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HOLOTHURIANS

(Sea cucumbers, Class Holothuroidea)

by C. Conand

GENERAL REMARKS

Notes on the phylum Echinodermata

The holothurians or sea cucumbers belong to the Echinodermata which form a very distinct phylum in the animal kingdom. Echinoderms are characterized by the possession of a radial symmetry (generally **pentamerous)**, an intradermic skeleton consisting of closely fitted plates, articulated plates, or **ossicles**, and a peculiar water vascular system of tubes filled with fluid. The phylum is divided into 5 classes of very different appearance (Fig. 1): the crinoids (or feather stars), holothuroids (or sea cucumbers), echinoids (or sea urchins), asteroids (or sea stars), and ophiuroids (or brittle stars). Echinoderms are almost exclusively marine, although a few species are found in brackish water.

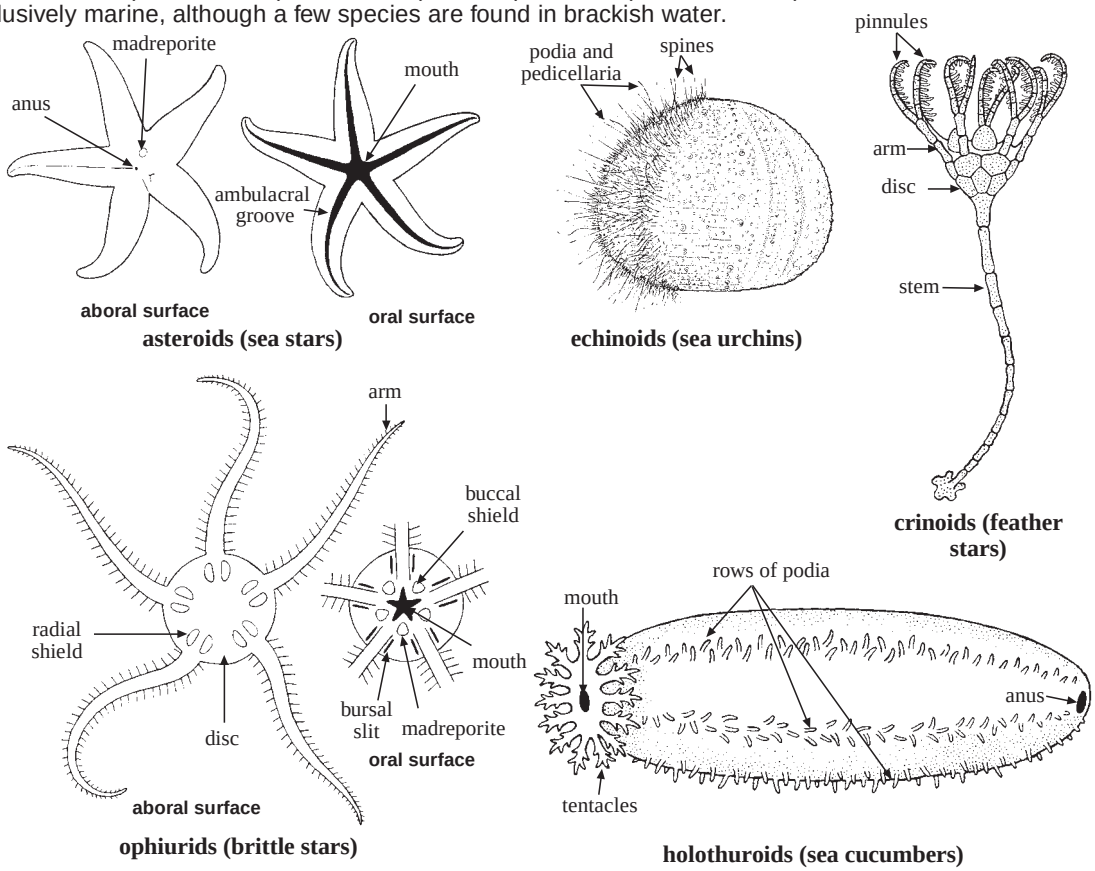


Fig. 1 the five classes of echinoderms

The body is of variable shape, rounded to cylindrical, or star-like, and subdivided into 10 areas (Fig. 2): 5 **radii** (or ambulacra) alternating with 5 **interradii** (or interambulacra). The radii correspond to the arms of the asteroids, ophiuroids, and crinoids, and to the rows of podia or papillae found in sea urchins and sea cucumbers. Some groups show a secondary bilateral symmetry. The holothurians are elongate orally-aborally and lie upon one side. Asteroids, echinoids, and ophiurids have the oral surface on the underside of body.

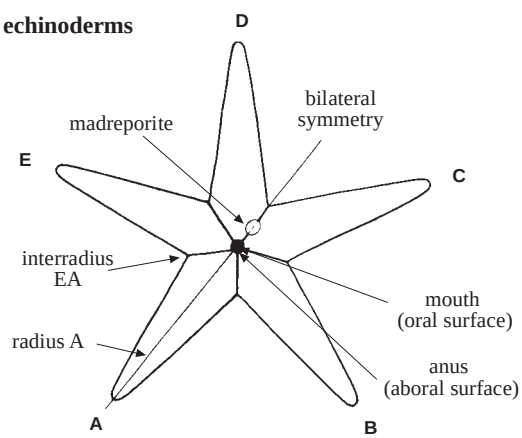


Fig. 2 schematic presentation of an echinoderm (following the Carpenter system for orientation)

The endoskeleton is produced by the dermis. It may be composed of closely fitted plates forming a rigid test or shell as in most echinoids, or articulated plates giving flexibility as in asteroids, ophiuroids, and crinoids, or consisting of calcareous spicules dispersed in the body wall, as seen in holothuroids. Spines and tubercules are parts of the endoskeleton and are covered by the epidermis. In addition, the body wall is composed of extracellular collagen-based material, the viscosity of which is controlled and provides rigidity or flexibility.

The general cavity (or coelomic cavity) contains the viscera. The water vascular system or **aquiferous system**, consists of a circumoral ring, from which arise radially water canals forming many extensions, the tube feet or **podia**. The **madreporite** is a plate with tiny pores which allows the communication with the environment. It is always situated in an interradial position and serves for the orientation: the opposite radius is called A and is followed, in a clockwise direction, by radii named B, C, D, and E (according to the "Carpenter system" for orientation, see Fig. 2).

Despite the differences between the classes, there are several common features in the digestive system of echinoderms. This system is conspicuously developed and attached by mesenteries to the body wall. Its shape is simple, either bag-like as in ophiuroids, or tube-like, looping in the general cavity as in crinoids, echinoids, and holothuroids. In asteroids, it forms conspicuous specialized organs. Structural variations appear progressively along the gut. A hemal system is associated with the digestive system. Its importance varies among the different classes.

The respiratory exchange partly occurs by means of the podia, and partly by specialized organs that differ among the classes.

The genital system is composed of a single gonad in holothuroids, a genital cord sending extensions to the pinnules of the arms in crinoids, and 5 gonads in the other classes. Sexes are generally separated, but cannot be distinguished externally. In most species, mature gametes are released into the sea. After fertilization, the development often passes planktonic larval stages with a bilateral symmetry, until the larvae metamorphose into benthic juveniles.

Species identification is done by examination of preserved specimens, mostly based on characters of the skeleton. Echinoderms should be preserved in alcohol, as formalin may dissolve the calcareous skeleton. In addition to the morphological characters, the colour, size, and ecology of live specimens can be useful for identification.

To date, approximately 6 000 described echinoderm species are known worldwide, living in all kinds of marine bottoms where they represent an important component of the benthic biomass. About 1 000 littoral species are known to occur in the Indo-West Pacific.

Among the 5 classes of echinoderms, only echinoids and holothuroids are of interest to fisheries. The holothurian fishery of the Western Central Pacific is the largest of the world (Conand, 1997).

External morphology of holothurians

Holothurians have an orally-aborally elongated body (Fig. 1). The body is formed like a short or long cylinder, with the mouth (at the anterior end) encircled by **tentacles**, and the **anus (**at the posterior end) often edged by papillae. The pentamerous symmetry is sometimes recognizable by the presence of 5 meridional **ambulacra** bearing **podia**. Holothurians often lay on the substrate with their ventral surface or **trivium**, formed by the radii A, B, and E in the Carpenter system for orientation. This creeping sole bears the locomotory podia, while on the dorsal surface, or **bivium**, the podia are often represented by papillae. Consequently, a secondary bilateral symmetry is evident. The body shape is different in the orders Apoda, members of which are vermiform, and Molpadida, members of which have a tail-like region bearing the anus. In the order Elasipoda, some extraordinary forms are found, with modified papillae making up sails.

The **mouth** is terminal or displaced dorsally, surrounded by a thin buccal membrane, and generally bordered by a circle of **tentacles** (Fig. 1). Tentacles are buccal podia containing extensions from the water vascular system. Their number varies between 10 and 30, generally being a multiple of 5. In the **Aspidochirotida** all tentacles are of the same size, but in the **Dendrochirotida** some tentacles are generally smaller. The shape of the tentacles differs among the various orders and is used as a key character (Fig. 3). In the Dendrochirotida they are **dendritic** (branching in an arborescent manner) and can reach a large size when extended. The Aspidochirotida and most Elasipoda have **peltate** tentacles, each with a central stalk. The Apoda have **pinnate** tentacles, with a central axis bearing series of digitations. The Molpadida have **digitate** tentacles, consisting of short projections with small terminal fingers. In all cases they are very retractile, particularly in the Dendrochirotida which have an **introvert** where the tentacles insert. The tentacles and the introvert can be contracted into the interior by a set of retractor muscles. These muscles also occur in a few Apoda and Molpadida, but not in the other orders.

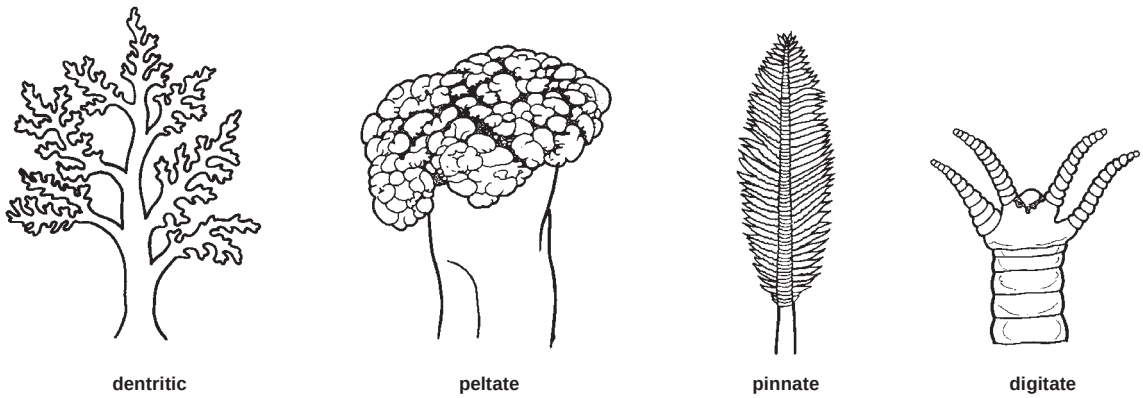


Fig. 3 basic types of tentacles

The body surface is thick, slimy in many species and wears warts, tubercules, or **papillae**. **Podia** appear on the body wall in 3 orders, but they are lacking in the Apoda and rare in the Molpadida. They typically have the form of locomotory tube feet: hollow tubular projections from the body wall form a stem, which allows the podium to lengthen, flex, or retract. It contains a branch of the water-vascular system and generally does not terminate in a concave sucker (as it is still often called), but in a flat disc, which allows the podium to adhere to the substratum during locomotion. Epidermal cells produce adhesive secretions. Internally the disc is supported by a large skeletal ossicle. Podia also can have the shape of papillae. The tube feet are rarely arranged in 5 regular rows, but generally they loose the discs on the dorsal surface and spread into the interradial areas. The **anus** is often displaced dorsally, encircled by small papillae or **anal teeth**. The coloration varies between species and sometimes also between individuals of the same species. The creeping sole is often brighter and lighter than the dorsal surface.

Body wall

The body wall is thin in Apodida and Molpadida, but thicker in the other orders, particularly in the Aspidochirota. It constitutes the part of the body that is processed for human consumption and therefore commercial species are characterized by a thick body wall. Its structure consists of a thin cuticle over the epidermis and a thick dermis underneath. The dermis is composed of connective tissue, enclosing the endoskeletal spicules or ossicles (see next paragraph). Below the dermis, a layer of circular muscles form a cylinder generally interrupted by 5 longitudinal muscle bands situated in the radial positions.

Spicules

Also called ossicles or deposits, spicules (Fig. 4) are characteristic of the class and of primary importance for identification. These are fenestrated (or perforated) calcareous bits of microscopic size. There is a wide variety of simple to complex shapes. **Rods** can be simple or branching, smooth, warty, or spiny. They can bear knobs at their ends, or are a characteristic C- or S-shape. Fenestrated **plates** also come in various forms. **Buttons** are oval ossicles, perforated with a varying number of holes arranged in 2 rows. **Tables** are more complicated. They appear as a perforated disc, bearing an erect **spire** (or tower) and show many variations according to the arrangement of its constituents. **Rosettes** are short rods subdivided into short branches. **Baskets** are concave, perforated plates. **Anchors** are peculiar of the family Synaptidae (order Apoda). They are orientated in the body wall, so that they support the attachment to the substrate during crawling, in the absence of podia. They are attached to an accompanying perforated plate. **Wheels** are characteristic of the family Chirodotidae (order Apoda) and are also found in the Elasipoda, which are best characterized by the presence of special spiny branched spicules. Miliary bodies (**grains**) are very tiny spicules found in some Stichopodidae. Apart from the body wall, spicules are found in the tentacles, the podia, and also in the mesenteries or other internal organs. Their developmental stages can differ from the definitive shapes in the adults and thus can make species identification difficult.

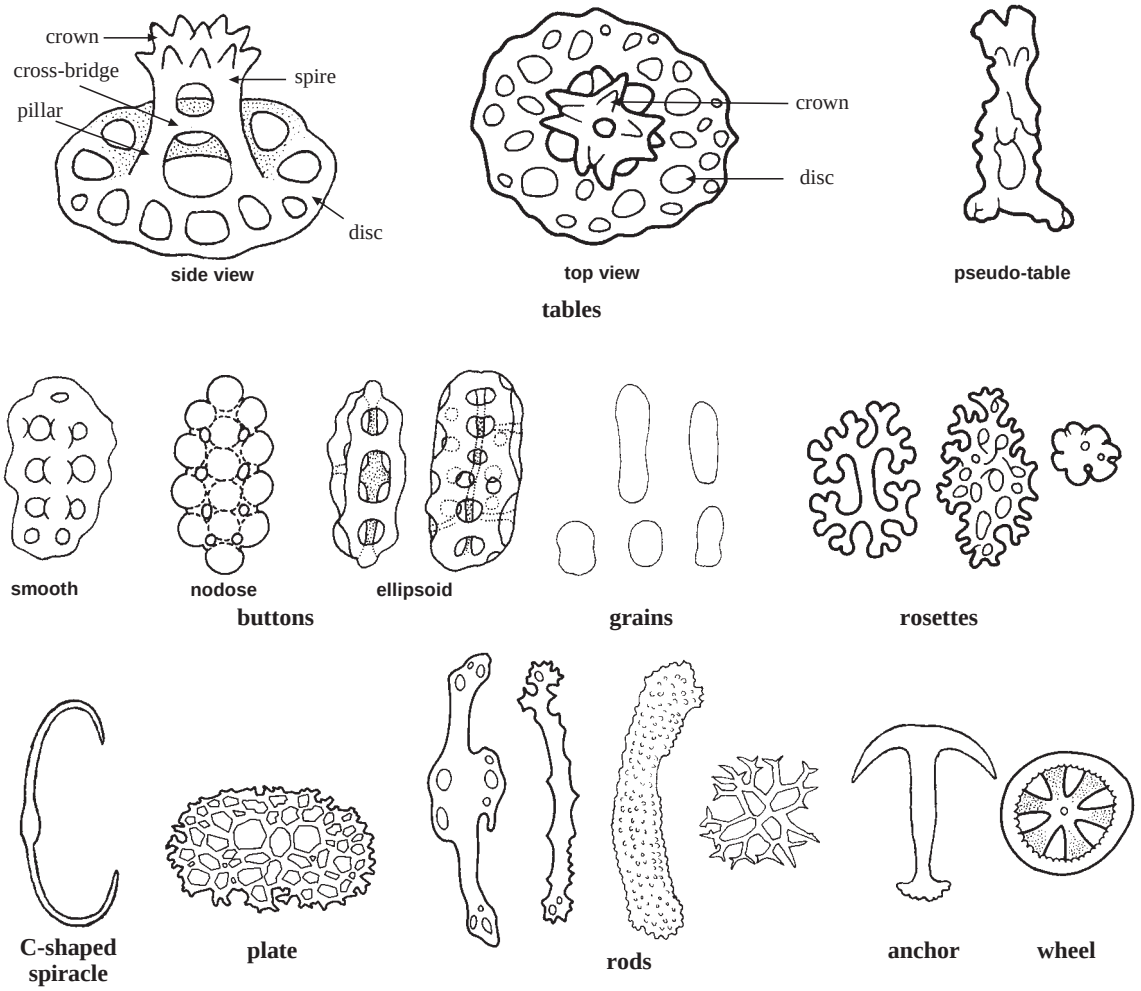


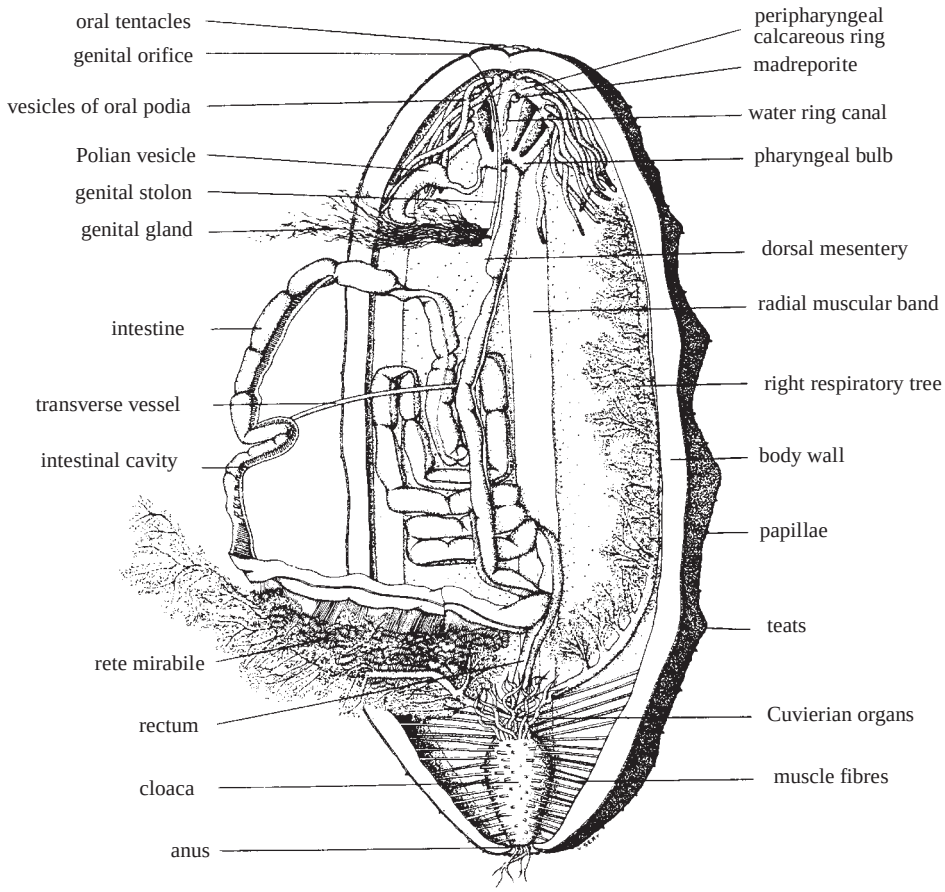
Fig. 4 basic types of spicules

Calcareous ring

A ring of usually 10 calcified plates encircles the pharynx. It is composed of alternating larger radial plates, opposite to the ambulacra, and smaller interradial plates. The plates may be simple or composed of smaller pieces. Longitudinal muscles attach to the radial plates.

Digestive system and connected organs

The gut is composed of a pharynx, an esophagus, a stomach, all of which are short structures, and a very long intestine (Fig. 5). The intestine consists of 3 portions, a descending, an ascending, and finally a descending loop which connects to both the rectum and the **cloaca** opening outwards through the anus. When present, **respiratory trees** are connected to the cloaca. The oxygenated water enters the body by these water lungs, which are found in all orders except the Apoda. **Cuvierian tubules**, present in several species of Aspidochirota, are generally considered as defensive structures. They are composed of sticky tubules attached to the base of the respiratory trees and can be expelled in some *Holothuria* and *Bohadschia* species through the cloaca towards the source of irritation.



(from Conand, 1986)

Fig. 5 anatomy of a holothuroid (*Holothuria nobilis*)

Reproductive system

In contrast to other echinoderms, the reproductive system of holothurians consists of a single **gonad** or genital gland (Fig. 5). The gonad is situated dorsal (interambulacrum CD) and composed of either 2 tufts of tubules, or only 1 tuft in many species of the family Holothuriidae. The sexes are generally separated and show little dimorphism unless in the period of maturing. The gonad is attached to the dorsal mesentery through which the **gonoduct** or genital stolon opening passes, leading to the outside by the **gonopore** (genital orifice) or a genital papilla. In most species, the mature gametes are freely released into the sea water. The spawning behaviour, observed in many Aspidochirota species, involves an upright posture of males and females followed by a swaying back and forth, while the gametes are being released.

Water vascular system, perivisceral coelom, and hemal system

The **water vascular system** (Fig. 5) is a coelomic space bordered by a mesothelium. It consists of the lumen of the buccal tentacles and the tube feet, a **water ring** around the esophagus, the **radial canals**, the **madreporic canal**, and the **Polian vesicles**. The perivisceral coelom is a large cavity containing watery proteinaceous coelomic fluid and different forms of cells (coelomocytes). The hemal system is well developed and composed of large hemal vessels along the gut, sinus, and lacunae. The hemal vessels associated with the gut can form a complex meshwork with the left respiratory tree, the **rete mirabile**, suggesting different functions of nutrient and gas transfers.

Habitat and biology

Holothurians are found throughout all oceans, at all latitudes, from the shore down to abyssal plains. They are usually benthic (living on the bottom); some species live on hard substrates, rocks, coral reefs, or as epizoites on plants or invertebrates; most of the species inhabit soft bottoms, on their surface or in the sediment. Among the commercial coastal holothurians, the Aspidochirota are predominant in the tropics, while the Dendrochirota are more common in temperate areas. The Aspidochirota from the tropical western

Pacific generally show a distribution reflecting the organization of the reef and lagoonal systems. Six different categories of species have therefore been defined, being characteristic of the main biotopes in which they occur: coral slopes (and passages), inner lagoons, inner reef flats, outer reef flats, outer lagoons, and coastal bays. The density and biomass increase from the outer reef slopes to the inner reef flats and coastal areas. Although there is much variation between the different sites, coral-slope species generally show lower densities and relatively large individual sizes, while species occurring on inner reef flats and inner lagoons show intermediate values, and those living on outer reef flats come in higher densities of smaller individuals. Most Aspidochirota species have comparatively few animal predators and their major effects in the reef communities are related to their deposit-feeding habits, as they are able to rework large amounts of sediments (bioturbation).

Fisheries

Holothurians have been harvested commercially for at least a thousand years, occasionally for the raw body wall or viscera, but mostly in order to be processed into a dry product called **bêche-de-mer**, **trépang**, or hai-sum, which is considered a delicacy by the Chinese. Harvesting in the tropics is usually done by hand, while collecting at low tide or by free-diving from small boats. The processing methods for bêche-de-mer include different stages of boiling, gutting, and drying, with variable procedures according to the species. Bêche-de-mer is then exported from the producer country to a central market such as Hong Kong, and then re-exported to the Chinese consumers. The economic significance of these artisanal fisheries is particularly important in less developed countries. The recent developments of these activities have led to a global increase of the catches, especially with a strong increase of the Hong Kong and Chinese markets, and the participation of new producer countries, with a shift of the exploited species, probably due to overcollecting.

Around 300 shallow-water species of holothurians are known to occur in the area, but only a few of them are of commercial interest. From 1990 to 1995, the reported yearly production of sea cucumbers in the Western Central Pacific ranged from around 6 800 to 9 000 t (FAO Yearbook of Fishery Statistics).

Identification note

As in other echinoderms, species identification is mostly done by examination of the skeletal parts of preserved specimens. Holothurians should be preserved in alcohol (70 %), as formalin may dissolve the calcareous skeleton. The calcareous ring can be readily observed after dissection.

The spicules, which are deeply hidden in the body wall, can be obtained by the following method:

1. Small pieces of body-wall tissue are removed from the bivium and the trivium, as well as the oral tentacles and podia, and dissected and macerated in sodium hypochlorite (bleach), or sodium hydroxide, in order to dissolve the organic material.
2. After washing in distilled water, the spicules are rinsed in alcohol and can be processed with a drop of a mountant (Canada balsam).
3. After processing, the spicules can be observed either on permanent slides with a light microscope, or prepared for scanning electron microscope.

GLOSSARY OF TECHNICAL TERMS

Anal teeth - radial calcareous papillae encircling the anus.

Bêche-de-mer - term used in the tropical Pacific for the processed product of sea cucumbers (see also **trepang**).

Bivium - the dorsal part of the body in the pentaradiate symmetry, with 2 radii.

Calacareous ring - internal collar of plates, generally 10, surrounding the pharynx.

Cloaca - anal cavity where the intestine ends.

Cuvierian tubules - threads becoming sticky when thrown out of the anus; used as a defense mechanism.

Dendritic - branching in an arborescent manner; used as descriptive term for the shape of tentacles in Dendrochirotida.

Digitate - finger-like.

Digitations - finger-like structures.

Fenestrated - having small window-like openings or holes.

Interradii (or interambulacra) - in the pentaradiate symmetry, the 5 areas between the rows of podia or papillae (Fig. 2).

Papillae - conical lumps on the surface of the body wall.

Pentamerous - having 5 radiating parts, resulting in a **pentaradiate symmetry**.

Peltate - with a central stalk.

Pinnate - feather-like.

Podia (or tube feet) - water-filled tubes used for locomotion.

Radii (or ambulacra) - in the pentaradiate symmetry, the 5 areas with podia or papillae.

Respiratory tree - arborescent organ (1 pair), opening in the cloaca.

Spicules - or ossicles, microscopic carbonate skeleton particles in the body wall, useful for species identification; they come in various shapes (Fig. 4).

Teats - large papillae.

Tentacles - buccal podia (Fig. 3).

Trépang - Malaysian name for sea cucumber, also used for the processed product (see also **bêche-de-mer**)

Trivium - the ventral surface of body in the pentaradiate symmetry, with 3 radii.

KEY TO THE SHALLOW-WATER ORDERS OF THE CLASS HOLOTHUROIDEA

1a. Podia absent; body vermiform; body wall thin, often translucent; dominant spicules in form of anchors with associated anchor plates tentacles pinnate; pharynx without retractor muscle; no respiratory tree . . . . . **Apodida**

1b. Podia present; body-wall moderately thick; body wall with dominant spicules in form of tables, perforated plates, buttons, rods, or rosettes . . . . . → **2**

2a. Tentacles peltate or pelyo-digitate; anterior end of body not introverted and associated with retractor muscles . . . . . **Aspidochirotida**
(the only order with commercial species in the area)

2b. Tentacles branched (dendritic); anterior end of body introverted, associated with retractor muscles . . . . . **Dendrochirotida**

ORDER ASPIDOCHIROTIDA

Diagnostic characters: Tentacles peltate, constituting a short stem ending in a disc covered by small digitations. Body wall bearing podia and/or papillae. Calcareous ring without posterior prolongation. Pharynx without special retractor muscles, but can be retracted within a fold of skin. Tentacle ampullae present. Respiratory trees well developed. Cuvierian organs present or absent. Dominant spicules in form of tables, buttons, rods, rosettes, or grains.

Key to the shallow-water families of Aspidochirotida occurring in the area

1a. Body with trivium (sole) usually flattened and dorsal bivium convex; gonads forming a single tuft appended to the left dorsal mesentery; Cuvierian organs present or absent; dominant spicules of form of tables, buttons (simple or modified), and rods (excluding C- and S-shaped rods) . . . . . **Holothuriidae** (p. 1165)

1b. Body square-shaped or trapezoidal in cross-section; Cuvierian organs always absent; gonads forming 2 tufts appended on each side of the dorsal mesentery; dominant spicules in form of branched rods and C-and S-shaped rods . . . . . **Stichopodidae** (p. 1185)