *Heterobrissus erinaceus* occurs between about 130 and 500 m, *Linopneustes* between 270 and 640 m, and *Plesiozonus* between 360 and 520 m. Elsewhere, *Linopneustes brachypetalus* is found at depths below 1,600 m (Mortensen 1950) ranging as far north as New Caledonia (Agassiz 1872), whereas *P. hirsutus* extends north to Indonesia. Collections in the Western Australian Museum indicate a similar asterostomatid fauna occurs on the North West Shelf (K.J.McNamara, unpublished data), where *L. brachypetalus* occurs at depths of 450–560 m and *Heterobrissus erinaceus* at 220 m.

Because Australian asterostomatids live in comparatively deep waters on the middle to outer continental shelf, very little is known of their feeding and reproductive behaviour or habitats. Sediments collected with *Linopneustes* and *Heterobrissus* species from the North West Shelf indicate that they inhabit muddy bottoms. A photographic census of large benthic organisms carried out in Suruga Bay, Japan, by Ohta (1983) provides some insight into some of the habits of one of these deep-water echinoids. Ohta recorded *Linopneustes fragilis* moving over the sediment and leaving a distinct, three-lobed trail. The absence of fascioles, or their weak development, is probably an indicator of absence of burrowing behaviour.

Family Spatangidae

Figure 10.43

The Spatangidae (**Fig. 10.43**) was established for echinoids with a subanal fasciole, but which lack peripetalous, lateroanal, internal or marginal fascioles (Gray 1825). This diagnosis has been generally accepted (Mortensen 1950; Fischer 1966), but other workers have suggested that some forms with peripetalous fascioles, in particular *Plethotaenia*, should also be included (Chesher 1968). However, due to the presence of characters such as a very deep anterior notch and multiple peripetalous fascioles, features not generally characteristic of spatangids, this course is not followed here.

Spatangids first appeared in the Eocene, and they could have evolved from the brissids by loss of the peripetalous fasciole. The most common living genus, *Spatangus*, has existed since the Eocene.

In addition to the nature of the fascioles, spatangids have four gonopores in an ethmolytic apical system, very small pores arranged in single lines in the anterior ambulacrum, and paired petals flush with the adjacent interambulacra. Primary spines may be present in some genera.

Spatangids are represented in Australian waters by two genera, *Spatangus and Granopatagus*, and two species: *Spatangus luetkeni* and *Granopatagus paucituberculatus*. The genera *Maretia*, *Nacospatangus* and *Paramaretia* are now classifed in the family Maretiidae because of their long wedge-shaped labral plate and short triangular sternum (Kroh & Smith 2010; Smith & Kroh 2011; Kroh & Mooi 2014).

Spatangus luetkeni (**Fig. 10.43**) inhabits waters from Sydney, New South Wales, to Bruny Island, Tasmania (O'Hara 2012). Its distribution is discontinuous; it also occurs in Japan and New Zealand (Rowe & Gates 1995). Observations of a stable population of *Spatangus luetkeni* from Botany Bay, New South Wales, indicate that this species prefers depths of at least 16 m where the water is calm (A.D.Miskelly, unpublished data).

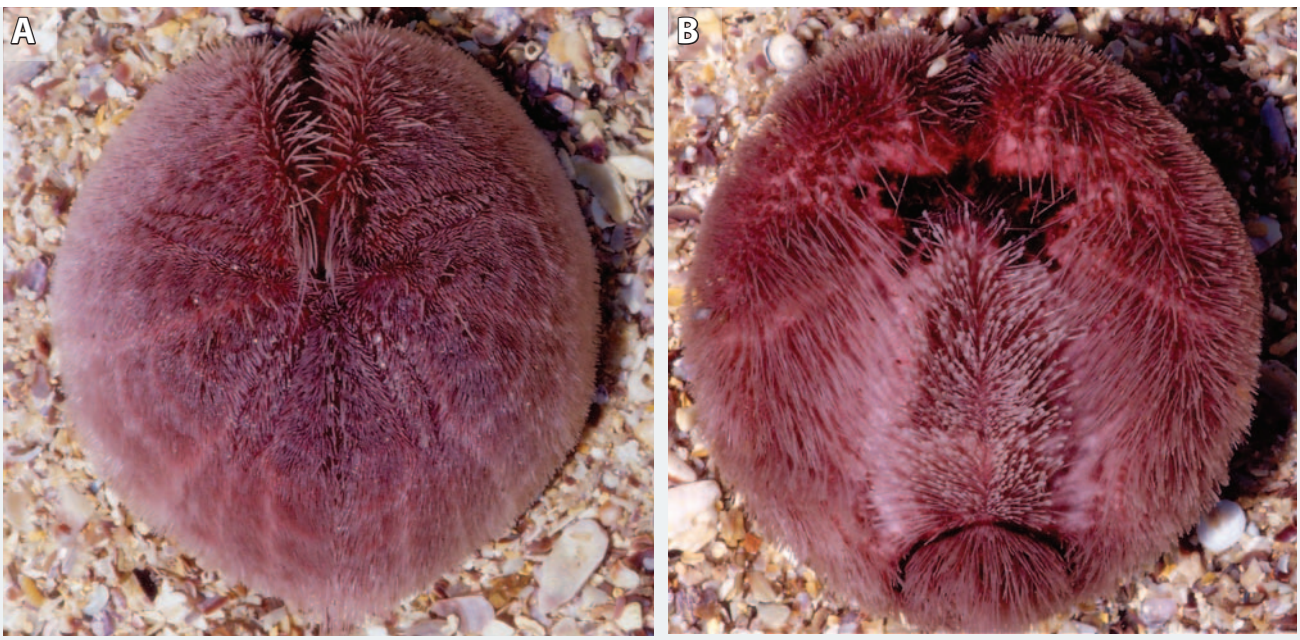


Figure 10.43 Family Spatangidae.

Spatangus luetkeni on coarse sand at Frenchmans Bay, La Perouse, New South Wales, at a depth of 16.5 m. Test length 90 mm.
A, aboral view.
B, oral view.

[A.D.Miskelly]

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It can be found in patches of sand and shellgrit, often adjacent to areas of algae. It does not burrow deeply, and generally leaves no trace of its presence, although a few defensive spines can be just visible through the substrate. The fresh dead test of *S. luetkeni* is purplish in colour, and in Botany Bay it occurs with species of *Echinocardium*, *Lovenia*, *Brissus* and *Metalia*.

Spatangids are usually quite large compared with related families, and in the case of *G. paucituberculatus*, a predominantly south-eastern species, it may grow up to 120 mm in test length. The overall similarity of the Spatangidae to the Brissidae is supported by the same size variation in the latter, as well as the presence or absence of an anterior notch and primary spines.

Almost all information on the behaviour of spatangids comes from studies of *Spatangus* by Nichols (1959a), who demonstrated that some species are shallow burrowers in coarse sediments. They burrow such that the dorsal surface of the test lies just beneath the sediment/water interface, larger apical spines and a single exhalant funnel maintaining an opening to the surface. In other spatangids the absence of funnel-building tube feet in the anterior ambulacrum and the lack of a peripetalous fasciole suggest that they are also shallow burrowers. However, some deeper water *Spatangus* species inhabit much finer sediments.

Family Eupatagidae

Figure 10.44

The family Eupatagidae is represented in Australia by a single genus, *Eupatagus,* and three species, two of which are endemic: *E. valenciennesii* (**Fig. 10.44**) and *E. flindersi*. *Eupatagus* is characterised by an oval test without an anterior notch, an ethmolytic apical disc, four gonopores and the madreporic plate projecting well posterior to the other plates of the apical disc. The anterior ambulacrum is narrow and flush. The remaining four ambulacra are petaloid and not sunken. The petals are distinctly bowed and tapered adapically. The periproct is comparatively large, and the peristome is kidney-shaped. The labral plate is elongate and wedge-shaped; almost as long as the following sternal plates. The plastron is short and triangular. The subanal fasciole is well developed and bilobed. The larger aboral tubercles bearing defensive spines are proportionately higher in *E. valenciennesii* than either *E. flindersi* or *E. rubellus*.

There are many fossil *Eupatagus* species worldwide. The type species is the extant *E. valenciennesii*. It typically occurs from off the coast of New South Wales from Port Stephens to Tasmania. However, a small denuded test found on One Tree Island, Queensland, is highly likely to be this species despite the unusual tropical locality (A.D.Miskelly, unpublished data). In New South Wales *E. valenciennesii* lives subtidally on sand, but in Victoria and Tasmania it is intertidal and species can be found easily at low tide on sandy areas. It is particularly common on Flinders Island where it feeds in coarse sand. Live individuals occur in sand burrows directly underneath small agglomerations of mollusc shells in depths of around 1–3 m, buried approximately 100 mm deep in the coarse sediment. The unspecialised morphology, petals not sunken and no anterior notch, dictates its preference for coarse sediment. Commensal bivalves have been observed attached to the long spines of the oral region around the phyllodes.

Eupatagus rubellus, an Indo-Pacific species, has recently been discovered in Australia. Schultz (2005) records it from Shark Bay, Western Australia, and a single live specimen has been found on Hicks Reef, Lizard Island, Queensland, buried in coralline sand at a depth of 12 m. *Eupatagus rubellus* is distinctly different from the other two species, *E. flindersi* and *E. valenciennesii*, in its reddish pigmentation of the plates when live, and its vaulted profile (A.D.Miskelly, unpublished data). The peripetalous fasciole is rudimentary. *Eupatagus rubellus* is the smallest of the species of *Eupatagus*, growing to a length of 48 mm.

The third species, *E. flindersi* appears to be the rarest and it has the smallest biogeographical distribution. It is known only from Goat Island, Victoria, and north-east Tasmania from Ringarooma Bay to Eddystone Point (O'Hara 2012). Few specimens are known and it differs from *E. valenciennesii* in having primary tubercles confined to the area between the anterior petals and the anterior margin of the test. *Eupatagus valenciennesii* has primary tubercles occurring between the anterior and posterior petals. It is known from a depth of 25 m.



Figure 10.44 Family Eupatagidae.
Eupatagus valenciennesii is an Australian endemic heart urchin found in the shallow waters of south-eastern Australia.
A, animal burying itself in coarse sediment. The spines on the oral surface are used to excavate the sediment outwards. This animal was found at Killiecrankie Beach, Flinders Island, Tasmania, at a depth of 3 m.
B, test found at Sawyers Bay, Flinders Island.
Test length 52 mm.
C, commensal galeommatoid bivalves adhere to the oral spines of living heart urchins.
[A.D.Miskelly]

Eupatagus valenciennesii broods its young. The juveniles are protected by dense spinecover in the region between the apical system and the posterior petals. It is not known how long the juveniles remain in position, as not all female specimens appear to have young on the aboral surface at any given time. The morphology of the test of females is different to males in that the test profile dips from the apical region to the posterior region, in between being quite flat. Males are more domed, and there is no difference in petal morphology between males and females. The juveniles are small, round and orange in colour, appearing quite inconspicuously under the protective spine canopy. Brooding occurs in summer (A.D.Miskelly, unpublished data). Some females examined in late February to early March were not brooding.

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Family Maretiidae

Figure 10.45

The Maretiidae are distributed around the entire Australian coastline from intertidal sand flats to the deep sea, where they are represented by five genera, *Maretia*, *Granobrissoides*, *Spatagobrissus*, *Paramaretia* and *Nacospatangus*, and eight species (O'Hara 2012; **Figs 10.2, 10.45**). *Granobrissoides* is endemic to Australia, as is the single species of *Spatagobrissus*, *S. incus*. *Paramaretia* is represented in Australia by *P. peloria* and *P. multituberculata*.

The Maretiidae have a fossil record from the Eocene to the Recent. They are distinguished from the Spatangidae by their long, wedge-shaped labral plate and short triangular sternum. They are further distinguished from the similar *Eupatagus* on the basis of development of fascioles. *Maretia* have only a subanal fasciole, while *Eupatagus* has in addition a peripetalous fasciole. The extinct *Spatagobrissus laubei* is known from the Middle Miocene Port Campbell Limestone, Rutledge Marl Member (McNamara *et al.* 1986). A second fossil species, *S. dermodyorum* (Holmes *et al.* 2005), is also known from the Middle Miocene. It was recently transferred from the Brissidae and placed in the Maretiidae due to the longitudinally elongate labral plate extending to ambulacral plate 2.

Maretia planulata is a tropical species growing to a length of 70 mm; it is generally found in shallow water, often exposed. Most specimens show alternating dark and light coloured areas on the adapical surface, not limited to any particular region. *Maretia planulata* is known as far south as Port Jackson, New South Wales, but here it is strictly subtidal, occurring on coarse shellgrit substrates at around 9–11 m depth (O'Hara 2012). The adapical surface is well tuberculated and supports long defensive spines that become erect when it is threatened by predators. A second species, *M. cordata,* is known only from Scott Reef, Western Australia (A.D.Miskelly, unpublished data). It is smaller, broader, and the spines are longer, thinner and more hair-like.

There are two living species of *Granobrissoides*, *G. dyscritus* (**Fig. 10.45B**) and *G. hirsutus,* and three fossil species, *G. australiae*, *G. tuberculata* and *G. paucituberculata* that appeared in the late Oligocene

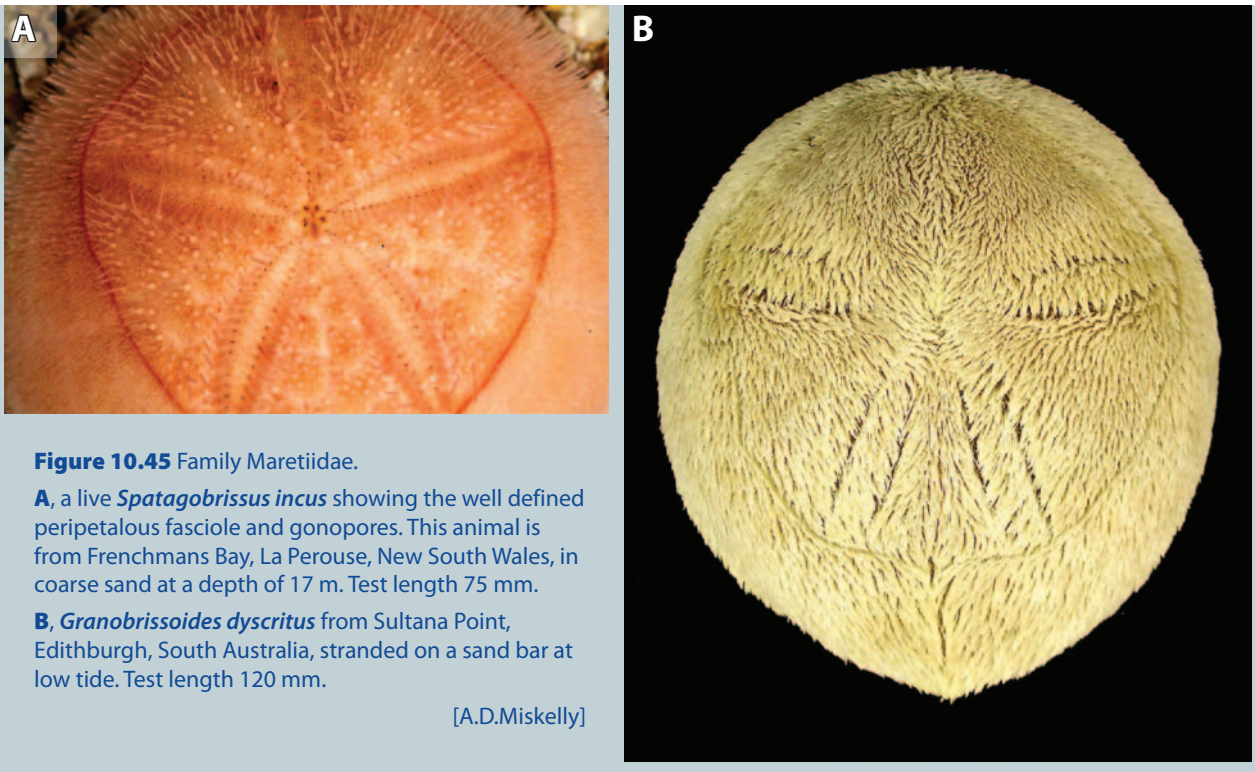


Figure 10.45 Family Maretiidae.

A, a live ***Spatagobrissus incus*** showing the well defined peripetalous fasciole and gonopores. This animal is from Frenchmans Bay, La Perouse, New South Wales, in coarse sand at a depth of 17 m. Test length 75 mm.

B, ***Granobrissoides dyscritus*** from Sultana Point, Edithburgh, South Australia, stranded on a sand bar at low tide. Test length 120 mm.

[A.D.Miskelly]

(McNamara & Ah Yee 1989). *Granobrissoides dyscritus* is an enigma. This large, conical species has been found live on only three occasions since it was first described from a single incomplete aboral fragment by Clark (1938). Three live specimens were discovered emerging from fine sand on the turn of the tide at Sultana Point, Edithburgh, South Australia (W.Rumball, personal communication). Despite its substantial size, growing to a length of approximately 120 mm, *G. dyscritus* is very finely tuberculate and denuded tests are quite shiny in appearance. The pore pairs of the petals diminish approximately one fifth of the distance away from the apical disc. The intertidal habitat for a heart urchin of this size is not known for any other species to occur in Australia. *Granobrissoides hirsutus* from southern Victoria and north-east Tasmania is poorly known (A.D.Miskelly, unpublished data).

Recent range extensions for *Spatagobrissus incus* (**Figs 10.2, 10.45A**) since its initial discovery in 1990 from the type locality east of Flinders Island, Tasmania, include west to Spencer Gulf, South Australia and north to Port Jackson, Sydney, New South Wales (A.D.Miskelly, unpublished data). *Spatagobrissus incus* is commonly found feeding in coarse shellgrit and rubble at depths of around 7.5 to 17 m. The live animal is flesh-pink, and has distinctly dark brown clavulae in the peripetalous fasciole, which is circular in outline. The subanal fasciole is similarly coloured, and anvil-shaped. There is a single pore pair on either side of the subanal fasciole (A.D.Miskelly, unpublished data).

Nacospatangus interruptus is known only on the west coast of Western Australia from the intertidal zone to 55 m (O'Hara 2012). The apical disc is ethmolytic, with three gonopores. The petals are not sunken and the aboral surface has no primary tubercles for defensive spines. The periproct is transversely elongate and markedly recessed. The colour of the living animal is dark purplish black.

Paramaretia is similar to *Nacospatangus*, except that there are four gonopores instead of three. It also grows much larger and there is an abundance of sunken primary tubercles on the adapical surface. Little is known of the biology of this genus, which occurs in deep water.

Family Loveniidae

Figure 10.46 & Box 10.6

The Loveniidae (**Fig. 10.46**) was erected to accommodate spatangoid genera with an internal fasciole (Lambert 1905), and while most also have a subanal fasciole, genera such as *Breynia* have an additional peripetalous fasciole. The apical system is ethmolytic, and the paired ambulacra are petaloid; the anterior row is short, runs transversely and terminates outside of the internal fasciole. Apart from *Echinocardium* (**Box 10.6**), the other members of the family are further distinguished by the presence of primary spines on the aboral surface. As with other spatangoid families in need of revision, the Loveniidae is probably a polyphyletic group. The earliest loveniid, a species of *Lovenia*, appeared in the Eocene.

The family includes five extant genera and 29 species (Kroh & Mooi 2014). *Lovenia* consists of 10 species, *Echinocardium* has 12, and they range from very widely distributed to more or less cosmopolitan. However the taxonomy of this genus is not settled, and cryptic species exist (Egea *et al*. 2016).

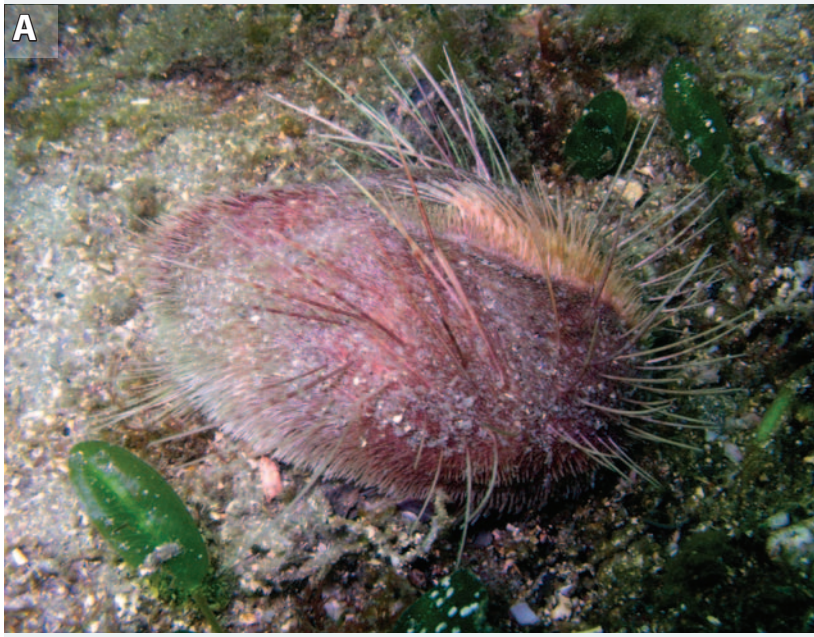
Four genera occur in Australian waters, *Breynia*, *Lovenia*, *Echinocardium* and *Pseudolovenia*. *Breynia* is represented by four species (McNamara 1982; A.D.Miskelly, unpublished data); *Lovenia* by four (McNamara & Henderson 1984; O'Hara 2012; A.D.Miskelly, unpublished data), *Echinocardium* by *E. cordatum*, which has a disjunct cosmopolitan distribution (David & Laurin 1996; Egea *et al*. 2016; **Box 10.6**); and *Pseudolovenia* by one species recently discovered off the Great Australian Bight. *Breynia* and *Lovenia* are clearly recognisable by the presence of large, primary spines on the aboral surfaces. The former has a diagnostic peripetalous fasciole, while this is lacking in *Lovenia*. Both have subanal as well as internal fascioles.

Echinocardium cordatum occurs in temperate waters, from off the southern Australian coast, and extends northward along the western and eastern coasts in sandy to muddy habitats (O'Hara 2012; Egea *et al*. 2016). This species has a nearly cosmopolitan, widespread disjunct, distribution; it also occurs in the western Pacific and North Atlantic oceans, southern Africa and the Gulf of

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California with a depth range from the intertidal to 250 m (Egea *et al*. 2016; **Box 10.6**). A recent study based on molecular analyses indicates that *E. cordatum* is a cryptic species complex with a mitochondrial clade distinct to Australia and New Zealand (Egea *et al*. 2016).

The four species of *Breynia* are distinguishable by the concentration of primary tubercles and spines on the aboral surface of the test. *Breynia australasiae* (**Fig. 10.46B**), a name formerly applied to all Australian members of the genus, has fewer primary tubercles and spines than the other common species, *B. desorii*. Furthermore, it has longer petals, a narrower peristome and a smaller periproct (McNamara 1982). These species are comparatively large, with test lengths up to about 120 mm. The third Australian species, *B. neanika*, is smaller and with fewer primary tubercles and spines, a flatter test and shorter petals, and a narrow, oval, subanal fasciole (McNamara 1982). A recent addition to the genus is *Breynia elegans*, a deepwater species that occurs north of Karratha, Western Australia. This species is flatter, very tuberculate and the test is thinner compared with *B. desorii* and *B. australasiae*. It grows to a test length of 120 mm.





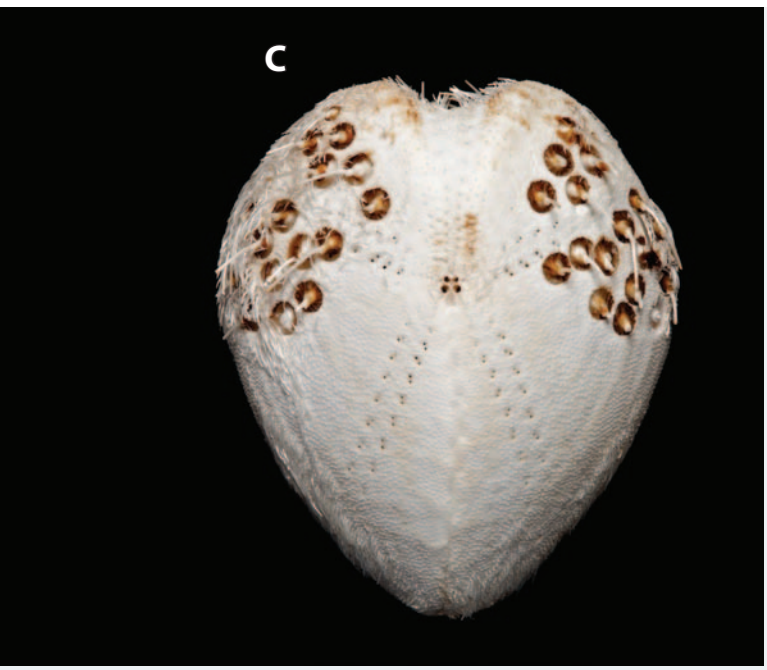


Figure 10.46 Family Loveniidae.

A, ***Lovenia elongata*** living among algae on fine silt at a depth of 7 m in Frenchmans Bay, La Perouse, New South Wales. The long barbed spines on the aboral surface stand erect when the animal is threatened. Test length 62 mm.

B, ***Breynia australasiae*** ploughing through carbonate sand at Swains Reef, Great Barrier Reef, Queensland, at 10 m. Test length 73 mm.

C, test of ***Pseudolovenia*** sp., aboral view, collected from the Great Australian Bight, between south of Nullarbor Station and Port Lincoln at approximately 1,000 m. This species has rudimentary pore pairs that constitute the petals. Test length 36 mm.

[A.D.Miskelly]

Box 10.6 The common heart urchin, *Echinocardium cordatum*



Figure a ***Echinocardium cordatum*** removed from its sandy burrow in a sheltered bay, Sydney, New South Wales. The spines form a dense coat; those on the upper surface, as seen here, are short and bristle-like.

[A.D.Miskelly]

Features The common heart urchin is actually heart-shaped (unlike many so-called 'heart urchins') with a prominent depression down the anterior side. It is covered in short sharp spines, these being elongate on the underside. It is generally a uniform light tan in colour, and it can grow to a length of 90 mm (**Fig. 2.36**).

Distribution This species is known from Exmouth in Western Australia south and eastwards around the southern Australian coast and up the east coast to southern Queensland at depths to 230 m. It also occurs in New Zealand, South Africa, Japan, California and Europe.

The widespread 'anti-tropical' distribution of this species is noteworthy, and several researchers have asked 'are these populations all the same species?' This could indicate that there is some continuing or relatively recent dispersal between populations, or that they have evolved into separate species, which implies a relict ancient distribution (see

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Chapter 5). Recent molecular investigations indicate that *Echinocardium cordatum* is a cryptic species complex with a mitochondrial clade distinct to Australia and New Zealand (Egea *et al*. 2016). This suggests that the species that occurs in Australia and New Zealand may be a different species, but determination of this awaits further research.

Fossils of *E. cordatum* have only been found from the Pliocene of Europe. *Echinocardium* was reported from Australia and New Zealand in the early to middle years of the nineteenth century. There is no reason to believe it was introduced into Australasia in the ballast water of ships. More research is clearly required.

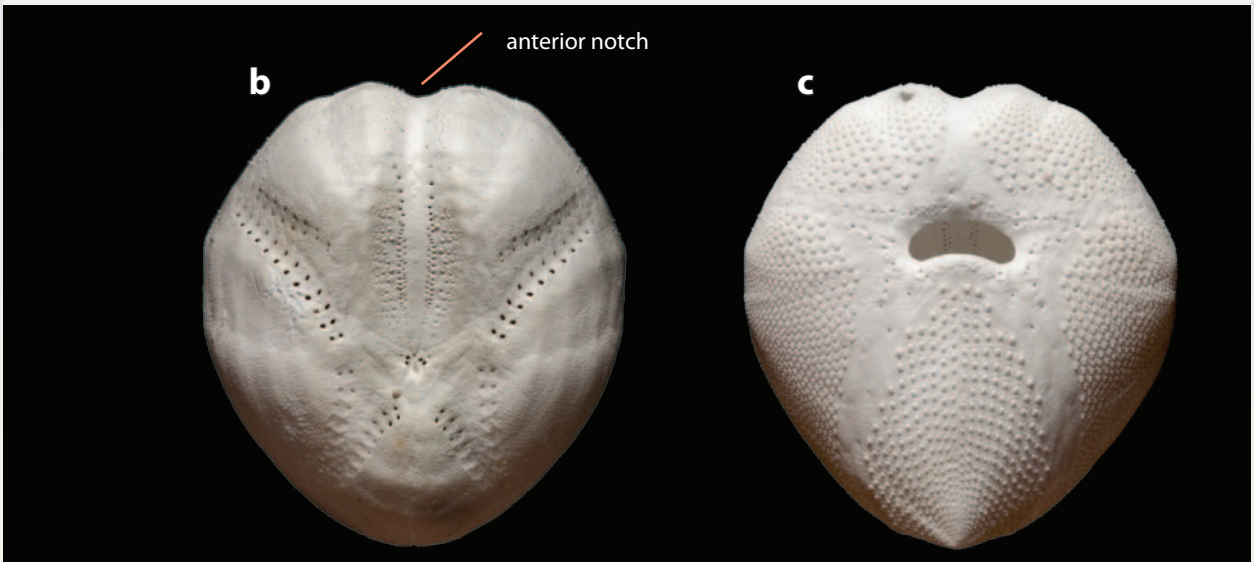
Way of life This species is common in bays and inlets where it plays an important role in bioturbating sediments. It is particularly common in Port Phillip and Western Port bays in Victoria, the D'Entrecasteaux Channel near Hobart, and in Sydney Harbour. It lives buried 80–150 mm underneath the seafloor. The only evidence of its presence is a shallow depression on the surface. Food collects in the depression and is transported down to the mouth by very long feeding tube feet. *Echinocardium* has a planktonic feeding larva.

Interaction with humans *Echinocardium* is vulnerable to dredging and is preyed upon by exotic pests such as the Northern Pacific seastar. Plankton researchers recently detected a marked increase in numbers of *Echinocardium* larvae in the European North Sea, suggesting that this species is benefiting from rising sea water temperatures.

Similar species In southern Australia, other heart urchins have a peripetalous fasciole, an obvious line of small spines and cilia that runs around the edges of the petals on the upper surface.

Order Spatangoida
Family Loveniidae
Species *Echinocardium cordatum* (Pennant, 1777)

Further reading David & Laurin 1996; Higgins 1974b, 1975; Kirby *et al*. 2007; Laurin *et al*. 1994; O'Hara 1999b; Egea *et al*. 2016



Figures b, c test of ***Echinocardium cordatum***.
b, aboral view.
c, oral view.

[A.D.Miskelly]

Lovenia elongata (**Fig. 10.46A**) differs from *L. gregalis* in having a broader test, a greater concentration of primary tubercles and spines, more arcuate petals, a larger peristome, and a deeply sunken periproct. *Lovenia triforis*, known from only one Australian specimen, has only three gonopores, and the anterior of *L. camarota* lacks a notch. The extant species of *Lovenia* are much larger than the fossil species, with test lengths up to 90 mm, more than twice the length of any extinct Australian species.

The single species of *Pseudolovenia* from the Great Australian Bight closely resembles *Pseudolovenia hirsuta*, a species found in Hawaii and Japan. Of the few Australian specimens known, the largest measures 36 mm in length, which, despite being an adult, is considerably smaller than the mature adult size of around 60 mm for *P. hirsuta*. Given the difference in size and the large biogeographical gap the recent Australian material of *Pseudolovenia* may be an undescribed species (A.D.Miskelly, personal observation). *Pseudolovenia* is an exclusively deep-water genus that differs from *Lovenia* in having sub-petaloid ambulacra in which the pore pairs are only rudimentary. The inner fasciole is present, yet not as pronounced as in *Lovenia*, and is concentrated close to the apical system. The large recessed tubercles which support long defensive spines are restricted to the anterior half of the test. Unlike *Lovenia* which has a deeply recessed periproct, *Pseudolovenia* has a periproct streamlined with the surrounding posterior area of the test. Examination of the stomach contents indicate that *Pseudolovenia* feeds on fine muddy sediment.

Lovenia first appeared in southern Australian waters in the Late Oligocene, where it also has a rich fossil record in Miocene sediments (Holmes 1993; **Fig. 10.6D**). *Breynia* is first recorded in Australia in the Middle Miocene, but only in north-western Australia (McNamara & Kendrick 1994). The structure and function of the spines and tube feet of *Echinocardium cordatum* are described in detail by De Ridder *et al.* (1987) and Flammang *et al.* (1991).

Breynia species are shallow-water dwellers, occurring from the intertidal down to a depth of 140 m (McNamara 1982). *Breynia desorii* is very abundant in the Kimberley region of north-west Australia, occurring at densities of up to 220,000, but more commonly at hundreds to thousands, per hectare (Keesing & Irvine 2013). A specimen of *B. desorii* was found buried in sand to 80 mm (McNamara 1982). Population densities are often very high, as indicated by the vast numbers that wash up on beaches, such as the Eighty Mile Beach in Western Australia, following cyclone activity. At local densities of up to 22 per square metre *B. desorii* is likely to play a major role in in bioturbation and nutrient recycling in sediment (Keesing & Irvine 2013). Despite being one of the more common shallow-water spatangoid echinoids in Australia, there is only one study (Keesing & Irvine 2013) of feeding and reproduction in *B. desorii*. McNamara (1982) describes the post-settlement ontogeny of *B. desorii*. *Breynia australasiae* can also occur in very high densities as evident in the large populations of this species in the lagoon at Lord Howe Island. The general ecology and habitat preferences of *Breynia* species remain poorly known.

Much more is known about the behaviour and habitats of *Lovenia elongata*, based on Red Sea populations (Ferber & Lawrence 1976). This species prefers clean, grassless, sandy bottoms in sheltered intertidal areas. While it lives in medium- to fine-grained sandy sediments, other species, such as the deeper water *L. gregalis*, inhabit foraminiferan muds (K.J.McNamara, unpublished data).

Studies of growth and reproduction have shown that *L. elongata* spawns in summer (Ferber & Lawrence 1976). Gametogenesis is not synchronous in all individuals; it begins in mid- to late winter, with a prolonged spawning period from spring through to late summer (Pearse & Cameron 1991). Subadults have a growth rate of 8–12 mm per year, and Ferber and Lawrence estimated that individuals can live for up to seven years. Keesing & Irvine (2013) suspect that *Breynia desorii* has a winter or dry season spawning. Gonadal development indicates attainment of maturity at test lengths of 45–54 mm, possibly in their second year.

Lovenia is a shallow burrower, usually living just below the sediment-water interface. It was observed emerging from Red Sea sediments exposed at low tide

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(Ferber & Lawrence 1976). Individuals were exposed subaerially for several hours during which time they moved actively over the sand at speeds up to 300 mm per minute. On the return of the tide the echinoids burrowed again.

Lovenia has a greater bathymetric range than *Breynia*, and whereas *L. elongata* was recorded from the intertidal zone to 94 m (Mortensen 1951), *L. gregalis*, from the North West Shelf, occurs in depths of 430–849 m (A.D.Miskelly, unpublished data), although elsewhere it extends to 930 m (Mortensen 1951). *Lovenia camarota* is known from between 20 m and 100 m, while *Echinocardium* occurs from the intertidal zone to depths of more than 200 m (Mortensen 1951). *Pseudolovenia* is the only loveniid that occurs in southern Australia at depths of around 1,000 m.

Loveniids, especially *Breynia* and *Lovenia*, are mainly tropical in their distribution. *Breynia australasiae* occurs as far south as about 30.5°S in Western Australia, and it extends around the northern Australian coast and down the east coast to about Port Macquarie, New South Wales, and Lord Howe Island (31°S). Other species have narrower distributions. Thus, *B. desorii* is restricted to the west coast, and *B. neanika* to the north. McNamara (1982) suggested that the eastern and northern species evolved from *B. desorii*, the latter occuring in rocks at least as old as Middle Pleistocene in Shark Bay, Western Australia (McNamara 1996).

Little is known about the biology and ecology of loveniids in Australian waters. In association with its very wide distribution, *E. cordatum* is the most studied spatangoid (Egea *et al*. 2016). It is recognised as an ecologically important species in soft sediment habitats where it can be superabundant (Nakamura 2001; Lohrer *et al*. 2004, 2008).

The genders of many loveniids can be readily discerned in this species because the gonopores of the females are much larger than those of the males. *Echinocardium cordatum* has an annual reproductive cycle, with small eggs and development through a planktotrophic echinopluteus larva with a planktonic period of ~40 days (Nunes & Jangoux 2007). In contrast, *Breynia australasiae* has large eggs and lecithotrophic development. Larval development and juvenile growth of *Echinocardium cordatum* has been described in detail by Nunes & Jangoux (2007).



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11: Class HOLOTHUROIDEA

Frank W.E. Rowe, Timothy D. O'Hara and Tania M. Bardsley

General description

Holothuroid echinoderms are commonly known as sea cucumbers or, in the Indo-Pacific region where some species are a culinary delicacy, trepang or bêche-de-mer. This has led to overfishing of species with some becoming locally extinct, and in 2014, thirteen species were placed on the vulnerable or extinction risk list by the IUCN (Purcell *et al.* 2014). The colloquial name is based on the more or less cylindrical form of the most common shallow-water or intertidal species (**Figs 11.1, 11.11b**). The mouth is located at one end (denoted anterior), with the anus at the opposite end (posterior) (**Fig. 11.2A**). Among the more unusual holothuroid morphologies are the limpet-shaped dendrochirotid family Psolidae (**Fig. 11.6A**) and the flask-shaped Rhopalodinidae, which occur in shallow waters, the deep-water Deimatidae with large stiff papillae (**Fig. 11.18**), and the pelagic, medusoid Pelagothuriidae (**Fig. 11.17**).

Comprehensive reviews of holothuroid biology include general accounts (Hyman 1955; Lawrence 1987) and reviews of functional morphology, histology and ultrastructure (Smiley 1994), feeding and nutrition (Massin 1982b; Roberts *et al.* 2000), reproduction and life histories (Smiley *et al.* 1991; McEdward & Miner 2001; Sewell & McEuen 2002), ecology (Purcell *et al.* 2016a) and global diversity (Paulay 2015). The biology of deepsea holothuroids is reviewed by Billett (1991). The most recent inventory of Australian holothuroid taxa is provided by the Australian Faunal Directory (O'Hara 2012).

Holothuroids have a pentamerous symmetry that is masked by bilateral symmetry. The ambulacra are indicated externally by five longitudinal bands of tube feet (podia) that can be restricted to more or less three bands on the underside (ventral, trivium). The upper two bands (dorsal, bivium) are often modified as sensory papillae. In some forms, such as the phyllophorid genus *Thyone*, unmodified tube feet can be scattered over the body. In the Synaptulida (formerly Apodida) and Molpadida, tube feet are absent, the five ambulacra being most readily recognised by the position of internal longitudinal muscle bands.

A ring of tentacles surrounds the mouth; the tentacles are used for feeding (see **Fig. 1.16**). The pharynx is surrounded and supported by a characteristic set of usually 10 plates, the calcareous ring (**Figs 1.17B, 11.2B**). The water vascular system comprises a circum-oral ring canal from which arises one or more stone canals leading to one or more madreporites lying in the coelom, and one or more blind-ending sacs (Polian

Figure 11.1 ***Holothuria atra*** (Holothuriidae) is a common and conspicuous sea cucumber throughout its range in the tropical Indo-west Pacific (Red Sea and East Africa to Australia) to depths of 20 m. It is often found lying exposed on shallow sand flats between reefs and sandy coastal beaches such as those of the Cocos Keeling Islands in northern Australia. It is a black-skinned sea cucumber usually growing to a length of 200 mm, but may grow up to 600 mm. Small animals tend to have a thin coating of sand covering the body, but often with round patches without sand so that the black skin shows through as a series of spots; large animals, usually found in deeper water, have no sand covering, or have a thick unbroken covering. ***Holothuria atra*** is commonly called the black sea cucumber or lolly fish.

[J.Freund]

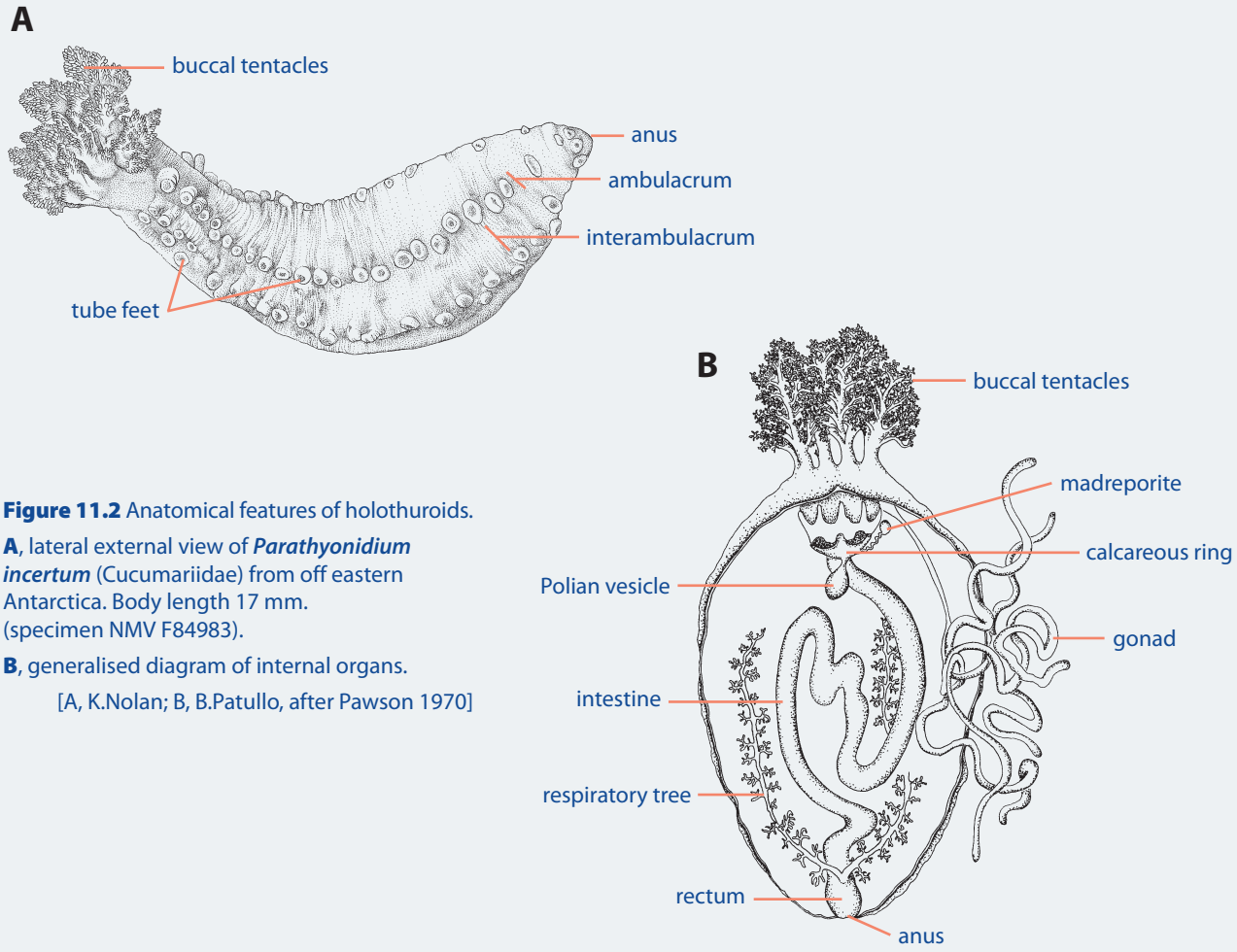


Figure 11.2 Anatomical features of holothuroids.
A, lateral external view of ***Parathyonidium incertum*** (Cucumariidae) from off eastern Antarctica. Body length 17 mm. (specimen NMV F84983).
B, generalised diagram of internal organs.
[A, K.Nolan; B, B.Patullo, after Pawson 1970]

vesicles). Five longitudinal canals also arise from the circumoral ring. They extend anteriorly and then turn and continue posteriorly along the ambulacra, giving rise to the tube foot/ampulla system. The buccal tentacles, and additional tentacles, arise directly from the circumoral ring in synaptulids and molpadids (Smiley 1994).

Ampullae of the tube feet lie in the coelom, and the tube feet themselves extend through the body wall. Molpadida have longitudinal canals, but no tube feet, whereas Synaptulida lack even the longitudinal canals. The coelom is capacious, containing a long digestive tract in an S-shaped loop (**Figs 11.2B, 11.15B**), and a solitary, dorsal gonad with a gonoduct leading to a gonopore that opens mid-dorsally close to the base of the buccal tentacles. A branched respiratory organ (present only in some Aspidochirotida, Dendrochirotida and Molpadida) and an associated Cuvierian (defence) organ (present in some Aspidochirotida) arise from the rectum (**Figs 2.18, 11.11D**).

The endoskeleton consists of microscopic ossicles of various shapes and sizes that are embedded in the body wall (Stricker 1985, 1986; **Figs 1.5C–E, 11.4**). Ossicles can be up to 5 mm long (for example, psolid scales), and either sparse or so dense that they make the body wall stiff and brittle. These ossicles are frequently used for the identification of holothuroids, especially at species level. They function in the body wall to form part of the spicule-reinforced connective tissue dermis, which together with the mutable characteristics of

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Table 11.1 Classification of the Holothuroidea. Only those groups recorded from the Australian region are included here.

Class Holothuroidea	
Order Dendrochirotida	Order Synaptulida
Family Paracucumidae	Family Chiridotidae
Family Psolidae	Family Synaptidae
Family Phyllophoridae	Family Myriotrochidae
Family Sclerodactylidae	Order Molpadida
Family Cucumariidae	Family Molpadiidae
Family Ypsilothuriidae	Family Caudinidae
Order Aspidochirotida	Family Gephyrothuriidae
Family Holothuriidae	
Family Stichopodidae	
Family Synallactidae	
Order Elasipodida	
Family Laetmogonidae	
Family Elpidiidae	
Family Psychropotidae	
Family Pelagothuriidae	
Family Deimatidae	

tissue provides structural support for the animal (see **Chapter 1; Box 1.1**). In juveniles the ossicles may deter settlement by small crustaceans (Smiley 1994). In the Synaptulida the ossicles are shaped like minute anchors with the sharp end pointing outward and give the animal traction when moving (Stricker 1985). As a result, synaptulids have a velcro-like feel on touch and readily stick to any surface.

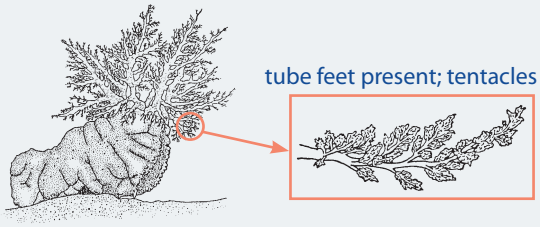
Reproduction and development in holothuroids is described in **Chapter 3**. Sexes are usually separate and generally indistinguishable externally, except for brooding species with dimorphic genital papillae (O'Loughlin 2001). A few taxa are hermaphroditic, and asexual reproduction by fission also occurs. Some fissiparous species like the tropical *Holothuria atra* and *Stichopus chloronotus* are among the most abundant and widespread species (Chao *et al.* 1993; Lee *et al.* 2008a). Reproduction usually involves spawning of gametes (**Fig. 3.2E**), but some species brood their young externally or internally. Species with small eggs develop through an auricularia planktotrophic larva (**Fig. 3.11F**) that then develops into a doliolaria larva which attaches to the benthos with its oral tentacles (Sewell & McEuen 2002). Species with direct development only have the doliolaria (Sewell & McEuen 2002). Doliolaria are barrel-shaped larvae that have uniform ciliation or can have bands of cilia (McEuen & Chia 1991; Sewell & McEuen 2002).

Holothuroids also have a propensity to eviscerate and then regenerate the lost internal structures (**Box 1.1**).

Holothuroids range in colour from dull, uniform blacks and browns to spectacular reds and yellows. Adults can be minute brooding forms, such as the southern Australian cucumariid *Neocnus bimarsupiis* (to 6 mm long; **Box 11.1**), or they can be large, bread-loaf-shaped species such as the tropical Australian and Indo-west Pacific stichopodids *Stichopus herrmanni* and *Thelenota anax*, which can be a metre or more in length.

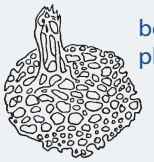
Holothuroids are suspension or deposit feeders and are epibenthic on all substrates or infaunal in soft substrates. While most are slow-moving, a few species are capable of swimming, and at least one family of elasipodids (Pelagothuriidae) is truly pelagic (**Fig. 11.17A**; **Box 1.5**). Holothuroids are found at all

ORDER DENDROCHIROTIDA

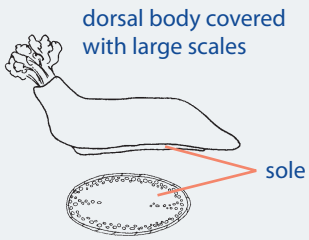


A Paracucumidae

cylindrical elongate tapered body



B Psolidae

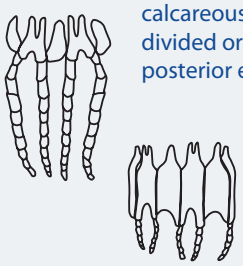


C Phyllophoridae

body not plated

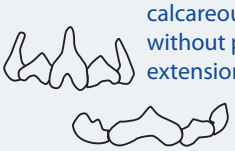


D Sclerodactylidae

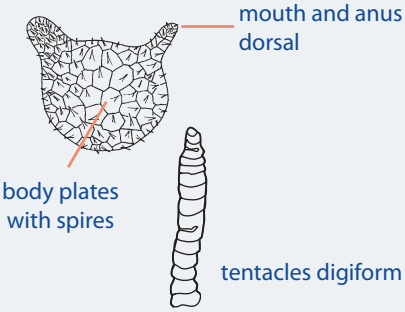


E Cucumariidae

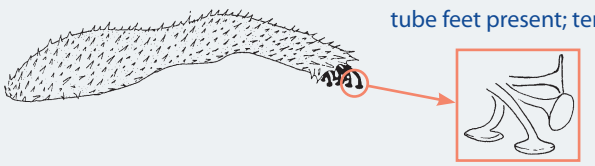
body not plated



F Ypsilothuriidae



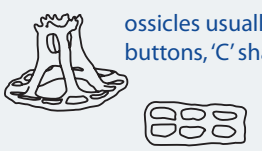
ORDER ASPIDOCHIROTIDA



G Holothuriidae

ventral surface of body rounded; tentacle ampullae present

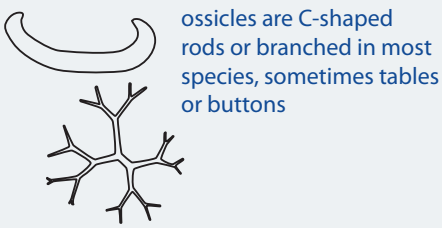




H Stichopodidae

ventral surface of body flat; tentacle ampullae present

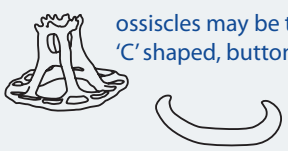




I Synallactidae

ventral surface of body rounded; tentacle ampullae absent

1 or 2 gonad tufts



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ORDER ELASIPODIDA — tube feet present; internal respiratory trees absent

J Laetmogonidae

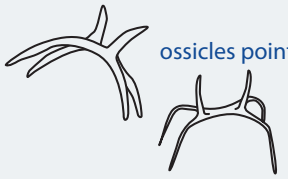
body gelatinous



ossicles include wheels

K Elpidiidae

body soft and oval-shaped; vellum anterior; mid-ventral tube feet absent



ossicles pointed branched rods

L Psychropotidae

body thick and gelatinous; vellum lateral; tube feet on mid-ventral surface



ossicles cross or rod shapes with extensions



M Pelagothuriidae

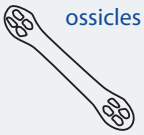
gelatinous body with anterior brim; ossicles and calcareous ring both absent



anterior brim

N Deimatidae

body parchment-like; papillae non-retractile

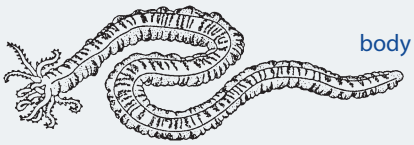


ossicles often spatulate

Figure 11.3 Diagrammatic key characteristics to the major holothuroid families.

[B.Patullo]

ORDER SYNAPTULIDA



body vermiform; tube feet absent

O Chiridotidae

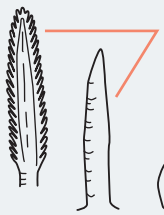


tentacles digitate



ossicles may be 6-spoked wheels, sigmoid hooks, or 'C' or bracket shapes

P Synaptidae



tentacles typically pinnate



ossicles anchor-shaped

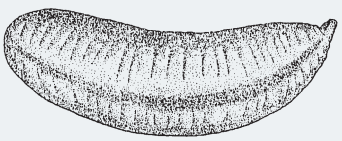
Q Myriotrochidae

tentacles various

ossicles 8–25-spoked wheels; 'S'- or 'C'- shapes absent



ORDER MOLPADIDA



body sausage-like; tube feet absent

R Molpadiidae



tentacles with terminal digit

S Caudinidae



tentacles with lateral digits (no terminal digit)

T Gephyrothuriidae

15 tentacles; ossicles absent



posterior body with caudal appendage

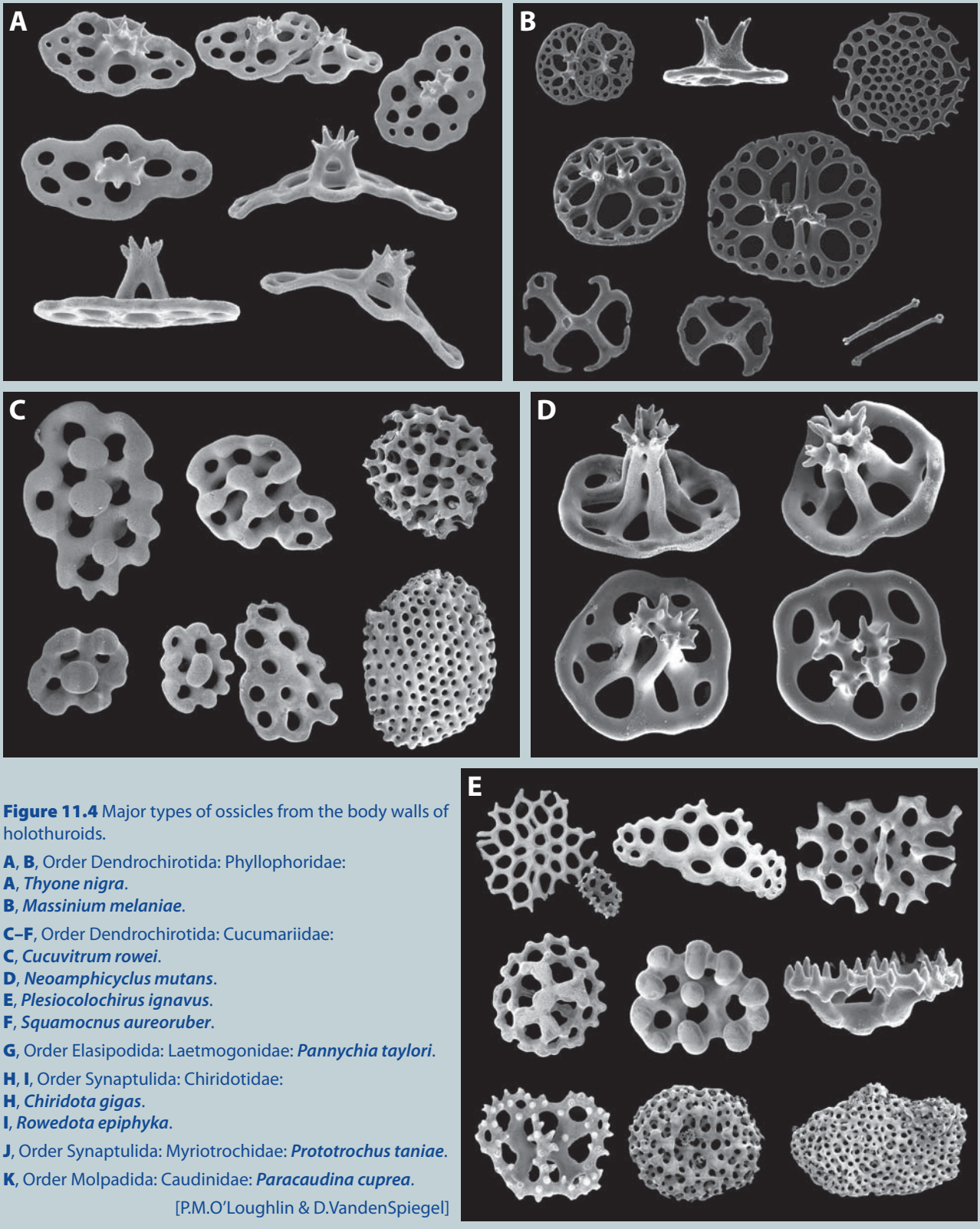


Figure 11.4 Major types of ossicles from the body walls of holothuroids.

A, **B**, Order Dendrochirotida: Phyllophoridae:
A, ***Thyone nigra***.
B, ***Massinium melaniae***.

C–F, Order Dendrochirotida: Cucumariidae:
C, ***Cucuvitrum rowei***.
D, ***Neoamphicyclus mutans***.
E, ***Plesiocolochirus ignavus***.
F, ***Squamocnus aureoruber***.

G, Order Elasipodida: Laetmogonidae: ***Pannychia taylori***.

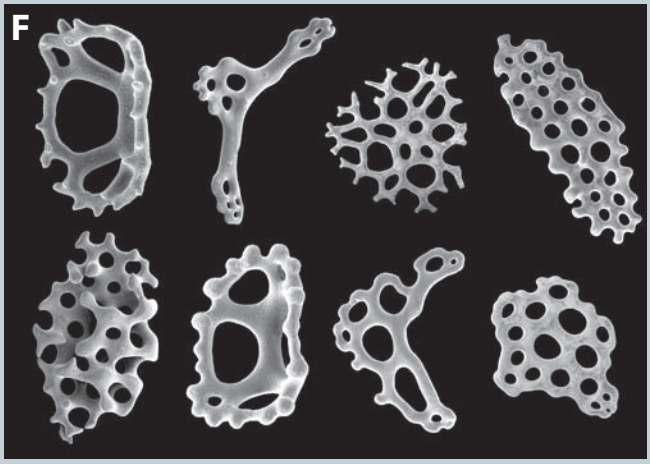
H, **I**, Order Synaptulida: Chiridotidae:
H, ***Chiridota gigas***.
I, ***Rowedota epiphyka***.

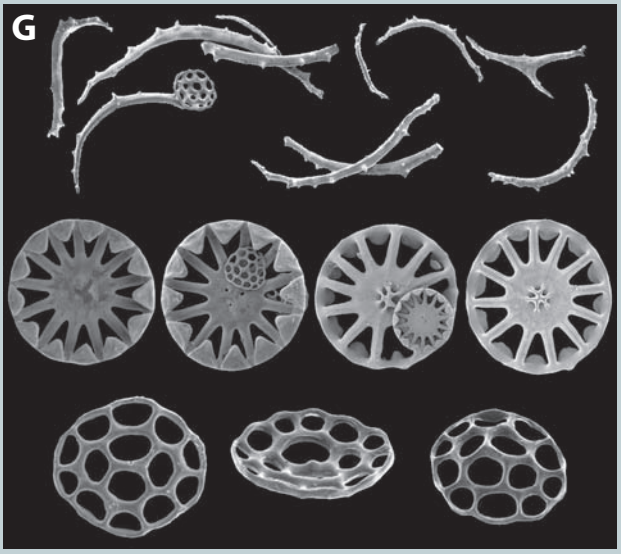
J, Order Synaptulida: Myriotrochidae: ***Prototrochus taniae***.

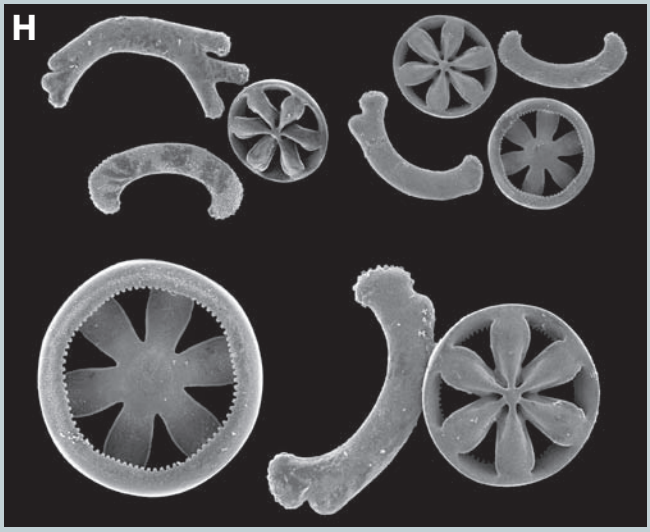
K, Order Molpadida: Caudinidae: ***Paracaudina cuprea***.

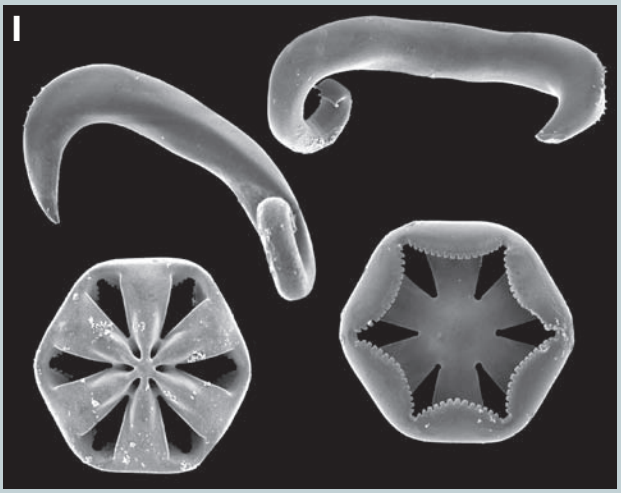
[P.M.O'Loughlin & D.VandenSpiegel]

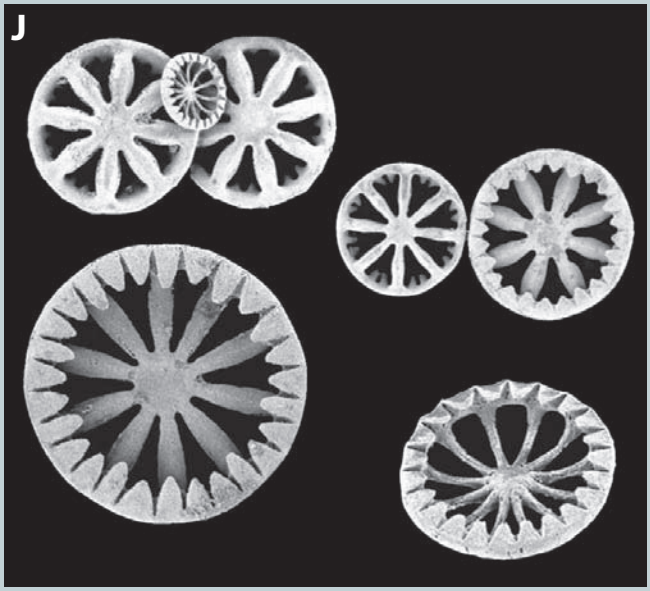
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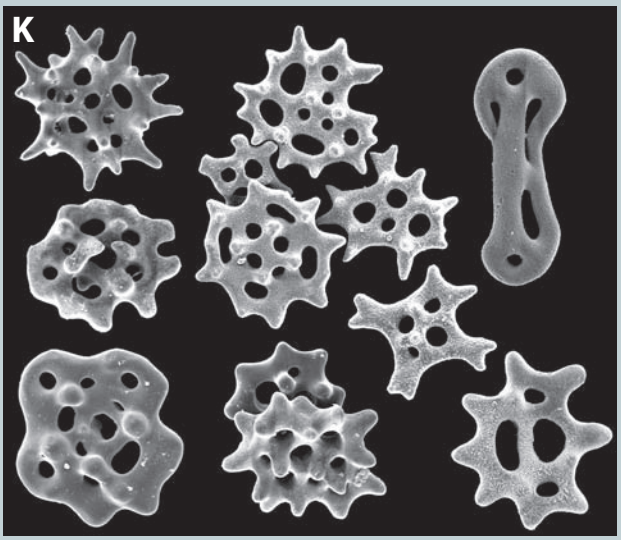

F


G


H


I


J


K

depths and in all seas, where they can be the dominant animals of the benthos (Marshall 1979; Smiley 1994).

Deposit-feeding holothuroids are ecologically important as bioturbators; individuals can pass enormous amounts of substrate through their bodies (Uthicke 1999; Roberts *et al.* 2000; **Fig. 1.18**) and large aggregations of suspension-feeding species are ecologically important in benthic-pelagic coupling (Hudson *et al.* 2004). Holothuroids are also important economically in some parts of the world where they are sold or traded as food, particularly in the Indo-Malayan region (Sloan 1985; Conand & Byrne 1993; Eriksson & Byrne 2015). A holothuroid fishery has existed in the tropics, including in northern Australia, for centuries (Vail & Russell 1989; Gudimova *et al.* 2004; Purcell 2014; Purcell *et al.* 2014; Eriksson & Byrne 2015; see **Chapter 4**).

Holothuroids are well represented in Australian waters, with some 20 of the 25 families, 92 of the 256 genera and 296 of the 1,722 known species (O'Hara 2012; Paulay 2015). A series of papers by O'Loughlin and colleagues have described or recorded numerous taxa from around Australia and eastern Antarctica (O'Loughlin *et al.* 1994, 2007, 2011a, 2011b, 2012, 2014a, 2014b, 2015; O'Loughlin 1998a, 2000, 2002, 2007; O'Loughlin & Alcock 2000; O'Loughlin & Ahearn 2005; O'Loughlin & VandenSpiegel 2007; O'Loughlin & Maric 2008). The earliest known extant Australian species to be described was *Ceto cuvieria* (as *Holothuria cuvieria*) in 1817, an endemic species from southern coasts (Pawson 1971c).

According to Smith (1988c), the fossil record for holothuroids is 'appalling', which is scarcely surprising given their skeletal form. Fewer than 20 species with body fossils have been found worldwide, most fossils being 'paraspecies', i.e. described from isolated ossicles only. An excellent revision of the fossil history was provided by Gilliland (1993), who noted that only 550 fossil paraspecies had been described, compared to some 1,700+ described extant species. Gilliland rejected about 100 paraspecies that he considered to be based on non-holothuroid fossil ossicles. The earliest unequivocal holothuroid microfossils are from the Ordovician, approximately 464 mya (Reich 2001). The earliest whole body fossil is *Porosothyone picketti* from the Late Silurian of the Yass Basin in Australia (Jell 2011).

Only three other fossil holothuroid taxa have been identified from Australia. *Eocaudina hexagona* and *Fissobractites subsymmetrica* in Late Triassic deposits from the northern slopes of Wombat Plateau, off north-western Australia, were known previously from between the eastern European Alps and Burma and from Austria, respectively, thus reinforcing hypotheses of their Tethyan affinities (Kristan-Tollman & Gramann 1992). The veracity of *Eocaudina* as a holothuroid was questioned by Gilliland (1993); *Fissobractites* is recognised as a dendrochirotid. The synaptulid species *Chiridota ingens* was described from Eocene deposits from Spring Creek, Victoria (Clark 1946).

Kerr & Kim (2001) provided the only quantitative cladistic analysis of the class Holothuroidea. They resolved the Synaptulida (=Apodida) as sister group to the rest of the modern holothuroids, followed by the Elasipodida, Aspidochirotida and Molpadida, with the Dendrochirotida the most highly derived group. Smirnov (2012) placed the synaptulids and elasipodids in separate subclasses, and recognised the distinctiveness of the Gephyrothuriidae by placing it in its own order. This phylogeny contradicts earlier theories that emphasised the 'primitiveness' of fully plated dendrochirotids such as *Placothuria* (Pawson 1966). However, it is consistent with the hypothesised evolution of larvae from ancestral feeding forms to derived, lecithotrophic (yolky) forms. All dendrochitids have either lecithotrophic larvae or brood their young, whereas many synaptulids and aspidochirotids have feeding auricularia larvae (McEdward & Miner 2001). Modern holothuroids probably arose in the Devonian, with at least six lineages that appear to have survived the Permian-Triassic mass extinction event (Kerr & Kim 2001).

The classification adopted here broadly follows Smirnov (2012); however, we have refrained from adopting his new subclass or new family-level taxa until they are confirmed by support from adequate molecular analyses. We have adopted the order name Synaptulida rather than Apodida to avoid confusion with similarly named taxa in insects, crustaceans, fish, amphibians and birds (Smirnov 2012).

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Order DENDROCHIROTIDA

Dendrochirotids usually have 10–30 richly branched tentacles (**Figs 1.16A,B, 11.9**); the introvert (the oral end including tentacles), can be retracted into the body (**Fig. 1.17**). Tube feet are usually well developed, and only rarely absent, and while respiratory trees are usually present, tentacle ampullae are not. A pair of gonad tufts occurs on each side of the dorsal mesentery. The calcareous ring can be simple or it can have long posterior processes. Body wall ossicles are shaped like perforated plates (often with knobs), multi-layered scales, cups or tables. In some species the ossicles overlap and form a protective armour or test (Pawson 1982a). See **Figure 11.3A–F** for an illustrated summary of family characteristics.

The taxonomy of dendrochirotids has evolved considerably since holothuroids with branched tentacles were initially recognised as a distinct group in the first half of the nineteenth century. Early classifications were based on external morphological features, such as the number of tentacles, the number and position of tube feet and body form. Species with 10 tentacles ('decachirotes', later Cucumariidae) were distinguished from those with more numerous tentacles ('polychirotes' or Phyllophoridae). Species with a distinct ventral sole, a dorsally orientated anus and mouth, and a heavily plated dorsal surface were later segregated into the Psolidae.

Panning (1949) and Heding & Panning (1954) transformed dendrochirotid taxonomy by using the form of the body wall ossicles and the calcareous ring as the principal characters separating subfamilies and genera. Panning (1949) revised the Cucumariidae, recognising five subfamilies (Cucumariinae, Colochirinae, Sclerodactylinae, Thyoninae and Ypsilothuriinae). Heding & Panning (1954) similarly recognised five subfamilies in the Phyllophoridae (Thyonidiinae, Cladolabinae, Phyllophorinae, Semperiellinae and Rhopalodininae).

Pawson & Fell (1965) and Pawson (1966) completed this transformation by revising dendrochirotid taxonomy at the familial and ordinal levels. Based on new evidence from the fossil record they regarded the form of the calcareous ring, and the shape of the tentacles and the body wall ossicles, as being more important diagnostic criteria than the number of tentacles. They separated forms with simple digitiform tentacles into a new order Dactylochirotida. Within the Dendrochirotida, species having simple calcareous rings (posterior processes rudimentary or lacking) were reassigned to the Cucumariidae (subfamilies Cucumariinae, Colochirinae and Thyonidiinae), those having complex calcareous rings with fragmented posterior processes to the Phyllophoridae (subfamilies Phyllophorinae, Semperiellinae and Thyoninae), and those with shorter, less fragmented rings to the Sclerodactylidae (subfamilies Sclerodactylinae and Cladolabinae). The aberrant genera *Placothuria* and *Paracucumis*, and later *Heterothyone* (Pawson 1970), with a complete covering of imbricating body wall ossicles, were referred to their own families (Placothuridae, Paracucumidae and Heterothyonidae, respectively).

However, dendrochirotid classification is still far from satisfactory, because convergent character states are common, and descriptions of many species are inadequate. A progressive revision of cucumariid genera by Panning (1962, 1964, 1966, 1971) has left many species in an uncertain taxonomic position. The Cucumariidae and the Psolidae are not distinguished clearly from each other (Gutt 1990; O'Loughlin & O'Hara 1992), and nor are the subfamilies of Phyllophoridae and Sclerodactylidae (Smirnov 2012). Some species with a sole and a dorsal surface with multi-layered imbricating plates (for example, *Neopsolidium* and *Echinopsolus*) could be assigned to either family. The distinction between the subfamilies Cucumariinae and Colochirinae is also unresolved. We have chosen not to adopt the family level classification of Smirnov (2012) until we have more supporting genetic evidence.

Three families, Rhopalodinidae, Vaneyellidae and Ypsilothuriidae, were formerly placed in the order Dactylochirotida. However, Smirnov (2012) does not regard them as a natural group and returned them to the Dendrochirotida. Only the Ypsilothuriidae is known from Australia. Rhopalodinidae are bizarre, flask-shaped holothuroids with a long proboscis-like

neck that includes both the mouth and anus (Thandar 2001). This is achieved by the dorsal interradius being greatly reduced so that the anal and oral openings lie adjacent to one another. Radial rows of tube feet appear externally as a whorl of ten 'semi-radii' from the bottom of the body (Cherbonnier 1988). The internal organs run as usual from mouth to anus. This unique body shape is presumably an adaptation to living in mud (Kerr & Kim 1999). The three rhopalodinid genera are restricted to continental shelf habitats off the west coast of Africa (Thandar 2001). A genetic phylogeny based on the nuclear 18S gene supported the monophyly of the Dendrochirotida (Lacey *et al.* 2005), and within the order, species cluster into cucumariid and phyllophorid/sclerodactylid clades. This study did not include any representatives of the Dactylochirotida or Psolidae, and a more comprehensive phylogeny based solely on morphology found the dactylochirotids to be nested within the dendrochirotid clade (Kerr & Kim 2001). Although the earliest fossil records of holothuroids resemble dendrochirotids (Reich 2001), both phylogenies suggest that the dendrochirotids are derived rather than primitive holothuroids.

Dendrochirotids are found worldwide, and while most occur in shallow water, a few species penetrate the abyssal zone. Only one dendrochirotid, *Cucumaria frondosa* from the North Atlantic, is commercially fished (Gudimova *et al.* 2004). There is no interest currently in fishing cucumariids in Australia. Dendrochirotids are suspension feeders, holding their tentacles out in flowing water (**Figs 1.16A,B, 11.6A, 11.7A, 11.9**) to capture particles on small sticky papullae on the surface of the tentacles (Fankboner 1981; Costelloe & Keegan 1984). The tentacles are placed into the mouth one at a time and the attached food particles are stripped off. In food-rich waters dendrochirotids can form aggregations of thousands of individuals (Costelloe & Keegan 1984; Eckert 2007). These aggregations are ecologically important in benthic-pelagic coupling. The phenomenon of evisceration (discarding internal organs) is exhibited by many dendrochirotids (**Box 1.1**). Following autotomy of internal ligaments and the supportive tissue at the anterior end, the entire digestive tract, feeding tentacles, the pharyngeal ossicles and sometimes the gonads are discarded primarily at the anterior end of the animal.

All dendrochirotids have large eggs and direct development. Most species, like *Sclerodactyla briareus* from the Atlantic, have planktonic doliolaria larvae while others brood their young (Pawson 1982a; O'Loughlin 1991, 1994, 2007; McEdward & Miner 2001; Sewell & McEuen 2002; O'Loughlin *et al.* 2009). There are also many species that are fissiparous, including *Cucuvitrum rowei* from south-east Australia (O'Loughlin *et al.* 2009).

Family Paracucumidae

Figure 11.5

The Paracucumidae are characterised by a complete covering of imbricate scales, the absence of a sole, and a simple calcareous ring that lacks posterior processes (Pawson 1982a). This family was established by Pawson & Fell (1965) to accommodate the aberrant Antarctic species *Paracucumis turricata* (formerly known as *P. antarctica*). The species is further characterised by the unusual shape of the body wall ossicles (round perforated scales with a thick central spire (**Fig. 11.3A**), the very long thin body shape, 12–13 tentacles, and rudimentary or non-existent tube feet (Heding & Panning 1954; Pawson 1982a; O'Loughlin 2002). The spires on the body wall ossicles give the animal a very rough feel.

A second Antarctic genus, *Crucella*, was added to the Paracucumaridae by Gutt (1990). It has 10 tentacles, tube feet all over the body, and non-imbricating, sometimes spinous, cross-shaped ossicles. *Crucella hystrix* has been reported from the Weddell, Amudsen and Ross seas, *C. scotiae* from the Ross Sea and *C. susannae* from the South Shetland Islands and Bamfield Strait (O'Loughlin *et al.* 2014b).

Paracucumis turricata (**Fig. 11.5**) has a circumpolar Antarctic distribution at depths of about 10–1,000 m, and has been recorded from a range of sites off the Australian Antarctic Territory (O'Loughlin *et al.* 1994; O'Loughlin 2002). This species is apparently a detritivore — its gut is often filled with detritus, including many diatoms (Pawson 1982a).

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Figure 11.5 Family Paracucumidae. The characteristically slender rough body of the Antarctic ***Paracucumis turricata*** is often broken into fragments on collection. (specimen NMV F68671)

[K.Nolan]

Family Psolidae

Figure 11.6

Psolids are characterised by the ventral surface which is soft and usually functions as a 'sole' that grips the substrate, and the dorsal surface which is generally covered with large imbricate scales. The anus and the mouth are often dorsal in position (**Fig. 11.3B**) and protected by rings of anal and oral valves (Pawson 1982a). There are 8–15 branched tentacles, and, in contrast to many holothuroids, psolids exhibit secondary bilateral symmetry (Pawson 1971a; Kerr & Kim 1999).

This cosmopolitan family is found at depths to 2,800 m (Pawson 1982a). They are most diverse in colder regions, particularly Antarctica; the most species-rich genera are *Psolus* and *Psolidium*. Species of *Psolus* are usually 'limpet'-shaped (**Fig. 11.6A**), with a low convex dorsal surface and a flattened sole (**Fig. 11.6B**). They lack tube feet on the dorsal surface, apart from a few specialised sensory feet on the introvert and around the anus. In addition to large, multi-layered dorsal scales, body wall ossicles include knobbed plates and cups. *Psolidium* species have a similar body wall shape and ossicles, but they differ in having a scattered covering of small tube feet on the dorsal surface which penetrate the protective scales (**Fig. 11.6C**).

Other genera include *Lissothuria*, from the Caribbean and Pacific coasts of Central America — these are U-shaped animals with scattered dorsal tube feet, and unique hourglass-shaped body wall ossicles (Pawson 1967). *Ekkentropelma* has a laterally directed anus and mouth; Pawson (1971a) speculated that this holothurian might adhere to vertical surfaces, with its anus and mouth in an upward position. The type species, *E. brychia*, is known from 2,763–2,818 m off the Antarctic Peninsula, and another occurs on the continental slope off South Africa (Thandar 2006). *Ceto*, which is endemic to southern Australia, has 15 tentacles and a thick leathery skin on the dorsal surface (Pawson 1971c).

Neopsolidium has comparatively small dorsal disc scales and thus occupies an intermediate position between the psolids and some cucumariids with a psolid-like body (*Apsolidium*, *Echinopsolus*, *Trachythyone*, *Psolidiella* and *Pseudopsolus*). Indeed, Gutt (1990), noting the continuous range of variation between the two families, suggested that the separation of dendrochiridote families is artificial. Certainly, using the current morphological characters, it is difficult to distinguish convergence of habit from true phylogenetic relationships.

Some *Echinopsolus* species are epizoic on sea urchin spines around Antarctica. Different species are commensal with different sea urchin species from the genera *Notocidaris* and *Ctenocidaris* (Gutt 1990; Massin 1992; O'Loughlin *et al.* 1994). They have

a narrow sole specialised for gripping spines, scattered dorsal papillae, and relatively small dorsal scales (to 0.6 mm). On the basis of reproductive characters, Bohn & Heß (2014) have recently expanded this genus to include non-epizoic species and transferred it to the Cucumariidae.

Thirteen species of Psolidae are known currently from Australia (Rowe & Gates 1995; O'Loughlin & Maric 2008). These include 12 species of the common genus *Psolidium* and the monotypic *Ceto cuvieria*, which occurs from Shark Bay, Western Australia to Bass Strait, Tasmania. Two species of *Psolus* previously recorded from Australia have been transferred to *Psolidium* (O'Loughlin & Maric 2008).

Antarctic psolids are difficult to identify, and these species require a comprehensive revision. Reproductive mechanisms can provide useful distinguishing characters (Carriol & Féral 1985). O'Loughlin *et al.* (1994) listed nine species from the Australian Antarctic Territory and O'Loughlin *et al.* (2015) found several around Heard Island, but others are known from the Weddell Sea, Antarctic Peninsula and other subantarctic islands. Several species of *Psolus* and *Psolidium* are known from the Macquarie Ridge (Davey & Whitfield 2013).

Most psolids live on the exposed surfaces of hard substrates such as rock or, less commonly, dead scallop shells or ascidians. A few exceptions are infaunal, such as *Psolus phantapus* from the North Atlantic Ocean (McKenzie 1991) and *Psolidium poriferum* from the Antarctic (Gutt 1991a). Once they become established, they are sedentary animals, or even effectively sessile, and these suspension feeders extend their branched tentacles into the water current.

Reproduction is almost exclusively sexual, although there is a report of asexual fissiparous reproduction in the northern European *Psolus valvatus* (Mortensen 1927). Psolids either produce pelagic doliolaria larvae or

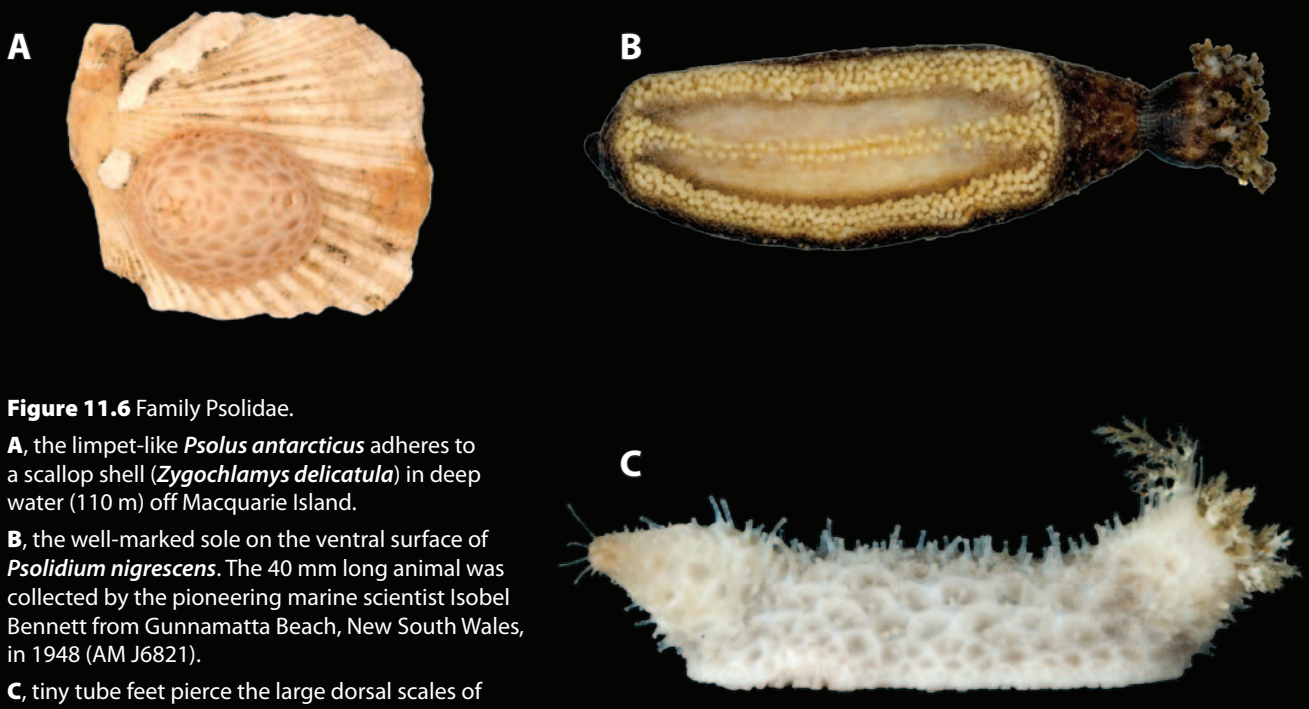


Figure 11.6 Family Psolidae.

A, the limpet-like ***Psolus antarcticus*** adheres to a scallop shell (***Zygochlamys delicatula***) in deep water (110 m) off Macquarie Island.

B, the well-marked sole on the ventral surface of ***Psolidium nigrescens***. The 40 mm long animal was collected by the pioneering marine scientist Isobel Bennett from Gunnamatta Beach, New South Wales, in 1948 (AM J6821).

C, tiny tube feet pierce the large dorsal scales of ***Psolidium***. Live ***Psolidium ravum*** from Portland, Victoria.

[A, C.Rowley; B,C, L.Altoff]

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brood their young (McEuen & Chia 1991). Adaptations for brooding vary considerably, particularly among Antarctic *Psolus* species. Thus, the female of *P. ephippifer* has specialised, table-like plates on the mid-dorsal surface which function as marsupia. *Psolus* (or *Echinopsolus*) *charcoti* has five external interradial marsupia, and *P. dubiosus* is reported to brood juveniles both in the gonads (Carriol & Féral 1985) and among the retracted tentacle crown (Gutt 1991b), suggesting that two species might have been confused here. Most species, however, retain their young under the sole, occasionally in special depressions or skin folds (for example, *P. antarcticus* and *P. punctatus*). Among the other genera, the Caribbean *Lissothuria antillensis* is a coelomic brooder, releasing the relatively large (1.0–1.5 mm) juveniles through the anus (Miller 1985). Brooding the juveniles until the dorsal scales are developed is an effective reproductive strategy as this 'armour' is a good shield against invertebrate predators (McEuen & Chia 1991).

Pelagic lecithotrophic larvae (doliolaria) are characteristic of some large northern hemisphere species such as *Psolus chitonoides*, *P. phantapus* and *Psolidium bullatum*. Female *P. chitonoides* produce large numbers (up to 34,700) of large eggs (600 µm diameter) that are released as a continuous 'rope' bound by a mucoid substance (McEuen 1988; McEuen & Chia 1991). Males help disperse sperm with their tentacles. The smaller *P. bullatum* releases fewer (to 3,074) and smaller sized eggs (330 µm diameter). Both males and females raise their anterior end and arch their back when spawning. The doliolaria larvae use their bands of cilia to swim down to the substratum for settlement and metamorphosis (McEuen & Chia 1991). Metamorphosis includes the development of the dorsal scales, flattening of the trivium and the development of the ventrolateral tube feet to form the sole (McEuen & Chia 1991).

Many psolids occupy exposed habitats that leave them vulnerable to predation. In response, the northern Pacific *Psolus chitonoides* has developed several defence mechanisms, including a protective dorsal armour, the production of saponins and other toxic chemicals to discourage predators, and the ability to quickly withdraw the tentacles and anus behind a series of protective valves (Bingham & Braithwaite 1986).

Family Phyllophoridae

Figure 11.7

The family Phyllophoridae has had a complicated taxonomic history. Originally created for all dendrochirotids with more than 10 tentacles, the family has been redefined several times based on different characteristics of the calcareous ring (Panning 1949; Heding & Panning 1954; Pawson & Fell 1965). In a recent classification, Smirnov (2012) removed the subfamilies Thyoninae and Semperillinae to a new family, the Thyonidae. However, Michonneau & Paulay (2014) cast doubt on the validity of these subfamilies, so we have retained the classification of Pawson (1982a) and Thandar (1990) until more evidence is available.

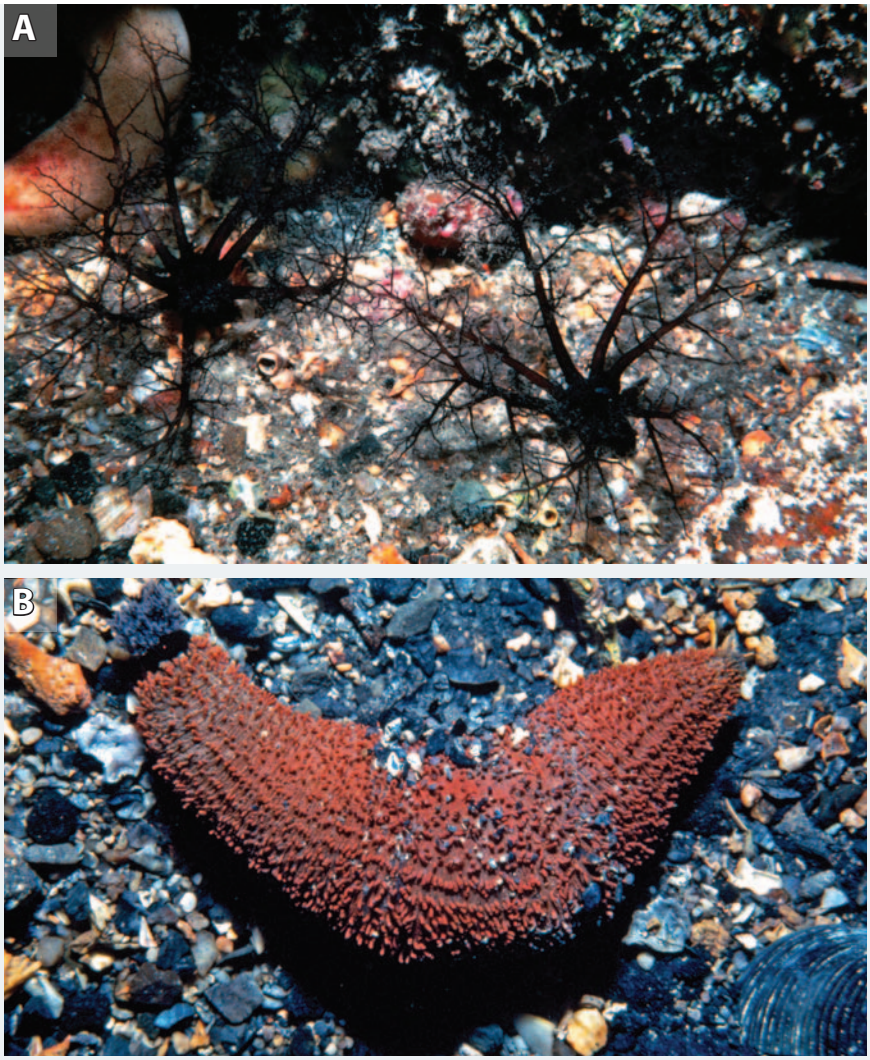
Phyllophorids are characterised by having a complex, fragmented calcareous ring that is often tubular, with short or long posterior processes (Pawson 1982a; Thandar 1990; **Fig. 11.3C**). The branched (dendritic) tentacles number 10–25, although usually either 10 or 20. The tube feet can be restricted to the ambulacra or can be more scattered, the dorsal ones usually smaller than the ventral ones and papilliform. Ossicles are generally shaped like tables, derivatives of tables, flat plates, buttons or rods (**Fig 11.4A,B**). The closely related Sclerodactylidae are distinguished by having short, tubular and comparatively unfragmented calcareous rings (Thandar 1989a).

Surprisingly little is known about the biology and life history of phyllophorids. The extended dendritic tentacles of some species indicate a filter-feeding habit (**Fig. 11.7A**). The larva of one species, *Phyllophorus urna*, from off Washington, USA, is a lecithotrophic benthic vitellaria (McEdward & Miner 2001). In Taiwan, *Phyrella fragilis* releases gametes from April to June, coinciding with a spring phytoplankton bloom (Chao *et al.* 1993). Specimens of *Thyone okeni* collected off Sydney regenerated their gut and tentacle crown within six weeks of evisceration (Tracey 1972).

Three species of *Lipotrapeza* are recorded for southern Australia (O'Loughlin *et al.* 2012). Members of this genus have 20 tentacles and knobbed rosette ossicles rather than tables. The brown and pink-coloured *Lipotrapeza vestiens* is common in sediment under

rocks in shallow water across southern Australia. The dorsal tube feet hold pieces of shellgrit, stones and other fragments of detritus over the body, presumably as a form of camouflage, and this species readily eviscerates when touched (Phillips *et al.* 1984). Occasionally, large numbers of individuals are washed ashore after storms (Clark 1946). The rarer red-brown *L. eichleri* from central Victoria has tube feet concentrated on the ventral side (O'Loughlin *et al.* 2012). *Lipotrapeza litusi*, described from a single specimen collected on Cottesloe beach, Perth, Western Australia, has tube feet with abundant rosette ossicles (O'Loughlin *et al.* 2012). The genus *Phyllostauros* was created recently for the aberrant species formerly known as *Lipotrapeza vercoi*, which has cross-shaped ossicles in the body wall and is known only from Gulf St Vincent in South Australia (O'Loughlin *et al.* 2012).

The taxonomy of the tropical genera is not settled. There are ongoing discussions about the limits and validity of the genera *Phyrella*, *Phyllophorella*, *Thyonidiella* and *Semperiella* (O'Loughlin *et al.* 2012, 2014a; Michonneau & Paulay 2014). The south-western Australian species formerly known as *Phyllophorus thyonoides* is a case in point. Based on the morphology of the calcareous ring it was transferred to *Phyllophorella*, but mitochondrial DNA data suggests it is a *Phyrella*. *Phyrella trapeza* is found in soft sediment across northern Australia (Rowe & Gates 1995). *Neothyonidium parvipedum* has



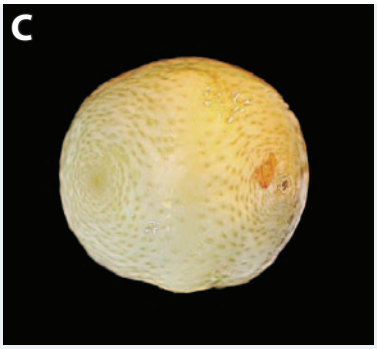


Figure 11.7 Family Phyllophoridae.
A, **B**, ***Thyone flindersi*** from Kangaroo Island, South Australia.
A, animal buried in sand with tentacles extended.
B, animal removed from its usually buried position.
C, the 40 mm sub-spherical body of ***Massinium bonapartum*** found in the muddy seafloor of the Joseph Bonaparte Gulf, northern Australia.
[A,B, K.Gowlett-Holmes; C, J.Keesing]

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only been recorded from the summit of the Wanganella Bank on the Norfolk Ridge north-west of New Zealand (Rowe 1989b).

One of the most important phyllophorid genera to emerge over the past decade is *Massinium* (**Fig. 11.7C**). Described in 2003 by Samyn & Thandar (2003) from a few species formerly in *Neothyonidium*, it now contains 11 species, many newly described from both northern and southern Australia (O'Loughlin *et al.* 2012, 2014a). *Massinium* species have 20 tentacles and a fragmented tubular calcareous ring with posterior processes that are joined distally. The extended tentacles of a buried, 100 mm long, *Massinium watsonae* are often seen by divers off south-eastern Tasmania (Edgar 1997 as *Neothyonidium* ? *dearmatum*). A new genus and species, *Triasemperia stola*, has been described recently from the continental shelf of northern Australia (O'Loughlin *et al.* 2014a). This genus differs in having unusual table-shaped ossicles with three pillars and a knobbed base that is similar to some *Stolus* species.

Thyone and *Stolus* have a complex tubular calcareous ring but only 10 tentacles, and are frequently placed in a separate subfamily (Thyoninae). They can be distinguished by their body wall ossicles, with 1- to 2-pillared table-shaped ossicles in *Thyone* and knobbed plates in *Stolus*. Rowe & Gates (1995) recorded eight species, and another five from southern Australia were described recently by O'Loughlin *et al.* (2012). The ossicles in *Thyone* typically degenerate with age and can be absent in the mid-body of adults, making identification difficult. *Thyone flindersi* is a small brown species (to 100 mm long) that lives buried in sand with only the retractable dendritic tentacles projecting into the water column (**Fig. 11.7A,B**). Formerly, it was confused with the New South Wales species *T. okeni* and Indo-Pacific species *T. venusta*. The Indo-Pacific *Hemithyone semperi*, with perforated button-shaped ossicles with cross-bars or 'bridges' on either side, is often placed in the Thyoninae, however, Smirnov (2012) noted the lack of fragmentation of the calcareous ring and questioned its affinity.

Family Sclerodactylidae

Figure 11.8

Sclerodactylids are characterised by having a short, complex calcareous ring with posterior processes. The ring is composed of separate radial and interradial elements, and the posterior processes can be fragmented or not (**Fig. 11.3D**). Tentacles number 10–20 and are branched, and although tube feet are usually scattered over the body, occasionally they can be restricted to the ambulacra. Ossicles are usually shaped like tables, flat plates or spinous rods (Pawson 1982a; Thandar 1989a).

Three subfamilies are recognised (Thandar 1989a), sometimes treated as families (Smirnov 2012). Sclerodactylinae and Sclerothyoninae have 10 tentacles, and they differ in the shape of the calcareous ring, i.e. tubular in the former and relatively short in the latter, with interradial and radial pieces united only at their basal ends. The third subfamily, Clabolabinae, have 15–20 tentacles in two or three circles. The three subfamilies constitute a heterogeneous assemblage, and include forms that are intermediate between the Phyllophoridae (with a complex calcareous ring) and the Cucumariidae (with a simple ring) (Thandar 1989a). The boundary between the Phyllophoridae and Sclerodactylidae is especially poorly defined (Thandar 1989a). In an alternative taxonomic scheme, Rowe & Gates (1995) emphasised the form of the body wall ossicles rather than the calcareous ring, placing genera with 4-spired tables in the Phyllophoridae and those with 2-spired tables in the Sclerodactylidae. Clearly, some phylogenetic revision is required. In the interim, Thandar's (1989a) taxonomy is adopted here, and *Havelockia*, with 4-spired tables and a short tubular calcareous ring, is retained in the Sclerodactylidae.

Seven species have been reported from Australia: *Afrocucumis africana*, *Havelockia versicolor*, *Globosita elnazae* and four species of *Cladolabes*. *Afrocucumis africana* is one of the few echinoderms that can tolerate the extreme environmental conditions of the intertidal zone (**Fig. 11.8**). This small species (~50 mm maximum length) is common across northern Australia, under coral or rock slabs, often with the ophiuroid *Ophiocoma scolopendrina* and small asterinids including *Cryptasterina* and *Ailsastra*



Figure 11.8 Family Sclerodactylidae.
The tough ***Afrocucumis africana*** survives under rocks in tropical intertidal habitats.
[L.Roediger]

species (M.Byrne, personal observation). Large specimens of *Cladolabes perspicillum* were known as 'footballs' on dredging vessels in Port Jackson in the early nineteenth century due to their habit of contracting their oral end and swelling mid-body (Clark 1946). *Globosita elnazae* from the continental shelf of northern Australia is up to 100 mm long and sub-spherical (O'Loughlin *et al*. 2014a).

Few studies have been published on the ecology or life history of sclerodactylids. Brooding has been reported for *Pachythyone rubra* from California and *Afrocucumis stracki* from Papua New Guinea (Chaffee 1982; Massin 2005; Eckert 2007). Juveniles develop within the coelom of *P. rubra*, breaking through the rectum wall and then being expelled through the anus or, more rarely, through evisceration (Chaffee 1982). *Sclerodactyla briareus* has a pelagic lecithotrophic larva (McEdward & Miner 2001). Various modes of reproduction have been recorded for disjunct populations of *Afrocucumis africana*, including brooding in a Japanese population (Ohshima 1916) and fission with occasional gonochoric reproduction in Taiwan (Chao *et al.* 1995), suggesting either the misidentification of some specimens or the presence of cryptic species.

Family Cucumariidae

Figure 11.9

The Cucumariidae have a simple calcareous ring that lacks posterior processes (**Fig. 11.3E**), 10–30 dendritic tentacles, and in the body wall have small ossicles that do not form an enclosing test (Pawson & Fell 1965). Three subfamilies are recognised: the Thyonidiinae with 10–30 tentacles and table-shaped ossicles (**Fig. 11.4D**), the Cucumariinae with 10 tentacles and plate-shaped ossicles, and the Colochirinae with 10 tentacles and plate- and cup-shaped ossicles (**Fig. 11.4E,F**) (Pawson & Fell 1965). The Thyonidiinae was raised to family rank by Smirnov (2012) who noted that it still may not be a natural group. The distinction between the Cucumariinae and Colochirinae is not sharply defined, and it is unclear whether all the derivative cup-like or cross-shaped ossicles are homologous. Their loss does not necessarily imply a close evolutionary relationship (O'Loughlin & O'Hara 1992).

The Cucumariidae is the largest of the dendrochirotid families with at least 60 genera and 200 species. They occur in a diverse range of habitats, from the Antarctic to the tropics and from the intertidal to abyssal depths. Rowe & Gates (1995) recorded 39 species from Australia, and seven others have been described subsequently (O'Loughlin 2000, 2007; O'Loughlin *et al*. 2014a). Additional undescribed species are known (P.M.O'Loughlin, personal communication).

Numerous small- to medium-sized cucumariids live across tropical Australia. *Leptopentacta grisea* is a rigid, U-shaped animal that lives in burrows. *Pseudocolochirus violaceus* has bright red ambulacra and yellow to blue interambulacra (**Fig. 11.9A,B**), *Cercodemas anceps* is yellow and pink (**Fig. 4.15**), *Colochirus robustus* is yellow and quadrangular-shaped (**Fig. 11.9C**), and *Mensamaria intercedens* is blue-black with bright red ambulacra (Cannon & Silver 1986). The first two species are suspension feeders that live a sedentary life exposed on rock or sand. Four species of *Actinocucumis* occur across northern Australia (O'Loughlin *et al.* 2014a).

Similarly, the southern Australian fauna includes many small shallow-water cucumariids (O'Loughlin & O'Hara 1992). Most have plate- and cup-shaped ossicles (**Fig. 11.4C,E**), although some genera have

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table-shaped derivatives (Fig. 11.4D). Two of the best-known species are *Plesiocolochirus ignavus*, white with orange flecks and common in algal holdfasts (Fig. 11.9D), and *Neoamphicyclus materiae*, a slate-grey species often found under rocks. The more abundant species on the continental shelf and upper slope (*Amphicyclus mortenseni*, *Neocucumis cauda* and *Neocucumella fracta*) have table ossicles.

Three cucumariids dominate the shallow-water holothuroid fauna of subantarctic Macquarie Island (O'Hara 1999a). *Pseudopsolus macquariensis* lives a sessile existence on the tops of intertidal rocks, rapidly extending its tentacle crown into incoming waves to feed in a manner similar to barnacles (T.D.O'Hara, unpublished data). *Trachythyone macphersonae* and *Pentactella laevigata* live under rocks, in crevices or in algal holdfasts. Populations of all three species on Macquarie Island are similar in form to those found on subantarctic islands to the west and presumably arrived on the more recently emerged Macquarie Island by rafting on kelp holdfasts (O'Hara 1998). A rich cucumariid fauna occurs on the continental shelves of East Antarctica and on Heard Island (O'Loughlin *et al.* 1994, 2015; O'Loughlin 2002). Important genera

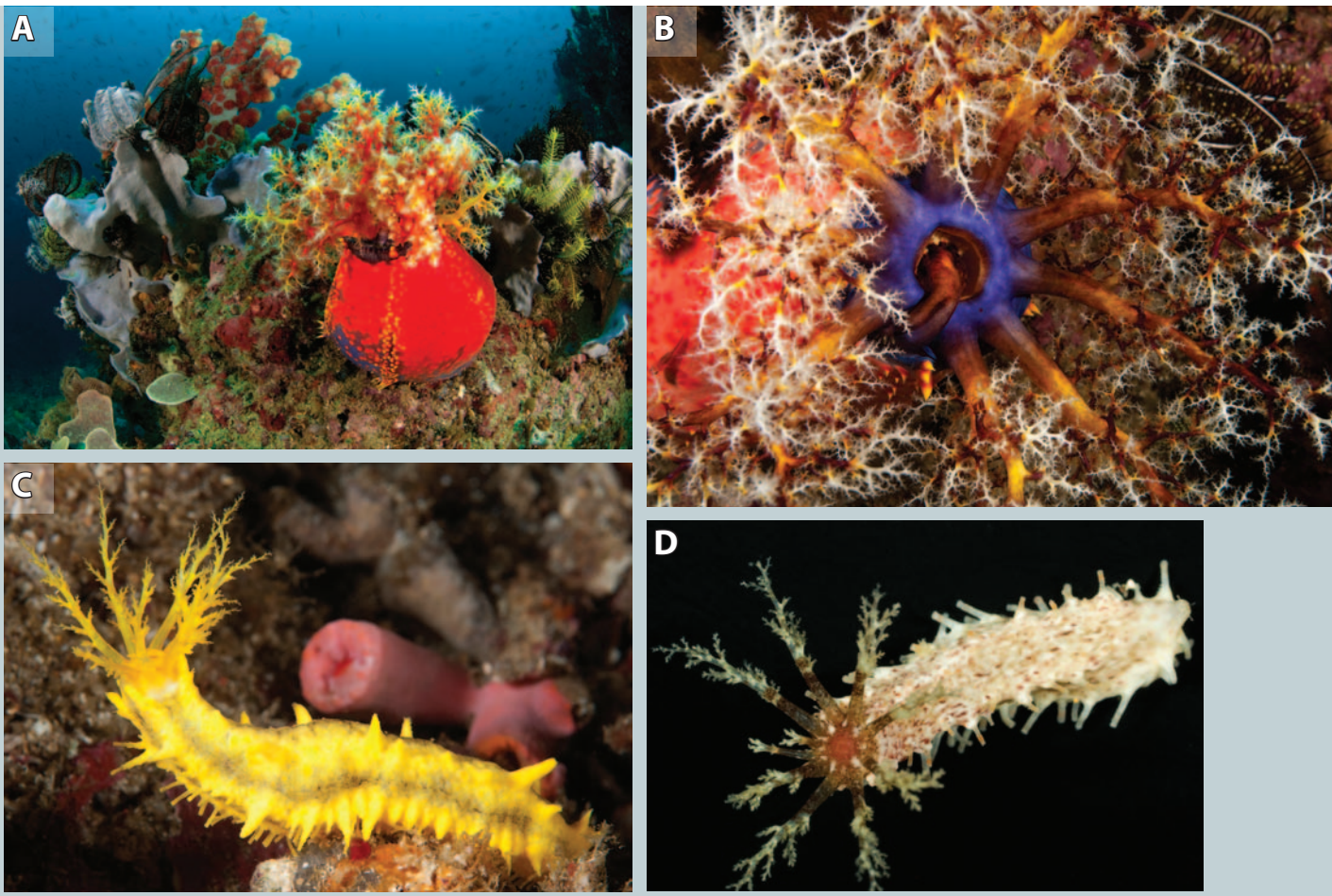


Figure 11.9 Family Cucumariidae.

A, **B**, the amazingly colourful ***Pseudocolochirus violaceus***, commonly know as a sea apple, is one of the most photographed holothuroids in the Indo-Pacific region. They extend their tentacles (**A**) to filter mainly plankton from the seawater. Each tentacle is brought to the mouth (**B**) to scrape off the captured plankton.

C, the bright yellow, quadrangular ***Colochirus robustus*** is frequently seen by divers across the tropical reefs from Australia to Korea.

D, the orange-flecked ***Plesiocolochirus ignavus*** is a common inhabitant of coastal rocky reefs of southern Australia.

[A,B, J.Freund; C, G.Bell; D, L.Altoff]

Box 11.1 *Neocnus bimarsupiis*

Features *Neocnus bimarsupiis* is a minute, dark-coloured sea cucumber that grows to only 6 mm in length. It is one of the many new species of small holothurians that have been discovered through careful collecting off the southern Australian coast over the past 35 years. This species has been found mainly on the fronds of the brown alga *Zonaria angustata* where it appears as a small, dark, oval protuberance.

The only visible tube feet are those on the under surface, and these help the animal grip the algal frond. It is presumed that the short bushy tentacles are extended into the water to feed during wave surges. The upper body is dominated by two large brood pouches near the tentacle crown. The pouches have small internal tube feet that can protrude from the small circular opening.

Frequently, the identity of holothurian species is confirmed by the shape and density of the small calcareous ossicles buried in the skin. However, this species has very few ossicles, mostly small branched or unbranched rods.

Distribution Found from Robe, South Australia, to Cape Paterson, Victoria, and the north-east coast of Tasmania, at depths down to 6 m.

Way of life It is likely that transfer of eggs from the gonad to the brood pouch occurs outside the body. Although the transfer process has not been determined, the two short grasping ventral tentacles and the minute, protruding suckered tube feet inside the brood pouches almost certainly play an important role. All specimens collected have female gonads, suggesting that this species is hermaphroditic or parthenogenetic.

Similar species Only one other species of *Neocnus* is known, *N. incubans* from the southern Mediterranean Sea. That species has only one large brood pouch. No other Australian species shares the combination of colour, form and brooding behaviour seen in *N. bimarsupiis*.

Order Dendrochirotida
Family Cucumariidae
Species *Neocnus bimarsupiis*
O'Loughlin & O'Hara, 1992

Further reading Cherbonnier 1972; O'Loughlin & O'Hara 1992



Neocnus bimarsupiis has two brood pouches on its dorsal body wall with tube feet to assist with the translocation of eggs.
[L.Altoff]

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include *Trachythyone*, *Ekmocucumis*, *Heterocucumis*, *Staurocucumis* and *Parathyonidium* (**Fig. 11.2A**). Many Antarctic species are suspension feeders, living a sedentary existence as epifauna or half-buried in sediment; several species are epizoic on bryozoans or sponges (Gutt 1991a).

One of the most interesting cucumariid attributes is the diversity of reproductive strategies and anatomical specialisations associated with reproduction. All cucumarids have lecithotrophic development with most species having pelagic doliolaria (McEdward & Miner 2001). O'Loughlin (1994) listed 30 species that brood their young, either in the gonads, coelom or in internal or external cavities or brood pouches. The minute black species *Neocnus bimarsupiis*, from south-eastern Australia, has two external marsupia on the dorsal body wall just behind the introvert (O'Loughlin & O'Hara 1992). O'Loughlin (1991) hypothesised that the two reduced ventral tentacles could grasp the released eggs and place them directly into the marsupium opening with the help of small extensible papillae within the marsupium (**Box 11.1**). *Neoamphicyclus lividus* and *N. materiae* brood large numbers of embryos (up to 500 or more) in the coelom (Hickman 1978; Materia *et al.* 1991; O'Loughlin & O'Hara 1992; O'Loughlin *et al.* 2009), while *Pentocnus bursatus* has sac-like brood chambers attached to the inner body wall (O'Loughlin & O'Hara 1992). Several Antarctic species are sexually dimorphic, the males having a temporary or permanent elongate genital papilla that could penetrate the openings of external brood pouches (O'Loughlin 2001).

Asexual reproduction occurs in some Cucumariidae. Several species are known to reproduce by fission, including the European *Ocnus planci*, *O. lacteus* and *O. brunneus* and the southern Australian *Squamocnus aureoruber* and *Cucuvitrum rowei* (O'Loughlin 1991, 1994; O'Loughlin *et al.* 2009). *Squamocnus aureoruber*, which lives in algal holdfasts on rocky reefs in shallow water (0–8 m), divides by constricting the mid-body to a thread that is then severed (O'Loughlin 1991).

Family Ypsilothuriidae

Figure 11.10

The Ypsilothuridae have a U-shaped body enclosed in an imbricate covering of large plate-like ossicles, each with a tall spire, and 8–10 digitate tentacles, some of which are larger than others (Pawson & Fell 1965; Pawson 1982a; **Fig. 11.3F**). The family includes three genera, *Ypsilothuria* with multi-layered ossicles and eight tentacles; *Ypsilocucumis* which has similar ossicles but 10 tentacles; and *Echinocucumis* with single-layered ossicles and 10 tentacles (Panning 1949; Pawson & Fell 1965). The recent discovery of a new genus, *Psolidothuria*, off South Africa, with spire-less plates and eight tentacles, has blurred the distinction between this family and the Vaneyellidae (Thandar 1998), known from two equatorial Indo-west Pacific genera, *Vaneyella* and *Mitsukuriella* (Pawson 1982a).

Several species of *Echinocucumis* and *Ypsilothuria* have been collected from the Tasman and Coral seas at depths of 800–1,600 m (P.M.O'Loughlin, personal communication). Specimens of *Y. bitentaculata* were found off Western Australia in 2005 and 2007 (**Fig. 11.10**). *Echinocucumis ampla* was described from off Heard Island (O'Loughlin *et al*. 2015).

Little is known about the biology of these animals. They appear to live in a U-shaped burrow with only the mouth and anus projecting, and the digitate tentacles could be adapted to feeding on detritus. The reproductive biology of *Y. bitentaculata*, from deep water of the North Atlantic Ocean, has been studied (Tyler & Gage 1983; Tyler *et al.* 1985b). This species has large eggs (to 350 µm diameter) indicative of larvae with abbreviated development, although there is no suggestion that it broods its young. Sexes are separate, each female bearing up to 50 eggs at various stages of development, but there is no evidence of an annual reproductive cycle.

The earliest undisputed fossil record is *Palaeoypsilus liassicus* from the Lower Jurassic (202 mya) of southern Britain (Gilliland 1993).

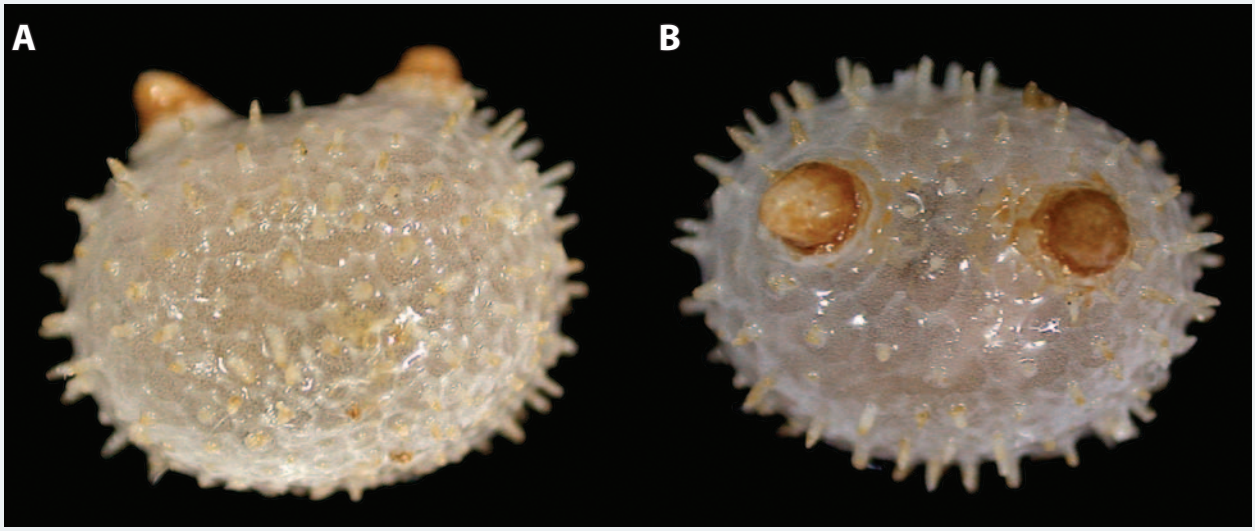


Figure 11.10 Family Ypsilothuriidae.

Ypsilothuria bitentaculata, found at a depth of 690 m off Ningaloo Reef, Western Australia, has both oral and anal ends orientated dorsally.
A, lateral view.
B, dorsal view.

[K.Gowlett-Holmes]

Order ASPIDOCHIROTIDA

Aspidochirotids have 15–30 shield-shaped tentacles (Pawson 1982a; **Fig. 1.16C**), and although tube feet and respiratory trees are usually present, there is no introvert. The gonads occur as one or two tufts, and the longitudinal muscles are usually in five double bands. The calcareous ring has larger radial than interradial segments, usually with a deep notch for a nerve in the centre of the distal margin, and body wall ossicles usually include tables. See **Figure 11.3G–I** for an illustrated summary of family characteristics. This order includes many of the largest holothuroids.

Traditionally, three families have been recognised: the predominantly shallow-water Holothuriidae and Stichopodidae, and the deep-water Synallactidae. These cluster on the available morphological cladograms of the Holothuroidea (Kerr & Kim 1999, 2001). The families are characterised by the disposition of their gonads and by the occurrence or otherwise of tentacle ampullae (Pawson 1982a). Smirnov (2012) recently transferred the Deimatidae from Elasipodida to Aspidochirotida, and referred the genus *Mesothuria* to a monotypic family. However, until these higher-level taxonomic changes are confirmed by genetic or cladistic data we retain the old classification for convenience.

Aspidochirotids are found worldwide, and while most occur in shallow water, a few species penetrate the abyssal zone. This order includes many species that are exploited commercially (see **Chapter 4**) and the biology and ecology of one of the most highly prized species, *Holothuria scabra*, has been extensively reviewed (Hamel *et al.* 2001). Aspidochirotids are deposit feeders, placing their spatula-like tentacles (**Figs 1.16C, 1.28**) in the substratum to capture particles on the surface of the tentacles and raking sediment into their mouths (Massin 1982b; Roberts *et al.* 2000).

The phenomenon of evisceration is exhibited by many aspidochirotids (**Box 1.1**). Following autotomy of internal ligaments the entire digestive tract, along with the respiratory trees, are discarded at the posterior end of the animal. Aspidochirotids have small eggs and development though a feeding auricularia larva (**Fig. 3.11F**) followed by the doliolaria stage (McEdward & Miner 2001).

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Family Holothuriidae

Figure 11.11

Holothuriids have long, slender tentacle ampullae, the gonad forms a single tuft on the left side of the dorsal mesentery, and body wall ossicles include table shapes and buttons (Pawson 1982a; **Fig. 11.3G**). This family includes many of the large species familiar to visitors to tropical coral reefs and bays. Some species with protein-rich body walls are collected for food and are the basis of important commercial fisheries (**Fig. 4.3**).

The Holothuriidae include five genera, by far the largest being *Holothuria*, with 172 species (Paulay 2015). This genus is characterised by the presence of perforated table-like or plate-like ossicles, a stout calcareous ring, a flattened ventral surface, and scattered conical sensory papillae on the dorsal surface (Rowe 1969). The genus was subdivided into 19 subgenera based on body wall ossicles (Rowe 1969), however, at least some of these probably deserve full generic status (O'Loughlin *et al.* 2007). Among the remaining genera, *Labidodemas*, with eight Indo-Pacific species, also has perforated table and plate ossicles, but its tube feet are mostly restricted to the five ambulacral rows, and it has narrow ribbon-like interradial pieces in the calcareous ring (Massin *et al.* 2004; Samyn *et al.* 2005). The monotypic *Pearsonothuria* (*P. graeffei*; **Figs 1.28, 2.16a**) has a stout ring with radial and interradial pieces of equal size, and knobbed pseudoplates and rosettes as body wall ossicles. *Actinopyga* and *Bohadschia* have only branched or lobed (rosettes) rods as body wall ossicles, while the former also has five prominent 'teeth' around the anus (Rowe 1969).

At least 60 species have been reported from Australia (Rowe & Gates 1995), most being restricted to shallow tropical waters. An exception, *Holothuria austrinabassa*, occurs on the continental shelf and slope (97–800 m) around southern Australia from Western Australia to off Portland, Victoria (39°S), making it the southernmost holothuriid (O'Loughlin *et al.* 2007). Interestingly, this species appears to be closely related to the most boreal taxon, *H. forskali* from the north-eastern Atlantic Ocean.

Molecular investigations are likely to result in many established 'species' being found to comprise additional 'cryptic' taxa. Recent examples include the discovery of more than one species within '*Holothuria nobilis*' (Uthicke *et al.* 2004a; **Fig. 4.3B,C**; **Box 4.1**), '*H. edulis*' (O'Loughlin *et al.* 2007), '*H. scabra*' (Massin *et al.* 2009; **Fig. 4.3A,D**) and '*Bohadschia marmorata*' (Clouse *et al.* 2005). The black striped *H. nigralutea* (**Fig. 11.11A**) is closely related to the pinkish *H. edulis* (**Fig. 11.11B**) (O'Loughlin *et al.* 2007). Other examples can have different colour patterns which are lost when preserved in ethanol in museum collections. Such discoveries have implications for commercial fisheries, which often assume a single stock when setting sustainable harvest limits (Uthicke *et al.* 2004a; Eriksson & Byrne 2015; **Box 4.1**).

Holothuriids are often abundant on sandy substrates in the tropics, with different species assemblages inhabiting inshore, mid-shelf and outer-shelf coral reefs (Hammond *et al.* 1985; Byrne *et al.* 2004b). They live in a range of habitats including sandy lagoons, seagrass beds, exposed reef flats and coral habitat, and due to their large size are often among the most conspicuous non-coral invertebrates in tropical and sub-tropical reefs (Hamel *et al.* 2001; Byrne *et al.* 2004b; Byrne 2008; Wolkenhauer *et al.* 2010; Purcell *et al.* 2016a). Being large deposit feeders, they play an important role in reworking the sediment (bioturbation), ingesting organic material, and nutrient recycling (Massin 1982a; Uthicke & Klumpp 1998; Roberts *et al.* 2000; Uthicke 2001b; Mangion *et al.* 2004). On the reef flat around Lizard Island, Queensland, *Holothuria atra* can consume up to 67 g dry weight of sediment per individual per day and, together with another common species, *Stichopus chloronotus*, has the potential to rework the top 50 mm of sediments in the area they inhabit over a year (Uthicke 1999). Another important bioturbator around the Great Barrier Reef is *Holothuria isuga* (**Fig. 2.38**). Some species appear to select sediment grains of a particular size (for example, *Actinopyga echinites*) whereas others do not (for example, *Holothuria atra*; **Fig. 11.1**), regardless of the size of the animal or tentacles (Massin & Doumen 1986).

Some species of *Holothuria*, *Labidodemas*, *Peasonothuria* and *Bohadschia* have a unique protective organ — white, sticky 'Cuvierian tubules' — that are often ejected from the anus or through the body wall when the animal is attacked or even handled (**Figs 2.18,**









Figure 11.11 Family Holothuriidae.

A, the strikingly coloured ***Holothuria nigralutea***, described only in 2007 from off north-west Australia, has since been discovered by SCUBA divers off Okinawa, Japan.

B, the pink ventral surface of ***Holothuria edulis*** is very characteristic. Despite being called the 'edible' sea cucumber, it does not support a high value fishery. This animal is from Ashmore Reef, off the north-west coast of Western Australia.

C, the flecked ***Holothuria hilla*** will reproduce asexually by fission during winter months. This species is nocturnal. This animal is from One Tree Island, Queensland.

D, Cuvierian tubules emerging from the anus of ***Bohadschia argus***.

[A, K.Gowlett-Holmes; B, W.Boyle; C, L.Roediger; D, C.Bryce]

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11.11D). These tubules can repel predators such as fish, and they can be regenerated within a matter of weeks (VandenSpiegel *et al.* 2000; Flammang *et al.* 2002). Other defence mechanisms include thickening of the body wall, toxins such as the red secretion holothurin released by *Holothuria atra* (Delia *et al.* 1977), body constriction and twisting in response to an attack by predatory molluscs (Kropp 1982), and the development of anal 'teeth' in *Actinopyga*, possibly a defence against the pearlfishes that infest holothuroid body cavities (**Fig. 2.24**). *Holothuria scabra* (**Fig. 4.3A**) has been shown to have a skin that contains anti-biofouling compounds that discourage the attachment of sessile molluscs (Selvin & Lipton 2004). However, the toxic chemicals exuded from the surface of *Holothuria* and *Bohadschia* also attract symbionts such as harlequin crabs (Caulier *et al.* 2013).

The reproductive cycle of holothuriids is variable: some species (for example, *H. impatiens*, *H. whitmaei*; *H. fuscogilva*) spawn seasonally, and others (for example, *H. edulis*) show no seasonal pattern (Harriott 1985; Ramofafia *et al.* 2000; Shiell & Uthicke 2006). In *H. scabra* in the Solomon Islands, gametogenesis occurs throughout the year (with a peak from September to December) making this a promising candidate for commercial aquaculture (Ramofafia *et al.* 2003). Although the potential for long-distance dispersal exists in many species, some remote populations show signs of being genetically distinct (Uthicke & Benzie 2001), with some genetic differences between populations dating back to the Late Pleistocene (Uthicke & Benzie 2003). The occurrence of distinct populations has implications for the sustainable management of these species (Uthicke & Benzie 2001), while low dispersal capability and slow growth can limit the capacity of local populations to recover from overfishing (Uthicke *et al.* 2004b). Natural hybrids between closely related species have been found, for example between *H. scabra* and *H. lessoni* (= *H. scabra versicolor*). However, these hybrids are likely to be sterile, as the population genetic structure does not show signs of introgression (Uthicke *et al.* 2005).

Several species of *Holothuria* can reproduce asexually by fission (**Fig. 3.8**), enabling rapid growth of local populations (Chao *et al.* 1994; Uthicke *et al.* 2001; Lee *et al.* 2008a). One of these, *H. atra*, can also reproduce sexually, thus facilitating dispersal to new sites (Uthicke *et al.* 2001). Fission and sexual spawning frequently occur in different seasons (Chao *et al.* 1994; Lee *et al.* 2008a; Thorne *et al.* 2013). *Holothuria atra* exists in two morphotypes, a small form which usually lives in the shallow intertidal that reproduces sexually and asexually, and a large form which usually lives in deeper water that only reproduces sexually (Uthicke *et al.* 2001; Lee *et al.* 2008a). It was thought that these may be two separate species, but this suggestion was not supported by genetic evidence (Uthicke *et al.* 2010). Interestingly if the small variety is translocated to deeper water it grows into large individuals that are only sexual reproducers. *Holothuria hilla* (**Fig. 11.11C**) and *H. difficilis*, species abundant on the Great Barrier Reef and Lord Howe Island, also reproduce asexually by fission and also have sexual reproduction (Lee *et al.* 2008b, 2009). *Holothuria difficilis* is found under boulders in the low intertidal and can reach high local densities, likely due to having a year-round pattern of fission (Lee *et al.* 2009).

Family Stichopodidae

Figure 11.12

Stichopodid holothurians have two gonad tufts, one on each side of the dorsal mesentery (**Fig. 11.3H**), no tentacle ampullae, body wall ossicles in the form of tables, C-shaped rods and, rarely, buttons, and, frequently, large warty projections on the dorsal surface (Pawson 1982a; **Fig. 11.3H**). Three of the nine genera occur in Australia — *Thelenota* and *Stichopus*, and the recently described *Australostichopus*. Most species occupy tropical shallow-water habitats, and they are often prominent members of the fauna around coral atolls (Sloan *et al.* 1979; Massin & Doumen 1986; Byrne *et al.* 2004b). Thirteen species are known from Australia (Rowe & Gates 1995; Lane 2008), although with at least two undescribed taxa from Lord Howe Island (Coleman 2007) and from Western Australia and Queensland (F.W.E.Rowe, unpublished data), as well as uncertainties regarding the identification of historical material this number is likely to increase. Most remarkably, the large and spectacularly coloured *Thelenota rubralineata* (**Fig. 11.12A**), also known as the 'candy-cane sea cucumber', was described only

relatively recently (Massin & Lane 1991) from the Indo-Malayan archipelago and, subsequently, was recorded from the northern Great Barrier Reef (Lane 2008).

Species of *Thelenota* (**Figs 4.1, 11.12A,C**) are some of the largest known holothuroids, reaching over a metre in length. They are characterised by the presence of dichotomously branched, thorny, rod-shaped ossicles, poorly developed table ossicles and the frequent occurrence of branched papillae on the dorsal surface (Samyn 2003). All three species have been reported from Australia, the most abundant being harvested under the common names 'amberfish' (*T. anax*) and 'prickly redfish' (*T. ananas*; **Fig. 4.1A**). *Stichopus*, the largest genus, with at least 21 species (Massin *et al.* 2002; Samyn 2003), is distinguished by the presence of well-developed table ossicles, 'C'-shaped ossicles and unbranched dorsal papillae. The temperate *S. mollis* from south-eastern Australia and New Zealand was transferred to a new genus, *Australostichopus*, because of its distinctive biochemistry (Moraes *et al.* 2004). It also lacks the 'C'-shaped rod ossicles that characterise *Stichopus*.

Several Australian *Stichopus* species are occasionally harvested in commercial quantities, including *S. chloronotus* ('greenfish'), and *S. herrmanni*, *S. ocellatus* and *S. vastus* (all known as 'curryfish'; **Box 4.1**). There is confusion among fishers about the identification of some species, with many specimens landed throughout the south-western Pacific as '*horrens*' (**Fig. 11.12B**) actually being *S. monotuberculatus* or *S. naso* (Byrne *et al.* 2010). Small experimental fisheries for *Australostichopus mollis* have been developed in New Zealand (see **Chapter 4**), but similar proposals for Victoria and Tasmania have floundered due to concerns about bioaccumulation of heavy metals and low yields (Barry & Parry 1993). Stichopodids are also fished in other parts of the world, one of the most infamous examples being the *Isostichopus fuscus* fishery on the Galapagos Islands. This fishery appears to be unsustainable due to over-harvesting and sporadic recruitment (Hearn *et al.* 2005).

The dull green *Stichopus chloronotus* is common on sand flats throughout the Great Barrier Reef and elsewere in the Indo-Pacific (Byrne *et al.* 2004b). The commercially important species *S. herrmanni* (**Fig. 4.3E**), now listed as vulnerable, is abundant in sandy lagoon habitats in the Great Barrier Reef in areas free of fishing (Eriksson *et al.* 2013). Other species, such as *S. monotuberculatus*, hide under coral slabs or in crevices during the day, emerging at night to feed. Several *Stichopus* species will disintegrate if handled for any length of time, an expression of change in the mutable connective tissue in the body wall (**Box 1.1**). Some species have the ability to shed sections of the body wall in response to attack by predatory molluscs (Kropp 1982).

Australostichopus is seen readily by divers around piers and rocky reefs in south-eastern Australia and New Zealand where it is the largest (up to 200 mm long) shallow-water holothuroid. Current, on-going, research (F.W.E.Rowe & M.Byrne, unpublished data) has determined *Australostichopus* comprises two species (*A. mollis* and *A. victoriae*) based on external morphology, colour pattern, molecular analysis and allopatric distribution. The brown *A. victoriae* extends from Houtman Abrolhos, Western Australia to Bass Strait, while the mottled *A. mollis* (**Fig. 1.1D**) occurs along the east coast of Tasmania, north to central New South Wales and east to New Zealand. The ecology and biology of *A. mollis* is very well studied in New Zealand, especially its feeding biology, role in sediment dynamics, reproduction and its potential for aquaculture (Sewell 1992; Slater & Carton 2007, 2009; MacTavish *et al.* 2012).

Stichopus chloronotus and *S. herrmanni* (**Fig. 4.3E**) are locally abundant on the Great Barrier Reef and due to their deposit feeding activity are major agents of bioturbation (Uthicke 1999; Eriksson *et al.* 2012). The deep-water Atlantic species *Parastichopus tremulus* has been reported to grasp sediment particles with its tentacles, preferring fine nutritionally rich sediment (Hudson *et al.* 2005).

Stichopodids exhibit sexual reproduction, and usually have separate sexes. A few hermaphroditic *Australostichopus mollis* have been collected (Sewell & Bergquist 1990; Sewell 1992). This species spawns between November and February in New Zealand, with a 3–4 week larval phase (Sewell & Bergquist 1990; Sewell 1992). Rarely seen juveniles differ from the adults in having a complete covering of soft balloon-like tubercules (R.S.Wilson *et al.* 2007). In addition to sexual reproduction, several stichopodid species,

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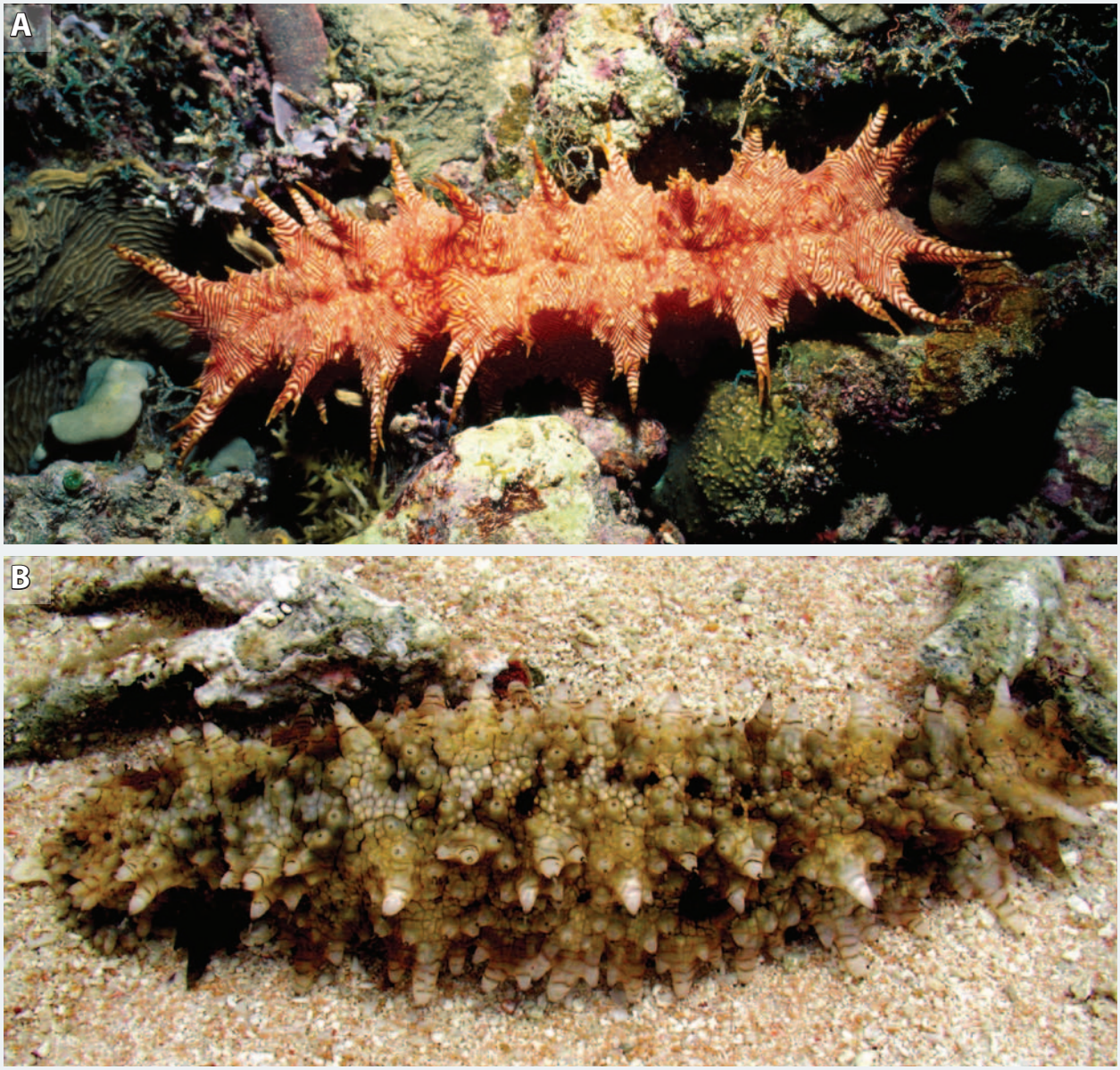


Figure 11.12 Family Stichopodidae.

A, the dramatic ***Thelenota rubralineata***, Madang, Papua New Guinea.

B, the widely distributed ***Stichopus horrens*** is nocturnal, hiding under coral rubble during the day. Raine Island, Great Barrier Reef, Queensland.

C, ***Thelenota ananas*** from Ashmore Reef, off north Western Australia, with its characteristic branched papillae over the dorsal surface.

[A, A.Flowers & L.Newman; B, M.Byrne; C, W.Boyle]

including *Stichopus chloronotus* and *S. naso*, reproduce asexually by fission, enabling rapid growth of local populations (Uthicke & Conand 2005). Although *Stichopus chloronotus* can reproduce asexually by dividing into anal and oral 'halves' (**Fig. 3.8**), sexual reproduction is also important, and populations show little genetic differentiation (Uthicke & Conand 2005).

Family Synallactidae

Figure 11.13

The deepsea family Synallactidae is defined as having peltate (shield-like) tentacles, an absence of tentacle ampullae, gonads in one or two tufts, and body wall ossicles that are table-shaped and, more rarely, 'C'-shaped rods or buttons (Pawson 1982a; **Fig. 11.3I**). The family has a cosmopolitan distribution, predominantly in deepsea habitats. The most recent inventory lists 17 genera and over 120 species (Paulay 2015).

The Synallactidae does not appear to be a well-founded family, seemingly containing a heterogeneous assembly of genera sharing only the lack of tentacle ampullae and deepwater distribution, which appears suggestive of a functional relationship between depth and ampullar development/requirement of the water-vascular system (F.W.E.Rowe, unpublished data). Moreover, Synallactidae include genera with one gonad tuft (*Mesothuria* and *Zygothuria*) and genera with two gonad tufts (all other genera), a characteristic used to distinguish the families Holothuriidae and Stichopodidae (both of which have tentacle ampullae and inhabit shallow water). Body form is also very variable among Synallactidae (for example, in *Synallactes*, *Pseudostichopus* and *Filithuria*). Several genera have been described with dendritic rather than peltate tentacles (for example, *Dendrothuria*, *Galatheathuria*, *Scotothuria*), whereas *Pseudostichopus* has rather nodulate tentacles. The variability of body wall ossicles is also considerable, showing similarities to holothuriids (for example, *Mesothuria*), stichopodids (for example, *Bathyplotes*), psychropotid elasipodids (for example, *Paelopatides*); or they can be absent (for example, *Pseudostichopus*). The taxonomy of the family was further confused by the inclusion of several genera in the molpadid family Gephyrothuriidae (Heding 1940), an error perpetuated for a time in the Australian fauna (Rowe & Gates 1995), but now rectified (O'Loughlin 1998b). Smirnov (2012), following the cladistic analysis and genetic data of Solís Marín (2003), placed *Mesothuria* and *Zygothuria* in a separate family, the Mesothuridae.

Two genera, *Pseudostichopus* and *Molpadiodemas*, have a distinctive pygal (vertical posterior) furrow in the body wall. Its function is unknown, but it possibly has a role in ensuring waste is disposed of as far away as possible from the animal (P.M.O'Loughlin, personal communication). The two genera differ in the position of tube feet, and the morphology of the longitudinal muscles and gonads (O'Loughlin & Ahearn 2005). Many of the species have been mis-identified in the past or have been mis-placed in other genera (such as *Echinomeseres*), so that historical records require confirmation. Three *Pseudostichopus* species (*P. hyalegerus*, *P. mollis* and *P. peripatus*) have been

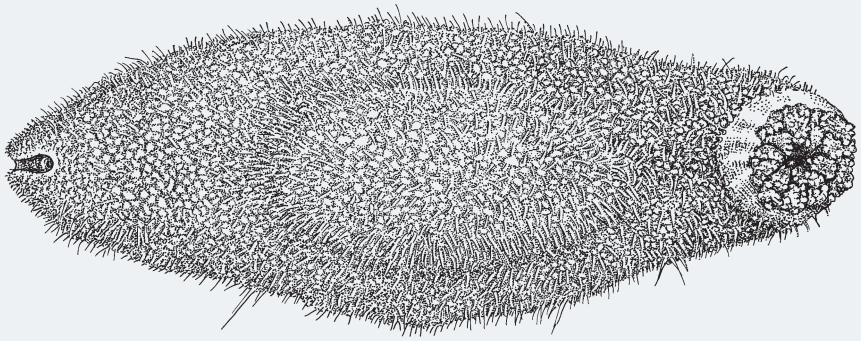


Figure 11.13 Family Synallactidae. ***Pseudostichopus spiculiferus*** embeds sponge spicules into its body wall, giving it a furry appearance. This animal was collected at a depth of 300 m in Prydz Bay, Antarctica. Ventral surface. Body length 100 mm. (specimen MNV F76598).

[K.Hollis]

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reported from the continental slope around Australia, and one from East Antarctica (*P. spiculiferus*) (O'Loughlin 2002; O'Loughlin & Ahearn 2005). Both *P. spiculiferus* and *P. hyalegerus* enclose themselves in a dense covering of sponge spicules (**Fig. 11.13**), and can easily be mistaken for small elongate sponges by inexperienced surveyors. *Molpadiodemas involutus* has been recorded from around Australia, and *M. crinitus* and *M. villosus* from East Antarctica.

Other genera recorded from Australia include *Mesothuria* (10 species), *Bathyplotes* (5), *Synallactes* (3), *Paelopatides* (2) and *Benthothuria* (1). In addition, several undescribed species (P.M.O'Loughlin, personal communication) have been collected from Australian and Antarctic waters (O'Loughlin *et al.* 1994, 2002; P.M.O'Loughlin, personal communication).

Ten synallactid species have been observed swimming, and, while they are not such efficient swimmers as members of the elasipodid family Pelagothuriidae, some have been recorded several hundred metres above the seabed (Miller & Pawson 1990) and, consequently, they could be regarded as benthopelagic. Others swim fitfully, and only in response to disturbance. Swimming occurs through undulation of the lateral brim, in a manner similar to cuttlefish, or by rolling and arching the body. Synallactids are deposit feeders (Neto *et al.* 2006), some species making deep burrows in the sediment (Massin 1982b; Moore & Roberts 1994). *Mesothuria* and *Pseudostichopus* have poorly developed tube feet and use body wall contraction to help them move across the seafloor (Billett 1991). One species, *Bathyplotes natans*, has been recorded as having lecithotrophic benthic larvae (McEdward & Miner 2001).

Order ELASIPODIDA

The Elasipodida is the dominant holothuroid order of the deep sea, with most species found only below 200 m. They are characterised by a lack of respiratory trees, having discoid tentacles with finger-like processes around the margin, and body wall ossicles in the form of wheels, crosses, perforated plates and/or pointed rods; see **Figure 11.3J–N**. They have characteristic ambulacral appendages, and the flat, ventral 'sole' is surrounded by extensible tube feet that are occasionally fused to form a brim-like swimming organ. Mid-ventral tube feet typically are reduced or absent. The dorsolateral margins are lined with sensory or respiratory papillae that are not connected to ampullae as in most other echinoderms. The oral end is orientated downwards, facilitating feeding on surface sediments (Hansen 1975).

This order is sometimes combined with Aspidochirotida in a subclass Aspidochirotacea due to their shared peltate tentacles (Pawson & Fell 1965). However, the ossicles are very different, and most similarities between the two orders are likely to be convergent (Hansen 1975; Smirnov 1984). The first fossils having the characteristic elasipodid ossicles are from the Devonian and Carboniferous periods, *viz.* the fossil family Protocaudinidae, characterised by having wheels with a central cross (Frizzell & Exline 1966). The order includes five families and at least 110 species (Hansen 1975). The families are distinguished by the morphology of the ossicles, calcareous ring, tube feet and papillae. Two suborders recognised by Hansen (1975) are not supported by quantitative cladistic analyses (Kerr & Kim 2001). Smirnov (2012) transferred the Deimatidae to the Aspidochirotida, arguing that the loss of the respiratory trees is a secondary development.

Elasipodids are adapted to life in the deep sea: species with extensible tube feet can use them like stilts to walk across the muddy seafloor, while fused tube feet or papillae can facilitate swimming. Many species are neutrally buoyant, being composed mostly of water, with relatively little organic matter in their body walls compared to other holothuroids. Deepsea photographs indicate that they are predominantly rake-feeders, grazing the surface layer, although some are opportunistic scavengers (Massin 1982b). Given their ubiquity they have potential to be useful bioindicators of human-induced disturbance such as that caused by deepsea mining for manganese nodules (Rodrigues *et al.* 2001). Many species are bioluminescent, emitting a bright blue light, particularly on dorsal papillae (Herring 1987). Despite the early origin of the order,

they should not be considered primitive forms capable of surviving only in the deep sea. Most of their unique structural and functional attributes are paedomorphic or specialisations for life at these depths (Hansen 1975).

Hansen (1975) documented the taxonomy, biology and biogeography of the group, and found evidence of distinct suites of species occupying 'bathyal' (200–400 to 1,800–2,600 m) and 'abyssal' (1,800–2,600 to 6,000 m) depths. The 'hadal' holothuroid fauna of the trenches was also unusual, with relatively few species, mainly in the family Elpidiidae, often occurring in great abundance. In the Kurile Trench, in the north-western Pacific Ocean, elasipodid holothuroids comprised up to 90% of all biomass at depths of 8,000–10,000 m (Zenkevitch & Birstein 1960). Hansen (1975) also argued that the unusual hadal fauna is more likely to be a product of the unusually rich sedimentation regime and young geological age of many trenches, rather than being influenced by water temperature or pressure. No single environmental factor appears to determine the distribution of elasipodid species; instead they are probably influenced by a combination of temperature, productivity and sediment type, with competition between species also being important. The bathyal holothuroids have a rather restricted geographical distribution, whereas many of the abyssal species are very widespread, some almost cosmopolitan. Many species in the south-western Pacific Ocean also occur in the North Atlantic Ocean. The central eastern Pacific has a few endemic abyssal species, perhaps because this comparatively nutrient-rich area is 'isolated' by the low-nutrient central Pacific (Sokolova 1972). A number of species appear to be endemic to geographically isolated trench systems.

The Abyssal Plane species *Amperima rosea* and *Ellipinion molle* (~4,000 m depth) exhibit pulses of very high local abundance that appear associated with the flux of phytodetritus to the deep seafloor (Billett *et al.* 2001). This so-called *Amperima* event of the mid-1990s indicates the opportunistic ecology of these boom-and-bust species (Wigham *et al.* 2003, Uthicke *et al.* 2009).

Family Laetmogonidae

Figure 11.14

Laetmogonidae are characterised by wheel-shaped ossicles (**Figs 11.3J, 11.4G**) with a central cross, gonads in one or more clusters of branched tubules, a typically gelatinous body wall, a weakly developed calcareous ring, and 15–20 tentacles (Hansen 1975). Fossil ossicles indicative of this family date back to the mid-Devonian (Kerr & Kim 2001).

The family includes six genera and 20 species (Paulay 2015). *Benthogone* has a distinctive ring of circum-oral papillae, and *Apodogaster* has a fused brim of ventrolateral papillae that lies outside the rows of tube feet. *Psychronaetes*, from the eastern Pacific, has a pronounced anterior 'head' with an irregular fringe of papillae (Pawson 1983), while *Pannychia* is distinguished from *Laetmogone* by the presence of mid-ventral tube feet and marginal teeth on the wheel ossicles (O'Loughlin *et al.* 2013). If a brim is present in these two genera it is formed from the fusion of ventrolateral tube feet (Hansen 1975). Laetmogonids occur predominantly on continental slopes, an exception being *Laetmogone*

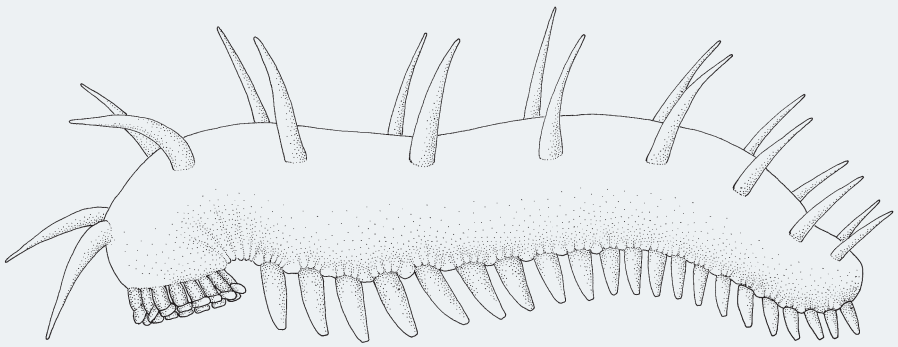


Figure 11.14 Family Laetmogonidae. The downturned mouth on ***Laetmogone wyvillethomsoni***, from Antarctic Prydz Bay, is an adaption to feeding on the seafloor. Body length 90 mm. (specimen NMV F68168).

[K.Nolan]

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wyvillethomsoni (**Fig. 11.14**) which is abyssal across the Southern Ocean, but rises to 200 m near the Antarctic continent (Hansen 1975; O'Loughlin 2002).

Three genera and 11 species are recorded from around Australia and off eastern Antarctica, including unpublished records of *Benthogone* off north-western Australia and undescribed species of *Laetmogone* and *Pannychia* (O'Loughlin *et al.* 1994; Rowe & Gates 1995; O'Loughlin 1998a; P.M.O'Loughlin, personal communication).

Although nothing is known of the biology of Australian species, detailed studies have been carried out on two north-eastern Atlantic species, *Benthogone rosea* and *Laetmogone violacea*. These appear to be selective feeders, and there is a greater concentration of chlorophyll in their gut than in surrounding sediments. They are spatially aggregated, probably in response to bottom currents winnowing planktonic detritus into hollows and around shallow mounds (Billett *et al.* 1988). Both species are bioluminescent, *L. violacea* emitting a brilliant blue light from the tips of the dorsal papillae when disturbed, while *B. rosea* has many tiny light spots all over the body (Herring 1974). Sexes are separate in both species and neither shows any pattern of reproductive seasonality (Tyler *et al.* 1985a). Egg size varies enormously, indicating variable life history strategies (Hansen 1975). There is a low level of genetic diversity within a population of *B. rosea* in the Bay of Biscay (Bisol *et al.* 1984).

Family Elpidiidae

Figure 11.15

Elpidiidae are characterised by a unique calcareous ring composed of five stellate radial pieces, body shape more or less globular, 10–12 tentacles, well-developed ventrolateral tube feet that are not fused into a brim, and no mid-ventral tube feet. Instead, many species

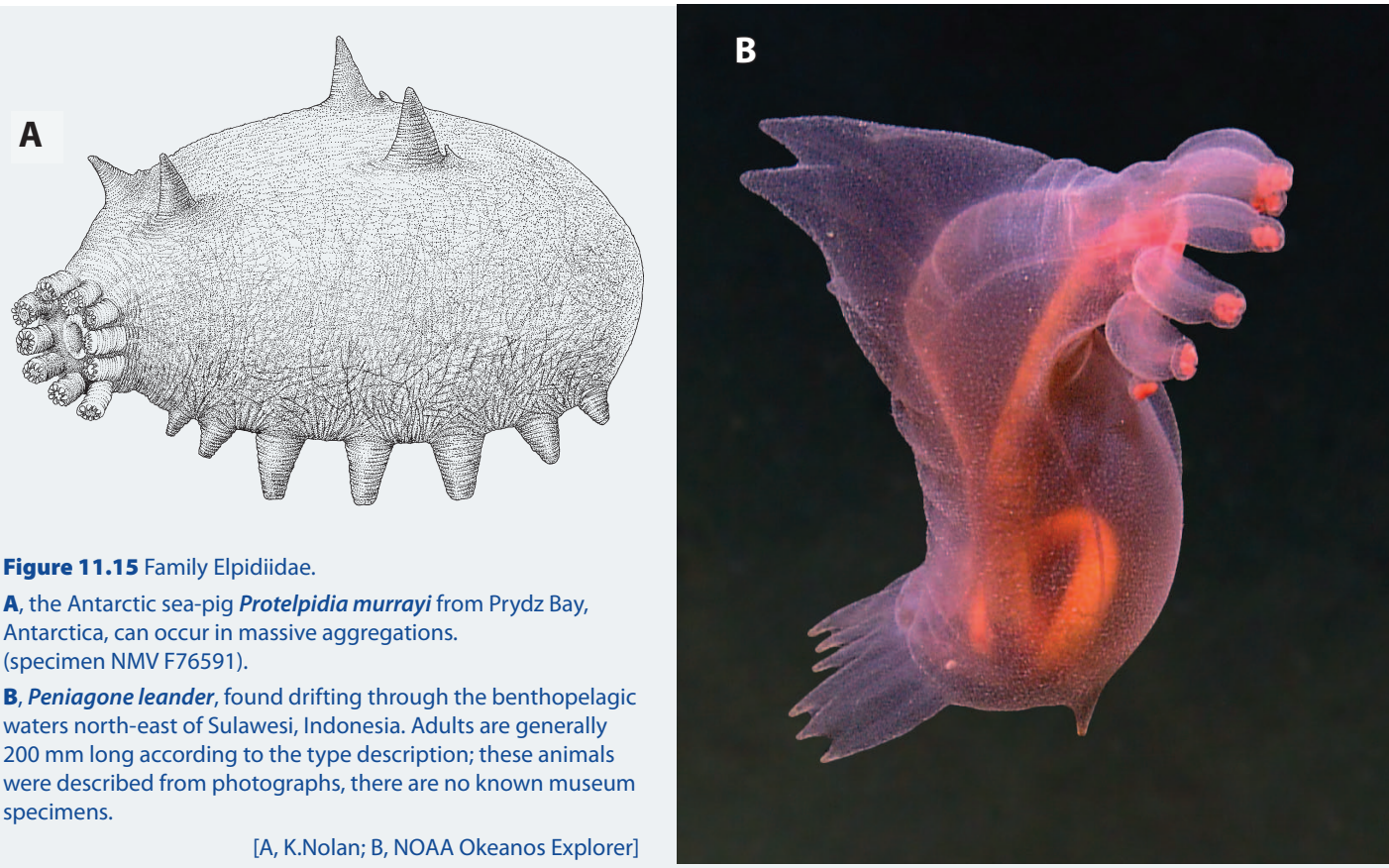


Figure 11.15 Family Elpidiidae.

A, the Antarctic sea-pig ***Protelpidia murrayi*** from Prydz Bay, Antarctica, can occur in massive aggregations. (specimen NMV F76591).

B, ***Peniagone leander***, found drifting through the benthopelagic waters north-east of Sulawesi, Indonesia. Adults are generally 200 mm long according to the type description; these animals were described from photographs, there are no known museum specimens.

[A, K.Nolan; B, NOAA Okeanos Explorer]

have a velum formed by the partial fusion of anterior dorsal papillae. When ossicles are present, they are in the form of spinous crosses or, very rarely, wheels (Hansen 1975; **Fig. 11.3K**).

Worldwide 13 genera and at least 100 species are known. The genera are mostly distinguished by the form of their body wall ossicles. The larger genera include *Peniagone* (32 species), *Elpidia* (22), *Ellipinion* (10), *Amperima* (8), *Achlyonice* (7) and *Scotoplanes* (5). *Elpidia* is somewhat aberrant in having distinctive ossicles that are rod-shaped with six arms and two perpendicular spines. Species of this genus lack a velum, and they have tentacle discs with marginal processes that are greatly enlarged along the aboral margin. This presumably gives the animals the ability to select sediment particles for organic content or size (Hansen 1975). Another genus, *Psychrelpidia*, shows some relationship with the Psychropotidae in having a unique brim formed from fused anterior dorsal and ventrolateral papillae, partly retractable tentacles and violet colouration (Hansen 1975). Gonads consist of clusters of tubules and are paired in *Peniagone* and *Psychrelpidia*, but unpaired in other genera (Hansen 1975). *Peniagone thieli* is bioluminescent, capable of emitting bright blue points of light over the dorsal surface, particularly on the tips of the podia and the two long anterior papillae (Herring 1974).

The development of a velum has been considered a specialised evolutionary development (Hansen 1975; Gebruk 1994), possibly facilitating swimming. Half the species of *Peniagone* can swim, and the benthopelagic *P. diaphana* (often referred to as *Scotoanassa translucida*) has been observed swimming by flexing the anterior and posterior ends of its body while it is in a vertical position (Pawson 1976; Billett *et al.* 1985; Tyler *et al.* 1985c). In contrast, *Scotoplanes*, lacking a velum, cannot swim, and it rolls away passively when disturbed by the bow wave of a submersible (Pawson 1976).

This family dominates many areas of the abyssal plain, and two species, *Scotoplanes globosa* and *Elpidia glacialis*, are frequently found in deepsea trenches at hadal depths. *Scotoplanes globosa*, often known as the 'sea-pig', is often described as one of the most abundant large (to 100 mm long) animals on the planet, although morphologically it appears to be a complex of similar species (Gebruk 1983). Elpidiids have adapted to the low nutrient conditions prevalent at these depths, having a highly developed intestinal system and limited food requirements (Hansen 1975). The peculiar calcareous ring and the small number of tentacles are likely to be paedomorphic rather than primitive features (Hansen 1975; Gebruk 1994).

Elpidia glacialis, *Protelpidia murrayi* (as *Scotoplanes globosa*; **Fig. 11.15**) and *Rhipidothuria racovitzai* (as *Achlyonice violaecuspidata*) have been reported in dense aggregations ('herds') in trenches bordering the Weddell Sea in Western Antarctica. Specimens of *R. racovitzai* were all facing away from the bottom current, suggesting that they minimise the section of the body exposed to the flow (Gutt & Piepenburg 1991). Herds of *Kolga hyalina* in the north-eastern Atlantic Ocean move in a coordinated group across the seafloor, perhaps in response to small-scale patchiness of organic matter (Billett & Hansen 1982), an optimal feeding strategy that reduces the number of animals that feed off the same patch of seafloor (Jumars & Gallagher 1982), or promotes reproductive success through spatial proximity of individuals (Billett 1991).

Elpidiid eggs are up to 2 mm in diameter, smaller than other families, but still of a size suggestive of abbreviated lecithotrophic development (Hansen 1975). Recruitment of *Peniagone diaphana* and *P. azorica* in the North Atlantic Ocean is probably infrequent and irregular, leading to patchy spatial distributions (Tyler *et al.* 1985c). *Kolga hyalina*, which can occur in large aggregations and then disappear from an area, has an opportunistic reproductive strategy that perhaps evades excessive predation on juveniles (Billett 1991). In the same region, populations of *Amperima rosea* rapidly increased over a few years possibly in response to fluctuating levels of plant detritus falling to the seafloor (Wigham *et al.* 2003). *Amperima rosea* produces small eggs (200 μm diameter) indicative of development through a feeding auricularia larva (Wigham *et al*. 2003). Reproduction occurs year-round and may be stimulated by environmental stimuli such as food supply (Wigham *et al*. 2003).

Species recorded from Australia include *Achlyonice margitae*, *Amperima furcata*, *Elpidia theeli*, *Peniagone challengeri* and *P. vitrea* as well as other undetermined

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taxa (O'Loughlin 1998a; P.M.O'Loughlin, personal communication). Both *P. challengeri* and *E. theeli* were described originally from abyssal depths off the south coast of Australia and Tasmania, respectively (Théel 1882; Hansen 1975). Another four species are reported from eastern Antarctica, including *Peniagone vignoni*, *Protelpidia murrayi* (**Fig. 11.15**; often misidentified as *Scotoplanes globosa*) and *Rhipidothuria racovitzai* (Gebruk 1990; O'Loughlin *et al.* 1994; O'Loughlin 2002; P.M.O'Loughlin, personal communication).

Family Psychropotidae

Figure 11.16

The Psychropotidae have a dorsoventrally flattened appearance with a brim formed from the fusion of ventrolateral tube feet. They also have mid-ventral tube feet, a gelatinous body wall with ossicles in the form of crosses with spinose tips or margins (**Fig.11.3L**), 15–20 tentacles, paired gonads and calcareous ring weakly developed or absent (Hansen 1975; Smirnov 2012).

The family includes three genera and 27 species (Paulay 2015). *Benthodytes* has the anus orientated dorsally, a circumoral ring of papillae that form a rim into which the tentacles can be withdrawn, and soft tentacle discs. *Psychropotes* and *Psycheotrephes* have the anus ventrally orientated (elongated into a 'tail' in *Psychropotes*), lack the circumoral papillae and have firm tentacle discs with marginal knobs. In addition, *Psychropotes* has an unpaired dorsal appendage. This family is mostly found on the abyssal plains with only a few species, especially *Benthodytes*, ranging onto the continental slope. Hansen (1975) has speculated that this family could have evolved entirely in the deep sea. Four species of *Benthodytes* and two species of *Psychropotes* are recorded from around Australia (Rowe & Gates 1995; O'Loughlin 1998a; P.M.O'Loughlin, personal communication; **Fig. 11.16**). None is known from the Australian Antarctic Territory, probably a reflection of a lack of abyssal sampling there.

All genera include species that can swim actively. *Benthodytes* species have been observed undulating their brim, in a manner similar to the swimming action of a cuttlefish (Pawson 1976), or slowly flexing the body in the vertical plane (Miller & Pawson 1990; **Box Fig. 1.5f**). However, they do not swim continually,

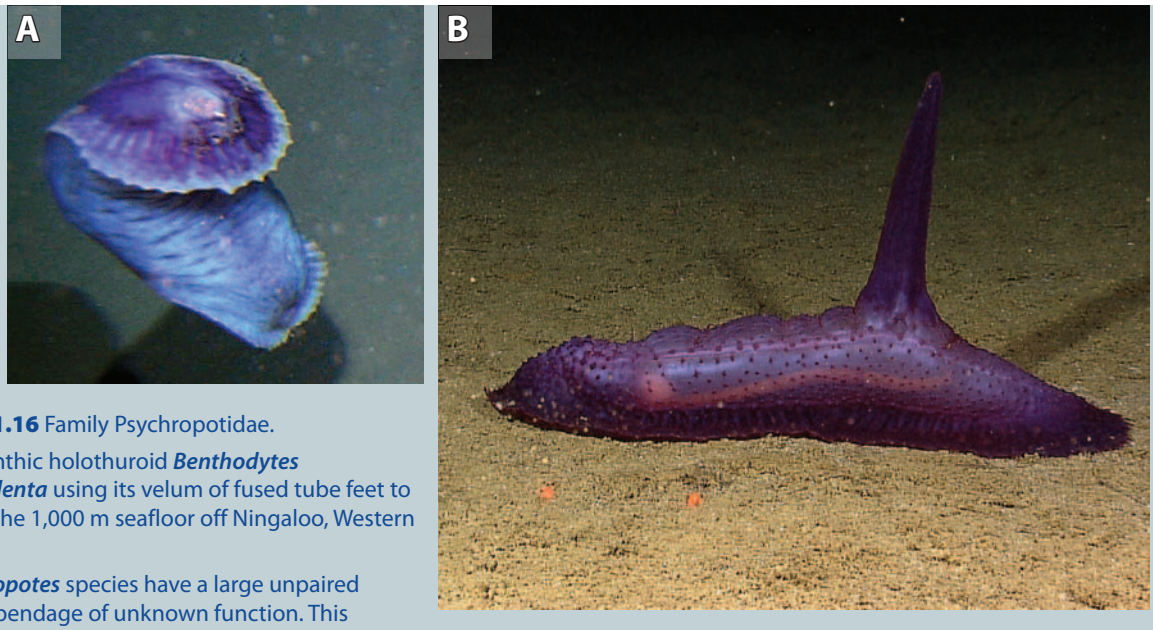


Figure 11.16 Family Psychropotidae.

A, the benthic holothuroid ***Benthodytes sanguinolenta*** using its velum of fused tube feet to swim off the 1,000 m seafloor off Ningaloo, Western Australia.

B, ***Psychropotes*** species have a large unpaired dorsal appendage of unknown function. This individual of ***P.*** cf. ***semperiana*** was photographed off Sulawesi, Indonesia.

[A, CSIRO; B, NOAA Okeanos Explorer Philippines]

but return to the seafloor to feed. Some species can be permanently benthopelagic as juveniles (Hansen 1975).

Benthodytes typica, which has been reported from Australia, lives on muddy sediments in the western Atlantic Ocean down to 4,000 m (Bisol *et al.* 1984). *Psychropotes longicauda* was observed to feed intermittently with cycles of filling and emptying the gut (Billett 1991; Moore & Roberts 1994).

One of the most interesting features of the Psychropotidae is the comparatively enormous size of their eggs. These can measure up to 4.4 mm in *Psychropotes longicauda*, which suggests that these eggs can develop directly into juveniles in the plankton (Billett 1991). Pelagic juveniles have been caught frequently in mid-water trawls, occasionally thousands of metres above the seafloor (Billett *et al.* 1985; Billet & Huggett 1987). Direct development could have the advantage of reducing vulnerability of juveniles to predation as there are few predators in abysso-pelagic waters (Billett 1991).

Family Pelagothuriidae

Figure 11.17

Pelagothuriids are a small specialised group of holothuroids characterised by their ability to swim using a flexible anterior brim (sometimes called a velum or veil; **Fig. 11.3M**) composed of fused tube feet. They lack a longitudinal row of mid-ventral tube feet, ossicles and a calcareous ring. These fragile animals are usually torn or distorted on collection, so knowledge of their anatomy and physiology is poor.

The family includes two species, *Enypniastes eximia* and *Pelagothuria natatrix* (**Box Fig. 1.5g**). Although only one species, *Enypniastes eximia*, has been recorded from waters around Australia (P.M.O'Loughlin, personal communication), both species are widespread, perhaps even cosmopolitan, in bathyal to hadal depths (500–7,060 m) (Gebruk 1989).

The swimming behaviour of both species has been observed in detail (Miller & Pawson 1990). *Enypniastes* is benthopelagic, only descending to the seabed to feed. It is generally observed swimming or drifting a few metres off the seabed, although on occasions it has been found well up in the water column and even at the surface. It is a bulbous animal with a large brim of 12 webbed conical

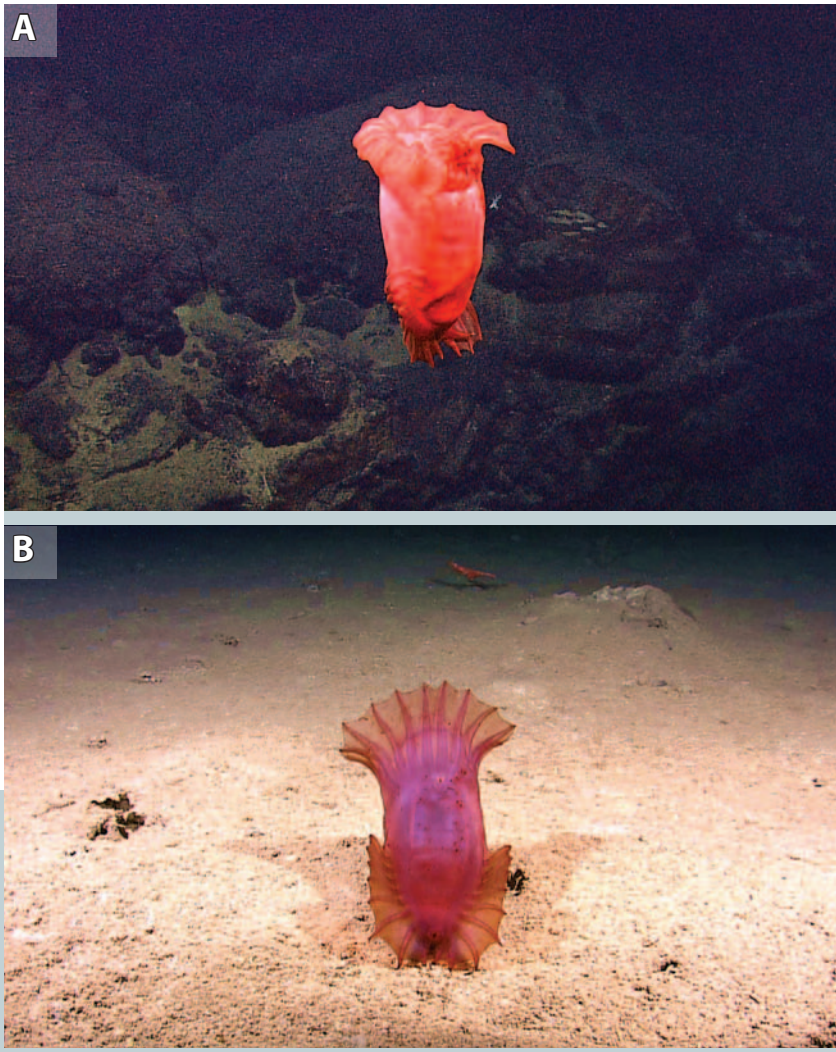


Figure 11.17 Family Pelagothuriidae.
The swimming holothurian ***Enypniastes eximia*** occurs worldwide, often in great abundance. Although pelagic (**A**), they feed off the seafloor (**B**).
[NOAA Okeanos Explorer Program, Galapagos Rift Expedition 2011]

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podia ringing the oral end, and two small posterolateral flaps with 10–15 webbed podia. The pulsating anterior brim is generally used to propel the animal and the posterior brim is for stabilisation. Unless in a strong current, movement is vertical with the mouth upward. After settling on the seafloor and lowering the anterior end, the tentacles are rapidly extended to grasp sediment and pass it to the mouth. Feeding lasts less than a minute before the animal ascends, possibly to avoid predators. Conversely, *Pelagothuria natatrix* appears to be truly pelagic. Its massively expanded anterior brim is held aloft like an upturned umbrella, possibly to catch detritus. Including the veil, *P. natatrix* reaches 160 mm in length. The reddish *E. eximia* is transparent, growing to 250 mm.

Family Deimatidae

Figure 11.18

This family has gonads forming a single cluster of unbranched tubules on either side of the body, these being more slender and numerous in males, a thin brittle body wall, and numerous body wall ossicles in the form of perforated plates, spatulate crosses and rods (Hansen 1975; **Fig. 11.3N**). Wheel ossicles are absent, and the calcareous ring is fragile and not separated into individual plates. Deimatids have between 15 and 20 tentacles, and the dorsal papillae are stiff and non-retractile; they lack respiratory trees. Smirnov (2012) has suggested transferring this family from the Elasipodida to Aspidochirotida on the basis that



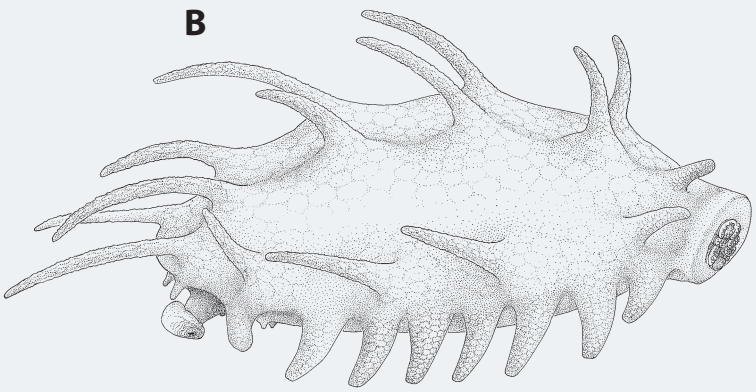


Figure 11.18 Family Deimatidae.

A, The numerous dorsal papillae on ***Orphnurgus glaber*** are probably used for respiration. Collected at a depth of 400 m off Ashmore Reef, north-western Australia. Dorsal view. Body length 130 mm. (specimen NMV F146595)

B, ***Deima validum***, found off Nowra, New South Wales, at depths of around 1,650 m, had a gut full of very fine mud. Body length 65 mm. (specimen NMV F77719)

[A, CSIRO; B, K.Nolan]

it has similar-shaped ossicles and calcareous ring to aspidochirotids, and interprets the lack of respiratory trees as a secondarily derived condition. Three genera are recognised (Hansen 1975; Paulay 2015), *viz. Deima* (2 species) with tentacles that can be retracted into the body and a specialised circumoral ring of papillae, and *Orphnurgus* (9 species) and *Oneirophanta* (2), which lack these features. The last two genera can be distinguished from one another by the morphology of the tentacle discs, these being covered in papillae and surrounded by ramified processes in *Orphnurgus*. This latter feature could be paedomorphic, as this tentacle form also occurs in juvenile *Oneirophanta mutabilis affinis* (Hansen 1975).

Four species have been recorded from near Australia. *Deima validum* (**Fig. 11.18B**) and *Oneirophanta mutabilis* have widespread, almost cosmopolitan, distributions, although populations in the eastern Pacific appear to be morphologically distinguishable at least at the subspecies level (Hansen 1975). *Deima validum* ranges from 750 to 4,820 m, whereas *O. mutabilis* is truly abyssal, occurring between 3,200 and 6,000 m. *Orphnurgus glaber* (**Fig. 11.18A**), known from a few specimens along Australia's north-western coast and the Lord Howe Rise, could be a complex of species (P.M.O'Loughlin, personal communication). The numerous species of *Orphnurgus* all have a limited distribution (Pawson 2002). There is also an undescribed species of *Oneirophanta* from off the New South Wales coast and around Lord Howe Island in depths of 800–3,100 m (P.M.O'Loughlin, personal communication).

Reproduction has been studied in populations of *Deima validum* and *Oneirophanta mutabilis*. The maximum egg size is 625–950 µm diameter, suggesting that they develop into lecithotrophic larva (Tyler *et al.* 1985b; Ramirez-Llodra *et al.* 2005). Intriguingly, no male specimens have been collected from the heavily sampled Porcupine Abyssal Plain in the north-eastern Atlantic Ocean, suggesting that this population is either parthenogenetic or their diet lacks organic compounds that are critical for sexual reproduction (Ramirez-Llodra *et al.* 2005). Males have been found in the closely related *O. mutabilis affinis*, which also broods its young in the ovaries (Hansen 1968, 1975). Such divergence in life history strategies suggests that this taxon should be treated as a species rather than subspecies. *Oneirophanta mutabilis* appears to feed and excrete continuously ('conveyor belt' feeder); its tentacles are digitate, enabling the animal to grasp sediment or rake it into the mouth (Moore & Roberts 1994).

Order SYNAPTULIDA

Members of the Synaptulida are worm-shaped animals with an elongate and roughly cylindrical body (**Figs 11.19, 11.20B**), completely lacking tube feet; see **Figure 11.3O–Q** for an illustrated summary of family characterisitcs. The descriptive former name 'Apodida' is no longer used, as there are similar names in other animal groups (Smirnov 2012). The body wall is very thin and often transparent, sometimes allowing the internal structures to be seen. The thin body wall is thought to facilitate gas exchange (Smiley *et al.* 1991) and is probably related to the absence of respiratory organs and a reduced haemal system. However, the body surface may be rough or sticky to the touch due to the presence of protruding ossicles, warty elevations or glands. Synaptulids have 10–25 simple, digitate or pinnate tentacles (**Fig. 1.16D**) and are unique among holothuroids in often having more than 10 plates in the calcareous ring, this being achieved by the insertion of additional interradial plates that correlate with the increased number of tentacles (Hyman 1955). The posterior margin of each plate can be somewhat concave or notched (Clark 1908a), but they lack the long posterior extensions seen in molpadids. Body wall ossicles can include miliary granules (very small calcareous granules), rods, wheels, sigmoid hooks, anchors and anchor plates (**Fig. 11.4**) or, rarely, they can be absent. Anal teeth and papillae, present in all other orders of holothuroids, are absent in the Synaptulida. Some species are also characterised by ciliated cups or vibratile urns, minute internal organs that appear

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to have an excretory function (Hyman 1955). These small, numerous, funnel-shaped bodies occur on the coelomic mesenteries or near the attachment of these to the body wall. Species range from a few millimetres to more than 3 m in length, the latter being among the longest echinoderms (Kerr 2001).

This order has been combined with the Molpadida, which also lack tube feet, in the subclass Apodacea (Pawson & Fell 1965). However, recent research confirms that the grouping of the two orders is unnatural, that the subclass arrangement does not reflect the evolutionary history of these animals (Kerr & Kim 2001). The few morphological features shared by these holothuroids have probably evolved in parallel, as adaptations to similar habitats and modes of life (Pawson & Fell 1965). Synaptulids are currently regarded as the most divergent group of holothuroids (Kerr & Kim 2001).

The Synaptulida comprises three families: the Chiridotidae, Synaptidae and Myriotrochidae. Numerous shared attributes of chiridotids and synaptids indicate a close relationship, while the myriotrochids appear more distant (Smirnov 1998; Kerr 2001). Characters including the form of the calcareous ring and body wall ossicles separate the families definitively, although the number and form of tentacles can also be diagnostic. Chiridotidae and Synaptidae are global in their distribution, mostly in shallow seas (Pawson 1982a). Myriotrochidae occur at greater depths and are described from polar regions and the Pacific, Indian and Atlantic oceans.

Family Chiridotidae

Figure 11.19

Adult chiridotids have 10, 12 or 18 digitate, peltato-digitate or pinnate tentacles (**Figs 11.3O, 11.19B**), although juveniles have bifurcate tentacles. Digitate tentacles are shortened, generally widened distally, with a few digits on each side, while in peltato-digitate tentacles the tentacle stalk is flattened and broadened distally. Plates of the calcareous ring lack the prominent anterior projections of the Myriotrochidae. Excavations for tentacle ampullae (small sac-like appendages arising from the tentacle canals) occur on the outer side of the calcareous ring. Body wall ossicles usually include miliary granules, curved rods, sigmoid hooks and wheels or wheel plates (**Figs 1.5C–E, 11.3O, 11.4H,I**). The wheels usually have six spokes (rarely 4–8), numerous tiny teeth on the inner rim and a star-shaped structure overlying a solid concave hub. The wheels can occur in aggregations, or they can be scattered throughout the body wall.

The family comprises 12 genera, six of which occur in Australian waters. Genera are distinguished by the number of tentacles, the combination of body wall ossicles and variations in ossicle morphology. Fourteen species are known from Australia and the Australian Antarctic Territory, the majority in temperate or polar regions, while five occur at subtropical or tropical latitudes. Australian species vary from just a few millimetres to about half a metre in length.

Chiridota gigas (**Figs 1.2H, 11.19A**) is the largest southern Australian synaptulid (Rowe 1982) and has been recorded from Tasmania, Victoria, New South Wales and New Zealand. This species can be distinguished by its pinkish colour and numerous white spots that are aggregations of wheel ossicles. The northern Australian *C. rigida* and *C. stuhlmanni* are found in shallow reef and coastal environments throughout the Indo-west Pacific region (Rowe & Gates 1995). Species of *Chiridota* generally have 10 or 12 tentacles (rarely 14), and their body wall ossicles include wheels and curved rods.

Polycheira rufescens occurs in shallow water in north-eastern Australia and throughout the Indo-west Pacific as far as East Africa. It can grow up to 270 mm in length and is dark reddish brown to black in colour, with slightly paler papillae that contain wheel ossicles (Thandar 1989b). Although *Polycheira* also exhibits wheel and rod ossicles in the body wall, the genus is easily differentiated from *Chiridota* by the presence of 18 tentacles (rarely 14–20).

The endemic Australian species *Scoliorhapis theeli* inhabits shallow temperate to subtropical waters from Western Australia to Victoria and Tasmania and north through New South Wales to north-eastern Australia (Rowe & Gates 1995). It is relatively uncommon and



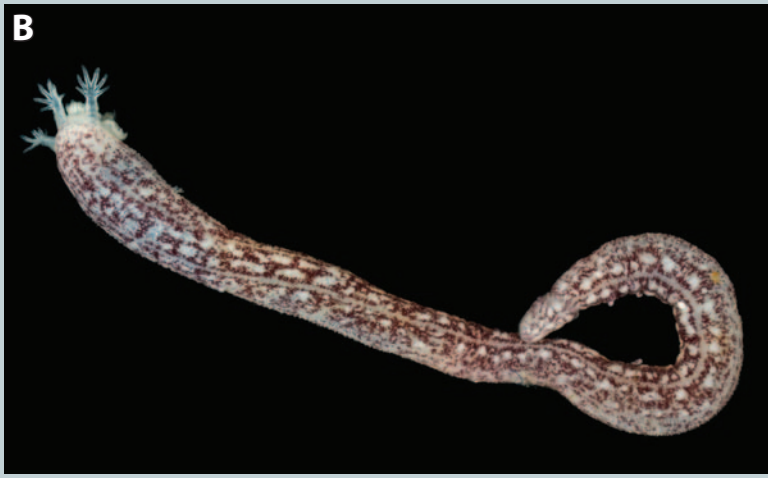


Figure 11.19 Family Chiridotidae.

A, the white flecks on the body of ***Chiridota gigas*** are composed of massed ossicles in the skin.

B, ***Rowedota epiphyka***, with hand-like or 'digitate' tentacles, lives under rocks along the coasts of southern Australia.

[A, W.Boyle; B, L.Altoff]

pinkish red in colour (Rowe 1982), although some material from Western Australia has been described as translucent whitish with numerous light purple papillae (Marsh & Pawson 1993). A preliminary analysis of Australian material in museum collections indicates that additional species of *Scoliorhapis* could be present here (P.M.O'Loughlin, personal communication). The genus is characterised by the presence of sigmoid hooks and the absence of wheel ossicles in the body wall. Hooks precede synaptulid wheels in the fossil record (Gilliland 1993), suggesting that *Scoliorhapis* could have evolved earlier than other chiridotids.

Archedota, described recently from the continental shelf in Bass Strait, has highly modified, irregular wheel ossicles (**Fig. 1.5D**) with spinous projections and no hook-like ossicles (O'Loughlin & VandenSpiegel 2007).

The remaining Australian chiridotid species were formerly grouped into two genera, *Taeniogyrus* and *Trochodota*, distinguished by the distribution of small teeth on the inner rim of the wheel ossicles, which are continuous in *Taeniogyrus* and non-continuous in *Trochodota* (Rowe 1976; O'Loughlin & VandenSpiegel 2007; **Fig. 11.4**). However, O'Loughlin & Vandenspiegel (2010) discovered that the type species of *Trochodota*, the Antarctic *Trochodota purpurea*, had continuous teeth after all, thus invalidating the genus. Consequently, the three southern Australian species formerly in *Trochodota* are now placed in a new genus *Rowedota*. *Rowedota allani* occurs in south-eastern Australia and is abundant in Port Phillip Bay, Victoria. This carmine-red to dark purple synaptulid can be up to 80 mm in length. The black *Rowedota shepherdi* can be found among algal epiphytes growing on seagrass in Corner Inlet, Victoria (T.D.O'Hara, unpublished data). The dark-flecked *Rowedota epiphyka* (**Fig. 11.19B**) lives on algae in the rocky shallows (O'Loughlin & VandenSpiegel 2007).

Taeniogyrus species include *T. roebucki*, found in sediment under rocks in shallow water in southern Australia. This red or brownish red species up to 80 mm in length is one of the most common species of the genus, and can occur in large clusters (Phillips *et al.* 1984). The minute *T. tantulus* has been found in massive aggregations (approximately 14,000 per square metre) on 10 m deep, offshore sediments in eastern Bass Strait (O'Loughlin & VandenSpiegel 2007).

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Several species of *Taeniogyrus*, including the Antarctic *T. contortus* and *T. magnibacula*, recently have been transferred to the genus *Sigmodota* on the basis that they have 12 tentacles rather than 10 as in other species (O'Loughlin & VandenSpiegel 2010).

Little is known of the biology of Chiridotidae. Larger species such as *Chiridota gigas*, in which ossicles form superficial mounds, have a rough or sticky body surface (Clark 1908a). Aside from having a protective function and giving the body some rigidity (Stricker 1986), ossicles can also provide traction against the substrate, thus aiding movement (Hyman 1955).

The tentacles of many chiridotids are digitate, their outer surface tending to be sticky (Roberts 1982). The external tentacle surface of the New Zealand species *Taeniogyrus dunedinensis* is known to secrete mucus (Pawson 1963). Tentacles can be extended randomly and flailed about to encounter food particles, or food particles can be collected during burrowing (Roberts 1982). *Taeniogyrus roebucki* is preyed upon by fish and has been recovered from the gut of Eastern School Whiting, *Sillago flindersi* (P.M.O'Loughlin, personal communication).

In Chiridotidae the sexes are generally separate (Lawrence & Herrera 2000), and collections of the temperate Australian species *Chiridota gigas*, *Rowedota allani* and *Taeniogyrus roebucki* include male and female specimens (Hickman 1962). *Chiridota gigas* spawns small eggs (~120 µm diameter) and has a feeding auricularia larva (Byrne *et al.* 2006). Species of *Taeniogyrus* exhibit a range of developmental modes. Thus, females of the Antarctic *Sigmodota contorta* incubate embryos inside the ovary (Smiley *et al.* 1991), and juveniles approximately 3 mm long are released through the genital opening (Clark 1908a). *Taeniogyrus dunedinensis*, from New Zealand, also broods, but embryos develop in the coelom (Smiley *et al.* 1991). In contrast, *T. australianus* is not viviparous, and the larvae have a planktonic developmental stage (Lawrence & Herrera 2000). The northern Australian *Polycheira rufescens* also has a planktonic larval stage, and spawning is correlated with phytoplankton growth in late summer (Chao *et al.* 1995). However, individuals of *P. rufescens* can change sex from male to female and back again in one reproductive season (Kubota & Tomari 1998; Arakaki *et al.* 1999). Asexual reproduction by fission, common among holothuroids, may occur in the Chiridotidae. For example, *C. gigas* can readily separate into two or several pieces when handled (Joshua 1914), but it is unknown whether any of the parts can survive and regenerate. However, in the Caribbean species *C. rotifera*, anterior ends can regenerate missing parts (Hadel *et al.* 1998).

Family Synaptidae

Figure 11.20

Synaptids are characterised by having 10–27 pinnate tentacles (**Fig. 1.16D**), although juveniles have simple tentacles (Smirnov 1998; **Fig. 11.3P**). Pinnate appendages consist of a central axis, usually tapered distally, with a row of digits along either side. The inner face of the tentacles often has sensory cups. As in the Chiridotidae, the plates of the calcareous ring lack prominent anterior projections, and excavations for tentacle ampullae occur on the outer side of the calcareous ring. Body wall ossicles only rarely are lacking, and they include miliary granules, anchors (**Fig. 11.3P**) and anchor plates. Wheel ossicles, similar to those found in chiridotids, occur in larval and postlarval synaptids, but they are absent from adults (Pawson 1971b).

The family includes 16 genera, eight of which are known from Australian waters. These are differentiated by the number of tentacles and by variation in the size and form of the ossicles. Most of the 22 Australian species have tropical distributions, although *Leptosynapta dolabrifera* and *Rynkatorpa hickmani* are found mainly at temperate localities (Rowe & Gates 1995).

Leptosynapta dolabrifera, one of the most common southern Australian holothuroids (**Fig. 11.20C**), varies from white to dark reddish purple, and can reach 150 mm in length (Phillips *et al.* 1984). It occurs in sediment in rocky or reef environments and in coastal waters from the intertidal down to 200 m (Rowe & Gates 1995). Like most synaptids, this species is rough to the touch due to the points of the minute anchor ossicles projecting from the thin body wall. The anchors are attached to the end of ovate, perforated

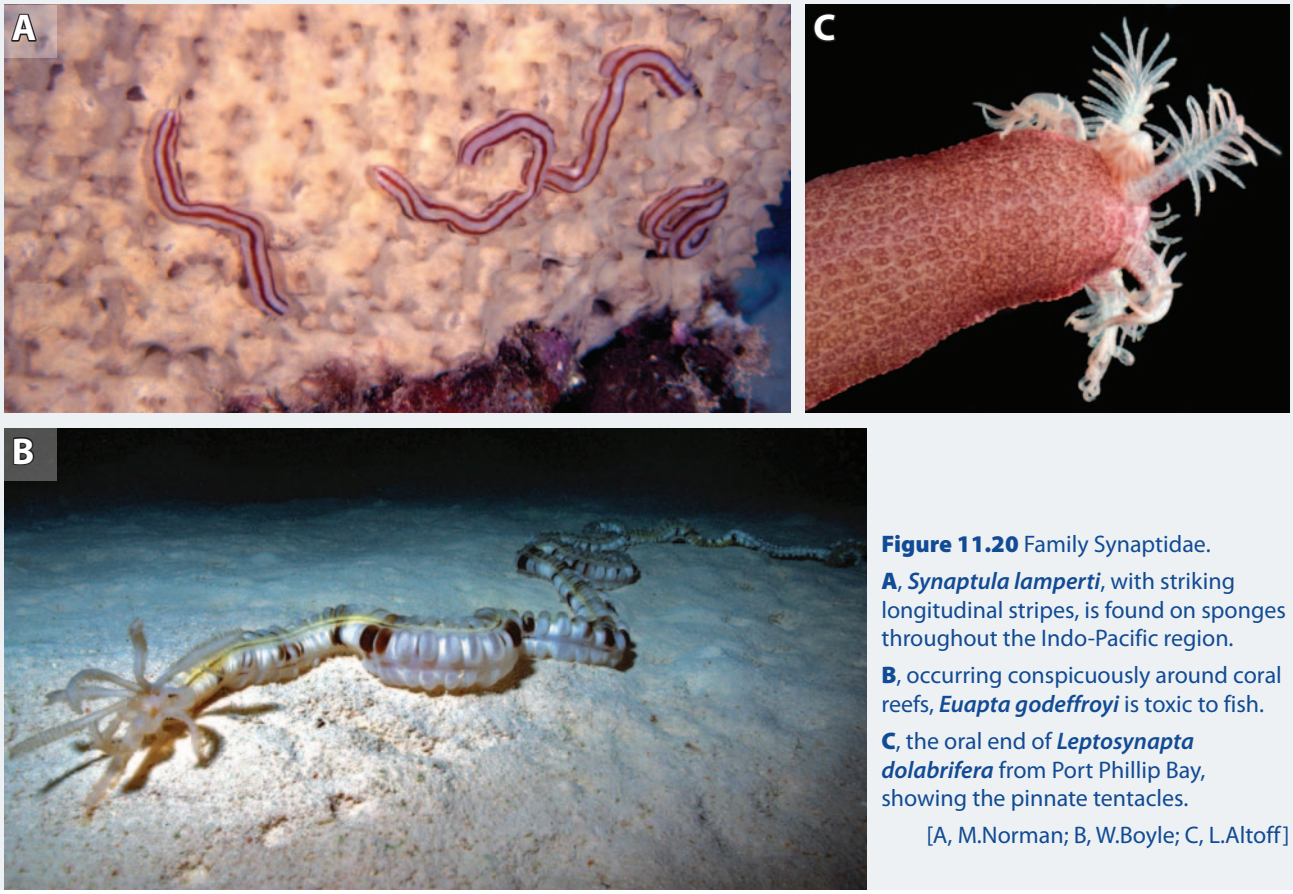


Figure 11.20 Family Synaptidae.

A, ***Synaptula lamperti***, with striking longitudinal stripes, is found on sponges throughout the Indo-Pacific region.

B, occurring conspicuously around coral reefs, ***Euapta godeffroyi*** is toxic to fish.

C, the oral end of ***Leptosynapta dolabrifera*** from Port Phillip Bay, showing the pinnate tentacles.

[A, M.Norman; B, W.Boyle; C, L.Altoff]

anchor plates, and they stand up from the plates at an angle of about 45 degrees. Stretching of the body wall causes the anchor to sink against the plate, bringing the pointed tips of their arms to the surface of the body wall without piercing it (Hyman 1955). This process gives synaptids some adhesion to the substrate and aids movement in the absence of tube feet. Locomotion is also facilitated by a combination of pulling motions by the tentacles and peristalsis of body musculature (Stricker 1985).

Synaptids include some of the longest echinoderms: some northern Australian species, such as *Synapta maculata* (**Fig. 1.16D**), can exceed 2 m in length. *Euapta godeffroyi* (**Fig. 11.20B**) is another long tropical species. *Synapta maculata*, common in shallow water in sand, reef or rubble environments and in seagrass beds, is found throughout the northern Indian Ocean from Indonesia to the Red Sea and East Africa (Rowe & Gates 1995). It is named for the black markings, or maculae, scattered over the brownish body. These animals generally feed by rhythmically furling and unfurling their pinnate tentacles. The unfurled tentacles spread over the substrate and detrital particles are collected between the nodules that cover their inner surfaces (Roberts 1982). Pinnate tentacles probably lack adhesive properties and operate mechanically by curling up and trapping surface particles for transfer to the mouth (Roberts 1982). The north-eastern Australian species *Opheodesoma grisea* also feeds in this way, and can consume diatoms, algae, small crustaceans, worms and other detritus (Massin 1982b). In contrast, the tropical *Synaptula lamperti* (**Fig. 11.20A**), found across northern Australia and Indonesia, is a highly specialised feeder and is found only in association with massive shallow water sponges (Gosliner *et al.* 1996). These holothurians derive at least part of their nutrition from

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sponge waste products (Hammond & Wilkinson 1989). Other species, including *Leptosynapta dolabrifera*, use tentacles to sweep sediment into the mouth selectively while burrowing. Nutrients are extracted through digestion and the residual material is egested as castings.

The anatomy and biology of the Synaptidae is quite well known compared to other synaptulid families. They have some complex sensory organs that are not found in other holothuroids. Wart-like elevations on the body surface include glandulo-sensory structures. With a ganglion under each elevation, these structures probably help to compensate for the lack of sensory information that might otherwise be provided by tube feet (Hyman 1955). Minute ciliated pits, known as sensory cups, occur on the inner surface of the tentacle stalk, and are thought to have a chemosensory function (Clark 1908a). These cups could allow synaptids to test the properties of the surrounding seawater and, possibly, provide information regarding palatability of particles collected by the tentacles (VandenSpiegel *et al.* 1998). Ocelli are innervated patches of pigmented cells that occur at the base of the tentacles in some genera and contain functional photoreceptive cells (Yamamoto & Yoshida 1978).

Many synaptids have separate sexes, and mature gametes are released into the water prior to fertilisation. The northern Australian species *Opheodesoma grisea* and *Synapta maculata* are known to spawn in late summer, and spawning is correlated with phytoplankton growth (Chao *et al.* 1995). Sexes are separate in *Leptosynapta dolabrifera* (Hickman 1962) but some synaptids, including other species of *Leptosynapta*, are hermaphroditic. In the latter, eggs and sperm usually develop simultaneously (Clark 1908a). The north-eastern Pacific species *L. clarki* is a protandric hermaphrodite in which individuals begin their reproductive lives as males but can change their sex, possibly more than once in their lifetime (Sewell 1994). The trigger for sex change is thought to be attainment of a certain size, in combination with some environmental or genetic factor (Sewell 1994). Some species of *Leptosynapta* and *Synaptula* brood embryos internally in either the coelom or ovary (Boolootian 1966), while *L. clarki* is an intra-ovarian brooder. Sperm are generally released externally and by some unknown mechanism enter the ovary to fertilise the eggs (Sewell 1994). The embryos are incubated in the ovary, receiving nourishment (Smiley *et al.* 1991), and functional juveniles 1–2 mm in length are released in spring (Sewell 1994). Some species of *Leptosynapta* can regenerate missing tissues through cell differentiation and/or migration. In *L. clarki*, regeneration always occurs from the anterior end, thus anterior pieces survive while posterior pieces die (Gibson & Burke 1983). A deepsea synaptid from the Atlantic Ocean, *Protankyra brychia*, has a planktotrophic larva that vertically migrates to surface waters (Pawson *et al.* 2003).

Soft-bodied organisms in shallow-water reef environments are especially vulnerable to predation. Many tropical holothuroids produce toxic or otherwise unpalatable compounds as a deterrent. Extracts of species of *Euapta* and *Leptosynapta* have been found to be highly toxic to fishes (Alender & Russell 1966).

Family Myriotrochidae

Figure 11.21

Myriotrochids have 10 or 12 digitate or peltato-digitate tentacles. Unlike chiridotids and synaptids, these holothuroids have plates of the calcareous ring with large anterior projections and excavations for tentacle ampullae on the anterior side. Body wall ossicles comprise wheels with numerous spokes, usually 8–25 (**Figs 11.3Q, 11.4J, 11.21**). The wheels can have large teeth or spines on the outer rim, and the inner rims can lack teeth or have large teeth. The wheel hubs can be perforated, solid or, rarely, with a 'button' (Gilliland 1993). Wheels are scattered throughout the body wall and are never aggregated, as in some chiridotids.

Worldwide the family includes eight genera and about 38 species, but only nine occur in the waters around Australia and Antarctica. *Prototrochus australis* has been reported from the Tasman Sea, and *Acanthotrochus antarcticus*, *Myriotrochus antarcticus* and *M. macquariensis* have been collected off the Australian Antarctic Territory or near Australian subantarctic islands (Belyaev & Mironov 1982; Smirnov & Bardsley 1997). Recently, five additional species of *Prototrochus* were described from the

Australian continental slope (O'Loughlin & VandenSpiegel 2007; O'Loughlin & MacIntosh 2015). Genera are distinguished mainly by the number of tentacles and by variation in the form of the wheel ossicles and the calcareous ring.

Myriotrochids, small synaptulids up to about 60 mm long, are found in soft sediments, generally in deepsea habitats, some specimens having been collected from 9,000 m. Some species are now thought to be essentially cosmopolitan, and the broad geographic separation of locality records could be the result of an uneven sampling of deepsea habitats as well the inherent difficulties associated with sampling infaunal animals in these environments (Gage & Billett 1986). Although myriotrochids can be locally common, very little is known of their biology. Intact specimens are rarely found in collections, fragmentation probably being a consequence of autotomy (Belyaev 1970; Gage & Billett 1986). Specimens of the subarctic species *Myriotrochus vitreus* separate into two pieces as soon as they are removed from water, the body dividing just posterior to the anterior end (Östergren 1902). Billett (1991) suggested that myriotrochids could produce large planktotrophic larvae that develop near the sea surface. Myriotrochids presumably process sediments and extract organic matter for nutrition (Pawson 1982a).

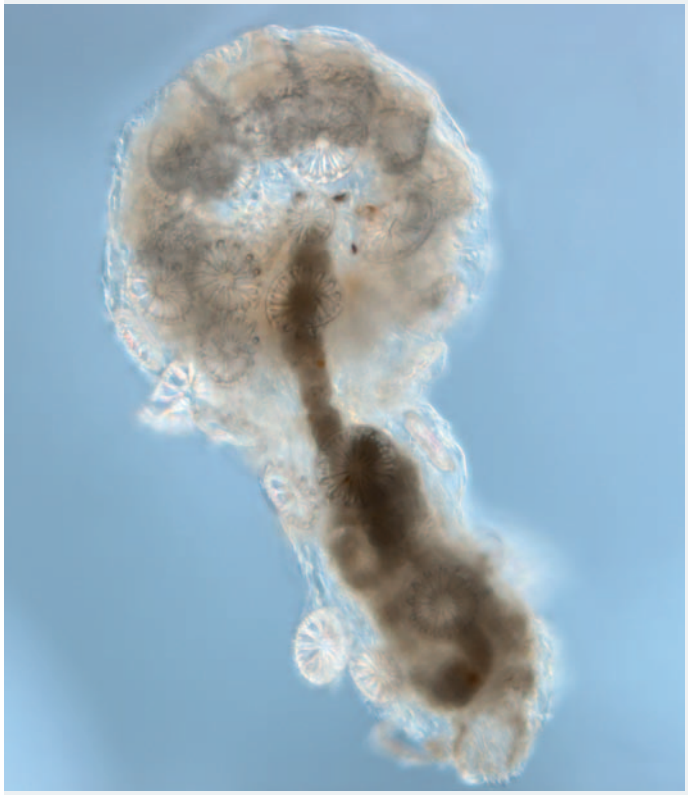


Figure 11.21 Family Myriotrochidae.
The oral end of the minute ***Prototrochus roniae*** known from the continental slope of the Great Australian Bight. Body length 0.9 mm. (speceimen SAM K4516)
[from O'Loughlin & MacIntosh 2015]

Order MOLPADIDA

Molpadids have a stout body that usually tapers posteriorly to a 'tail' (**Figs 11.22–11.24**). They lack tube feet, and the body wall is generally thick and firm. However, the family Eupyrgidae (not in Australia) is unusual in having a rigid, continuous 'test' (Kerr & Kim 2001). Respiratory trees and a well-developed haemal system facilitate gas exchange which is presumably otherwise reduced by the thickened body wall. Additional characteristics include 15 simple or digitate tentacles and radial plates of the calcareous ring having long posterior extensions. Body wall ossicles include tables, fusiform rods, racquets, anchor plates, anchors and crossed cups (see Gilliland (1993) for detailed descriptions and illustrations of these ossicle types); rarely, ossicles are absent. Orange and egg-shaped phosphatic deposits can also occur. Anal papillae, derived from tube feet, represent the only body surface remnants of these structures in the order (Hyman 1955), and anal teeth are known from only a few species (Gilliland 1993). See **Figure 11.3R–T** for a illustrated summary of family characterisitcs.

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The order was considered to include four families: the Molpadiidae, Caudinidae, Gephyrothuriidae and Eupyrgidae. However, recent analysis indicates the placement of the Gephyrothuriidae and Eupyrgidae within the Molpadida is problematic (Kerr & Kim 2001); Smirnov (2012) removed the Gephyrothuriidae to a new order. The families are distinguished by variation in overall body shape, and the form of the tentacles and body wall ossicles. The Molpadiidae and Caudinidae have essentially cosmopolitan distributions and live at depths ranging from the shallows to over 5,000 m (Pawson 1982a; Pawson *et al.* 2001). Gephyrothuriidae occur in deep water (some records below 8,000 m) and have been recorded from the Pacific, Indian and Atlantic oceans. Eupyrgidae are known only from Arctic latitudes and off Korea (Pawson 1982a). Molpadids show many morphological similarities to dendrochirotid holothuroids (Pawson 1982a) and a possible relationship between these groups is supported by the fossil record (Gilliland 1993).

Very little is known of the biology of molpadids. They are generally found buried in mud or soft sand, lying vertically or obliquely in the sediment with the anterior end orientated downward and the posterior end near the surface (Pawson 1982a). A combination of tentacles 'digging' into the sediment and peristaltic movements of the body musculature provide the mechanism for burrowing (Hyman 1955). As the animals burrow, sediment is ingested, usually non-selectively, and organic matter is extracted through digestion (Pawson 1982a; Pawson *et al.* 2001). Waste is voided as a cloud of sediment that builds up into a conical mound surrounding the animal's 'tail' (Massin 1982b). Molpadids mix the sediment through their feeding activities and locomotion; they are considered to be important bioturbators in some regions (Billett 1991). The orientation of the posterior end near to the surface of the sediment also facilitates respiration by the respiratory trees via the cloaca (Pawson 1982a). Deepsea species generally produce large, yolky eggs, and development probably involves a non-feeding larval stage (Billett 1991).

Family Molpadiidae

Figure 11.22

Molpadiids are usually characterised by tentacles having lateral digits and a terminal digit (**Fig. 11.3R**). However, the eastern Pacific genus *Ceraplectana* is distinguished by the presence of 10 claw-shaped tentacles (Clark 1908b). The radial plates of the calcareous ring have well-developed posterior extensions, and body wall ossicles can include triradiate and fusiform tables, fusiform rods, racquets, anchor plates and anchors. Phosphatic deposits can also be present and appear as

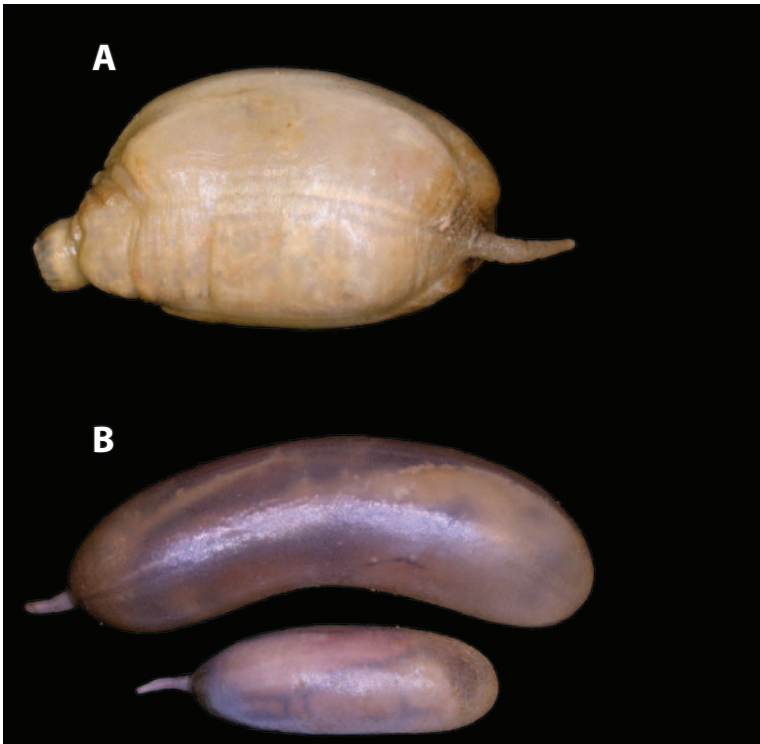


Figure 11.22 Family Molpadiidae.
A, an undescribed species of ***Molpadia*** from 1,920 m on the Lord Howe Rise. (specimen NMV F97705)
B, the sausage-shaped ***Molpadia lenticulum*** collected by the NORFANZ expedition on the Lord Howe Rise. (specimen MNV F 97706)
[K.Gowlett-Holmes]

pale orange to red granules of varying size. Anal teeth are rare, and are triangular or Y-shaped perforated ossicles (Gilliland 1993).

In addition to calcareous ossicles, many species of *Molpadia* have phosphatic deposits in the body wall. These minute, hard, subspherical structures are composed of amorphous hydrous ferric phosphate (Smiley *et al.* 1991). Phosphatic deposits develop as part of unique and radical transformation of the *Molpadia* 'skeleton'. As the animals grow and age, calcareous ossicles are resorbed while phosphatic granules are deposited (Pawson *et al.* 2001). However, the formation of calcareous ossicles can continue in the anterior and posterior parts of the body (Dubois & Chen 1989), and ossicles in the 'tail' do not become transformed into phosphatic deposits (Pawson *et al.* 2001). Partly resorbed ossicles have been observed inside some developing phosphatic granules, but most granules are deposited in areas of the body wall where ossicles do not occur, indicating that nucleation and accretion of granules does not depend on the presence of calcite (Dubois & Chen 1989). As individuals grow, their greyish-white bodies change to light or dark red or almost black due to the accumulation of ferric phosphate (Pawson *et al.* 2001). This phenomenon could be adaptive to low-oxygen environments, as a phosphatic skeleton is possibly more stable than a calcitic one under these conditions (Rhoads & Morse 1971).

The family includes three genera: *Cherbonniera*, *Heteromolpadia* and *Molpadia*. They are characterised primarily by tentacle number and form, as well as the combination and form of body wall ossicles. Only *Molpadia* is known from Australian waters, where it is represented by six species (P.M.O'Loughlin, personal communication) (**Fig. 11.22A,B**). These are differentiated by the variation in the form of body wall ossicles and by the presence or absence of phosphatic deposits.

Molpadia andamanensis is known from northern and eastern Australia at depths of 100–338 m and throughout the eastern Indo-west Pacific region (Rowe & Gates 1995). Recent research indicates this species also occurs off south-eastern Australia to depths below 2,000 m (P.M.O'Loughlin, personal communication). Its colour is deep reddish purple with the oral disc light grey (Clark 1946). *Molpadia dissimilis* is rather similar in appearance, and also occurs off New South Wales and on the continental slope of south-eastern Australia at 90–1,256 m (Rowe & Gates 1995). *Molpadia scabrum* is rusty-red in colour, with the tentacles and the tip of the tail white (Cannon & Silver 1986); it occurs in tropical waters off northern Australia and throughout the western Pacific Ocean, and has been collected from depths of 12–918 m (Rowe & Gates 1995). *Molpadia abyssicola*, *M. granulata* and *M. musculus* have recently been collected from eastern and south-eastern Australia at depths of 4,866 m, 1,150 m and 402–2,180 m, respectively (P.M.O'Loughlin, personal communication). *Molpadia lenticulum* (**Fig. 11.22B**) and an undescribed species (**Fig. 11.22A**) are present on Lord Howe Rise. There are also several species known from around Antarctica (O'Loughlin *et al.* 2011a) and across the Kerguelen-Heard Island plateau (O'Loughlin *et al.* 2015).



Figure 11.23 Family Caudinidae.
The rust-coloured species ***Paracaudina cuprea*** is usually completely buried in the seafloor of bays across southern Australia.
[W.Boyle]

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Family Caudinidae

Figure 11.23

Caudinids have tentacles with one or two pairs of lateral digits, but they lack a terminal digit (Pawson & Liao 1992; **Fig. 11.3S**), and the tail can be reduced or absent (species of *Acaudina*). The radial plates of the calcareous ring have long posterior projections, a trait that is shared with Molpadiidae. Body wall ossicles can include crossed cups, 3- and 5-pillared tables, perforated plates and irregular rods (Pawson & Liao 1992; Gilliland 1993; **Fig. 11.4K**). Phosphatic deposits and anal teeth are usually absent.

The family includes five genera, three of which occur in Australian waters. These are differentiated by the extent of the 'tail', the number of tentacle digits, and the combination and form of body wall ossicles. Twelve species have been recorded from Australian waters (Rowe & Gates 1995; O'Loughlin *et al*. 2011b).

Two species of *Acaudina* occur in northern Australia and are also found throughout the eastern Indo-west Pacific (Rowe & Gates 1995). *Acaudina leucoprocta* is purplish-brown or deep purple, with the posterior end white (Clark 1938), while *A. molpadioides* is pale grey with yellowish or brownish tentacles (Clark 1938). *Hedingia albicans* has been recorded from depths of 846–2,700 m off New South Wales, essentially it has a discontinuous cosmopolitan distribution (Rowe & Gates 1995).

Until recently four species of *Paracaudina* were listed for Australian waters. *Paracaudina chilensis* is a tropical species that occurs in northern Australia and in the eastern Pacific Ocean and west-central Atlantic Ocean (Rowe & Gates 1995). Three other species were considered to be temperate: *P. australis*, *P. luticola* and *P. tetrapora*. A review of the genus in Australian and New Zealand waters (O'Loughlin *et al.* 2011b), however, described five new species from southern and north-eastern Australia. Southern populations, formerly considered to be *P. australis*, are now called *P. cuprea* (**Fig. 11.23**), with *P. australis* restricted to northern and eastern Australia and perhaps Singapore. Another southern species referred to by Rowe (1982) as '*Paracaudina* sp.' is often seen along the beaches of Port Phillip Bay after storms, and has been named *P. bacillis*. The identification of species requires the examination of body wall ossicles. However, live colour can be a guide to some species: *P. australis* is a translucent pinkish-white, *P. cuprea* is rusty yellow-red and the other species are more or less off-white.

Family Gephyrothuriidae

Figure 11.24

Gephyrothuriids are unique among molpadids in having a barrel-shaped body. Although the posterior 'tail' is lacking, a caudal appendage is present as an extension of the cloaca (O'Loughlin 1998b; **Fig. 11.3T**). Whip-like papillae can occur on the dorsal surface, or

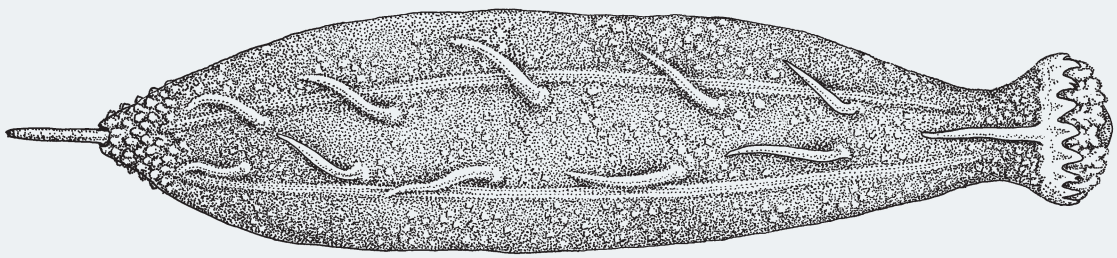


Figure 11.24 Family Gephyrothuriidae.

The tail on ***Gephyrothuria alcocki*** is actually an extension of the internal cloaca. Collected from off Nowra, New South Wales, 1,650 m. Dorsal view. Body length 35 mm. (specimen NMV F78394)

[K.Hollis]

rudimentary papillae can be present on the dorsal and lateral surfaces (Pawson 1982a). Tentacles bear two or three pairs of digits but they lack terminal digits and ampullae. Plates of the calcareous ring are fused and lack the posterior projections of Molpadiidae. Calcareous ossicles and phosphatic deposits are also absent (O'Loughlin 1998b).

The family consists of two monotypic genera (O'Loughlin 1998b). *Gephyrothuria alcocki* (**Fig. 11.24**) is cosmopolitan and has been collected from the eastern Australian continental slope to a depth of 1,750 m, while *Hadalothuria wolffi* occurs off Papua New Guinea at depths of 8,810–8,940 m (O'Loughlin 1998b). The two species are distinguished by external features: the form of the body and variation in papillae, and by internal features including the form of the calcareous ring and gonads.

Although little is known of the biology of gephyrothuriids, it is thought that they have a mode of life similar to molpadids (Pawson *et al.* 2001). Sexes are separate in *G. alcocki*, and adult males have a prominent genital papilla (O'Loughlin 1998b, 2001).

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