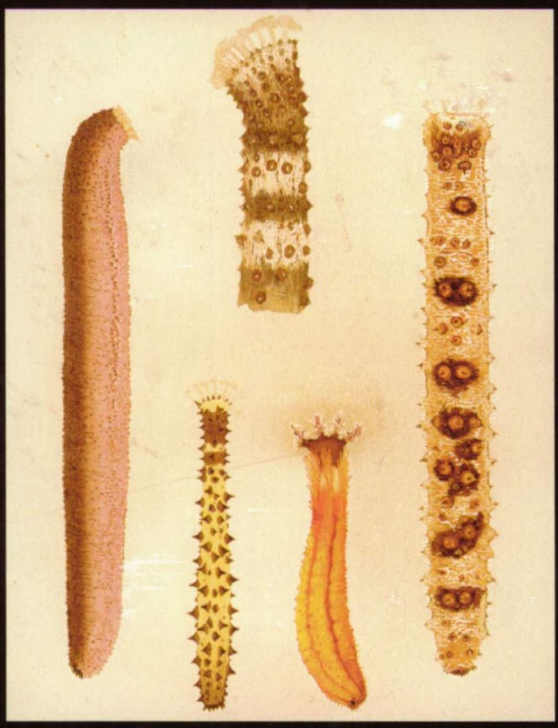
Towards an understanding of the shallow-water holothuroid fauna (Echinodermata: Holothuroidea) of the western Indian Ocean



Yves Samyn

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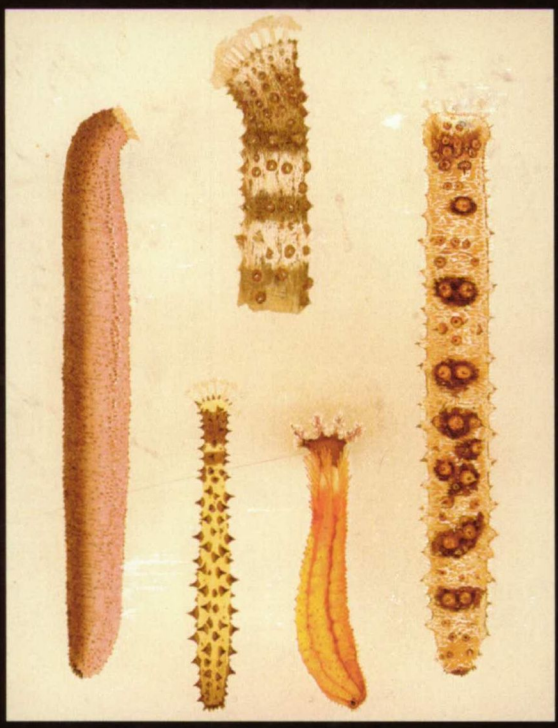

Yves Samyn

To C. Massin and A.S. Thandar
For teaching me to dive in the murky waters of holothuroid taxonomy

"Without taxonomy to give shape to the bricks, and systematics to tell us how to put them together, the house of biological science is a meaningless jumble"

R.M. May, 1990

"R. May's brick and cement are necessary for constructing a solid building, but let's make sure we have enough brick-makers and bricklayers to build a stable biodiversity house"

Y. Samyn & C. Massin, 2002

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A Dissertation Presented in Candidacy for the Degree of Doctor of Philosophy

VRIJE UNIVERSITEIT BRUSSEL
Faculteit der Wetenschappen
Laboratorium voor Ecologie & Systematiek
Academiejaar 2002-2003

Promotor: Prof. M. H. Daro
Vrije Universiteit Brussel
Laboratorium voor Ecologie & Systematiek

The research presented in this Ph.D. was made possible thanks to the collaboration of:

Funding agencies
Research Council – Vrije Universiteit Brussel
Fund for Scientific Research - Flanders
Department Science, Innovation and Media - Ministry of the Flemish Community
Vlaamse Interuniversitaire Raad

Non-funding agencies
Royal Belgian Institute of natural Sciences, Belgium
Royal Museum for central Africa, Belgium
Muséum national d'Histoire naturelle, France
Natural History Museum, United Kingdom
Zoological Museum University of Copenhagen, Denmark
Museum of Comparative Zoology, Harvard University Camebridge, USA
Natural History Museum of Los Angeles County, USA
National Museum of natural History, Smithsonian Institute, USA
National Museum of natural History, The Netherlands
Zoological Institute and Museum, Hamburg University, Germanny
Institute of Marine Sciences and Limnology, National University of Mexico, Mexico
Kenya Wildlife Services – Mombasa, Kenya
KwaZulu-Natal Nature Conservation Sevices – Durban, Republic of South Africa
Zoology Department – University of Durban-Westville, Republic of South Africa
Vlaams Instituut van de Zee – Oostende, Belgium

Brussels, May 2003

The research presented in this Ph.D. was carried out in the framework of the projects 'Causal factors of biodiversity: community, phylogeny and biogeography: a comparative study of tropical and subtropical estuaries and lagoons' (FWO), 'Biodiversity studies on seaweeds and echinoderms in the transition between temperate southern Africa and the tropical western Indian Ocean' (Vl.G.BIL 98/84), and 'Marine, shallow-water benthic algae and echinoderms of KwaZulu-Natal, Republic of South Africa' (Vl.G.BIL 01/46).

This Ph.D. thesis holds a collection of peer-reviewed scientific papers which have appeared lately. The differences in style as employed by the publishers/editors of the different scientific journals (titles, artwork, figure legends, references, abrreviations, acknowledgments, etc.) were retained as it is believed that these do not obstruct the contents. The same rule of thumb applies to the as yet unpublished material (marked as *in prep.*) written in function of submission to scientific journals.

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Towards an understanding of the shallow-water holothuroid (Echinodermata: Holothuroidea) fauna of the western Indian Ocean

Preface

"All interpretations made by a scientist are hypotheses, and all hypotheses are tentative. They must forever be tested and they must be revised if found to be unsatisfactory."

E. Mayr[1], 1982: 831

Ever since reading S.J. Gould's preface to his book *Wonderful Life* (1989), I kept my senses open for Akira Kurosawa's movie *Rashomon* (1950) for I was intrigued about why an eminent evolutionary biologist like Gould talks about a seemingly fait-divers (actually it is a brilliant master piece) in cinematography to preface a most interesting book on Precambrian life. Why?, you are most probably asking. Well, Gould's (too) brief explanation of Kurosawa's message had surprised me. According to Gould, Kurosawa had meant that a complicated story like the one narrated in *Rashomon* could never be told in the same way by any two observers or participants. I began to wonder if such was the case in biological problems as well? Were my high school science- (and non-science by the way) teachers, with their unambiguous theories and law-like truths, wrong? Could it be that there was less certitude than was dictated to us, ignorant scholars and students *in spe*? "Yes", answered Dr. D. Roggen, one of my zoology professors, each and every fact, theory and even law should or rather must be questioned at all times! In fact, his phrase "Science is not the immediate construction of what is true, but a gradual destruction of what is false", might seem obvious at first, but it actually means that historically we have been overwhelmed by non-truths, voluntary or not. It is up to us, scientists and non-scientists alike, to actually prove or reject the various hypotheses that are and have been presented to us through time. For the slightly more experienced biologist I have now become, Dr. Roggen's statement no longer comes as a surprise for I have hard-learned that biological systems, whatever the level at which we study them, are invariably extremely complex, definitely more intricate as Kurosawa's magnificent morality sketch of medieval Japan.

Perhaps nowhere in biology is Dr. Roggen's phrase better embodied as in taxonomy and systematics, scientific disciplines that through a sophisticated set of nomenclatural rules, keep track of the historical opinions toward the status of the study object. Indeed, synonymies are much the language of taxonomists and very few fellow-biologists, that is non-taxonomists and necessarily end-users of taxonomic research, understand the value of these lists. To these colleagues, scientific names are solely metaphysical, pragmatic indexes that allow information storage and information retrieval. To taxonomists (and evolutionary biologists in general) on the other hand, they are falsifiable hypotheses about causation of relatedness (common descent) and similarity between organisms. Thus, attention must be called to the striking differences between identification and classification. While the first process can be done by any layperson who has access to a good classification and an ordered mind, the second endeavour can only be accomplished by the specialized taxonomist who questions the causation of the identification keys at all times. By necessity, in the present dissertation, both processes are important for this convergence will not only facilitate future taxonomic research, but it will put the understanding of the observed biodiversity patterns in an evolutionary framework.

Anyway, years after reading Gould's (1989) book, I had the opportunity to see *Rashomon* myself and it became clear to me that if life was just a movie, we as biologists are in fact both observer and judge, but should never be the story maker, a role reserved for the evolutionary forces that shape(d) nature, whatever these are. So, even if there's an objective truth out there, it's a grail to be sought after, but as it is a non-dogmatic one we might just find it some day and if we fail we can always contempt ourselves that we have approximated it to our satisfaction. This heuristic *aurea mediocritas* might seem a daring conjecture to the reductionistic bio(techno)logist, but to the holistic biologist it is just the rule to that very fun emergence called life! Enjoy the ride.

Brussel, April 2003

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[1] Mayr E. 1982. The Growth of Biological Thought. Diversity, Evolution and Inheritance. Belknap Press of Harvard University Press. Cambridge, Massachusetts. 974 pp.

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Chapter One

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Introduction

"We must needs confesse, that fishes within stone shells, have small or no sense, as namely oysters. Many are of the nature of very Plants, to wit, those that they call Holothuria: also Pulmones, resembling the lungs of a beast: and Star-fishes, made in forme of starres (such stars I meane as it pleaseth the painter to draw)."

Plinius, book 9: chapter XLVII (as translated by Holland, 1601)

"Les holothuries, que les anciens comprenoient assez ordinairement sous le nom vague de *purgamenta maris* ou de *pudenda marina*, a cause de quelques resemblance avec l'organe excitateur mâle de l'homme, se trouvent, à ce qu'il paroît, dans toutes les mers, dont elles habitent essentiellement le parties les plus profondes, jusqu'à trois cents pieds et plus: c'est même à cela que semble être due la singularité qu'offrent ces animaux, de vomir pour ainsi dire leur canal intestinal, à cause de la grande différence de pression."

de Blainville, 1821: 311.

1. What are holothuroids?

The Holothuroidea, commonly known as sea cucumbers, are one of the five extant classes of echinoderms (see Barker *et al.* 1986 for the erection of a sixth existing class, the Concentricycloidea; Smith 1988 and Janies & Mooi 1999 for the subsequent narrow, cladistic, classification of it). This highly successful class has a fossil record extending back some 460-500 million years to Lower Ordovician (Gilliland 1993; Reich 1999; 2001) and has invaded every part of the marine realm, from the intertidal to the deep ocean trenches and from the polar to the tropical regions. Holothuroids (the more widely used term "holothurian" is here restricted for species belonging to the genus *Holothuria*; holothuriids is likewise restricted for those species that belong to the family Holothuriidae) are the second most diverse echinoderm class, with some 200 described genera containing some 1600 extant species (Smiley & Pawson ±1990, complemented with references missed by these authors and with descriptions dated after 1990). Like their closest relatives, the echinoids (Smith and Littlewood 1997; Littlewood *et al.* 1997), the body lacks arms (in the elasipodids the extensions are greatly enlarged tube feet used for swimming or walking rather than arms in the strict sense of the word). Mouth and anus are almost invariantly located at opposite poles (sometimes turned dorsally or ventrally at the ends of the longitudinal axis) and the ambulacral and interambulacral areas are arranged meridionally around the polar axis, which is lengthened to give the typical elongated sausage shape. A notable exception to this general pattern is presented by the Rhopalodinidae R. Perrier, 1902 that are characterized by a flask-shaped body with the mouth and anus opening at the tip of a long proboscis-like structure (Thandar 2001 and references therein). The vermiform to cylindrical shape of most holothuroids gives them a bilateral symmetrical appearance, a pattern especially visible in some members of the orders Aspidochirotida and Dendrochirotida (Psolidae) which are modified dorso-ventrally with a more or less flattened ventral side (commonly referred to as the sole). Nevertheless, the animal has a typical secondarily derived (the larvae have a bilateral symmetry) pentaradiate symmetry as evidenced by the calcareous ring, which is usually composed of ten calcareous pieces (five radial and five interradial pieces), although more than ten elements can be found in members of the Apodida or a mosaic of numerous pieces in some members of the Dendrochirotida. This structure serves as the attachment site for the longitudinal and, if present, the introvert retractor muscles, supports the pharynx and the perioesophagal ring, the five radial canals (absent in the order Apodida) and the nerve ring. The radial canals terminate in the tube feet (also called podia, *i.e.* pedicels with sucking disc and end plate) and papillae (without sucking disc and end plate). The five-fold symmetry is further visible in the five longitudinal muscles. Overall, the ventral surface of a holothuroid, the trivium, is composed of three ambulacral and two interambulacral areas; the dorsal surface, the bivium, consists of two ambulacral and three interambulacral areas. Tube feet and papillae are *per definition* arranged along the ambulacral areas although radial distribution is often obscured or absent altogether due to scattering (into the interambulacral areas) or reduction of the pedicels. In fact, the orders Apodida and Molpadida lack tube feet or papillae, though it must be emphasized that buccal tentacles are nothing but modified buccal tube feet that are highly retractable. Hereby, it must be noted that some holothuroids (e.g. Dendrochirotida) possess retractor muscles to redraw the buccal tentacles and the introvert into the body wall. Another diagnostic feature of the Holothuroidea is the highly reduced

(microscopic) stereomic calcareous skeleton that has a mesodermal origin. It has been demonstrated (Schmidt 1925; 1932; Panning 1931a; 1931c; 1933) that the spicules of holothuroids consist of a single crystal of calcite. These ossicles (also termed spicules or sclerites or deposits) can be found in virtually every organ of the holothuroid, although some species have lost their spiculation in all or in some body parts (e.g. *Holothuria (Mertensiothuria) leucospilota* (Brandt, 1835) lacks ossicles in the tentacles, some *Thyone* spp. lack ossicles throughout their body wall but have retained them in their pedicels,...). Gilliland (1993) quite correctly stressed that a single species can present several different types of ossicles (each type called a morphotype by him), whereby he calls the summation of all the ossicles the morphotype assemblage. This morphotype assemblage can change with age whereby, according to Massin (1994), four different types of variation can occur with increasing body size: (i) ossicles may gradually increase in size, with little modification to the general form, (ii) ossicles gradually regress and may completely disappear throughout the body, (iii) ossicles gradually disappear apart from the distal ends of the animal and the pedicels and (iv) early ossicles from the body wall are replaced by new, other forms. Cutress (1996), upon detailed examination of twelve Caribbean aspidochirotids, added that ossicles of aspidochirotids may not only become larger with increasing body size, but may also shrink and become simpler when a species grows. Massin *et al.* (2000) arrived at the same conclusion upon study of the changes in *H. (Metriatyla) scabra* individuals of different sizes. In regard to the mechanisms that underlie these transformations, we are, regrettably, largely in the dark. Cutress (1996) believed that these changes are the consequence of continual dissolution and redeposition of calcite. Massin (1994:145) on the other hand, noted that "the relationship between ossicle changes and increasing size and physiological, ecological or geographical data is unknown". However, as the ossicle assemblage of a species is a keystone character to arrive at its identification (and a main guide to its classification), we are dependent on it, but we must, however, follow Féral's (1980) suggestion that the size of specimens is very important to arrive at a trustworthy identification.

Be as it may, some 20 different types of ossicles are commonly discerned and are used in identification and classification. For clarity of the present dissertation, only the most common ones are here described; some of these are here illustrated (pls I & II). Rarer ossicles like hourglasses, racquets, towers,..., not encountered during the present study, are omitted. For these I refer to Gilliland (1993). The present descriptions are based on a variety of papers dealing with holothuroid taxonomy and paleontology (Panning 1931b-1935a-d; Tortonese 1937-38; Deichmann 1958; Caso 1964; Rowe 1969; Clark & Rowe 1971; Rowe & Doty 1977; Cherbonnier 1980; 1988; Gilliland 1993; Solis-Marin pers. comm.) as well as on personal observations. As several of the historical or regionally important papers were written in French (e.g. Cherbonnier), German (e.g. Panning), or Spanish (e.g. Caso), ossicle names are also given in these languages.

- ***Anchor*** (German: *Anker*; French: *ancre*; Spanish: *ancla*) (see also plate 1A) Ossicle shaped as an anchor. Anterior end of the shaft terminates in two (three has been reported but this is exceptional) arms (*flukes*) which may be smooth or laterally finely dented; the central area (*vertex*) between the arms opposite the shaft sometimes with minute knob-like projections; flukes often slightly raised distally out of the horizontal plane; posterior end of the shaft (*stock*) finely rugose or branching; stock end of the anchor (*keel*) articulated with the corresponding anchor plate by connective tissue (after Clark & Rowe 1971: 173; Gilliland 1993: 52). Anchor size (and sometimes also shape) often varies between the anterior and posterior end of the body in Apodida. In the Molpadiidae, anchor-alikes (cfr. *tables*) can be found. These have a saucer-shaped stock, perforated by three large holes and occasionally three small additional holes, with raising from the disc three beams that coalescence very rapidly (after Gilliland 1993: 52, plate 8 figs 5, 6).
- ***Anchor plate*** (German: *Ankerplatte*; French: *plaque anchorale*; Spanish: *placa ancla*) (see also plate 1B). Ossicles shaped as rounded, oval, pyriform or rectangular plates with the anterior side of the plate usually wider than the posterior side. Anterior side with large, smooth or variably denticulate holes (usually seven of which one in the centre, but *Rynkatorpa* has two larger central holes and *Protankyra* & *Synapta* are multi-perforated); posterior side with smaller, generally smooth, holes. Anchor plates can be abruptly contracted posteriorly (thus lacking a hole on each side) or not (thus with a large hole on each side); an arch-like smooth or toothed transverse bar (*bridge*) usually more or less well developed near the posterior end of the plate; this bridge forms the articulation point for the anchor with the anchor plate (after Clark & Rowe 1971: 173; Gilliland 1993: 52). Molpadiid anchor-plates have a large central area and three variously developed arms (see Gilliland 1993: 44, text-fig. 4F).

- ***Basket* or *Cup*** (German: *Korb*; French: *corbeille*; Spanish: *cesta* or *canasta*) (see also plate 1C). Three-dimensional concavo-convex perforated plates with smooth or toothed edges; baskets can be shallow or deep (after Clark & Rowe 1971: 174). According to Gilliland (1993), these ossicles are restricted to the dendrochirotid families Heterothyonidae, Cucumariidae, Sclerodactylidae and Psolidae and to the dactylochirote *Rhopalodina compacta* Cherbonnier, 1959 where they are very small (25 µm in diameter) and form 'rudimentary cups'.
- ***Button*** (German: *Schnalle*; French: *bouton* or *boucle*; Spanish: *botón*) (see also plate 1D, E, G). Ossicle pierced by a variable number of regular to irregular holes that are usually arranged in pairs; rim of button may be smooth, spiny or knobbed, straight, undulating or irregular; surface of button smooth (occasionally with a median optical discontinuity) or knobbed; thickness of button variable (after Clark & Rowe 1971: 174).
  In the Aspidochirotida [Holothuriidae and as communicated to me by Rowe a minority of species in the Stichopodidae (see also Samyn in press)], buttons are usually oval to rectangular, with a smooth, knobbed or occasionally spiny rim; the holes are usually arranged in two rows (occasionally one or more than two), positioned parallel to the median axis of the button and with no terminal hole. The number of holes varies from two to over 20 (see also *plate*). Basically button types differ from each other in the number and width of the holes, the nature of the rim and the rugosity of the surface. Very rugose buttons can transform into more intricate structures called fenestrated ellipsoids (see below).
  Buttons, as presented by some dendrochirotids, are typically oval to diamond-shaped and have four holes which are arranged in a cross. Additional holes frequently can be added on either side of the terminal hole. These forms are best described as dendrochirotid buttons as it is believed that these are analogous to aspidochirotid buttons (buttons *sensu stricto*). According to Gilliland (1993: 26) dendrochirotid buttons can also be divided in smooth, knobbed and thickened forms.
- ***End-plate*** (German: *Endscheibe*; French: *plaque terminale*; Spanish: *placa de la ventosa*) (see also plate 2A, B). An end-plate is a multiperforated ossicle found in the terminal part of tube feet. Fully formed end-plates are circular in outline and have their rim smooth or ragged; the central part often is slightly concave. The number, size, arrangement and regularity of the holes vary between higher-level taxa. The diameter of the end-plate is variable (75-500 µm in diameter), but in some groups species-specific. The large central holes can be overgrown by a secondary layer thus forming an irregular meshwork (after Clark & Rowe 1971: 174; Gilliland 1993: 15).
- ***Fenestrated ellipsoid*** (German: *gefensterte* or *durchbrochene Hohlkugeln* or *Hohlkörper*; French: *ellipsoïde fenestré*; Spanish: *elipsoide festoneado*) (see also plate 2C). Buttons with knobs interconnecting to form a three-dimensional fenestrated structure; number, size and arrangement of holes and knobs variable (after Clark & Rowe 1971: 174).
- ***Fenestrated sphere*** (German: *dicht gelagerte Türme*; French: *sphère fenestré*; Spanish: *esfera festoneada*) (see also plate 2D). Modified tables (see below) with the spire low; its peripheral spines connected to projections from the margin of the disc, forming a rounded hollow fenestrated structure (from Clark & Rowe 1971: 174; after Deichmann 1958: 321).
- ***Grain* or *Granule*** (German: *Körner*; French: *grain*; Spanish: *grano* or *gránulo*) (see also plate 2E). Small, solid imperforated (*grain*) or perforated (*granule*) ossicle (see also *rosette*).
- ***Lenticular plate*** (also known as *scale*) (German: *Platte*; French: *plaque lenticulaire*; Spanish: *placa lenticular*). Very thick, perforated, sometimes knobbed plate shaped like a double-convex lens. The thickening of the plate often obliterates the holes. Such plates are typical of several dendrochirotid families (Placothuriidae, Heterothyonidae, Psolidae and occasionally also in the Cucumariidae and the Sclerodactylidae) and can imbricate to form a 'test', which can cover the body to a certain degree. The anal and oral valves as found in some psolids have a similar ultrastructure (after Clark & Rowe 1971: 174; Gilliland 1993: 28).
- ***Miliary granule*** (German: *biscuitförmige Kalkkörper*; French: *corpuscules crépus*; Spanish: *gránulo miliar*) (see also plate 1K). Usually very small (5-30 µm in diameter) ossicles; shape from blebs to rods to rosette-alikes; they can be found in synaptids and chiridotids.
- ***Perforated plate*** (German: *Gefensterte Platte*; French: *plaque perforé*; Spanish: *placa perforada*) (see also plate 2F, G). Ossicles of various size and structure that are commonly divided on the basis of the length-width ratio, the arrangement of the perforations, the rugosity and the thickness of the plate. The number of different types is almost proportional to the number of authors that

described them. Gilliland (1993: 22, 24) made a brave effort to distinguish four types in the orders Dendrochirotida and Dactylochirotida). As his division can serve as the basis of further systematic cataloguing, it is here given.

- ***Simple plates***: thin and unsculptured plate with the holes regularly arranged over the whole area of the plate and with the hole size rather uniform (see Gilliland 1993: 22, 19, pl. 3 fig. 2, 23, pl. 5 fig. 3).
- ***Thickened plates:*** as simple plates, but thickened.
- ***Knobbed plates***: as simple plates but with knobs or other verrucosities on the plate surface.
- ***Plates with trabeculae***: plates with 'ribs' or trabeculae over the surface, or an incipient secondary layer (from Gilliland 1993: 24).

As said before, perforated plates are so omnipresent in the different holothuroid orders that it is difficult to list all of them in well-defined categories. Within the Aspidochirotida (predominant order in the present dissertation), perforated plates can be divided into those derived from the button and those formed from the rosette-*bauplan*. The first type has its holes arranged in two or more rather regular rows (Holothuriidae), while the second type has its holes arranged more randomly (Stichopodidae).

- ***Primary cross*** (German: *Gabelstab*; French: *croix primaire*; Spanish: *cruz de malta* or *cruz primaria*). Four-armed cross with central to subcentral elevation with variable ornamentation; arms are generally perforated. Found in dactylochirotids, dendrochirotids and certain aspidochirotids (Synallactidae and juveniles of some Holothuriidae).
- ***Pseudo-buttons*** (German: *Falsche Schnalle*; French: *pseudo-bouton*; Spanish: *pseudo-botones*). Irregular, incomplete or reduced buttons.
- ***Pseudo-table*** (German: *unregelmäßige Körper*; French: *pseudo-tourelle*; Spanish: *pseudo-tabla*) (see also plate 2H, J). Table with the disc reduced and the spire often low. Pseudotable is the name commonly employed to designate the table-alikes as found in *Pearsonothuria graeffei* (Semper, 1868) and *Thelenota* spp. It is highly debateable whether or not pseudotables are homologous to true tables (see *table*).
- ***Rods*** (German: *Kalkstäbchen* or *Stützstäbe*; French: *bâtonnet*; Spanish: *barrotes*). Elongated bar-like ossicle which may be thickened centrally and/or distally; perforated or not; branching or not. Various types of rods can be discerned according to the taxon (after Gilliland 1993: 21, 31, 46).
  - *Spectacles*: rods with perforated, expanded ends; short rods with widened ends that develop into button-alikes or 'lozenges'; elongated spectacles can be found in dactylochirotids and dendrochirotids
  - *Curved rods*: rods that are fragile to robust, non-branching to highly branching, non-perforated to perforated, smooth to rugose (see Gilliland 1993: 21, 23, pl. 4 figs 6, 8)
  - *Parallel-sided rods*: relative wide, flat rods that lack distinct, expanded ends; perforated distally or overall (see Gilliland 1993: 21,19 fig. 8).
  - *Fusiform rods*: only in dendrochirotids; close to parallel-sided rods; distal ends not expanded (see Gilliland 1993: 21,10, pl. 1 fig. 6)
  - *Irregular rods*: rods characterised by an overall irregularity, both in the rim, the widening and in the degree and position of the perforations (see Gilliland 1993: 21, 26, pl. 5 fig. 6).
  - *C-and S-shaped rods*: slender, curved rods, with sometimes a central thickening, found in the Elpidiidae (Elasipodida); Holothuriidae (only in *Holothuria (Stichothuria) coronopertusa* Cherbonnier & Féral, 1984), Stichopodidae and Synallactidae (Aspidochirotida); in the Stichopodidae S-shaped, and more intricate rods can also be found. The C-shaped rods of the Elasipodida and Aspidochirotida are considered analogue by Hansen (1975), a view that is generally accepted. It is currently under investigation whether the C-shaped rods as found in the three holothuriid families are homologues or analogues.
  - *Aspidochirotid perforated rods* (see also plate 2): type of rods found in some holothuriid subgenera. These rods may be: expanded distally and/or centrally, straight to slightly kinked to curved; perforated overall or only in the expanded areas. Two main types can be discerned:

        - *Holothuriidae:* perforations are mostly two by two, giving rise to a regular perforated rod, which by many authors is called an elongated plate (see also *plate*).
        - *Stichopodidae:* perforations are more random, giving rise to an irregular perforated rod (see also *plate*). In the dorsal papillae these rods typically have the central part expanded to one side; the perforations are found therein.
    - *Apodan rods*: usually round in cross-section, 50-250 µm long; Gilliland (1993: 46, 48) discerns six types:
        - *Smooth 'bracket' shaped rods*
        - *Irregular 'bracket' shaped rods*
        - *Synaptid spectacles*
        - *Accessory plates*
        - *Slender, variably curved rods*
        - *Sigmoid rods*
- ***Rosette*** (German: *Rosette*; French: *rosette*; Spanish: *roseta*) (see also plate 1J): rosettes form from dichotomously (terminal and lateral) branched rods; branches may variously anastomose to form perforated deposits. Often the general appearance is rather button-like, though rosettes differ from buttons in having the holes of various sizes and in having a single terminal perforation. As there's quite a bit of confusion in the literature as to the description of a rosette, it is here defined for the different orders, families, and genera.
    - Dendrochirotida: small, highly branched rod with the branches folded inwards, sometimes anastamosing to form holes; the end of the branches may be swollen to form an elaborate ossicle. Found predominantly in the tentacles.
    - Aspidochirotida
        - Holothuriidae (for a detailed description see also Panning 1935d: 11, 12, 16-18).
            - *Actinopyga*-type rosette: dichotomously branched rods; branching both distally and laterally (one to several) along the median axis, branches can anastomose; end of branches lobed or spiny.
            - *Bohadschia*-type rosette: from simple unbranched solid grains to variously dichotomously branched rods; branching predominately distally with zero to one lateral branch; end of branches swollen, always smooth; branches can anastomose.
            - *Holothuria*-type rosette: basically a bifurcate rod with the terminal branches growing under angles of 120°; eventually branches anastomose thus forming large, sideward perforations and always a terminal hole.
                - *Halodeima & Acanthotrapeza*-type: basically a *Holothuria*-type rosette going from simple branched rods to small perforated deposits with smooth to spiny margin.
                - *Stauropora & Pearsonothuria*-type: irregular *Holothuria*-type rosette, giving rise to plate-like ossicles, especially in the tentacles (only in *Pearsonothuria*) and the tube feet; those from the body wall are simpler and only occasionally form plates.
        - Stichopodidae: branched rods; beyond the primary dichotomy, branching irregular; branching predominantly distally with branches incurved; branches occasionally anastomose; end of branches slightly swollen.
    - Elasipodida: same type as in Dendrochirotida.
    - Apodida: no true rosettes (see miliary granules) although the formation appears to be the same.
- ***Table*** (German: *Türme*; French: *table*; Spanish: *tabla*) (see also plate 2L); tables originate from multi-armed (usually four) deposits which branch distally. These branches anastomosing to form a perforated disc, on which arise a variable number of vertical pillars; these pillars can be variously connected to each other (cross-beam or bridge) to form the spire; the spire ends in a cluster of spines or in a crown.

- Table disc (German: *Scheibe*; French: *disque*; Spanish: *discos*): circular to sub-circular to quadrangular to four-armed base plate with a smooth, undulating or rugose rim; flat or raised; perforated by one or four central holes and a highly variable number of peripheral holes; bearing the pillars of the spire.
- Spire (German: *Aufsatz*; French: *tourelle*; Spanish: *espiras*): consists of two, three or four pillars that raise from the disc and end in the crown; pillars parallel to each other or turned inwards toward the top (tack-like). Height of the spire is determined relative to the disc diameter: high when spire-length exceeds disc diameter, moderate when spire-length equals disc diameter and low when spire-length less than disc diameter; spire can be reduced to knobs on the disc or totally absent ("table reduced to the disc").
- Cross-beam or bridge (German: *Querleiste*; French: *entretoise*; Spanish: *puente*): connection between the pillars; number of cross-beams variable (from zero to over five).
- Crown (German: *Krone*; French: *couronne*; Spanish: *corona*): cluster or ring of spines of various forms that terminates the spire.

Tables are found in a large number of taxa; they differ from each other in one or several of the table parts mentioned above.

- ***Wheels*** (German: *Rädchen*; French: *roue*; Spanish: *rueda*) (see also plate 2M): circular ossicles with six or more spokes leading to the peripheral rim; restricted to the Chiridotidae and Myriotrochidae (Apodida)(after Clark & Rowe 1971: 174). Round concavo-convex wheels, similar to chiridotids wheels, can be found in the auricularia larvae of synaptids (Mortensen 1938; Pawson 1971).

2. Classification history[1]

"The holothurians are the least-known class of echinoderms, the difficulties in the way of preserving them in museums, and the notable unattractiveness of the preserved specimens, being serious handicaps."

H.L. Clark, 1946: 383

Nowadays, general body morphology; presence and positioning of tube feet and papillae; shape, position and number of tentacles; presence of tentacle ampullae; gross and fine morphology of the calcareous ring; number of tufts of gonad; and shape, size, distribution, abundance and position (for instance superficial *versus* deep in the body wall; anterior or posterior side of the body wall;...) of microscopic ossicles from various tissues are the main characters used for identifying (and classifying) holothuroids. It can come as no surprise that this has not always been the case and that the *modus*, the criteria and the ultimate role(s) of classification mark the *zeitgeist* (and to a certain extent the paradigm) wherein the researcher tried to attain his goal. Mayr (1982, chapter 4) quite impressively assembled the (general) beliefs toward classification in the intellectual milieu of each historical period. However, whereas Mayr cannot be called incomplete in his endeavour, he lacked space to treat every group with the attention it deserves. Thus, hereunder, an attempt is made to reconstruct the history of the classification of holothuroids. Such an archival enterprise not only demonstrates the rich controversies and scientific disputes that shape(d) holothuroid classification, but also delivers clues to an ultimate holothuroid classification.

However, as documenting and discussing the complete history of classification of all the currently recognized holothuroid taxa makes a dissertation on its own, I opted to discuss the complete history of the Holothuroidea only up to roughly the beginning of the twentieth century. For the last century, I deliberately restricted myself to the family best represented in the present work: the Holothuriidae.

2.1. The epoch of natural philosophy

"It is not a hyperbole for us to say that all of biology is a footnote to Aristotle. He defined the field, outlined the major problems, and accumulated data to provide answers – he set the course."

J. A. Moore, 1993: 33

[1] Parts 2.1 to 2.5 of this essay will shortly be made suitable for submission to the *Archives of Natural History*; an abridged version of part 2.6 has been incorporated in Samyn *et al.* (in prep.)

Even though the Chinese were undoubtedly gathering sea cucumbers for soup long before our western civilisation tried to comprehend these animals, it is customary - but most certainly not completely correct - to use the knowledge of the early classical philosophers and naturalists as the beginning of natural history for this group of animals[1]. Of these early western naturalists, the Greek Aristotle [384-322 BC], together with his friend Theophratus [371-287 BC], whom Aristotle had met in Athens when both studied at Plato's school and with whom he undertook biological excursions in the neighbourhood of Assus and on the Island of Lesbos (Ferwerda 2000), undoubtedly set the scene for (western) natural history. Together with the Roman compiler Plinius [23-79], these men rank amongst the most influential naturalists of their time. Aristotle (even if he presumably drew a lot of information from his predecessors, most probably from the ideas of Hippocrates) deserves the credit of being the father of the science of classification, and the praise of being the first to do so by means of the surprisingly modern way of inspection (Mayr 1982). Aristotle is the first to use the name *holothourion*; Plinius (as translated by Holland 1601) preferred the name *cucumis marinus*. However, the meaning that the above naturalists *avant-la-lettre* gave to these names had hardly anything to do with sea cucumbers as we know them in the Modern Times [e.g. de Blainville's (1821; see also Gill 1907b) definition in his 'Dictionaire des Sciences Naturelles']. Rather the classical philosophers defined sea cucumbers as a kind of motionless marine animals that differ from sponges and alikes only by not being attached to the substrate (Aristotles; De partibus animalium: 681a18) or even plants [Plinius; The History of the World, book 9: chapter 47, as translated by Holland 1601; but see also Ludwig 1889-92 who believed that Plinius' *Cucumis marinus* is the same as *Cucumaria planci*, which is now classified as *Ocnus planci* (Brandt, 1835)].

2.2. The epoch of downward classification

Holothuroids were unambiguously recognized as an animal group, under the name *genitale marinum*, only as late as the middle of the sixteenth century. At this point in time, the Frenchman Pierre Belon [1517-1564] recognized that the locomotory system of holothuroids is comparable to that of sea urchins and starfish (Belon 1553). Shortly hereafter, Rondelet [1507-1566] gave the first graphical representation of a true sea cucumber [presumably *Ocnus planci* (Brandt, 1835)] and was the first author who, with certainty, employed Aristotle's name *holothurion* for a sea cucumber in the present sense of the name (Rondelet 1554). However, as Ludwig (1889-92) noted, Rondelet mixed sea cucumbers with other phyla. Be as it may, hereafter, until the mid eighteenth century, sea cucumbers received attention only on short commons. For instance, Columna (1616) used the name *pudendum regale* for a species (*Stichopus regalis* according to Ludwig 1889-92), while Aldrovandi (1642) and Bianchi (1766) further recognised true sea cucumber species.

It is, however, important to note that the classifications employed by these medieval naturalists were exclusively based on the principle of logic division or *downward classification*, a method that proceeds by dividing large classes of organisms into subsets until the last dichotomy in the specimen collection leads to the identification of the specimen (which thus gets the lowest taxonomic rank). This cannot come as a surprise, as these naturalists were convinced that the living world was designed by a supreme God and thus necessarily unchangeable (God creates once and has not made mistakes...). To these men, the search and the identification of the lowest ranks stood for the discovery and the description of the unchanging *essences* or - if you want – the living building blocks in God's original creation scheme[2]. It is philosophically interesting, but in the same time conceptually disappointing that the mental framework of these scientists (one tentatively could refer to them as Thomists; *i.e.* those who where heavily influenced by the reasoning of Thomas Aquinas [1225-1274]), goes back to Plato's thoughts which draw on the fact that the living world is made up from a limited number of fixed and unchanging forms (*eide* sensu Plato)[3] and which takes

[1] The same (western world) dogmatic start applies to the study of other living forms (some of us even have the tendency to extrapolate this narrow window upon the study of societies and their associated cultural and religious beliefs). It is thus extremely unfortunate that the ancient writings of non-western societies, to date, remain largely inaccessible or ignored.

[2] In fact, Newton's often quoted *Principia*, is a mathematically framed search for God's creation and the ways used by God to sustain nature and its history (Amati 2001).

[3] Mayr (1982) draws on Delbrück (1971) and Balme (1980) to emphasize the distinction between Plato and his followers and the Aristotelian school. Plato had a true essentialist view, whereby the world is composed

God as first cause of all essences. To these adepts of natural theology, these essences or *eide* or *esse* or species (choose the terminology that fits you best as a reader, but essence is in my opinion the best option) were nothing else but the propagations of God's magnificent (read "physically and metaphysically not truly understood, but unquestionable as it was not only described in the Bible, but also philosophically reasoned on by Thomas Aquinas") creation of one female and one male per essence. Consequently, the classifications made by these naturalists differed from one another in the number of recognized species, the number and kind of characters used, and - in more advanced stages - on the weighting of the different kinds of characters. The principles of downward classification are for instance clearly reflected in the classifications produced by notable naturalists like Linnaeus (even though in his later works he more or less abandoned this principle; see also hereunder) and is still in use today in keys of taxonomic revisions, monographs and field identification guides. Nowadays however, this method serves only the purpose of identification and not of classification *an sich*, as the system not only fails as an heuristic research program but also does not allow information storage nor retrieval of it. Mayr (1982) gives convincing evidence that during the last quarter of the eighteenth century, the method of *upward classification* slowly began to be adopted, even by original opponents as Linnaeus. This method proceeds through assemblage of related (similar) species into taxa and subsequently through grouping of the most similar of these newly formed taxa into higher ones, and this until a complete hierarchy of taxa has been formed.

2.3. The transition to upward classification

The eighteenth century is marked by the discovery of an almost unimaginable diversity of life forms in the different corners of the world and especially in the tropics. This explosion of organisms quickly made classification based on single characters (essences) and weighting of these characters according to presumed functional importance, virtually impossible. Gradually, naturalists understood that downward classification had to be abandoned and that compositional or upward classification would yield better and, above all, faster results. However, in order to be successful, it was realised that the concept of essentialism had to be replaced by the concept of a fundamental, holistic unit: the species. However, in a world dominated by theology, abandonment of essentialism was not easily achieved. Upward classification became like a mistress to zoological systematics: one could not longer live without her, but one was unwilling to be seen with her.

Largely inspired by Ray [1628-1705][1], Linnaeus [1707-1778] - renown for his standardization of taxonomy and nomenclature, whereby he invented binomial nomenclature and telegram-style diagnoses – was one of the first who came into conflict with downward classification. The Linnean categories Kingdom, Class, Order, Genus and species can be seen as one of the first attempts to devise a system that orders the complex and varied natural world [but see also Aristotle's *eidos*, *genos*, *diaphora* (Ferwerda 2000)]. Linneaus, however, continued to use Platonic philosophy and Thomistic logic, which resulted in dichotomous classifications. Linnean categories thus are best seen as a reflection of his strong belief in the *scala naturae*, wherein the fixed species are arranged according to degree of complexity (*Unitas in omni specie ordinem ducit;* as written in the introduction of his *Systema naturae*), rather than according to natural relationship. Linnaeus described very few holothuroids. In fact in the tenth edition of his *Systema naturae* (1758: 657)

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of an unchangeable universal order or *cosmos* created by several gods (through spontaneous generation), as such there is no place for change (evolution) whatsoever; the essences (*eide*) exist and will continue to do so. Aristotle, on the other hand, was a proponent of the viewpoint that neither creation nor extinction has ever existed, but that an unilinear gradation (later writers will refer to this as the *scala naturae*) in living entities (Aristotle also used the term *eide*) can be observed. According to Delbrück (1971), Aristotle's notion of *eide* can be compared to that of the 'unmoved mover', DNA or the carrier of genetic information in the present sense. Aristotle, thus, was by far the true essentialist that Plato (and his medieval followers) never ceased to be.

[1] J. Ray holds his place in the annals of systematic zoology as the first to use a species concept in a modern sense. His supposed 'cynical' definition of species - I quote verbatim: "species are merely what competent naturalists say they are" - later was adopted in Darwin's (1859) *Origin* (McQuat 2001).

the genus[1] *Holothuria*, placed in the class Vermes, contained only four species, which bear no resemblance to sea cucumbers in the modern sense of the word (one species belongs to the Acnidaria and three species belong to the Tunicata). It is only in the twelfth edition of his *Systema naturae* (1767: 1089) that, in addition to the above species, four sea cucumbers in the present sense of the name (and one worm) were included. In this later edition, Linnaeus kept the name *Holothuria* but drastically changed the diagnosis to accommodate true holothuroids. Gill (1907b: 494) used a rather sharp pen to Linnaeus' change of diagnosis and accused the *British Association for the Advancement of Science* that "they preferred homage to an individual rather than truth to a principle, (by insisting) on the twelfth edition as the initial volume of zoological nomenclature". Gill (1907a) proposed to disregard the name *Holothuria* and all its derivatives and suggested that Bohadschiidae may replace it, a name he took from Jaeger (1833). He was not followed in this action (see also Opinion 80, 1924).

Buffon [1707-1788], Linneaus' contemporary peer was not that interested in identifying all the organisms, but had a genuine interest in understanding the natural diversity he observed (Mayr 1982; Gould 2001). To attain this goal, he drew on the total *habitus* of organisms (all body parts, including internal anatomy, behavior and distribution), rather than on single characters as did Linnaeus. In the end he concluded that Linnaeus' essentialistic principles of classification should be abandoned as species are subject to change. Unfortunately, Buffon did not arrive at a classification governed by the principles of upward division. This is curious for his *Histoire naturelle* - a 44-volume encyclopaedia dealing with natural history - contained such extremely detailed comparative anatomical studies that it could have allowed recognition of natural taxa. Regrettably, Buffon chose the least scientific of all systems to arrive at a classification: the utilitarian one (for man, obviously). As Buffon and Linnaeus apparently had an antagonistic effect on each other, their theories never were allowed to truly interact. However, by the end of their careers both naturalists tried to resolve their conflicts: Buffon gradually adopted the Linnaean categories, while Linneaus considered Buffon's process of hybridisation (Mayr 1982). To my knowledge, Buffon did not study any species of sea cucumber, but and his total habitus approach need mentioning as this novel investigation style clearly paved the way for the coming generations of taxonomists.

In the late eighteenth, early nineteenth century, several other cornerstone players in zoological systematics entered the arena. The most influential of these undoubtly was Cuvier [1769-1832]. This great French comparative anatomist and palaeontologist *avant-la-lettre* had a very large influence on naturalists. Cuvier's thoughts dictated that knowledge of an anatomical structure acquires meaning only when its structure is known. He further firmly believed that animals are characterised by fixed (that is non-evolving), natural characters. By detailed studies of the internal anatomy of very diverse animals (a noteworthy difference with Buffon who concentrated mainly on vertebrates), Cuvier discovered a plethora of new characters and (mainly internal) organization types. Cuvier, as Buffon before him, quite successfully correlated several characters that he weighted according to functional importance (those dealing with the nutritive, the circulatory and the nervous system received the highest value), to arrive at a classification. Although conceptually his classification cannot be called truly upward (there was still the search for essences, resulting in classifications that were built by logical division), his system (1812) resulted in the destruction of the belief in the *scala naturae* (nature's ladder). Cuvier created four branches (*embranchement*), which showed hardly any overlap: *Animaux vertébrés*, *Animaux mollusques*, *Animaux articulés* and *Animaux rayonnés* or *zoophytes*. The last of these – the Radiata – is of importance in the present essay, as an elaboration of upward thinking led to the discovery that its composition was highly heterogeneous and needed splitting in more distinct phyla (Meckel 1821; Leuckaert 1848): the Echinodermata and the Coelenterata (now further split into Cnidaria and Acnidaria). It would however be erroneous to state that Cuvier did not recognise holothuroids from other echinoderms or from other phyla (used in the present sense of the rank) as in his *zoophytes* he discerned several classes, one of them being the *Echinodermes* (Cuvier 1817). Herein he further distinguished two orders: *les pédicellés* and *les échinoderme sans pieds*. Cuvier's first order holds representatives of various echinoderm classes (as we know them today); his second order holds four families: *les molpadies*, *les miriades*, *les priapules* and *les siponcles*, the first of these holds true holothuroids in which he recognised six groups.

[1] To Linnaeus, genera were the cornerstone of classification whereby he firmly believed that they were natural groups. In most instances, Linnaeus's genera have lost the hierarchical valuation which we give them today.

In the shadow of Cuvier, another Frenchman of great importance calls attention: de Blainville [1777-1850]. This man, who at Cuvier's death, took over the Chair of the Department of Comparative Anatomy in the Muséum National d'Histoire Naturelle (Paris), had no trouble in integrating comparative anatomy into systematic zoology and was one of the first to construct [hereby largely drawing on Tiedemann's (1816[1]) dissertation] a detailed, and surprisingly modern definition of holothuroids. De Blainville (1821) proposed to name the group *polycérodermaires* and attributed the family rank to it. He arranged the few species known at that time into five unnamed groups (A to E), which he based on general body form, tentacle morphology, distribution of tube feet and internal anatomy. As such, de Blainville's approach relied heavily on that of Cuvier, but, as it largely abandoned the functionality criterion, it can be considered more upward.
In the same period yet another French naturalist was very important in the pragmatic reconceptualization of zoological classification: Lamarck [1744-1829]. Cuvier's influence on Lamarck is clearly visible when one goes through his *Philosophie Zoologique* (1809[2]). It is thus not surprising that, in terms of classification theory, Lamarck's early concepts largely resembled those of Cuvier (differing in that he ranked his taxa according to degree of perfection; a reflection of his firm belief in the *scala naturae*). Later, Lamarck's ideas became more dynamic, and as he allowed branching of the (presumed) single lineage, almost phylogenetic. Hereby he put forward the hypothesis that animals acquire useful characters during their lifetimes (only when they are subject to different conditions and this through physical forces), which they then pass on to their offspring (Lamarck 1815: 11-12; 181-182). However, as outlined by Mayr (1982) and Bowler (1989), this theorem (evolution by transmutation) was largely unsuccessful. Be as it may, Lamarck's contributions to holothuroid systematics are extremely important. For instance he divided the *Division de radiaires* into two orders: *Radiaires mollasses* and *Radiaires échinodermes*. In the last order he created three classes: *les Stellérides*, *les Echinides* and *les Fistulides*. It is in this last section that we find the holothuroids. These were further separated into *Holothuries* (genus *Holothuria*) and *Fistulaires* (genus *Fistularia*). In *Holothuria*, a name we know since Aristotle, he placed species with non-peltate tentacles (mainly dendrochirotids); in *Fistularia*, a name he took from Forskål (1775)[1], he placed species with peltate tentacles (species now placed in *Holothuria*).
So given the *zeitgeist* - with the explosion of live forms that were brought home from various expeditions and the realization that weighting of characters according to functional importance not necessarily yielded natural groups - it can not come as a surprise that the eight- and early nineteenth holothuroid specialists gradually produced classifications that abandoned the ideas of essentialism and the *scala naturae*, and slowly began to adopt the principles of upward classification. However, given the doctrine of Cuvier's ideas, their classifications were mainly based on comparative anatomy, hereby stressing physiological (proximate) causation. This was to change in a fortnight[3] when C. Darwin [1809-1882] published his theory of natural selection in *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (1859), better known as *The Origin of Species* (but see also Wallace 1855). Darwin (1859) not only argued (and to a great extend proved) that individual variability gives selective advantage to the fittest organisms, enabling them to produce more offspring with the same advantageous qualities, but also put forward the hypothesis of a common ancestor to all species. This theory, as Mayr (1997: 93) notes "supplied the justification for the method of upward classification". As

[1] Reference to be found in Ludwig (1889-92).
[2] "D' abord, je changeai la dénomination de ma classe des échinodermes en celle de radiaires, afin d' y réunir les méduses et les genres qui en sont voisins. Cette classe, malgré son utilité et la nécessité qu' en font les caractères de ces animaux, n' a pas encore été adoptée par les naturalistes." (Lamarck 1809: 123)
[3] It is an extreme simplification to jump from the post-Linnean era (with Buffon; Cuvier, Lamarck as principal actors) to the Darwinian era; but for the sake of this essay, there's hardly any harm in doing so as during that period few conceptual innovations were made in regard to the classification of holothuroids. It is in this period that people like Owen [1804-1892], some called him the "British Cuvier", others the "champion of natural theology", developed important concepts like analogy and homology. These puzzling concepts were in the pre-*Origin* time (when no theory of evolution was available) elegantly explained by some (not all) of the *Naturphilosophen*, who sought to express the law and harmony in nature by using numerical systems. As *five* was the most popular number at that time (Mayr 1982), the *quinarian* system was developed. The quinarians arranged all organisms on circles (five on each circle) whereby those positioned on the same circle were united by affinity whereas those on overlapping circles revealed analogies. To my knowledge, this system was never employed for holothuroids.

such, it was able to give the final blow to the Lamarckian notion of evolution (drive towards perfection; e.g. the belief in the *scala naturae*) and supplied a two-step (natural selection acting on variability in natural population and common descent) causal theory on evolutionary change.

The period between 1750 and 1859 was thus clearly pregnant with evidence that allowed a conceptual renovation of holothuroid systematics. According to Ludwig (1889-92), Bohadsch (1761[1]) and Gaertner (1761[1]) were the first to produce a thorough anatomical description of true sea cucumbers (hereby employing the name *Hydra*). These two pioneers not only recognized that the specimens they had before them were related to sea-urchins and starfish (as did Belon two centuries earlier), but their description of external and internal anatomy shows that they (especially Bohadsch) attributed functionality to the structures they observed (e.g. tentacles were attributed a food-acquisition function, at the oral side the gonadal opening was recognised,...). Somewhat later, Strussenfeldt (1767[1]) gave an even more detailed description of the anatomy of a dendrochirotid. Pallas (1774[1]) was the first to examine a non-European species (from Cape of Good Hope). However, as outlined by Ludwig (1889-92), his description was less correct than the ones his colleagues (especially Strussenfeldt) had previously produced. After these early attempts, more and more species were described from various localities (Gunner 1770[1]; Forskål 1775[1]; O.F. Müller 1776[1]; 1788[1]; Pennant 1777[1]; Dicquemare 1778[1]; Fabricius 1780[1]). Without doubt, these descriptive studies prepared the ground for further comparative anatomical insights. As already mentioned, it was Cuvier - with his superior knowledge on the internal anatomy of invertebrates - who integrated (and supplemented) the available anatomical knowledge into a true classification (see above). Holothuroid classification now quickly gained *momentum* as Tiedemann (1816[1]), Oken (1816[1]), Goldfuss (1820[1]), Chamisso & Eysenhardt (1815[1]); Lamarck (1809; 1815; 1816), Lessueur (1824), Delle Chiaje (1823-1829[1]), Risso (1826[1]), Fleming (1828[1]), Rüppel & Leuckaert (1828[1]), Eschscholtz (1829-33[1]), de Blainville (1830), Lesson (1830), Quoy & Gaimard (1833[1]), Jaeger (1833), Brandt (1835), Burmeister (1837), Grube (1840), Forbes (1841), Troschel (1846), Gray (1848; 1853), von Siebold (1848), J. Müller (1850), Bronn (1860) and Dujardin & Hupé (1862[1]) all attempted to arrive at a holothuroid classification. It would lead us to far to discuss all of these attempts in their detail (see for instance Ludwig 1889-92, part D). However, even if all the above classifications are to a large extent interconnected, two of these classifications are noteworthy in regard to their influence on subsequent taxonomists: the one proposed by Jaeger (1833) and the one designed by Brandt (1835). It is thus worth to portrait these with a bit more colour.

Jaeger (1833) partially followed Cuvier and Oken in regarding body morphology and, to a lesser extent, position of tube feet as the determining characters in classifying sea cucumbers. In addition however, Jaeger also considered the presence or absence of respiratory trees to arrive at a classification of the genus *Holothuria* (taxonomic rank *sensu* Linnaeus; *i.e.* the present class Holothuroidea). Basically Jaeger (1833) discerned three large groups ("subgenera"; *i.e.* orders in the present sense): *Cucumaria* comprising those species that (possibly) lack respiratory trees and have their tube feet arranged in rows; *Tiedemannia* holding those species with a cylindrical body, with no distinction between ventral and dorsal side, no respiratory trees and poorly developed tube feet; and *Holothuria* containing those forms with non cylindrical body, with distinction between dorsal and ventral side and with respiratory trees. The tribes he discerned in his subgenera correspond to a large extent to some genera we know today (but note that his *Cucumaria* tribe *Minyas* does not hold sea cucumbers). A translation (from Latin to German) of Jaeger's (1833) classification can be found in Ludwig (1889-92: 306).

Brandt's (1835) classification - even if Ludwig (1889-92: 306) refers to it as "Viel gekünstelter" and Deichmann (1958: 282) as "the poorest, most artificial of all" – also deserves a closer look. Brandt (1835) grouped true holothurians (his family Holothuriae) together with sipunculids (his families Sipunculacea and Thalassemata) in the order Holothurina. Brandt (1835) divided the family Holothuriae into two main groups: those with tube feet (Pedatae) and those without tube feet (Apodes). Even though Brandt's (1835) classification was based on a very limited number of species and only on anatomical features, two remarkable observations can be made from it: (i) the division between those species with peltate (Aspidochirotida) and those species with branching tentacles (Dendrochirotida) is still in use today, albeit these groups are now attributed a higher rank and (ii) recent cladistic evidence (Kerr & Kim 2001) provides some support for his division of Apodes (now Apodacea) in Pneumonophorae (now Molpadida) and Apneumones (now Apodida). A free translation (from Latin) of Brandt's (1835) higher-level classification is given in table 1.

[1] Reference to be found in Ludwig (1889-92).

Familia Holothuriae
I. Pedatae [species with pedicels more or less developed, variously distributed]
A. Homiopodes [species with pedicels similar in size and shape]
a. Dendropneumones [species with highly branched respiratory trees, free or attached; pedicels distributed over total body surface or solely ventrally]
aa. Peripodes [pedicels visible in five rows or over the whole body]
bb. Hypopodes [pedicels slightly visible]
b. Apneumones [species without respiratory tree]
B. Heteropodes [species with two different types of pedicels: cylindrical with flattened apex, distributed ventrally sprouting from pores; or conical with the majority plus minus teat-like distributed dorsally; dendritic respiratory tree; gonad split]
a. Stichopodes [Ventral pedicels distributed in three, four or five bands in the median area]
b. Sporadipodes [Few ventral pedicels distributed without order]
aa. Aspidochirotae [peltate tentacles]
bb. Dendrochirotae [branched tentacles]
II. Apodes [species with dendritic, semi-dendritic or no respiratory tree attached to the body mesenteries]
A. Pneumonophorae [respiratory tree obvious]
B. Apneumones [respiratory tree absent]

Table 1. Brandt's (1835) higher-level classification.

Grube (1840), clearly building further on Lamarck (1816), Lessueur (1824), Brandt (1835) and Burmeister (1837), attributed a higher taxonomic weight to the morphology of the tentacles and discerned three groups: *Aspidochirotae*, *Dendrochirotae* and *Chiridotae*. Troschel (1846) not only used the shape of the tentacles, but also their number and position, a *modus* that enabled him to delimit some new genera. Initially Grube (1840) and Troschel's (1846) attempts were virtually ignored in England (see for instance Forbes 1841 and Gray 1848) and Germany (see for instance von Siebold 1848) where the older systems were further elaborated. J. Müller (1850), on the other hand, recognised the value of Grube's system and concluded that presence or absence of respiratory trees is weightier than presence or absence of tube feet. As such, he discriminated between the group without respiratory trees (*Lungenlose*; now Apodida) and the group with respiratory trees (*Lungentragende*). The latter he further divided into those without tube feet (*Fusslose*; now *Molpadiida*) and those with tube feet (*Fussige*; now Aspidochirotida and Dendrochirotida). Shortly hereafter another breakthrough was made when Gray (1853) described a peculiar flask-shaped deep-sea species from Congo. For this species, he created the new genus *Rhopalodina*. Gray (1853) and Bronn (1860) believed this genus to be so different from the other holothuroids that they proposed to classify it in a family or even an order of its own. Bronn (1860) even went so far as to propose the order Decacrenida for *Rhopalodina* and Pentacrenida for all the other holothuroids. For the division of the latter taxon he combined Brandt (1835) and J. Müller's (1850) system, but confusingly used new names for most of his taxa [e.g. his two suborders Apodia (= Brandt's Apodes) and Eupodia (=Brandt's Pedatae)]. Nevertheless, Bronn (1860) deserves the credit of being the first to recognize the position of all the then known holothuroids as the class Holothurioidea.

2.4. The post *Origin* period

By the mid-nineteenth century, comparative anatomy had matured enough to recognise natural groups that were, by a largely upward-approach, placed in a hierarchical classification. However, as the reconstructed archetypes lacked a credible causal explanation, they remained to a large extent hollow until they were reinterpreted with Darwin's (1859) paradigm of the common ancestry.
Selenka (1867), according to H.L. Clark (1908[1]) the first to study holothurians with a modern systematic point of view, was one of the first who could have defended his holothuroid classification by using the extraordinary explanatory powers of Darwin's (1859) theory of common descent and (gradual) origin of

[1] The publication date of H.L. Clark's important monograph *"The apodous holothurians"* has in the past predominantly been dated from 1907, but as Pawson *et al.* (2001) have demonstrated that this date is not in accordance with article 21.2 of the International Code of Zoological Nomenclature. I comply with Pawson *et al.* (2001) and thus refer to Clark's work as H.L. Clark (1908).

species. Unfortunately, Selenka's (1867) writings give no indication of a search in that direction. Instead, Selenka (1867) continued in the traditional descriptive style. Hereby, he chose to elaborate J. Müller's (1850) system and distributed the species into two different orders: the Pneumonophora [confusingly also noted as Dendropneumona by him (1867: 305)] for those species with respiratory trees and the Apneumona for those species without respiratory trees. Selenka (1867) divided the Pneumonophora in three separate families (Aspidochirotae, Dendrochirotae and Lisomatidae) while he believed that the Apneumona held only the family Synaptidae. A free translation (from German) of the characters used by Selenka is given in table 2.

	Pneumonophora			**Apneumona**
Character	Aspidochirotae	Dendrochirotae	Lisomatidae	Synaptidae
Presence of respiratory tree	+	+	+	-
Left respiratory tree encircled with blood-vessels	+	±	±	-
Tentacles tree-shaped	-	+	-	-
Presence of retractor-muscles of calcareous ring	-	+	-	-
Presence of tube feet	+	+	-	-
Intestine with one loop	+	+	+	±
Presence of hermaphroditism	-	-	-	+
Gonadal pore in inner side of tentacle crown	-	+	-	-
Presence of tentacular ampullae	+	-	±	-
Presence of Cuvierian tubules	±	-	±	-

Table 2. Classification based on comparative anatomical studies as proposed by Selenka (1867).

Almost simultaneously, Semper (1868) released an impressive work on the sea cucumbers of the Indo-Pacific. Semper, as Gray (1853) and Bronn (1860) before him, placed the genus *Rhopalodina* separate from the other holothuroids and proposed a new class (Diplostomidea) to accommodate it. The other species he kept in the class Holothurioidea which he, like Selenka (1867), divided into two orders: Apneumona and Pneumophora. However, Semper (1868), contrary to Selenka (1867), clearly adopted Darwin's theory of common descent as is evident from his phrase (p. 186) "Freilich ist auch heutigen Tages die genetische Methode, welche im Stammbaum nicht bloss den Ausdruck zufälliger Aehnlichkeit, sondern auch den der genealogischen Abstammung sieht, noch durchaus nicht allgemein zur Geltung gekommen; aber sie giebt dennoch einen Prüfstein ab für die Richtigkeit derjenigen Resultate, die wir bisher auf dem fast allein eingeschlagen Wege der vergleichenden Anatomie gewonnen haben." Semper thus actively searched for the characteristics of the inferred common ancestor. By using Haeckel's (1866) recapitulation theory - the theory that states that ontogenic stages recapitulate the adult stage of the ancestors - Semper deduced that sea cucumbers without tube feet and with simple tentacles (Synaptidae and Molpadidae) represent the most ancient forms; those with papillae and tube feet are less ancient and those with solely tube feet represent the most recent ones. His consistent use of the recapitulation theory also made him conclude that the structure of the calcareous ring and the ossicles must receive a very low phylogenetic value as these structures acquire their final morphology only in the last stages of development. This is reflected in his classification where these structures are only used to distinguish species from each other. Be as it may, it is safe to state that Semper (1868) was the first holothuroid taxonomist who clearly attempted to incorporate phylogeny of sea cucumbers into a classification.

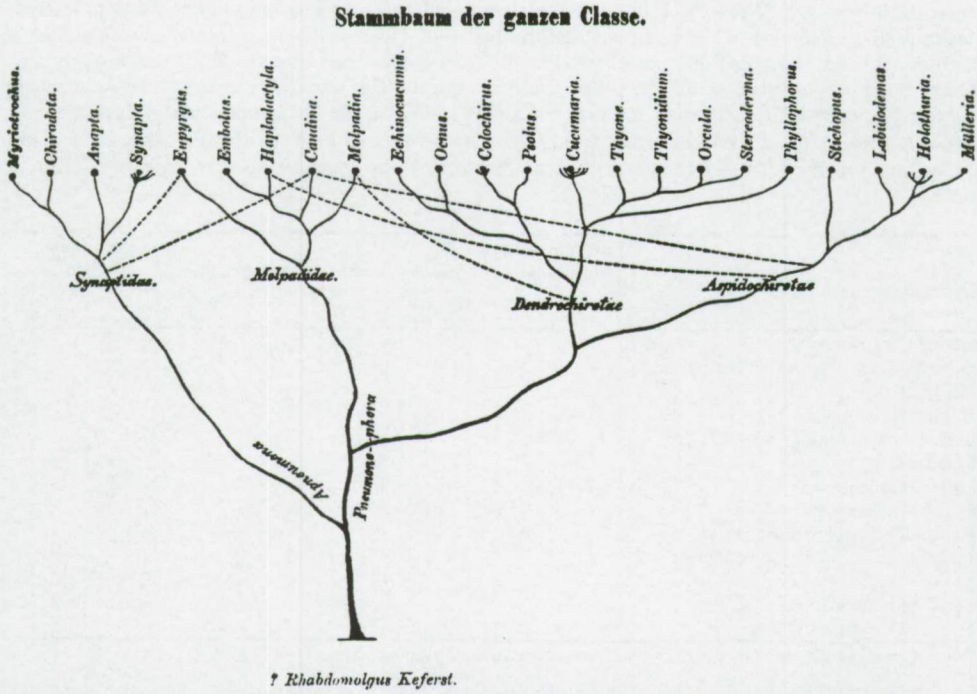

Figure 1. Phylogenetic tree for the Holothuroidea, according to Semper (1868). This graphical representation shows that Semper not only utilised an upward classification, but also applied the concept of common descent. Hereby, he searched for inferred common ancestors by applying the recapitulation theory (remark his tentative common ancestor, *Rhabdomolgus Keferst.*).

Somewhat later Théel (1879), who had at his disposition a large collection of deep-sea species, felt justified to create a new order to accommodate the large number of new species he had discovered. He defended this decision rather vaguely, I cite: "Most of the species living in the great depths offer such considerable peculiarities that I think it convenient to form for them a new order, Elasmopoda, equivalent to those already known, Pedata and Apoda" (Théel 1879: 3, but see also his diagnosis on page 4). Within his new order Théel recognised three families: the Elpidiidae, the Deimatidae and the Psychropotidae. Hereafter, Lampert (1885) followed Semper (1868) and Théel (1879), but in the same time considered parts of Selenka's (1867) lower level classification. Lampert (1885) believed that the character presence of tube feet holds more phylogenetic information than the presence and the structure of the respiratory trees, which he called *inconstanter*. Lampert (1885) discerned three orders: Pedata, Elasipoda and Apoda. Within the Pedata he recognised the families Aspidochirotae, Dendrochirotae and Rhopalodinidae; in the Elasipoda, he placed the families Elpidiidae, Deimatidae and Psychropotidae; and in the Apoda, he discerned the suborder Pneumonophora with the family Molpadidae and the suborder Apneumona with the family Synaptidae. Théel's (1886) final classification thus largely mirrored Lampert's (1885) one. Hereafter, Ludwig (1889-1892) made an important summary of all the known classifications and made a brave approach to construct the ultimate classification whereby he considered 19 different key-characters. The characters Ludwig (1889-92) investigated were: (1) general body form; (2) body colouration; (3) ossicles of the body wall; (4) presence of anal teeth; (5) structure of sensory organs; (6) structure of the longitudinal musculature; (7) presence of retractor muscles; (8) structure of the calcareous ring; (9) number, size, positioning and form of the tentacles; (10) presence and size of the tentacle ampullae; (11) morphology, position and (to a certain extent) number of tube feet; (12) form, size and colour of the stone canal(s); (13) number of Polian vesicles; (14) structure of the gonad; (15) fine-structure of the digestive system; (16) presence and size of respiratory trees; (17) presence of Cuvierian tubules; (18) presence of ciliated funnels and (19) the complexity of the blood vessel system. He proposed two orders: Actinopoda, grouping the

species with tube feet and Paractinopoda for those species lacking tube feet. He put Théel's (1879) Elasmopoda (as Elasipoda) as a family of the Actinopoda. His schematic representations [1889-92: 326 (reproduced in fig. 2), 328, 334, 336, 339, 343, 352, 356] again show clearly that he truly adopted an upward system. Moreover, just as Semper (1868), Lampert (1885) and Théel (1886) before him, he considered horizontal (*i.e.* geographic) and vertical (*i.e.* bathymetrical) distributions to strengthen his classification. As H.L. Clark (1908) correctly observed, Ludwig's (1889-92) classification was also the first to incorporate embryological evidence.

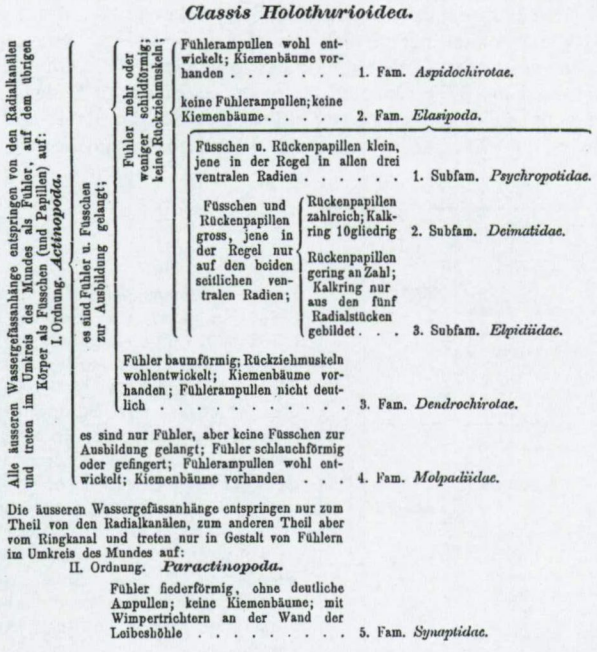

Figure 2. Ludwig's (1889-92) classification of the Holothuroidea. A truly upward approach is clearly visible.

It cannot be denied that Ludwig's (1889-92) classification was to a large extent based upon the search for evolutionary relationships. Hereby, he argued that his families – Dendrochirotae, Molpadiidae and Synaptidae – have originated from a common dendrochirotid-like ancestor, form one *Hauptstamm* (*Dendrochirotenstamm*); he further argued that a second lineage has originated from an aspidochirotid-like ancestor (*Aspidochirotenstamm*) which gave rise to his families Aspidochirotae and Elasipoda. Several remarks can be made from Ludwig's (1889-92) phylogeny. In regard to the inferred common ancestor, the *Urholothurie*, Ludwig, even though he postulated that his two main lineages have respectively an aspidochirotid-like and a dendrochirotid-like ancestor, believed his *Urholothurie* "ähnliecher geblieben sind als die Abzweigungen der Elasipoden, Molpadiiden und Synaptiden" and that of these three families the synaptids are the oldest and in the same time most diverged group. By doing so he was able to justify his division between those with tube feet (Order Actinopoda) and those without tube feet (Order Paractinopoda). However, from a modern point of view this implies that his order Actinopoda is non-monophyletic (fig. 3). Again this comes as no surprise, as since 1859 (to now), the relation between classification and phylogeny has remained controversial. Most probably this was due to the fact that the causal mechanism of evolution (natural selection or descent with modification as Darwin often called it) was not truly understood or searched for during those days. Here, a clear difference with Darwin (1859, chapters 4 and 13), who observed *within* a theoretical framework, is visible. A citation from Darwin's (1859: 404) most popular book can illustrate this best: " I believe that the arrangement of the groups within each class, in due subordination and relation to the other groups, must be strictly genealogical in order to be natural; but that the *amount* of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different

genera, families, sections or orders." Clearly, Ludwig (and many of his predecessors) did not adopt the last section of this line of thought.

In 1896, Haeckel produced an important, but often ignored, work that integrated paleontological evidence with comparative anatomy and ontogeny. Haeckel understood, perhaps better then anybody else during his time that classification had to be based on phylogeny. Haeckel thus was preoccupied in developing a method that would reveal the phylogeny. As said before, Haeckel (1866) was particularly interested in the heuristic method of recapitulation. As such it is not surprising that Haeckel (1896: 379) saw sea cucumbers with their reduced calcareous skeleton (as in the larvae of other echinoderms) as the most primitive group amongst the extant echinoderms. Haeckel (1896), undoubtedly aware of Ludwig's flaw in regard to the monophyly of the Actinopoda proposed a new classification that corresponded perfectly with the phylogenetic scenario he had elaborated. However, apart from adding a new group [the *Pelagothurien* (order Nectothuriae), deep sea forms discovered in 1893], changing the names and ranks of Ludwig's (1889-92) classification and shuffling the groups as to attain monophyly of the subclasses, his higher-level classification largely followed that of Ludwig (1889-92). This becomes clear when Ludwig and Haeckel's phylogenies are put next to each other (fig. 3).

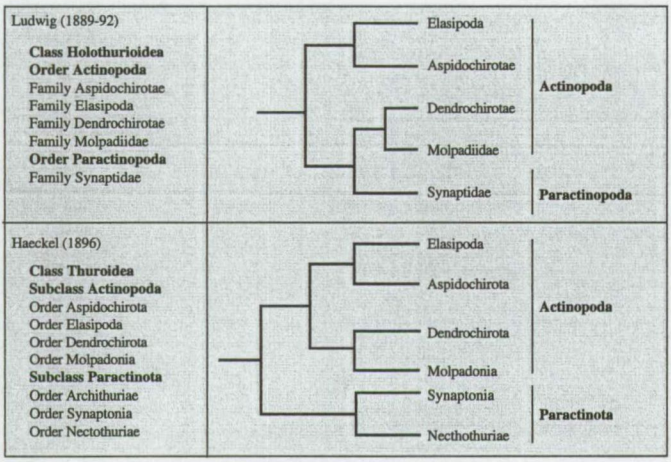

Figure 3. Comparison of Ludwig's (1889-92: 454) and Haeckel's (1896: 380, 439) phylogenetic trees as rendered into cladograms. Whereas Ludwig's (1889-92) classification not completely satisfies the monophyly criterion, Haeckel (1896) clearly balanced his classification with what he believed to be the correct genealogy. Haeckel's "hypothetische gemeinsame Stammgruppe aller Holothurien", the extinct Archituriae is not depicted on the cladogram; he classified them under the Paractinota.

Haeckel's (1896) changes in the higher-level systematics mark the *zeitgeist* of the early post-Darwinian era. Indeed, the consistent use of the theory of recapitulation in the deciphering of phylogeny and the subsequent incorporation of the genealogy into classifications was in that era much the pre-occupation of many taxonomists. Even though the recapitulation theory (*sensu* Haeckel, not von Baer) is now known to be invalid[1], it boosted comparative embryological and anatomical studies, which, in turn, resulted in complementary taxonomic insights and new classifications. Östergren (1898), for instance, further divided the then already well-established family Synaptidae into three subfamilies (later raised to family rank) because of differences in the calcareous deposits. He discerned the Synaptinae with anchors and anchor-plates (only miliary granules in the genus *Anapta*); the Chiridotinae with 6-spoked wheels or sigmoid or bracket-shaped particles and never anchors and the Myriotrochinae with 8-or more-spoked wheels.

Thus, with the coming of the new century several new classifications quickly emerged: Sluiter (1901), Perrier (1902), Delage & Hérouard (1904), MacBride (1906), Östergren (1907), Fisher (1907), H.L. Clark (1908; apodids only), and others. Surprisingly, of these, only Östergren (1907) makes immediate reference to Haeckel's (1896) important work. Östergren's reconstructed phylogeny (copied in fig. 4) is, however, difficult to analyse. Undoubtedly this is the result of his *Cuvierian philosophy* that "wenn wir den systematischen und phylogenetischen Wert eines organes richtig beurteilen wollen, die Funktion desselben eingehend kennen müssen (p. 191)". As such he places great emphasis on food acquisition, distribution, movement, defence, respiration, and the form and function of the ossicles. Östergren (1907) recognised the

[1] Gould's (1977) jewel of a book neatly "recapitulates" the history and the scientific beliefs of the recapitulation theory.

same five orders as Ludwig (1889-92), whereby he argued that elasipods are the most ancient group and that the *Urholothurie* most probably resembled them. He continued this line of thought by stating that, if the common ancestor had respiratory trees, it would resemble the synallactids, or, if respiratory trees were absent, deimatids. Similarly he hypothesized that mobile species, with well-developed tube feet and covering themselves with alien objects, evolved into the psychropotid/pelagothuriid lineage. In congruence with his predecessors, Östergren recognized that apodids are to be positioned separate from the other orders, but his view on the splitting off of the dendrochirotids, aspidochirotids and molpadiids remains rather vague, especially in regard to the Synallactidae, which he placed as a family of the elasipods.

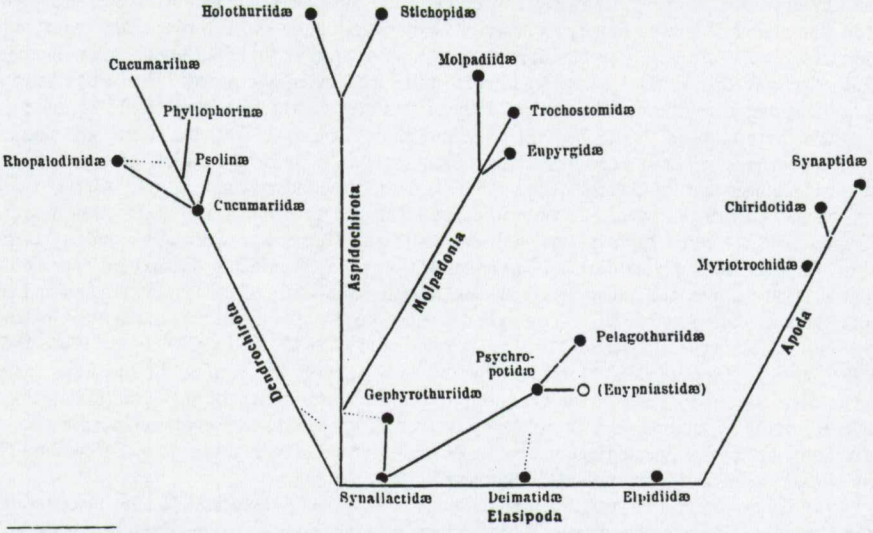

Figure 4. Östergren's (1907) evolutionary tree. His base line, holding the elasipods, is deliberately kept horizontal to allow the scenario where respiratory trees can be retained or lost in the neighbouring families. The dotted lines represent alternatives on the origin of the Psychropotidae, Gephyrothuriidae, Dendrochirotida and Rhopalodinidae.

Östergren's (1907) classification was however largely overshadowed by Fisher's (1907) important treatise on the holothurians of the Hawaiian Islands. It is important to note that Fisher (1907) tried to stabilize the seemingly ever-changing names by calling attention to the nomenclatural inconsistencies in the previous classifications (but see also Gill 1907a, b). As such he recognised[1] the order Actinopoda - holding the families Holothuriidae (with subfamilies Holothuriinae and Synallactinae), Elpidiidae (with as subfamily Deimatinae) and Cucumariidae (with as subfamilies Cucumariinae and Psolinae) – and the Paractinopoda (with as family Synaptidae). Deichmann (1930), in an important treatise on the holothuroids of the western part of the Atlantic Ocean, retained the elasipods as a distinct order and recognised four additional orders: Aspidochirotida, Dendrochirotida, Molpadonia and Apoda. Basically this ordinal classification is nowadays retained, with a sixth order, Dactylochirotida, proposed by Pawson & Fell (1965).

From these early attempts to classify holothuroids it is difficult to see a punctuated shift from down-to upward division; rather the two principles were intermixed for a long time. So clearly, Cuvier's legacy of employing comparative anatomy - with every organ assigned a defined function – continued to have a major impact. On the other hand, it became increasingly clear that additional diagnostic characters would have to be used if a consensus classification - that is a classification independent of the number of species, the types and weighting of characters - was ever to be reached. This was especially true at the subfamily level (term used in the present content meaning). *Deus ex machina*, ossicles or spicules, of which, according to Ludwig (1889-92), the first type (an anchor from the body wall of an apodid) was purposefully

[1] As Fisher (1907) only dealt with Hawaiian species, his classification only applies to this selected group.

described[1] by Lesson (1830), seemed to be just the kind characters that could resolve the classification impasses of that time even though, contrary to Cuvier's doctrine, no immediate function could be assigned to these characters (but see for instance Östergren 1907).
Microscopic observation of these ossicles (by the 1860-1870s microscopy truly had come of age, making it possible to study not only the larger ossicles like anchors and anchor plates, but also the much smaller ossicles like tables and buttons) revealed that the morphologically delimited taxa could also be recognised on the level of the ossicle assemblage; multi-character taxonomy gradually became common, first by default, later by intent. Indeed, by the start of the twentieth century most of the currently known ossicle types had already been described. However, whereas in the old (early nineteenth to twentieth century) system this knowledge was used mostly to describe at the level of the species, twentieth century authors increasingly used these characters to classify the multitude of species they had under study. Deichmann (1948: 330) captured this shift of character-interest quite well when she noted: "There has been some tendency to consider them (the ossicles) trivial, rather fortuitous characters, which should be more or less ignored, while the emphasis should be laid upon morphological structures; the more one studies the spicules, however, the more it becomes evident that there is a definite relation between the larger morphological features and the pattern of the spicules, though secondary changes may often obscure the latter". So by the start of the twentieth century, usage of ossicle assemblage in constructing holothuroid classifications had delivered quite a few well-defined taxa. These taxa were subsequently critically analysed by a new breed of taxonomist: a taxonomist who was clearly utilising the upward approach (with consideration of all the available characters), was aware of the non-fixity of the taxa he studied and sought to incorporate an evolutionary causality (common descent) into his classification. This can for instance be illustrated with the attempts of Pearson (1914) and Panning (1931b-1935a-d; 1940; 1941; 1944; 1951) to classify the family Holothuriidae. Moreover, by the 1950's, with the coming of the *New Synthesis*, taxonomists also started to pose direct questions concerning the causes of the structural changes in phylogeny. By doing so, comparative morphology was transformed into true evolutionary morphology, a frameshift that significantly boosted understanding of the proposed classifications [e.g. Deichmann (1958) and Rowe (1969) on the taxonomy of the Holothuriidae].
Finally, in 1965, Pawson & Fell took up the challenge to propose a classification that incorporates the evolutionary relationships and which reflects the Linnean scheme. They abandoned number of tentacles as a criterion for diagnosing major taxa and, instead, gave greater importance to the shape of the calcareous ring, the shape of the tentacles and the ossicles of the body wall. By doing so, they proposed three new subclasses and six orders. One of these orders, the Dactylochirotida (grouping species with finger-like tentacles and a testaceous body wall) was new. This classification is still in use today, even though recently it has received some criticism (Kerr & Kim 2001). In figure five, Pawson & Fell's (1965) hierarchical classification and the transformation into a phylogeny as made by Kerr & Kim (2001) is given.

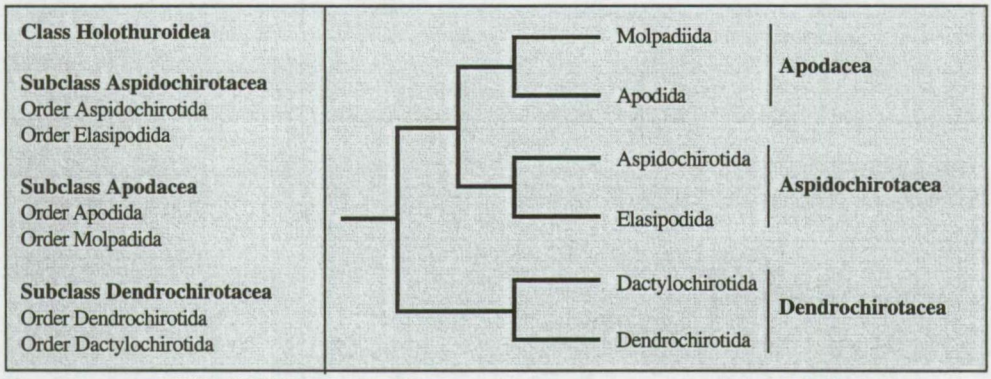

Figure 5. Pawson & Fell's (1965) Linnean classification rendered to a phylogeny (from Kerr & Kim 2001).

[1] Ludwig (1889-92) correctly noted that Strussenfelt (1767) had painted the large scales of *Psolus phantapus*, but that it is only since Lesson (1830) that ossicles were realized to be part of the body wall of holothuroids.

Even if the clades as proposed by Pawson & Fell (1965) are fairly well defined and have been used by most subsequent authors (e.g. Cherbonnier, Liao, Lambert, Massin, O'Loughlin, Rowe, Thandar, ...), consensus over their monophyly has not be reached and as such the higher level taxonomy of Holothuroidea remains problematic. Hansen (1975), for instance, noted that grouping of Elasipodida with Aspidochirotida on the basis of presence of peltate tentacles excludes some elasipodids, notably members of *Orphnurgus* [see also Pawson (2002) for an up to date key to this genus] Consequently, Hansen (1975) rejected the subclass Aspidochirotacea. It must, however, be noted that Pawson & Fell (1965; see also Pawson 1982), were aware of the possibility of convergence in their classification. For instance, they suggested that the Apodacea, holothuroids without tube feet, might be non-monophyletic and that the observed similarities between the Apodida and the Molpadiida might be the result of convergent evolution rather than of common descent.

2.5. The last two decades – *cladistics* enters classification

The last fifteen years saw the coming of phylogenetic techniques to decipher the relationships between the five extant classes of echinoderms. This novel approach significantly added to our understanding of the inter-classis relationships of which a consensus is now more or less apparent (Littlewood *et al.* 1997; Janies 2001). However, until the last couple of years, surprisingly few cladistic studies were devoted to uncover the relationships *within* the Holothuroidea. Littlewood *et al.*'s (1997) sequence analyses of small and partial large rRNA subunits of some holothuroids (a single aspidochirotid; two apodids; three dendrochirotids and one elasipodid) revealed a close relationship between dendrochirotids and aspidochirotids. However, the two different genes sequenced by the latter authors returned a different position for the apodids and the elasipods. Kerr (2000) enlarged Littlewood *et al.*'s (1997) analysis with other published sequences (Raff *et al.* 1988; Wada & Satoh 1994) in an attempt to resolve the relationships between four of Pawson & Fell's (1965) six orders of holothuroids. Kerr's (2000) study revealed a well-supported (Apodida,(Elasipodida,(Aspidochirotida, Dendrochirotida))) topology. He tentatively concluded that apodids and not dendrochirotids (Pawson & Fell 1965) are to be considered the most divergent group of living holothuroids, a scenario that can be traced back to Semper's (1868), on comparative anatomy based, phylogenetic tree (see also fig. 1; also Ludwig's 1889-92 description of the *Urholothurie*). Kerr (2000) further correctly emphasized that his (and Littlewood *et al.*'s 1997) results rendered the subclass Aspidochirotacea paraphyletic. In an ensuing cladistic analysis on a relatively large morphological dataset Kerr & Kim (2001) corroborated their earlier result and in addition suggested that all three subclasses as proposed by Pawson & Fell (1965) are non-monophyletic and, moreover, that only four of Pawson & Fell's (1965) six taxonomic orders received strong support as clades (monophyly of Molpadiida and Dendrochirotida[1] questioned). Kerr & Kim's (2001) phylogeny of the Holothuroidea as inferred from morphological analyses and the stratigraphic record is reproduced in figure 6.

So, despite the fact that classification of holothuroids has a long and rich history, basic questions – even at higher taxonomic levels – on the classification and evolution remain. Kerr & Kim's (2001) important observation (p. 77) that "differences, at the level of orders and subclasses, however, indicate that several groups as currently defined have not been cladistically diagnosed, that is not via the most parsimonious ascription of character states" is here remembered. As such, old as well as recent taxonomic revisions [a.o. Smirnov (1989) on the Synaptidae; O'Loughlin (1998) on the Gephyrothuriidae; Thandar (2001) on the Rhopalodinidae] will have to pass the scrutinizing test of cladistic analysis before they can be considered stable and reflecting common descent (see also Samyn *et al.* Submitted, chapter 4; Samyn In preparation, chapter 7; Kerr 2001; Kerr *et al.* Submitted, annex). Undoubtedly, in the long-run (that is when enough well-preserved tissue material is available) molecular systematics can and will further guide our quest for a natural classification.

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[1] Even though Kerr & Kim's (2001) cladistic analysis of the higher-level taxonomy (up to family) is a thoughtful analysis, it also has its drawbacks. For instance, it is not surprising that the Phyllophoridae returned unresolved as the authors chose the "outsider" *Afrocucumis africana* (Semper, 1868) as the representative species of the Cucumariidae (Massin pers. comm.). Likewise, these authors scored a mere 47 characters of which only nine dealt with the ossicle assemblage; as such it seems that they have omitted quite a few parsimony informative characters (presence of rosettes, presence of holothuriid buttons, presence of several table types...). Their results are thus best treated as preliminary.

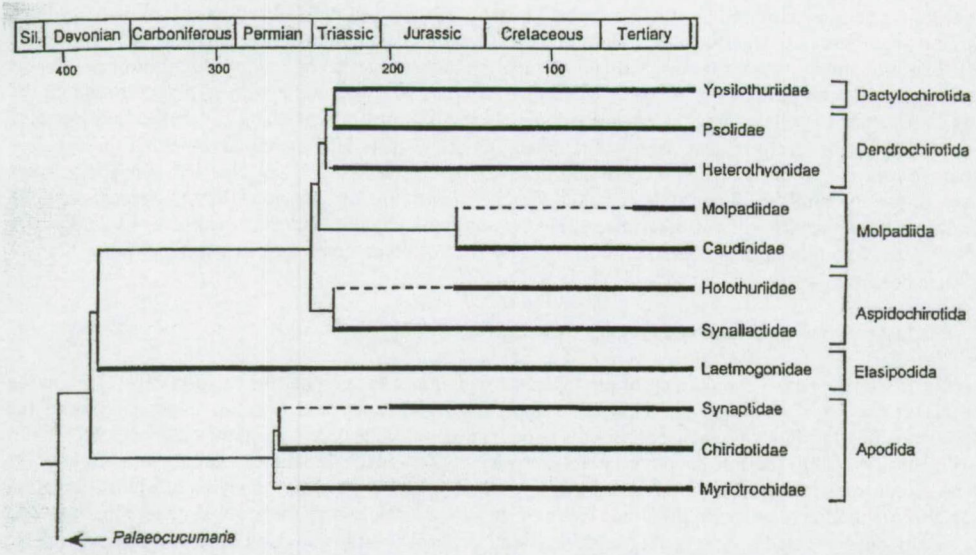

Figure 6. Kerr & Kim's (2001: 78) inferred phylogeny of the Holothuroidea as based on a morphological dataset and the stratigraphic record of the oldest fossil representatives. Thin solid lines represent the phylogeny as obtained from their cladistic study; thick solid lines represent the range of occurrence and thin dashed lines indicate ghost range.

2.6. The Holothuriidae (Holothuroidea: Aspidochirotida) as a *casus*

As the present dissertation deals to a large extent with the Holothuriidae, I think it is well worth the effort to discuss the recent history of that particular taxon, as this will help the reader to get a better grasp on the subject.

Within the Aspidochirotida, three to four families are nowadays recognised: the Gephyrothuriidae[1]; the Holothuriidae; the Stichopodidae and the Synallactidae (see for instance Rowe & Gates 1995). The monophyly of the Aspidochirotida is still debated (Kerr & Kim 2001). Even though some recent evidence points to the monophyly of the Holothuriidae (Appeltans 2002; Massin *et al.* in press, Kerr *et al* in prep.), the evidence for a non-monophyletic status is forthcoming (pers. observ.; Massin, Rowe & Thandar pers comm.). Whatever the case, as most authors agree that this family is a true natural group and as the classification that currently applies to it has remained virtually unchanged since it was proposed by Rowe (1969; but see also James 198, Massin *et al.* in press and Samyn *et al.* in prep. for the taxonomic status and systematic position of the genus *Labidodemas*; Cherbonnier 1980 and Thandar 1988 for the addition of two new subgenera; Samyn & Massin (in press) for the revision of the subgenus *Mertensiothuria*; and Samyn *et al.* in prep. for the revision of the *arenicola* complex), it will here be treated as such.

The name Holothuriidae is attributed to Ludwig (1894), but as Gill (1907a) correctly pointed out, Gray used the name Holothuridae (spelling *sensu* Gray) as early as 1848. Before 1894, Brandt's (1835) name Aspidochirotae was commonly used to designate the Holothuriidae. Ludwig (1883) for instance recognised three genera within the Aspidochirotae: *Stichopus* Brandt, 1835, *Mülleria* Jaeger, 1833 and *Holothuria* Semper, 1868 (non Linnaeus, without giving an explanation). Within *Holothuria* he further recognised four groups: *Stichopus*, *Bohadschia*, *Sporadipus* and *Holothuria* sensu stricto. In subsequent publications Ludwig (e.g. 1886; 1887, 1899) abandoned his division of *Holothuria*, but still recognised the three genera he had recognised in 1883. In 1896, Haeckel, based upon his studies of embryology, palaeontology and

[1] It is symptomatic for the taxonomy of the Holothuroidea that the systematic position of the Gephyrothuriidae Deichmann, 1940 (a taxon characterized by the absence of ossicles in many body tissues) is still debated. For instance, while Rowe (*in* Rowe & Gates 1995) maintains this family within the Aspidochirotida, Pawson *et al.* (2001) place them under the Molpadiida. Kerr & Kim (2001) chose the golden mean and omitted them from their phylogenetic analysis.

phylogeny, recognised that some of the genera attributed to the Holothuriidae warrant a family on their own and thus he erected the Stichopodidae. In this action he was initially only followed by Östergren (1907) and later Mortensen (1927). Not surprisingly, the latter was at that time studying the larval forms of different echinoderms, with regard especially to their importance for classification[1]. Nevertheless, it was only after Deichmann's (1938) work that this family was commonly incorporated in classifications. In the mean time some important (they are still cited daily) new works were published. Amongst the most important ones were those by Fisher (1907) and Mitsukuri (1912). Both these authors recognised two subfamilies in the Holothuriidae: the Holothuriinae Ludwig and the Synallactinae Ludwig (both were later raised to family level). According to Fisher (1907) the Holothuriinae (now Holothuriidae) hold four genera: *Actinopyga* Bronn, 1860; *Holothuria* Linnaeus, 1767; *Labidodemas* Selenka, 1867 and *Stichopus* Brandt, 1835, whereby in a footnote he correctly points to the fact that it has been shown earlier that the name *Mülleria* Jaeger, 1833 (for which *Actinopyga* is the replacement name) is at least three times pre-occupied (Férussac 1823[2], molluscs; Desmarest 1825[1], crustaceans; Fleming 1828[1], other echinoderms). Mitsukuri (1912), apart from retaining *Mülleria* as a valid taxon-name, adheres to the same taxonomy[3].

Clearly, the many changes in the Holothuroidea (see also Gill 1907a; Clark & Rowe 1967) confused a number of authors. This confusion, as already noted above, was most probably due to the fact that the original generic name *Holothuria* Linnaeus, 1758 included only species other than echinoderms. More than a century later, despite the efforts of many to bring order to the nomenclature, the issue was still not settled. Deichmann (1958) for instance, proposed to regard *Holothuria* as a colloquial name, but Clark & Rowe (1967) and Rowe (1969: 9; see also Gill 1907a,b) correctly disagreed with this decision for "In 1924 (Opinion 80) the generic name *Holothuria* Linnaeus, 1767, as restricted by Brugière, 1791, with type-species *H. tremula* Linnaeus, 1767 (non Gunnerus, 1767) = *H. tubulosa* Gmelin, 1790, was placed on the Official List of Generic Names in Zoology" and "this action therefore firmly established the generic name *Holothuria* in the present sense rather than the original one of Linnaeus, 1758".

Synoptically spoken, at the beginning of the twentieth century, many authors divided the family Holothuriidae on the basis of presence and/or absence of anal teeth and the position of tube feet, whereby two genera, *Mülleria* Jaeger and *Holothuria* Linnaeus, were recognised. Pearson (1914) examined "a large number of species [sic]" belonging to these two genera and proposed a re-classification arguing that the number and arrangement of tentacles, Polian vesicles, stone canals and Cuvierian tubules should be disregarded for classification purposes. This because he believed that these characters were too variable (even within the limits of the species) to hold evolutionary significance. Instead, he suggested that comparative study of the calcareous ring, the ossicle assemblage and the arrangement of tube feet and papillae would yield a more natural ("in accordance with relationship [sic]") classification. Pearson (1914) grouped *Mülleria* and *Holothuria* (*sensu stricto*) under the single genus *Holothuria* (*sensu extenso*) wherein he discerned five subgenera: *Actinopyga* Bronn, 1860, *Argiodia* Pearson, 1914, *Bohadschia* Jaeger, 1833, *Halodeima* Pearson, 1914 and *Thymiosycia* Pearson, 1914. The first two subgenera contained species formerly classified under *Mülleria* while the latter three subgenera contained species formerly classified under *Holothuria sensu stricto* (see figure 7).

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[1] Again, it comes as no surprise that embryological studies on echinoderms received a lot of attention in the beginning of the twentieth century, as during that time embryology had truly come of age. Hereby echinoderms, of which gametes could relatively easily be obtained, were amongst the preferred experimental animals.

[2] Reference to be found in Fisher (1907).

[3] Even though Mitsukuri (1912) referred *Labidodemas leucopus* Haacke, 1880 and *L. neglectum* Haacke, 1880 to the synonymy of *Holothuria monacaria* Lesson, 1830 [=*H. (Mertensiothuria) hilla* Lesson, 1830], this does not imply that Mitsukuri did not recognise *Labidodemas* as a valid genus, rather it means that he had no representative species of it in the collection he studied.

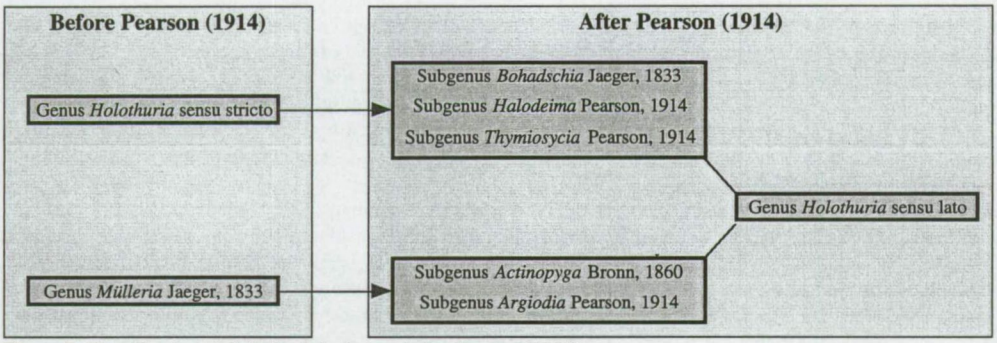

Figure 7. Classification of *Holothuria* before and after Pearson (1914).

Pearson (1914) further believed that *Actinopyga* and *Bohadschia* (with the ambulacral appendages more or less arranged in rows; the ossicles in the form rosettes and rods; the calcareous ring without anterior & posterior projections, but with deep ampullary notches and the interradial pieces almost as high as the radial pieces) represent the primitive condition whereas *Argiodia, Halodeima* and *Thymiosycia* (with scattered ambulacral appendages, table and button ossicles and a calcareous ring with pronounced anterior and posterior projections and a deep indentation between the radial and interradial pieces) are the more advanced forms. Even though he believed that anal teeth are the result of convergent evolution, he did consider this character in his classification. Pearson's schematic relationship of the sub-genera and the cladistic transformation into a phylogeny is given in figure 8.

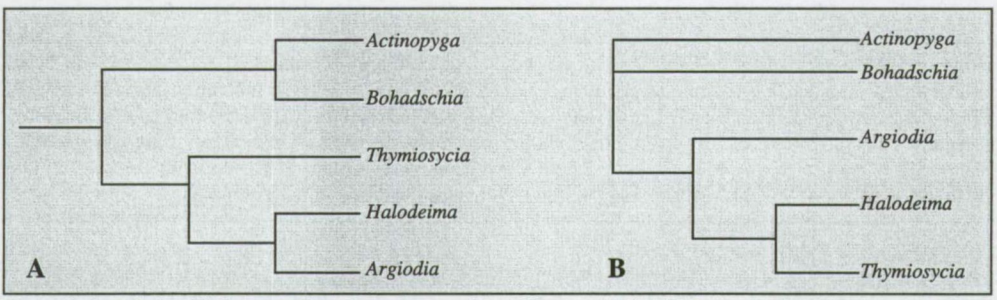

Figure 8. A. Relationship between the subgenera according to Pearson (1914); **B.** Pearson's classification rendered into a phylogeny.

H.L. Clark (1921) completely ignored Pearson's (1914) classification and opted to follow Fisher's (1907) classification, albeit with some modifications *vis-à-vis* the rank of the Holothuriidae. He divided the latter family into five genera: *Actinopyga* Bronn, 1860; *Labidodemas* Selenka, 1867; *Holothuria* Linnaeus, 1767; *Stichopus* Brandt, 1835 and *Thelenota* Brandt, 1835; a classification that was largely followed by subsequent authors (a.o. H.L. Clark 1922; 1923; Deichmann 1926; Domantay 1933; ...). It is, as noted above, however incomprehensible that these eminent holothuroid taxonomists systematically ignored Haeckel's (1896; see also Östergren 1907) important revision that had separated the Stichopodidae from the Holothuriidae.

Panning's (1931b; 1935a-d) revision of *Holothuria* stands as a series of highly significant works in the classification of *Holothuria*. Not only did Panning consider virtually all the available literature (a merit on its own in the turbulent *interbellum*), he also critically analysed most of it and listed virtually complete synonym lists. Panning's *magnum opus* was perhaps a bit too descriptive and hence conservative as was noted by Deichmann (1958, see also Rowe 1969: 121) who fulminated: "this magnificent work suffers from his dependence in too many cases on the accounts of earlier writers; hence many errors have been perpetuated and related forms have been placed far apart." Be it as it may, Panning's insights into holothurian α-taxonomy clearly paved the way for β-taxonomy that was to follow in the coming decades. Panning (1931b; 1935a-d) tried to follow Pearson's (1914) classification but rapidly (and understandably)

came into conflict with his observations. Panning (1931b) gave three pertinent reasons why Pearson's system needed rethinking. Firstly he argued that, Pearson's new taxa were too vaguely described and that the latter refrained from stating clearly which species they contained. Secondly he noticed that, Pearson separated *Thymiosycia* from *Halodeima* on only a single character (*i.e. Halodeima* with tube feet and papillae, *Thymiosycia* with papillae only), which to Panning was insufficient justification (he chose to put *Thymiosycia* as a synonym of *Halodeima*). Thirdly he opposed Pearson's arbitrariness in not considering the geographic distribution (Atlantic versus Pacific) of the different species, and argued that by doing so Pearson necessarily overlooked a large number of synonyms. In 1931(b), Panning recognized *Actinopyga* Bronn, *Bohadschia* Jaeger, *Halodeima* Pearson and *Microthele* Brandt [Panning correctly recognized that Brandt's (1835) *Microthele* has priority over Pearson's (1914) *Argiodia* even though he did not acknowledge it the original (Brandt 1835) meaning] as subgenera in *Holothuria* (*sensu* Pearson). By 1935 (a-d), Panning had altered and refined his classification: on Fisher's advice (1935a: 24) he opted to group Pearson's (1914) subgenera *Halodeima* and *Thymiosycia* in the subgenus *Holothuria sensu stricto*. Thus Panning (1935a-d) now recognized four subgenera in the genus *Holothuria s.l.*: *Actinopyga, Bohadschia, Microthele* and *Holothuria s.s*, whereby he believed (1935a: 25) that *Actinopyga* was most closely related to *Microthele* and *Bohadschia* with *Holothuria s.s.* Based upon his studies of the optical properties of ossicles, Panning (1928; 1931a; 1931c; 1933; hereby partially drawing on Hérouard 1889; 1925 and Perrier 1902; but see also Schmidt 1925; 1932) concluded that the subgenus *Holothuria* best be split in two groups, those with rosettes and those with true buttons. He defined rosettes as small, thin plates that develop from a rod which bifurcates at each end (*Gabelstab*), the terminal branches equally growing at an angle of 120° from the rods and eventually (can) anastomosing, thus forming large, lateral perforations and always a pair of terminal holes. As such, the central perforations are often rather large and elongate / oval, while the branches are generally thin and the overall shape of the rosette is irregular. True buttons on the other hand, even if they are also thin plates, arise from a non-terminally branching primary rod (*ungegabelten Primärstab*) that develops lateral projections perpendicular to the primary rod. As such, when these projections curl and eventually anastomose, forming pairs of lateral perforations, one on each side of the median rod, are formed; terminal holes are absent. Moreover, in true buttons, the holes are generally smaller and more roundish and the rim of the button (when it is fully formed) is rather smooth, giving the impression of a "finished ossicle". Figure 9 gives Panning's (1951) drawings on the position of the optical axes as present in rosette-like buttons and in true buttons as well as scaled drawings of the two ossicle types.

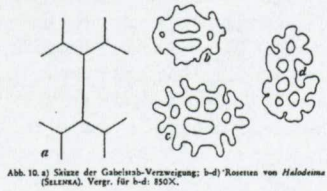

Abb. 10. a) Skizze der Gabelstab-Verzweigung; b-d) Rosetten von *Halodeima grisea* (Selenka). Vergr. für b-d: 850X.

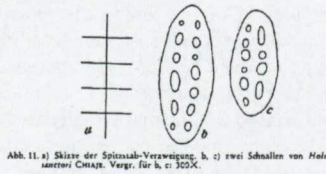

Abb. 11. a) Skizze der Spitzstab-Verzweigung. b, c) zwei Schnallen von *Holothuria sanctori* Chiaje. Vergr. für b, c: 305X.

Figure 9. Rosettes versus buttons according to Panning (1951: 178). Top: rosettes of *Holothuria (Halodeima) grisea* Selenka, 1867; with a schematic representation of the bifurcate rod. Bottom: true buttons of *Holothuria (Platyperona) sanctori* Delle Chiaje, 1823, with a schematic representation of the branching of the primary rod.

Panning, even though he continually defended his line of reasoning (see also citation at the beginning of chapter 3), failed to develop his observations into an unambiguous classification of *Holothuria* and was drawn to the conclusion that "Dies sind die Formen der beiden Kalkkörperarten im Regelfalle; über Abweichungen und Zwischenstufen mag an anderer Stelle die Rede sein [sic.]" (Panning 1935a: 25). Perhaps this is the reason why he stated that he did not want to burden the systematics of the subgenus *Holothuria* with yet other names and why, instead, he created two large groups. His *Abteilung A* grouped those species with rosettes and rosette-like buttons, while his *Abteilung B* clustered those species that possess true buttons. To the latter he put the name *Sporadipus*, a designation originally given by Brandt (1835). In these two subdivisions he (1935a-d) discerned several smaller groups, which he based almost

exclusively on ossicle assemblage. As such, he created five 'Reiche" in Abteilung A and eight 'Reiche' in Abteilung B (*Sporadipus*). By 1940, Panning revised his treatment of *Holothuria s.l.* He now treated 'presence of anal teeth' as a convergent character and thus no longer considered *Actinopyga* and *Microthele* to be the most closely related taxa ("Dass beide Untergattungen Afterzähne haben, ist nur eine Konvergenz, über die wir allerdings nicht weiter urteilen können, da wir die Bedeutung dieser Gebilde nicht kennen", page 523). Moreover, as he thought *Actinopyga* Bronn, 1860 and *Bohadschia* Jaeger, 1833 differed from one another only by the presence of anal teeth (in *Actinopyga*); he put *Actinopyga* as a subgenus of *Bohadschia*. Further, he raised his *Abteilung A* to genus level which he named *Halodeima* Pearson, 1914; and his *Abteilung B* he split into the genera *Microthele* Brandt, 1935 and *Holothuria* Linneaus, 1767, confusingly noting that under certain circumstances *Microthele* has to be seen as "nur eine Untergattung von *Holothuria*" (p. 524). By 1944, Panning reached his final classification of *Holothuria*; now recognising five genera: *Actinopyga, Bohadschia, Halodeima, Holothuria* and *Microthele*. This classification was accepted and used by subsequent taxonomists (e.g. Tortonese, Cherbonnier, ...), though in 1946, H.L. Clark noted that (my square brackets): "the natural classification of this family [Holothuriidae] has yet to be discovered. It is a large group with scores of species, but the attempts to break it up into genera have as yet proved unsatisfactory. The genus *Actinopyga* is apparently a natural group and its species are easily recognised. *Labidodemas* is much less satisfactory, and the number of component species is doubtful (monotypic). The rest of the family are best retained in the old genus *Holothuria.* Pearson (1913-1914) started out on the task of breaking up the genus, but he made little progress and his work has never been continued. Panning (1931b-1935) attacked the problem de novo and gave promise of reaching some helpful conclusions, but he was diverted into a different line of work and his results were incomplete. Neither Pearson nor Panning had access to sufficient material to enable him fully to meet the problems, and it seems best to continue using the name *Holothuria* in the old sense until someone with access to at least half the named species can concentrate on the problem". H.L. Clark (1946), who at that time must have seen an uncountable number of specimens, thus clearly urged for a new start. Deichmann, who had access to the important collections brought home by the Velero III and IV, took the challenge and, in 1958, presented a new classification. She rejected Panning's and H.L. Clark's classifications to a large extent. On generic level, she accepted Panning's (1944) view on *Actinopyga, Bohadschia* and *Microthele* (even though she, as Panning before her, unfortunately failed to recognize *Microthele* in Brandt's (1835) original sense), but, in addition, she recognized that the small genus *Labidodemas* Selenka, 1867 (in which she, in 1938, had described the species *L. americanum*), did not belong to *Holothuria* s.l. (Panning 1935c). Enigmatically, she (1958: 311) changed *Halodeima*, which she "accepted with minor changes" to her new *Ludwigothuria.* More radical was her decision to split the genus *Holothuria* into several new genera and to abandon the old name *Holothuria* completely (hereby disregarding Opinion 80, see also above). This division of *Holothuria* was, so she said herself, "foreshadowed in the key which W.K. Fisher made for the Hawaiian holothurians in 1907". As Rowe (1969: 122) noted, Deichmann (1958) relied quite heavily on the ecological position of the different taxa she studied to get to a more natural classification. This cannot come as a surprise as the years before the great evolutionary biologist Ernst Mayr [1904-], had elaborated his views on how new species form and adapt to changes in an environment.

In the late fifties, this line of reasoning led Mayr (1957) to the formulation of the biological species concept, currently defined by him as follows: "I define a biological species as groups of interbreeding natural populations that are reproductively isolated from other such groups" or even "a biological species is a reproductively cohesive assemblage of populations" (Mayr 2000: 17). As a good taxonomist, Deichmann must have been heavily influenced by these new conceptualisations[1] that shaped organismal biology in the aftermath of the Second World War. But as Levin (1999: 15) correctly notes "all the known hierarchic ecological classifications, including the most carefully reasoned, are vulnerable from the standpoint of close compliance with formal rules of classification". Be it as it may, Deichmann's (1958) classification

[1] This new movement, often referred to as *evolutionary morphology*, so notes Mayr (1982: 468) "typically starts with the ancestor and asks what evolutionary processes were responsible for the divergence of the descendants. Typical questions for this school are: Why and how did the ancestral type type give rise to new morphological types? To what extent was a change in niche occupation or, indeed, the invasion of an entirely new adaptive zone responsible for the anatomical reconstruction? What was the nature of the selection pressures? Was behaviour the pacemaker of the ecological shift? What was the nature of the population in which the decisive shift occurred?"

was interesting in its novelty and is worth critical study. Rowe (1969) took the latter challenge when he revised the complete Holothuriidae. Rowe (1969: 119) correctly pointed out that by creating 11 new generic names " Deichmann has disregarded a number of appropriate prior genus-group names of Brandt (1835), Jaeger (1833), Haacke (1880) and Pearson (1914) on the grounds of poor definition, most of these names *are* available under the Rules, being associated with recognized species, those of Jaeger and Brandt needing only designations of type-species in order to qualify for recognition under the Rules" (see also Clark & Rowe 1967).
A detailed discussion of Deichmann's (1958) classification can be found in Rowe (1969) who, in one of his first, but grand, works on holothuroids, argued that Deichmann's taxonomic groups are better regarded as subgenera in *Holothuria* rather than genera on their own. Rowe thus agreed largely with Panning's (1939) generic classification (although he placed *Microthele* and *Halodeima* at subgeneric level), and with Deichmann (1958), regarding *Labidodemas,* albeit his phrase "In truth I think *Labidodemas* may even prove to warrant separation at family level" caused some commotion during the last two decades (James 1981; Massin *et al.* in press; see also chapter 4). Rowe (1969:122-123) summarised the supraspecific taxa (my brackets) when he presented "a table of the supraspecific taxa with their type-species represented in her (Deichmann's 1958) paper together with their present disposition" This table is here reproduced with permission (table 2).

Genus-group name	Type-species	Present disposition [anno 1969]
Labidodemas Selenka, 1867	*L. semperianum* Selenka, 1867	Valid genus
Microthele: Deichmann, 1958 (non Brandt, 1835)	*Holothuria sanctori* Delle Chiaje, 1823	*Holothuria (Platyperona)* subg. nov.; type-species *Holothuria difficilis* Semper, 1868
Brandtothuria Deichmann, 1958	*H. arenicola* Semper, 1868	*H. (Thymiosycia)* Pearson, 1914; type-species *Fistularia impatiens* Forskål, 1775
Lessonothuria Deichmann, 1958	*H. pardalis* Selenka, 1867	Valid subgenus
Mertensiothuria Deichmann, 1958	*Stichopus leucospilota* Brandt, 1835	Valid subgenus
Semperothuria Deichmann, 1958	*Holothuria languens* Selenka, 1867	Valid subgenus
Irenothuria Deichmann, 1958	*I. maccullochi* Deichmann, 1958	Valid subgenus
Vaneyothuria Deichmann, 1958	*Holothuria lentiginosa* v. Marenzeller, 1893	Valid subgenus
Ludwigothuria Deichmann, 1958	*H. atra* Jaeger, 1833	*Holothuria (Halodeima) atra* Pearson, 1914; type-species *H. atra* Jaeger, 1833
Selenkothuria Deichmann, 1958	*H. lubrica* Selenka, 1867	Valid subgenus
Fossothuria Deichmann, 1958	*Stichopus rigidus* Selenka, 1867	*H. (Cystipus)* Haacke, 1880; type-species *C. pleuripus* Haacke, 1880, a junior subjective synonym of *rigidus* Selenka, 1867
Jaegerothuria Deichmann, 1958	*Holothuria inhabilis* Selenka, 1867	*H. (Cystipus)* Haacke, 1880
Theelothuria Deichmann, 1958	*H. princeps* Selenka, 1867	Valid subgenus

Table 2. Supraspecific taxa with their type species with the disposition according to Rowe (1969) (from Rowe 1969: 122-123).

In addition Rowe (1969) described five new subgenera to accommodate the species that did not fitted in Deichmann's (1958) revised supraspecific taxa. These are: *Acanthotrapeza* with type-species *Holothuria pyxis* Selenka, 1867; *Metriatyla* with type-species *H. scabra* Jaeger, 1833; *Panningothuria* with type-species *H. forskali* Delle Chiaje, 1823; *Platyperona* with type-species *H. difficilis* Semper, 1868 and *Stauropora* with type-species *H. discrepans* Semper, 1868. Based on ossicle complexity, Rowe (1969, text-fig. 1, p. 125, table 1, 165) constructed a hypothetical evolutionary tree for the genus *Holothuria*. This tree, as he says so himself (Rowe 1969: 124), involves "speculations that should at least form the basis for future argument". Indeed, these speculations are not the least; in fact they involve one of the most intricate problems in evolutionary thought, namely direction of evolution. Deichmann (1958: 276) argued that "most

primitive are undoubtedly those with numerous regular tables and regular smooth buttons, somewhat reminiscent of certain synallactid-like members of the Stichopodidae", whilst "a more advanced stage is indicated by the presence of irregular buttons, or the development of rosettes, or the reduction of the inner layer of spicules, while the tables have become variously modified". Rowe (1969) on the other hand reasoned that the species with plates and no tables or buttons might be the more primitive and that regular tables and buttons are present in more advanced forms. Ecologically speaking, that means that according to Deichmann (1958), surf-zone species are more advanced, while to Rowe (1969) these are the most primitive. If we take this argumentation to the current classification that would mean that *Actinopyga*, *Bohadschia*, and the holothurian subgenera *Semperothuria* and *Selenkothuria*, are the youngest clades according to Deichmann (1958) and later Levin (1999), whereas according to Rowe (1969) and later Thandar (1988; 1994) the reverse is more likely.

I'd like to conclude this discussion with a phrase I took from Goodwin's (1995: 23) most enjoyable book. "There's more to scientific debate than facts and theories." Although, this phrase is here taken out of his context (Goodwin used it to illustrate the debating power of T.H. Huxley against the theologically oriented Mivart who attacked Darwinism), I think it holds a universal, humanistic truth: people classify for it gives not only depth and meaning to the nature of Life, but also "divine" mental satisfaction that sets us free from the metaphoric paradigms that we have been dictated far too often! As such, taxonomy and its related scientific disciplines provide us with falsifiable keys that can unlock the extraordinary colours of nature.

3. Why study sea cucumbers of the western Indian Ocean?

If the more patient reader is still with me after this exasperating discussion of sea cucumber classification, it might be time to devote some words to the extrinsic and intrinsic need to study the holothuroids of the western Indian Ocean.

The extrinsic need to assess holothuroid biodiversity is obvious when one realizes that ever since the Middle Ages, holothuroids have been harvested for human consumption (Conand & Byrne 1993; Conand 1998; 2001), with the processed product commonly known as Beche-de-mer. While in the early days harvesting was only done in the consuming countries of the Far East, market demands have shifted exploitation-grounds towards the western Indian Ocean during the last two decades (Marshall *et al.* 2001). As not a single species of holothurian is currently[1] listed in the CITES Red Data Books, protection of this ecologically important faunal component is nowadays addressed indirectly in two ways. The first approach works at a holistic, but geographically small scale, and involves the creation of marine parks and reserves. The Kenyan government, for instance, has addressed some of the problems of over fishing by gazetting marine protected areas which maybe fully protected (marine parks) or partially protected (marine reserves) allowing limited fishing. It has been demonstrated worldwide that such protected areas can be effective and do hold potential in the conservation of marine biota; for instance a large body of literature and my own observations indicate that reserves sometimes act as refugia for intensely exploited species. However, it is equally clear that the potential effectiveness of reserves on their own is limited, since the scale and variability of fundamental biological processes (consider the influence of currents on the dispersion of organisms) are often much larger than reserves can encompass, hereby forcing us to conserve outside as well as inside reserves. The second (Malthusian) approach tries to satisfy the market by producing top-commercial species *ad libitum* through aqua cultural means (e.g. Hamel *et al.* 2001 on *Holothuria (Metriatyla) scabra*). Even if both of these approaches apparently lead to good results, they unfortunately also have their drawbacks. Firstly, in eastern Africa, most of the protected marine areas were established during colonial times when focus was on attractivety rather than on biological value, hence the effectiveness and the patterns that shaped these areas remain largely elusive. Secondly, even if mariculture

[1] A tentative list with the names of the top-commercial and over-havested species has recently been submitted and is now under consideration by CITES (Massin pers. comm.). It must however be noted that as reliable identification of holothurians depends on microscopic examination of the ossicle assemblage, a time consuming process that requires extensive expert knowledge – it will be unfeasable to check even a minority of the specimens that are traded. Moreover, the first processing of holothurians for beche-de-mer renders the species hardly identifiable for the ossicles from the body wall have been scraped away.

yields excellent immediate results (at least for the species that have been studied intensively) the influences on the ecosystem are largely unknown, but experiences in other localities with other groups have warned us that functionality of an ecosystem can change drastically through these practices (Naylor *et al.* 2000).
On the intrinsic level, it is equally clear that we'll have to grasp the processes that shape(d) the observed biodiversity. It is predominantly at this level that this dissertation is acting and as such its aim can synoptically be put as: assembling the basic levels of scientific understanding that are essential to get to sustainable conservation of sea cucumbers in the western Indian Ocean (Samyn 2000). The *modus operandi* to attain this goal will be discussed in the next chapters.

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Plate 1

A. Anchor of body wall of *Euapta godeffroyi* (Semper, 1868). 1=vertex; 2=fluke; 3=shaft; 4=stock; 5=keel.

B. Anchor-plate of body wall of *Euapta godeffroyi* (Semper, 1868). 1=anterior side; 2=bridge; 3=posterior side.

C. Basket of body wall of *Aslia lefevrei* (Barrois, 1882). (from Gilliland 1993: 19, pl. 3 fig. 7).

D. Smooth button of body wall of *Pawsonia saxicola* (Brady & Robertson, 1871). (from Gilliland 1993: 9, pl. 1 fig. 6).

E. Knobbed button of *Stolus buccalis* (Stimpson, 1855).

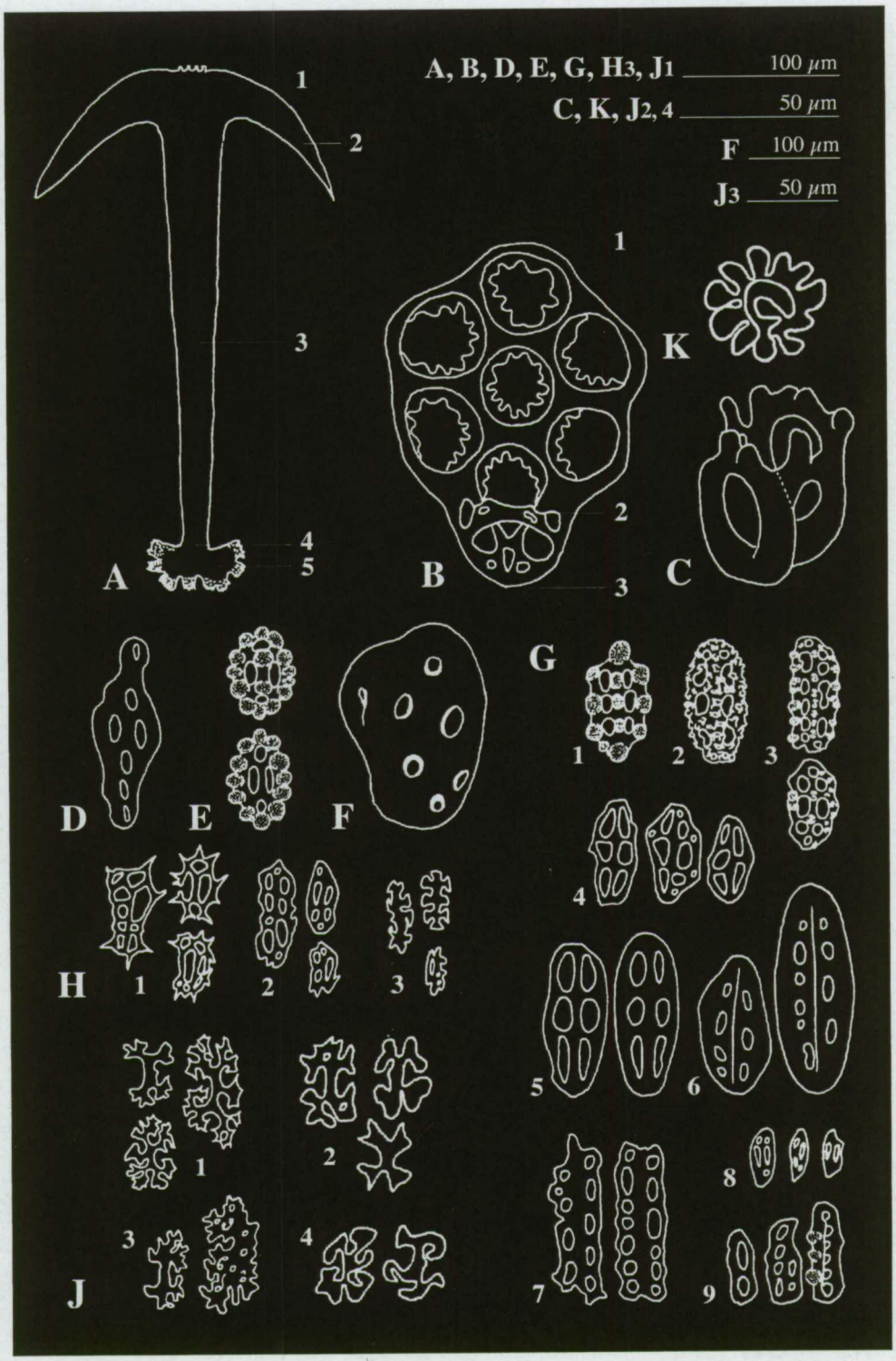
F. Thickened button from *Paracucumaria hyndmani* (Panning, 1949) (from Gilliland 1993: 23, pl. 4 fig. 2).

G. Button types from the body wall of different Holothuriidae spp.: 1. Regular, knobbed button of *Holothuria (Cystipus) rigida* Selenka, 1867; 2. Regular, rugose button of *H. (Holothuria) tubulosa* Gmelin, 1790 (from Rowe 1969: 153, fig. 17b); 3. Regular, knobbed buttons of *H. (Metriatyla) scabra* Jaeger, 1833; 4. Irregular buttons of *H. (Mertensiothuria) leucospilota* (Brandt, 1835); 5. regular buttons of *H. (Thymiosycia) impatiens* (Forskål, 1775); 6. Regular buttons with median longitudinal ridge of *H. (Platyperona) difficilis* Semper, 1868; 7. Elongate, plate-like buttons of *H. (Vaneyothuria) suspecta* Cherbonnier, 1958; 8. Irregular buttons of *H. (Stauropora) fuscocinerea* Jaeger, 1833; 9. Irregular buttons of *H. (Lessonothuria) verrucosa* Selenka, 1867.

H. Rosette types from the body wall of different Holothuriidae spp.: 1. Spiny, button-like rosettes of *Holothuria (Acanthotrapeza) pyxis* Selenka, 1867 (from Rowe 1969: 139, fig. 8b); 2. Undulating, button-like rosettes of *H. (Halodeima) edulis* Lesson, 1830; 3. Irregular rosettes of *Holothuria (Stauropora) pervicax* Selenka, 1867.

J. Rosette types from the body wall of different aspidochirotid spp.: 1. Rod-like rosettes of *Actinopyga echinites* (Jaeger, 1833); 2. Rod-like rosettes of *Bohadschia cousteaui* Cherbonnier, 1954; 3. Irregular rosettes of *Pearsonothuria graeffei* (Semper, 1868); 4. Slender rosettes of the body wall of *Stichopus monotuberculatus* (Quoy & Gaimard, 1833).

K. Miliary granule of the body wall of *Synaptula recta* (Semper, 1868).


A, B, D, E, G, H3, J1 100 μm
C, K, J2, 4 50 μm
F 100 μm
J3 50 μm
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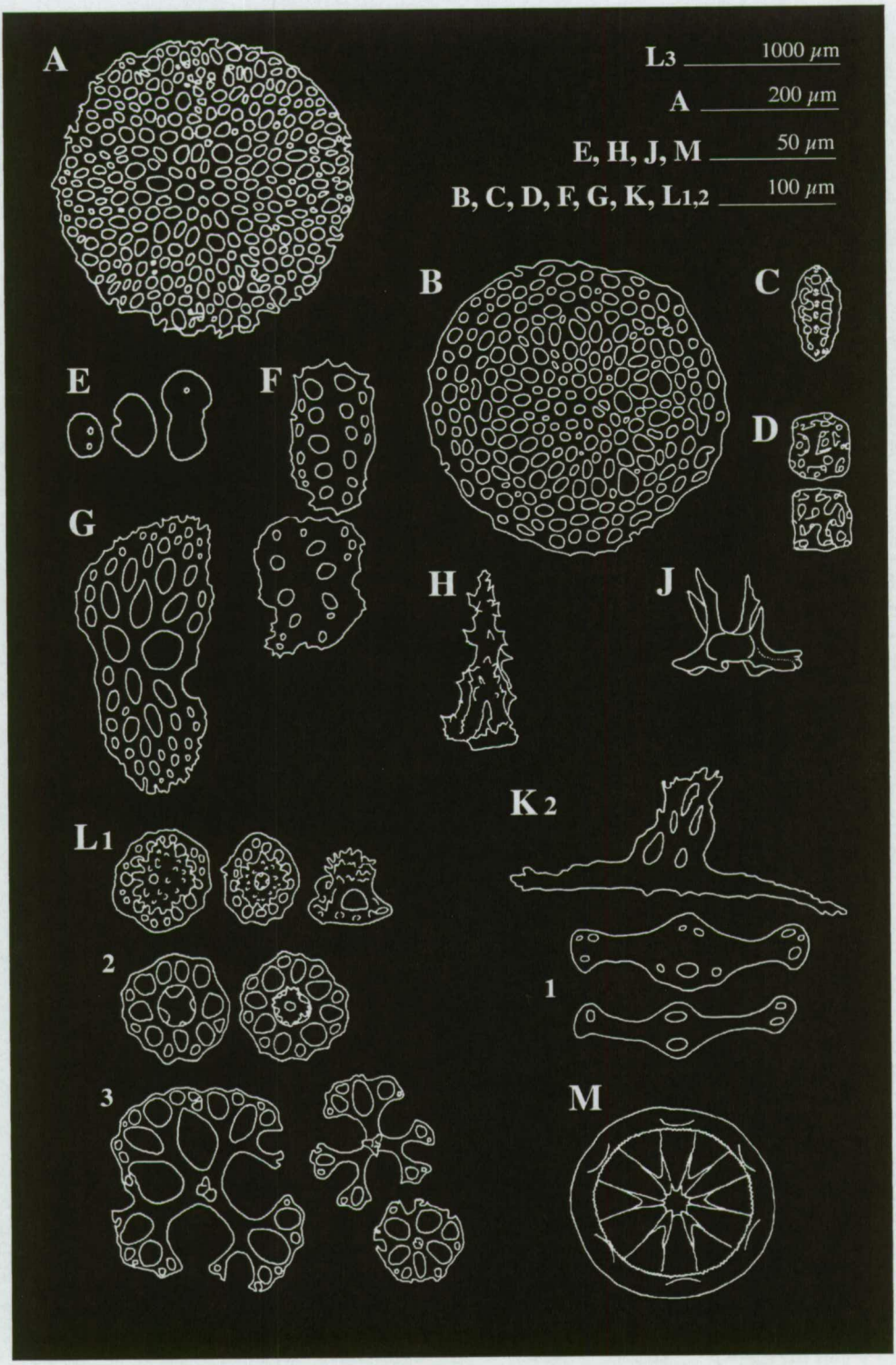
K

Plate 2

A. End-plate of a ventral tube feet of *Holothuria (Halodeima) atra* Jaeger, 1833.
B. End-plate of a ventral tube feet of *Thyone* sp.
C. Fenestrated ellipsoid of the body wall of *Holothuria (Microthele) nobilis* (Selenka, 1867).
D. Fenestrated sphere of the body wall of *Holothuria (cystipus) rigida* Selenka, 1867 (from Rowe 1969: 155, fig. 18b, c).
E. Grains of the body wall of *Bohadschia atra* Massin, Rasolofonirina, Conand & Samyn, 1999 (from Massin *et al.* 1999:152, fig. 1G).
F. Button-derived plates of the tube feet of *Holothuria (Platyperona) difficilis* Semper, 1868.
G. Rosette-derived plate of the tube feet of *Stichopus herrmanni* Semper, 1868.
H. Pseudotable of the body wall of *Pearsonothuria graeffei* (Semper, 1868).
J. Pseudotable of the dorsal papillae of *Thelenota ananas* (Jaeger, 1833). (from Cherbonnier 1988: 154, fig. 63D).
K. Aspidochirotid rods of the tube feet: 1. *Holothuria (Thymiosycia) impatiens* (Forskål, 1775); 2. *Stichopus herrmanni* Semper, 1868.
L. Aspidochirotid table types: 1. *Holothuria* type, here of the body wall of *H. (Microthele) nobilis* (Selenka, 1867); 2. *Mesothuria* type, here of the body wall of *M. intestinalis* (Ascanius & Rathke, 1767); 3. *Synallactes* type, here of the dorsal papillae of *S. challengeri* (Théel, 1886) (from Massin 1992: 314, fig. 2F).
M. Wheels of the body wall of *Polycheira fusca* (Quoy & Gaimard, 1833) (from Cherbonnier 1988: 271, fig. 121A)


A
L3 1000 μm
A 200 μm
E, H, J, M 50 μm
B, C, D, F, G, K, L1,2 100 μm
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Chapter Two

Modus operandi

"So kommt es, daß man unmöglich ein wahres Bild von der Natur der Kalkkörper gewinnen kan, wenn man aus den Familien und Gattungen Stichproben nimmt. Vielmehr muß man sich zunächst eine eng begrenzte Gruppe vornehmen, muß dafür aber in dieser die Kalkkörper mit äußerster Gründlichkeit untersuchen; man muß vom selben Tier sich die Kalkkörper aller Körperteile ansehen, und zwar aus der Bauchhaut wie aus der Rückenhaut, aus der Mundhaut wie aus dem Afterbezirk, ans der Fühlern wie den Papillen und Füßen: man muß sie in großer Zahl in geduldiger Kleinarbeit zeichnen und vergleichen, erst dann wird man mit Sicherheit ein Bild ihrer wahren Natur entwerfen können".

Panning, 1931: 206.

Introduction

The Committee on Biological Diversity in Marine Systems (1995) has characterized biological diversity (or biodiversity) as comprising three levels: (i) diversity among ecosystems, (ii) phyletic diversity, or diversity of species within an ecosystem, and (iii) genetic diversity within species. To understand these three layers, we primordial need to construct a sound taxonomic framework. This is especially true for the study of phyletic diversity which cannot be considered separately from the taxonomic information on which it is based (Vecchione *et al.* 2000).

The intrinsic (comprehension of biodiversity) and extrinsic (safeguarding and eventual sustainable exploitation of biodiversity) need to study holothuroid biodiversity has already been briefly touched in the previous chapter. Here, I will focus on the type of information and on the *modus* of acquiring such information to get to a description and an imperative baseline understanding of the biodiversity of shallow-water (up to 50 m depth) holothuroids of the western Indian Ocean. The latter area is here arbitrarily defined as the area comprising the shallow waters (up to 50 m depth) from Suez to Cape Town and from East Africa (Red Sea and Persian Gulf included) up to 65° East (fig. 1).



Fig. 1. The western Indian Ocean as study area.

Types of information

It has been argued elsewhere (Samyn 2000) that understanding biodiversity involves the grasping of several levels of information. Undoubtedly, the discovery and description of species from local areas constitutes the baseline information. Hereafter, if decisions are to be made about preserving species, we must also comprehend the relationships among species from different areas and examine the evolutionary uniqueness of the species in their respective areas. The *modus operandi* to attain this goal involves three strongly intertwined stages.

1. In a first instance, description of local fauna's depends on proper identification of organisms. In this regard the importance of a stable taxonomic knowledge is of paramount importance. However, as can be expected from a notoriously difficult group like holothuroids, the status of the taxonomic information varies considerably among taxa and among geographical regions. Thus, the first stage of the present research involved the creation of reliable and up-to date taxonomic lists for the total western Indian Ocean. As it is financially unrealistic and sometimes impossible (e.g. Somalia which is nowadays politically too unstable to harvest specimens) to obtain *de novo* representative samples from the total area, I opted to thoroughly investigate two accessible areas along the East African Coast: tropical Kenya and subtropical KwaZulu-Natal, Republic of South Africa. Further, by using all the available literature and some important museum collections (e.g. specimens from the Seychelles and

Inhaca collected by the ULB and the Royal Africa Museum that are deposited in the Royal Africa Museum) I was able to get to the desired checklists for the total region

2. The second stage is in my opinion best seen as a pragmatic quality control of the former phase. Indeed, while building the taxonomic lists (α-taxonomy), my colleagues and myself paid special care to the systematics (β-taxonomy) as it, at least partially, depends on the recognition of natural groups (monophyletic branches or clades) and the taxonomic rank we attribute to them to enable us to formulate further causal explanations (for instance determination of evolutionary trajectories, biogeographic distributions, ...). An ardent commitment to the latter point can be found in Mayr & Bock (2002) who quite correctly emphasize that biological classifications (and phylogenies) of organisms are historical-narrative explanations that are dependent on the nomological-deductive theory of evolution.
3. Once a trustworthy dataset is obtained, it becomes possible to put the biodiversity patterns in a zoogeographical context.

Detailed methodologies for acquiring these three types of information can be found in the *materials and methods* section of the different papers that are bundled in the present dissertation (see ensuing chapters). Here it suffices to briefly discuss the study area and the methodology of specimen-acquisition.

Choosing the study areas

As said repeatedly before, a first step in every biodiversity assessment involves knowing which species live where. Here I thoroughly studied the holothuroid fauna of a limited number of relatively accessible regions along the East African Coast. Choice of the study areas was chiefly guided by the amount of study that already has been performed in the different regions of the WIO, although the geological, physical and biological oceanography of the regions were also taken into consideration. Geological, physical and biological oceanography is further discussed in chapter six; whereas study effort is discussed here since this parameter determines the conditions within which the present research was shaped.

In regard to study effort it is very clear that some areas have historically received more attention than others. The efforts published prior to and including the present study are here listed:

Red Sea (northern part, including Gulfs of Suez and Aqaba): Cherbonnier (1954a; 1955; 1963; 1967; 1979a, b); A.M. Clark (1952); H.L. Clark (1908); Daniel & Halder (1974); Erwe (1919); Fisher (1907); Gray (1872); Heding (1928; 1931); Heding & Panning (1954); Helfer (1911; 1912; 1913); Hérouard (1893); Hughes & Gamble (1977); James (1969); James & Pearse (1969); Lampert (1885; 1896); Mitsikuri (1912); Mortensen (1926; 1937); Panning (1944; 1951); Pearson (1913); Price (1982); Samyn (unpublished data[1]); Samyn & Massin (in press[1]); Selenka (1867; 1868); Théel (1886); Tortonese (1977)

Red Sea (central part): Cherbonnier (1954a; 1955; 1979b); A.M. Clark & Rowe (1971); H.L. Clark (1908); Daniel & Halder (1974); De Blainville (1821); Erwe (1919); Fisher (1907); Heding & Panning (1954); Lampert (1885); Ludwig (1875; 1877); Mitsikuri (1912); Panning (1944); Pearson (1914a); Price (1982); Selenka (1867; 1868); Semper (1868; 1869); Théel (1886); Tortonese (1979)

Red Sea (southern part): Cherbonnier (1954a; 1955; 1963; 1967); A.M. Clark (1951); Ludwig (1886); Mitsikuri (1912); Tortonese (1936a; 1936b; 1937-38; 1953a)

Gulf of Aden: Cherbonnier (1954a; 1955); H.L. Clark (1908); Daniel & Halder (1974); Lampert (1885); Ludwig (1883; 1887); Mitsikuri (1912); Semper (1868; 1869); Théel (1886); Vaney (1905)

Somalia: Ludwig (1883); Panning (1944); Tortonese (1980)

Persian Gulf: Clark & Rowe (1971); Daniel & Halder (1974); Fisher (1907); Heding (1940); Koehler & Vaney (1908); Price (1981; 1982; 1983)

Arabian Sea: Clark & Rowe (1971); Daniel & Halder (1974); Levin (1979); Price (1982)

Soccotra: Levin (1979)

Kenya: Humphreys (1981); Levin (1979); Massin *et al.* (1999[1]); Obura *et al.* (1998); Panning (1941); Samyn (in press[1]); Samyn & Vanden Berghe (2000[1]); Samyn *et al.* (2001[1]); Tervuren collection (see Samyn, in press[1])

Tanzania (chiefly Zanzibar): Cherbonnier (1974; 1988); H.L. Clark (1908; 1924); Daniel & Halder (1974); Deichmann (1948); Fisher (1907); Heding (1929; 1931); Lampert (1885; 1896); Ludwig (1875; 1881; 1887; 1899); Massin *et al.* (1999[1]); Mitsikuri (1912); Panning (1941; 1944; 1949); Samyn (in press[1]); Selenka (1867); Semper (1868; 1869); Tervuren collection (see Samyn, in press[1]); Théel (1886)

[1] Records gathered after the onset of the present research.

Mozambique: Bell (1884); Cherbonnier (1952a; 1970a; 1988); H.L. Clark (1908; 1923); Daniel & Halder (1974); Fisher (1907); Forskål (1775); Kalk (1958; 1959); Lampert (1885); Ludwig (1883; 1899); Mitsikuri (1912); Müller (1850); Panning (1944); Pearson (1910); Perrier (1893); Samyn (unpublished data[2]); Selenka (1867); Semper (1868; 1869); Sloan *et al.* (1979); Tervuren collection (see Samyn, in press[2]); Thandar (1984, 1985; 1987a; 1987b; 1989c; 1990; 1991); Thandar & Rowe (1989); Théel (1886)

South Africa: Cherbonnier (1952a; 1953b; 1954b; 1970a); H.L. Clark (1923); Daniel & Halder (1974); De Blainville (1821); Deichmann (1944; 1948); Fisher (1907); Heding (1938); John (1939); Lampert (1885); Ludwig (1875; 1882; 1887); Mitsikuri (1912); Panning (1944); Pearson (1914a); Rajpal & Thandar (1998); Samyn (unpublished data[2]); Semper (1868); Thandar (1977; 1984, 1985; 1986; 1987a; 1987b; 1989a; 1989b; 1989c; 1990; 1991; 1994; 1996; 2001); Thandar & Rowe (1989); Théel (1886); Samyn & Thandar (in press[2]); Massin *et al.* (in press[2])

Madagascar: Bell (1884); Cherbonnier (1970b; 1988); Ludwig (1883); Massin *et al.* (1999[2]); Massin (personal communication[2]); Théel (1886)

Mascarene Islands: Arakaki and Fagoonee (1996); Cherbonnier (1952b; 1953a; 1988); A.M. Clark & Rowe (1971); H.L. Clark (1908); Conand (1999); Daniel & Halder (1974); De Blainville (1821); Fisher (1907); Haacke (1880); Heding (1928); Heding & Panning (1954); Hoffmann (1874); Lampert (1885; 1889a; 1989b); Ludwig (1883; 1887); Mitsikuri (1912); Panning (1944); Quoy & Gaimard (1833); Selenka (1867); Semper (1868); Théel (1886)

Amirante Islands: Bell (1884); A.M. Clark (1984); Daniel & Halder (1974); Hughes & Gamble (1977); Lampert (1885); Ludwig (1899); Mitsikuri (1912); Pearson (1913); Price (1971); Sloan *et al.* (1979); Théel (1886)

From this extensive survey, it became evident that locations like the Persian Gulf, the Arabian Sea, Soccotra, Somalia, Kenya, southern Tanzania and central Mozambique have received relatively little attention, while the Red Sea, Madagascar, South Africa and the Islands of the western Indian Ocean have been better studied. After taking into account the accessibility, the habitat diversity (e.g. presence of coral reefs, sea grass beds, mangrove forests) and the oceanography (currents), two areas were chosen (see fig. 2 & 3). First, the poorly known tropical coastline of Kenya, with inclusion of the totally unknown western coast of Pemba Island (Tanzania); and secund, the relatively well studied subtropical coast of KwaZulu-Natal (South Africa) at the edge of coral reef distribution.



Fig. 2. Settings of the tropical (Kenya) and the subtropical (KwaZulu-Natal) coast. While the former (pictures A & C) is characterised by well-developed fringing reefs with associated lagoons, seagrass beds and extensive mangrove forests, the latter (pictures B & D) is characterised by isolated patches of corals, no lagoons, hardly any sea grass beds and mangrove forests, strong wave action and high dunes with dense vegetation. (Photo A by B. Van Bogaert; B-D by author).

[2] Records gathered after the onset of the present research.

Of added value is that previous collections from (nearly) the same areas permitted comparison with the *de novo* estimates of holothuroid biodiversity. Indeed, the Royal Africa Museum in Tervuren (Belgium) not only holds a relatively largely unidentified (a minority of these specimens was identified by notable holothuroid taxonomists like G. Cherbonnier and F.W.E. Rowe) holothuroid collection from Inhaca (southern Mozambique) and the Seychelles (brought home by the Université Libre de Bruxelles in the late sixties), but also part of Humphreys' (1981) collection (identified by A.M. Clark in the late seventies) from Kenya and Zanzibar.

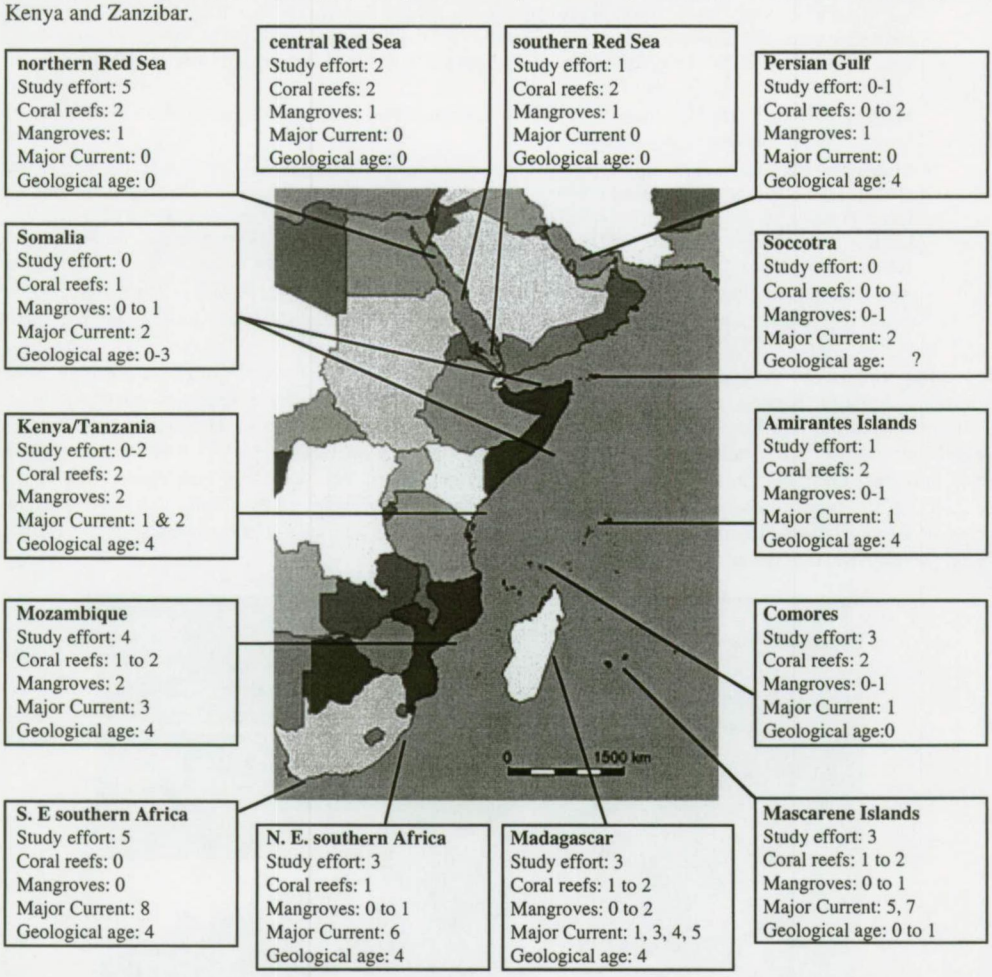

Fig. 3. Selective exclusion of subareas in the western Indian Ocean took into account the amount of research performed in that particular area, the geological, physical and biological oceanography and the accessibility. Study effort: 0 (very low), 1 (low), 2 (moderate), 3 (good), 4 (very good), 5 (excellent); coral reef development: 0 (absent), 1 (patches only), 2 (well-developed fringing reefs); sea grass beds: 0 (absent), 1 (poorly developed), 2 (well-developed); mangroves: 0 (absent), 1 (poorly developed), 2 (well-developed); major currents: 0 (no major current), 1 (North Equatorial Current), 2 (Somali Current, reverses seasonally with monsoon), 3 (Mozambique Current), 4 (South Equatorial Current), 5 (East Madagascar Current), 6 (Agulhas Current), 7 (Return Agulhas Current), 8. Benguela Current; geological age: 0 (0-5 million years), 1 (6-10 million years), 2 (11-20 million years), 3 (21-30 million years), 4 (31- +65 million years).

Building a representative specimen collection

In the past, holothuroid samples were gathered by handpicking in the intertidal or by dredging. With the advent of SCUBA-diving selective sampling at greater depth in shallow waters became feasible. This

technological innovation greatly augmented the effectiveness of sampling. Moreover, SCUBA-diving allowed observation of a species *in situ*, thus greatly improving our understanding of the ecology of the species.



Fig. 4. Left: sampling with the aid of SCUBA. SCUBA diving has its main advantage in that selective sampling at greater depth (up to 40 m) and description of the habitat wherein a species lives, becomes possible. Here, making notes on *Thelenota ananas* (Jaeger, 1833) as found in the Mombasa Marine National Park, Kenya. Right: intertidal collecting at Sodwana Bay (Republic of South Africa) (Photo A by B. Van Bogaert; photo B by I. Tallon)

The specimens studied here were collected during four separate expeditions [July to August 1997; April 1998 (prospecting only); July to August 1998 and April 1999] to several sites along the Kenya Coast and along the western coastline of Pemba Island, Tanzania as well as during three expeditions [August 1999; July 2000 and February 2001] to KwaZulu-Natal, Republic of South Africa. Maps of the sampling sites can be found in Samyn (in press) and in Samyn & Thandar (2003). In Kenya and along the Pemba Coast, collecting was done in the coral gardens, the sea grass beds as well as on sandy bottoms; for logistic reasons (accessibility and time budget) Kenyan mangrove forests were not sampled. In South Africa, we sampled on sandy bottoms, on coarse grained substrate as well as in the underdeveloped coral gardens. Both in Kenya and in South Africa, collecting was done chiefly during day-time (± 85% of dives) although, whereever possible, some night dives were also performed (for instance 25% of dives along the Pemba coast were night dives). Collecting always was a joint effort between the VUB and local authorities. For Kenya this was the Kenya Marine Fisheries and Research Institute, the Kenya Wildlife Services and WWF Kenya; for South Africa this was the KwaZulu Natal Nature Conservation Service, and the University of Durban-Westville.

Upon collection, specimens were always kept separate from each other by using simple plastic bags. Such physical separation of live specimens minimised potential antagonistic reaction of one species against another (*e.g.* expulsion of Cuvierian tubules; evisceration). Once ashore, specimens were anaesthetized in roughly 5% magnesium chloride for at least 4 hours (an individual was considered completely anaesthetized when, after turning it on its dorsal side, it ceased moving), transferred to 100% buffered alcohol for 24 hours, and transferred to 70 % buffered alcohol for permanent storage (see fig. 5).



Fig. 5. Sampling methodology: from left to right: field lab; specimens [here *Bohadschia subrubra* (Quoy & Gaimard, 1833)] are kept separate from each other by plastic bags; relaxation and anaesthetization with ± 5% magnesium chloride; transfer to alcohol for transport [here *Neostichopus grammatus* (H.L. Clark, 1923)] (all photo's by I. Tallon).

Several specimens have been deposited in the Royal Belgian Institute of Natural Science, Brussels; the Royal Africa Museum, Tervuren; the Muséum National d'Histoire Naturelle, Paris; and the Smithsonian Institute, Washington (Massin *et al.* 1999; Samyn & Vanden Berghe 2000; Samyn *et al.* 2001; Samyn & Massin in press; Massin *et al.* in press; Samyn in press; Samyn & Thandar in press). Ultimately, the remainder of the collected specimens will be deposited in the two main natural history museums of Belgium (Royal Belgian Institute for Natural Science Brussels and the Royal Africa Museum, Tervuren), while duplicates will be deposited in other important museums.

Identification

As outlined in the previous chapter, identification of holothuroids depends to a large extend on the shape, the size and the distribution of the ossicles in the different body parts. Ossicles were removed from the

tissue in household bleach, washed in two changes of distilled water and illustrated with the camera lucida. Where thought necessary, scanning electron microscopy was also used. In this case, the ossicles were passed through two changes of absolute alcohol and transferred with a fine pipette together with a little alcohol on to a specimen stub to which they normally stick once the alcohol evaporates; hereafter they were sputter-coated with gold for five minutes at 30-40mA and photographed with a Philips SEM 500. Identification was done by using established keys for a region (a.o. Cherbonnier's 1988 key for the holothuroids of Madagascar) or a taxon (e.g. Heding's 1928 key for the Synaptidae) or a combination of both. Whenever there was a doubt over the identification, the original description and where possible the type series and reliably identified representative specimens coming from other localities were also examined. The latter was possible thanks to the collegial and kind help of many colleagues in different museums and research institutes world wide, who always and readily supplied loans of the necessary voucher specimens.

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Chapter Three

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A new species of *Bohadschia* (Echinodermata, Holothuroidea) from the Western Indian Ocean with a redescription of *Bohadschia subrubra* (QUOY & GAIMARD, 1833)

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ABSTRACT

Bohadschia atra sp. nov. from the Western Indian Ocean is described and compared with *Bohadschia subrubra* (QUOY & GAIMARD, 1833). *B. subrubra* is redescribed and compared to the new species and related *Bohadschia* species. The shape of the ossicles varies with body size for both species.

Key-words

Echinodermata, Holothuroidea, *Bohadschia*, new species, ossicle changes, Western Indian Ocean.

RÉSUMÉ

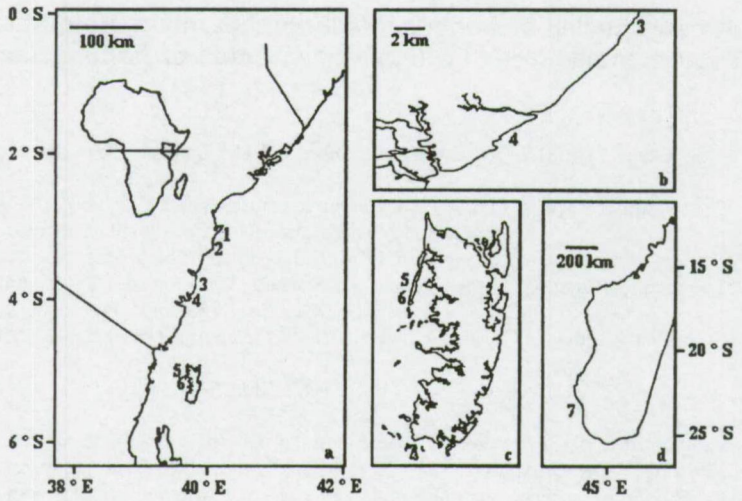
Bohadschia atra sp. nov., vivant dans la partie ouest de l'ocean indien, est décrite et comparée à *Bohadschia subrubra* (QUOY & GAIMARD, 1833). *B. subrubra* est redécrite et comparée à la nouvelle espèce ainsi qu'à d'autres espèces de *Bohadschia*. Pour les deux espèces décrites, la forme des spicules varie en fonction de la taille du corps.

Mots-clefs

Echinodermata, Holothuroidea, *Bohadschia*, nouvelle espèce, variation de la spiculation, Océan Indian ouest.

Introduction

Recent collections on the Grand Récif of Toliara (Tuléar), Madagascar, along the Kenyan Coast (Mombasa, Shariani) and on the reefs of Pemba Island (Fundu South Reef), Tanzania (see map) yielded large specimens of two shallow-water species belonging to the genus *Bohadschia*. One species is considered new to science, whilst the second, the little-known *B. subrubra* (QUOY & GAIMARD, 1833) is shown to be fairly wide-spread in the western region of the Indian Ocean.



Map
Map with observation sites (a) and maps with collection sites (b)(c)(d).
Kenya.
1: Malindi Marine National Park;
2: Watamu Marine National Park;
3: Shariani;
4: Mombasa Marine National Park.
Tanzania.
Pemba Island.:
5: Fundu North Reef;
6: Fundu South Reef.
Madagascar.
7: Tuléar.

Taxonomy

Family Holothuriidae LUDWIG, 1894
Genus *Bohadschia* JAEGER, 1833

Bohadschia atra sp. nov.
Fig. 1 (A-J), Fig. 2(A-E), Pl. 1B, D

Bohadschia subrubra; CHERBONNIER, 1988: 40, fig. 13 (A-K); ROWE & RICHMOND, 1997: 302 (text).
Bohadschia sp.; ROWE & RICHMOND, 1997: 303 (fig.).

Material

Holotype: Mayotte (Comores), 1977, 8 m depth, coll. Ph. BOUCHET, MNHNP, Ec HN-7133; Paratypes: Tanzania (Pemba Island, Fundu South Reef), 21-vii-1998, 12 m depth, coll. Y. SAMYN, IRSNB, IG 28 268/Fun90-91 (2 specimens); Kenya (Mombasa), 12-viii-1997, 10 m depth, coll. Y. SAMYN, IRSNB, IG 28 268/Mom12 (1 specimen); Kenya (Shariani), 3-viii-1997, 2 m depth, coll. Y. SAMYN, IRSNB, IG 28 268/Sharll (1 specimen); Kenya (Mombasa), 10-viii-1998, 2 m depth, coll. Y. SAMYN, IRSNB, IG 28 268/Mom60-61 (2 specimens); Toliara (Tulear, Madagascar), several specimens observed and photographed (see pl. 1D).

Description

Preserved specimens from 108 X 32 to 270 X 65 mm. Living specimens up to 400 mm long and 150 mm wide. Dorsal surface deep brown to black with small round, brown-red spots (pl. IB, D). Each red spot surrounds the base of at least one dorsal papillae. On some specimens transverse brown-red bands are more visible anteriorly than posteriorly. Ventral surface brown to light brown covered by numerous small, black tube feet, spread without alignment over both the ambulacral and interambulacral areas. Dorsal papillae also black, without alignment. Tube feet more numerous than the dorsal papillae. Mouth ventral, anus dorsal without anal teeth; tentacles 18-20, black; body wall 2-5 mm thick.

Calcareous ring stout with radial pieces at least twice as large as the interradial ones; radial pieces (fig. IA) with a central notch and two lateral hollows. One Polian vesicle, one stone canal; long tentacular ampullae. Gonad well developed comprising a bunch of very long and thin undivided tubules. Cuvierian tubules very numerous.

Ossicles of body wall granules and rosettes. Large specimens (>25 cm) with rosettes only (figs 1B, C) somewhat larger dorsally (fig. 1B) than ventrally (fig. 1C). Medium (15-24 cm) and small (<14 cm)

specimens with massive rosettes (fig. 1H), some rod-like (fig. 1J), and perforated grains ventrally (fig. 1G)(exceptionally an unperforated grain can be observed); with branched rosettes (fig. F) dorsally.
Ventral tube feet without any ossicles except an end plate 285-300 mm across in large specimens; with rods 110-210 mm long (fig. lE) and an end plate in medium specimens; with a few rods (fig. 2A) 50-110 mm long, perforated grains (fig. 2B), rosettes (fig. 2C) and an end plate 360-400 mm across in small specimens. Dorsal papillae of medium specimens with rods (cf. CHERBONNIER 1988: fig. 13H, I), those of small specimens with rosette only (fig. 2D).

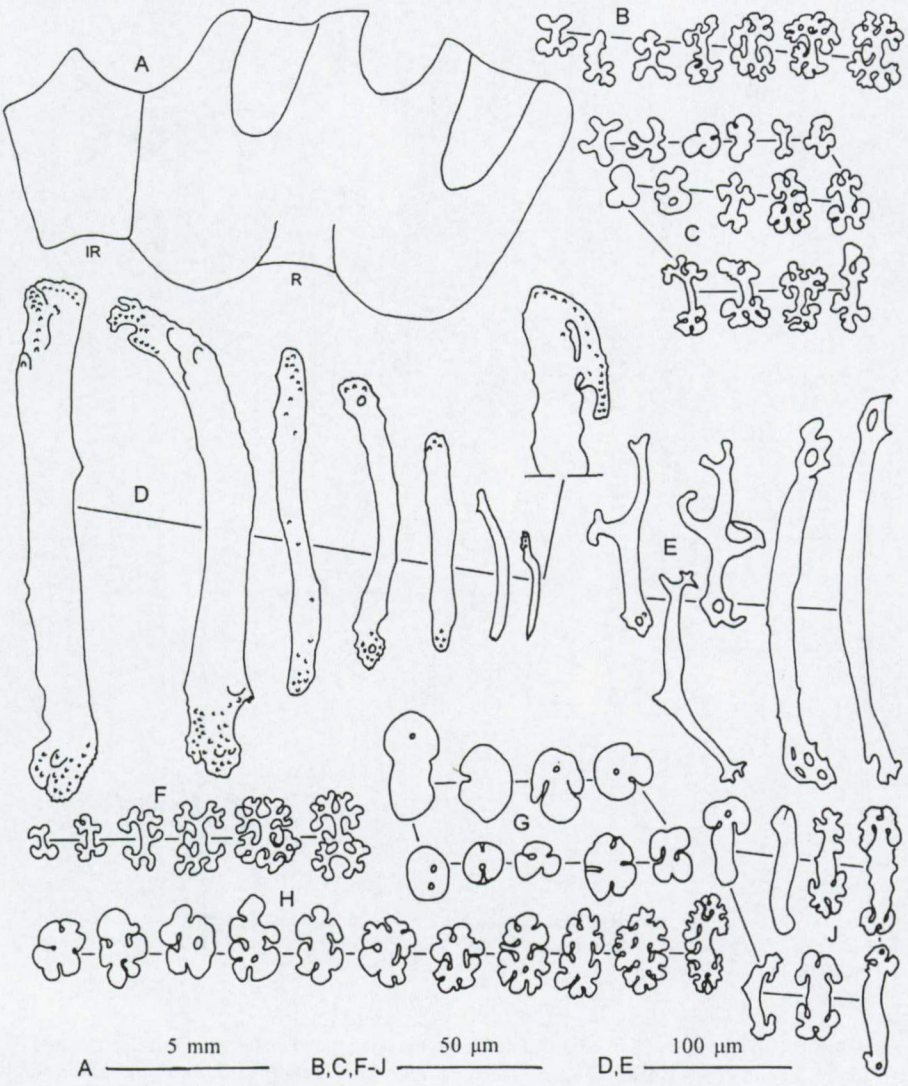


Fig.1. *Bohadschia atra* nov. sp. A: calcareous ring (r: radial plate; ir: interradial plate) (L=270 mm); B: rosettes of dorsal body wall (L=270 mm); C: rosettes of ventral body wall (L=270 mm); D: rods of the tentacles (L=270 mm); E: rods of the tube feet (holotype, L=220 mm); F: rosettes of dorsal body wall (L=108 mm); G: perforated grains of ventral body wall (L=108 mm); H: rosettes of ventral body wall (L=108 mm); J: small rods of ventral body wall (L=108 mm)

Tentacles of large specimens with spiny rods (fig. 1D) sometimes bent at the extremities (fig. 1D), 80-360 mm long; in medium specimens rods up to 340 mm long (cf. CHERBONNIER, 1988, fig. 13F); in small specimens rods 100-330 mm long (fig. 2E).

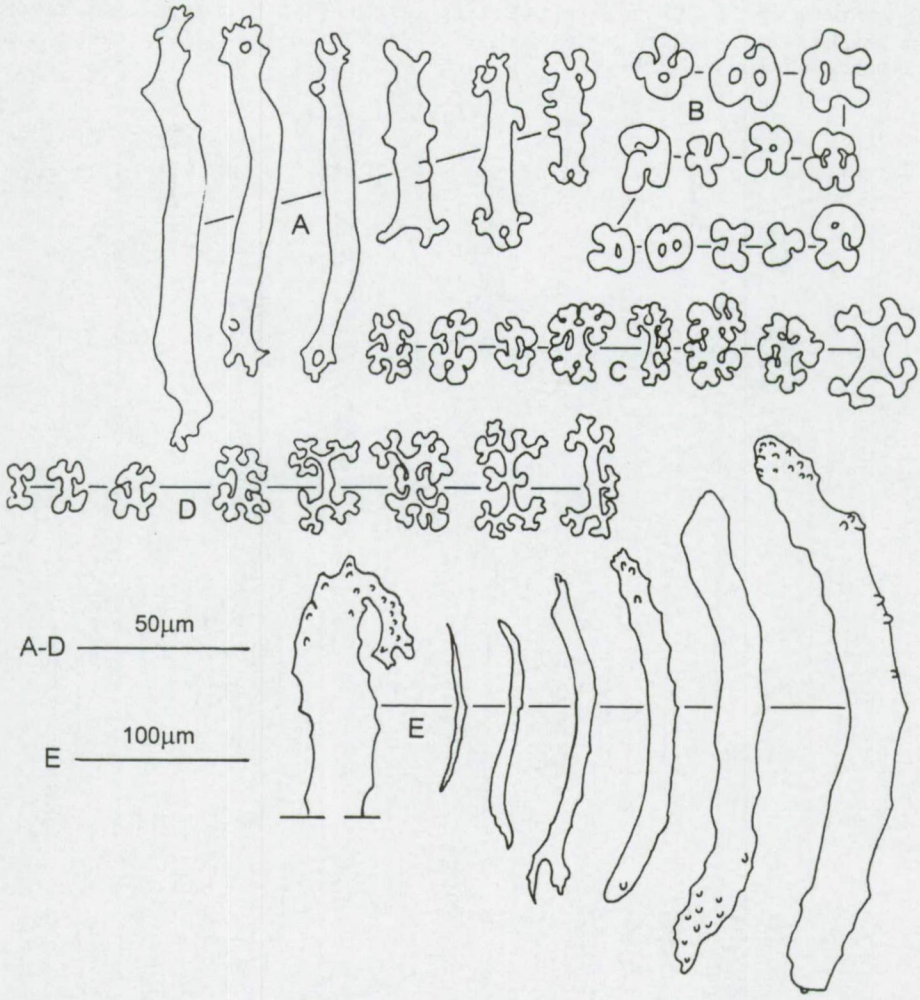


Fig.2. *Bohadschia atra nov. sp.* A: rods of ventral tube feet (L=108 mm); B: perforated grains of ventral tube feet (L=108 mm); C: rosettes of ventral tube feet (L=108 mm); D: rosettes of dorsal papillae (L=108 mm); E: rods of the tentacles (L=108 mm).

Ecology

B. atra dwells in shallow (up to 12 m depth) inner reefs, on sandy patches between coral heads and on the leeward side of seagrass beds (mainly *Thalassodendron ciliata*). Contrary to *B. subrubra* it has not been observed on coral rubble. *B. atra* has been observed feeding on sand, faeces also composed of sand, no rubble.

Distribution

Madagascar (Toliara), Comores (Mayotte), Kenya [Mombasa, Shariani; Watamu & Malindi (SAMYN, pers. observ.)]; Tanzania (Pemba Island: Fundu South Reef).

Etymology
Atra means black and refers to the black colour pattern of the body wall.
Discussion
Species belonging to the genus *Bohadschia* are difficult to identify and unfortunately to add to the confusion, *B. atra* nov. sp. has, in the past, been misidentified as *B. subrubra* (cf. CHERBONNIER, 1988). Moreover, there is an inversion in the text referring to *B. subrubra* and *B. sp* (here *B. atra* nov. sp.) in ROWE & RICHMOND (1997).
B. atra is easy to distinguish from all the other *Bohadschia* species by its dorsal black to deep brown colour with red dots and by its black tube feet and papillae. The misidentification by CHERBONNIER (1988) is surprising because the original description by QUOY & GAIMARD (1833) clearly states that the colour of the dorsal side is light brown with deep brown patches and that the ventral side is white with yellowish tube feet ("Le dessus du corps, sur fond terre de Sienne clair, a de large taches irregulières terre de Sienne calcinée (. . .) Le dessous du ventre est blanc parsemé irrégulièrement d'un grand nombre de suçoirs d'un jaune légèrement verdâtre"). This does not fit with the specimen from Madagascar described by CHERBONNIER (1988). This specimen is brown ventrally with black tube feet.
Bohadschia atra can not be a black form of *B. subrubra* because their ossicles are quite different. Ossicles of the tentacles of *B. atra* are always slightly curved rods with spinose extremities whereas those of *B. subrubra* are much more intricate mainly in small specimens. Moreover, *B. atra*, whatever the size, does not have unperforated grains (with a very few exceptions) whereas they are present and numerous in medium and large *B. subrubra*. Perforated grains are present in small *B. atra* and absent in large ones. It is the reverse for *B. subrubra*. Dorsal and ventral tube feet are present in *B. subrubra* whereas *B. atra* has ventral tube feet and dorsal papillae.
Bohadschia argus (JAEGER, 1833) presents ossicles quite similar to the ones of *B. atra* nov. sp. (see PANNING, 1944: fig. 8). Both species present ventrally the same kind of perforated grains and massive rosettes. However, they clearly differ in their colour pattern. *B. argus* has irregular, very large, dorsal ocelli always surrounded by a whitish space whereas *B. atra* has small, regular ocelli never lined with a whitish space. Moreover, the dorsal papillae of *B. argus* are translucent whereas those of *B. atra* are black. *B. argus* presents also numerous variations in its colour pattern (PANNING, 1944; FÉRAL & CHERBONNIER, 1986) whereas B. atra has a constant colour pattern.

Bohadschia subrubra (QUOY & GAIMARD, 1833)

Fig. 3(A-G), Fig. 4 (A-P), Fig. 5 (A-G), Pl. lA, C, D

Holothuria subrubra QUOY & GAIMARD, 1833: 136; HOFFMANN, 1874: 55.
Bohadschia subrubra; CHERBONNIER, 1952: 36, fig. 14(A-J); A.M. CLARK & ROWE, 1971:176; ROWE & RICHMOND, 1997: 303.
Bohadschia sp.; ROWE & RICHMOND, 1997: 302 (text).

Material
Madagascar, Grand Recif of Toliara, inner reef flat, 9-iii-97, coll. C. CONAND (2 specimens); Kenya (Shariani), 3-viii-1997, 1 m depth, coll. Y. SAMYN, IRSNB IG 28 628/Shar 10 (1 specimen); Kenya (Mombasa), viii-1998, 14 - 18 m depth, coll. Y. SAMYN, IRSNB IG 28 628/ Mom89-92-93-94 (4 specimens); Tanzania (Pemba Island, Fundu North Reef), 20-vii-1997, 14 ill depth, coll. Y. SAMYN, IRSNB IG 28628/Fun7 (1 specimen).
Description
Specimens from 113 X 48 to 250 X 75 mm. Living specimens 130 to 350 mm long (pl. 1). Colour of living specimens brown-orange background with a patchwork of irregular, large, black patches (pl. lA-D). Specimens from Madagascar are more orange (pl. 1D) than the ones from Kenya (pl. 1C). In alcohol dorsal surface beige-brown with irregular black patches; ventral surface grey-white with minute brown-black spots. Limit between dorsal and ventral surfaces well marked by a dotted brown line. Tube feet white, numerous, densely crowded, spread without alignment on the whole dorsal and ventral surfaces. Mouth ventral, anus dorsal without anal teeth. Tentacles 18, grey-white. Body wall 2-5 mm thick. Calcareous ring stout with radial plates twice as large as interradial plates (fig. 3A); radial plates with a deep central notch and two lateral hollows (fig. 3A). One Polian vesicle, one stone canal; tentacular ampullae 33-35 mm long. Gonads well developed, made of a bunch of long, undivided tubules. Cuvierian tubules present, numerous, white.

Ossicles of body wall granules and rosettes. Large specimens (> 15 cm) with numerous unperforated granules (fig. 3B) and small rosettes (fig. 3C) ventrally and rosettes only (fig. 3D) dorsally; small specimens (<15 cm) with numerous large rosettes (fig. 3E) and a few granules (fig. 3F) ventrally, and rosettes only (fig. 3G) dorsally. Small rosettes, dorsally located, slightly larger in large specimens than in small ones: maximum 41 and 33 μm long, respectively.

Ossicles of tube feet rods, rosettes and granules. Ventral tube feet of the large specimens with rods, 17-210 μm long (figs 4A-B), granules (fig. 4C) and a few rosettes (fig. 4D); end plate 500-650 μm across. Dorsal tube feet of the large specimens with rods, 35-230 μm long (figs 4E-F) and rosettes (fig. 4G); end plate 450-500 μm across. Ventral tube feet of the small specimens with rods, 40-310 μm long (figs 4H-1) and a few rosettes (fig. 4K); end plates 400-450 μm across. Dorsal tube feet of the small specimens with rods 50-250 μm long (figs 4L-M), numerous large rosettes (fig. 4N) and a few irregular bodies (fig. 4P); end plate 260-360 μm across.

In the tentacles rods only. Large specimens with regular rods, 25-410 μm long with spiny extremities (figs 5A-B); a few with forked or perforated extremities (fig. 5C). Small specimens with rods 35-540 μm long (figs 5D-E), very often with irregular extremities (fig. 5F); numerous irregular rods (fig. 5G).

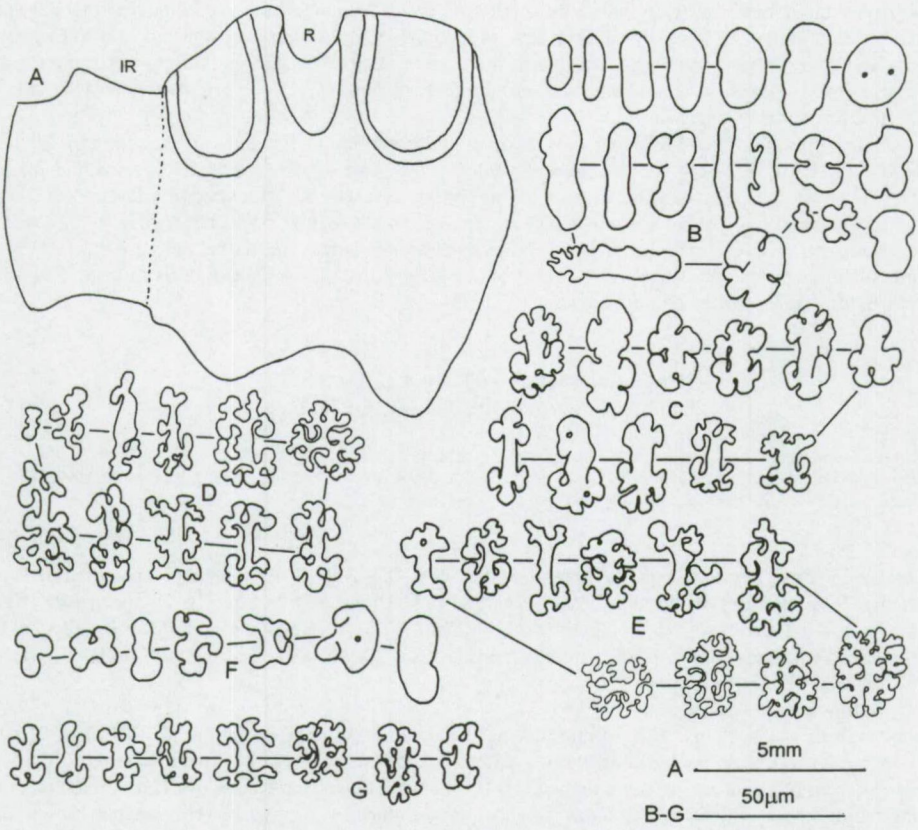


Fig.3. *Bohadschia subrubra* (QUOY & GAIMARD, 1833). Calcareous ring and body wall ossicles. A: calcareous ring (r: radial plate; ir: interradial plate); B: ventral granules of a large specimen; C: ventral rosettes of a large specimen; D: Dorsal rosettes of a large specimen; E: ventral rosettes of a small specimen; F: ventral granules of a small specimen; G: dorsal rosettes of a small specimen.

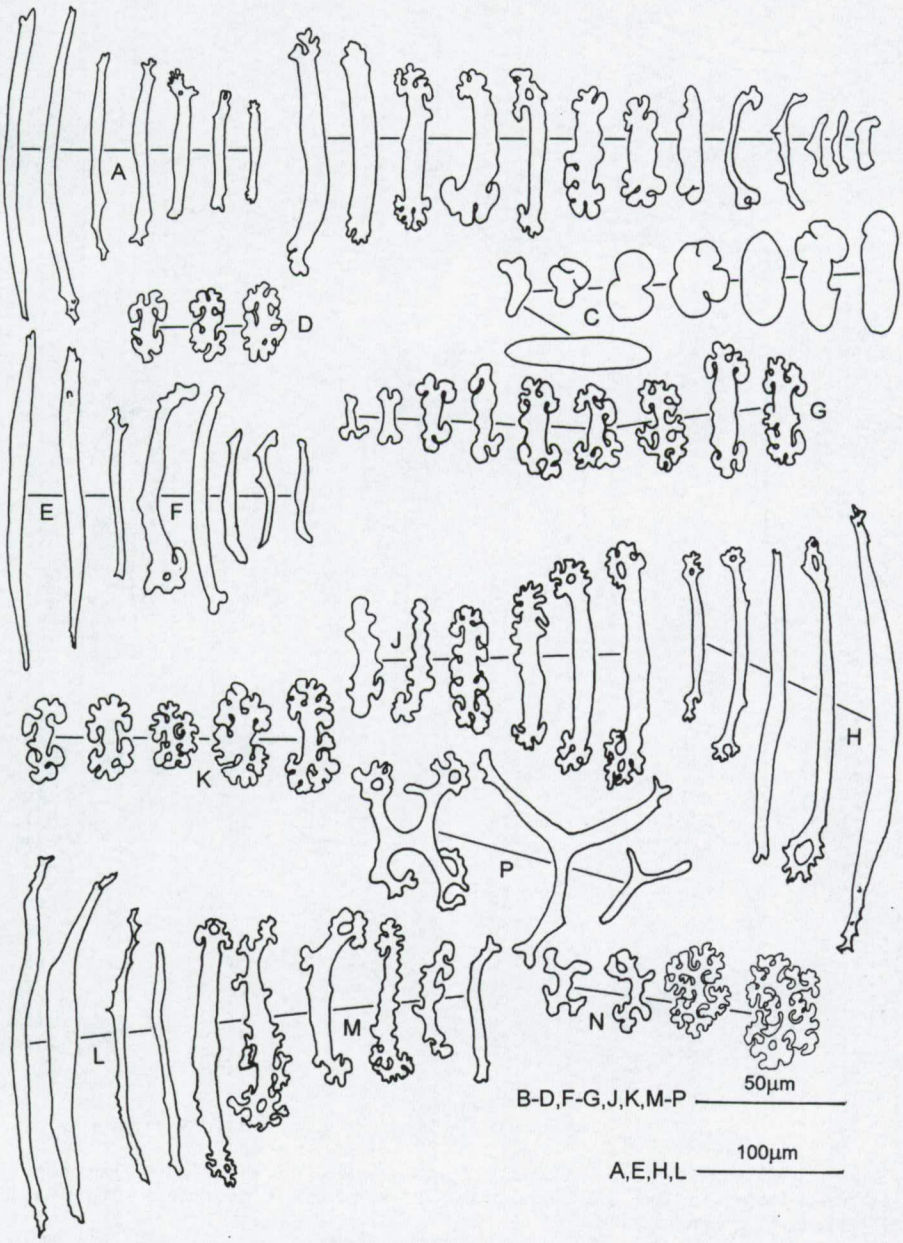


Fig. 4. *Bohadschia subrubra* (QUOY & GAIMARD, 1833). Tube feet ossicles. A & B: ventral rods of large specimen; C: ventral granules of a large specimen; D: ventral rosettes of a large specimen; E & F: dorsal rods of a large specimen; G: dorsal rosettes of a large specimen; H&J: ventral rods of a small specimen; K: ventral rosettes of a small specimen; L & M: dorsal rods of a small specimen; N: dorsal rosettes of a small specimen; P: dorsal irregular bodies of a small specimen

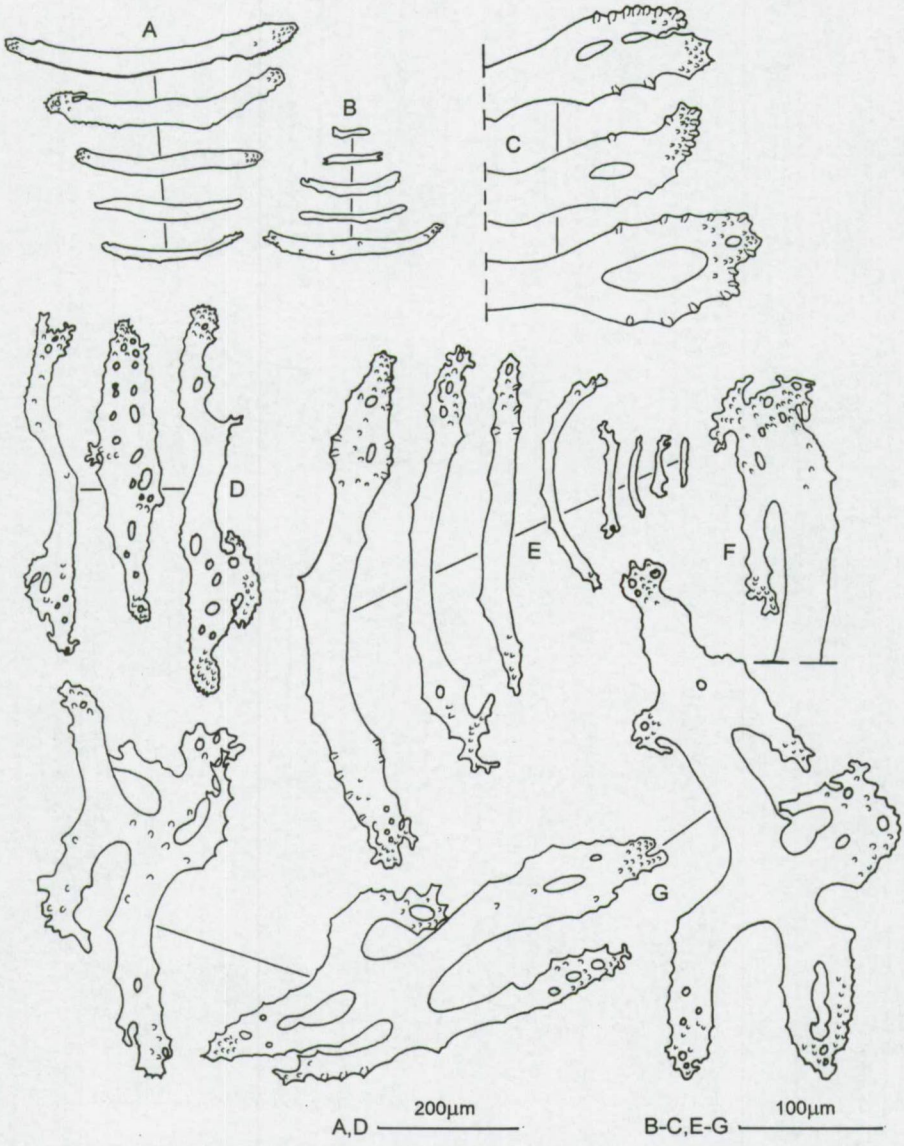


Fig. 5. *Bohadschia subrubra* (QUOY & GAIMARD, 1833). Tentacular ossicles. A & B: rods of a large specimen; C: rod extremities of a large specimen; D & E: regular rods of a small specimen; F: rod extremity of a small specimen; G: irregular rods of a small specimen

Ecology

Bohadschia subrubra lives in the intertidal zone on inner flats of the barrier reef near Toliara. It is generally found on sandy areas located in between alive or dead coral heads. It is also often found inside coral cavities. This particularity is recognised by the local Madagascan names "Falalijaka madrasy" or "Falalijaka bato" which mean"rocky *Bohadschia*". Obviously this species has long been known to Madagascan fishermen. *B. subrubra* has also been observed on the sea-grass beds of the inner flat and on

deeper sandy-muddy bottoms (Nosy Bé, P. LABOUTE, see pl. IA; pers. communiction). The species is also able to live on coral rubble (Zélée Banks, Mayotte; P. DURVILLE, photo and pers. observation of C. CONAND).

Geographical range

Madagascar (Toliara Reef, Nosy Bé), **Mauritius** (ile aux Cerfs), Kenya (Mombassa, Shariani), Tanzania (Pemba Island, Fundu North Reef).

Discussion

In a given area (Madagascar or Kenya) large and small specimens have the same colour pattern. However, their ossicles are so different that they could be considered as separated species. Some *Bohadschia* species, e.g. *Bohadschia marmorata* (JAEGER, 1833), are known to present changes in their ossicles with increasing body size (PANNING 1944, ROWE & DOTY 1977). This led to a lot of confusion and several species have been succes-sively lumped and split again (PANNING 1929, 1944, Rowe & DOTY 1977, CHERBONNIER 1988, ROWE & GATES 1995). *Bohadschia subrubra* is yet another example showing high ossicle variability within a *Bohadschia* species.

B. subrubra exhibits a range of colour pattern similar to the one described by ROWE & DOTY (1977) for *B. marmorata* from Guam. However, the orange-brown background has never been mentioned for *B. marmorata.* The ossicles of *B. subrubra* show characteristic of *B. marmorata* and *B. cousteaui* CHERBONNIER, 1954, which are both present in Madagascar (CHERBONNIER 1988). The ossicles of the tentacles show the same evolution in *B. subrubra* and *B. cousteaui.* Those of the small specimens of *B. subrubra* (135 mm long; figs 3C-D) are identical to those of the *B. cousteaui* (130 and 140 mm long) described by CHERBONNIER (1988: figs 151-1). Whereas the ossicles of the tentacles of the large specimens of *B. subrubra.* (230 mm long; figs 3A-B) are identical to those of the *B. cousteaui* (212 mm long) described by CHERBONNIER (1954, 1955: pl. 23, figs j-k). However, *B. cousteaui* differs from *B. subrubra* by the colour pattern and by the presence of numerous unperforated ventral granules whatever the size of the specimens. Moreover, the complexity of the ossicles of *B. marmorata* increases with increasing size (ROWE & DOTY 1977) whereas it is the reverse for *B. subrubra:* rosettes and tentacular rods are more complex in the small specimens than in the large ones.

The most characteristic features of *B. subrubra* are the presence of rosettes in the tube feet whatever the size of the specimen and particularly the large, complex rosettes in the tube feet of the small specimens, and the colour of the body wall.

Acknowledgments

It is a pleasure to thanks Drs. E. Vanden Berghe and F.W.E. Rowe for reading critically this manuscript and improving the English; Dr. N. Ameziane-Cominardi (Museum National d'Histoire Naturelle, Paris) for the loan of material. Dr. E. Okemwa, director of the Kenya Marine Fisheries Research Institute, who provided to Y.S. space and facilities for the first processing of the samples at his institute. Partial financial support of Y.S. came from the Onderzoeksraad of the Free University Brussels. Logistic assistance in the Mombasa Marine National Park was provided to Y.S. by Kenya Wildlife Services, through Dr. N.A. Muthiga. Autorisation to study the Kenyan echinoderms came from the Office of the President through Mr. J.E. Ekirapa. The field assistance of B. Van Bogaert who helped Y.S. with the collection of the specimens is greatly appreciated. Dr. E. Mara, Director of IH-SM Toliara, Madagascar provided logistic assistance to R.R. and C.C.

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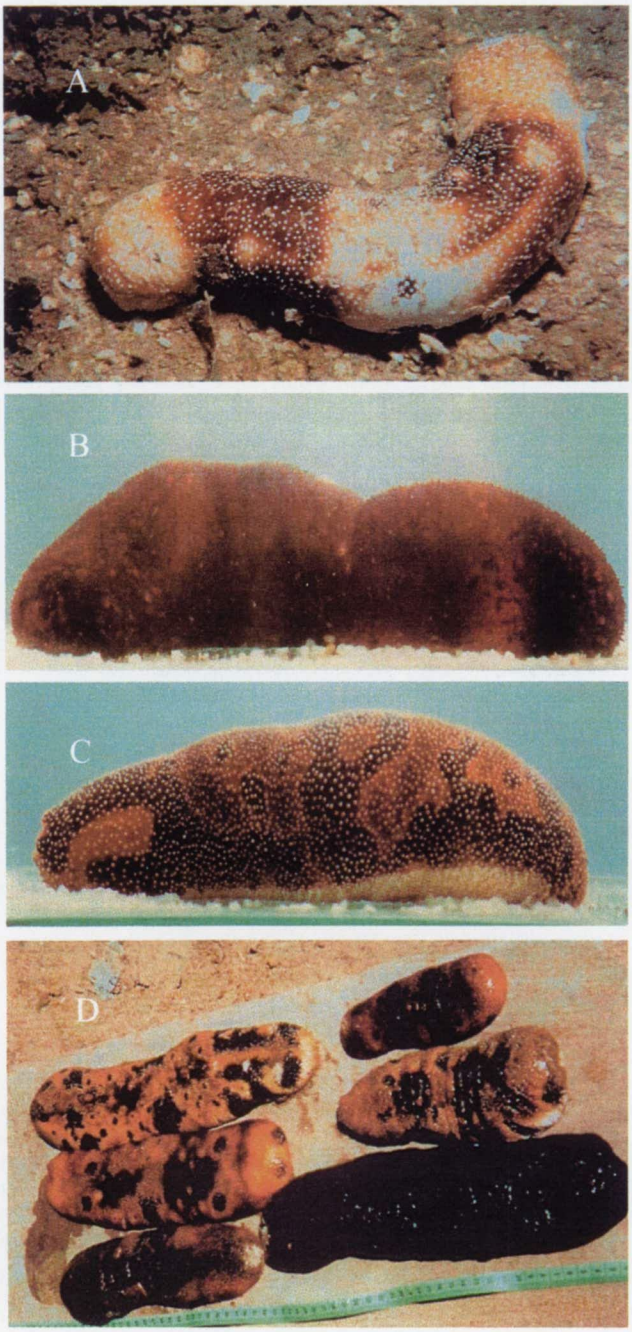

Pl. 1.
A. *Bohadschia subrubra* (QUOY & GAIMARD, 1833) on a sandy-muddy bottom at 10 m depth, near Nosy Bé (photo P. LABOUTE, IRD).
B. *Bohadschia atra* nov sp. from Kenya (photo Y. SAMYN)
C. *Bohadschia subrubra* (QUOY & GAIMARD, 1833) from Kenya (photo Y. SAMYN).
D. Colour range of freshly collected *Bohadschia subrubra* with one *Bohadschia atra* nov sp. (black one) from Madagascar (photo C. CONAND)

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A new species of *Holothuria* (Aspidochirotida, Holothuriidae) from Kenya

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ABSTRACT

Samyn Y., Massin C., Muthiga N.A. 2001. A new species of *Holothuria* (Aspidochirotida, Holothuriidae) from Kenya. *Annls Mus. R. Afr. Centr. (Zool.)* 285: 101-110. A new species, *Holothuria (Mertensiothuria) arenacava* (Echinodermata, Holothuroidea) from the littoral waters of Kenya is described. This species is characterized by its sand-burrowing behaviour, by its small tentacles, by the variously developed tables, corpuscules, buttons, plates and rods in the tube feet, and by the smooth, spiny and knobbed rods in the tentacles.

Keywords - Echinodermata, Holothuroidea, *Holothuria,* new species.

RÉSUMÉ

Holothuria (Mertensiothuria) arenacava sp. nov. (Echinodermata, Holothuroidea), provenant des eaux littorales du Kenya, est décrite. L'espèce se caractérise par son comportement fouisseur, par ses petits tentacules et par les spicules de ses podia (tables plus ou moins développées, corpuscules, boutons, plaques et baguettes) et de ses tentacules (baguettes lisses, noduleuses ou épineuses).

Introduction

The Kenyan Coast has been intensively investigated by SCUBA diving for echinoderms between 1997 and 1999. This survey has resulted in an annotated checklist of the echinoids and holothurians from the Kiunga Marine National Reserve adding several echinoid and holothurian species to the Kenyan fauna (Samyn & Vanden Berghe, in press). Further collecting from the Mombasa Marine National Reserve (1998-2000) yielded several specimens of a burrowing holothurian which is new to science, the description of which is the object of the present note.

Material and methods

Material originates from 2 expeditions, August 1998 and April 2000, resulting from a joint effort by the Free University of Brussels (Unit of Ecology & Systematics) and Kenya Wildlife Service. Collecting was done by hand-picking while SCUBA diving down to depths of 12 m. Although the new species is a sand-burrowing species, destructive sampling techniques like dredging were never used.
The specimens were anaesthetized in 5 % magnesium chloride for 5 hours, transferred to 100 % buffered alcohol for one day and transferred to 70 % buffered alcohol for permanent storage. Ossicles were prepared for light microscopy as described by Massin (1999).
The holotype and 3 paratypes are deposited in the collections of the Royal Belgian Institute of Natural Science, Brussels (RBINS), under the number IG 28628. Two paratypes are deposited in the collections of the Royal African Museum, Brussels (RAM), under the numbers MRAC 1662 and 1663, two paratypes are deposited in the collections of the Muséum National d'Histoire Naturelle, Paris (MNHNP), under the numbers EcHh 8070 and EcHh 8071, two paratypes in the collections of the Smithsonian Institution, Washington (SI), under the number USNM E53097 and USNM E53098 and two paratypes in the

collections of the British Museum of Natural History, London (BMNH), under the numbers NHM 2000.2414 and NHM 2000.2415.
Material has been compared with species from the collections of the RBINS and with the type material of *Holothuria (Mertensiothuria) papillifera* Heding in Mortensen, 1938 from the Zoologisk Museum (ZM), Copenhagen.

Taxonomy

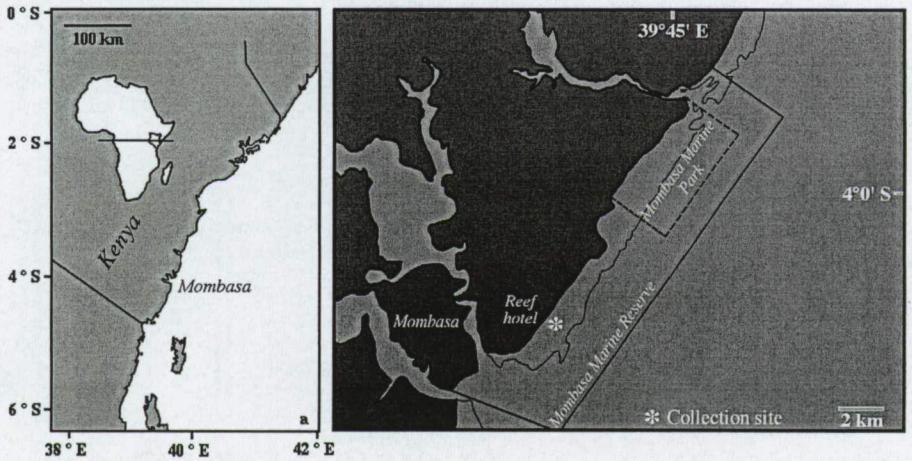
Family Holothuriidae LUDWIG, 1894
Genus *Holothuria* LINNAEUS, 1767
Subgenus *Mertensiothuria* DEICHMANN, 1958
Holothuria (Mertensiothuria) arencava sp. nov.

Material

Holotype: KENYA, Mombasa, VIII.1998, 11 m depth, coll. Y. Samyn (IRSNB IG 28628/ KMom/9897-6)
Paratypes in the collections of IRSNB: KENYA, Mombasa, VIII.1998, 12 m depth, coll. Y. Samyn (IRSNB IG 28628/KMom/9897-2); KENYA, Mombasa, VIII.1998, 12 m depth, coll. Y. Samyn, (IRSNB IG 28628/KMom/9897-3); KENYA, Mombasa, IV.2000, 10 m depth, coll. N.A. Muthiga (IRSNB IG 28628/KMom/0002-2).
Paratypes in the collections of RAM: KENYA, Mombasa, VIII.1998, 9 m depth, coll. Y. Samyn (MRAC 1662/K.Mom/9897-1); KENYA, Mombasa, IV.2000, 10 m depth, coll. N.A. Muthiga, (MRAC 1663/K.Mom/0002-1).
Paratypes in the collections of MNHNP: KENYA, Mombasa, VIII.1998, 10 m depth, coll. Y. Samyn, (EcHh8070/KMom/9897-4); KENYA, Mombasa, IV.2000, 10 m depth, coll. N.A. Muthiga (EcHh8071/KMom/0002-3).
Paratypes in the collections of SI: KENYA, Mombasa, VIII.1998, 11 m depth, coll. Y. Samyn, (USNM E53098/KMom/9897-5); KENYA, Mombasa, IV. 2000, 10 m depth, coll. N.A. Muthiga, (USNME53097/KMom/0002-4).
Paratypes in the collections of BMNH: KENYA, Mombasa, VIII.1998, 10 m depth, coll. Y. Samyn, (NHM 2000.2414/KMom/9897-7); KENYA, Mombasa, IV.2000, 10 m depth, coll. N.A. Muthiga, (NHM 2000.2415/KMom/0002-5).

Type locality

Mombasa Marine National Reserve, off the Reef Hotel (Map 1).



Map 1. Collection site marked by the asterisk

Description

Preserved specimens range between 160 x 40 to 190 x 48 mm in length and breadth, respectively. Living specimens range up to approximately 250 x 50 mm. Colour in life identical to colour in alcohol. Trivium uniform chestnut brown, bivium chestnut brown with sometimes an orange-brown median area, anus underlined with orange-brown in some specimens. Body wall with numerous, irregular transversal wrinkles. Five clearly distinguishable longitudinal grooves in the ambulacral areas, over the total body length. Body wall covered by numerous short, brown cylindrical tube feet, distributed evenly over both the radial and interradial areas. Bivium also bears a few conical papillae of the same colour. Mouth ventral, surrounded by 20 small tentacles; one specimen with only 12 tentacles (eight dorsal and four ventral, the latter reduced). Tentacle crown surrounded dorsally by a semicircle of light brown conical papillae. Anus terminal, surrounded by a semicircle of chestnut brown, conical papillae. Longitudinal muscles bifid, prominent. Body wall up to 8 mm thick. Cuvierian organs present. Calcareous ring (fig 1K) with radial plates almost twice the width and one and a half times the length of the interradial ones. Single, well developed Polian vesicle, 1/6 of the body length. Stone canal (Fig. 1L) very short, contorted, ending in an irregular quadrangular madreporic plate. Respiratory trees dendritic, very long extending forward to reach the calcareous ring.

Ossicles of the ventral and dorsal body wall (Fig.1) consist of tables, buttons and corpuscules (plates with 2-3 holes). Tables (Figs 1A, C, E, G) numerous, disc 45 to 67 µm across, perforated by four central holes and 5-14 peripheral holes of various sizes; disc quadrangular or more rounded with a spinose rim; pillars short (0-1 cross beam) ending in a spiny crown with a large central opening; sometimes, pillars reduced to knobs. Buttons (Figs 1B, D, F, H) numerous, 25 to 55 µm long, with 3-4 pairs of irregular holes; rim of button smooth but irregular. Corpuscules (Figs 1D, F, H), from 20 to 30 µm long, with 2-3 holes; more numerous in small specimens. Ventral tube feet with plates, buttons, modified buttons, corpuscules, rods and tables. Plates (Fig. 2B) up to 75 µm long, with up to four columns of holes. Buttons in large specimens (Fig. 2B) up to 85 µm long and 43 µm wide, mostly with 2-3 rows of holes. Buttons in small specimens (Fig. 2D), up to 70 µm long, always with 2-4 pairs of holes. Some buttons reduced to rods (Fig. 2B). Some small corpuscules (Fig. 2D), up to 25 µm long, with two holes. Tables similar in small and large specimens (Figs 2A,C); disc from 30 to 48 µm across with a rim always more or less spinose; disc always perforated by four large central holes and a variable number of peripheral holes; spire variably developed, often reduced to only a few knobs. End plate of ventral tube feet up to 765 µm across. Ventral tube feet at the anal side with similar poorly developed tables (Fig. 2E); numerous perforated rods (Fig. 2F) up to 110 µm long; end plate, small, only 80 µm across (Fig. 2G); numerous buttons (Fig. 2H), always with 1-6 pairs of irregular holes. Oral papillae in small specimens with simple rods (Fig. 3A), sometimes perforated at the extremities, from 30 to 110 µm long; buttons (Fig. 3B) with 2-5 pairs of holes, up to 75 µm long; some small corpuscules (Fig. 3B) with 2-4 holes. Oral papillae in large specimens with buttons (Fig. 3C) and variously developed tables (Fig. 3D). Dorsal papillae with buttons (Fig. 3G), from 30 to 85 µm long, with 2-7 pairs of irregular holes; complex rods derived from the largest plate-like buttons (Fig. 3E); tables (Fig. 3F) similar to the ones in the body wall. Dorsal tube feet with tables (Fig. 3H), buttons (Fig. 3J), and rods (Fig. 3K) similar to the ones in the ventral tube feet, both in size and in shape. End plate of dorsal tube feet 500-600 µm across. Tentacles with smooth, spiny and knobbed rods (Figs 3N, P), 35 to 160 µm long.

Ecology

Holothuria (Mertensiothuria) arenacava lives in the sand at depths ranging from 9 to 12 meters. The animal lies flat, just below sand surface, only exposing a part of its dorsal surface.

Distribution

Holothuria (Mertensiothuria) arenacava is only known from the type locality.

Etymology

The name *arenacava* refers to the sand-burrowing behavior of the species; *arena* meaning sand and *cava* is derived from *cavare*, meaning to dig.

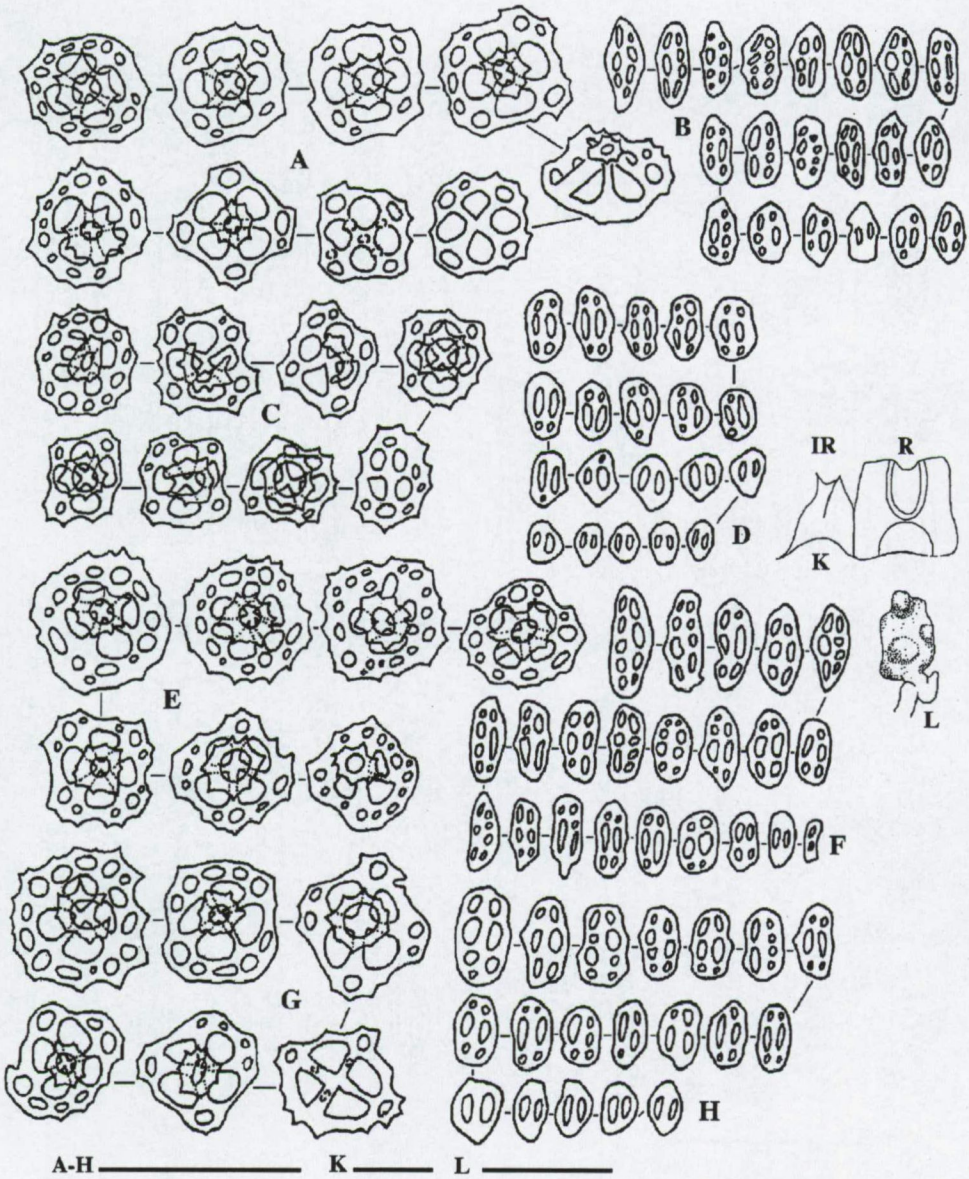


Fig. 1. *Holothuria (Mertensiothuria) arenacava* sp. nov. A. Tables of ventral body wall (L=160 mm); B. Buttons of ventral body wall (L=160 mm); C. Tables of ventral body wall (L=73 mm); D. Buttons and corpuscules of ventral body wall (L=73 mm); E. Tables of dorsal body wall (L=160 mm); F. Buttons and corpuscules of dorsal body wall (L=160 mm); G. Tables of dorsal body wall (L=73 mm); H. Buttons and corpuscules of dorsal body wall (L=73 mm); K. Calcareous ring (L=160 mm); L. Stone canal and madreporic plate (L=73 mm). Scale bar A-H represents 100 µm; scale bar K represents 5 mm; scale bar L represents 5 mm.

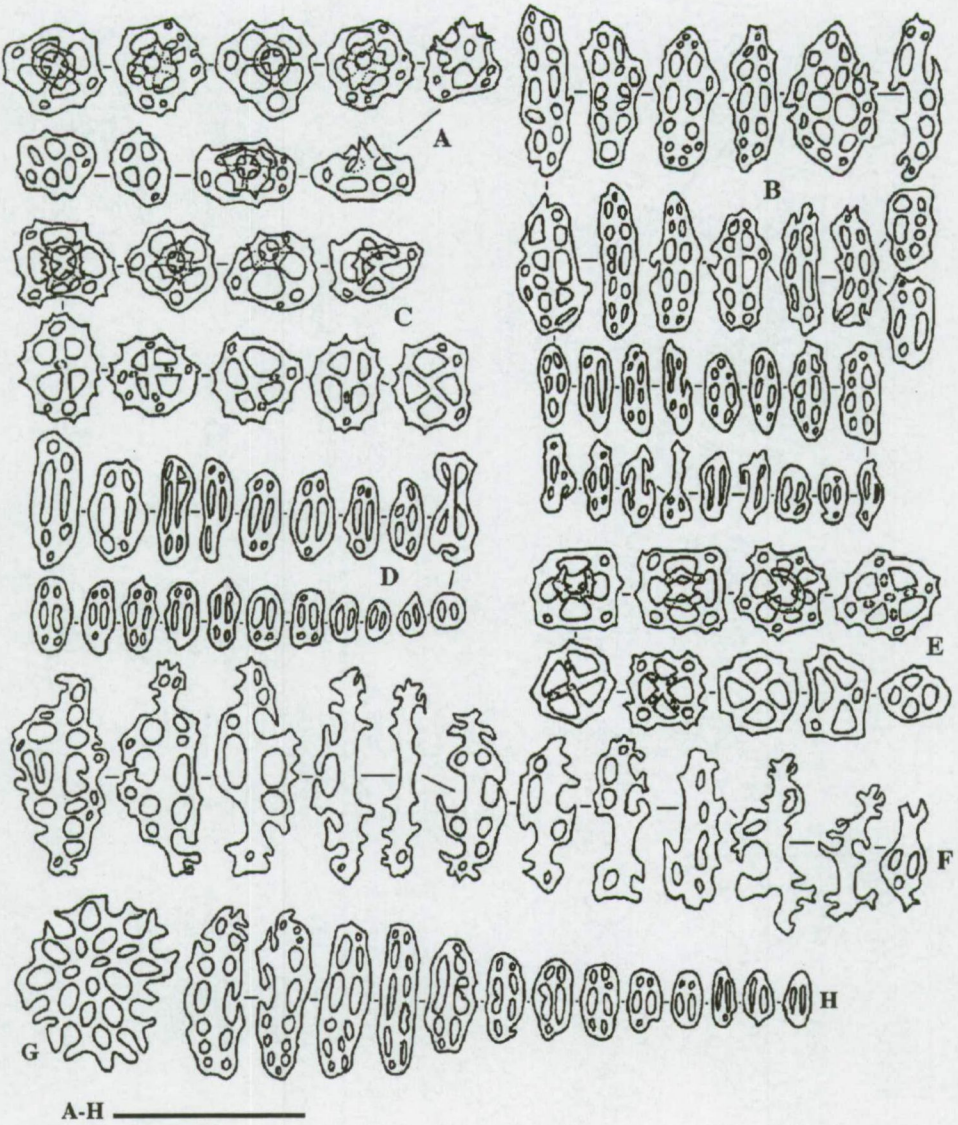


Fig. 2. *Holothuria (Mertensiothuria) arenacava* sp. nov. A. Tables of ventral tube feet (L=160 mm); B. Buttons and plates of ventral tube feet (L=160 mm); C. Tables of ventral tube feet (L=73 mm); D. Buttons and corpuscules of ventral tube feet (L=73 mm); E. Tables of ventral tube feet at anal side (L=73 mm); F. Plates and rods of ventral tube feet at anal side (L=73 mm); G. Endplate of ventral tube feet at anal side (L= 73 mm); H. Plates, buttons and corpuscules of ventral tube feet at anal side (L=73 mm). Scale bar A-H represents 100 µm.

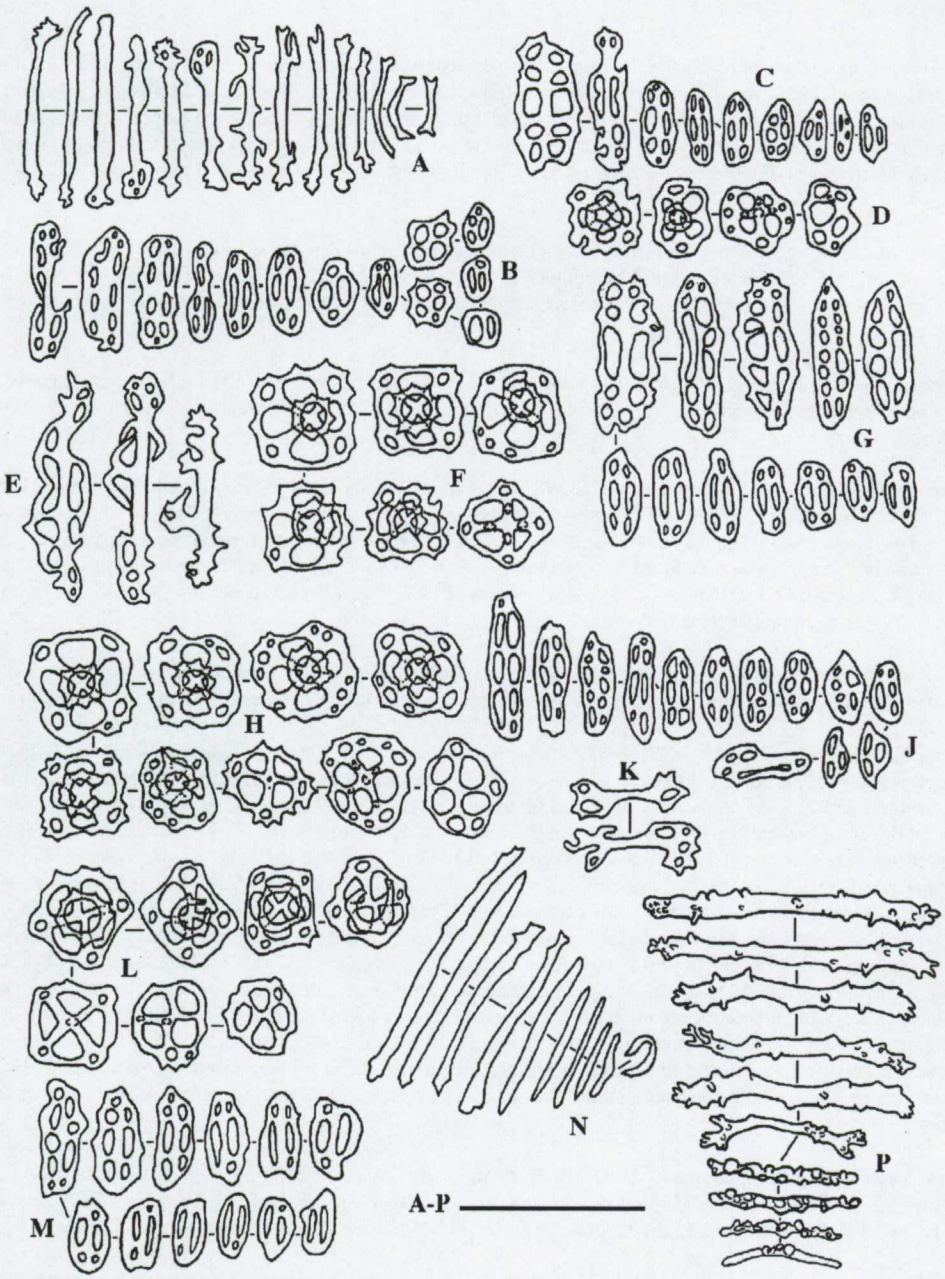


Fig. 3. *Holothuria (Mertensiothuria) arenacava* sp. nov. A. rods of oral papille (L=73 mm); B. Plates, buttons and corpuscules of oral papille (L=73 mm); C. Plates and buttons of oral papille (L=160 mm); D. Tables of oral papille (L=160 mm); E. Rods of dorsal papille (L=73 mm); F. Tables of dorsal papille (L= 73 mm); G. Plates and buttons of dorsal papille (L=73 mm). H. Tables of dorsal tube feet (L=160 mm); J. Buttons of dorsal tube feet (L=160 mm); K. Rods of dorsal tube feet; L. Tables of dorsal tube feet (L=73 mm); M. Buttons of dorsal tube feet (L=73 mm); N. Smooth rods of tentacles; P. Knobbed rods of tentacles. Scale bar A-P represents 100 μm.

Discussion

The species described here clearly belongs to the subgenus *Mertensiothuria* Deichmann, 1958, by the calcareous ring which has radial plates which are almost twice as wide as the interradial plates, by the body wall which always contains tables with a spiny disc and wide central, variously developed crown, by the irregular buttons, perforated by 4-8 holes, and by the dorsal and ventral tube feet that contain similar elongated buttons, perforated by 2-4 rows of holes, small plates, variously developed tables, and perforated rods.

At present seven species are generally included in the subgenus *Mertensiothuria*: *H. (M.) albofusca* Cherbonnier, 1988, *H. (M.) artensis* Cherbonnier & Féral, 1984, *H. (M.) exilis* Koehler & Vaney, 1908, *H. (M.) fuscorubra* Théel 1886, *H. (M.) leucospilota* Brandt, *1835, H. (M.) papillifera* Heding in Mortensen, 1938, and *H. (M.) platei* Ludwig, 1898.

Rowe (1969) states that *H. (M.) papillifera* is probably conspecific with *H. (M.) leucospilota.* However, examination of the type material of *H. (M.) papillifera* showed that it is clearly distinct from *H. (M.) leucospilota.*

Formerly *Holothuria canaliculata* Tan Tiu, 1981, *H. dietrichii* Ludwig, 1875, *H. dofleinii* Augustin, 1908, *H. fuscocinerea* Jaeger, 1833 and *H. pervicax* Selenka, 1867 were recognized within the subgenus *Mertensiothuria.* According to Rowe (in Rowe & Gates 1995) which re-examined the type material, *H. dietrichii* is a junior synonym of *Thyone papuensis* Théel, 1886. The others have been moved to the subgenus *Stauropora* by Rowe (in Rowe & Gates 1995). Moreover, according to this author *H. canaliculata* is a junior synonym of *H. dofleinii.*

From all known species within the genus *Mertensiothuria, H. (M.) arenacava* sp. nov. is readily distinguished from all the known species allocated to the subgenus *Mertensiothuria* by its burrowing habit.

Of the known species, *H. (M.) albofusca, H. (M.) fuscorubra, H. (M.) leucospilota,* and *H. (M.) papillifera* are species which are known to occur in the western Indian Ocean and/or the Red Sea (table 1). *H. (M.) leucospilota* and *H. (M.) fuscorubra* have a similar colour pattern as *H. (M.) arenacava*, but these species present different ossicles in the tube feet and the tentacles. The tube feet *of H. (M.) leucospilota* present large plates, whereas *H. (M.) arenacava* presents only small plates; the tentacles *of H. (M.) leucospilota* are characterized by the absence of ossicles (Cherbonnier 1988, Massin 1999), while *H. (M.) arenacava* presents characteristic smooth, spiny and knobbed rods. Ossicles of *H. (M.) fuscorubra* are very similar to the ones of *H. (M.) leucospilota*, besides small rods in the tentacles (Cherbonnier 1951). Nevertheless, these rods are very different from the ones found in *H. (M.) arenacava. H. (M.) albofusca* is only known from 3 specimens from Madagascar, hence intraspecific variation in this species is largely undocumented. However, its typical colouration pattern with a chocolate brown dorsal side, a white yellowish ventral side and anus circled by chestnut brown is distinct from the more uniform colouration of *H. (M.) arenacava.* Moreover, the ventral tube feet of *H. (M.) albofusca* are characterized by the presence of only large plates (Cherbonnier 1988) while the ventral tube feet of *H. (M.) arenacava* possess tables, buttons and small plates.

H. (M.) exilis from the Andaman Islands (Koehler & Vaney 1908), *H. (M.) papillifera* from the Red Sea (Heding in Mortensen 1938), *H. (M.) platei* from Juan Fernandez (Ludwig 1898, Panning 1935), and *H. (M.) artensis* from New Caledonia (Cherbonnier & Féral 1984) are only known from the type locality.

H. (M.) exilis is another species only known from a single 2 cm long specimen: grayish chestnut brown body; 20 yellowish tentacles; pedicels spread in bivium, in rows in trivium; presenting tables with smooth rim of disc and low or no spire, very short, sparsely knobbed rods and corpuscules in the body wall; in the tube feet tables with pointed spire with 2-3 cross-beams. General body morphology and the absence of buttons make it markedly distinct from *H. (M.) arenacava.* However, it should be noted that in their description Koehler & Vaney (1908) stated that *H. exilis* is systematically very close to *H. pervicax* Selenka, 1867. In his important review on the Holothuriidae Rowe (1969) also noted that *H. exilis* 'will

Current species name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Distribution
H. (Mertensiothuria) albofusca Cherbonnier, 1988												x			Madagascar only
H. (Mertensiothuria) dofleini Augustin, 1908													x		Indo-West Pacific
cited as Holothuria dofleinii Augustin				x											(East Africa & Japan)
H. (Mertensiothuria) fuscocinera Jaeger, 1833							x			x	x	x		x	Red Sea; Indo-West Pacific
cited as *Holothuria curiosa* Ludwig				x											
cited as *Holothuria fusco-cinerea* Jäger					x										
H. (Mertensiothuria) fuscorubra Théel, 1886													x		Indo-West Pacific
cited as *Holothuria fusco-rubra* Théel					x										
H. (Mertensiothuria) leucospilota Brandt, 1835							x	x	x	x	x	x	x	x	Red Sea; Indo-Pacific
cited as *Holothuria vagabunda*	x														
cited as *Holothuria vagabunda Selenka*			x	x	x										
H. (Mertesniothuria) papillifera Heding, 1938						x									Red Sea
H. (Mertensiothuria) pervicax Selenka, 1867		x	x				x	x	x	x	x	x	x		Red Sea; Indo-Pacific

Table 1. Littoral holothurians within the subgenus *Mertensiothuria* from eastern Africa, the Red Sea and the western Indian Ocean Islands. 1. Bell, 1884[1]; 2. Lampert, 1896[2]; 3. Ludwig, 1899[3], 4. Pearson, 1910[4]; 5. Pearson, 1913[5]; 6. Heding in Mortensen, 1938; 7. Clark & Rowe, 1971[6]; 8. Sloan et al, 1979[7]; 9. Tortonese (1949; 1951; 1980)[8]; 10. Humphreys, 1981[9]; 11. Clark, 1984[10]; 12. Cherbonnier, 1988[11]; 13. Rowe & Richmond, 1997[12]; 14. Samyn & Vanden Berghe, in press[13].

[1] Bell (1884) lists echinoderms from Mozambique, the Seychelles, Darros Islands, the Amirante Islands, and from Glorieuses Islands.

[2] Lampert (1896) describes a collection made mainly in the surroundings of Zanzibar, but sampled also in the Suez region and in the Red Sea

[3] Ludwig (1899) briefly describes a collection of echinoderms from the Zanzibar area, i.e. the area bordering the East African coast, from the equator to ± 20° South, comprising British-East Africa, German East Africa and Portuguese Mozambique, the Island Juan de Nova in the Mozambique Channel, Madagascar (with Nosy-Bé and Nosy-Faly), Mayotte, the Comores, the Glorieuses Islands and Aldabra. In addition the echinoderm fauna of Amirante Islands and the Seychelles are also considered.

[4] Pearson (1910) gives a brief but concise description of the holothurians from the Kerimba Archipelago (Mozambique).

[5] Pearson (1913) describes the holothurians in the waters which lie between latitudes 30°N and 30°S and longitudes 30°E and 130°E, an area which falls out of the scope of this paper. Consequently, only the species which have a discrete record in the surroundings of our study region are included in this list.

[6] Clark & Rowe (1971) lump the holothurians from East Africa and Madagascar in one group, the Islands of the western Indian Ocean in a second group and the Mascarene Islands in a third group. All three geographical areas are considered in this table.

[7] Sloan et al. (1979) briefly describe the echinoderms from Aldabra.

[8] The echinoderm fauna of Somalia has been described by Tortonese. This list summarizes the holothurians described in 3 papers (1949; 1951; 1980).

[9] Humphreys (1981) gives a checklist of the echinoderms from Kenya and Zanzibar.

[10] Clark (1984) lists of echinoderms from the Seychelles, whereby she also includes the species known from Aldabra, from the Mascarene Islands and/or from East Africa/Madagascar.

[11] Cherbonnier (1988) describes and discusses the holothurians from Madagascar (a few species are also from Zanzibar, the Comores and Glorieuses Islands).

[12] Rowe & Richmond (1997) briefly describe the echinoderms found in the western Indian Ocean, i.e. 'from about central Somalia to the center Kwazulu-Natal coast of South-Africa, embracing the islands of Madagascar, the Comores, Zanzibar, la Réunion, Mauritius and the Seychelles.'

[13] Samyn & Vanden Berghe (in press) give an annotated checklist of the echinoids and the holothurians of the Kiunga Marine Reserve, Kenya, bordering Somalia. Hereby they also discuss local distribution.

prove to be conspecific with *H. pervicax* Selenka, 1867' [sic]. Later, Rowe (in Rowe & Gates 1995) placed *H. pervicax* in the subgenus *Stauropora* after re-examination of the type material of *H. pervicax*. Several requests to the Indian Museum in Calcutta by one of us (CM) were left unanswered, hence we consider the material as being temporarily unavailable. Therefore we cannot make conclusions on the validity of *H.exilis*.

H. (M.) papillifera is yet another poorly described species (Heding in Mortensen 1938), characterized by its lack of Cuvierian organs, by tables with well developed disc, pillars united by a single cross-beam and ending in a spiny crown, by very regular, 50 µm long buttons with 6 angular holes, rods in the tentacles and 30-40 µm long oval rings in the longitudinal muscles. Again, these characteristics (especially the regular buttons and the oval rings) are markedly distinct from *H. (M.) arenacava*. Moreover, *H. (M.) papillifera* is characterized by very large, soft dorsal papillae which have not been observed in *H. (M.) arenacava*. *H. (M.) platei* presents large plates in the dorsal and (even longer) in the ventral tube feet; irregular, smooth, variously developed buttons with 6 pairs of holes, and poorly developed tables without spire in the body wall; whereas *H. (M.) arenacava* presents well developed tables, buttons of various sizes in the body wall, and rods, buttons, small plates and tables in the tube feet and papillae.

It appears that *Holothuria (Mertensiothuria) arenacava* has most affinity with the recently described *H. (M.) artensis* Cherbonnier & Féral, 1984, by the tables, the buttons and by the presence of both smooth and spiny rods in the tentacles. However, they differ strikingly by the ossicles of dorsal tube feet: only rosettes for *H. (M.) artensis* versus buttons, corpuscules, tables and rods for *H. (M.) arenacava*. Moreover, the tube feet of *H. (M) arenacava* do not contain the X-shaped rods and rosettes specific of *H. (M.) artensis*.

Acknowledgments

We wish to thank Drs F.W.E Rowe and E. Vanden Berghe for critically reviewing the manuscript; Kenya Wildlife Service for providing us with logistics for sampling in the Mombasa Marine National Reserve, Dr C. Nielsen (ZM), Copenhagen, for the loan of type material of *H. (M.) papillifera*
Financial support came from the *Research Council* (OZR) of the Free University Brussels (VUB), and from the Flemish Fund for Scientific Research (FWO). Authorisation to study the Kenyan echinoderms came from the Office of the President through J.E. Ekirapa.

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Massinium, a new genus in the holothuroid family Phyllophoridae (Echinodermata: Holothuroidea: Dendrochirotida) with description of a new south-west Indian Ocean species *M. maculosum*

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ABSTRACT

Several specimens of a phyllophorid holothuroid collected from off the KwaZulu-Natal coast, Republic of South Africa, represent a species new to science. In the structure of the calcareous ring and the absence of tables from the body wall it resembles *Neothyonidium magnum* and *N. arthroprocessum*. In all three species the posterior processes of the calcareous ring are distally joined. Hence, they do not correspond with the diagnosis of *Neothyonidium* as defined by its type species, *N. hawaiense*, and are now assembled in the new genus *Massinium*. The new species is described as *Massinium maculosum*. The three species are keyed and a distribution map is provided.

Key words

Holothuroidea, Phyllophoridae, *Massinium* gen. nov., *Massinium maculosum* sp. nov., taxonomy

Introduction

The genus *Neothyonidium* was erected by DEICHMANN (1938) to separate those forms with 20 tentacles positioned in two well-defined circles and a calcareous ring with long posterior prolongations, formerly classified in *Thyonidium* Düben & Koren, 1844 and *Phyllophorus* Grube, 1840. Unfortunately, DEICHMANN (1938) refrained from giving a complete diagnosis of the genus. Instead, the character of the genus was covered by only two phrases in a key to the Phyllophoridae of the eastern Pacific ['Tentacles arranged in an external circle of five pairs of large tentacles and an inner circle of much smaller tentacles, five deeply divided or five pairs' and 'Calcareous ring tall, tubular with long deeply divided posterior prolongations and long narrow interradials' (DEICHMANN 1938: 379)]. Only a single species was included by DEICHMANN (1938): *N. hawaiiense* (Fisher, 1907), the designated type species by monotypy.
HEDING & PANNING (1954) followed DEICHMANN (1938) in recognizing the systematic value of the calcareous ring in the classification of phyllophorids. These authors elaborated DEICHMANN's (1938) diagnosis of the genus *Neothyonidium* by adding two-pillared tables as an additional diagnostic character. By doing so, HEDING & PANNING (1954) recognised *Neothyonidium hawaiiense* (Fisher, 1907) as type species of the genus, to which they also assigned *Phyllophorus inflatus* Sluiter, 1901; *P. dearmatus* Dendy & Hindle, 1907; *P. intermedius* Koehler & Vaney, 1908; *P. vultur* Sluiter, 1914; *P. minutus* Ohshima, 1915; *Thyonidium magnum* (Ludwig, 1882) and with doubt *P. parvus* (Ludwig, 1881). However, they down-graded *T. alexandri* Fisher, 1907 as a synonym of *N. hawaiiense*. Unfortunately, the descriptions given by HEDING & PANNING (1954) are in too many cases largely dependent on the accounts of earlier writers. Since then, PAWSON (1965) described *N. armatum* from New Zealand; CHERBONNIER (1988) *N. dissimilis* from Madagascar; ROWE (1989) *N. parvipedum* from the north-eastern Tasmania; THANDAR (1989) *N. arthroprocessum* from South Africa and LIAO & PAWSON (2001) *N. spiniferum* from China. In addition, ROWE (*in* ROWE & GATES 1995) resurrected *T. alexandri* from the synonymy of *N. hawaiiense* as a valid species. A critical review of *Neothyonidium* is beyond the scope of this paper, but it is safe to state that several species assigned to it may not belong to this genus and others may be conspecifics of some well-known species.

THANDAR (1989) emended the diagnosis of the genus *Neothyonidium* to accommodate the southern-African *N. arthroprocessum*, characterised by its peculiar U-shaped deposits in the body wall. At that time he justified this inclusion by stating that the rods of *N. arthroprocessum* may be table derivatives. Later on, additional records of *N. arthroprocessum* revealed that these deposits are derived from minute buttons rather than from tables (THANDAR 1996). On the basis of a new species of a phyllophorid holothuroid - here described from the east coast of South Africa - characterised by possessing only rosette-shaped granules and "pseudobuttons" in the body wall, it became clear that the emended diagnosis of *Neothyonidium* (THANDAR 1989; see also 1996) could not be upheld. In fact, both *N. arthroprocessum* and the new species belong to another natural group without body wall tables. Moreover, a careful study of the calcareous ring, internal morphology and ossicle assemblage revealed that these two species, together with the tropical west Pacific *N. magnum* (Ludwig, 1882), constitute a well-defined lineage, not corresponding with the diagnosis of *Neothyonidium* as defined by its type species, excellently described by FISHER (1907). This lineage thus constitutes a new genus, here diagnosed as *Massinium*, characterised by the following synapomorphies: a complex calcareous ring with the posterior processes distally linked to each other; four polian vesicles and a body wall that is always devoid of tables. Moreover, in *N. arthroprocessum* and in the new species, the respiratory trees are extremely complex, with a richly-branched subsidiary trunk to each tree. Unfortunately, since we have only anterior fragments of *N. magnum* at our disposal, the detailed structure of its respiratory trees remains poorly described. The new species is here described as *M. maculosum*.

Materials and methods

During recent surveys of the echinoderm fauna of KwaZulu-Natal (Republic of South Africa), several specimens belonging to a species new to science, were found. Collecting was done by SCUBA-diving to depths of a maximum of 44 m, but specimens belonging to the new species were found between 17 and 20 m. Specimens were anaesthetized in 5% magnesium chloride during 4 hours, transferred to 100% buffered alcohol for 24 hours, and then to 70% buffered alcohol for permanent storage. They were studied according to conventional methods outlined by workers such as FISHER (1907), DEICHMANN (1948), ROWE & DOTY (1977) and MASSIN (1999), amongst others. Ossicles were removed in household bleach, washed in two changes of distilled water and illustrated with the camera lucida. For scanning electron microscopy, the ossicles were passed through two changes of absolute alcohol and transferred with a fine pipette together with a little alcohol on to a specimen stub to which they normally stick once the alcohol evaporates. They were then sputter-coated with gold for 5 minutes at 30-40 mA and photographed with a Philips SEM 500.

Results

Family PHYLLOPHORIDAE Oestergren, 1907
Subfamily Semperiellinae Heding & Panning, 1954

Genus *Massinium* gen. nov.

Diagnosis. Dendrochirotid holothuroids with twenty tentacles arranged in two circles of 10 + 10; anus encircled by calcareous teeth; calcareous ring complex, elongated, tubular, with both radial and interradial plates fragmented into a mosaic of small pieces, pronlonged posteriorly with posterior processes distally-linked to adjoining processes of neighbouring plates forming a ribbon-like structure beneath the water-vascular ring; Polian vesicles large, four; ossicles of body wall comprise rods or rosette-shaped deposits, tables always absent; introvert with two-pillared tables and numerous rosettes and/or rods.

Type species. Massinium maculosum sp. nov.

Etymology. This genus is named after Dr. Claude Massin of the Royal Belgian Institute of Natural Sciences, Section Malacology, in recognition of his excellent contributions to the taxonomy of holothuroids. The gender is neuter.

Key to the genus *Massinium*

1 Body wall ossicles comprise soleley rods of variable form, never rosette-like, with minute, often occluded perforations at ends; introvert with two-pillared tables, rods and rosette-shaped bodies .. .. ***M. arthroprocessum*** **(Thandar, 1989)**

1' Body wall ossicles comprise only rosette-like bodies 2

2 Outer tentacles devoid of ossicles; introvert with tables and rosettes; body colour off-white to grey, mottled liberally with dark brown; tentacles with white shaft dashed with brown, tentacle tips spotted with yellow and white ..... ***M. maculosum*** **sp. nov.**

2' Ossicles of outer ring of tentacles include rosettes; introvert with tables only; body colour yellow to brown, tenacles darker brown ..... ***M. magnum*** **(Ludwig, 1882)**

***Massinium maculosum* sp. nov.**
(Figs 1 - 5)

Diagnosis. Medium sized, U-shaped phyllophorid with bloated mid-body and relatively short anterior and posterior ends. Anus surrounded by teeth and papillae, variously developed. Ossicles of body wall short, thick, flat, oval to round rosette-shaped rods and "pseudobuttons", often with minute perforations. Introvert ossicles include tables and rosettes. Tentacles of outer ring without ossicles, tentacles of inner ring with rods and rosettes.



Fig. 1 - *Massinium maculosum* sp. nov. as photographed after removal from the substrate at Sodwana Bay, 2-Mile Reef. (Picture by R. Anderson).

Etymology. The name maculosum refers to the conspicuous colouration of the whitish shaft of the tentacles, mottled with dark-brown and yellow.

Name bearing type. Holotype SAM A27882 (specimen with detached calcareous ring)

Type locality. Mabibi, KwaZulu-Natal Republic of South Africa (Fig. 5).

Material examined. Holotype (specimen with detached calcareous ring), RSAKZN/01122, SAM A27882, 13.ii.2001, 20 m, SCUBA-diving, Y. Samyn. Paratype 1 (calcareous ring only), RSAKZN/01121(a), SAM A27883, other data same as holotype. Paratype 2 (calcareous ring only), RSAKZN/99217, SAM A27884, 17.viii.1999, Sodwana Bay (2-Mile Reef), 14 m; SCUBA-diving, Y. Samyn & P. Timm. Paratype 3 (specimen with calcareous ring attached), RSAKZN/01121(b), MRAC 1701, other data same as holotype. Paratype 4 (calcareous ring only), RSAKZN/99139, MRAC 1702, 12.viii.1999, Sodwana Bay (9-Mile Reef), 17 m, SCUBA-Diving, Y. Samyn. Paratype 5 (specimen devoid of calcareous ring),

RSAKZN/01124, NHM 2003.570, other data same as holotype. Paratype 6 (calcareous ring only), RSAKZN/01123, NHM 2003.571, other data same as holotype.

Description. Holotype (Fig.2A). Specimen entire, well-preserved but with ventral surface slightly ruptured and calcareous ring detached Body form cylindrical, somewhat U-shaped, with the mid-body bloated and with narrower anterior and posterior ends. Length along ventral surface 150 mm, height of mid-body 41 mm, anterior and posterior ends 30 mm and 40 mm in length and 11 mm and 17 mm in diameter respectively. Color light yellow to off-white, mottled with dark brown, more pronounced at the ends. Body wall thin and smooth in bloated part; thick and wrinkled proximally and distally. Body wall podia papilliform, scattered, more numerous proximally and distally, with dark narrow rings encircling reduced suckers. Tentacles 20, in two circles of 10+10, well branched, outer tentacles with whitish stalks spotted with dark brown, branches black proximally and white at tips, inner tentacles much shorter, also with whitish stalks and uniformly black branches. Largest tentacle about 30 mm long. Anus encircled by five groups of papillae, with 4-7 papillae per group. Single papilla of one group heavily calcified, appearing as a tooth covering most of the anal opening; another tooth underdeveloped, not covering anus.

Calcareous ring (see that of paratype 4: Fig. 4H) 42 mm in length, distinctly tubular with radial and interradial plates fused for three-quarter of their length, both radial and interradial plates broken into a mosaic; radial plates anteriorly bifid, with depressions for attachment of retractor muscles; anterior of interradial plates pointed. Posterior processes of radial plates short, broad, bifurcating and uniting with adjacent process of neighboring plates to form a ribbon-like structure encircled by the water vascular ring. Polian vesicles four (one per interradius except the mid-dorsal), up to 25 mm long. Stone canal single, slightly shorter than polian vesicles, free, terminating in an ovoid, well-calcified madreporic body. Gonad (testis) in two tufts, well-developed, white, branched, mostly dichotomously. Respiratory trees remarkably well-developed, reaching anterior end of body, with heavily branched subsidiary trunks extending both to the level of the calcareous ring and beneath the cloaca; exact origin and ramifications of the subsidiary branches could not be determined without further damage to the holotype.

Ossicles of the dorsal and ventral body wall similar - comprising small, thick, flat, elongated to roundish bodies in the form of rods, rosettes and "pseudobuttons", the latter evidently derived from rosettes (Fig. 2B, C, 3A-C). Elongate ventral deposits 27-40 μm long (mean 34.5 μm) and 13-24 μm broad (mean 19.5 μm). Roundish ventral deposits 24-42 μm long (mean 28.6 μm) and 18-41 μm broad (mean 25.8 μm). Elongate dorsal deposits 27-45 μm long (mean 35 μm) and 14-27 μm broad (mean 17.8 μm). Roundish dorsal deposits fewer, 23-25 μm long (mean 24.7 μm) and 19-23 μm broad (mean 22 μm). Rosettes of dorsal body wall more abundant and more complex. Some ossicles large and bone-shaped, dorsally 26-51 μm long (mean 39 μm) and 6-14 μm wide (mean 8.3 μm); ventrally 37-49 μm long (mean 45 μm) and 6-11 μm broad (mean 8.6 μm). "Pseudobuttons" oval, irregular, multilocular, more dominant ventrally, holes minute, larger in ventral body wall (Fig. 3D, E). Ventral podial deposits in the form of tables, plates, rods and rosettes similar to those of body wall (Fig. 2F). Tables with smooth ovoid discs, 50-75 μm long, perforated by four large central holes and a variable number of irregularly positioned peripheral ones. Spires of moderate height, comprising two pillars united by a single cross bar or cross bar absent, pillars diverging distally to terminate in two spiny tips. Rods straight, smooth, elongate, with terminal perforations and/or processes. Some rods irregular with medial processes or formed into plate-like deposits with several perforations in the middle and/or the tips. End-plates with numerous holes, not varying in size peripherally (Fig. 4G). Dorsal podia without tables; other deposits similar to those of ventral podia. Introvert podia with tables and rods (Fig. 4B). Anal podia with tables and rosettes (Fig. 4E, F). Large tentacles (from outer ring) without deposits. Small tentacles (from inner ring) comprise tables at their roots, similar to those of introvert, rosettes and slender rods at their tips; rods straight or slightly curved with crinkly apices (Fig. 4C, D). Introvert deposits comprise tables and rosettes (Figs 2D, E; 3F, G). Tables with large subcircular to oval discs with smooth margins and perforated by four large central holes and usually a single circle of smaller holes, the latter 3-12 in number. Table discs 69-135 μm long (mean 100 μm) and 55-104 μm wide (mean 79 μm); spire 30-53 μm high (mean 45 μm), with a single cross bar and 2-6 terminal teeth. Occasionally pillars reduced to knobs on surface of disc. Rosettes similar to those of body wall, 23-53 μm long (mean 37 μm).

Paratype 1. Represented by calcareous ring and tentacles only. Introvert bordered by numerous podia arranged in rows in the radii. Tentacles as in holotype, longest 24 mm. Polian vesicles four, of unequal

length, longest 29 mm. Stone canal free, slightly twisted proximally. Madreporite poorly calcified, slightly wider than stone canal.

Paratype 2. Represented by calcareous ring, tentacles and anterior fragment of body wall. Polian vesicles four, two branched proximally and one terminally, giving the impression that there are more than four polian vesicles. Stone canal typical but very much coiled proximally. Madreporite as in holotype. Body wall ossicles typical. Ossicles absent from large tentacles. Small tentacles include rods, rosettes and tables, table discs subcircular to oval with four large central perforations and numerous smaller perforations, up to 20, in one or two circles. Spire high, consisting of two pillars and one or two cross-bars, terminating in four teeth. Rosettes similar to those of body wall. Rods straight or curved, with one to two terminal perforations.

Paratype 3. Same form and colouration as holotype, with eviscerated calcareous ring still attached to main body. Length along ventral surface 130 mm, height of mid-body 32 mm, anterior and posterior ends 20 mm and 9 mm respectively. Anus encircled by four calcareous teeth of which one is best developed, each bordered by three to four papillae. Calcareous ring as in holotype, fragmented. Polian vesicles four, elongate, up to 37 mm, tubular. Stone canal free, slightly twisted proximally, madreporite hardly distinguishable from stone canal. Tentacles as in holotype, number difficult to determine as inner circle is obscured within oral cavity. Length of larger tentacles variable, up to 20 mm. Ossicles of ventral and dorsal body wall similar to holotype, 33-59 μm long (mean 46 μm); introvert tables with discs 104-137 μm long (mean 114 μm).

Paratype 4 (Fig. 4H). Represented by the calcareous ring and tentacles as illustrated. Calcareous ring 50 mm in length, best preserved of all type material.

Paratype 5. Specimen small without calcareous ring. Colour as in holotype but dark speckling more pronounced, obscuring the lighter areas of the skin. Length along ventral surface 75 mm, height of mid-body 21 mm, anterior and posterior ends 15 mm and 9 mm respectively. Five equally-sized anal teeth, each bordered by four papillae. Body wall ossicles similar to holotype, 31-60 μm long (mean 40 μm).

Paratype 6. Represented only by calcareous ring and a fragmented part of the body wall. Four polian vesicles, single free stone canal, proximally coiled. Madreporite ovoid, slightly wider than stone canal.

Ecology. This species lives burried deeply in sand, under boulders and coral debris exposing its tentacle crown only when feeding. Upon slightest disturbance, even shading, the tentacle crown and the introvert are swiftly retracted into the body leaving no trace of the animal. Individuals were observed to be actively feeding during daytime (recorded observations : 11h00-13h45; no observations were made at night). The species appears to be more common at Mabibi where, during 108 dive-minutes, six individuals were spotted whereas at Sodwana, only two individuals were spotted during roughly the same period of time at the 9-Mile Reef and just one at the 2-Mile Reef, in more than nine hours of underwater observations. Depth range 14-21 meters.

Geographical distribution. For now only known from northern KwaZulu-Natal (Republic of South Africa) (Fig.5).

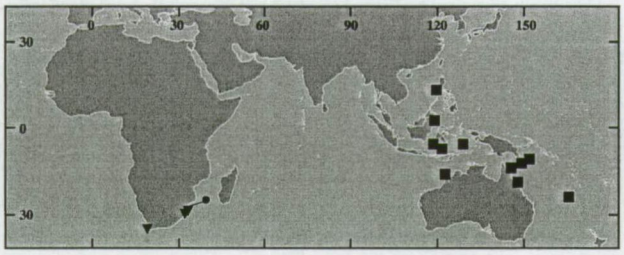

Figure 5. Distribution of the currently known *Massinium* spp.: *Massinium arthroprocessum* (Thandar, 1989) is represented by triangles; *M. maculosum* sp. nov. by a circle; *M. magnum* (Ludwig, 1882) by squares.

Discussion

Massinium maculosum comes very close to *Massinium magnum* (Ludwig, 1882), differing from it in the colouration of the tentacles, the absence of ossicles from the tentacles of the outer ring and the form of the body wall deposits. The original description of *M. magnum* was based only on the introvert and the

calcareous ring. Only SLUITER (1901), DOMANTAY (1933) and CHERBONNIER (1980) claim to have studied complete specimens of this species. However, CHERBONNIER (1980), who also examined LUDWIG's (1882) type, is of the opinion that both Sluiter's and Domantay's specimens may not be the true *M. magnum* as there are significant differences in the form of the introvert tables – those of the holotype are according to him 'absolument identiques' [sic] to his specimens in having multilocular discs with one or more series of peripheral holes in contrast to Sluiter's and Domantay's specimens which have fewer peripheral perforations, restricted in an incomplete or a single series. SLUITER (1901) unfortunately failed to describe the colour of his specimens; DOMANTAY (1933), on the other hand, described the colouration of his specimens accurately. The latter author noted that the tentacles are deep chocolate brown in life and almost black in contracted condition; the introvert is brown and the body wall is almost white. We have examined the introvert in specimens of *M. magnum* described by MASSIN (1999) from Sulawesi (Indonesia) and also in two undescribed specimens collected by Massin from Papua New Guinea. As stated by MASSIN (1999) the introvert of his Sulawesi specimens contains only tables. We here corroborate MASSIN's (1999) observations and further state that this is also true for his Papua specimens. However, the introvert tables of the Sulawesi specimen have tall spires and few peripheral holes, many of which alternate with the large central holes; whereas those of the Papua specimens have moderate to low spires and more peripheral holes. It is therefore certain that *M. magnum* is either a highly variable species or a species-complex. This is corroborated by colour illustrations of *M. magnum* given by FÉRAL & CHERBONNIER (1986) from New Caledonia, GOSLINER *et al.* (1996) from Papua New Guinea and MASSIN (1999) from Sulawesi. Hence a redescription of *M. magnum*, based on all the available material, is urgent and will the subject of our next investigation.

In his revision of the southern African phyllophorids, THANDAR (1990) listed only *M. arthroprocessum* in the subfamily Semperiellinae. The new species now increases to two the number of species in this subfamily occuring in southern Africa.

Massinium is distributed throughout the tropical and subtropical Indo-West Pacific Ocean: *M. magnum* is known from the tropical West Pacific, whereas *M. arthroprocessum* and *M. maculosum* for now are restricted to the subtropical West Indian Ocean. The distribution is mapped in fig. 5.

Acknowledgments

We thank Dr. C. Massin (IRSNB), Brussels, for allowing us to study specimens of *N. magnum* from Papua New Guinea and Sulawesi. Financial support came from the Flemish Community [Bilateral (international) Scientific and Technological cooperation; project numbers BIL98/84 and BIL01/46).

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Appendix

Museum acronyms

MRAC	Muséum Royal de l'Afrique centrale, Tervuren, Belgium
NHM	Natural History Museum, London, United Kingdom
SAM	South African Museum, Cape Town, Republic of South Africa
IRSNB	Institut royal des Sciences naturelles de Belgique, Brussels, Belgium

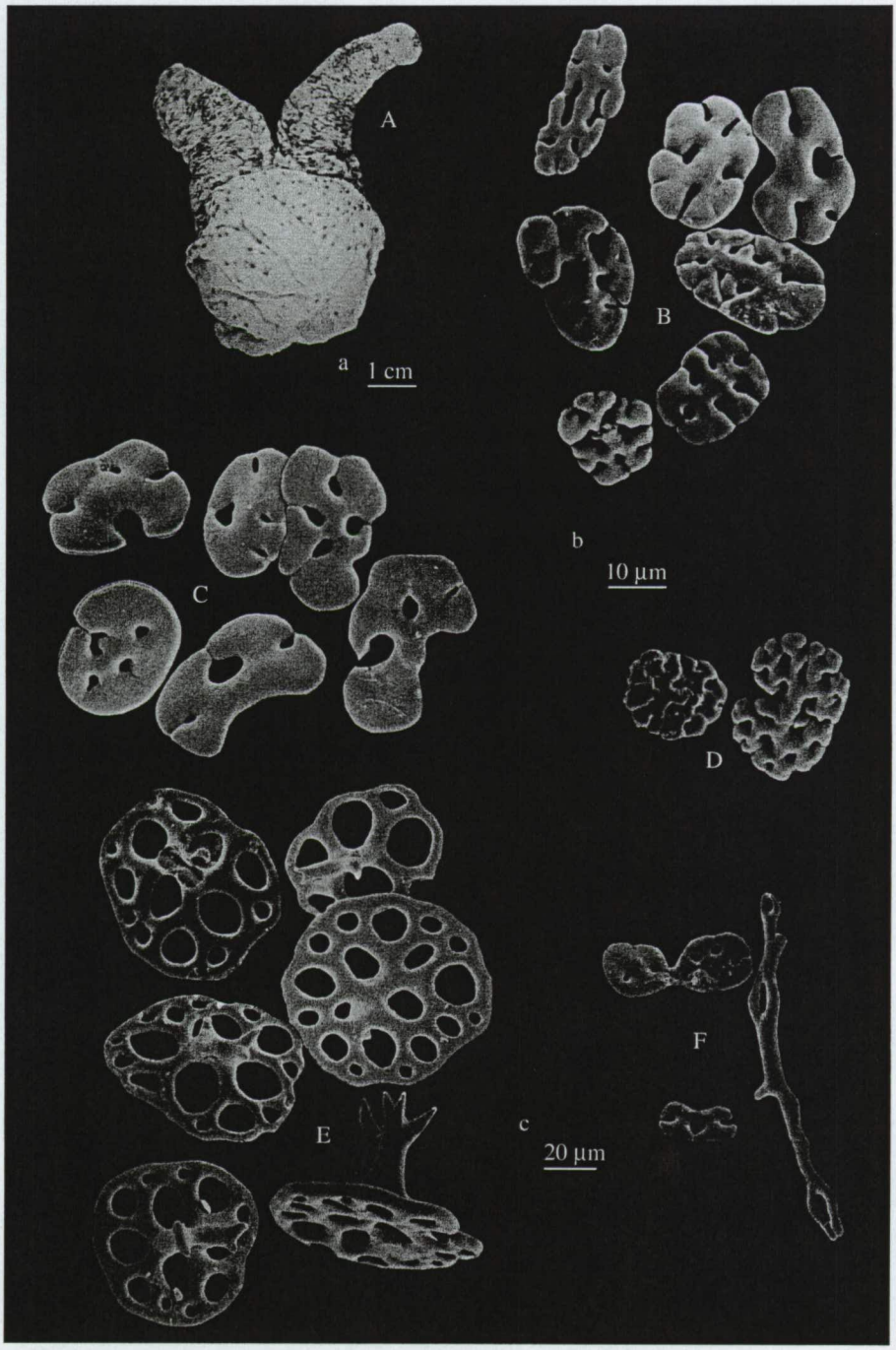

Figure 2. *Massinium maculosum* sp. nov. A, entire; B, rosette-shaped ossicles from mid-dorsal body wall; C, rosette-shaped ossicles from mid-ventral body wall; D, rosettes from the introvert; E, tables from the introvert; F, podial deposits. (A - scale a; B, C, D & F - scale b; E - scale c)

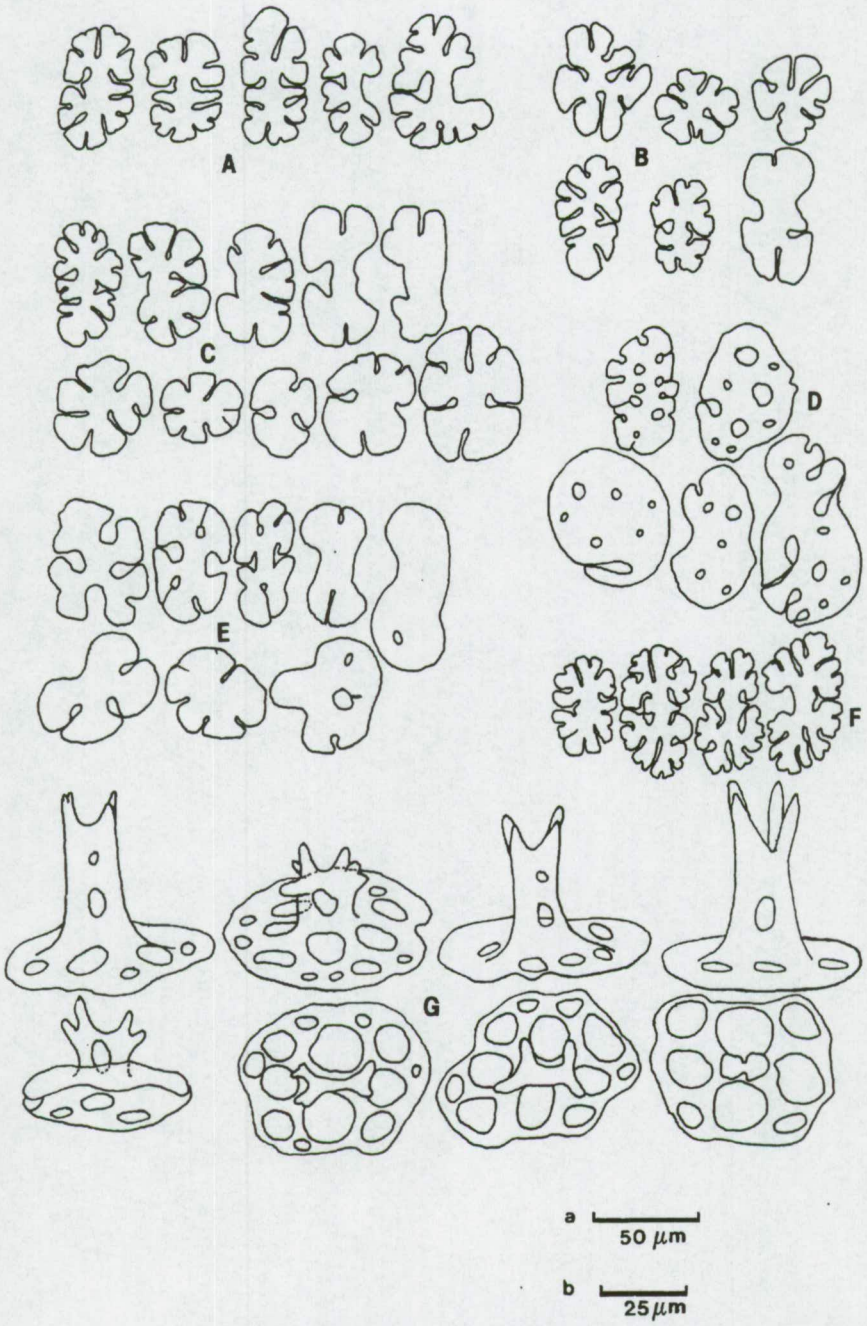

Figure 3. *Massinium maculosum* sp. nov. Ossicles. A, rosette-shaped deposits from antero-dorsal body wall; B, rosette shaped plates from antero-ventral body wall; C, rosette-shaped deposits from mid-dorsal body wall; D, pseudobuttons from dorsal body wall; E, pseudobuttons from ventral body wall; F, Rosettes from introvert; G. tables from introvert. (A-F - scale b; G - scale a)

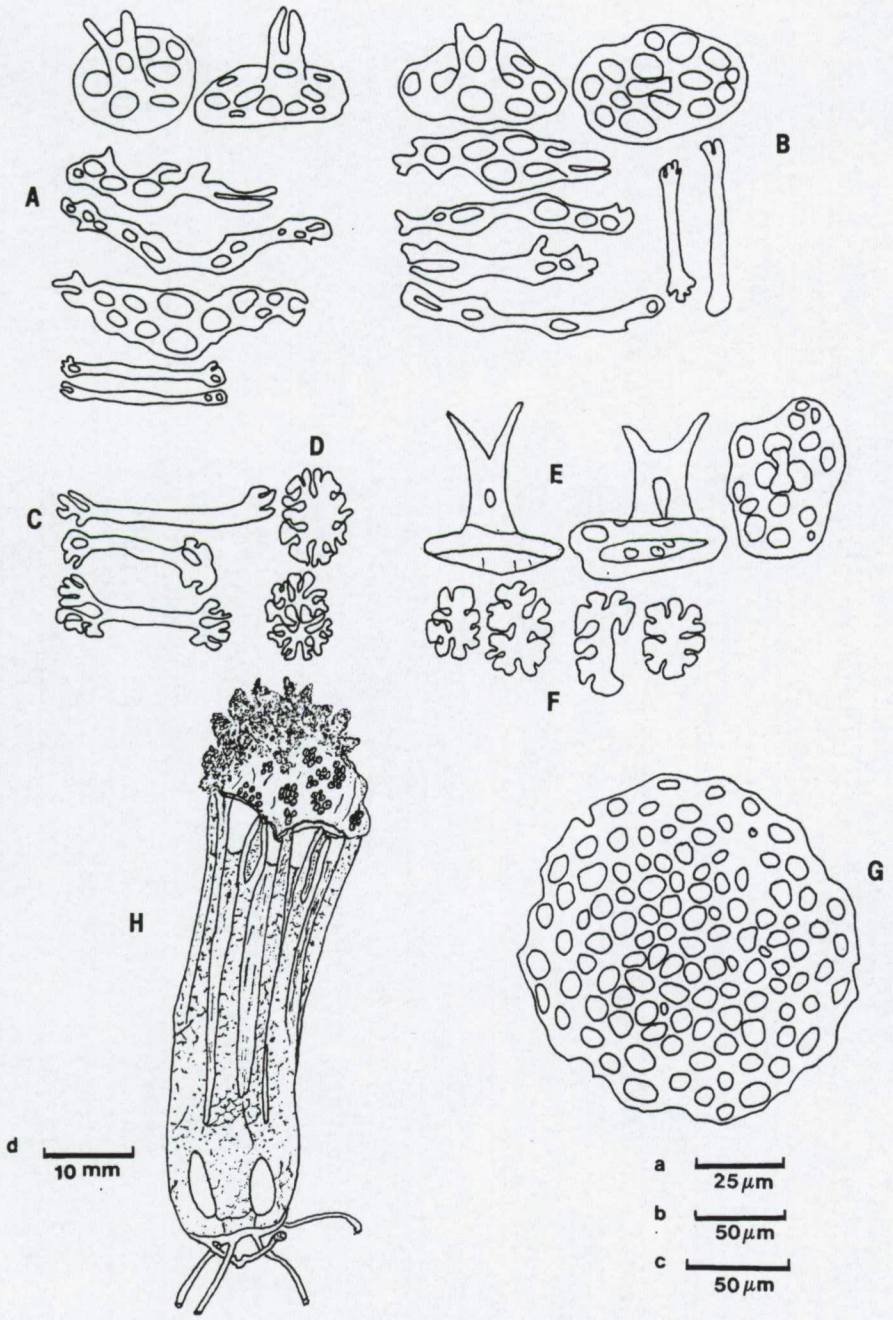

Figure 4. *Massinium maculosum* sp. nov. Calcareous ring and ossicles. A, introvert deposits; B, introvert podial deposits; C, rods of tentacle of inner ring; D, rosettes of tentacle of inner ring; E, tables from anal podia; F, rosettes from anal region; G, end-plate from pedicel; H, calcareous ring of paratype 4 showing tentacles, four polian vesicles and a single stone canal. (A, B & E – scale c; C, D & F – scale a; G – scale b & H – scale d)

Chapter Four

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The holothurian subgenus Mertensiothuria (Aspidochirotida: Holothuriidae) revisited

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ABSTRACT

Mertensiothuria is one of the 20 subgenera currently recognised under *Holothuria*. The diagnosis of the subgenus is amended with new information on the ossicles found in the longitudinal muscles. The number of species of *Mertensiothuria* considered to be valid at present is six. These species are redescribed on the basis of new material, type and non-type museum material and on re-evaluation of literature. Two of them, *Holothuria hilla*, and *Holothuria aphanes* are transferred from the subgenus *Thymiosycia* to *Mertensiothuria*. Four species formerly referred to *Mertensiothuria* are removed; provisionally they are not referred to any of the known subgenera of *Holothuria*. Full annotated descriptions or (where the type material was not available) references to the literature are given for each species. An identification key is given to the species belonging to the subgenus *Mertensiothuria*.

Keywords

Echinodermata - *Holothuria* - *Mertensiothuria* - Holothuroidea - redescription - systematics

Introduction

The subgeneric name *Mertensiothuria* was one of the 13 genera Deichmann (1958) created to arrange the mass of species formerly gathered under the generic name *Holothuria* Linnaeus, 1767. Deichmann (1958) designated *Stichopus (Gymnochirota) leucospilota* Brandt, 1835, for which *Holothuria (Mertensiothuria) leucospilota* (Brandt, 1835) is now the valid name, as the type-species. Rowe (1969) reviewed the family Holothuriidae Ludwig, 1894 and suggested that the taxa created by Deichmann (1958) should be regarded as subgenera rather than genera. In this important taxonomic paper, Rowe (1969) recognised six species under *Mertensiothuria*: *Holothuria exilis* Koehler and Vaney, 1908, *H. fuscocinerea* Jaeger, 1833, *H. leucospilota* (Brandt, 1835), *H. papillifera* Heding *in* Mortensen, 1938, *H. pervicax* Selenka, 1867, and *H. platei* Ludwig, 1898. With doubt, Rowe (1969) also assigned *H. dietrichii* Ludwig, 1875 to the subgenus *Mertensiothuria*. Later on, after examination of type material, Rowe (*in* Rowe and Gates, 1995) considered *H. dietrichii* as a junior synonym of *Thyone papuensis* Théel, 1886. Hereafter, *H. dofleinii* Augustin, 1908 (Rowe, *in* Rowe and Richmond, 1997) and four new species - *H. (Mertensiothuria) albofusca* Cherbonnier, 1988 from Madagascar, *H. (M.) arenacava* Samyn, Massin and Muthiga, 2001 from Kenya, H. *(M.) artensis* Cherbonnier and Féral, 1984 from New Caledonia, *H. (M.) canaliculata* Tan Tiu, 1981 from the Philippines - have been added to the subgenus. Moreover, *H. fuscorubra* Théel, 1886 (Rowe, *in* Rowe and Gates, 1995; Rowe, *in* Rowe and Richmond, 1997; Samyn, Massin and Muthiga, 2001) was raised from synonymy with *H. (M.) leucospilota*. Of the species mentioned above, *H. dofleinii* (with *H. canaliculata* as junior synonym), *H. fuscocinerea* and *H. pervicax* have been transferred to the subgenus *Stauropora* (Rowe, *in* Rowe and Gates, 1995); the later transfer of *H. dofleinii* and *H. pervicax* back to *Mertensiothuria* by Rowe (*in* Rowe and Richmond, 1997) was made in error (Rowe, pers. comm.).

Thus, prior to this study, eight species were retained in this subgenus. Each of these is here discussed separately in terms of complete synonymy (or reference to complete synonymy), name-bearing type, status and location of the type, type locality, full taxonomic description, synoptic diagnosis, some notes on the ecology, and known geographical distribution. Their diagnostic characters are tabulated in an identification key. Since ossicles of the longitudinal muscles play an important role in the amended diagnosis of the subgenus *Mertensiothuria*, we have checked for their presence in different genera belonging to the family

Holothuriidae: *Actinopyga, Bohadschia, Holothuria, Pearsonothuria* and *Labidodemas*. Within the genus *Holothuria*, the following subgenera have been checked: *Acanthotrapeza, Cystipus, Halodeima, Holothuria, Lessonothuria, Mertensiothuria, Metriatyla, Microthele, Panningothuria, Platyperona, Roweiothuria, Semperothuria, Stauropora, Stichothuria, Theelothuria, Thymiosycia, Vaneyothuria* and four *Holothuria* species presently not allocated to a given subgenus.

Taxonomy

Family Holothuriidae Ludwig, 1894
Genus *Holothuria* Linnaeus, 1767
Subgenus *Mertensiothuria* Deichmann, 1958

Diagnosis [Type-species *Stichopus leucospilota* Brandt, 1835]

Size moderate to large (up to 400 mm long); body often cylindrical in shape, although some species display a flattened trivium. Often fugitive species, reflected by a relatively thin, smooth body wall, covered by numerous, more or less irregularly arranged, ventral tube feet, and by less numerous irregularly arranged dorsal papillae and tube feet. Calcareous ring stout with the radial plates almost twice as long as the interradial plates. Ossicles of the body wall consist of poorly developed tables and irregular buttons, perforated by three to six pairs of holes. Ventral tube feet with rods, buttons, and wide plates. Longitudinal muscles contain ossicles varying in shape from rods to C-shape ossicles, rings and small, smooth buttons.

Key to the subgenus *Mertensiothuria*

1. Ossicles absent in the tentacles 2
   Ossicles present in the tentacles 3
2. Buttons rather irregular with three to four pairs of holes; disc of tables round to quadrangular; spire low to moderate with one to two cross beams; crown mostly complete; perforated rods present in dorsal tube feet; often found in semi-cryptic locations ..... *H. leucospilota*
   Buttons rather regular with two to three pairs of holes; disc of tables generally quadrangular; spire low with one or no cross beam; crown often incomplete; perforated rods absent in dorsal tube feet; often found in exposed locations ..... *H. fuscorubra*
3. Tube feet buttons and plates longer then 100 µm ..... *H. albofusca*
   Tube feet buttons and plates less then 90 µm long 4
4. Dorsal papillae long to very long; rods of tentacles longer than 400 µm; rods of dorsal papillae with numerous lateral spines and holes 5
   Dorsal papillae short; rods of tentacles less then 250 µm long; rods of dorsal papillae nearly smooth with a few holes at the extremities ..... *H. hilla*
5. Some large tentacle rods with wide, ragged extremities ..... *H. aphanes*
   All large tentacle rods with narrow, spiny extremities ..... *H. papillifera*

Systematic account

Holothuria (Mertensiothuria) albofusca Cherbonnier, 1988
(figures 1A-E, 11A, 12A, B)

Holothuria (Mertensiothuria) albofusca Cherbonnier, 1988: 114, fig. 46; Samyn *et al.*, 2001: 104, 107.

Original name; *Holothuria (Mertensiothuria) albofusca* Cherbonnier, 1988.
Name bearing type; Holotype, MNHNP EcHh2753; Paratype MNHNP EcHh2770.

Type locality; Madagascar (Navetsy, Nosy Bé).
Current status; *Holothuria (Mertensiothuria) albofusca* Cherbonnier, 1988.
Material examined; Republic of South Africa (KwaZulu-Natal, Bhanga Nek), August 1999, 30 m depth, coll. Y. Samyn, MRAC 1664/RSAKZN/99145 (one specimen); Holotype MNHNP EcHh2753.
Description; The specimen from the Republic of South Africa measures, after preservation, 101 mm in length and 17 mm in width and is slightly flattened ventrally. Body colour in alcohol similar to colour in life: dorsal side uniform brown (figure 12A), ventral side uniform yellowish (figure 12B). Ventral tube feet sparsely distributed and more or less restricted to three to four rows in each ambulacral area; light, uniform chestnut brown in colouring. Dorsal and lateral tube feet restricted mostly to longitudinal rows in the ambulacral areas; very sparsely distributed; uniform, dark brown in colouring. Mouth ventral, surrounded by 20 tentacles only 5 mm in length, yellowish, with few, oval brown dots on the stalk near the mouth. Peristome with same colour and pattern as tentacles. Tentacle basis surrounded dorsally by a semicircle of papillae of the same colour as the dorsal tube feet. Anus terminal, unguarded, with narrow chestnut-brown ring. Longitudinal muscles bifid, well developed. Cuvierian tubules prominent. Two long Polian vesicles (one third of body length). Left respiratory tree reaching up to the calcareous ring. Body wall up to 2 mm thick, with black dots under the transversal and longitudinal muscles. Gonad whitish, finely tubular.
Ossicles: body wall with smooth, irregular buttons, 55-85 µm long, with three to four (occasionally five) pairs of holes (figure 1A, B); tables with disc 45-60 µm across, perforated by four central holes, 10-12 peripheral holes, spire with a single cross-beam and ending in a more or less spiny crown (figure 1A, B). Ventral tube feet (figure 1C) with large multi-perforated plates, from 85 x 45 µm up to 150 x 120 µm; irregular buttons, up to 120 µm long, with three to six pairs of holes; tables with shape and size similar to the ones in the body wall; end plate up to 460 µm across. Dorsal tube feet (figure 1D) with smooth, perforated rods, 100 to 200 µm long; buttons and tables similar in shape and size to the ones in the body wall; end plate up to 160 µm across. Tentacles (figure 1E) with smooth or slightly spiny and perforated rods from 15 to 260 µm long. Longitudinal muscles with rods and rings, 20-30 µm long (figure 11A).
Ecology; *Holothuria (Mertensiothuria) albofusca* is known to thrive in sea-grass beds or 'dans une dune hydraulique terrigène' (Cherbonnier, 1988). The specimen from KwaZulu-Natal was found at 30 m depth, on a sandy bottom.
Geographical distribution; Western Indian Ocean, for now restricted to Madagascar (Nosy Bé) and Republic of South Africa (KwaZulu-Natal).
Diagnosis; See Cherbonnier, 1988: 114, figure 46; present note.
Proposed status; *Holothuria (Mertensiothuria) albofusca* Cherbonnier, 1988.
Comments; Prior to the present study, *Holothuria (Mertensiothuria) albofusca* was only known from three specimens held in the Paris National Museum of Natural History (Cherbonnier, 1988). The *H. (M.) albofusca* found at Bhanga Nek, Republic of South Africa is now considered to be from the most southern edge of the distribution area of this species. The South African specimen differs slightly from the ones described by Cherbonnier (1988). First, our specimen has 20 tentacles with characteristic brown, oval dots on the stalk just under the crown, a character not described on the 18 tentacles of Cherbonnier's (1988) specimens. Second, our specimen bears two long (one third of body length) Polian vesicles, contrary to a small one for the holotype of *H. (M.) albofusca* (Cherbonnier, 1988). Re-examination of the holotype shows that the tube feet have three kinds of ossicles (large perforated plates, buttons and tables) instead of a single one (large perforated plates) as mentioned by Cherbonnier (1988). This fits with the specimen from South Africa. The tentacles hold rods, 15-250 µm long. The presence of small rods and rings in the longitudinal muscles is a new observation.

Holothuria (Mertensiothuria) aphanes Lampert, 1885
(figures 2A-J, 3A-H, 12C, D)

Holothuria aphanes Lampert, 1885: 242; Ludwig, 1889-92: 329; Oestergren, 1898: 235, figs 3, 4; Sluiter, 1901: 16; Panning, 1935c: 87 (cited as a synonym of *H. impatiens*); Panning, 1935d: 14; Cherbonnier, 1955: 149, pl. 31, fig. a-o.
Holothuria (Thymiosycia) aphanes: Rowe, 1969: 147; Clark and Rowe, 1971: 178; Price, 1982: 11; Cherbonnier, 1988: 93.

Original name; *Holothuria aphanes* Lampert, 1885.
Name bearing type; ? Stadliches Museum für Naturkunde, Stuttgart.
Type locality; Egypt (Kosseir, Red Sea).
Current status; *Holothuria (Thymiosycia) aphanes* Lampert, 1885.

Material examined; Red Sea (Aqaba), 09-xii-1985, 3m depth, coll. Féral and Labat, MNHNP EcHh7174 (one specimen).

Description; Specimen 270 mm long, 25 mm wide anteriorly and 40 mm at mid body. Colour in alcohol deep brown dorsally with yellowish tube feet (figure 12C); yellowish ventrally with white tube feet ending in a yellow sucker (figure 12D); tentacles greenish. General aspect very similar to *Holothuria (Thymiosycia) impatiens* (Forskål, 1775) and *Holothuria (Mertensiothuria) papillifera* Heding, *in* Mortensen, 1938. Dorsal tube feet up to 8 mm long, more or less aligned in five to six rows. Ventral tube feet conical, located along the ambulacral areas in three double rows. Tentacles short, 20. Mouth ventral, anus terminal. Specimen auto-eviscerated; only the right respiratory tree remains. Longitudinal muscles with two wide, thin folds. Calcareous ring massive (figure 2A); radial plates quadrangular with an anterior notch; interrradial plates as wide as the radial ones but low and with a strong anterior tooth (figure 2A). Tentacle ampullae short (11 mm long); four Polian vesicles: two medium (4-5 mm long) and two very small (1-2 mm long); one contorted stone canal going upwards and ending in an ovoid madreporic plate (figure 2B).

Ossicles: dorsal and ventral body wall with buttons and tables. Buttons numerous, most of them very regular with three pairs of holes (figure 2D); some with four to five pairs of holes (figure 2D). Buttons from the ventral body wall slightly smaller (58-75 µm long) than the ones from the dorsal body wall (67-90 µm long)(figure 2D, E). Tables (figure 2C) with a rounded disc with smooth margin, perforated by four large central and 10-12 peripheral holes; four pillars united by one cross-beam and ending in a very small crown of short, blunt spines. Tables 50-60 µm across and more or less 50 µm high.

In the dorsal tube feet same ossicles as in the dorsal body wall. Top of the dorsal tube feet with rods (figure 2J), 140-220 µm long, with a few lateral holes, which are located close to the small end plate (180-200 µm across). Ventral tube feet present tables, often with a reduced number of peripheral holes (figure 2H); buttons similar to the ones of the ventral body wall (figure 2G) but smaller and more irregular; and large perforated plates (figure 2F) located close to the end plate (350-400 µm across). Longitudinal muscles with rings (figure 3A), C-shape (figure 3B) and button like ossicles, 15-40 µm long (figure 3C). Tentacles with rods only: some narrow, straight or slightly curved, 40-520 µm long (figure 3D, E), some more massive with wide ragged extremities (figure 3F), and some small, 20-50 µm long, S-shape (figure 3G) and C-shape ossicles (figure 3H), located at the top of the tentacles.

Diagnosis; Present note.

Ecology; No information.

Geographical distribution; Egypt (Aqaba, Kosseir) and Djibouti (Gulf of Aden); ? Indonesia (Siau Island).

Proposed status; *Holothuria (Mertensiothuria) aphanes* Lampert, 1885.

Comments; *H. aphanes* was considered a synonym of *H. impatiens* by Oestergren (1898). Panning (1935c) agreed with this opinion. Rowe (1969) revived it from this synonymy and regarded *H. aphanes* as a valid species; we agree with this opinion as *H. aphanes* is distinct from *H. impatiens* in several ways. First, the tables of the body wall of *H. aphanes* have a very small and narrow crown of spines at the top of the pillars whereas *H. impatiens* has a larger crown. Second, the ventral tube feet of *H. aphanes* have large perforated plates typical of the subgenus *Mertensiothuria*, but not the rods with two central holes and enlarged extremities typical of *H. impatiens*. Moreover, the presence of very characteristic ossicles in the longitudinal muscles of *H. aphanes* (already mentioned by Oestergren, 1898) but not in those of *H. impatiens* is an additional character to separate the species. Because the ossicles located in the muscles of *H. aphanes* are so close to those typical of the subgenus *Mertensiothuria*, and because the tables of *H. aphanes* are very similar to those of *H. hilla* and *H. albofusca*, *H. aphanes* is moved from the subgenus *Thymiosycia* to the subgenus *Mertensiothuria*.

H. papillifera is morphologically very close to *H. aphanes*, both described from nearly the same type locality (Ghardaqa and Kosseir, respectively). Since the intraspecific variability of both species is not known, *H. papillifera* is possibly a junior synonym of *H. aphanes*. At present both species are separated by the shape of the tentacle rods and by the size of their ossicles: tables of the body wall *of H. papillifera* are larger than those of *H. aphanes* whereas the buttons of *H. papillifera* are smaller than those of *H. aphanes*, and this for specimens of similar size (220 and 270 mm long, respectively).

Holothuria aphanes seems restricted to the Red Sea, making Sluiter's (1901) record from Indonesia dubious.

Holothuria arenacava Samyn, Massin and Muthiga, 2001

Holothuria (Mertensiothuria) arenacava Samyn, Massin and Muthiga, 2001: 102, figs 1-3.

Original name; *Holothuria (Mertensiothuria) arenacava* Samyn, Massin and Muthiga, 2001.
Name bearing type; Holotype, IRSNB IG 28628/KMom/9897-6; Paratypes, IRSNB IG 28628/KMom/9897-2, IRSNB IG 28628/KMom/9897-3, IRSNB IG 28628/KMom/0002-2; MRAC 1662/KMom/9897-1, MRAC 1663/KMom/0002-1, MNHNP EcHh8070/KMom/9897-4, MNHNP EcHh8071/KMom/0002-3, SI E53097/KMom/0002-4, SI E53098/KMom/9897-5, NHM 2000.2414/KMom/9897-7, NHM 2000.2415/KMom/0002-5.
Type locality; Kenya (Mombasa).
Current status; *Holothuria (Mertensiothuria) arenacava* Samyn, Massin and Muthiga, 2001.
Material examined; See Samyn, Massin and Muthiga, 2001; Kenya (Mombasa), August-1998, 14 m depth, coll. Y. SAMYN, IRSNB IG 28268/KMom/9853 (one specimen).
Description; See Samyn *et al.*, 2001: 102, figures 1-3.
Diagnosis; See Samyn *et al.*, 2001: 102, figures 1-3.
Ecology; *Holothuria arenacava* lives in the sand at depths ranging from 9 to 12 m. The animal lies flat, just below the sand surface, only exposing part of its dorsal surface.
Geographical distribution; For now only known from the type locality (Mombasa).
Proposed status; *Holothuria arenacava* Samyn, Massin and Muthiga, 2001 (provisionally not referred to a known subgenus).
Comments; Recently, we described *H. arenacava* as a new holothurian species from Kenya, and placed it in the subgenus *Mertensiothuria* (Samyn *et al.*, 2001). Indeed, the morphology of the calcareous ring and the ossicles from the body wall, the dorsal and ventral tube feet agree very well with the diagnosis of *Mertensiothuria*. However, *H. arenacava,* having no ossicles in the longitudinal muscles, can no longer be retained in the subgenus *Mertensiothuria*. For now, we do not refer it to any of the known subgenera.

Holothuria artensis Cherbonnier and Féral, 1984

Holothuria (Mertensiothuria) artensis Cherbonnier and Féral, 1984: 678, fig. 9, pl. IB.

Original name; *Holothuria (Mertensiothuria) artensis* Cherbonnier and Féral, 1984.
Name bearing type; Holotype, MNHNP, microslides of ossicles without reference number.
Type locality; New Caledonia (Ile Art, Archipel des Belep).
Current status; *Holothuria (Mertensiothuria) artensis* Cherbonnier and Féral, 1984.
Material examined; None.
Description; See Cherbonnier and Féral, 1984: 678, fig. 9, pl. IB.
Diagnosis; See Cherbonnier and Féral, 1984: 678, fig. 9, pl. IB.
Ecology; Cherbonnier and Féral (1984) provide no description on the ecology of *H. (M.) artensis*, but state that the gut contains a mixture of brown mud and coarse sand.
Geographical distribution; Only known from the type locality (Ile Art).
Proposed status; *Holothuria artensis* Cherbonnier and Féral, 1984.
Comments; It is not possible to discuss the status of *Holothuria artensis* because the holotype (the single known specimen; MNHNP EcHh3117) is currently untraceable. The specimen labelled MNHNP EcHh3117 and supposedly illustrated as the holotype by Cherbonnier and Féral (1984: plate IB) is **not** *H. artensis* but a species of *Bohadschia*. Since the holotype of *Bohadschia maculisparsa* Cherbonnier and Féral, 1984 is labelled MNHNP EcHh3107 we thought that a switch of labels might have occurred between the specimens of those two species. However, the specimen MNHNP EcHh3107 is definitely the holotype of *B. maculisparsa*. A search needs to be carried out in the huge holothurian collections of the MNHNP to find the missing holotype of *H. artensis*. In the meantime, ossicle preparations of *H. artensis* held in the MNHNP and which accord with Cherbonnier and Féral's figures (1984: figure 9 A-M), should be considered as originating from the holotype. Presence or absence of ossicles in the muscles cannot be ascertained as no ossicle preparations of this tissue were made by Cherbonnier. Provisionally, the species will not be maintained in the subgenus *Mertensiothuria* or referred to another subgenus within the genus *Holothuria*.

Holothuria exilis Koehler and Vaney, 1908

Holothuria exilis Koehler and Vaney, 1908: 17, pl. 1, figs 11-15; Panning, 1935d: 8, fig. 112.
Holothuria (Mertensiothuria) exilis: Rowe, 1969: 149.
Holothuria (Stauropora) pervicax: Samyn *et al.*, 2001: 104.

Original name; *Holothuria exilis* Koehler and Vaney, 1908.
Name bearing type; Holotype, IM 5618/6.
Type locality; India (Andaman Isles).
Current status; *Holothuria exilis* Koehler and Vaney, 1908.
Material examined; None.
Description; See Koehler and Vaney, 1908: 17, pl. 1, figures 11-15.
Diagnosis; See Koehler and Vaney, 1908: 17, pl. 1, figures 11-15.
Ecology; Unknown.
Geographical distribution; Only known from the type locality.
Proposed status; *Holothuria exilis* Koehler and Vaney, 1908.
Comments; In their description, Koehler and Vaney (1908) already noted that *H. exilis* is very close to *H. pervicax* Selenka, 1867. In his review of the Holothuriidae Rowe (1969) noted that *H. exilis* 'will prove to be conspecific with *H. pervicax* Selenka, 1867' [sic]. After re-examination of the type material of *H. pervicax*, Rowe (*in* Rowe and Gates, 1995) placed *H. pervicax* in the subgenus *Stauropora*. The type material of *H. exilis* is held in the Museum of Calcutta, but is in poor condition (Haldar, pers. comm.) and can only be examined on site. Although there are some presumptions that *H. exilis* is a junior synonym of *H. pervicax* and may therefore be referable to *Stauropora*, we will provisionally not allocate *H. exilis* to a given subgenus. Only a careful, on-site study of the type material will allow the matter to be settled.

Holothuria (Mertensiothuria) fuscorubra Théel, 1886
(figures 4A-L, 11B, 12E)

Holothuria fusco-rubra Théel, 1886: 182, pl. 7, fig. 2; Sluiter, 1901: 15; H.L. Clark, 1902: 527; Fisher, 1907: 661, pl. 68, fig. 3, 3a-e; Pearson, 1913: 77, pl. 11, fig. 16a-d; Schmidt, 1925: 134; Cherbonnier, 1951: 32, pl. XI, figs 11-18, pl. XIII, figs 1-12, 14; Deichmann, 1958: 298 (cited as a synonym of *H. (M.) leucospilota*); Rowe, 1969: 164 (cited as a synonym of *H. (M.) leucospilota*).
Holothuria fuscorubra: H.L. Clark, 1925: 103.
Holothuria (Holothuria) curiosa var. *fusco-rubra*: Panning, 1931: 208, 209, fig. 1b; Panning, 1933: 132, figs 7-10; Panning, 1935d: 5, fig. 108; Panning, 1935e: 18, 26, fig. 19.
Holothuria (Mertensiothuria) fusco-rubra: Marsh *et al.*, 1993: 64.
Holothuria (Mertensiothuria) fuscorubra: Rowe and Gates, 1995: 293; Rowe and Richmond, 1997: 304; Samyn *et al.*, 2001: 104, 107.
Holothuria isuga Mitsukuri, 1912: 87, text fig. 18.
Holothuria pardalis?: Heding, 1940: 123, fig. 6.

Original name; *Holothuria fusco-rubra* Théel, 1886.
Name bearing type; Holotype, NHM 1886.10.2.173.
Type locality; Hawaiian Is (as Sandwich Isles).
Current status; *Holothuria (Mertensiothuria) fuscorubra* Théel, 1886
Material examined; Tuvalu (Ellice Islands, north and south ends Nukufetau), 1952, unknown depth, coll. Challenger, NHM 1952.5.7.1 (one specimen).
Description; Medium sized, voluminous species with length of live specimens up to 400 mm (Rowe and Richmond, 1997). Ventral and dorsal body colour in alcohol uniform chestnut brown (figure 12E). Body wall with many transversal folds after preservation. Ventral and dorsal tube feet sparsely distributed, more densely crowded in the ambulacral areas than in the interambulacral ones. Mouth ventral, surrounded by 20 (Fisher, 1907; Cherbonnier, 1951) green to chestnut brown tentacles. Anus terminal surrounded by a single ring of papillae. Very well developed bifid longitudinal muscles. Cuvierian tubules present according to Cherbonnier (1951), but not reported from the examined specimen.
Ossicles: in the ventral and dorsal body wall (figure 4A-D) tables and buttons. Tables of the ventral body wall (figure 4A) numerous, disc 40-60 µm across, perforated by four central holes and four to ten peripheral holes of various sizes; disc quadrangular or more rounded with a spiny rim; pillars short (single cross-beam) ending in a spiny crown with a large central opening; often crown incomplete. Tables of the dorsal body wall (figure 4C) similar in shape but with discs of 53-70 µm across. Buttons of ventral and

dorsal body wall (figure 4B, D) numerous, 40-60 µm long, with three pairs of regular holes; rim of button always smooth, slightly irregular. Ventral tube feet with plates, buttons and tables (figure 4E-G); plates (figure 4E) up to 110 µm long and 75 µm wide, with up to four rows of holes of different sizes; buttons (figure 4F) numerous, up to 75 µm long, with three to four (occasionaly five) pairs of holes, rim of button smooth, but highly irregular; tables similar in shape as the ones in the body wall, however, crown more often only partially formed. Dorsal tube feet with plates, buttons and tables (figure 4H-K); plates (figure 4K) up to 110 µm long and 75 µm wide, up to four rows of holes of different sizes; tables and buttons (figure 4H, J) similar to the ones in the ventral tube feet. Anal papillae (figure 4K) with rods, 40-155 µm long, sometimes perforated by one or several holes. Longitudinal muscles (figure 11B) with rings and rods from 25 to 42 µm long, rods often perforated by one or two holes.

Diagnosis; Present note.

Ecology; Not specified in the original description. The gut of NHM 1952.5.7.1 contains coarse sand. According to Rowe (*in* Rowe and Gates, 1995) it has a benthic, inshore, detritus- and deposit-feeding habit. Rowe (pers. comm.) notes that *H. (M.) fuscorubra* tends to live in exposed locations and that a mucus coating often envelops the animal.

Geographical distribution; Tropical Indo-west Pacific (Rowe and Gates, 1995).

Proposed status; *Holothuria (Mertensiothuria) fuscorubra* Théel, 1886.

Comments; Although Cherbonnier (1951) noted small rods with lengths of about 50 µm in the tentacles, these were not observed by us in the material examined. We agree with Rowe (*in* Rowe and Gates, 1995) in raising *H. (M.) fuscorubra* from synonymy of *H.(M.) leucospilota* since comparison of the ossicle assemblage of individuals of similar body length (77 mm length for *H. (M.) fuscorubra* versus 80 mm length for *H. (M.) leucospilota*) reveals several differences: (i) the disc of the tables found in the body wall of *H. (M.) leucospilota* is round to slightly quadrangular and moderatly spinose (figure 6B, G) while for *H. (M.) fuscorubra* it tends to be more quadrangular and more spinose (figure 4A, C); (ii) the spire of the tables found in the body wall of *H. (M.) leucospilota* (figure 6B, G) generally is better developed, with one or two cross-beams, as that of *H. (M.) fuscorubra*, with one or no cross-beam (figure 4A, C); (iii) the crown of the tables found in the body wall is generally narrow, but rather well developed in *H. (M.) leucospilota*, while for *H. (M.) fuscorubra* it is often reduced (as already observed by Théel, 1886; Sluiter, 1901; Pearson, 1913 and Cherbonnier, 1951), or when present wide; (iv) the number of peripheral holes in the table discs of *H. (M.) leucospilota* is greater (figure 6B, G) than that present in *H. (M.) fuscorubra*; (v) the buttons of *H. (M.) leucospilota* have three to four pairs of irregular holes and an irregular rim (figure 6D, H), while those of *H. (M.) fuscorubra* have two to three pairs of holes and have a more regular outline (figure 4B, D); (vi) the plates in the ventral tube feet of *H. (M.) leucospilota* are elongated to oval, perforated by numerous small holes (figure 6L), while in *H. (M.) fuscorubra* they are wider with large perforations (figure 4E); (vii) the dorsal tube feet of *H. (M.) leucospilota* have no plates *per se* but variously perforated rods (figure 6T), while those of *H. (M.) fuscorubra* show well-developed plates of various sizes (figure 4K) and no rods. In addition, Rowe (pers. comm.) observed that *H. (M.) fuscorubra* lives in more exposed locations whereas *H. (M.) leucospilota* is almost invariably found in semi-cryptic locations (see also figure 12G), and that *H. (M.) fuscorubra* tends to develop a mucus envelope around its body. It is, however, noteworthy that Rowe (pers. comm.) is uncertain whether these observations are associated with growth and changes in ecology with age, or whether they are true characteristics of the species.

Holothuria (Mertensiothuria) hilla Lesson, 1830
(figures 5A-E, 11C, 12F)

Holothuria (Thymiosycia) hilla: Massin, 1999: 55 (synonymy and records before 1999); Leonardo and Cowan, 1984: 38, text fig.;Liao, 1998: 80; Samyn, 2000: 15, tab. 1; Lane *et al.*, 2000: 489; Samyn and Vanden Berghe, 2000; Schoppe, 2000: 113, text fig.

Original name; *Holothuria hilla* Lesson, 1830.

Name bearing type; Holotype, MNHNP EcHh542

Type locality; Society Islands (Borabora).

Current status; *Holothuria (Thymiosycia) hilla* Lesson, 1830.

Material examined; Kenya (Kiunga Marine Reserve), April 1999, 2 m depth, coll. Y. Samyn, IRSNB IG 28628/KKiun/9942 (one specimen); Kenya (Kiunga Marine Reserve), April 1999, 3 m depth, coll. Y.

Samyn, IRSNB IG 28628/KKiun/9943 (three specimens); Kenya (Mombasa), August 1998, 5 m depth, coll. Y. Samyn, MRAC 1665/KMom/9857 (one specimen); Kenya (Kisite), August 1998, 6 m depth, coll. Y. Samyn, MRAC 1666/KKis/98102 (one specimen); Madagascar (Tuléar), October 1998, Grand Récif at low tide, coll. I. Eeckhaut *et al.*, IRSNB IG 29142 (one specimen).

Description; Medium sized species; preserved specimens from 42 x 14 mm to 135 x 20 mm, live specimens up to 30 % larger. Body cylindrical; colour in alcohol similar to the colour in life (figure 12F); bivium brown with yellow spots corresponding to large dorsal papillae; trivium beige-brown with white-yellow spots corresponding to large tube feet which are distributed in three to four rows in the ambulacral areas. Mouth ventral, surrounded by 20 very short, dirty-yellow tentacles. Anus terminal, not surrounded by papillae. Tentacle ampullae short. Single to two Polian vesicles. Single, curled stone canal ending in a spherical madreporic plate. Body wall, smooth, a few mm thick. Longitudinal muscles bifid, well developed. Cuvierian tubules numerous.

Ossicles: dorsal and ventral body wall with similar tables and buttons (figure 5A, B), though fewer tables are found in the ventral body wall. Tables (figure 5A, B) 52 -67 µm across; rim of disc smooth, circular to quadrangular in outline; disc perforated by four large central holes and nine to 13 smaller peripheral holes; spire consists of four short pillars, single cross-beam, small moderately spiny crown with a small central hole. Buttons (figure 5A, B) with rim smooth but irregular, 70-100 µm long and 25-45 µm wide, with three to six pairs of irregular holes. Tentacles with rods 45-145 µm long, extremities slightly spiny (figure 5C). Dorsal papillae with buttons, button-like plates and rods (figure 5D); buttons similar to the ones in the body wall, but up to 125 µm long; rods up to 200 µm long, often with distal or median perforations. Ventral tube feet characterized by large plates and buttons (figure 5E). Plates 110 -160 µm long and 55-75 µm wide, with two to five longitudinal rows of irregular holes; buttons similar to those of the body wall. Longitudinal muscles with rings, C-shape ossicles and irregular buttons with one pair of holes, 17-40 µm long (figure 11C).

Ecology; The fugitive *H. (M.) hilla* is found under coral debris and under live coral slabs. Massin (1999) notes that *H. (M.) hilla* often occupies the same habitat as *H. (Thymiosycia) impatiens* and *H. (M.) leucospilota*. Depth range 0-30 m (Rowe, *in* Rowe and Gates, 1995).

Geographical distribution; Rowe and Gates (1995) note a tropical Indo-west Pacific distribution. Massin's distribution map (1999: 56), however, shows subtropical records (Japan, Tasman Sea, South West Australia, Northern Red Sea, Persian Gulf).

Diagnosis; Present note.

Proposed status; *Holothuria (Mertensiothuria) hilla* Lesson, 1830.

Comments; Although *H. (M.) hilla* is a well-known, easily identifiable species from the Indo-west Pacific, its systematic position is changed from the subgenus *Thymiosycia* to *Mertensiothuria* in the present note. This taxonomic decision is justified by the presence of rings, C-shape ossicles and small irregular buttons in the longitudinal muscles (figure 11C), a diagnostic character restricted to the subgenus *Mertensiothuria*. This claim is further confirmed by investigation of the longitudinal muscles of *H. (Thymiosycia) impatiens* Forskål, 1775, the type species of *Thymiosycia*, and of *H. (T.) thomasi* Pawson and Caycedo, 1980, as these species do not have ossicles in their longitudinal muscles (see also table 1). The form and distribution of the other ossicles in the different body parts (especially the large plates in the tube feet) agrees better with the diagnosis of *Mertensiothuria* than that of *Thymiosycia* in which it was formerly placed. Moreover, the ossicles (tables and buttons) of *H. (M.) hilla* are close to those of *H. (M.) albofusca* (see Cherbonnier, 1988).

The ossicles found in the longitudinal muscles of *H. (T.) arenicola* Semper, 1868 (figure 11K) are pseudobuttons rather than the rods to C-shape ossicles, rings and small smooth buttons, here considered diagnostic for *Mertensiothuria*. For now, it suffices to note that further examination of the longitudinal muscles of other species currently classified under *Thymiosycia* most probably will bring additional insights into the systematics of the Holothuriidae.

Holothuria (Mertensiothuria) leucospilota (Brandt, 1835)
(figures 6A-P, 11D, 12G)

Holothuria (Mertensiothuria) leucospilota: Massin, 1999: 27 (synonymy and records before 1999); Conand, 1998: 1178, text fig.; Liao, 1998: 80; Lane *et al.*, 2000: 489; Samyn, 2000: 15, tab.1; Samyn and Vanden Berghe, 2000; Samyn *et al.*, 2001: 104, 107.

Original name; *Stichopus (Gymnochirota) leucospilota* Brandt, 1835.
Name bearing type; Status and whereabouts undetermined (Rowe and Gates, 1995); neotype, NHM 1968.7.3.105-6 (by present designation).
Type locality; Solomon Islands.
Current status; *Holothuria (Mertensiothuria) leucospilota* (Brandt, 1835).
Material examined - Solomon Islands, date of collection unknown, depth unknown, coll. H.G. Vevers, NHM 1968.7.3.105-6 (three specimens, including the neotype: 80 mm in length); Solomon Islands, date of collection unknown, depth unknown, coll. H.G. Vevers, NHM 1968.7.3.104 (two specimens); Kenya (Kanamai), July 1997, 2 m depth, coll. Y. Samyn, MRAC 1667/KKan9701 (one specimen); Tanzania (Pemba Island, Mesali), July 1998, 1-5 m depth, coll. Y. Samyn, MRAC 1668/TMes9954-55-56 (three specimens); Kenya (Kiunga Marine Reserve), April 1999, 1-3 m depth, coll. Y. Samyn, IRSNB IG28268/KKiun9932-33 (two specimens); Republic of South Africa (Durban, Vetch Peer), 3 m depth, coll. Y. Samyn, MRAC 1669/RSAKZN0016 (two specimens); Republic of South Africa (Sodwana Bay), 8 m depth, coll. Y. Samyn, MRAC 1670/RSAKZN00131 (one specimen).
Description; Intermediate to large cylindrical and elongate species, length in alcohol up to 300 mm. Colour in life: very dark brownish red to black (figure 12G); colour in alcohol brownish with the ventral side somewhat lighter. Ventral tube feet large, relatively short, with brown to grey sucking disc, distributed in the ambulacral areas, and scattering into the interambulacral areas. Bivium with soft, brown papillae in the ambulacral areas. Mouth ventral surrounded by 20 large, black tentacles. Anus terminal, unguarded. Calcareous ring stout with very large radial plates more then three times as wide as the pointed interradial plates. Single club-shaped Polian vesicle. Single stone canal. Cuvierian tubules very thin, abundant, readily ejected.
Ossicles: body wall with tables (figure 6A-C, F, G, J) and buttons (figure 6D, E, H, K). Tables (figure 6A-C, F, G, J) numerous; disc 40-70 µm across, perforated by four central holes and four to 12 peripheral holes of similar size; disc round to quadrangular in outline, rim smooth to spiny; pillars long (one to three cross-beams) in small specimens and short (single cross-beam) in longer specimens; spiny crown with a large central opening, crown narrow in small individuals and wider in longer individuals. Buttons (figure 6D, E, H, K) absent in the body wall of the smallest specimen, more numerous with increasing body length, 40-70 µm long, with two to four (occasionally five) pairs of irregular holes; rim of buttons smooth but irregular; generally larger in the dorsal (figure 6D, E) than in the ventral body wall (figure 6H, K). Dorsal tube feet with rods, buttons and tables (figure 6Q-V). Rods from 50-190 µm variously perforated; buttons and tables similar to those of the body wall. Ventral tube feet with large plates, buttons and tables (figure 6L-P). Plates 60-120 µm long, buttons and tables similar to those of the body wall. No ossicles in the tentacles. Longitudinal muscles with simple or perforated rods and rings (figure 11D).
Diagnosis; See Cherbonnier, 1988: 112, figure 45; present note.
Ecology; This species often displays a semi-cryptic behaviour, whereby it hides two thirds of its body under a coral block (see also figure 12G). Sometimes it can be found exposed on coral rubble or coarse sand. It is mainly an eulittoral species, never observed deeper than 8 m.
Geographical distribution; Tropical and subtropical Indo-Pacific Ocean (see also distribution map Massin, 1999: 29).
Proposed status; *Holothuria (Mertensiothuria) leucospilota* (Brandt, 1835).
Comments; As the status and whereabouts of the type material of *H. (M.) leucospilota* was undetermined until now (Rowe and Gates 1995) we find it opportune to create a neotype in the present note. We believe that such designation is obligatory to define the nominal taxon objectively. Unfortunately attempts to obtain specimens of *H. (M.) leucospilota* from the original type locality, i.e. Marshall Island (Ualan), were not succesful. However, a search through the huge collection of the Natural History Museum, London resulted in several specimens from the Solomon Islands. The largest specimen in NHM 1968.7.3.105-6 is here designated as the neotype. Following article 76.3 of the International Code of Zoological Nomenclature, the Solomon Islands are now considered the type locality of *H. (M.) leucospilota.*
It has been documented for several species in *Holothuria* that the size, appearance and prevalence of ossicle types changes with age (Cutress, 1996; Massin, 1999; Massin, Mercier and Hamel, 2000). Examination of several specimens of *H. (M.) leucospilota* of different lengths reveals that as the holothurian increases in size: (i) buttons become more abundant (the smallest specimen, 33 mm in length, has no buttons in the

body wall) and tables tend to disappear, (ii) the rim of the disc of the tables becomes more spiny (iii) the spire of the tables decreases in length and (iv) the crown becomes wider.
Up till now, Erwe (1913) and Panning (1931; 1935e; 1944) described pseudobuttons (as 'unvollkommene Schnallen' and 'falsche Schnallen') from the longitudinal muscles of *H. leucospilota*. Erwe (1913, fig. 13b) also mentioned rods in these muscles. It is remarkable that these important systematic accounts were ignored for so long.

Holothuria (Mertensiothuria) papillifera Heding *in* Mortensen, 1938
(figures 7A-M, 8A-J, 12H-K)

Holothuria papillifera Heding *in* Mortensen, 1938: 55, pl. XI, figs 1-3.
Holothuria (Mertensiothuria) papillifera: Rowe, 1969: 149; Clark and Rowe, 1971: 176; Price, 1982: 11; Samyn *et al.*, 2001: 104, 107.

Original name; *Holothuria papillifera* Heding *in* Mortensen, 1938.
Name bearing type; Syntype series ZM Karaf n°85, 25.10.1937; lectotype by present designation, ZM Karaf n°85/1 (largest specimen of the type serie), paralectotypes ZM Karaf n°85/2,3.
Type locality; Egypt (Ghardaqa).
Current status; *Holothuria (Mertensiothuria) papillifera* Heding *in* Mortensen, 1938.
Material examined; ZM Lectotype and two paralectotypes.
Description; Medium size to large specimens (lectotype 225 x 20-30 mm; paralectotypes 165 x 30-50 mm and 160 x 20-30 mm); body club-shaped, narrow anteriorly, much larger posteriorly. Colour of living specimen uniform greyish-brown. Colour in alcohol brown dorsally (figure 12H), beige to light brown ventrally (figure12K). Mouth ventral, anus terminal. Twenty short, yellowish tentacles surrounded by a circle of papillae. Dorsally, numerous, large conical papillae without alignment (figure 12J). Ventrally, tube feet densely crowded in the ambulacral as well as in the interambulacral areas (figure 12J).
Calcareous ring (figure 7A) typical of the subgenus *Mertensiothuria*; two long Polian vesicles (one-sixth of body length) and two very short (± 2% of body length), contorted stone canals (figure 7B); tentacle ampullae very short (2 to 2.5 % body length). Cuvierian tubules numerous, whitish, very thin.
Ossicles: in the body wall tables and buttons. Dorsally, tables few with disc 45-75 µm across, round to quadrangular (figure 7C), perforated by four central and nine to ten peripheral holes; four pillars united by one cross beam and ending in a small crown of spines; table height ± 50 µm. Buttons regular with three to five pairs of holes (three pairs being the most frequent), 55-85 µm long (figure 7D); a few irregular buttons (figure 7E). In the ventral body wall same types of ossicle, tables (figure 7F) being more numerous and buttons (figure 7G) smaller than dorsally. At the base of the dorsal papillae same ossicles as in the dorsal body wall. At the top of the papillae, tables (figure 7H), buttons (figure 7J) generally with three pairs of holes and rods, 200-230 µm long, with lateral processes (figure 7K). In the dorsal papillae of the paralectotype, 165 mm long, the buttons have generally four to five pairs of holes and lateral processes of the rods are perforated (figure 7L). In the tube feet buttons (figure 7M), irregular perforated plates (figure 8A), large, regular perforated plates, from 70 x 85 µm to 95 x120 µm (figure 8B), and small tables (figure 8C), 50-55 µm across. In the paralectoptype 165 mm long, ossicles of the tube feet somewhat larger, especially the regular and irregular perforated plates (figure 8D and 8E, respectively). In the tentacles rods, spiny at the extremities (figure 8F, G), 30-500 µm long. The smallest rods, 30-45 µm long, C-or S-shape (figure 8H). In the longitudinal muscles numerous regular to irregular C-shape and O-ring ossicles (figure 8J), 10-65 µm long.
Diagnosis; Present note.
Ecology; Unknown.
Geographical distribution; Up to now only recorded from the Red Sea (Ghardaqa, Abu Sadaf and Abu Fanadir).
Proposed status; *Holothuria (Mertensiothuria) papillifera* Heding *in* Mortensen, 1938.
Comments; The original description of *H. (M.) papillifera* given by Heding (*in* Mortensen, 1938) in a foot-note (without any illustration) is very succinct. Since the type series is available in the collection of the ZM, we take the opportunity to describe and illustrate the species, and to designate a lectotype and paralectotypes.
Heding (*in* Mortensen, 1938) suggested that *H. (M.) papillifera* is very close to *H. (M.) leucospilota*. Rowe (1969) suggested it is possibly conspecific with *H. (M.) leucospilota*. Examination of the type series

confirms that both species are close to each other. Moreover, presence or absence of Cuvierian tubules is no longer a distinctive character (Heding *in* Mortensen, 1938) since both species possess them. The main characters separating *H. (M.) papillifera* from *H. (M.) leucospilota* are the greyish brown colour of the body wall, the long, soft dorsal papillae, the tables with a smooth disc margin, a very narrow crown of spines at the top of the tables, the rods of the dorsal papillae with lateral perforated processes and the presence of ossicles in the tentacles.

Holothuria platei Ludwig, 1898
(figures 9A-G, 10A-F)

Holothuira platei Ludwig, 1898, 432, pl. 56, figs 1-14.
Holothuria Platei: Deichmann *et al.*, 1924: 381, text fig. 1.
Holothuria (Holothuria) platei: Panning, 1935d: 11, text fig. 118.
Mertensiothuria platei: Deichmann, 1958: 229, pl. 3, figs 10-12; Codoceo, 1976: 91; Rozbaczylo and Castilla, 1987: 185; Ramirez and Osorio, 2000: 7.
Holothuria (Mertensiothuria) platei: Rowe, 1969: 149; Samyn *et al.*, 2001: 104, 107.

Original name; *Holothuria platei* Ludwig, 1898.
Name bearing type; Holotype,?ZMH (according to Deichmann 1958:300); existence of type undetermined (Rowe, pers. comm.).
Type locality; Chile (Juan Fernández).
Current status; *Holothuria (Mertensiothuria) platei* Ludwig, 1898
Material examined; Chile (Juan Fernández Island, Bahia del Pade, stat. 39), 26 August 1908, coll. Svenska Mag. Exped. 1907-1908, ZM 30/5 (one specimen); Chile (Juan Fernández Island, Massatierra), April 1917, coll K. Bäckstrom, ZM 30/5-29 (one specimen); Chile (Juan Fernández Island), MNUHB 3932 (two specimens) and MNUHB 3933 (one specimen).
Description; Medium size to large specimens (100-230 mm long), cylindrical with mouth and anus terminal. Colour in life varying from brown to almost black dorsally and from light brown to pale greyish white ventrally; tentacles dark brown. Colour in alcohol nearly the same but somewhat faded. Tube feet densely crowded ventrally, present in ambulacral and interambulacral areas. They are wide, short with a terminal disc 0.8 to 1.2 mm across. Dorsally the tube feet are small, much less numerous than ventrally, without terminal disc and scattered without alignment. Mouth surrounded by 20 very large, bushy tentacles; anus surrounded by five groups of three to four papillae. Calcareous ring with radial plates at least twice as long as the interradial ones; interradial plates with a sharp central tooth, radial plates quadrangular with a central notch on the anterior margin (figure 9A). One very long Polian vesicle (one-quarter of body length) and very long tentacle ampullae (one-fifth to one-sixth of body length). One very short stone canal ending in an ovoid madreporic plate. Longitudinal muscles very large (10-11 mm wide), undivided. Right respiratory tree going up to the calcareous ring. Cuvierian tubules present, but not observed in all specimens.
Ossicles: in the body wall, tables and buttons. Tables very few, with only a single broken one observed in one specimen. Dorsal body wall with buttons (figure 9B); early buttons as rods (figure 9B). Ventral body wall with irregular (figure 9C) and regular (figure 9D) buttons. Buttons generally 100-120 µm long with six to seven pairs of holes. Ventral tube feet with perforated plates (figure 10A; from 70 x 140 µm up to 125 x 190 µm) located close to the end plate, regular (figure 9E) and irregular (figure 9F) buttons, some rod-like with perforated extremities (figure 9G); end plates ± 800 µm across. Dorsal tube feet with a small end plate (± 250 µm across), buttons (figure 10B) and rods (figure 10C); rods longer (up to 210 µm long) than in the ventral tube feet (up to 130 µm long). Few ossicles in the tentacles, in the shaft as well as in the extremities: spiny and knobbed rods, 125-400 µm long (figure 10D, E), sometimes with forked or tree like extremities (figure 10F). No ossicles observed in the longitudinal muscles.
Diagnosis; Present note.
Ecology; The species lives in the intertidal zone (Codoceo, 1976; Ramirez and Osorio, 2000). It is attached to rocks in the surf zone or concealed under large stones. When it lives in coarse sand bottoms it is covered with various debris (pebbles, pieces of algae, calcareous tube worms,...). The bushy tentacles are extended in the water column. However, intestinal content reveals mainly coarse detrital material (Codoceo, 1976). The species reaches high population densities: 20-25 specimens/m^2 (Ramirez and Osorio, 2000).
Geographical distribution; At present only known from the type locality (Juan Fernández Is.).
Proposed status; *Holothuria platei* Ludwig, 1898 (provisionally not referred to a known subgenus).

Comments; With its huge bushy tentacles, the very large perforated plates in the tube feet, the large regular buttons with up to six to seven pairs of holes and the absence of ossicles in the longitudinal muscles, *Holothuria platei* does not fit well within the genus *Mertensiothuria*. The bushy tentacles are very similar to the ones of *Holothuria (Semperothuria) cinerascens* (Brandt, 1835) (see Massin, 1996) and to those of several species belonging to the subgenus *Selenkothuria* (Deichmann, 1938, 1958; Caso, 1954). This is most probably a convergence indicating a suspension feeding role of the tentacles. The ossicles of *H. platei* are very different from *H. cinarescens* and from all the known species belonging to the subgenus *Selenkothuria*. As already noted by Deichmann (1958), *H. platei* occupies a rather isolated position. Reduced tables and large buttons seem to belong to *Mertensiothuria*. However, because of the absence of ossicles in the longitudinal muscles, because of the huge size of the perforated plates of the tube feet and because of the size and shape of the tentacle ossicles the species can no longer be maintained in the subgenus *Mertensiothuria*. Provisionally, it will not be referred to a known subgenus.

Presence of ossicles in the longitudinal muscles of Holothuriidae

Table 1 summarizes the presence/absence of ossicles in the longitudinal muscles of 49 species of Holothuriidae. Only 13 of the investigated species possess ossicles in the longitudinal muscles. These ossicles can be very similar to those of the body wall e.g. *H. (S.) pervicax* (figure 11E) and *H.(C.) rigida* Selenka, 1867 (figure 11F), or be represented by rods e.g. *Actinopyga* sp. (figure 11G), *Actinopyga echinites* (Jaeger, 1833) (figure 11f *in* Erwe, 1913) and *Pearsonothuria graeffei* (Semper, 1868) (figure 11J) or elongated grains e.g. *Actinopyga mauritiana* (Quoy and Gaimard, 1833) (figure 11H). Six species i.e. *H. (M.) albofusca*, *H. (M.) aphanes*, *H. (M.) fuscorubra*, *H. (M.) leucospilota*, *H. (M.) papillifera* and *H. (M.) hilla* have nearly the same kind of ossicle in the longitudinal muscles (figures 3A-C, 8J, 11 A-D). These are typically rods, C-shape and oblong ossicles together with small smooth buttons (one pair of holes). The presence of these types of ossicle is characteristic of the subgenus *Mertensiothuria*. Panning (1933: figure 11a-d) reported the presence of pseudobuttons in the longitudinal muscles of *H. (Thymiosycia) arenicola* Semper, 1868; an observation which is here confirmed.

Discussion

Pearson (1914) was the first who tried to arrange the mass of species under the name *Holothuria* Linnaeus, 1767 into manageable groups. As he was working on specimens mainly originating from the Indian Ocean, his analysis was bound to be incomplete for the distribution of *Holothuria* is (now) known to be quasi cosmopolitan (Tortonese, 1965; Rowe, 1969; Tommasi, 1969; Clark and Rowe, 1971; Maluf, 1988; Hendler *et al.*, 1995; Massin, 1999). It is not known to occur in Arctic, Antarctic and abyssal areas. Pearson (1914) recognised within the genus *Holothuria* five subgenera; *Bohadschia*, *Actinopyga*, *Argiodia*, *Halodeima* and *Thymiosycia*. When Panning (1929-35) reviewed the bulk of species under *Holothuria* he recognised *Actinopyga*, *Bohadschia*, *Holothuria*, and *Microthele* as subgenera, but retained the majority of the species under *Holothuria sensu stricto*. In 1944, Panning revised this viewpoint and elevated *Actinopyga*, *Bohadschia* and *Microthele* to generic rank. Deichmann (1958) later re-evaluated *Holothuria*, on the basis of new East Pacific material. As Deichmann did not recognise the genus *Holothuria sensu* Linnaeus, 1758, thereby disregarding the Official List of Generic Names in Zoology (see Rowe, 1969), she described 13 genera of which *Mertensiothuria* was one. Rowe (1969) revised the Holothuriidae and suggested that Deichmann's taxa should be regarded as subgenera rather than genera. Rowe (1969) further stated that: (i) *Brandtothuria* Deichmann, 1958 and *Paramicrothele* Caso, 1964 are junior synonyms of *Thymiosycia* Pearson, 1914; (ii) *Fossothuria* Deichmann, 1958 and *Jaegerothuria* Deichmann, 1958 are junior synonyms of *Cystipus* Haacke, 1880; (iii) *Ludwigothuria* Deichmann, 1958 is the junior synonym of *Halodeima* Pearson, 1914; (iv) *Microthele* sensu Deichmann, 1958 has nothing to do with *Microthele* Brandt, 1835 hence, *Microthele* sensu Deichmann, 1958 was replaced with a new *subgenus*, i.e. *Platyperona* Rowe, 1969. Rowe (1969) erected five other new subgenera to accomodate the remaining species. Later on, two other new subgenera, *Stichothuria* and *Roweothuria*, have been added by Cherbonnier (1980) and Thandar (1988), respectively.

Of the ten species described and discussed in the present review, we believe that only six *i.e. H. (M.) albofusca, H. (M.) aphanes, H. (M.) fuscorubra, H. (M.) hilla, H. (M.) leucospilota* and *H. (M.) papillifera.* can be retained with certainty within *Mertensiothuria*. Following examination of type and other relevant specimens, *H. (M.) arenacava* and *H. (M.) platei* are removed from *Mertensiothuria,* though not reassigned to another subgenus. Although, we have not been able to examine the type specimens of *H. (M.) artensis* and *H. (M.) exilis,* we believe that neither species can be included in the subgenus *Mertensiothuria*, but we are unable to allocate them to another subgenus of *Holothuria* at this time.

The presence of rods, small smooth buttons, C-shape, and O-ring ossicles in the longitudinal muscles was until now described for *H. papillifera* (Heding *in* Mortensen, 1938), *H. aphanes* (Oestergren, 1898), *H. hilla* (Erwe 1919) and *H. leucospilota* (Erwe, 1913; Panning, 1931; 1935e; 1944). However, as these are present in all the species retained with certainty within the subgenus *Mertensiothuria*, they are now considered to be a valid diagnostic character to identify *Mertensiothuria.*

Acknowledgments

It is with great pleasure that we thank Dr. F.W.E Rowe for sharing his extensive knowledge on the Holothuriidae with us and for critically reviewing the manuscript; Dr C. Nielsen (ZM), Copenhagen, for the loan of type material of *H. (M.) papillifera* and of specimens of *H. (M.) platei*; Dr. N. Ameziane Cominardi (MNHNP), Paris, for the loan of type material of *H. (M.) albofusca, H.(M.) artensis* (microslides of ossicles), *H. (S.) coronopertusa* and *Bohadschia maculisparsa* and of specimens of *H. (M.) aphanes*; Dr P. Bartsch and C. Lueter (MNUHB), Berlin for the loan of specimes of *H. (M.) platei,* Dr. S. Halsey (NHM), London, for the loan of non-type material of *H. (M.) fuscorubra* and for providing several specimens of *H. (M.) leucospilota*; Dr. C. Ahearn (SI) for the loan of type material of *H. (T.) thomasi*; Dr. D. VandenSpiegel (MRAC), Tervuren, for the loan of specimens of *H. (V.) suspecta* and for photographing *H. (M.) aphanes, H. (M.) fuscorubra* and *H. (M.) papillifera*. Financial support came from the Flemish Fund for Scientific Research (project number G.0086.96), and from the Flemish Community (project number BIL98/84).

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Appendix

Museum acronyms

IM	Indian Museum, Calcutta, India
IRSNB	Institut royal des Sciences naturelles de Belgique, Brussels, Belgium
MGH	Museum Goddefroyi, Hamburg, Germany
MNHNP	Muséum national d'Histoire naturelle, Paris, France
MNUHB	Museum für Naturkunde an der Universität Humboldt zu Berlin, Berlin, Germany
MRAC	Muséum royal d' Afrique centrale, Tervuren, Belgium
NHM	Natural History Museum, London, England
SI	Smithsonian Institution, Washington, USA
SMNS	Stadliches Museum fuer Naturkunde, Stuttgart, Germany
ZM	Zoological Museum, Copenhagen, Denmark
ZMH	Zoologisches Museum für Hamburg, Hamburg, Germany

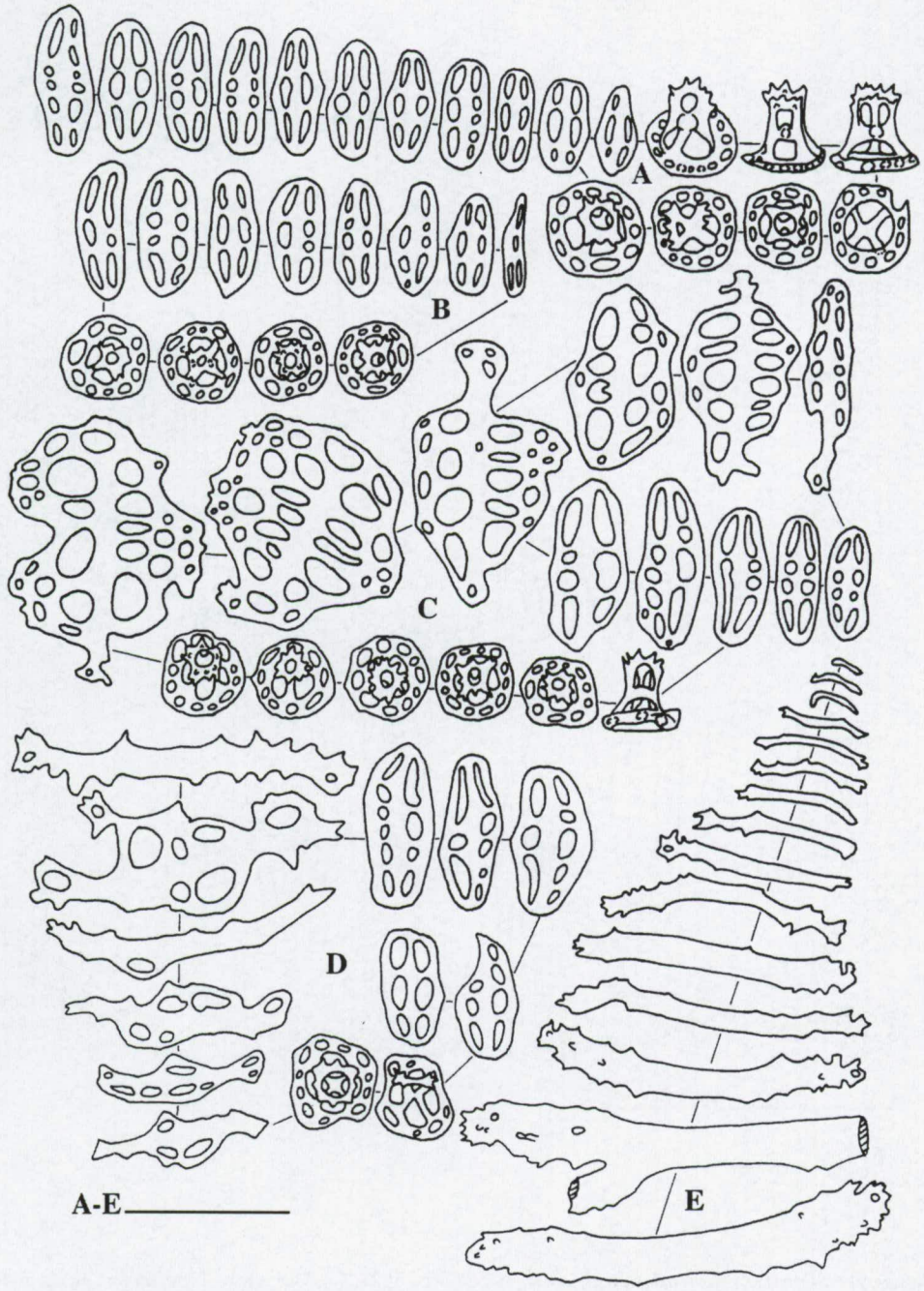


Figure 1. *Holothuria (Mertensiothuria) albofusca* Cherbonnier, 1988. L=101 mm. A. Buttons and tables of dorsal body wall; B. Buttons and tables of ventral body wall; C. Plates, buttons and tables of ventral tube feet; D. Perforated rods, tables and buttons of dorsal tube feet; E. Rods of tentacle. Scale bars A-E represent 100 μm.

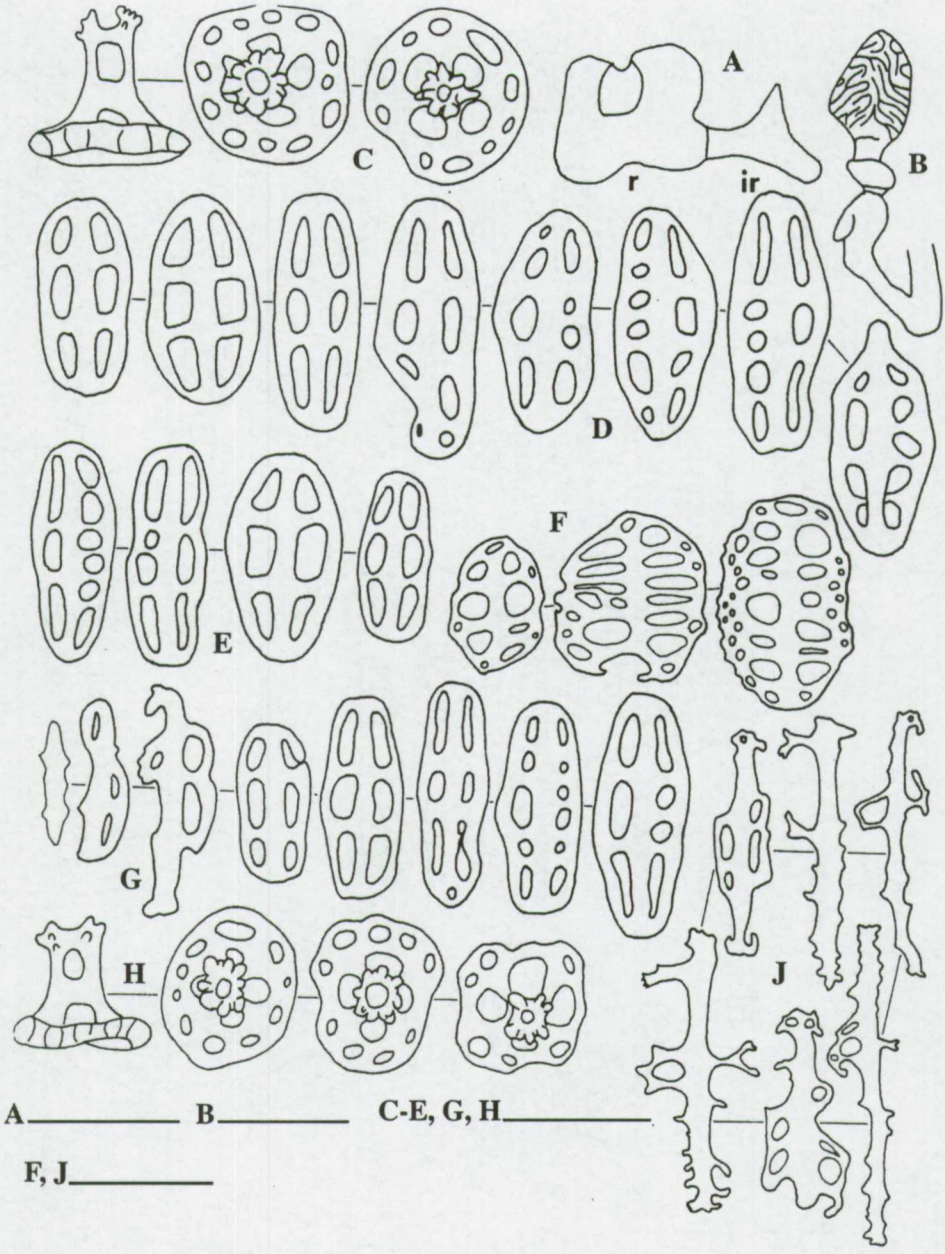
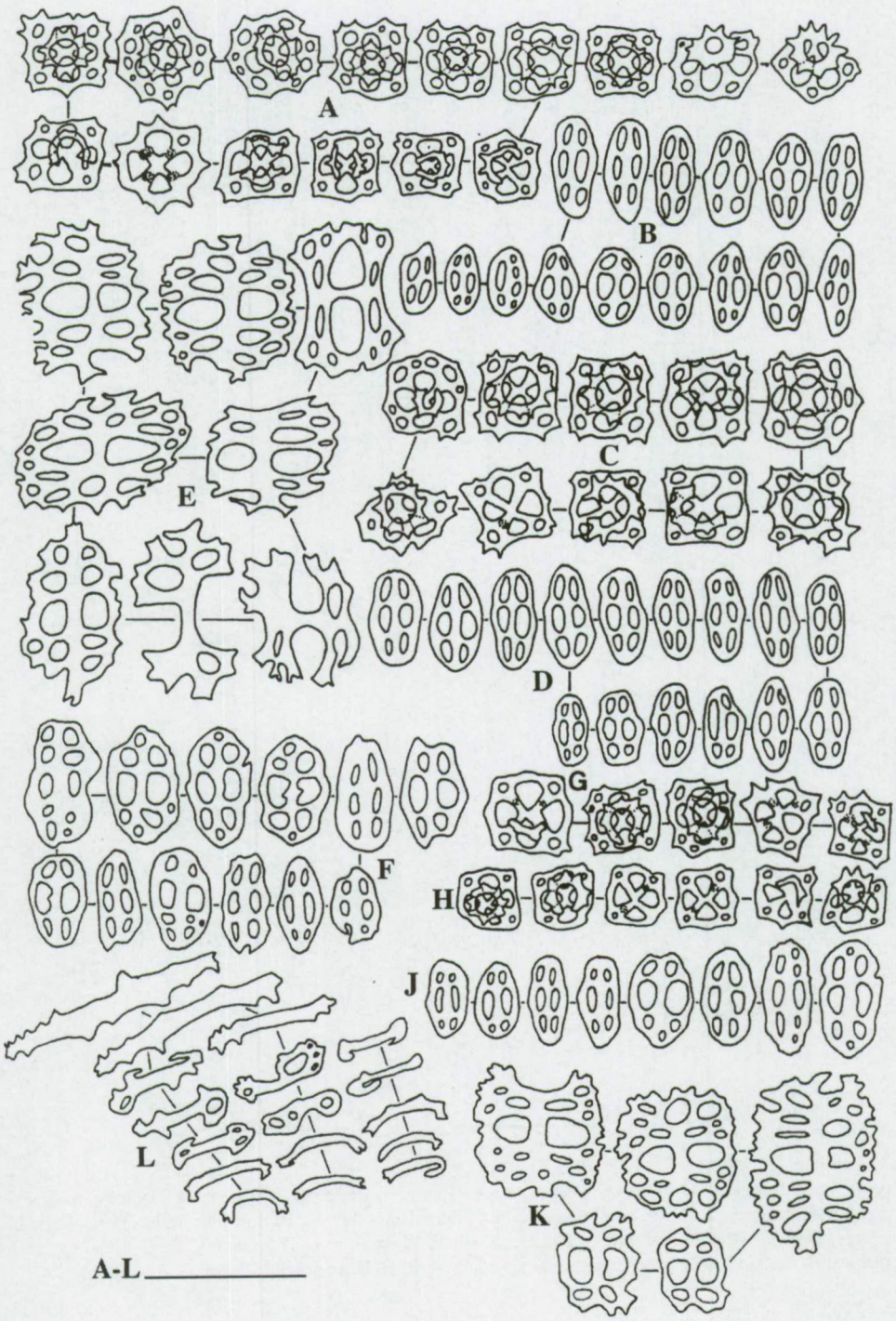


Figure 2. *Holothuria (Mertensiothuria) aphanes* Lampert, 1885. L=270 mm. A. Calcareous ring (r: radial plate; ir: interradial plate); B. Stone canal and madreporic plate; C. Tables of dorsal body wall; D. Buttons of dorsal body wall; E. Buttons of ventral body wall; F. Perforated plates of ventral tube feet; G. Buttons of ventral tube feet; H. Tables of ventral tube feet; J. Rods of dorsal tube feet. Scale bar A represents 5 mm; B = 2 mm; F, J. = 100 μm; C-E, G, H = 50 μm.



Figure 3. *Holothuria (Mertensiothuria) aphanes* Lampert, 1885. L=270 mm. A. Oblong ossicles of longitudinal muscles; B. C-shape ossicles of longitudinal muscles; C. Button like ossicles of longitudinal muscles; D & E. Straight, narrow rods of tentacles; F. Massive rods of tentacles; G. C-shape ossicles of tentacles; H. S-shape ossicles of tentacles. Scale bar A-C, E, G, H represents 50 μm; D, F = 100 μm.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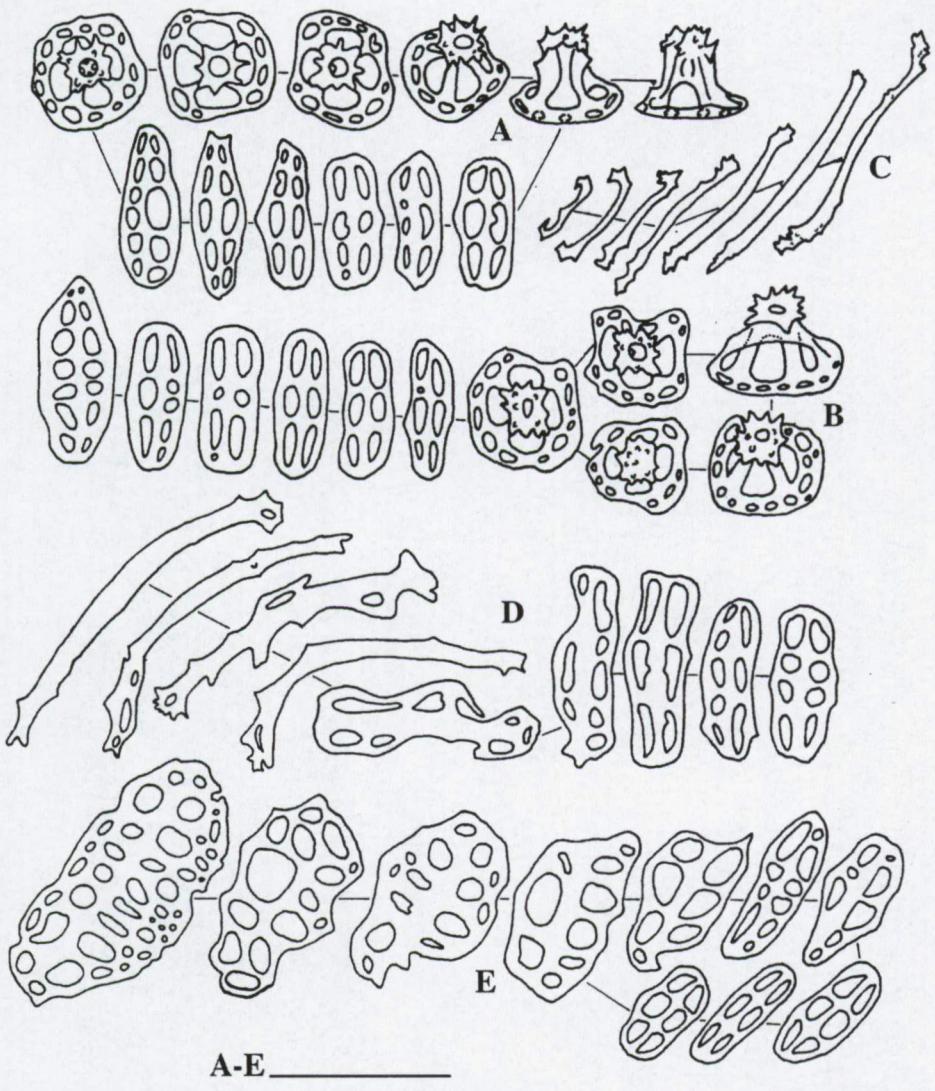


Figure 5. *Holothuria (Mertensiothuria) hilla* Lesson, 1830. L=113 mm. A. Tables and buttons of dorsal body wall; B. Tables and buttons of ventral body wall; C. Rods of tentacles; D. Buttons, button-like plates and rods of dorsal papillae; E. Plates and buttons of ventral tube feet. Scale bar A-E represents 100 μm.

Figure 4 (opposite page). *Holothuria (Mertensiothuria) fuscorubra* Théel, 1886. L=74 mm. A. Tables of ventral body wall; B. Buttons of ventral body wall; C. Tables of dorsal body wall; D. Buttons of dorsal body wall; E. Plates of ventral tube feet; F. Buttons of ventral tube feet; G. Tables of ventral tube feet; H. Tables of dorsal tube feet; J. Buttons of dorsal tube feet; K. Plates of dorsal tube feet; L. Rods of anal papillae. Scale bar A-L represents 100 μm.

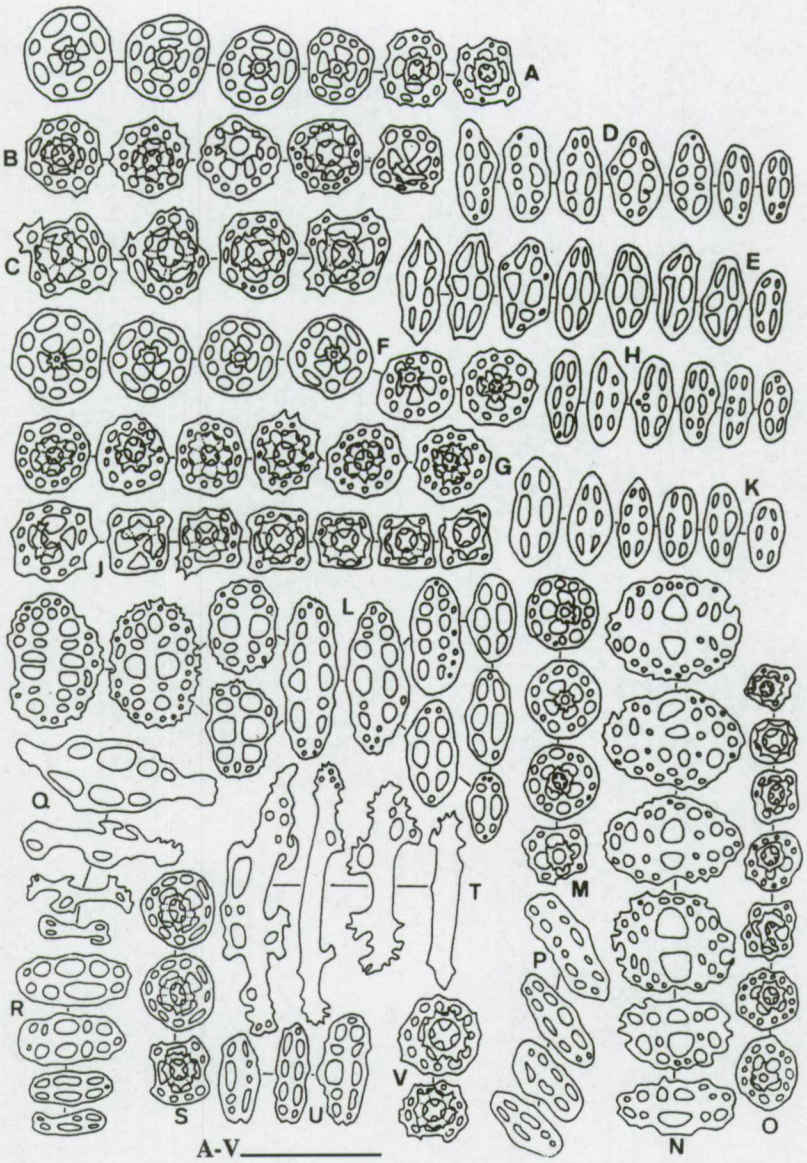


Figure 6. *Holothuria (Mertensiothuria) leucospilota* (Brandt, 1835). A. Tables of dorsal body wall (L=33 mm); B. Tables of dorsal body wall (L=80 mm); C. Tables of dorsal body wall (L=220 mm); D. Buttons of dorsal body wall (L=80 mm); E. Buttons of dorsal body wall (L=220 mm); F. Tables of ventral body wall (L=33 mm); G. Tables of ventral body wall (L=80 mm); H. Buttons of ventral body wall (L=80 mm); J. Tables of ventral body wall (L=220 mm); K Buttons of dorsal body wall (L=220 mm); L. Plates and buttons of ventral tube feet (L=33 mm); M. Tables of ventral tube feet (L=33 mm). N. Plates of ventral tube feet (L=80 mm); O. Tables of ventral tube feet (L=80 mm); P. Buttons of ventral tube feet (L=80 mm); Q. Rod-like plates of dorsal tube feet (L=33 mm); R. Buttons of dorsal tube feet (L=33 mm); S. Tables of dorsal tube feet (L=33 mm); T. Rods of dorsal tube feet (L=80 mm); U. Buttons of dorsal tube feet (L=80 mm); V. Tables of dorsal tube feet (L=80 mm). Scale bar A-V represents 100 µm. Illustrations B, D, G, H, N-P, T-V are based on the neotype.



Figure 7. *Holothuria (Mertensiothuria) papillifera* Heding *in* Mortensen, 1938. A. Calcareous ring (r: radial plate; ir: interradial plate) (L=225 mm); B. Stone canal (L=225 mm); C. Tables of dorsal body wall (L=225 mm); D. Regular buttons of dorsal body wall (L=225 mm); E. Irregular buttons of dorsal body wall (L=225 mm); F. Tables of ventral body wall (L=225 mm); G. Buttons of ventral body wall (L=225 mm); H. Tables of top of dorsal papillae (L=225 mm); J. Buttons of top of dorsal papillae (L=225 mm); K. Rods of top of dorsal papillae (L=225 mm); L. Rods of top of dorsal papillae (L=165 mm); M. Buttons of tube feet (L=225 mm). Scale bar A, B represents 5 mm; C-J, M = 50 μm; K, L = 100 μm.

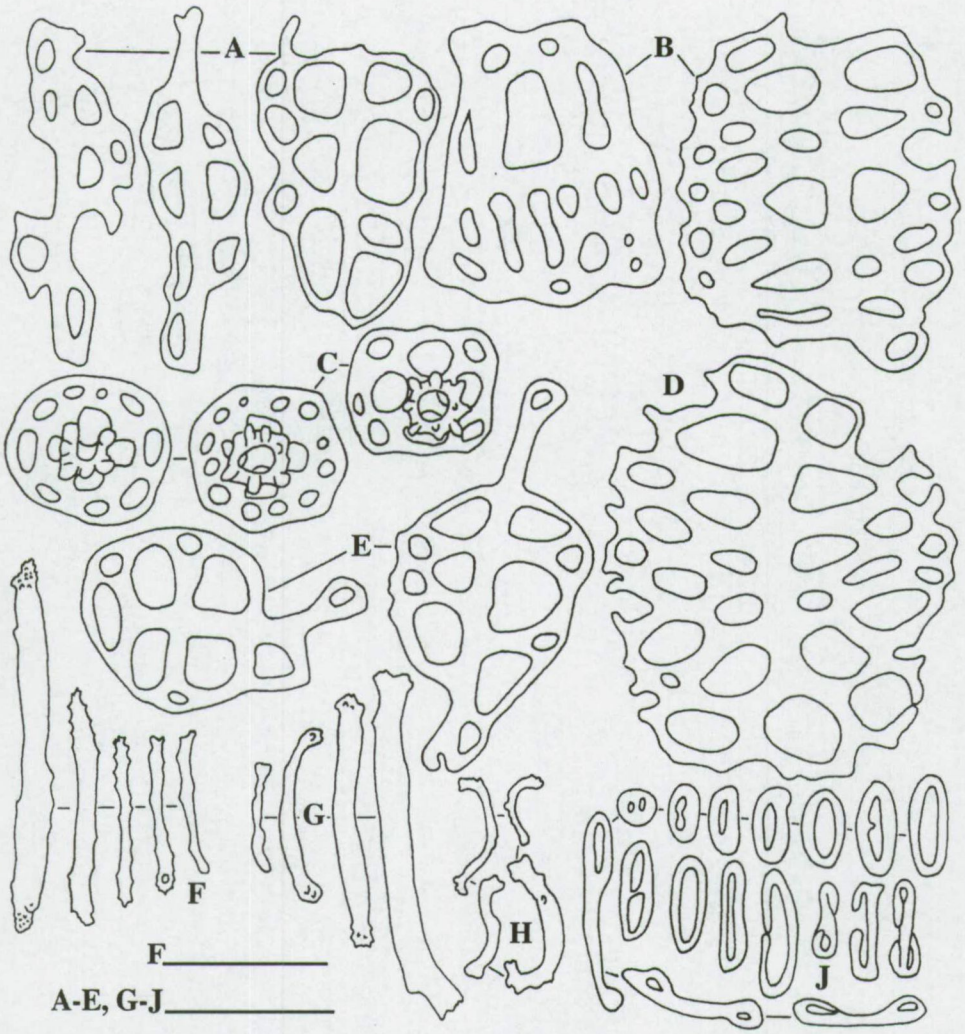
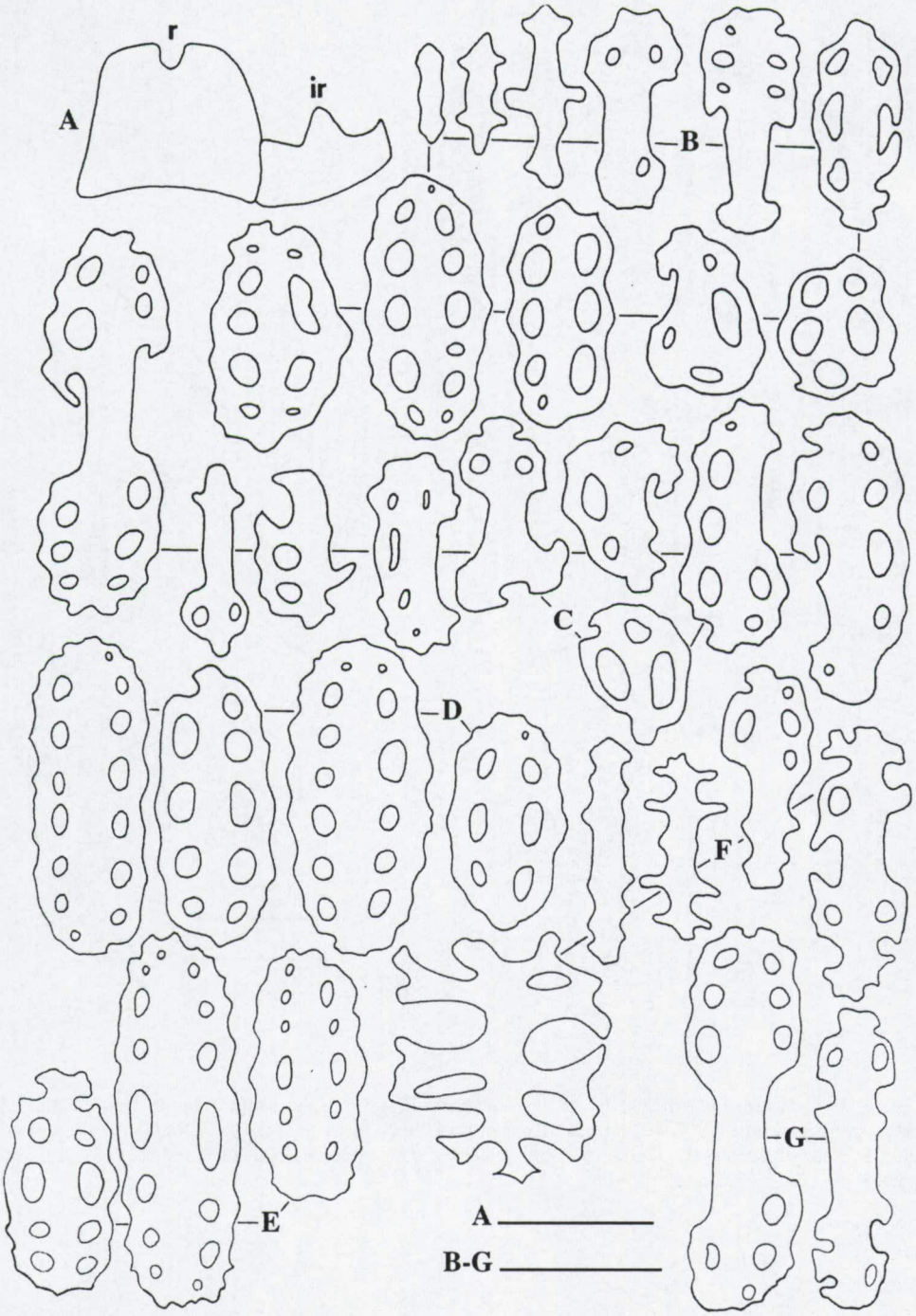


Figure 8. *Holothuria (Mertensiothuria) papillifera* Heding *in* Mortensen, 1938. A. Irregular perforated plates of ventral tube feet (L= 225 mm); B. Regular perforated plates of ventral tube feet (L= 225 mm); C. Tables of ventral tube feet (L= 225 mm); D. Regular perforated plate of ventral tube feet (L= 165 mm); E. Irregular perforated plates of ventral tube feet (L= 165 mm); F-H. Rods of tentacles (L= 225 mm); J. Ossicles of longitudinal muscles (L=225 mm). Scale bar F represents 200 μm; A-E, G-J = 50 μm.

Figure 9 (opposite page). *Holothuria platei* Ludwig, 1875. A. Calcareous ring (r: radial plate; ir: interradial plate) (L=120 mm); B. Buttons and rods of dorsal body wall (L=92 mm); C. Irregular buttons of ventral body wall (L=92 mm); D. Regular buttons of ventral body wall (L=92 mm); E. Regular buttons of ventral tube feet (L=92 mm); F. Irregular buttons of ventral tube feet (L=92 mm); G. Rod-like buttons of ventral tube feet (L=92 mm). Scale bar A represents 5 mm; B-G = 50 μm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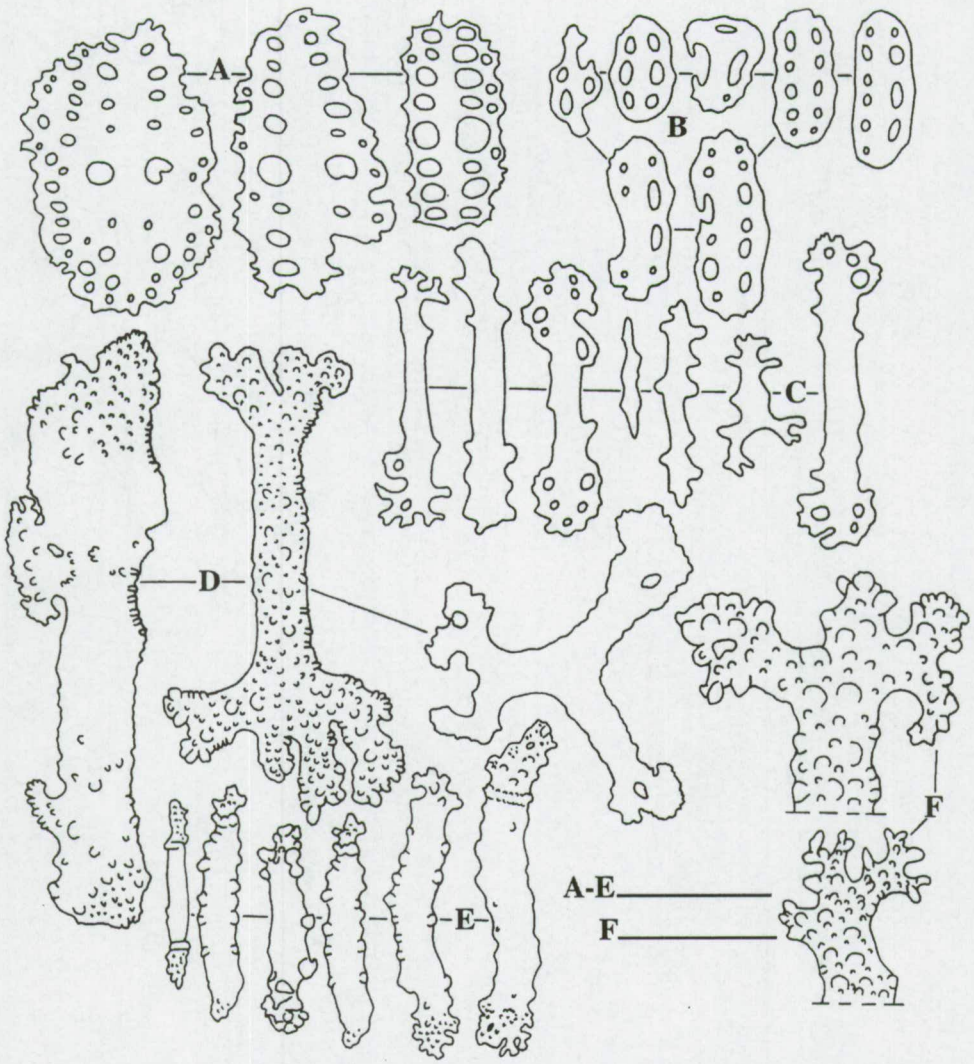

Figure 10. *Holothuria platei* Ludwig, 1875. A. Perforated plates of the ventral tube feet (L=92 mm); B. Buttons of dorsal tube feet (L=92 mm); C. Rods of dorsal tube feet (L=92 mm); D. Rods of tentacle (L=72 mm); E. Rods of tentacle (L=120 mm); F. Enlargment of the extremities of tentacle rods (L=72 mm). Scale bar A-E represents 100 μm; F = 50 μm.

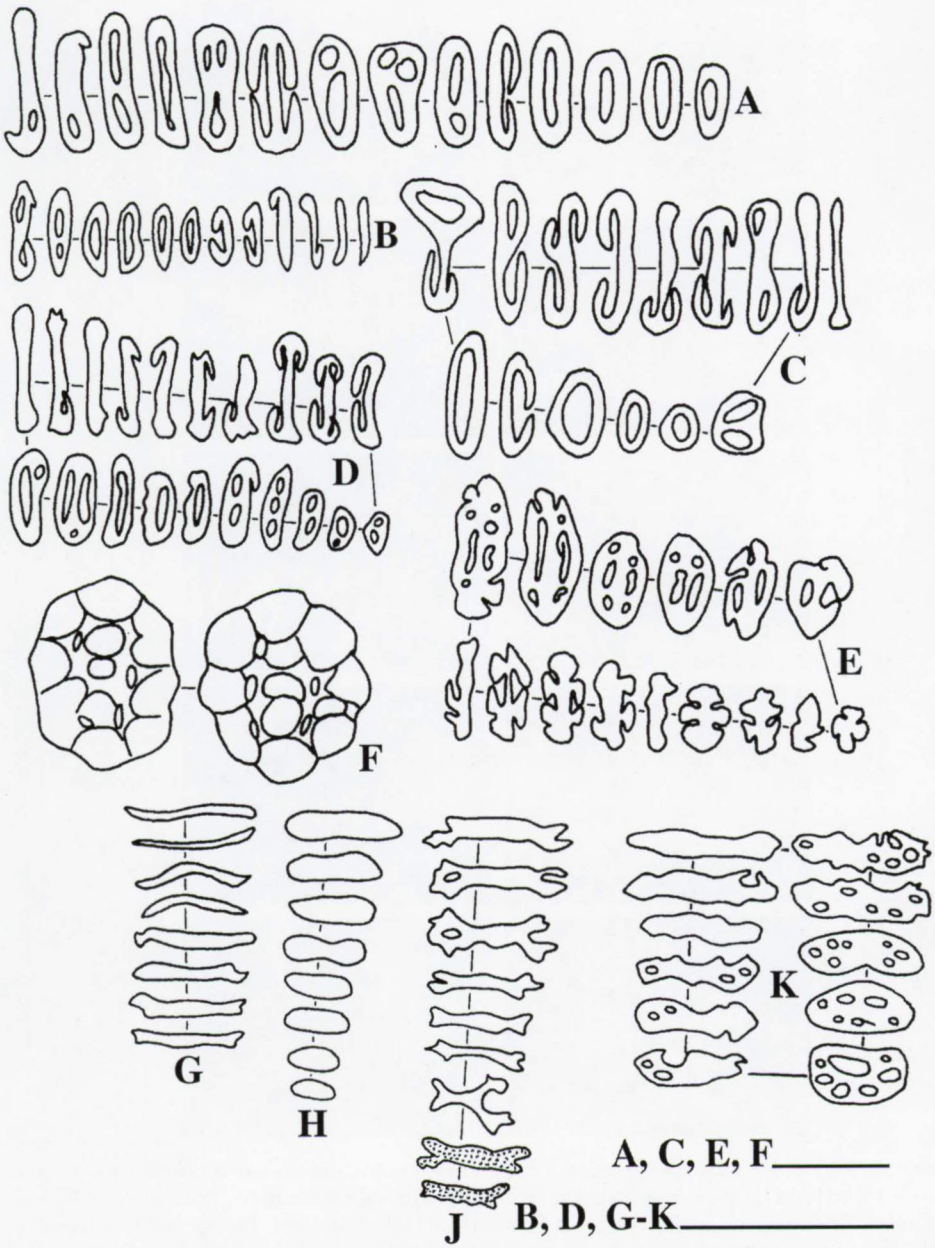

Figure 11. Ossicles of longitudinal muscles presented by different members of the family Holothuriidae. A. *H. (Mertensiothuria) albofusca* Cherbonnier, 1988; B. *H. (Mertensiothuria) fuscorubra* Théel, 1886; C. *H. (Mertensiothuria) hilla* Lesson, 1830; D. *H. (Mertensiothuria) leucospilota* (Brandt, 1835); E. *H. (Stauropora) pervicax* Selenka, 1867; F. *H. (Cystipus) rigida* (Selenka, 1867); G. *Actinopyga* sp.; H. *Actinopyga mauritiana* (Quoy & Gaimard, 1833); J. *Pearsonothuria graeffei* (Semper, 1868); K. *H. (T.) arenicola* Semper, 1868. Scale bar A, C, E, F represents 50 μm; B, D, G-K = 100 μm.

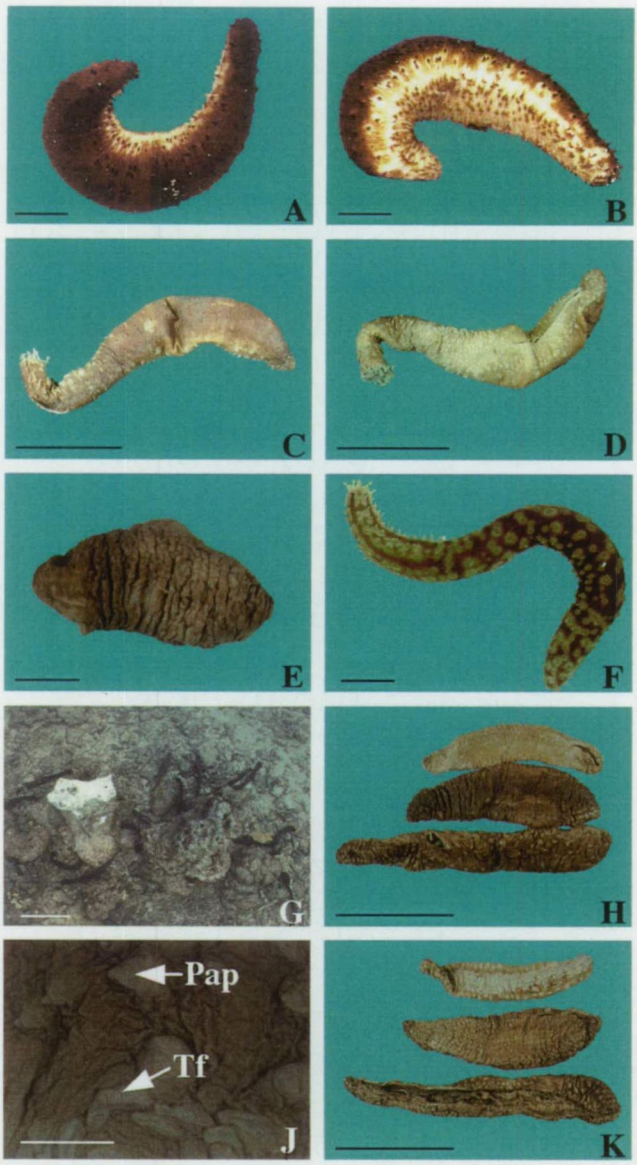

Figure 12. Plate of the valid species retained in the subgenus *Mertensiothuria*. A. Dorsal view of *H. (M.) albofusca* Cherbonnier, 1988 from Republic of South Africa (KwaZulu-Natal, Bhanga Nek); B. Ventral view of *H. (M.) albofusca* from Republic of South Africa (KwaZulu-Natal, Bhanga Nek); C. Dorsal view of *H. (M.) aphanes* Lampert, 1885 from Egypt; D. Ventral view of *H. (M.) aphanes* from Egypt; E. Dorsal view of *H. (M.) fuscorubra* (Théel, 1886) from Tuvalu; F. *Holothuria (Mertensiothuria) hilla* Lesson, 1830 from Indonesia; G. *Holothuria (Mertensiothuria) leucospilota* (Brandt, 1835) from Papua New Guinea; H. Dorsal view of *H. (M.) papillifera* Heding *in* Mortensen, 1938 from Egypt; J. Detail of papillae and tube feet of *H. (M.) papillifera* from Egypt; K. Ventral view of *H. (M.) papillifera* Heding *in* Mortensen, 1938 from Egypt Scale bar A, B, E represents 2 cm; C, D, H, K = 10 cm; F = 3 cm; G = 20 cm; J = 1 cm. (Photo's A, B: Samyn; photo's F, G: Massin; photo's C; D, E, H-K: VandenSpiegel).

GENUS	SUBGENUS	SPECIES OBSERVED	PRESENCE	TYPES OF OSSICLES
Actinopyga	-	*A. echinites*	yes	smooth rods
		A. mauritiana	yes	elongated grains
		A. sp.	yes	smooth rods
Bohadschia	-	*B. atra*	no	-
		B. marmorata	no	-
		B. subrubra	no	-
Gastrothuria	-	none	unknown	unknown
Holothuria	*Acanthotrapeza*	*H. (A.) coluber*	no	-
	Cystipus	*H. (C.) rigida*	yes	knobbed buttons
	Halodeima	*H. (H.) atra*	no	-
		H. (H.) edulis	no	-
	Holothuria	*H. (H.) tubulosa*	no	-
		H. (H.) mammata	no	-
	Irenothuria	none	unknown	unknown
	Lessonothuria	*H. (L.) pardalis*	no	-
	Mertensiothuria	*H. (M.) albofusca*	yes	buttons, oblong rings
		H. (M.) aphanes *	yes	rods, buttons, oblong rings
		H. (M.) fuscorubra	yes	rods, buttons, oblong rings
		H. (M.) hilla *	yes	rods, buttons, oblong rings
		H. (M.) leucospilota	yes	rods, buttons, oblong rings
		H. (M.) papillifera	yes	rods, buttons, oblong rings
	Metriatyla	*H. (M.) albiventer*	no	-
		H. (M.) scabra	no	-
	Microthele	*H. (M.) nobilis*	no	-
		H. (M.) fuscopunctata	no	-
	Panningothuria	*H. (P.) forskali*	no	-
	Paraholothuria	none	unknown	unknown
	Platyperona	*H. (P.) difficilis*	no	-
		H. (P.) excellens	no	-
	Roweiothuria	*H. (R.) poli*	no	-
		H. (R.) arguinensis	no	-
	Selenkothuria	none	unknown	unknown
	Semperothuria	*H. (S.) cinerascens*	no	-
		H. (S.) flavomaculata	no	-
	Stauropora	*H. (S.) fuscocinerea*	no	-
		H. (S.) pervicax	yes	knobbed buttons
		H. (S.) olivacea	no	-
		H. (S.) discrepans	no	-
		H. (S.) hawaiiensis	no	-
	Stichothuria	*H. (S.) coronopertusa*	no	-
	Theelothuria	*H. (T.) maculosa*	no	-
		H. (T.) turriscelsa	no	-
	Thymiosycia	*H. (T.) arenicola*	yes	rods, pseudobuttons
		H. (T.) impatiens	no	-
		H. (T.) thomasi	no	-
	Vaneyothuria	*H. (V.) suspecta*	no	-
	Undetermined	*H. arenacava*	no	-
		H. artensis	unknown	unknown
		H. exilis	unknown	unknown
		H. platei	no	-
Labidodemas	-	*L. pertinax*	no	-
		L. rugosum	no	-
Pearsonothuria	-	*P. graeffei*	yes	spiny rods

TABLE 1. Presence or absence of ossicles in the longitudinal muscles of members of the Holothuriidae family.

* Species formerly classified under the subgenus *Thymiosycia.*

The genus *Labidodemas* (Holothuroidea: Aspidochirotida) revisited with description of three new species and with re-positioning of *Holothuria (Irenothuria) maccullochi* Deichmann, 1958

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ABSTRACT

Prior to the present revision the taxon *Labidodemas* comprised *Labidodemas americanum*, *L. pertinax*, *L. rugosum* and *L. semperianum*. An up-to-date re-evaluation of the group proved that at least four additional species need to be assigned to it. Three of these are new to science: one has recently been discovered in the shallow-waters of KwaZulu-Natal, Republic of South Africa; one originates from Low Island, Australia and was erroneously identified as *L. semperianum* and one stems from South-West Sulawesi, again erroneously identified as *L. semperianum*. In addition, *Holothuria maccullochi*, classified in the monotypic subgenus *Irenothuria*, and *Holothuria proceraspina* are assigned to *Labidodemas*; the former as a valid species and the latter as a synonym of *L. semperianum*. Annotated taxonomic descriptions, distribution maps and an identification key are given.
The new observation that *L. americanum* holds Cuvierian tubules suggests that its rank remains at generic level rather than at family level as was recently proposed.

Keywords

Holothuroidea, Holothuriidae, Labidodematidae, *Labidodemas*, *Holothuria (Irenothuria) maccullochi*, new species, new combination, systematics.

Introduction

Currently, five nominal genera are commonly recognised in the family Holothuriidae: *Actinopyga* Bronn, 1860, *Bohadschia* Jaeger, 1833, *Holothuria* Linneaus, 1767, *Labidodemas* Selenka, 1867 and *Pearsonothuria* Levin, 1984. Although the monophyletic origin of these genera has never been fully tested, no author has, since Rowe's revision of the Holothuriidae (1969), doubted their validity. In fact, the rank that is accorded to these genera is accepted by all but one subsequent author. Indeed, James (1981) took Rowe's (1969: 126) phrase 'In truth I think *Labidodemas* may even prove to warrant separation at family level' quite literally and erected the family Labidodematidae. However, the diagnostic characters that James (1981) attributes to the Labidodematidae are not only not autapomorphic, but can also not be used to distinguish and separate the Labidodematidae from the Holothuriidae. We think it is imprudent, and at this stage even problematic, to treat *Labidodemas* as anything else but a valid genus in the Holothuriidae, until a phylogenetic analysis (be it a cladistic or an evolutionary one) indicates that the rank needs up-or downgrading.
The present paper re-describes the four species currently classified under *Labidodemas*, adds three species new to science, assigns *Holothuria (Irenothuria) maccullochi* Deichmann, 1958 to it and recognises *H. proceraspina* as a synonym of *L. semperianum*. All eight species are keyed and distribution maps are given.

Museum acronyms

ICML-UNAM, Institute of Marine Sciences and Limnology – National University of Mexico, Mexico; IRSNB, Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; NHM, Natural History Museum, London, UK; NHM LAC, Natural History Museum Los Angeles County, Los Angeles, USA; RmcA, Royal Museum for central Africa, Tervuren, Belgium; RMNH, Nationaal Natuurhistorisch Museum (Naturalis), Leiden, Netherlands; USNM, National Museum of Natural History, Washington D.C., USA; ZMG, Zoologisches Museum Göttingen, Göttingen, Germany; ZMH, Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Hamburg, Germanny.

Taxonomy

Family HOLOTHURIIDAE Ludwig, 1894
Genus *Labidodemas* Selenka, 1867

Emended Diagnosis (after Deichmann, 1938: 363 and Rowe, 1969: 132)

[Type-species *Labidodemas semperianum* Selenka, 1867; by monotypy]

Size medium to moderate (100 to 200 mm long); body has two distinct morphotypes: vermiform or more cylindrical; ventral tube feet mainly in ambulacral areas, in one to four rows (sometimes also spread into the interambulacral areas); dorsal papillae and tube feet in ambulacral and often also in interambulacral areas, or absent altogether; anal papillae present or absent. Species fugitive to fossorial, with thin body wall and 20 tentacles. Tentacle ampullae short (1/12 to 1/100 of body length). Calcareous ring with massive radial pieces and narrow ribbon-like interradial pieces. Body wall ossicles consist of variously developed tables, either with disc reduced and spire low, ending in a cluster of firm, often clavate, spines frequently longer than radius of table disc, or with disc well developed and with low to moderate spire ending in a cluster of firm spines or a wide, centrally perforated crown; buttons (when present), usually with rim smooth to slightly knobbed, some buttons spiny, often irregular and incompletely formed; in most cases minute, occasionally perforate, branching or curved rods also present. Tube feet ossicles similar to those of body wall, with in addition rounded perforated plates. Tentacles always with smooth to slightly spiny rods. Longitudinal, transversal and cloacal retractor muscles devoid of ossicles. Cuvierian tubules present or absent.

Key to the genus *Labidodemas*

1 Tables with large disc perforated at least by two circles of peripheral holes **2**
1' Tables with small disc without peripheral holes or with one circle of peripheral holes **3**
2 Cuvierian tubules absent, tables with high spire. . . . . ***L. maccullochi***
2' Cuvierian tubules present, tables with low spire or no spire . . . . . ***L. americanum***
3 Tables with low spire; table crown > table disc **4**
3' Tables with low or high spire; table crown < table disc **5**
4 Tables disc spiny, with very few or without peripheral holes, four central holes; table crown with four long acute spines, occasionally bifurcated distally; table crown > table disc; buttons absent in body wall . . . . . ***L. quadripartitum* sp. nov.**
4' Tables disc spiny, with one circle of peripheral holes, four to six central holes; table crown with four to five long spines most of them bifurcated distally; table crown > table disc; buttons present in dorsal body wall . . . . . ***L. semperianum***
4" Table disc smooth, with one circle of peripheral holes, five to eight central holes; table crown with five to eight huge spines deeply bifurcated distally; table crown >> table disc (up to twice the

diameter); buttons present in dorsal and ventral body wall ..... ***L. pseudosemperianum* sp. nov.**

5 Table spire high, buttons present and smooth ..... ***L. rugosum***

5' Table spire low, buttons present or absent; if present, spiny **6**

6 Table disc with peripheral holes; table crown very irregular, buttons present .. ***L. spineum* sp. nov**

6' Table disc nearly always without peripheral holes, buttons absent; table crown regular ..... ***L. pertinax***

Systematic account

Labidodemas americanum Deichmann, 1938
(figure 1A-F; map 1)

Labidodemas americanum Deichmann, 1938: 363, text-figures 1-5; Clark H.L., 1946: 421; Domantay, 1953: 136; Deichmann, 1958: 286, pl.1, figure 5; Caso, 1961: 373; Rowe, 1969: 133; James, 1981: 2; Maluf, 1988: 159; Maluf, 1991: 360; Nepote, 1998: 25.

Labidodemas americanum?; Brusca and Thomson, 1975: 46.

Original name - *Labidodemas americanum* Deichmann, 1938.

Name-bearing type - MCZ Number not given.

Type locality - Jasper Island (Costa Rica).

Material examined - Mexico (Colima, La Peruena, Morro Pulpito), 10 January 1995, coll. F. Solis-Marin, USNM E51623 (one specimen); Mexico (Nayarit, Punta de Mita, Corral del Mangle), May 1995, 3 m depth, coll. C. Vizcarra, USNM E51619 (one specimen); Galapagos Islands (South Seymour Island), 19 January 1938, shore, NHMLAC 452-1 (two specimens); Costa Rica (Coco Islands, Chatham Bay), 14 January 1938, shore, NHMLAC 452-2 (two specimens); Galapagos Islands (Tower Island, Darwin Bay), 16 January 1938, shore, NHMLAC 452-3 (one specimen); Galapagos Islands (Osborn Island), 9 December 1934, intertidal, NHMLAC 452-5 (two specimens); Mexico (Gulf of California, Espiritu Santo Island), 23 February 1936, shore, NHMLAC 452-6, (three specimens); Mexico (Gulf of California, Calerita), 5 February 1997, coll. C. Sanchez Oritz and F. Solis-Marin, intertidal pool, ICML-UNAM 5.42.7 (three specimens); Mexico (Bahia de Banderas, Marieta Islands, Redonda Island,), 22 March 1996, coll. F. Solis-Marin and C. Nepote, 15 m, ICML-UNAM 5.42.1 (one specimen); Mexico (Revillagigedo's Archipelago, Isla Socorro, Colima), 16 February 1992, ICML-UNAM 5.42.5 (two specimens); Galapagos Islands (Osborn Island, Hood Island), 19 December 1934, coll. F.C. Ziesenhenne, intertidal pool, ICML-UNAM 5.42.0 (one specimen); Mexico (Nayarit, Punta de Mita), 20 May 1995, unknown depth, coll. Y. Rodriguez, ICML-UNAM 5.42.3 (one specimen).

Diagnosis - See Deichmann, 1938: 363, text-figures 1-5; present revision.

Description - Colour of living specimens varies from green and almost transparent to yellowish. Colour in alcohol white to beige with yellow-brown tube feet to brown with brown-black tube feet. Specimens small (from 21 x 10 to 80 x 14-19 mm). Body cylindrical, slightly tapering anteriorly. Mouth and anus terminal, with large opening (nearly as wide as body). Mouth generally surrounded by 20 short tentacles. Ventrally, tube feet restricted to ambulacral areas; a zigzag pattern in lateral ambulacra, in double row mid-ventrally. Dorsally, tube feet few, scattered over the whole dorsal side, more or less aligned in four to five rows. Anal papillae absent. Calcareous ring (figure 1A) ribbon-like with large quadrangular radial plates and small, narrow, triangular, interradial ones, anteriorly pointed. Radial plates with a small central anterior notch (attachment of the longitudinal muscle) surrounded by two small concavities (figure 1A) and a large posterior concavity. Polian vesicle single, one-tenth of body length; stone canal single, almost straight, anteriorly directed, ending in an ovoid madreporic plate close to calcareous ring. Tentacle ampullae very short (± 3% of body length). Tube feet ampullae visible on inner side of body wall. Gonad not observed. Cuvierian tubules brown to greenish, numerous, short and thick. Intestine contains coarse coral pieces up to 4.9 x 4.6 x 2 mm.

Ossicles: Body wall and tube feet with tables only. Tables often reduced to disc (figure 1B), perforated by four large central holes and one (rarely two) circle(s) of smaller peripheral holes. Tables of body wall 50-75

µm across; rim of disc slightly knobbed or spiny (figure 1B), diameter of crown of spines 20-25% of disc diameter. Tables of tube feet derived from primary crosses (figure 1C, D), smaller (40-65 µm across) than those of body wall; disc often without peripheral holes. End plate of tube feet smaller dorsally (300-375 µm across) than ventrally (400-450 µm across). Tentacles hold short rods, 20-100 µm long, with central node (figure 1E); longer, branched and/or spiny rods in smaller specimens (figure 1F).

Ecology - Observation of *Labidodemas americanum* in their natural habitat in Bahia de La Paz (Gulf of California) and in Jalisco (Mexico) (F. Solis Marin, personal communication), shows that the species lives amongst pebbles and small rocks in shallow tidal pools or in waters up to 17 m depth. In the tidal pools of Bahia de La Paz, fissiparous behaviour was observed in one relatively long individual (Solis-Marin, personal communication). Such behaviour has been reported for other members of the Holothuriidae (Emson and Wilkie, 1980; Jaquemet *et al.*, 1999), but hitherto not in *Labidodemas*. It is interesting to note that we, as Deichmann (1938: 364), failed to locate the gonad in all the specimens studied.

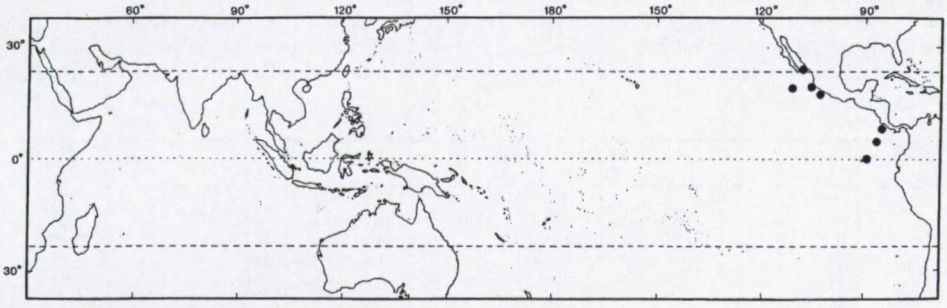
Geographical distribution (see map 1) - Costa Rica (Jasper Island, Cocos Islands), Galapagos Islands (Osborn Island, Tower Island, South Seymour Island).

New geographical records made in present work: Mexico (Calerita, Bahia de Banderas, Marieta Islands, Redonda Island, Revillagigedo's Archipelago, Isla Socorro, Colima, Jalisco, La Peruena, Punta Mita, Pulmo Reef, Espiritu Santo Island, Bahia de La Paz).

Comments - Deichmann (1938) described two contracted specimens from Jasper Island (Costa Rica) as *L. americanum*. By doing so, she was the first to break the monotypy of the genus, as previous new species in *Labidodemas* all proved to be junior synonyms of *L. semperianum* or some *Holothuria* species (Sluiter, 1901; H.L. Clark, 1921; Panning, 1935a, b). H.L. Clark (1946) expressed some doubt about the generic status of Deichmann's species, but refrained from assigning it to another genus: 'Deichmann's *Labidodemas americanum* (1938) from the west coast of Costa Rica lacks the very characteristic tables of *semperianum*, and I am sceptical as to the two being congeneric' (H.L. Clark, 1946: footnote on page 421). Later, in 1958, Deichmann had the opportunity to examine 13 additional specimens that were collected in the Galapagos Islands, Cocos Island and Espiritu Santo Island by the Hancock expeditions. She identified these specimens again as *L. americanum*, but unfortunately illustrated only a single ossicle and also did not address H.L. Clark's (1946) reservations.

Examination of several specimens from the NHMLAC (Hancock material) and the USNM leaves no doubt that *L. americanum* is a valid species. It can easily be distinguished from the other *Labidodemas spp.*, by the presence of Cuvierian tubules, by the absence of rods and buttons in the body wall and by the reduced table spire. The number of ossicles present in the body wall is highly variable from one specimen to another.

The small size of the tentacles and the ampullae, and the very coarse intestinal content show that *L. americanum* is clearly a non-selective feeder, only able to push very rough material into the mouth. Ingestion and ejection of such rough material is facilitated respectively by the wide opening of mouth and anus.



Map 1. Distribution of *Labidodemas americanum* Deichmann, 1938.

Labidodemas maccullochi (Deichmann, 1958)
(figures 2A-L, 3A-V; map 2)

Irenothuria maccullochi Deichmann, 1958: 306, pl. 4 figures 1-4; Caso, 1965:268, text fig 16, pls IV(1-4), V (1-2).
Holothuria (Irenothuria) maccullochi; Rowe, 1969: 142, figure 11a, b.; Maluf, 1988: 157.
Holothuria maccullochi; Hickman, 1998: 55 (colour picture), 65.

Original name - *Irenothuria maccullochi* Deichmann, 1958.

Name-bearing type - Holotype NHMLAC 232-34; paratype NHMLAC 256-34b.

Type locality - Puerto Utria (Columbia).

Current status - *Labidodemas maccullochi* (Deichmann, 1958).

Material examined - Columbia (Puerto Utria, Velero III station 232-34: 5°59'10''N, 77°20'20''W), 14 February 1934, shore, rock, coll. Hancock expedition, NHMLAC 232-34 (holotype); Costa Rica (South of Mala pt., Port Culebra, Velero III station 256.34, 10°36'30''N, 85°42'15''W), 24 February 1934, coll. Hancock expedition, NHMLAC 256-34b (paratype); Columbia (Octavia Bay, Velero III station 433.35: 6°49'50''N, 77°41'35''W), 27 January 1935, shore, coll. Hancock expedition, NHMLAC 433-35; Panama (Bahia Honda, Velero III station 861.38, 7°44'25''N, 81°32'45''W), 1 Mach 1938, shore, rock, coll. Hancock expedition, NHMLAC 861-38; Mexico (Bahia California, 7°44'25''N, 81°32'45''W), 16 August 1996, rock, sand, 15.9 m depth, coll. Ramirez-Murillo, ICML-UNAM 5.42.8 (two specimens identified as *Labidodemas americanum*).

Diagnosis - See Deichmann, 1958: 306; present revision.

Description - Medium to large species, live specimens up to 260 mm long (Hickman, 1998); preserved specimens from 41 to 220 mm long. Body cylindrical, but ventral side somewhat flattened. Body colour in life 'deep, brick red' (Hickman, 1998: 55), or as 'an unusually dark coloured *Brandtothuria impatiens'* (Deichmann, 1958: 307). Live specimens characterised by ventral tube feet that are 'yellow and arranged in irregular double rows', and dorsal papillae that are 'scattered, small and papilliform' (Hickman, 1998: 55). Preserved specimens with ventral tube feet arranged in somewhat irregular double rows in each ambulacrum and with dorsal papillae fewer in number and scattered over the bivium. Skin thin (1-3 mm thick), gritty to the touch. Mouth terminal surrounded by 20 tentacles; occasionally two of these positioned closer to the mouth than the rest. Anus terminal, very large, unguarded by anal papillae. Inner body wall with distinct dark-brown spots. Cuvierian tubules absent. Tentacle ampullae short (1/20 of body length in the 220 mm specimen). Two well-developed Polian vesicles (one-tenth of body length in the 220 mm specimen). Single, heavily twisted stone canal, short (4.5 mm long in the 220 mm specimen) ending in an ovoid madreporic plate. Calcareous ring ribbon-like, composed of large radial pieces and low interradial ones; radial pieces with deep posterior concavity; anteriorly a central notch (attachment for the longitudinal muscle) surrounded by two small concavities (figure 2A); interradial pieces very slender with a well developed anterior tooth (figure 2A). Digestive tract filled with very coarse debris, ranging from sand and coral pieces to shell fragments and spine fragments of cidarid sea urchins.
Ossicles: Tentacles with variously developed rods, generally smooth but some minute knobs rugosities can be found (figure 2B, C). Ventral and dorsal body wall with numerous tables only (figures 2D-L, 3A-D). Diameter of tables of dorsal body wall varies from one specimen to another but without clear relationships with body length (see table 1)

Length of specimens (mm)	Diameter of tables from dorsal body wall (μm)	Locality	Figures
41	85-150	Costa Rica	2D
51	110-175	Columbia	2E
98	110-235	Columbia	2F
100	100-185	Mexico, Baja California	2G
140	80-125	Mexico, Baja California	2H
220	215-235	Panama	2L

Table 1. Length of specimens versus table sizes and localities for *Labidodemas maccullochi* (Deichmann, 1958).

Disc perforated by numerous holes sometimes arranged in two to three circles around the four central holes which are slightly wider then the rest (figures 2D-L, 3A-D), rim of disc spiny; spire moderately high to

high; generally one cross beam although the pillars can be connected two by two near the apex giving the impression of a crown; pillars diverge near the tip, tapering to a point. Tables of ventral body wall similar to those of dorsal body wall, but generally somewhat smaller and with the pillars more often connected to each other (figures 2K, L, 3A-D). Dorsal papillae with tables, rods, pseudo-buttons and wide plates (figure 3E-P). Tables similar to those of body wall but the reduced type (disc only); type specimen holds numerous tables with a low spire; smallest specimen (41 mm) only with reduced tables (figure 3E) slightly knobbed rods (figure 3F) and pseudo-buttons (figure 3G), specimens from Bahia Claifornia (L=100 and 140 mm) with reduced as well as well developed tables (always smaller than those from the body wall) (figure 3J, L), variously perforated rods (figure 3K, N), buttons to wide plates (figure 3H, M); the longest specimen (L=220 mm) with variously developed tables, rods and pseudo-buttons, never with wide plates (figure 3O-P). Ventral tube feet with an ossicle assemblage similar to that of dorsal papillae, however, without wide plates (figure 3Q-V).

Ecology (after Deichmann, 1958 and Hickman, 1998) - Rare species occurring at tide level, covered with sand while foraging. The specimens from Bahia California were found subtidally, at depths of ± 16 m.

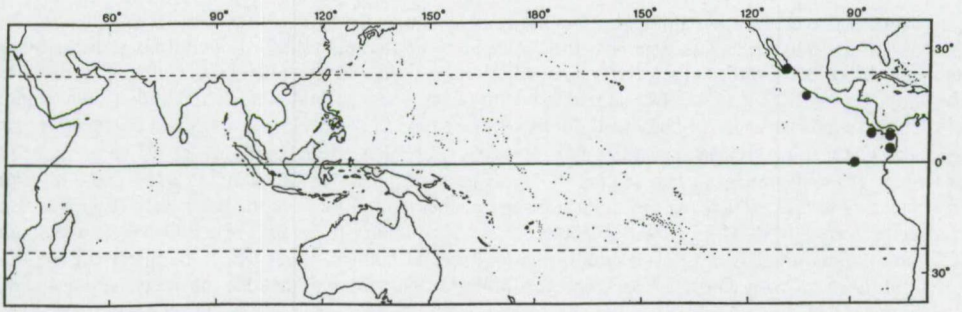
Geographic distribution (see map 2) - From the Gulf of California to Columbia and the Galápagos Islands.

Comments - As can be seen on the original labels, Domantay, in 1949 and 1950, seems to be the first who attempted to identify the NHMLAC specimens. He put the name *Holothuria mortenseni* sp. nov. to them, after the first collector, T. Mortensen, who, in 1916, had found the species in Panama. Domantay (1953: 135) published the name *Holothuria mortenseni* sp. nov. in a list, without any description or illustration. Under the rules of the International Code of Zoological Nomenclature, Domantay's name *mortenseni* is not valid (article 9.6: labels of specimens do not constitute published work; article 13.1.1: to be available a new name published after 1931 must be accompanied by a description or a definition that states in word characters that are purported to differentiate the taxon) and Deichmann's (1958) name *maccullochi* must be retained. The specimens here examined are to a large extend the same as those Deichmann (1958) studied (Hancock material). Deichmann (1958: 307) noted that 'The Hancock material ranges in length from 4 to 20 cm. No striking differences were found between the spicules in these different age groups except that they become slightly larger with advancing age [Sic.]'. The present observations substantiate Deichmann's (1958) observations. However, we are at present not able to construct unambiguous growth series as not enough material is available to us.

Deichmann's (1958) statement that Cuvierian tubules are present in some individuals could not be asserted, hence we believe that Deichmann's (1958) specimen series holds an additional species. *L. americanum* is a likely candidate as it thrives in the same region and has a comparable habit, but it is strange that Deichmann failed to recognise it as such for she had created *L. americanum* 20 years earlier.

It is interesting to note that the calcareous ring of *L. maccullochi* is very similar to the one of *L. americanum*. Both species share also two circles of peripheral holes in the table discs, a character which is not present in the other species belonging to the genus *Labidodemas*.

It is tempting to create a new species for the two specimens from Bahia California, as these differ from the other material in possessing wide plates in the dorsal papillae (figure 3H, M). It could be coincidental, but they were also found subtidally rather then intertidally as has always been reported for *L. maccullochi*. However, we refrain from doing so because the ossicle assemblage from the dorsal papillae of the type could not be examined since these could not be located on the poorly preserved specimen. For now, we keep a conservative attitude and attribute the observed differences to geographic variation. As such, two discrete populations are discernible: one in Bahia California and one on the west coast of northern South America. The specimens from the Galápagos Islands most probably belong to the southern population as Hickman (1998: 65) reports that the 'dorsal papillae contain a few supporting rods with perforated ends, and small perforated discs of various shapes' [Sic.], exactly as Deichmann (1958) put in the diagnosis of *Irenothuria*.



Map 2. Distribution of *Labidodemas maccullochi* (Deichmann, 1958)

Labidodemas pertinax (Ludwig, 1875)
(figure 4A-K; map 3)

Holothuria pertinax Ludwig, 1875: 100, pl. 7 figure 50; Théel, 1886: 208; Cherbonnier, 1955: 139, fig 3a-j; Cherbonnier, 1967: 63.
Holothuria (Holothuria) pertinax; Panning, 1935a: 75, figure 57.
Labidodemas pertinax; Cherbonnier, 1988: 52, pl. 18A-L; Marsh *et al.*, 1993: 57; Rowe and Gates, 1995: 304; Liao, 1997: 92, figure 52a-d; Samyn and Vanden Berghe, 2000: 25, pl. 2D; Samyn, 2000: 15; Lane *et al.*, 2000: 489.
Labidodemas semperianum; Rowe, 1969: 132, figure 4 only (not text); Clark and Rowe, 1971: 176 (part); Liao, 1975: 209, figure 9(1-7) (non *L. semperianum* Selenka, 1867); Humphreys, 1981: 33 (non *L. semperianum* Selenka, 1867); Massin, 1999: 61, figure 49 (specimen IRSNB IG.28251/197: non *L. semperianum* Selenka, 1867).
Labidodemas semperiana; Clark and Rowe, 1971: pl. 28 figure 12 (*lapsus calami* for *Labidodemas semperianum*; non *L. semperianum* Selenka, 1867).
Labidodemas petinax; Rowe and Richmond, 1997: 302 (*lapsus calami* for *Labidodemas pertinax*)

Original name - *Holothuria pertinax* Ludwig, 1875.

Name-bearing type - Holotype ZMH E. 2608.

Type locality - Samoa (as Navigator Islands).

Current status - *Labidodemas pertinax* (Ludwig, 1875).

Material examined - Samoa, collecting date and depth unknown, coll. Kubary, ZMH. E.2608 (Mus. Godeffroyi 9946, holotype); Republic of South Africa (KwaZulu-Natal, Sodwana Bay, 7 Mile Reef), February 2000, 23 m depth, coll. Y. Samyn, RMcA1692/RSAKZN/0064 (one specimen); Republic of South Africa (KwaZulu-Natal, Sodwana Bay, 2 Mile Reef), February 2001, 12 m depth, coll. Y. Samyn, RMcA1693/RSAKZN/0156 (one specimen); Kenya (Kiunga Marine Reserve, Mkomani), April 1999, 1 m depth, coll. Y. Samyn, IRSNB IG 28 268/KKiun/9919 (one specimen); Kenya (Kiunga Marine Reserve, Mlango wa Bomani), April 1999, 1-4 m depth, coll. Y. Samyn, IRSNB IG 28 268/KKiun/9920 (two specimens); Indonesia (Java Sea), NHM 89.6.15.34 (one specimen); Maldives, NHM 1955.10.14.48 (one specimen); Indonesia (Celebes Islands, Kapoposang), 28 September 1994, 5 m depth, under a coral slab, coll. C. Massin, IRSNB IG.28251/197 (one specimen identified as *L. semperianum*); Kenya (Watamu), 20 August 1969, beneath rock, coll. W. Humphreys, NHM 1979.2.5.229 (one specimen identified as *L. semperianum*); Maldives (Male Atoll, Dunidu Island), 18 March 1964, 4 m depth, coll. F. Ziesenhenne, USNM E11583 (one specimen); Papua New Guinea (Hansa Bay, Laing Island, K3), 12 October 1996, 1 m depth under rocks, coll. J-M Ouin, IRSNB IG 28455/36 (one specimen).

Diagnosis - See Cherbonnier, 1988: 51, figure 18.

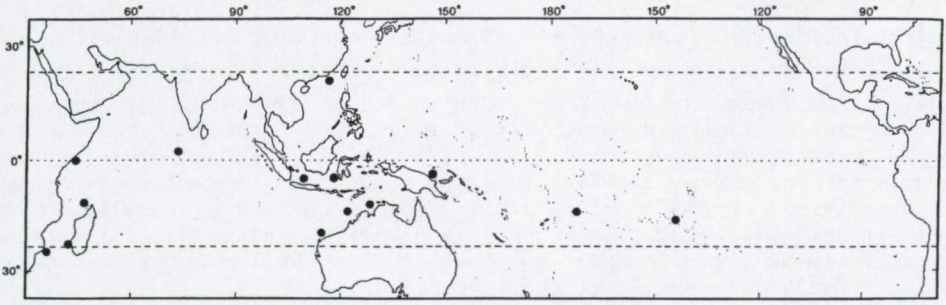
Description - Small to medium-sized species, preserved specimens 84 to 152 mm long and ten to 19 mm wide. Body cylindrical, tapering anteriorly, mouth and anus terminal. Colour in life and alcohol identical: uniform white dorsally with a very faint yellow to pinkish shine ventrally; mouth surrounded by a 5 mm wide dark-purple to brown ring in largest specimen and 1 mm wide in smallest specimens. Skin thin, gritty to the touch. Mouth surrounded by 20 (occasionally fewer), small, dirty white, tentacles. Tentacle ampullae very short: 1.5 to 4 mm long for specimens 88 to 100 mm long. Ventral side with long, cylindrical, yellow to brownish tube feet in ambulacral areas (in two rows in median ambulacrum); dorsal side with fewer, short, whitish tube feet and papillae somewhat scattered in ambulacra and interambulacra. Cuvierian tubules absent. Calcareous ring slender with massive radial pieces, each with anterior notch, and interradial pieces minute, ribbon-like, each with one anterior tooth-like projection (figure 4K).

Ossicles: Tentacles with smooth rods, 25-50 µm long, slightly rugose at extremities (fig 4A). Ventral and dorsal body wall with small, 25-65 µm long, rods similar to those of tentacles (figure 4B, D), some more stout rods (figure 4C) and tables (figure 4E, F). Rods more abundant in ventral than in dorsal body wall; the reverse for the tables. Tables with disc 40-60 µm across, perforated by four central holes and occasionally some small peripheral holes (see Cherbonnier, 1988: 52 figure 18A, B, D, H); rim of disc regularly spiny; height of spire lower than width of disc; spire with single cross beam or none, ending in a crown with a wide central opening; diameter of crown 60-90 % of disc diameter (figure 4E, F). Ventral tube feet with rods similar to those of body wall in addition to more stout rods, 45-75 µm long, occasionally branched and/or perforated (figure 4G); some ill-formed tables (disc and occasionally one or two pillars) present (figure 4H). Dorsal papillae with rods similar to those of ventral tube feet (figure 4J).

Ecology - Shallow-water species reported from tidal pools up to depths of 23 m; deposit/detritus feeder; hides under coral slabs, in and on coarse coral debris and small rocks.

Geographical distribution (see map 3) - Madagascar (Glorious Islands), Kenya, Maldives, Java Sea, Australia (N.W. Coast, W.A., Scott Reef), Samoa.
New geographical records made in present work: South Africa (KwaZulu-Natal), Madagascar (Tuléar), China, Tahiti.

Comments - Rowe (1969) did not distinguish between *L. semperianum* and *L. pertinax*, and used the latter species (specimen NHM 1955.10.14.48 from the Maldives) to illustrate the ossicles of *L. semperianum* in his revision of the Holothuriidae. Cherbonnier (1970) correctly noted that the ossicles illustrated by Rowe (1969) are different from those typical of *L. semperianum*. Regrettably, he explained this anomaly by stating that Rowe (1969) perhaps illustrated ossicles from tube feet or corroded ossicles. In 1971, Rowe (*in* Clark and Rowe) illustrated specimen NHM 89.6.15.34 as *L. semperiana*. An examination of his illustration clearly shows that it is *L. pertinax*. It was only in 1988, on the basis of two specimens from Glorious Islands and one from the NHM collections, that Cherbonnier (1988) realised that *H. pertinax* is a valid species in *Labidodemas*. It has been treated as such since then (Marsh *et al.*, 1993; Rowe and Gates, 1995; Liao, 1997; Rowe and Richmond, 1997; Samyn and Vanden Berghe, 2000; Samyn, 2000; Lane *et al.*, 2000). The present revision corroborates this finding.



Map 3. Distribution of *Labidodemas pertinax* (Ludwig, 1875).

Labidodemas pseudosemperianum sp. nov.
(figures 5A-K, 6A-G; map 4)

Labidodemas semperianum; Massin, 1999: 61, figures 49, 111f (non *L. semperianum* Selenka, 1867).

Name bearing type - Holotype RMNH Ech 6087.

Material examined - Indonesia (Celebes, Kapoposang), 30 September 1994, 5 m depth under a coral slab, coll. C. Massin, RMNH Ech 6087 (holotype); Mariana Islands (Guam, Tumon Bay, 14 August 1992, 1 m depth under rocks, outer reef flat at south part of bay, coll. A. Kerr, USNM E 53083 (one specimen).

Diagnosis - Medium-sized species, body cylindrical, white-pink with yellow tube feet; around the mouth colour deep pink to brown. Calcareous ring ribbon-like; ventral body wall with tables and buttons; dorsal body wall with tables, buttons, pseudo-buttons and rods; disc of tables smooth; spire of tables low, single

cross beam; crown of spines with two to ten central holes and five to eight huge, often deeply bifurcated spines; crown of spines up to twice the diameter of the table disc.

Description - Holotype 120 x 10 mm; specimen from Guam 48 x 11 mm. Living holotype white pink with pink-brown around the mouth; in alcohol uniformly white. Body cylindrical with mouth and anus terminal; mouth surrounded by 20 tentacles; few long, slender, slightly conical papillae scattered over the whole bivium, presenting a vague alignment in three double rows close to the mouth and the anus. Tube feet very long, restricted to the ambulacra; in each ambulacrum two rows of tube feet in a zigzag pattern. Calcareous ring ribbon like, composed of massive radial pieces and narrow interradial pieces (cf. fig. 49 in Massin, 1999). One Polian vesicle and one stone canal going upwards and ending in a muriform madreporic plate. Digestive tract filled with very rough calcareous sand. Cuvierian tubules not observed; tentacle ampullae short (1/12 to 1/20 of body length).

Ossicles: Dorsal body wall with tables (figure 5A-B), buttons (figure 5C), pseudo-buttons (figure 5D) and rods (figure 5E). Table disc 70-95 µm across with five to eight central holes and 5-15 peripheral holes; rim of disc smooth, sometimes with single long spine (figure 5A). Table spire low with one cross beam and ending in a crown of spines with two to ten central holes and five to eight huge spines, most of these deeply bifurcated distally; table crown always larger than table disc (up to twice the table disc; figure 5A). Buttons very irregular, 40-70 µm long, with two to four pairs of holes (figure 5C); numerous in the holotype, rare in the specimen from Guam. Rods and pseudo-buttons present only in the specimen from Guam (figure 5D-E). Ventral body wall with tables (figure 5F) and buttons (figure 5G) similar to those of dorsal body wall; a few irregular rods in the specimen from Guam. Dorsal tube feet with plates and tables; close to the end plate, perforated plates with spiny edge (figure 5H); mid of tube feet hold tables with reduced crown of spines (figure 5J); base of tube feet with tables, 40-60 µm across, similar to those of body wall (figure 5K).Ventral tube feet with numerous rods (figure 6D), some of them C-shaped (figure 6E), and a few pseudo-buttons (figure 6F); base of tube feet with few tables similar to those of body wall (figure 6C) in addition to many reduced tables (figure 6B); close to end-plate spiny perforated plates (tables reduced to disc) also present (figure 6A). Tentacles with small rods, 15-60 µm long, straight, curved, and Y-shaped (figure 6G).

Etymology - The name *pseudosemperianum* refers to the close similarity between the new species and *Labidodemas semperianum.*

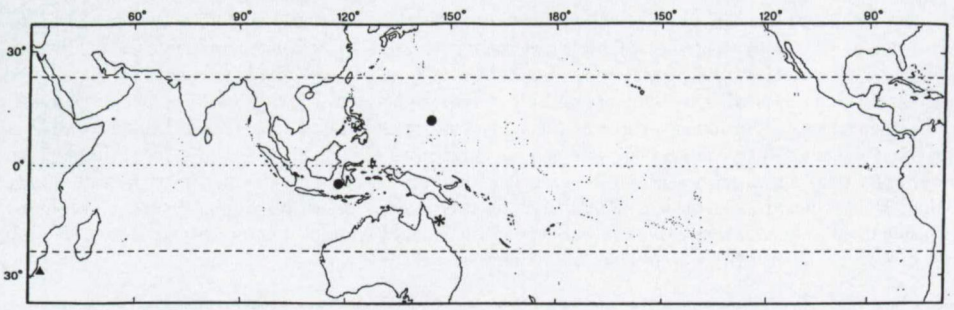
Geographical distribution (see map 4) - Indonesia (Celebes, Kapoposang); Mariana Islands (Guam).

Ecology - Shallow waters (1-5 m depth) under coral rocks; digestive tract filled with rough sand.

Comments - At first glance (general morphological and anatomical aspects), *Labidodemas pseudosemperianum* is hard to distinguish from *L. semperianum* or *L. pertinax.* However, close examination of the ossicles (mainly the tables) reveals clear differences (see table 2) which can not be linked to the size of the specimens. The two examined specimens of *L. pseudosemperianum* are 120 and 48 mm long and both have smooth table discs whereas all the examined specimens of *L. semperianum* (from 64 to 125 mm long) have spiny table discs. If the observed ossicle variation should be dependent on the body length, one would expect to find more spiny or knobbed ossicles with increasing body size (Massin, 1994; Massin *et al.*, 2000); the reverse is true in the present situation.

The three main characters specific to *L. pseudosemperianum* are: (i) the smooth edge of the table disc, (ii) the numerous holes of the crown of spines and (iii) the presence of buttons in the dorsal and ventral body wall. As the other characters (see table 2) show a progressive change from *L. quadripartitum* sp. nov. (see below) over *L. semperianum* to *L. pseudosemperianum,* one could suspect a highly variable species. However, as these variations could not be linked to zoogeography, ecology or to the size of the specimens, such can not be the case. Moreover, a highly variable species would be exceptional within the genus *Labidodemas*, as all the other species show little, if any, variation through their distribution area and their size.

Up to now, *L. pseudosemperianum* is restricted to the West-Pacific shallow-waters.



Map 4. Distribution of *L. pseudosemperianum* sp. nov. (dots); L. *quadripartitum* sp. nov. (triangle) and *L. spineum* sp. nov. (asterisks).

Labidodemas quadripartitum sp. nov.
(figure 7A-G; map 4)

Name bearing type - Holotype RMcA1694/RSAKZN/0196.

Type locality - Sodwana Bay, 1/4 Mile Reef (Republic of South Africa).

Material examined - Republic of South Africa (KwaZulu-Natal, Sodwana Bay, 1/4 Mile Reef), February 2001, 12 m depth, coll. Y. Samyn, RMcA1694/RSAKZN/0196 (holotype).

Diagnosis - Medium-sized species; body vermiform; dorsal body wall whitish, ventral body wall reddish; calcareous ring ribbon-like; ventral body wall with tables only; dorsal body wall with tables and rods; tables with rim of disc spinose; spire of table low, single cross-beam; crown of tables with four huge (occasionally slightly bifurcated) spines, wider than disc diameter.

Description - Specimen 110 mm long and 8 mm wide at its widest point. Body vermiform, tapering anteriorly with mouth and anus terminal. Colour in life similar to colour in alcohol: dorsally whitish yellow, ventrally claret-red. Skin thin (1-2 mm), rather smooth to the touch. Mouth terminal, tentacles retracted; number could not be determined. Anus small, terminal. Anal papillae absent. Ventral side with short but wide brownish tube feet distributed in three rows in ambulacral areas; dorsal side at first sight apparently without tube feet or papillae, but examination of inner body wall reveals large tube feet ampullae in ambulacral areas. Cuvierian tubules absent. Calcareous ring ribbon-like, with radial pieces 2.5 times height of interradials; radial pieces massive, with medial depression for longitudinal muscle, posterior margin slightly concave; interradial pieces brittle, anteriorly with tooth-like projection (figure7F). Stone canal contorted, ending in large madreporic plate (figure 7G). Tentacle ampullae very short (1-2 mm long). Gonad not observed.

Ossicles: Dorsal and ventral body wall devoid of buttons. Ventral body wall (figure 7A) with tables only; tables disc 45-60 µm across, perforated by four large central holes and zero to occasionally six peripheral holes; rim of disc spinose, height of spire equal to width of disc, spire with single cross-beam and ending in a crown with four huge spines that occasionally bifurcate distally, crown of spines considerably wider than disc. Dorsal body wall with tables and rods (figure 7B, C); tables (figure 7B) with disc 30-60 µm across, perforated by four large central holes and zero to one peripheral hole, rim of disc moderately to very spinose, spire often reduced to knobs on disc, but occasionally persists as high as width of disc but then with a single cross beam that ends in a four-spined crown, usually not wider than disc; rods, 35-50 µm long, straight or with slightly undulating margins (figure 7C). Ventral tube feet with tables and rods (figure 7D, E); tables mostly reduced to disc, 33-42 µm across, perforated by three to four central holes and occasionally a single peripheral one, rim of disc slightly spinose, spire reduced to two or four knobs on surface of disc; rods 33-55 µm long, branched medially or distally, often perforated by one to several holes.

Etymology - The name *quadripartitum* refers to the crown of the tables that ends in four huge spines; *quadripartitum* (Latin) meaning split into four.

Ecology - The single specimen was collected at 12 m depth; over coarse sand under and between several large slabs of dead coral and rock.

Geographical distribution (see map 4) - For now only known to the type locality.

Comments - The new species, with its ribbon-like calcareous ring, its ventral side with three rows of tube feet and dorsal side with two rows of tube feet, and its ossicle assemblage, undoubtedly belongs to *Labidodemas*. Nevertheless, the general body morphology of *L. quadripartitum* is unique to the genus. The dorsal body wall is yellowish to light brown and at first sight seems devoid of tube feet or papillae; however, inspection of the inner surface of the body wall reveals large tube feet ampullae in all five ambulacra. The ventral body wall is claret-red and has three rows of wide brownish tube feet. Although we have currently only one specimen at our disposal it is unlikely that this species will ever present a body wall that is translucent. The ossicle assemblage reveals that *L. quadripartitum* is very close to *L. semperianum* and *L. pseudosemperianum*, but several differences warrant it new species status. Table 2 lists the differences in the body wall ossicles of the three species.

Character	*L. quadripartitum* sp. nov.	*L. semperianum* Selenka, 1867	*L. pseudosemperianum* sp. nov.
Tables	• disc with 4 central holes • disc with 0-2 (occasionally 6) peripheral holes • disc 30-60 µm across • rim of disc spiny • crown with 4 huge spines that occasionally bifurcate distally • table disc < table crown • crown of spines with 1 central hole • dorsal tables few	• disc with 4-6 central holes • disc with 5-10 peripheral holes • disc 55-90 µm across • rim of disc spiny • crown with 4-5 huge spines that bifurcate slightly distally • table disc ≤ table crown • crown of spines with 1 (occasionally 2) central hole • dorsal tables numerous	• Disc with 5-8 central holes • disc with 5-15 peripheral holes • disc 70-95 µm across • rim of the disc smooth • crown with 5-8 huge spines that bifurcate deeply distally • table disc << table crown (crown up to twice the disc) • crown of spines with 2-10 central holes • dorsal tables numerous
Ventral buttons	absent	absent	present
Dorsal buttons	absent	present	present

Table 2. Differences in body wall ossicles of *L. quadripartitum* sp. nov., *Labidodemas semperianum* Selenka, 1867, and *L. pseudosemperianum* sp. nov.

Labidodemas rugosum (Ludwig, 1875)
(figure 8A-L; map 5)

Holothuria rugosa Ludwig, 1875: 110, pl.7, fig 33d-e; Pearson, 1913: 82 (synonymy and records before 1908).
Holothuria (Holothuria) rugosa; Panning, 1935a: 75.
Labidodemas rugosum; Rowe, 1969: 133; Levin, 1979: 20; James, 1981: 83; Mukhopadhyay, 1991: 408; Rowe and Gates, 1995: 304; Rowe and Richmond, 1997: 302; Massin, 1999: 58, figures 46a-j, 47a-c, 48 (records before 1998); Lane *et al.*, 2000: 489.
Holothuria triremis Sluiter, 1901: 19, pl. 6, figure 3a-c
? Holothuria triremis; Pearson, 1913: 82.
Holothuria (Halodeima) trimensis; Panning, 1931: 119 (*lapsus calami* for *Holothuria triremis* Sluiter, 1901)

Original name - *Holothuria rugosa* Ludwig, 1875.

Name-bearing type - Holotype ZMH E.2625.

Type locality - Samoa (as Navigator Islands).

Current status - *Labidodemas rugosum* (Ludwig, 1875).

Material examined - Samoa, collecting date and depth unknown, coll. Dr. Graeffe, ZMH E.2625 (Mus. Godeffroyi 9937, holotype); Republic of South Africa (KwaZulu-Natal, Sodwana Bay, 2 Mile Reef), July 2001, 15 m depth, coll. Y. Samyn, RMcA1695/RSAKZN/0099 (one specimen); Indonesia (Celebes Islands, Kudingareng Keke), 5 October 1994, 2 m depth, coll. C. Massin, IRSNB IG.28251/256 (one specimen); Papua New Guinea (Hansa Bay, Laing Island, L4), 18 October 1996, reef flat at low tide, under rock, coll. C. Massin, IRSNB IG28455/55 (one specimen); Papua New Guinea (Hansa Bay, Laing Island, K3), 20 October 1996, reef flat at low tide, coll. J.M.Ouin, IRSNB IG28455/62 (two specimens); British Indian Ocean Territory (Chagos Archipelago, Diego Garcia), 07 August 1967, coll. J.D. Taylor, NHM 1969.5.27.22 (2 specimens); British Indian Ocean Territory (Chagos Archipelago, Diego Garcia), 08 August 1967, sublittoral fringe, coll. J.D. Taylor, NHM 1969.5.27.23.26 (5 specimens).

Diagnosis - See Cherbonnier, 1988: 53-55, figure19.

Description - Small to medium-sized species; preserved specimens 67 to 133 mm long and four to 20 mm wide. Body cylindrical, mouth and anus terminal. Colour in life uniform whitish with yellowish tube feet; fading slightly after preservation. Skin thin (1-2 mm thick), but rather gritty to the touch. Mouth terminal

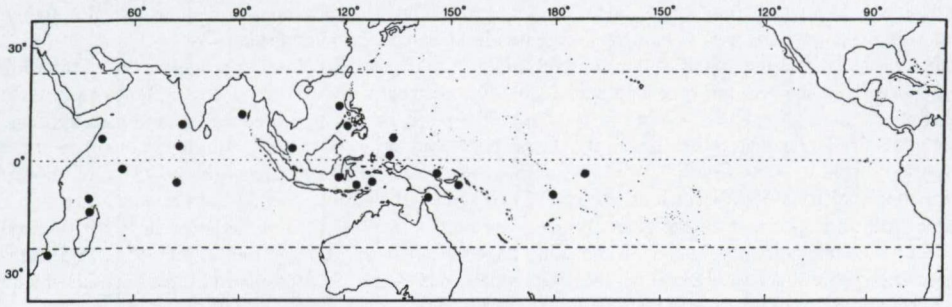
surrounded by 20 small, yellowish tentacles. Ventral side with tube feet in three to four rows in median ambulacrum and in two rows in each lateral ambulacrum; some tube feet in interambulacral areas. Dorsal side with whitish papillae and short yellowish tube feet more or less confined to ambulacra, but also scattered in interambulacra. Ampullae of tube feet conspicuous on inner side of body wall. Cuvierian tubules absent. Tentacle ampullae short (1/12 body length). Single, well developed Polian vesicle (one-sixth of body length). Single, small (4 mm), straight stone canal ending in minute madreporic plate (figure 8L). Calcareous ring composed of huge radial pieces and slender interradials; posterior margin of ring undulating; radial pieces with anterior notch, and central depression for longitudinal muscle; interradial pieces ribbon-like with minute anterior tooth-like projection (figure 8K). Digestive tract filled with rough coral sand and pieces of coral smaller than in *L. americanum*.

Ossicles: Tentacles with simple, straight or curved, smooth rods, 25-85 µm long (figure 8A). Ventral and dorsal body wall with similar tables and buttons (figure 8B-E). Table discs 65-90 µm across, perforated by four large central holes and 6-11 peripheral holes; rim of disc very spinose; margin of disc slightly turned upward; height of spire equal to diameter of disc; spire with four undulating pillars, united by one or two cross beams and terminating in crown consisting of cluster of stout spines; crown occasionally with small central perforation (figure 8B, C). Buttons, 45-85 µm long, with two to six pairs of irregular holes, margins smooth, but undulating (figure 8D, E). Ventral tube feet with tables and buttons (figure 8F, G): tables similar in shape to those of body wall, but disc only 45-65 µm across; crown of spines less developed but often perforated by central hole; spire occasionally reduced to knobs on surface of disc (figure 8F); buttons plate-like, surrounding end-plate, 70-100 µm long, generally rim more irregular than that of body wall buttons (figure 8G). Dorsal papillae with tables and buttons: tables similar in shape to those of body wall, but generally smaller (figure 8H); buttons very irregular, often rod-like, generally larger than those of body wall (figure 8J).

Ecology - Found in shallow waters, always less then 20 meters deep (Lane *et al.*, 2000); deposit / detritus feeder; under coral slabs and in and on coarse coral debris. Gut of the South African, and Chagos specimens filled with coarse sand.

Geographical distribution (See map 5) - If compared with figure 48 in Massin (1999: 61), the following new localities are here added: Republic of South Africa (KwaZulu-Natal), Malaysia, northern part of the Philippines.

Comments - In his revision of the Holothuriidae, Rowe (1969) realised that *H. rugosa* Ludwig, 1875, because of its body form and ribbon-like calcareous ring, belongs in *Labidodemas*. It has been treated as such since then and the present revision corroborates this.



Map 5. Distribution of *Labidodemas rugosum* (Ludwig, 1875).

Labidodemas semperianum Selenka, 1867
(figures 9A-J, 10A-H; map 6; figure 11A-L for *L. selenkianum*)

Labidodemas Semperianum Selenka, 1867: 309, pl. 17, figures. 1-3.
Labidodemas semperianum Selenka, 1867; Rowe and Richmond, 1997: 302; Massin, 1999: 61 (records before 1998, partim); Lane *et al.*, 2000: 489; Samyn, 2000: 15; Marsh, 2000a: 26; Marsh, 2000b: 101.
Labidodemas dubiosum Ludwig, 1875: 98, pl. 7, figure 25; Lampert, 1885: 110; Théel, 1886: 189.
Labidodemas egestosum Sluiter, 1901: 22.
? Labidodemas Selenkianum Semper, 1868: 77; Lampert, 1885: 110.
? Labidodemas selenkianum; Théel, 1886: 188.

Labidodemas semperlanum; Allen and Steene, 1994: 245 (*lapsus calami* for *L. semperianum*).
Labidodemas semprianum; Arakaki and Fagoonee, 1996: 122 (*lapsus calami* for *L. semperianum*).
? *Holothuria pertinax*; Sluiter 1887: 186, pl. 1, figure 1-2.
Labidodemas pertinax; Rowe and Doty, 1977: figures 3b, 5g [non *L. pertinax* (Ludwig, 1875)].
Labidodemas sp.; Price and Reid, 1985: 3 (here identified as *L. semperianum*).
Holothuria proceraspina Cherbonnier, 1967: 62, figure 3a-o (syn. nov.); Price, 1982: 11; Tortonese, 1977: 275.

Original name - *Labidodemas semperianum* Selenka, 1867.

Name-bearing type - Syntypes ZMG (no number given by Selenka, 1867), MCZ 736 (2 specimens). As the syntypes of the ZMG are untraceable (Troester, personal communication), a lectotype and a paralectotype are here designated in the MCZ 736 material: as lectotype the dissected specimen (75 mm long) and as paralectotype the non dissected specimen (90 mm long) are chosen.

Type locality - Formerly Hawaiian Islands (as Sandwich-Inseln) but now Society Islands according to the designation of lectotype.

Current status - *Labidodemas semperianum* Selenka, 1867.

Material examined - Society Islands, collecting date, depth and collector unknown, MCZ 736 (two specimens); Maldives (Male Atoll, Dunidu Island), 18 March 1964, 4 m depth, coll. F. Ziesenhenne, USNM E11583 (one specimen identified as *L. pertinax*); Philippine Islands, 26 May 1978, 6-7 m depth, USNM E24458 (one specimen); Indonesia (Sumatra, Pula Wé), 1980-1981, 2 m depth, sublittoral rock, coll. A. Price, NHM 1999.2148 (one specimen); Philippine Islands (La Onoy Gulf, Luzon Island), 5 April 1989, intertidal, USNM E40771 (one specimen identified as *L. rugosum*); China, collecting date and depth unknown, coll. Kpt. Schnehagen, ZMH. E. 2933 (one specimen identified as *L. pertinax*); Fidji, collecting date and depth unknown, coll. Dr. Graeffe, ZMH E.2674 (Mus. Godeffroy 1170, holotype of *L. selenkianum* Semper, 1868).

Diagnosis - Cherbonnier, 1970: 566, figure A-P; present revision.
Description - The lectotype and paralectotype are cylindrical, 70 x 20 and 90 x 15 mm, respectively. Both type specimens are grey-white in alcohol; mouth and anus terminal; lectotype with 12 tentacles visible but, most probably the number is 20 as in all the other species belonging to the genus *Labidodemas*. Ventral tube feet very long, cylindrical and only present in the ambulacral areas; each ambulacrum with two rows of tube feet in a zigzag pattern, more densely crowded at mid body and fewer close to mouth and anus. Dorsally tube feet few, dispersed in ambulacral and interambulacral areas; no clear alignment visible. Body wall gritty to the touch. Calcareous ring of the lectotype ribbon-like with large quadrangular radial plates and very thin interradial plates (figure 9A). One huge Polian vesicle (one-third of body length); tentacle ampullae very short (1-2 mm long); stone canal not observed. Vesicles of ventral tube feet prominent. Gonad well developed, made of several very large tubules. Cuvierian tubules absent.
Ossicles: In the ventral body wall of the lectotype tables only (figure 9B), 55-80 μm across; rim of the table disc spiny with sometimes one very long spine; table disc perforated by four to six central holes and five to ten peripheral holes; spire low, ending in four to six long spines, most of them bifurcated distally; table crown generally larger than table disc. In the dorsal body wall tables (figure 9C) similar to the ones of the ventral body wall, buttons (figure 9D) 60-75 μm long, sometimes knobbed, pseudo-buttons (figure 9E) 55-65 μm long and rods 50-70 μm long (figure 9F). Number of buttons, pseudo-buttons and rods highly variable from one specimen to the other. In some specimens they seem to be gathered in heaps. Ventral tube feet have tables that are reduced to the spiny edged disc (figure 9G) and rods (figure 9H). End plates more or less 500 μm across. Dorsal papillae with small rods (figure 9J) and no end plate. Tentacles with rods 20-60 μm long, very similar to the ones of *Labidodemas pseudosemperianum* (cf. fig. 6G).
The paralectotype (figure 10A, B), the specimens from Maldives (figure 10C) and the Philippines (figure 10D-H) show very few variations from the lectotype. Re-examination of the holotype of *Labidodemas selenkianum* Semper, 1868 (figure 11A-L) shows somewhat corroded ossicles; the tables have a reduced crown but the general aspect is very similar to that of *L. semperianum*

Ecology - Lives under coral slabs and coral rocks in shallow water (0-10 m depth).

Geographical distribution (see map 6) - The following new localities are added since Massin's (1999: 62, figure 50) publication: China, South China Sea, Montebello Islands, Christmas Island; Pitcairn Islands. Moreover, Kenya has to be removed from Massin's (1999) map, since Humphreys' (1981) record of *L. semperianum* (NHM 1979.2.5.229, identified by A.M. Clark) proved to be *L. pertinax* after examination.

Celebes (Indonesia) also needs to be omitted since Massin's records (1999) of *L. semperianum* (RMNH Ech 6087 and IRSNB IG 28251/197) proved to be *L. pseudosemperianum* and *L. pertinax*, respectively.

Comments - *Labidodemas semperianum*, with its wide Indo-Pacific distribution, is one of those species which seems easy to identify due to its very characteristic ossicle assemblage (especially the tables). However, re-examination of material from IRSNB, MCZ, NHM, RMNH and ZMH revealed many misidentifications with, very often, a confusion between *L semperianum* and *L. pertinax*. This confusion undoubtedly results from the similar external aspects of both species. As such, when one sample includes several specimens they are often designated under a single species name whereas careful examination of the ossicles of all the specimens in the sample reveals several species.

Cherbonnier (1970) gave a very good description of *L. semperianum* but, unfortunately, it was based on non-type material from Marshall Islands (Guam). According to Rowe and Gates (1995), syntypes are housed in the ZMG and the MCZ. The ZMG type series is currently untraceable in the ZMG (Troester, personal communication) whereas MCZ syntypes are available. To stabilise the taxonomy of *L. semperianum*, we here designate a lectotype and a paralectotype (see name-bearing type). Selenka (1867) examined material from ZMG and MCZ and indicated that all the material was coming from Hawaiian Islands (as Sandwich Inseln). However, on the original label of the two syntypes from MCZ, the locality mentioned is 'Society Islands'. With the designation of a lectotype among the syntypes from MCZ, the type locality thus can no longer be the Hawaiian Islands but becomes the Society Islands.

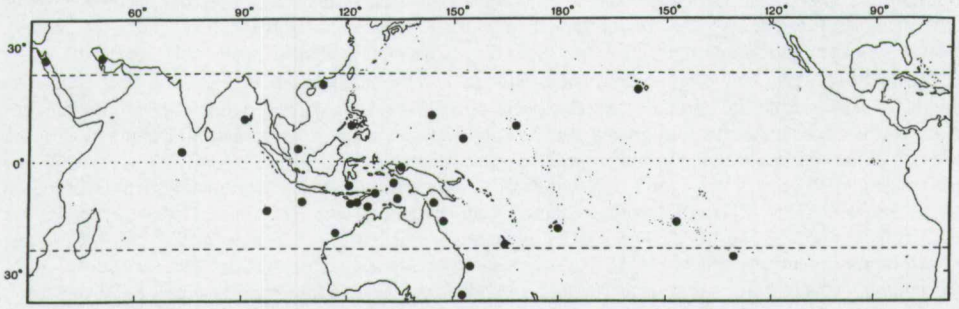
Material from Maldives (figure 10C), and the Philippines (figure 10D-H) shows few variations from the type material. A specimen from China (ZMH E 2933) has some tables of the ventral body wall with table crown much larger than table disc. However, unlike *L. pseudosemperianum*, the spines of the crown are only occasionally divided distally. Moreover, tables reduced to the disc (with spiny edge), coming from the apex of ventral tube feet, have fewer but larger spines than those from ventral tube feet of the holotype of *L. spineum*.

In terms of ossicle assemblage, the most constant features are: (i) presence of buttons and rods dorsally but not ventrally, (ii) rim of table disc spiny and (iii) diameter of table crown equal to or slightly larger than diameter of table disc. These characters allow separation of *L. semperianum* from the two closely allied new species that are here described: *L. quadripartitum* and *L. pseudosemperianum*.

After re-evaluation of the original description, *Holothuria proceraspina* Cherbonnier, 1967 is here recognised as a junior synonym of *Labidodemas semperianum*. Indeed, the body morphology of *H. proceraspina* as described by Cherbonnier (1967) – 'Il est entièrement blanc jaunâtre, sauf la partie orale qui est brune tout autour de la bouche. Le tégument est peu épais, lisse, plissé. Les pieds ventraux sont peu nombreux et dispersés sur les radius et les interradius, à l'exception de la région anale où ils s'alignent sur deux rangs sur le radius médian et sur un rang sur les radius latéraux' [Sic] - the structure of the calcareous ring (Cherbonnier, 1967: 62, figure 3m) and the ossicle assemblage (Cherbonnier, 1967: 62, figure 3a-l, o) are typical of *Labidodemas*. Cherbonnier (1967) implicitly came to the same conclusion as in his remarks he states that the form of the tables are reminiscent of the majority of species under *Halodeima* and of *Holothuria pertinax* Ludwig, 1875 (now *L. pertinax*). It should, however, be noted that the structure of the calcareous ring of *H. proceraspina* - 'Couronne calcaire petite mais bien calcifiée, à larges et hautes radiales, à courtes interradiales triangulaires' [Sic.] - conflicts with that of *Halodeima* (now a subgenus of *Holothuria*) (see Rowe, 1969: 137, figure 7a), but Cherbonnier (1967) was correct to recognise that *L. pertinax* is very close to *H. proceraspina*. However, *L. pertinax* differs from *H. proceraspina* in lacking buttons in the body wall. In fact four species currently recognised in *Labidodemas* possess buttons in the body wall: *L. semperianum* , *L. pseudosemperianum*, *L spineum* sp. nov. (for description see below) and *L. rugosum*; the ossicle assemblage of the first of these is identical to that of *H. proceraspina*, hence the decision for synonymy. Re-examination of *Labidodemas* sp. collected by Price (Price and Reid, 1985) in Indonesia reveals that this specimen almost certainly is also *L. semperianum*.

Re-examination of the type material of *L. selenkianum* Semper, 1868 shows that the ossicles are partly eroded by the preserving fluid. This could explain the reduced table crown and the eroded rim of the table discs. As the general morphological aspect and the ossicle assemblage of the holotype are very close to *L. semperianum* as the species is here defined, it is tempting to accept the decision of Sluiter (1901) and many authors after him (a.o. Cherbonnier, 1970; Rowe and Gates, 1995), to regard *L. selenkianum* as a mere synonym of *L. semperianum*. However, we feel reluctant to base the final judgement on *L. selenkianum* with only a single specimen (with eroded ossicles) at hand. As such, our list of synonyms of *L. semperianum* marks *L. selenkianum* with a question mark. The here, for the very first time, depicted (figure

11) ossicle assemblage of the holotype will, once more material is available, allow definite rejection or acceptance of this species.



Map 6. Distribution of *Labidodemas semperianum* Selenka, 1867.

Labidodemas spineum sp. nov.
(figures 12A-N, 13A-G; map 4)

Name-bearing type - Holotype NHM 1974.12.3.42.43 (L=125 mm); paratype NHM 1974.12.3.42.43 (L=112 mm).

Type locality - Low Island, Great Barrier Reef, Australia.

Material examined - Australia (Low Island, Great Barrier Reef), 1973, sand flat (LWM), coll. P. Gibbs, NHM 1974.12.3.42.43 under the name *L. semperianum* (holotype and paratype).

Diagnosis - Medium-sized species; 20 short tentacles. Ribbon-like calcareous ring. Tables, buttons and rods present in body wall and tube feet. Buttons and rods spiny. Tables with quadrangular or triangular disc, with low spire without cross beam, crown irregular.

Description - The holotype is 125 x 11-14 mm and the paratype 112 x 8-11 mm. Body cylindrical, worm-like, tapering anteriorly. Colour in alcohol white-beige with both extremities brown; tube feet same colour as body wall. Mouth and anus terminal. Mouth surrounded by 20 short tentacles; anus wide, surrounded by five groups of paired papillae. Ventrally, tube feet restricted to ambulacra; lateral ambulacra with one row of tube feet in a zigzag pattern, median ambulacrum with two rows of tube feet. Dorsally, tube feet present in ambulacral and interambulacral areas, small, arranged in about five to six rows.

Calcareous ring ribbon-like (figure 12A) with large quadrangular radial plates and narrow interradial plates with short anterior projection. Radial plate with small anterior notch and indentation for insertion of longitudinal muscle. Two Polian vesicles, the larger one-seventh of body length. Single stone canal. Tentacle ampullae very short (1 mm long); tube feet ampullae visible on inner side of body wall. Specimens partly eviscerated (gonad, part of intestine, and left respiratory tree missing). Presence/absence of Cuvierian tubules could not be ascertained because specimens are partly eviscerated. Segment of digestive tract still present, filled with rough coral sand.

Ossicles: Both dorsal and ventral body wall with tables, rods, and buttons. Dorsally, tables irregular with a spiny quadrangular disc (figure 12B) (very often triangular in the paratype; figure 12E), 50-80 µm across, perforated by four large central holes and four to ten peripheral ones; four short pillars without cross beam, ending in a crown of spines (figure 12B, E), often irregular (figure 12B). Spire low (figure 12E). Tables of ventral body wall similar to dorsal tables (figure 12G, J) in size and shape, but sometimes reduced to disc only (figure 12G). Buttons spiny (figure 12C, H, K), 35-50 µm long, with two to four pairs of holes; rods short, 30-35 µm long, often spiny (figure 12D, F, K), either straight or C-shaped. Some ossicles intermediate between rods and buttons (figure 12H, K). Tube feet with ossicles similar to those of body wall. Tables 45-85 µm across (figures 12L, N, 13A, D), often reduced to disc only (figure 13A). Buttons 45-55 µm long (figure 13B, E), rare or absent in dorsal tube feet. Rods spiny, 30-60 µm long (figures 12M, 13C, F), sometimes branching at extremities (figure 13F). Some ossicles (pseudo-buttons) with intermediate stages between buttons and rods (figure 13C). End plate of dorsal tube feet 125 µm across. In tentacles small rods, 10-50 µm long (figure 13G).

Etymology - The name *spineum*, Latin, means spiny and refers to the numerous spines covering the buttons and the rods from the body wall and the tube feet.

Ecology - No data currently available.

Geographical distribution (see map 4) - Only known from the type locality.

Comments - Rods and buttons are similar in holotype and paratype but the tables are quite different. In the holotype, seen from above, they are *rugosum*-like whereas in the paratype they are *pertinax*-like. The tables of *L. spineum* differ from those of *L. rugosum* by the very low spire without cross beam and from those of *L. pertinax* by a more irregular crown of spines and the triangular shape of some discs. *Labidodemas spineum* is very easy to separate from all the other *Labidodemas spp.* because it is the only species with spiny buttons and rods in the body wall.

Discussion

Historical overview

Since Selenka (1867), several authors have described other, not well defined (H.L. Clark, 1946), species in *Labidodemas*: *L. dubiosum* Ludwig, 1875 from Tahiti and *L. selenkianum* Semper, 1868 from Viti Levu Islands (Fiji). Both these species were referred to the synonymy of *L. semperianum* by Sluiter (1901; subsequently followed by H.L. Clark, 1921). The 18 mm long *Labidodemas egestosum* Sluiter, 1901 from Saleyer (Indonesia), marked by the total absence of ossicles and calcareous ring, is a dubious species. Even Sluiter (1901) considered this form as being abnormal. It was also referred to the synonymy of *L. semperianum* by H.L. Clark (1921). Ludwig (1883) referred *L. leucopus* Haacke, 1880 and *L. neglectum* Haacke, 1880 from Mauritius to the synonymy of *Holothuria monacaria* Lesson, 1830 and *Holothuria decorata* Marenzeller, 1881, respectively. He also referred *L. punctulatum* Haacke, 1880 from Mauritius to the synonymy of *Holothuria lineata* Ludwig, 1874 (see also Pearson, 1910). Mitsikuri (1912) referred *L. leucopus*, *L. neglectum* and *H. decorata* to the synonymy of *H. monacaria* [= *H. (Mertensiothuria) hilla* Lesson, 1830]. Panning (1935a) and Rowe (1969), on the other hand, referred both *L. leucopus* and *L. neglectum* to the synonymy of *Holothuria monacaria* and *L. punctulatum* to the synonymy of *H. (Lessonothuria) pardalis* Selenka, 1867 (Panning, 1935b; see also Rowe, 1969). Table 3 summarises the history of the taxonomy of *Labidodemas*.

Nominal species as they have appeared in literature	Present disposition and authority
Labidodemas americanum Deichmann 1938	No change
Irenothuria maccullochi Deichmann, 1958	*Labidodemas maccullochi* (Deichmann, 1958): present work
Holothuria pertinax Ludwig, 1875	*Labidodemas pertinax* (Ludwig, 1875): Cherbonnier, 1988
Holothuria rugosa Ludwig, 1875	*Labidodemas rugosum* (Ludwig, 1875): Rowe, 1969
Holothuria triremis Sluiter, 1901	*Labidodemas rugosum* (Ludwig, 1875): Panning, 1935a
Labidodemas semperianum Selenka, 1867	No change
Labidodemas dubiosum Ludwig, 1875	*Labidodemas semperianum* Selenka, 1867: Sluiter, 1901, here confirmed
Labidodemas selenkianum Semper, 1868	*Labidodemas semperianum* Selenka, 1867: Sluiter, 1901, here (temporarily) confirmed
Labidodemas egestosum Sluiter, 1901	*Labidodemas semperianum* Selenka, 1867: H.L. Clark, 1921
Holothuria proceraspina Cherbonnier, 1967	*Labidodemas semperianum* Selenka, 1867: present work
Labidodemas leucopus Haacke, 1880	*Holothuria (Mertensiothuria) hilla* Lesson, 1830: Ludwig, 1883 (as *H. (Holothuria) monacaria* Lesson, 1830)
Labidodemas neglectum Haacke, 1880	*Holothuria (Mertensiothuria) hilla* Lesson, 1830: Ludwig, 1883 (as *Holothuria decorata* Marenzeller, 1881)
Labidodemas punctulatum Haacke, 1880	*Holothuria (Lessonothuria) pardalis* Selenka, 1867: Panning 1935b (as *H. (Holothuria) pardalis* Selenka, 1867)

Table 3. Nominal *Labidodemas* spp. versus the present disposition and authority.

The large number of synonyms recorded in table 3 is symptomatic of the turbulent, and at times even chaotic, classification history of the Holothuriidae. Whereas Selenka's (1867) taxon *Labidodemas* was accepted by most subsequent workers (a.o. Semper, 1868; Ludwig, 1875; 1883; Haacke, 1880; Lampert, 1885; Sluiter, 1901; Fisher, 1907; H.L. Clark, 1921; Deichmann, 1938; 1958; Rowe, 1969) it remained in the background until in 1969, Rowe created some controversies in regard to the taxonomic rank that should

be attributed to it. This lead to a re-description of *L. semperianum* (Cherbonnier, 1970), the creation of the Labidodematidae (James, 1981) and to the re-positioning of *H. pertinax* (Cherbonnier, 1988). Despite these bold decisions, many inconsistencies still pertained in literature. *Labidodemas semperianum*, for example, has numerous buttons according to Selenka (1867), Fisher, (1907), Cherbonnier (1970), Cannon and Silver (1986) and the present revision, few buttons according to Semper (1868), present work (specimen from Guam), or no buttons according to Domantay (1934) .
The present work, based on available type material and numerous voucher specimens from different, representive localities, thus not only exposed a large number of misidentifications, revealed an erroneous classification (*Holothuria (Irenothuria) maccullochi*) and a synonym (*H. proceraspina*), but also uncovered the presence of Cuvierian tubules in one species (*L. americanum*).

Systematic implications

In 1981, James erected the Labidodematidae in order to give a higher rank to the aberrant (but not unique!) characters of *Labidodemas vis-à-vis* the other genera in the family Holothuriidae. In his distinct and not too accurate diagnosis of the new family, James (1981) stressed that the tube feet and papillae of *Labidodemas* spp. are confined to the ambulacra, that the ambulacral and interambulacral areas are disproportional in size and that the body wall is translucent. With our current knowledge of the Holothuriidae, it is problematic to accept this diagnosis at family level. Indeed, the characters given by James (1981) are not only plesiomorphic, as evidenced by the fact that some species (or at least the juveniles) belonging to *Actinopyga, Bohadschia, Holothuria* and *Pearsonothuria* also have their tube feet restricted to the ambulacral areas, but, they also do not apply to all the species currently classified in *Labidodemas* (e.g. the tube feet in *L. quadripartitum* do spread into the interambulacral areas). Moreover, a character of higher taxonomic value (unique to *Labidodemas*) was ignored by James (1981): the ribbon-like structure of the calcareous ring. Despite this, the ossicle assemblage characterising the different species of *Labidodemas*, is typical of the family Holothuriidae since variously developed tables in combination with rods and/or buttons are also found in *Holothuria* and *Pearsonothuria.* The fact that *L. americanum* possesses Cuvierian tubules, a feature common to several species within the Holothuriidae, not only in *Holothuria* but also in *Actinopyga, Bohadschia and Pearsonothuria* convincingly justifies the retention of *Labidodemas* within the family Holothuriidae. In regard to the taxonomic rank that should be attributed to it, we believe it is best to maintain a conservative attitude and keep *Labidodemas* on generic level within the Holothuriidae.
Nevetheless, we urge for a phylogenetic analysis to determine if *Labidodemas*'s fossorial life style, its reduced peltate tentacles, its tube feet and papillae mostly restricted to the ambulacral areas, its ribbon-like calcareous ring, its (presumably) non-functional Cuvierian tubules (only present in *L. americanum*), its extremely variable ossicle assemblage, its non-selective feeding strategy and its wide Indo-Pacific distribution, represents the primitive condition as Levin (1999) convincingly argues or if it represents the derived form. If the latter will turn out to be the case, *Labidodemas* has closest affinity with *Holothuria* and may ultimately even prove to be part of it.

Geographical distribution

Labidodemas is restricted to the Indo-Pacific. L. *pertinax* (map 3) and *L. rugosum* (map 5) have a wide Indo-Pacific distribution. *Labidodemas pseudosemperianum* (map 4) is up to now restricted to the West Pacific. *Labidodemas americanum* and *L. maccullochi*, on the other hand, are restricted to the tropical eastern Pacific region (map 1, 2). *Labidodemas quadripartitum* and *L. spineum* are to date only known from the type locality: Sodwana Bay (Republic of South Africa) and Low Island (Australia), respectively (map 4). From a biogeographical point of view, it is interesting to note that Humphreys' (1981) record from Kenya (NHM 1979.2.5.229) of *L. semperianum* should be *L. pertinax*. This implies that *L. semperianum* is not present along the coastline of eastern Africa; the records of Cherbonnier (1967) of *Holothuria proceraspina* and those of Tortonese (1977) of *H. proceraspina* and *L. semperianum* from the Gulf of Aqaba appear to be valid. On the other hand, Price's (1981) determination of *L. semperianum* from the Persian Gulf was based on the key of Clark and Rowe (1971), hence it is not impossible that this record may also prove to be *L. pertinax* (see also comments under *L. pertinax*); similarly Price's (1983) record from the Arabian Gulf coast of Saudi Arabia, identified as *L. semperianum* most possibly is *L. pertinax* rather than *L. semperianum* for the ossicle assemblage described (tables with short spire ending in a cross

with up to five forked branches and minute rods) contradicts Selenka's (1867), Cherbonnier's (1970) and the present description where buttons have been described. Hence the distribution of *L. semperianum* most possibly is narrower than is generally assumed (map 6).
However, given the many misidentifications and erroneous classifications uncovered in the present revision, it is not improbable that careful re-examination of all the *Labidodemas* specimens deposited in museums world wide, will still alter the distribution maps as they are here provided.deposited in museums world wide, will still alter the distribution maps as they are here provided.

Acknowledgments

It is with great pleasure that we thank Drs F.W.E. Rowe and D. Pawson for critically reviewing this manuscript. This work would not have been possible without the kind help of many of our colleagues in different museums worldwide. It is with great pleasure that we thank Dr. J.F. Bertrand (MCZ), Massachusetts; Dr. S. Halsey (NHM), London; Dr. G. Hendler (NHM LAC), Los Angeles; Dr. C. Ahearn (USNM), Washington, Dr Maya-Best (RMNH), Leiden and Dr. A. Laguarda Figueras (ICML-UNAM), Mexico for sending us type and non-type material of several species; sincere thanks also to Dr. H. Ruhberg and Mr. P. Stewie for welcoming one of us (YS) at the ZMH. Financial support came from the Flemish Fund for Scientific Research (project number G.0086.96), the Ministry of the Flemish Community (project number BIL98/84 and BIL01/46) and the Research Council of the Free University of Brussels (travel grants to Kenya and the Republic of South Africa).

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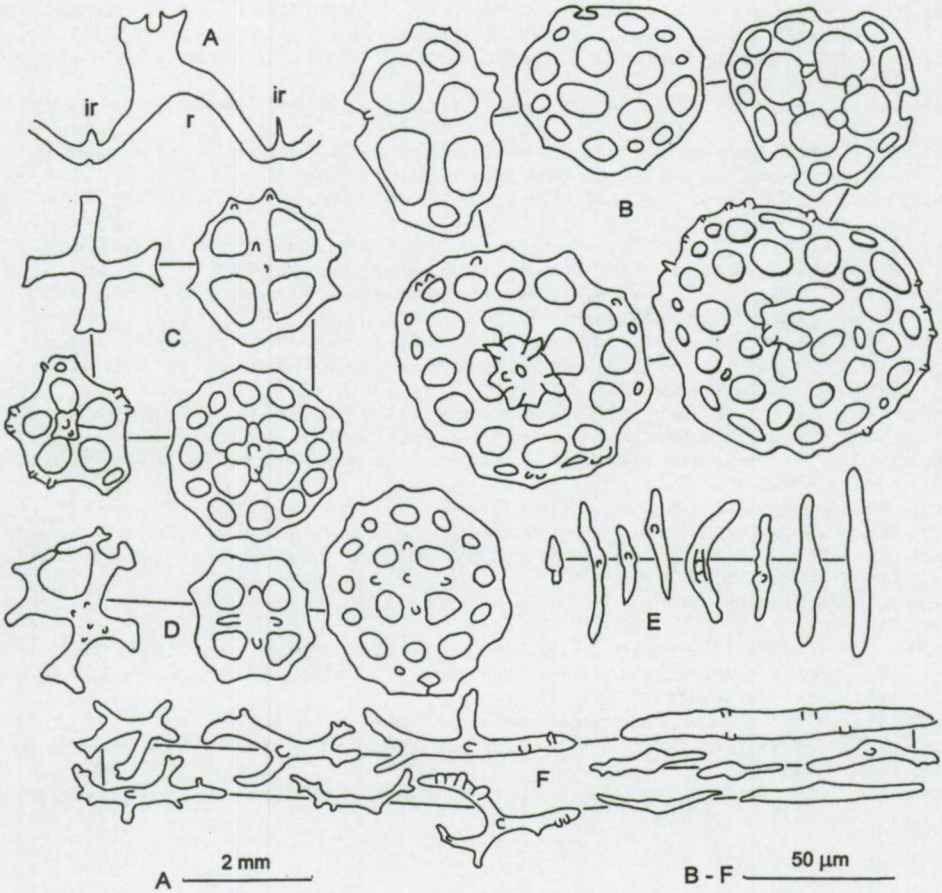

Figure 1. *Labidodemas americanum* Deichmann, 1938. (A) calcareous ring (r=radial plate; ir= interradial plate) (L = 40 mm); (B) tables of body wall (L = 85 mm); (C) tables of dorsal tube feet (L = 85 mm); (D) tables of ventral tube feet (L = 85 mm); (E) rods of tentacles (L = 85 mm); (F) rods of tentacles (L = 70 mm). Scale bars: (A) 2 mm; (B-F) 50 µm.

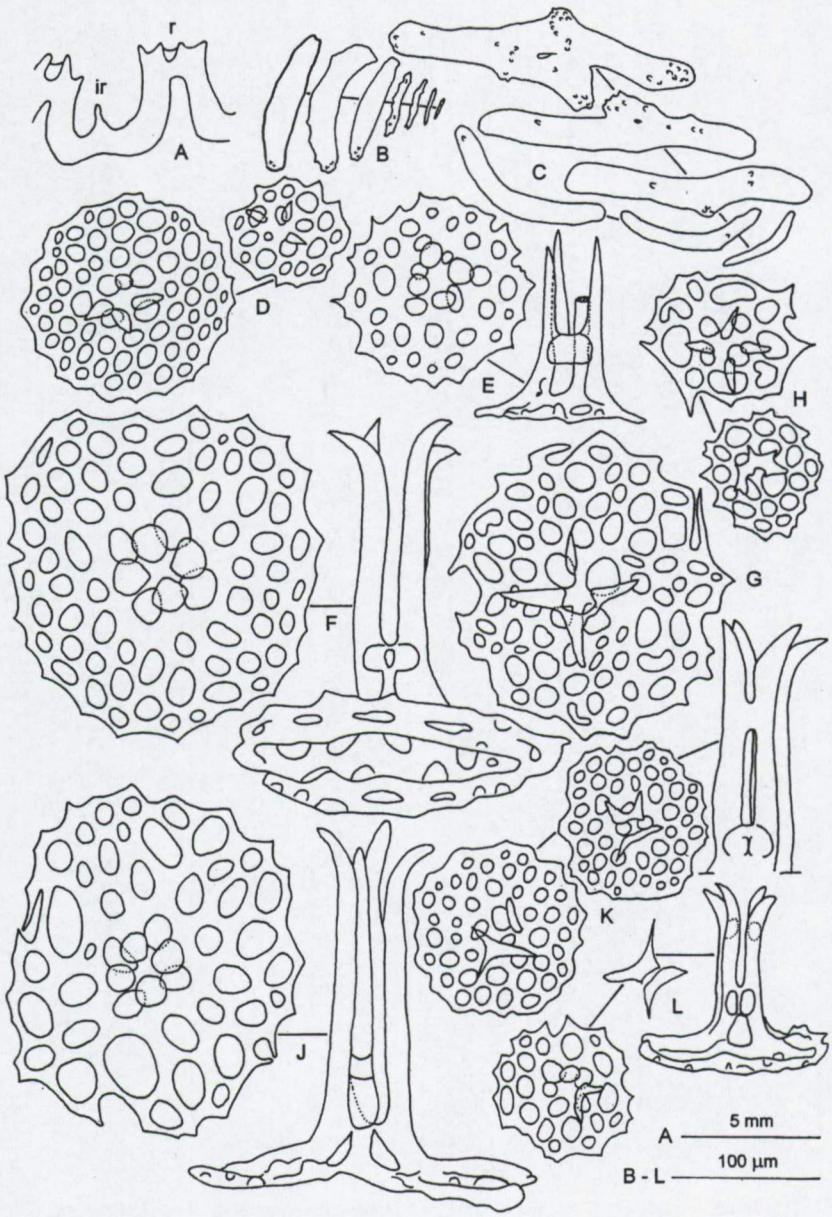

Figure 2. *Labidodemas maccullochi* (Deichmann, 1958). (A) calcareous ring (r=radial plate; ir=interradial plate) (L = 98 mm, holotype); (B) rods of tentacles (L = 98 mm, holotype); (C) rods of tentacles (L = 220 mm); (D) tables of dorsal body wall (L = 41 mm, paratype); (E) tables of dorsal body wall (L = 51 mm); (F) tables of dorsal body wall (L = 98 mm, holotype); (G) tables of dorsal body wall (L = 100 mm); (H) tables of dorsal body wall (L = 140 mm); (J) tables of dorsal body wall (L = 220 mm); (K) tables of ventral body wall (L = 41 mm, paratype); (L) tables of ventral body wall (L = 51 mm). Scale bars: (A) 5 mm; (B-L) 100µm.

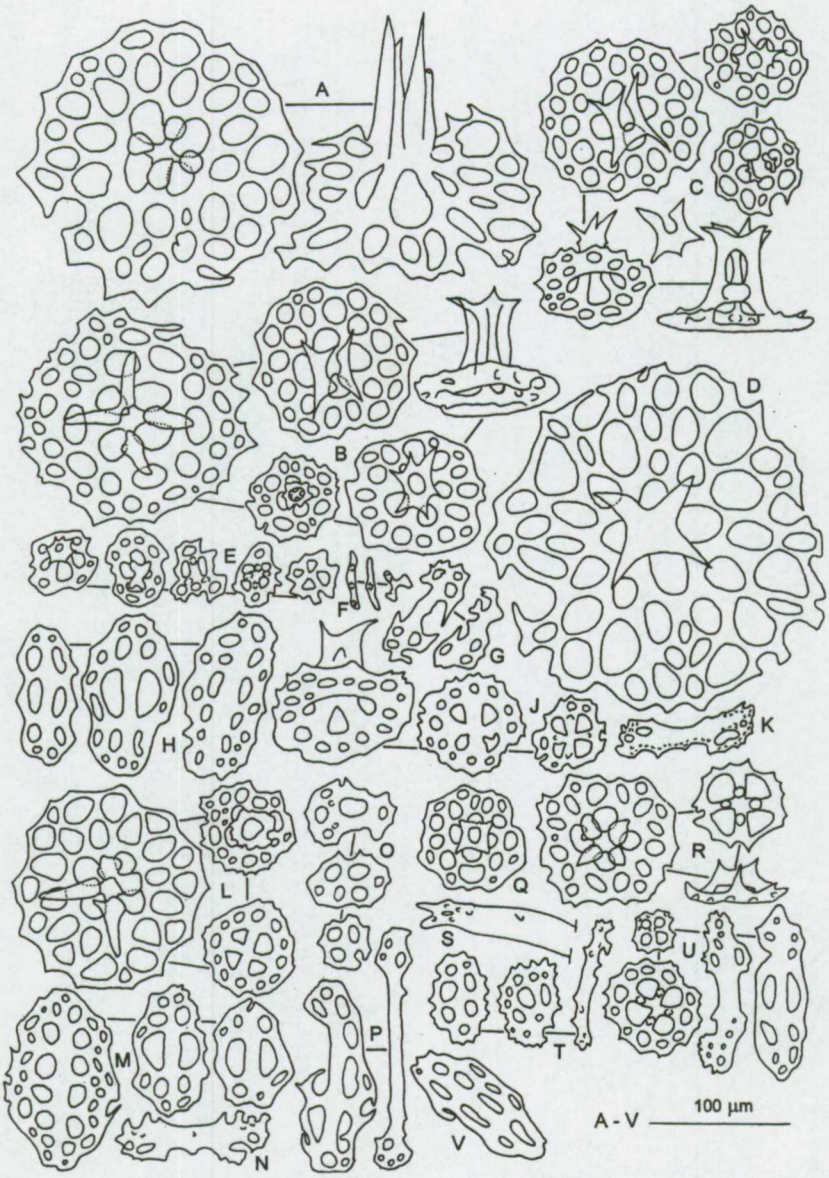

Figure 3. *Labidodemas maccullochi* (Deichmann, 1958). (A) tables of ventral body wall (L = 98 mm, holotype); (B) tables of ventral body wall (L = 100 mm); (C) tables of ventral body wall (L = 140 mm); (D) table of ventral body wall (L = 220 mm); (E) reduced tables of dorsal papillae (L = 41 mm, paratype); (F) rods of dorsal papillae (L = 41 mm, paratype); (G) pseudo-buttons of dorsal papillae (L = 41 mm, paratype); (H) buttons to perforated plates of dorsal papillae (L = 100 mm); (J) table and tables reduced to the disc of dorsal papillae (L = 100 mm); (K) rugose, perforated rod of dorsal papillae (L = 100 mm); (L) tables and table reduced to disc of dorsal papillae (L = 140 mm); (M) buttons and perforated plate of dorsal papillae (L = 140 mm); (N) rugose, perforated rod of dorsal papillae (L = 140 mm); (O) tables reduced to the disc of dorsal papillae (L = 220 mm); (P) pseudo-plate and perforated rod of dorsal papillae (L = 220 mm); (Q) table of ventral tube feet (L = 41 mm, paratype); (R) tables of ventral tube feet (L = 98 mm, holotype); (S) fragment of perforated rod of ventral tube feet (L = 98 mm, holotype); (T) pseudo-buttons and rod of ventral tube feet (L = 100 mm); (U) Reduced tables and pseudo-plates of ventral tube feet (L = 140 mm); (V) irregular button of ventral tube feet (L = 220 mm). Scale bar: (A-V) 100 µm.

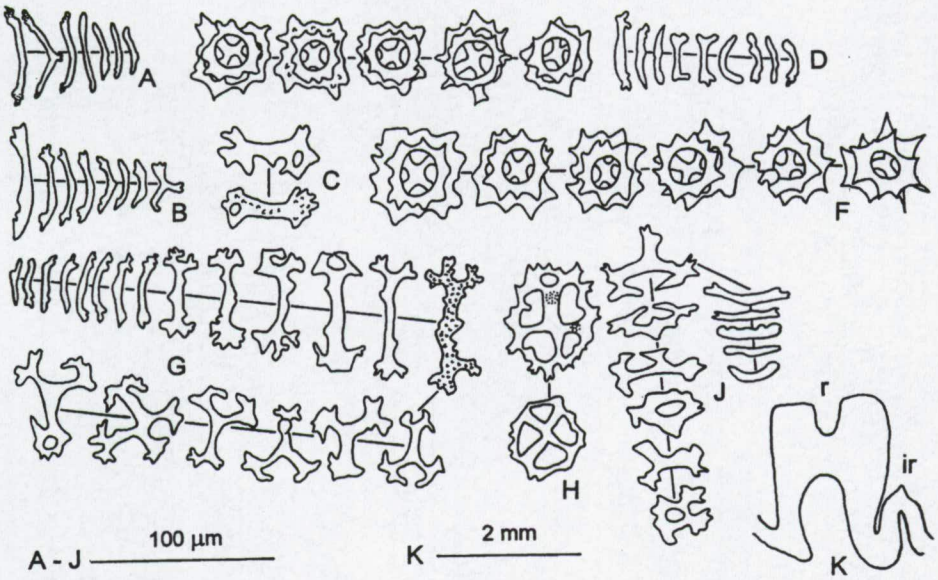

Figure 4. *Labidodemas pertinax* (Ludwig, 1875) (L=140 mm). (A) rods of tentacles; (B) and (C) rods of ventral body wall; (D) rods of dorsal body wall; (E) tables of ventral body wall; (F) tables of dorsal body wall; (G) rods of ventral tube feet; (H) tables of ventral tube feet; (J) rods of dorsal papillae; (K) calcareous ring (r=radial plate; ir=interradial plate). Scale bars: (A-J) 100 µm; (K) 2 mm.



Figure 5. *Labidodemas pseudosemperianum* sp. nov. (A) tables of dorsal body wall (holotype); (B) table of dorsal body wall (USNM E53083); (C) buttons of dorsal body wall (holotype); (D) pseudo-buttons of dorsal body wall (USNM E53083); (E) rods of dorsal body wall (USNM E53083); (F) table of ventral body wall (holotype); (G) buttons of ventral body wall (holotype); (H) tables reduced to disc of dorsal tube feet (holotype); (J) reduced table of dorsal tube feet (holotype); (K) tables of dorsal tube feet. Scale bar (A-K) 50 µm.

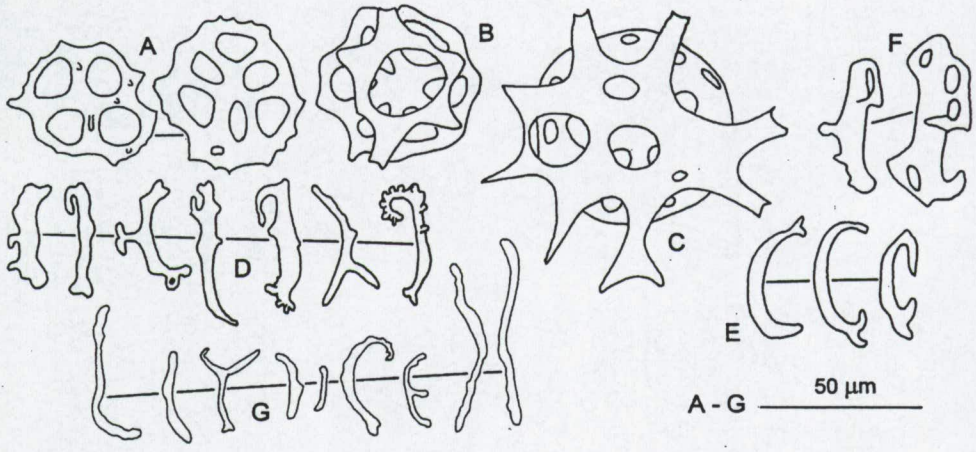

Figure 6. *Labidodemas pseudosemperianum* sp. nov. Holotype. (A) tables reduced to disc of ventral tube feet; (B) reduced table of ventral tube feet; (C) table of ventral tube feet; (D) rods of ventral tube feet; (E) C-shaped rods of ventral tube feet; (F) pseudo-buttons of ventral tube feet; (G) rods of tentacles. Scale bar (A-G) 50 µm.

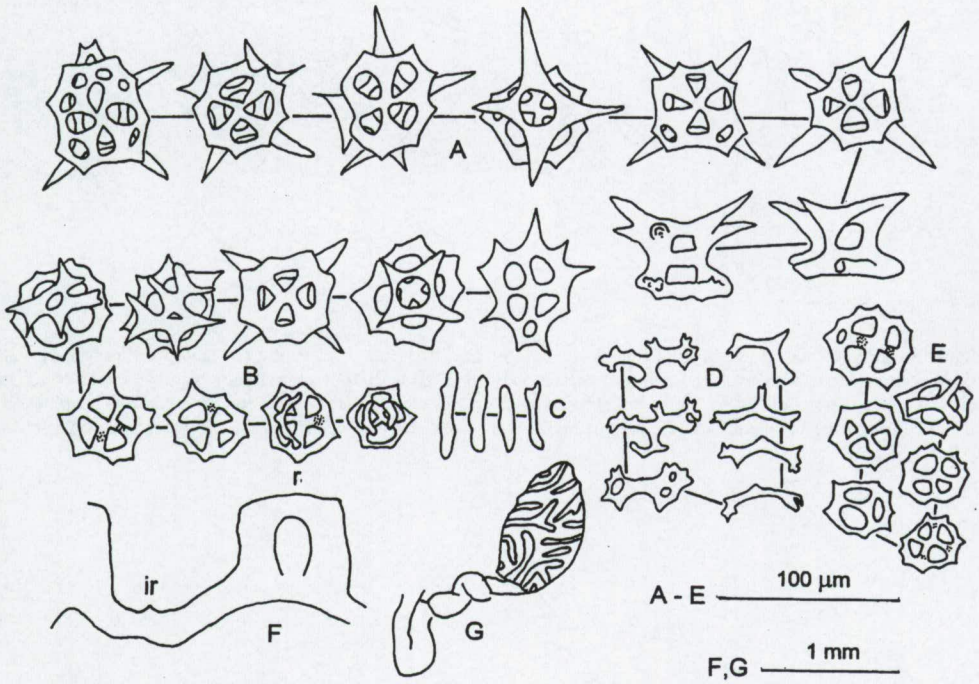

Figure 7. *Labidodemas quadripartitum* sp. nov. (L=110 mm). (A) tables of ventral body wall; (B) tables of dorsal body wall; (C) rods of dorsal body wall; (D) rods of ventral tube feet; (E) tables of ventral tube feet; (F) calcareous ring (r=radial plate; ir=interradial plate); (G) stone canal and madreporic plate. Scale bars (A-E) 100 µm; (F, G) 1 mm.

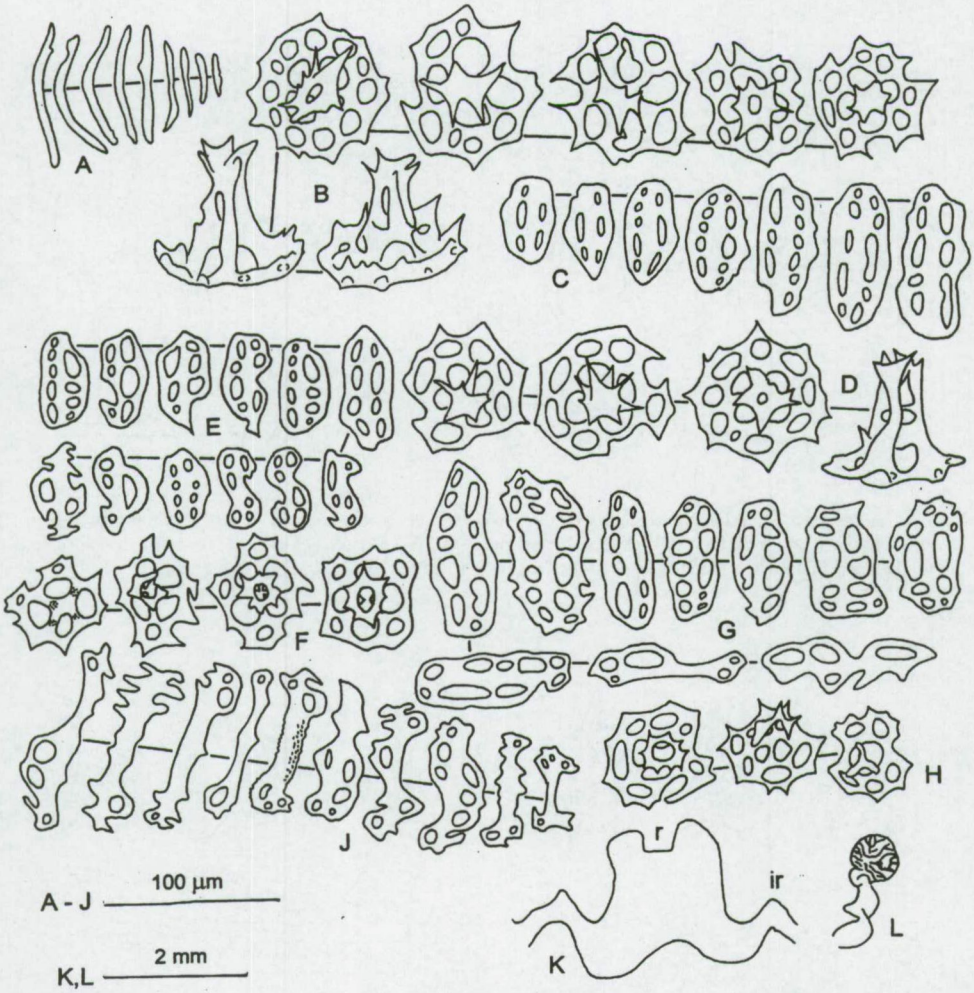

Figure 8. *Labidodemas rugosum* (Ludwig, 1875). (L=130 mm). (A) rods of tentacles; (B) tables of dorsal body wall; (C) buttons of dorsal body wall; (D) tables of ventral body wall; (E) buttons of ventral body wall; (F) tables of ventral tube feet; (G) buttons of ventral tube feet; (H) tables of dorsal papillae; (J) buttons to rods of dorsal papillae; (K) calcareous ring (r=radial plate; ir=interradial plate); (L) stone canal and madreporic plate. Scale bars: (A-J) 100 µm; (K, L) 2 mm.



Figure 9. *Labidodemas semperianum* Selenka, 1867. Lectotype. (A) calcareous ring (ir: interradial plate; r: radial plate); (B) tables of ventral body wall; (C) tables of dorsal body wall; (D) buttons of dorsal body wall; (E) pseudo-buttons of dorsal body wall; (F) rods of dorsal body wall; (G) spiny perforated plates of ventral tube feet; (H) rods of ventral tube feet; (J) rods of dorsal papillae. Scale bars (A) 5 mm; (B-J) 50 µm.

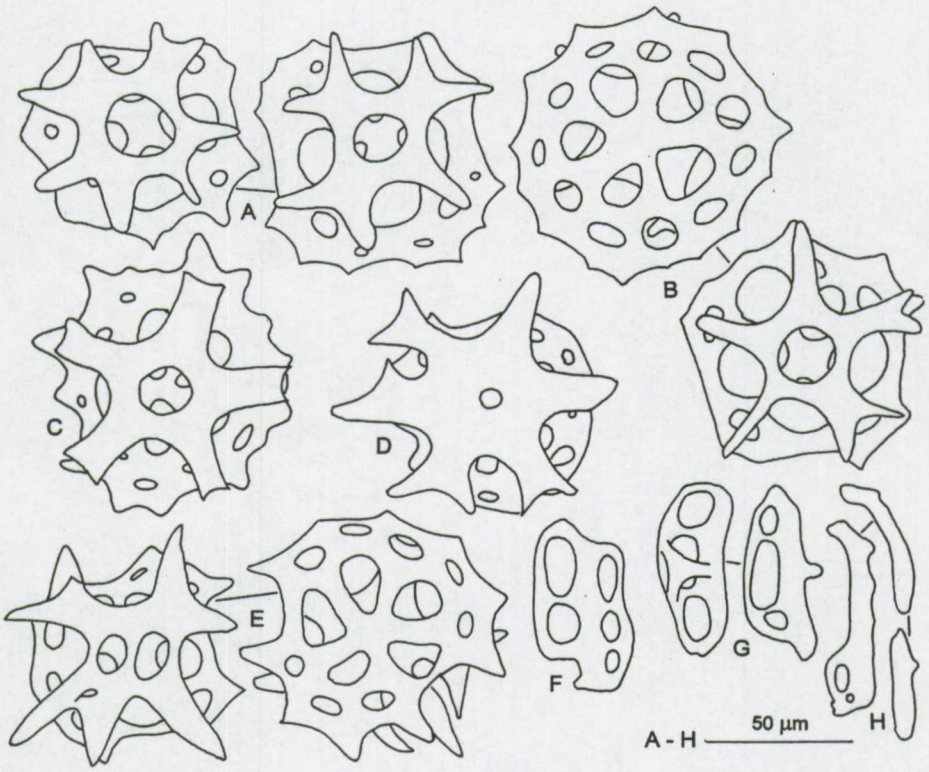

Figure 10. *Labidodemas semperianum* Selenka, 1867. (A) tables of dorsal body wall (paralectotype); (B) tables of ventral body wall (paralectotype); (C) table of dorsal body wall (USNM E11583); (D) table of dorsal body wall (USNM E40771); (E) tables of ventral body wall (USNM E40771); (F) buttons of dorsal body wall (USNM E40771); (G) pseudo-buttons of dorsal body wall (USNM E40771); (H) rods of the dorsal body wall (USNM E40771). Scale bar (A-H) 50 µm.

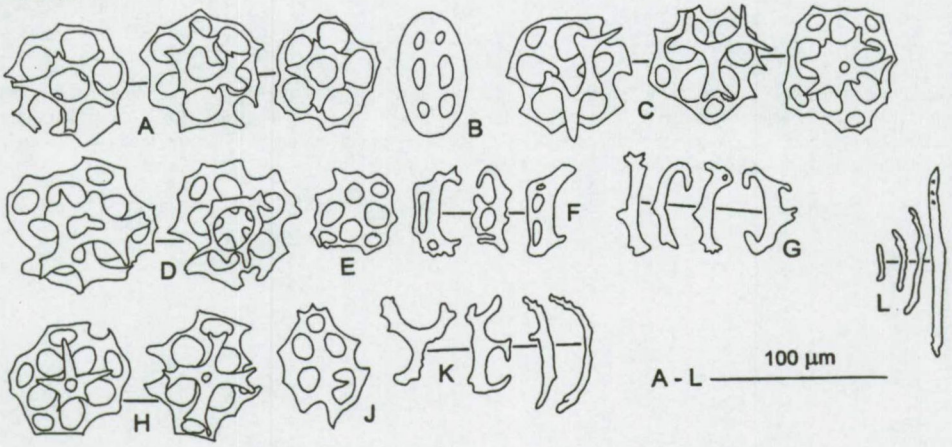

Figure 11. *Labidodemas selenkianum* Semper, 1868 (holotype); (A) tables of dorsal body wall; (B) button of dorsal body wall; (C) tables of ventral body wall; (D) tables of dorsal tube feet; (E) spiny perforated plate of dorsal tube feet; (F) pseudo-buttons of dorsal tube feet; (G) rods of dorsal tube feet; (H) tables of ventral tube feet; (J) perforated plate of ventral tube feet; (K) rods of ventral tube feet; (L) rods of tentacles. Scale bar (A-H) 100 µm.

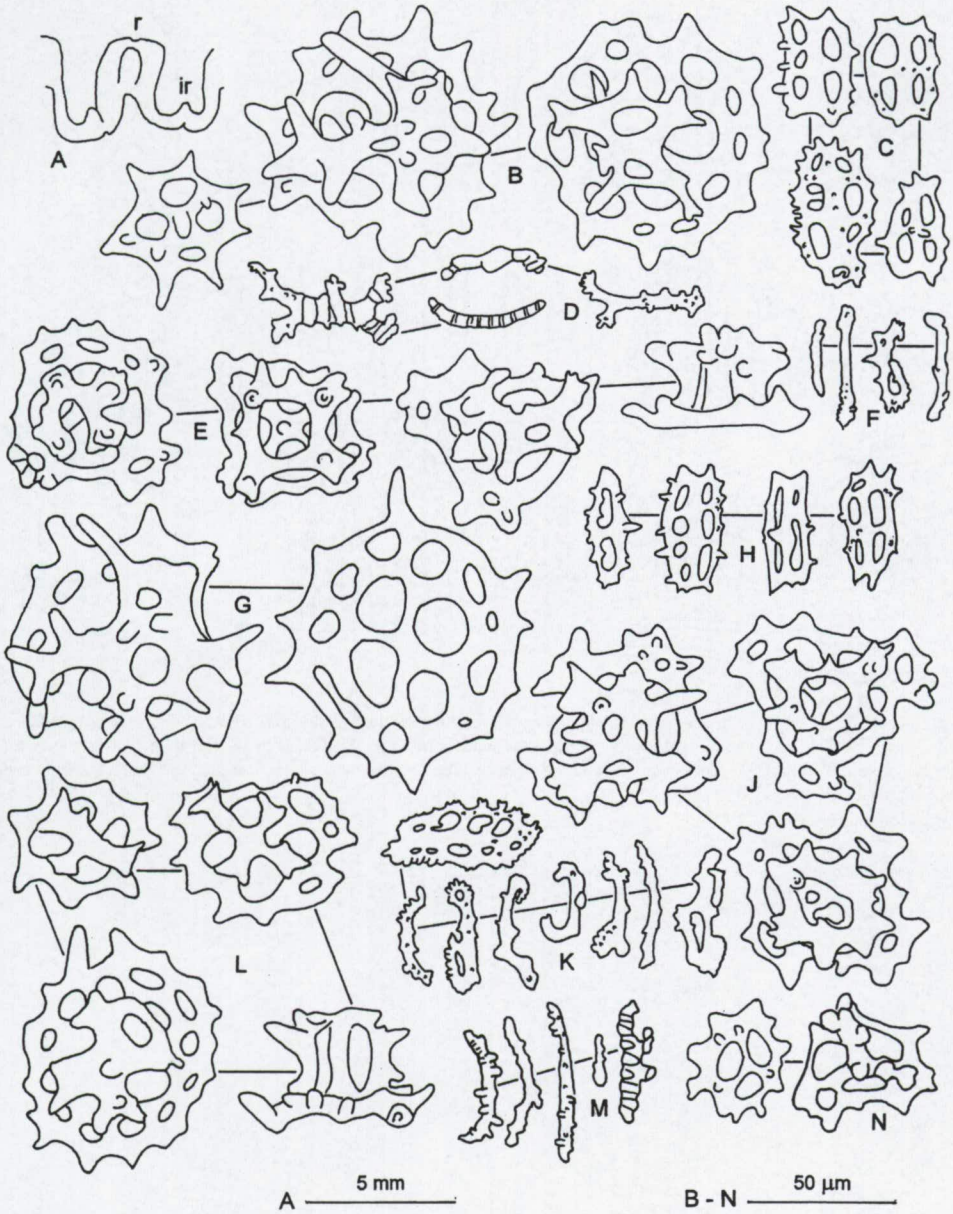

Figure 12. *Labidodemas spineum* sp. nov. (A) calcareous ring (r=radial plate; ir=interradial plate)(holotype); (B) tables of dorsal body wall (holotype); (C) buttons of dorsal body wall (holotype); (D) rods of dorsal body wall (holotype); (E) tables of dorsal body wall (paratype); (F) rods of dorsal body wall (paratype); (G) tables of ventral body wall (holotype); (H) buttons of ventral body wall (holotype); (J) tables of ventral body wall (paratype); (K) rods and buttons of ventral body wall (paratype); (L) tables of dorsal tube feet (holotype); (M) rods of dorsal tube feet (holotype); (N) tables of dorsal tube feet (paratype). Scale bar (A) 5 mm; (B-N) 50 µm.

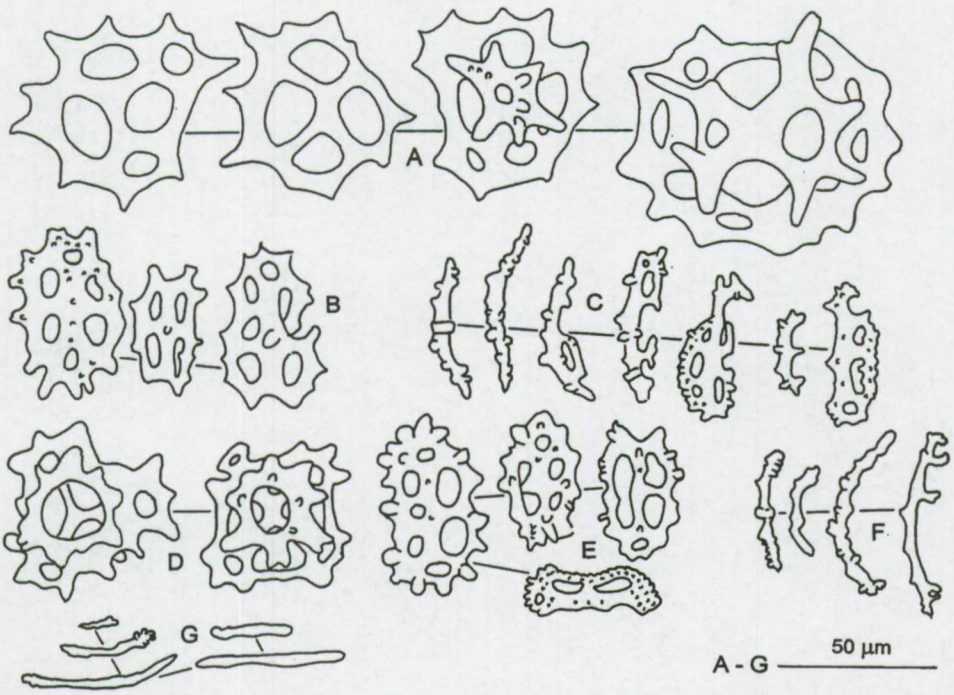

Figure 13. *Labidodemas spineum* sp. nov. (A) tables of ventral tube feet (holotype); (B) buttons of ventral tube feet (holotype); (C) rods and pseudo buttons of ventral tube feet (holotype); (D) tables of ventral tube feet (paratype); (E) buttons of ventral tube feet (paratype); (F) rods of ventral tube feet (paratype); (G) rods of the tentacles (holotype). Scale bar (A-G) 50 µm.

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Phylogeny of *Labidodemas* and the Holothuriidae (Holothuroidea: Aspidochirotida) as inferred from morphology

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ABSTRACT

The Holothuriidae is one of the three established families within the large holothuroid order Aspidochirotida. The approximately 185 recognized species of this family are commonly classified in five nominal genera, *Actinopyga*, *Bohadschia*, *Holothuria*, *Pearsonothuria* and *Labidodemas*. Maximum parsimony analyses on morphological characters, as inferred from type and non-type material of the five genera, revealed that *Labidodemas* comprises highly derived species that arose from within the genus *Holothuria*. The paraphyletic status of the latter, large (148 assumed valid species) and morphologically diverse genus has recently been recognized and is here confirmed and discussed. Nevertheless, we adopt a Darwinian or eclectic classification for *Labidodemas* which we retain at generic level within the Holothuriidae. Further, by comparing our phylogeny of the Holothuriidae with past and present classifications of its genera and subgenera we make suggestions concerning possible taxonomic changes.

Keywords

Phylogeny - systematics - morphology - eclectic taxonomy - classification - evolution - Holothuriidae - Holothuroidea - *Labidodemas* - *Holothuria* - *Actinopyga* - *Bohaschia* - *Pearsonothuria*

Introduction

Recently Massin, Samyn & Thandar (in press) reviewed the holothuroid genus *Labidodemas* Selenka, 1867, describing three new species and transferring two species from *Holothuria* Linnaeus, 1767, one being a synonym of the type species and one being a valid species. Most interestingly, Massin *et al.* (in press) were the first to discover that one species in *Labidodemas* (*L. americanum* Deichmann, 1938) possesses Cuvierian tubules. This new finding allowed Massin *et al* (in press) to question the family rank that James (1981; see also Rowe 1969 for a more balanced view of ranking) had attributed to the group. As the other four genera in the Holothuriidae – *Actinopyga* Bronn, 1860; *Bohadschia* Jaeger, 1833; *Pearsonothuria* Levin, 1984 and *Holothuria* Linneaus, 1767 – also have representatives possessing this organ, Massin *et al.* (in press) argued that *Labidodemas* is best kept within the Holothuriidae. By doing so the latter authors regarded presence of Cuvierian tubules as a synapomorphic character of the Holothuriidae, absence of Cuvierian tubules being due to secondary loss. In regard to the taxonomic rank, Massin *et al.* (in press) gave high weight to the ribbon-like form of the calcareous ring and proposed retaining *Labidodemas* at generic level. However, these authors urged that a phylogenetic analysis be carried out to determine the exact systematic position and taxonomic rank of *Labidodemas*. Such a study has recently been conducted by two independent teams. Kerr *et al* (submitted), on the basis of a 16S mtDNA sequence, and our team (Appeltans, 2002), on the basis of morphological characters, who found that *Labidodemas* indeed falls

within the Holothuriidae, more specifically within the genus *Holothuria*. However, as Kerr *et al.* (submitted) and Appeltans (2002) were not in the position to use all the currently existing species within *Labidodemas* spp., they could not accurately test its monophyly or present a phylogeny. As such, these authors were not in the position to argue conclusively on the taxonomic rank that should be attributed to *Labidodemas*.

In the present paper, we performed a cladistic analysis on 132 morphological characters that were drawn from type and non-type species of the five currently recognized holothuriid genera. This analysis allows objective selection between two recent scenarios that attempted to explain the direction of evolution in *Holothuria*. The first was formulated by Deichmann (1958: 276), who considered *Labidodemas* as a sister genus of *Holothuria sensu lato* (Pearson, 1914), argueing that within *Holothuria* "most primitive are undoubtedly those with numerous regular tables and regular smooth buttons, somewhat reminiscent of certain synallactid-like members of the Stichopodidae", whilst "a more advanced stage is indicated by the presence of irregular buttons, or the development of rosettes, or the reduction of the inner layer of spicules, while the tables have become variously modified". The second is attributed to Rowe (1969) who also regarded *Labidodemas* as a sister clade to the other holothuriid genera (but see also James, 1981; Massin *et al.*, in press) but, contrary to Deichmann (1958), reasoned that species with plates, and without tables or buttons represent the more primitive condition, whereas those with regular tables and buttons represent the more advanced forms. Interestingly, Massin *et al.* (2000), following their detailed study of the ontogeny of ossicles in *Holothuria (Metriatyla) scabra* Jaeger, 1833, came to the conclusion that absence of buttons and presence of tables with tall spire are plesiomorph characters in the evolution of the Holothuriidae. From an ecological point of view this implies that, according to Deichmann (1958), holothurian surf-zone species (inhabiting exposed places such as rock-crevices) and holothurian rock-clinging species are more advanced, whilst according to Rowe (1969; pers. comm.) the latter forms are to be considered primitive. Whereas Deichmann (1958) did not provide a satisfying explanation for her line of reasoning, Rowe (1969; pers. comm.) underlines that his views are based on the conclusions of Pawson & Fell (1965), who argued that dendrochirotids (with dendritic tentacles) are more primitive than aspidochirotids (predominantly peltate tentacles). Thus, to Rowe (1969; pers. comm.) holothurians with more dendritiform tentacles (as found in the subgenera *Selenkothuria* Deichmann, 1958 and *Semperothuria* Deichmann, 1958) are to be considered more primitive. In regard to the evolution of the genera, neither Deichmann (1958) nor Rowe (1969) took position, although Rowe (pers. comm.) nowadays advocates that *Actinopyga* and *Bohadschia* are derived possibly through the *Pearsonothuria* form which is (i) more *Holothuria*-like in body form and (ii) appears to have highly modified tables (raquets) and very complex rosettes.

Systematics of the Holothuriidae through time

Ever since it's description, the alpha- and beta-taxonomy of *Labidodemas* Selenka, 1867 has been the subject of a considerable and often conflicting debate (Massin *et al.*, submitted and references therein). This is hardly surprising as the taxonomic history of *Holothuria* and the Holothuriidae has been the subject of much, at times chaotic, debate which is here briefly reviewed.

At the beginning of the twentieth century, the Holothuriidae were commonly divided on the basis of presence and/or absence of anal teeth and the position of tube feet whereby two genera, *Mülleria* Jaeger and *Holothuria* Linnaeus, were recognized. Pearson (1914), after examination of "a large number of species [sic]", proposed a re-classification arguing that the number and arrangement of tentacles, Polian vesicles, stone canals and Cuvierian tubules must be disregarded for classification purposes. Instead, he utilised the structure of the calcareous ring, the ossicle assemblage and the arrangement of tube feet and papillae to arrive at a classification that is "in accordance with relationship [sic]"). Pearson (1914) grouped *Mülleria* and *Holothuria* (*sensu stricto*) under the single genus *Holothuria* (*sensu extenso*) wherein he discerned five subgenera: *Actinopyga* Bronn, 1860, *Argiodia* Pearson, 1914, *Bohadschia* Jaeger, 1833, *Halodeima* Pearson, 1914 and *Thymiosycia* Pearson, 1914. The first two subgenera contained species formerly classified under *Mülleria* while the latter three subgenera held species formerly classified under *Holothuria* sensu stricto (fig. 1).

Pearson (1914) further believed that *Actinopyga* and *Bohadschia* (with the ambulacral appendages more or less arranged in rows; the ossicles in the form rosettes and rods; the calcareous ring without anterior & posterior projections, but with deep ampullary notches and the interradial pieces almost as high as the radial pieces) represent the primitive condition whereas *Argiodia, Halodeima* and *Thymiosycia* (with scattered ambulacral appendages, table and button ossicles and a calcareous ring with pronounced anterior and

posterior projections and a deep indentation between the radial and interradial pieces) are the more advanced forms.

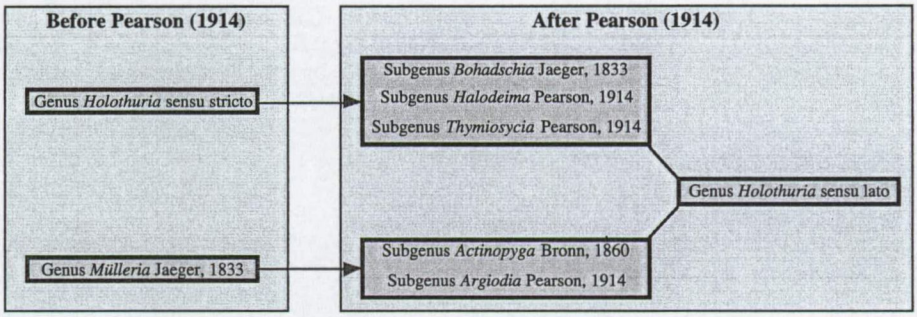

Figure 1. Classification of the genus *Holothuria* before and after Pearson's (1914) revision.

H.L. Clark (1921) completely ignored Pearson's (1914) work and opted to follow Fisher's (1907) classification, albeit with some modifications *vis-à-vis* the rank of the Holothuriidae which he divided into five genera: *Actinopyga* Bronn, 1860; *Labidodemas* Selenka, 1867; *Holothuria* Linnaeus, 1767; *Stichopus* Brandt, 1835 and *Thelenota* Brandt, 1835. This classification was largely followed by subsequent authors (a.o. H.L. Clark, 1922; 1923; Deichmann, 1926; Domantay, 1933). It is unclear why this generation of taxonomists systematically ignored Haeckel's (1896; see also Östergren, 1907) important revision separating the Stichopodidae from the Holothuriidae. Panning's (1931b; 1935a-d) revision of *Holothuria* stands as a series of highly significant works in the classification of *Holothuria*. Not only did Panning consider virtually all the available literature (a merit on its own in the turbulent *interbellum*), he also critically analysed most of it and listed virtually complete synonym lists. Panning's *magnum opus* was perhaps a bit too descriptive and conservative as was noted by Deichmann (1958, see also Rowe, 1969: 121) who stated: "this magnificent work suffers from his dependence in too many cases on the accounts of earlier writers; hence many errors have been perpetuated and related forms have been placed far apart." Be it as it may, Panning's insights into holothurian α-taxonomy clearly paved the way for the β-taxonomy that was to follow in the coming decades. Panning (1931b; 1935a-d) tried to follow Pearson's (1914) classification but rapidly (and understandably) came into conflict with the latter's observations. Panning, in his first paper (1931b) gave three pertinent reasons why Pearson's system needed rethinking. Firstly he argued that, Pearson's new taxa were too vaguely described and that it was not clearly stated which species they contained. Secondly he noticed that Pearson separated *Thymiosycia* from *Halodeima* on only a single character (*i.e. Halodeima* with tube feet and papillae, *Thymiosycia* with papillae only), which to Panning was insufficient justification (he chose to put *Thymiosycia* as a synonym of *Halodeima*). Thirdly he opposed Pearson's arbitrariness in not considering the geographic distribution (Atlantic versus Pacific) of the different species, and argued that by doing so Pearson had necessarily overlooked a large number of synonyms. In 1931(b), Panning recognized *Actinopyga* Bronn, *Bohadschia* Jaeger, *Halodeima* Pearson and *Microthele* Brandt [Panning correctly recognized that Brandt's (1835) *Microthele* has priority over Pearson's (1914) *Argiodia* even though he did not acknowledge it in the original (Brandt, 1835) meaning] as subgenera in *Holothuria* (*sensu* Pearson). By 1935(a-d), Panning had altered and refined his classification: on Fisher's advice (see 1935a: 24) he grouped Pearson's (1914) subgenera *Halodeima* and *Thymiosycia* in the subgenus *Holothuria sensu stricto*. Thus, Panning (1935a-d) now recognized four subgenera in the genus *Holothuria s.l.*: *Actinopyga, Bohadschia, Microthele* and *Holothuria s.s,* whereby he believed (1935a: 25) that *Actinopyga* was most closely related to *Microthele* and *Bohadschia* to *Holothuria s.s.* Based upon his studies of the optical properties of ossicles, Panning (1928; 1931a; 1931c; 1933; hereby partially drawing on Hérouard 1889; 1925 and Perrier 1902; but see also Schmidt, 1925; 1932) concluded that the subgenus *Holothuria* was best split in two groups, those with rosettes and those with true buttons. He defined rosettes as small, thin plates that develop from a rod which bifurcates at each end (*Gabelstab*), the terminal branches equally growing at an angle of 120° from the rod and eventually (can) anastomosing, thus forming large, lateral perforations and always a pair of terminal holes. As such, the central perforations are often rather large and non-roundish while the branches are generally thin and

the overall shape of the rosette is irregular. True buttons on the other hand, even if they are *an sich* also thin plates, arise from a non-terminally branching primary rod (*ungegabelten Primärstab*) that develops lateral projections perpendicular to the primary rod. As such, when these projections bifurcate at their ends and eventually anastomose, pairs of opposite perforations, one either side of the median rod, are formed; terminal holes are absent. Moreover, in true buttons, the holes are generally smaller and more roundish and the rim of the button (when it is fully formed) is rather smooth, giving the impression of a "finished ossicle". Fig. 2 gives Panning's (1951) drawings on the position of the optical axes as present in rosette-like buttons and in true buttons as well as scaled drawings of the two ossicle types.

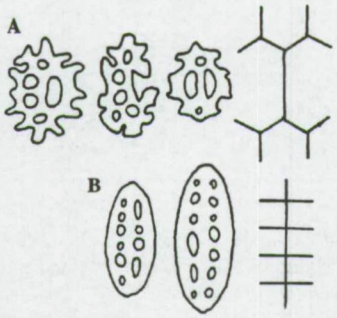

Figure 2. Rosettes versus buttons according to Panning (1951: 178). Top: rosettes of *Holothuria (Halodeima) grisea* Selenka, 1867; with a schematic representation of the bifurcate rod. Bottom: true buttons of *Holothuria (Platyperona) sanctori* Delle Chiaje, 1823, with a schematic representation of the branching of the primary rod.

Panning, even though he continually defended his line of reasoning, unfortunately failed to develop his observations into an unambiguous classification of *Holothuria* and was drawn to the conclusion that "Dies sind die Formen der beiden Kalkkörperarten im Regelfalle; über Abweichungen und Zwischenstufen mag an anderer Stelle die Rede sein [sic.]; (Panning, 1935a: 25). Perhaps this is the reason why he stated that he did not want to burden the systematics of the subgenus *Holothuria* with yet other names and why he instead created two large groups. His *Abteilung A* grouped those species with rosettes and rosette-like buttons, while his *Abteilung B* clustered those species that possess true buttons. To the latter he put the name *Sporadipus*, a designation originally given by Brandt (1835). In these two subdivisions he (1935a-d) discerned several smaller groups, which he based almost exclusively on ossicle assemblage. As such, he created five 'Reiche" in *Abteilung A* and eight 'Reiche' in *Abteilung B* (*Sporadipus*). By 1940 (p. 523), Panning realised that (our brackets) "Dass beide Untergattungen (*Actinopyga* and *Microthele*) Afterzähne haben, ist nur eine Konvergenz, über die wir allerdings nicht weiter urteilen können, da wir die Bedeutung dieser Gebilde nicht kennen" and that thus *Actinopyga* and *Microthele* can no longer be considered closely related taxa. Moreover, as he thought *Actinopyga* Bronn, 1860 and *Bohadschia* Jaeger, 1833 differed from one another only by the presence of anal teeth (in *Actinopyga*); he put *Actinopyga* as a subgenus of *Bohadschia*. Further, he raised his *Abteilung A* to genus level which he named *Halodeima* Pearson, 1914; and his *Abteilung B* he split into the genera *Microthele* Brandt, 1935 and *Holothuria* Linneaus, 1767, confusingly noting that under certain circumstances *Microthele* has to be seen as "nur eine Untergattung von *Holothuria*" (Panning, 1940: 524). By 1944, Panning reached his final classification of *Holothuria*; now recognising five genera: *Actinopyga, Bohadschia, Halodeima, Holothuria* and *Microthele*. This classification was accepted and used by subsequent taxonomists (e.g. Tortonese, Cherbonnier,...), though in 1946, H.L. Clark noted that (our square brackets): "the natural classification of this family [Holothuriidae] has yet to be discovered. It is a large group with scores of species, but the attempts to break it up into genera have as yet proved unsatisfactory. The genus *Actinopyga* is apparently a natural group and its species are easily recognized. *Labidodemas* is much less satisfactory, and the number of component species is doubtful (monotypic). The rest of the family are best retained in the old genus *Holothuria*. Pearson (1913-1914) started out on the task of breaking up the genus, but he made little progress and his work has never been continued. Panning (1931b-1935) attacked the problem *de novo* and gave promise of reaching some helpful conclusions, but he was diverted into a different line of work and his results were incomplete. Neither Pearson nor Panning had access to sufficient material to enable him fully to meet the problems, and it seems best to continue using the name *Holothuria* in the old sense until someone with access to at least half the named species can concentrate on the problem". H.L. Clark (1946), who at that time must have examined an uncountable number of specimens, thus clearly urged for a new start. Deichmann, who had

access to the important collections brought home by the Velero III and IV, took up the challenge and, in 1958, presented a new classification. She rejected Pearson's, Panning's and H.L. Clark's classifications to a large extent. At generic level, she accepted Panning's (1940; 1944) view of *Actinopyga, Bohadschia* and *Microthele* (even though she, as Panning before her, unfortunately failed to recognize *Microthele* in Brandt's (1835) original sense). In addition, she recognized that the small genus *Labidodemas* Selenka, 1867 (in which she, in 1938, had described the species *L. americanum*), did not belong to *Holothuria* s.l. (Panning, 1935c), but stands on its own. Enigmatically, she (1958: 311) changed *Halodeima*, which she "accepted with minor changes" to *Ludwigothuria* Deichmann, 1958. More radical was her decision to split the genus *Holothuria* into several new genera and to abandon the old name *Holothuria* completely. Clark & Rowe (1967) and Rowe (1969: 9; see also Gill, 1907a,b) correctly disagreed with this latter decision for "In 1924 (Opinion 80) the generic name *Holothuria* Linnaeus, 1767, as restricted by Bruguière, 1791, with type-species *H. tremula* Linnaeus, 1767 (non Gunnerus, 1767) = *H. tubulosa* Gmelin, 1790, was placed on the Official List of Generic Names in Zoology" and "this action therefore firmly established the generic name *Holothuria* in the present sense rather than the original one of Linnaeus, 1758". Irrespective of the last nomenclatural flaw, it is clear that Deichmann's (1958) division of *Holothuria* was, as she said herself, "foreshadowed in the key which W.K. Fisher made for the Hawaiian holothurians in 1907". This decision, as noted by Rowe (1969: 122), relied quite heavily on the ecological position of the different taxa she studied. This again comes as no surprise as Deichmann clearly was a product of a new movement, which is now referred to as *evolutionary morphology*. This school, so notes Mayr (1982: 468), typically asks questions such as "Why and how did the ancestral type give rise to new morphological types? To what extent was a change in niche occupation or, indeed, the invasion of an entirely new adaptive zone responsible for the anatomical reconstruction? What was the nature of the selection pressures? Was behaviour the pacemaker of the ecological shift? What was the nature of the population in which the decisive shift occurred?". Hardly anybody will nowadays dispute that the answers to these grand questions unmistakably can resolve many of the classificationary impasses, but getting these is another cup of tea. Be it as it may, Deichmann's (1958) classification was interesting in its novelty and definitely worth critical study. Rowe (1969) took up the latter challenge when he revised the complete Holothuriidae. Rowe (1969: 119) correctly pointed out that by creating 11 new generic names " Deichmann has disregarded a number of appropriate prior genus-group names of Brandt (1835), Jaeger (1833), Haacke (1880) and Pearson (1914) on the grounds of poor definition, most of these names *are* available under the Rules, being associated with recognized species, those of Jaeger and Brandt needing only designations of type-species in order to qualify for recognition under the Rules". In the end, Rowe (1969) came to the conclusion that Deichmann's taxonomic groups are best regarded as subgenera of *Holothuria*, which he considered a monophyletic group. Rowe thus agreed largely with Panning's (1940; 1944) generic classification (although he placed *Microthele* and *Halodeima* at subgeneric level), and with Deichmann (1958) in regard to the position of *Labidodemas*. Albeit his phrase (Rowe 1969: 126) "In truth I think *Labidodemas* may even prove to warrant separation at family level" caused some commotion during the last two decades (James, 1981; Massin *et al.*, submitted). Rowe (1969:122-123) summarised the supraspecific taxa (our brackets) when he presented "a table of the supraspecific taxa with their type-species represented in her (Deichmann's 1958) paper together with their present disposition" This table is here reproduced with permission (table 4).

Table 4. Supraspecific taxa with their type species with the disposition according to Rowe (1969) (from Rowe, 1969: 122-123).

Genus-group name	Type-species	Disposition (anno 1969)
Labidodemas Selenka, 1867	*L. semperianum* Selenka, 1867	Valid genus
Microthele: Deichmann, 1958 (non Brandt, 1835)	*Holothuria sanctori* Delle Chiaje, 1823	*Holothuria (Platyperona)* subg. nov.; type-species *Holothuria difficilis* Semper, 1868
Brandtothuria Deichmann, 1958	*H. arenicola* Semper, 1868	*H. (Thymiosycia)* Pearson, 1914; type-species *Fistularia impatiens* Forskål, 1775
Lessonothuria Deichmann, 1958	*H. pardalis* Selenka, 1867	Valid subgenus
Mertensiothuria Deichmann, 1958	*Stichopus leucospilota* Brandt, 1835	Valid subgenus
Semperothuria Deichmann, 1958	*Holothuria languens* Selenka, 1867	Valid subgenus
Irenothuria Deichmann, 1958	*I. maccullochi* Deichmann, 1958	Valid subgenus
Vaneyothuria Deichmann, 1958	*Holothuria lentiginosa* v. Marenzeller, 1893	Valid subgenus
Ludwigothuria Deichmann, 1958	*H. atra* Jaeger, 1833	*Holothuria (Halodeima) atra* Pearson, 1914; type-species *H. atra* Jaeger, 1833
Selenkothuria Deichmann, 1958	*H. lubrica* Selenka, 1867	Valid subgenus
Fossothuria Deichmann, 1958	*Stichopus rigidus* Selenka, 1867	*H. (Cystipus)* Haacke, 1880; type-species *C. pleuripus* Haacke, 1880, a junior

		subjective synonym of *Stichopus rigidus* Selenka, 1867
Jaegerothuria Deichmann, 1958	*Holothuria inhabilis* Selenka, 1867	*H. (Cystipus)* Haacke, 1880
Theelothuria Deichmann, 1958	*H. princeps* Selenka, 1867	Valid subgenus

In addition, Rowe (1969) described five new subgenera to accommodate the species that could not be fitted in Deichmann's (1958) revised supraspecific taxa. These are: *Acanthotrapeza* with type-species *Holothuria pyxis* Selenka, 1867; *Metriatyla* with type-species *H. scabra* Jaeger, 1833; *Panningothuria* with type-species *H. forskali* Delle Chiaje, 1823; *Platyperona* with type-species *H. difficilis* Semper, 1868 and *Stauropora* with type-species *H. discrepans* Semper, 1868. Based on ossicle complexity, Rowe (1969, text-fig. 1, p. 125, table 1, p. 165) constructed a hypothetical evolutionary tree for the genus *Holothuria*. This tree, as he says so himself (Rowe, 1969: 124), involves "speculations that should at least form the basis for future argument". These speculations are not minor and in fact involve one of the most intricate problems in evolutionary thought, namely the direction of evolution. Synoptically spoken, according to Pearson (1914, partim), Rowe (1969) and later Thandar (1988; 1994), surf-zone and rock-clinging species (generally characterized by the absence of well developed tables and true buttons) represent the more primitive condition from which evolved the fugitive and fossorial species (generally characterized by well-developed tables and true buttons), whereas according to Deichmann (1958) and later Levin (1999) the reverse scenario is more likely.

Materials and Methods

Rooting

Recent morphological (Kerr & Kim, 2001; Appeltans, 2002) and molecular (Kerr *et al.*, submitted) evidence suggests that the most proximate extant holothuroid group to the Holothuriidae is the Stichopodidae. Therefore, the type species of two stichopodid genera [*Stichopus chloronotus* Brandt, 1835 and *Thelenota ananas* (Jaeger, 1833)] were utilised to polarize the characters of the ingroup.

Taxon selection

According to the latest views [Smiley & Pawson, ±1990 (unpublished manuscript); Samyn, in press; Massin *et al.*, in press], the family Holothuriidae comprises 184 species which are commonly classified into five genera: *Actinopyga* with 16 species; *Bohadschia* possessing 11 species; *Holothuria* 148 species; *Labidodemas* comprising eight species and *Pearsonothuria* monotypic. It must be noted that the above species counts have to remain tentative as quite a few of them will prove to be but synonyms or, on the other hand, cryptic species and new species continue to be described. Characters from three out of five of these genera, are taken from their type species. As we lacked specimens of the type species of *Bohadschia* [*B. marmorata* Jaeger, 1833], we used the recently described *Bohadschia atra* Massin *et al.*, 1999 as proxy. For *Holothuria* we examined seven of its subgenera (out of the 18 currently recognized subgenera; see also Rowe, 1969; Samyn & Massin, in press; Samyn, in press). These subgenera were chosen in such a fashion that they reflect the large morphological variation within the large genus *Holothuria* as it is currently perceived. For *Labidodemas* all eight currently known species were included. The chosen taxa are given in table 1.

Table 1. Taxa used in this study. Only *B. atra* is not the type species of the genus, for *Holothuria* we utilised the type species of seven representative subgenera.

Family Holothuriidae Ludwig, 1874
- Genus *Actinopyga* Bronn, 1860
  - *Actinopyga echinites* (Jaeger, 1833)
- Genus *Bohadschia* Jaeger, 1833
  - *Bohadschia atra* Massin, Rasolofonirina, Conand & Samyn, 1999
- Genus *Holothuria* Linnaeus, 1767
  - *Holothuria (Cystipus) rigida* (Selenka, 1867)
  - *Holothuria (Halodeima) atra* Jaeger, 1833
  - *Holothuria (Lessonothuria) pardalis* Selenka, 1867
  - *Holothuria (Mertensiothuria) leucospilota* (Brandt, 1835)
  - *Holothuria (Metriatyla) scabra* Jaeger, 1833
  - *Holothuria (Microthele) nobilis* (Selenka, 1867)

Holothuria (Semperothuria) cinerascens Brandt, 1835
Genus *Labidodemas* Selenka, 1867
Labidodemas americanum Deichmann, 1938
Labidodemas maccullochi (Deichmann, 1958)
Labidodemas pertinax (Ludwig, 1875)
Labidodemas pseudosemperianum Massin, Samyn & Thandar (in press)
Labidodemas quadripartitum Massin, Samyn & Thandar (in press)
Labidodemas rugosum (Ludwig, 1875)
Labidodemas semperianum Selenka, 1867
Labidodemas spineum Massin, Samyn & Thandar (in press)
Genus *Pearsonothuria* Levin, Kalin & Stonink, 1984
Pearsonothuria graeffei (Semper, 1868)
Family Stichopodidae Haeckel, 1896
Genus *Stichopus* Brandt, 1835
Stichopus chloronotus Brandt, 1835
Genus *Thelenota* H.L. Clark, 1921
Thelenota ananas (Jaeger, 1833)

Character selection

Recently, Samyn & Massin (in press) utilized presence of ossicles in the longitudinal muscles to amend the diagnosis of the holothurian subgenus *Mertensiothuria* Deichmann, 1958. To assess the validity of their claim these authors simultaneously investigated the ossicle-content of the longitudinal muscles of *Pearsonothuria graeffei*, three *Actinopyga* species, two *Bohadschia* species, two *Labidodemas* species and one to six species belonging to 18 of the *Holothuria* subgenera. They found that *Actinopyga*, *Pearsonothuria* and four subgenera of *Holothuria* possess ossicles in the longitudinal muscle. Massin *et al.* (in press), in their revision of *Labidodemas*, extended this survey to include the transversal (or circular) and cloacal-retractor muscles and concluded that ossicles are always absent in the musculature of *Labidodemas* spp. The present study, includes data not only the ossicle content of the musculature, but, also the presence or absence of ossicles in gonad and cloaca. As the latter tissues have only sporadically been investigated (Cherbonnier & Féral, 1984; Liao, 1980; Samyn & Massin, in press; Massin *et al.*, in press; Rowe, pers. comm.) in terms of ossicle content, we here illustrate some of the ossicles recovered from the cloaca (fig. 3).

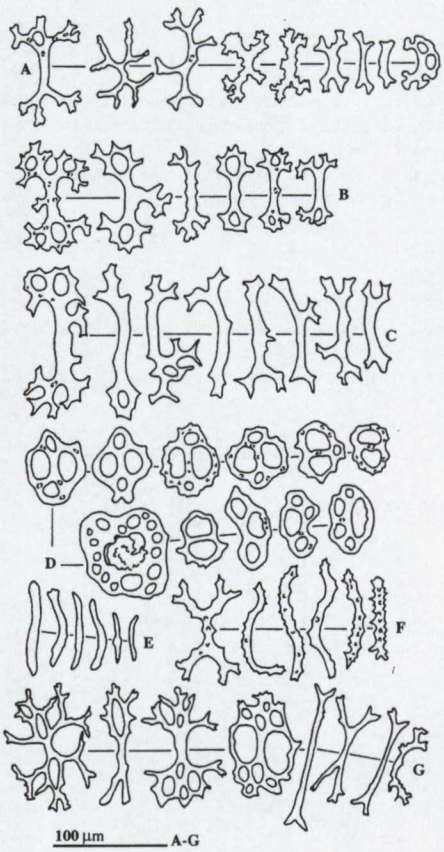

Figure 3. Ossicles of the cloaca. A. *Actinopyga echinites* (Jaeger, 1833); B. *Pearsonothuria graeffei* (Semper, 1868); C. *Bohadschia atra* Massin, Rasolonofirina, Conand & Samyn 1999; D. *Holothuria (Metriatyla) scabra* Jaeger, 1833; E. *Labidodemas pertinax* (Ludwig, 1875); F. *Stichopus chloronotus* Brandt, 1835; G. *Thelenota ananas* (Jaeger, 1833). The scale bar A-D & F-G represents 100 µm; E represents 50 µm.

Overall, 132 discrete characters dealing with the gross external and internal morphology (13 characters each), ecology (three characters), ossicle assemblage of the different body parts and organs (102 characters) were selected. In addition, one character dealt with the known broad distribution of the investigated taxa (Massin, 1999; Massin *et al.*, 1999; Massin *et al.*, in press; Samyn, in press). These characters with their respective states are given in table 2. Description of the employed characters and their respective states can be found in the revisionary work of Rowe (1969; see also Clark & Rowe, 1971) or in recent monographies on Malagasy (Cherbonnier, 1988), Indonesian (Massin, 1999) or East African (Samyn, in press) shallow-water holothuroids.

Table 2. Investigated characters with their respective character states.

External morphology

1. *Overall shape:* 0=cylindrical; 1=convex; 2=quadrangular
2. *Tentacle size:* 0=small; 1=large
3. *Tentacle shape:* 0=peltate, indentions shallow; 1=peltate, indentions deep; 2=peltate, indentions very deep
4. *Thickness of BW (of live specimens):* 0=<1 mm; 1=1-4 mm; 2=+4 mm
5. *Position of mouth:* 0=terminal; 1=ventral
6. *Position of anus:* 0=terminal; 1=superterminal to dorsal
7. *Arrangement of ventral tube feet:* 0=in radial areas only; 1=some also spread in interradial areas; 2=overall spreading
8. *Arrangement of dorsal tube feet and/or papillae:* 0=present, in radial areas only; 1=present, overall spreading
9. *Presence of enlarged dorsal and/or lateral papillae:* 0=absent; 1=present
10. *Presence of anal appendages:* 0=absent; 1=present, anal papillae; 2=present, anal teeth
11. *Presence of collar of papillae around mouth:* 0=absent; 1=present, not fused; 2= present, fused at base
12. *Rugosity of body wall:* 0=smooth; 1=rough to the touch
13. *Firmness of body wall:* 0=firm; 1=very soft (collapsible if animal disturbed)

Internal morphology

14. *Proportion of radial/interradial plates:* 0=length radial plate up to 1,5 length of interradial plate; 1=length radial plate 1,5-2 times longer than length interradial plate; 2=length radial plate 2-3 times longer than interradial plate; 3= length radial plates more than three times longer than length interradial plate
15. *Morphology of radial plates:* 0=posterior side radial plate straight or slightly indented or convex; 1=posterior side radial plate largely indented, ribbon-like; 2=radial plate with posterior medial prolongations
16. *Cuvierian tubules:* 0=absent; 1=present
17. *Expellability of Cuvierian tubules:* 0=non-expellable; 1=expellable
18. *Adhesivity of Cuvierian tubules:* 0=non-adhesive; 1=adhesive
19. *Appearance of Cuvierian tubules:* 0=long, thin; 1=thick, globulous; 2=short,thin
20. *Structure of Cuvierian tubules:* 0=proximal half of trunk similar in structure to distal half of trunk; 1=proximal half of trunk dissimilar in structure to distal half of trunk
21. *Number of attachment sites of Cuvierian tubules:* 0=less than ten attachment sites; 1=more than 10 attachment sites
22. *Number of Polian vesicles:* 0=one; 1=two or more
23. *Length of Polian vesicles:* 0=short (less than 1/12 of body length); 1=long (more than 1/12 of body length)
24. *Number of stone canals:* 0=one; 1=two or more
25. *Length of stone canals:* 0=short (less than 1/12 of body length); 1=long (more than 1/12 of body length)
26. *Gonad tuft:* 0=one tuft; 1=two tufts

Ecology

27. *Nature of substratum:* 0=sand and/or rubble; 1=turf algae; 2=living corals and sponges
28. *Hiding behaviour:* 0=body never concealed; 1=body partially concealed; 2=body completely concealed
29. *Host to carapids:* 0=never reported as host to pearlfish; 1=reported as host to pearlfish

Ossicle assemblage of the body wall

30. *Regular tables:* 0=absent; 1=present
31. *Pseudo-tables:* 0=absent; 1=present
32. *Hollow fenestrated spheres:* 0=absent; 1=present
33. *Rim of disc of regular tables:* 0=smooth; 1=moderately spiny; 2= spiny
34. *Rugosity of disc of regular tables:* 0=smooth; 1=knobbed
35. *Structure of disc of regular table:* 0=flat; 1=raised at rim

36. *Size of table disc of regular table:* 0=reduced; 1=not reduced
37. *Number of central holes in table disc of regular table:* 0=four; 1=variable (never solely four)
38. *Number of peripheral holes in table disc of regular table:* 0=absent; 1=present, in one ring; 2=present, in more than one ring
39. *Height of spire of regular table:* 0=low (height less than disc diameter); 1=moderate (height up to 1,5 times disc diameter); 2=high (height more than twice the disc diameter)
40. *Number of pillars of regular table:* 0=four; 1=variable (never solely four)
41. *Crown of spire of regular table:* 0=absent; 1=present
42. *Structure of crown of spire of regular table:* 0=cluster of spines; 1=regular ring with central opening; 2=irregular ring with one or more central opening(s); 3=Maltese cross
43. *Length of spines on crown of regular table:* 0=short; 1=medium; 2=long
44. *Bifurcation of spines on crown of regular table:* 0=absent; 1=present
45. *Buttons:* 0=absent; 1=present
46. *Ellipsoidal buttons:* 0=absent; 1=present
47. *Rim of buttons:* 0=smooth, not spinose; 1=spinose; 2=undulating
48. *Symmetry of buttons:* 0=regular; 1=irregular
49. *Rugosity of buttons:* 0=smooth; 1=with small knobs; 2=with large knobs
50. *Number of holes in buttons:* 0=generally three pairs of holes; 1=often more than three pairs of holes
51. *Opening of holes in buttons:* 0=open; 1=almost close
52. *Presence of rods:* 0=absent; 1=present
53. *Rugosity of rods:* 0=smooth; 1=slightly rugose; 2=very rugose
54. *Perforation of rods:* 0=not perforated; 1=perforated distally
55. *Complexity of rods:* 0=non-branching; 1=branching
56. *C-, S-, X- shaped rods:* 0=absent; 1=present
57. *Rosettes:* 0=absent; 1=button-like rosettes; 2=rod-like rosettes

Ossicle assemblage tentacles

58. *Ossicles:* 0=absent; 1=present
59. *Rugosity of tentacle-rods:* 0=smooth: 1=moderately spiny; 2= spiny
60. *Rosette-like branched rods:* 0=absent; 1=present
61. *Other ossicles:* 0=absent; 1=present, irregular plate-like branched rods; 2=present, reduced tables

Ossicle assemblage longitudinal muscles

62. *Ossicles:* 0=absent; 1=present
63. *Structure of ossicels:* 0=non-spinose rods to oblong rings to button-like ossicles (pseudobuttons); 1=ossicles present as spiny rods of various shape; 2=ossicles present as C-to S-shaped rods or derivatives

Ossicle assemblage cloacal retractor muscles

64. *Ossicles:* 0=absent; 1=present
65. *Structure of ossicles:* 0=non-spinose rods to oblong rings to button like ossicles (pseudobuttons); 1=reduced tables; 2=spiny rods of various shape

Ossicle assemblage transversal (circular) muscles

66. *Ossicles:* 0=absent; 1=present
67. *Structure of ossicles:* 0=non-spinose rods to oblong rings to button-like ossicles (pseudobuttons); 1=spiny rods of various shape; 2=C-to S-shaped rods

Ossicle assemblage cloaca

68. *Ossicles:* 0=absent; 1=present
69. *Structure of ossicles:* 0=spiny rods of various shape; 1=C-to S-shaped rods; 2=reduced tables

Ossicle assemblage ventral pedicels

70. *Regular tables:* 0=absent; 1=present; 2=rare
71. *Pseudo-tables:* 0=absent; 1=present
72. *Rim of disc of regular tables:* 0=smooth: 1=moderately spiny; 2= spiny
73. *Rugosity of disc of regular tables:* 0=smooth; 1=knobbed
74. *Structure of disc of regular table:* 0=flat; 1=raised at rim
75. *Size of table disc of regular table:* 0=reduced; 1=not reduced
76. *Number of central holes in table disc of regular table:* 0=four; 1=variable (never solely four)
77. *Number of peripheral holes in table disc of regular table:* 0=absent; 1=present, in one ring; 2=present, in more than one ring

78. *Height of spire of regular table:* 0=low (height less than disc diameter); 1=moderate (height up to 1,5 times disc diameter); 2=high (height more then twice the disc diameter)
79. *Number of pillars of regular table:* 0=four; 1=variable (never solely four)
80. *Crown of spire of regular table:* 0=absent; 1=present
81. *Structure of crown of spire of regular table:* 0=cluster of spines; 1=regular ring with central opening; 2=irregular ring with one or more central opening(s); 3=Maltese cross
82. *Length of spines on crown of regular table:* 0=short; 1=medium; 2=long
83. *Bifurcation of spines on crown of regular table:* 0=absent; 1=present
84. *Regular buttons:* 0=absent; 1=present
85. *Ellipsoidal buttons:* 0=absent; 1=present
86. *Rim of buttons*: 0=smooth, not spinose; 1=spinose; 2=undulating; 3=knobbed
87. *Symmetry of buttons:* 0=regular; 1=irregular
88. *Rugosity of buttons:* 0=smooth; 1=with small knobs; 2=with large knobs
89. *Number of holes in buttons:* 0=generally three pairs of holes; 1=often more than three pairs of holes
90. *Opening of holes in buttons:* 0=open; 1=almost close
91. *Plates:* 0=absent; 1=present
92. *Structure of plates:* 0=wide regular; 1=elongate regular; 2=irregular; 3=pseudoplates
93. *Rods:* 0=absent; 1=present
94. *Rugosity of rods:* 0=smooth; 1=slightly rugose; 2=very rugose
95. *Perforation of rods:* 0=not perforated; 1=perforated distally; 2=perforated overall
96. *Complexity of rods:* 0=non-branching; 1= branching; 2=central and distal widening; 3=central widening only
97. *Rosettes:* 0=absent; 1=button-like rosettes; 2=rod-like rosettes
98. *Grains:* 0=absent; 1=present

Ossicle assemblage dorsal pedicels

99. *Regular tables:* 0=absent; 1=present
100. *Pseudo-tables:* 0=absent; 1=present, with disc; 2=present, without disc
101. *Rim of disc of regular tables:* 0=smooth: 1=moderately spiny; 2=spiny
102. *Rugosity of disc of regular table:* 0=smooth; 1=knobbed
103. *Structure of disc of regular table:* 0=flat; 1=raised at rim
104. *Size of table disc of regular table:* 0=reduced; 1=not reduced
105. *Number of central holes in table disc of regular table:* 0=four; 1=variable (never solely four)
106. *Number of peripheral holes in table disc of regular table:* 0=absent; 1=present, in one ring; 2=present, in more than one ring
107. *Height of spire of regular table:* 0=low (height less than table diameter); 1=moderate (height up to 1,5 times disc diameter); 2=high (height more than twice the disc diameter)
108. *Number of pillars of regular table:* 0=four; 1=variable (never solely four)
109. *Crown of spire of regular table:* 0=absent; 1=present
110. *Structure of crown of spire of regular table:* 0=cluster of spines; 1=regular ring with central opening; 2=irregular ring with one or more central opening(s); 3=Maltese cross
111. *Length of spines on crown of regular table:* 0=short; 1=medium; 2=long
112. *Bifurcation of spines on crown of regular table:* 0=absent; 1=present
113. *Buttons:* 0=absent; 1=present
114. *Ellipsoidal buttons:* 0=absent; 1=present
115. *Rim of buttons:* 0=smooth, not spinose: 1=spinose; 2=undulating
116. *Symmetry of buttons:* 0=regular; 1=irregular
117. *Rugosity of buttons:* 0=smooth; 1=with small knobs; 2=with large knobs
118. *Number of holes in buttons:* 0=generally three pairs of holes; 1=often more than threepairs of holes
119. *Opening of holes in buttons:* 0=open; 1=almost close
120. *Plates:* 0=absent; 1=present
121. *Structure of plates:* 0=wide regular; 1=elongate regular; 2=irregular
122. *Rods:* 0=absent; 1=present, not curved 2=present, curved
123. *Rugosity of rods:* 0=smooth; 1=slightly rugose; 2=very rugose
124. *Perforation of rods:* 0=not perforated; 1=perforated distally; 2=perforated overall
125. *Complexity of rods:* 0=non-branching; 1= branching; 2=central and distal widening
126. *Rosettes:* 0=absent; 1=present, button-like; 2=present, rod-like
127. *C-, S-,X- shaped rods:* 0=absent; 1=present

Ossicle assemblage anal papillae
128. *Tables:* 0=absent; 1=present, regular; 2=present, tack-like
129. *Buttons:* 0=absent; 1=present
130. *Rods:* 0=absent; 1=present

Ossicle assemblage gonad
131. *Gonad:* 0=devoid of ossicles; 1=with ossicles

Distribution
132. *Ocean:* 0=West Indian; 1=Indo-West Pacific; 2=East Pacific

Because the recognition of species within holothuriid genera relies heavily on the variation in shape of the ossicles, we were obliged to utilize several characters that referred to the same ossicle type. Such characters (e.g. 30 & 32-44 for the table ossicles of the body wall) were scored with hierarchically related characters states, even though this provoked the coding of character inapplicability in quite a number of cases.
The dataset employed here includes 77 binary and 55 multistate characters; it is represented in table 3.

Phylogenetic analyses

Cladistic analyses were performed by using the computer program *PAUP*4.0b10 (PPC/Altivec)* (Swofford, 2002) for MacIntosh. Due to the high number of taxa and characters, we preferred the heuristic search algorithm to the branch-and-bound one. Heuristic searches were carried out with the following options: keep best trees only; starting tree(s) for branch-swapping obtained via stepwise addition and when multiple starting trees exist, swapping was allowed only on the best tree; stepwise addition in a random sequence with 10^5 replicates initiated from a random tree whereby, a single tree was held at each step; branch-swapping algorithm set to tree bisection-recognition (TBR) whereby multiple trees were saved (steepest descent not in effect) but swapping was allowed only on the best tree. Heuristic searches were run under the maximum-parsimony optimality criterion with the following options: branches were collapsed when their maximum length is zero. All characters were run unordered whereby the state optimisation was achieved through accelerated transformation (ACCTRAN); internal nodes were allowed states that are not observed in terminal taxa; multiple states were treated as polymorphisms; gaps as missing data. Consistency index (CI), retention index (RI) and rescaled consistency index (RC) calculated with minimum-possible single-character lengths.
Because we consider equal weighting of characters to be an improbable and unnatural situation (not all characters bear the same information-content and / or predictive value), we reweighted on the RC, an action that gives higher relative weight to those characters that are more consistent with initial heuristic cladograms and, as such, a greater weight to parsimony informative characters (Bosselaers & Jocqué, 2000).
Data quality of the best tree(s) were assessed by bootstrapping using 500 randomly obtained replicates under the heuristic search, by examination of the skewness of 10^6 randomly generated trees from the dataset, as well as by the Bremer or decay index (number of evolutionary steps required to break down a clade). To test if the most parsimonious cladogram(s) as obtained here are statistically superior to the cladograms obtained through classical β-taxonomy (f.i. by Rowe 1969), we analysed them with a normal approximation of a Wilcoxon signed-rank test, as well as with a binomial sign test of winning sites as implemented in *PAUP**. In all analyses, the outgroup (Stichopodidae) was set as a monophyletic sister group to the ingroup.

Table 3. Character matrix. Missing coding are indicated by "?", polymorphic state (01) is indicated by "a"; (02) by "b"; (012) by "c"; (12) by "d" and (13) by "e". Not applicable characters are indicated by "_"

Taxon	1-10	11-20	21-30	31-40	41-50	51-60	61-70
Actinopyga echinites	1102101112	0000010021	0a1a001000	00_____	____00____	_1a0a02110	0111210100
Bohadschia atra	110d112100	1000011100	1010000010	00_____	____00____	_0___02120	00_0_0_100
Holothuria (Cystipus) rigida	1011102101	010200____	_101000201	0101010100	1100112021	00___00100	00_0_0_0_1
Holothuria (Halodeima) atra	1111102100	000200____	_101000001	00100a0110	131100____	_0___01110	00_0_0_0_1
Holothuria (Lessonothuria) pardalis	1011101100	010200____	_110000201	00a01101c0	1100102a00	00___00110	00_0_0_0_1
Holothuria (Mertensiothuria) leucospilota	1111102100	0002011100	1010000101	0010010100	1100100a00	00___000__	_1010100_1
Holothuria (Metriatyla) scabra	110d102100	110200____	_110100001	0000010d10	1100102020	0110100120	00_110_121
Holothuria (Microthele) nobilis	1102112112	0101010110	1aa0000011	0000010110	1a0011b121	00___00120	20_0_0_0_1
Holothuria (Semperothuria) cinerascens	1121001101	100200____	_11aa00101	00100a0a10	131100____	_1200001c1	00_0_0_0_1
Labidodemas americanum	0011000100	0103110?10	1010000201	001a010200	a10000____	_0___00100	00_0_0_0_1
Labidodemas pseudosemperianum	0010000000	010310____	_000000201	0000011101	1221100101	0100000100	00_0_0_0_1
Labidodemas maccullochi	0011000100	010310____	_110000201	0010010220	a12000____	_0___00110	00_0_0_0_1
Labidodemas quadripartitum	1011000000	000310____	_0100?0201	0020000a00	112a00____	_1000000__	_0_0_0_0_1
Labidodemas rugosum	0011001100	010310____	_010000201	0020a10110	aa1010b10a	00___00100	00_0_0_0_1
Labidodemas pertinax	0011000100	010310____	_100000201	0020000010	110000____	_1aaa001a0	00_0_0_101
Labidodemas semperianum	0010000001	010310____	_010100201	00d0011101	12211001a0	0100000100	00_0_0_0_1
Labidodemas spineum	001a000001	010310____	_110000201	00daa11101	1dda101a10	0110a00100	00_0_0_0_1
Pearsonothuria graeffei	1101110100	1000010100	1011002010	10_____	____00____	_0___021_1	011120_100
Stichopus chloronotus	2101101010	201120____	_a1a010011	0010010110	131a00____	_0___10110	d1d0_121a1
Thelenota ananas	2102102110	201120____	_101010010	00_____	____00____	_110100121	1111211100

	71-80	81-90	91-100	101-110	111-120	121-132
Actinopyga echinites	0_____	___00_____	0_10012100	_____	__00_____0	_100110___11
Bohadschia atra	0_____	___00_____	0_10012100	_____	__00_____0	_10a110___01
Holothuria (Cystipus) rigida	0010101001	1001020210	0_10220010	0a01010011	001020d100	_20220010101
Holothuria (Halodeima) atra	0a0000aa01	31100_____	130___1010	0000001013	0100_____0	_100000___01
Holothuria (Lessonothuria) pardalis	0a0a101a01	10010b1000	1a0___0010	a01a011011	00102a0a00	_201000___01
Holothuria (Mertensiothuria) leucospilota	0100101001	1001000000	1a0___0010	a001010011	0010ba0a00	_10b000___11
Holothuria (Metriatyla) scabra	000010d101	10010b0100	1110220010	00010d1011	0a10201a00	_102200___01
Holothuria (Microthele) nobilis	0000101101	d001100210	1a10b30010	000101101d	0001_____1	110b100___01
Holothuria (Semperothuria) cinerascens	000000a101	31100_____	0_1daa00a0	0000001013	1100_____0	_12a00000101
Labidodemas americanum	010010c00a	a0000_____	0_0___0010	10000a0a0_	__00_____0	_0___0000002
Labidodemas pseudosemperianum	0b0011a01a	d211001000	0_10a00010	b0011a01ad	da00_____0	_0___00___01
Labidodemas maccullochi	020010ca0a	a1000_____	0_0___0010	20000a000_	__10ba0a01	1110100___02
Labidodemas quadripartitum	0200000000	__000_____	0_10110010	200000000_	__00_____0	_110100___?0
Labidodemas rugosum	020a10100a	1a01021010	110___0010	201a01a011	10102a0100	_102000___01
Labidodemas pertinax	020000000a	10000_____	0_1a010010	d00000000_	__00_____0	_110000___01
Labidodemas semperianum	02001100aa	dd100_____	011aa00110	10011a01ad	1a00_____0	_10a00000111
Labidodemas spineum	020a11a0aa	d21101ad00	0_11a00010	20aa1a0aad	a1101ad000	_11a00010101
Pearsonothuria graeffei	1_____	___00_____	120___2001	_____	__00_____0	_100d10___11
Stichopus chloronotus	020010100a	10000_____	1210be0010	100001001e	0a00_____0	_10001100011
Thelenota ananas	0_____	___00_____	1211010002	_____	__00_____0	_1d0100___11

Results

Phylogenetic position of Labidodemas and other holothuriid genera

Of the 132 characters, five proved constant, 28 were parsimony uninformative, leaving 99 informative sites. The equally weighted maximum parsimony analysis returned four shortest trees of length 464 (402 when uninformative characters are excluded), a strict consensus of which is presented in figure 4. This tree has a CI of 0.70 (0.65 when uninformative characters are excluded), a RI of 0.60 and a RC of 0.42 (0.39 with uninformative characters excluded). The highly left skewed (g_1 = -0.47; P<0.01) frequency distribution of the tree lengths suggests that our dataset contains considerable hierarchical signal (Hillis & Huelsenbeck, 1992). Unfortunately, however, the bootstrap percentages for many internal nodes were moderate to small (*i.e* bootsrap values below 70%).

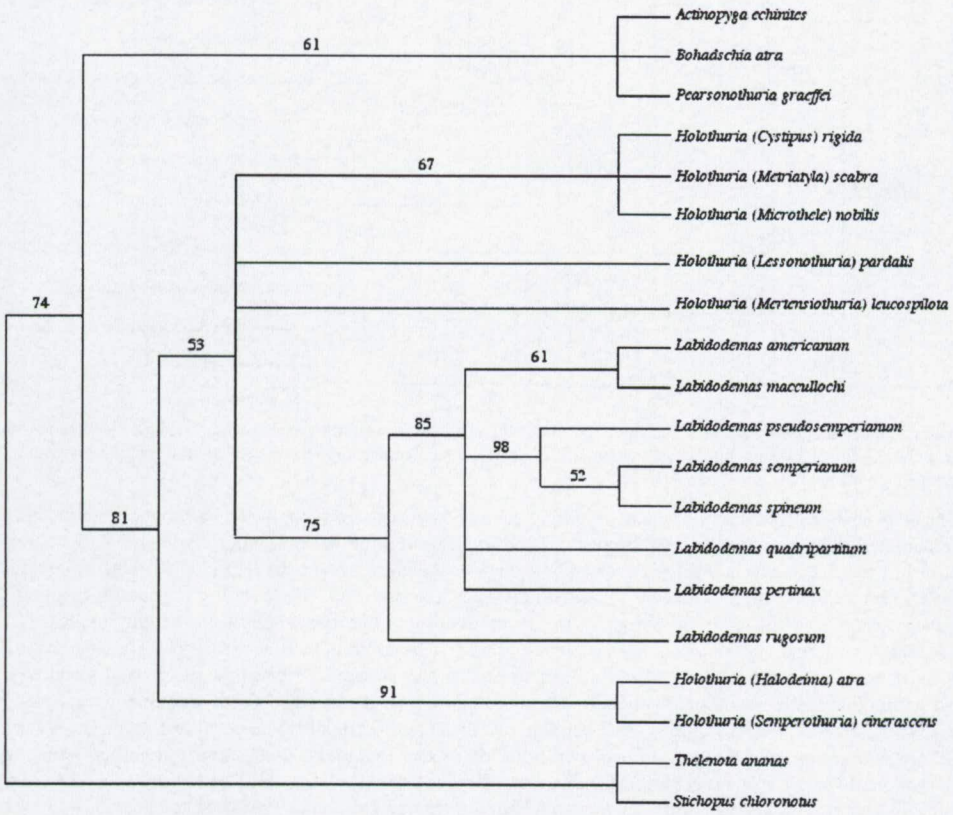

Figure 4. Bootstrap 50% majority rule consensus tree of four trees as recovered under the equal weighting scheme. Values above branches represent bootstrap percentages (500 replicates).

Reweighting on the basis of the RC resulted in a single, fully resolved tree (fig. 5), which has a length of 93.64 steps (68.64 when uninformative characters excluded), a CI of 0.81 (0.74 when parsimony-uninformative excluded), a RI of 0.82, and a RC of 0.65 (0.59 when parsimony uninformative excluded).

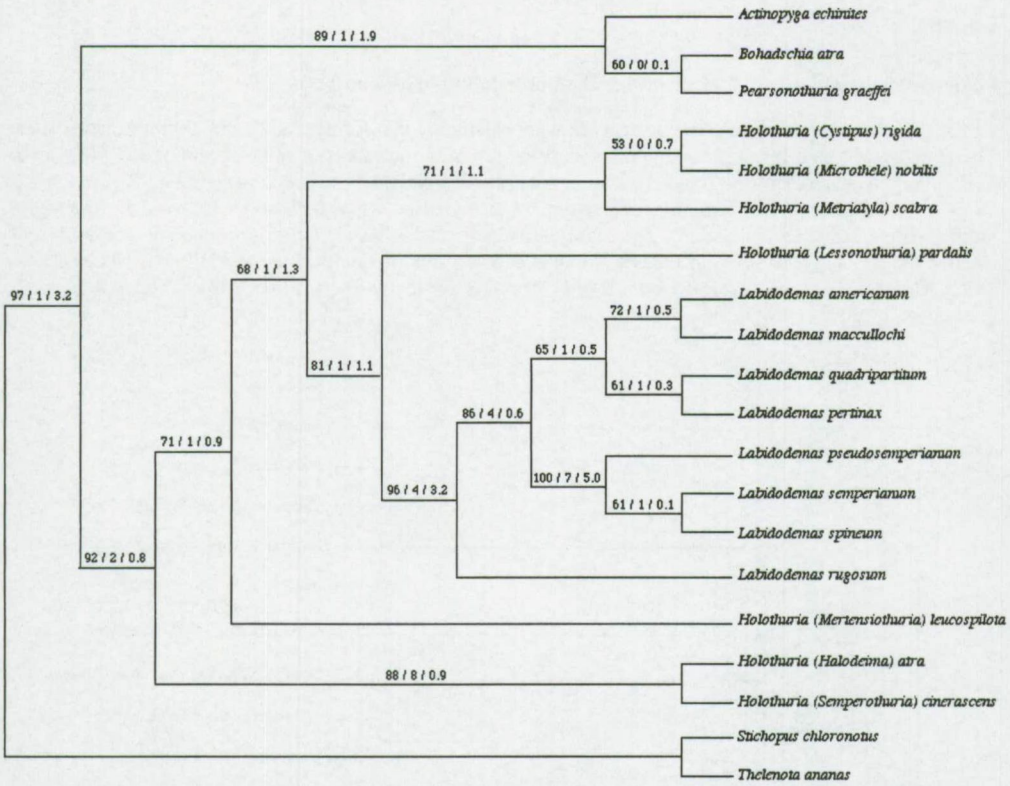

Figure 5. Single most parsimonious tree obtained under the successive weighting (on the RC) scheme. Values above the branches indicate percent bootstrap support (500 replicates) / Bremer support values as obtained under equal / successive weighting.

As can be seen from figs 4 and 5, each weighting scheme returned *Labidodemas* as a monophyletic clade. The calculated bootstrap and Bremer support proved to be quite high for the major clades (96% bootstrap support and 4 / 3.2 decay index for equal and successive weighting respectively) (fig. 5). Unfortunately, however, the relationships between the different *Labidodemas* spp. were not completely resolved. However, a clear pattern is visible: *L. rugosum* occupies the basal position to the clades (*L. Pseudosemperianum* (*L. spineum, L. semperianum*)) and ((*L. americanum, L. maccullochi*),(*L. pertinax, L. quadripartitum*)), with the latter two clades sister to each other. However, *Labidodemas* proved to be well nested within the genus *Holothuria* which, if we retain *Labidodemas* as a valid genus, acquires paraphyletic status. Within *Holothuria*, two major, well-supported clades are discernable. The basal one is formed by the subgenera *Halodeima* and *Semperothuria*, while the other one includes *Labidodemas* together with the other examined *Holothuria* subgenera. This again confirms the paraphyletic status of *Holothuria*. The other holothuriid genera, *Actinopyga*, *Bohadschia* and *Pearsonothuria* (the latter two as sister genera, however with low node support) are positioned at the base of the Holothuriidae. Unfortunately, the overall support for this clade under the reweighted analysis proved moderate to weak (bootstrap percentage 68 %; Bremer support only 1.3).

To further test if *Holothuria* is indeed paraphyletic, we compared the single most parsimonious tree as obtained after successive weighting to the shortest tree where *Holothuria* is restrained as a monophyletic group [cfr. Rowe's (1969) scheme]. This tree proved to be significant longer (reweighted tree length=71.53; N=21, z=-2.29, P=0.027; winning sites=16, P=0.027). On the other hand the most parsimonious tree always proved to be identical in length to the tree where the subgenera *Halodeima* and *Semperothuria* are set as one clade. As Kerr *et al.* (submitted) placed *Bohadschia* and *Pearsonothuria* within *Holothuria*, we tested the length of such a tree. First, we analysed the tree where *Bohadschia, Pearsonothuria, Labidodemas* and *Holothuria* (without its subgenera *Halodeima* and *Semperothuria*) form

one clade. This tree proved to be significantly longer (reweighted tree length=73.23; N=13, z=-2.70, P=0.0070; 11 wining sites, P=0.025) than the most parsimonious one. Moreover, the tree where the holothurian subgenera *Halodeima* and *Semperothuria* are included in the (*Holothuria*, *Labidodemas*, *Bohadschia*, *Pearsonothuria*) clade was not significantly longer (tree length=70.51; N=5, z=-0.68, P=0.50; 3 winning sites, P=1.0) than the most parsimonious one. On the other hand, the tree where *Halodeima*, *Semperothuria*, *Bohadschia* and *Pearsonothuria* are constrained to form a single clade, again was significantly longer (N=14, z=-2.42, P=0.0155; 11 wining sites, P=0.057).

Discussion

Phylogeny

Labidodemas as recently revised by Massin *et al* (in press) is here conclusively confirmed to be a monophyletic lineage. Moreover, as already indicated by Appeltans (2002) and Kerr *et al.* (submitted), *Labidodemas* occupies a derived position within *Holothuria*. As we have examined only seven out of the 18 currently assumed valid *Holothuria* subgenera (excluding the nominal subgenus), it is difficult to discuss the phylogeny of the latter genus in all the details it deserves. Nevertheless, after analysing several constrained topologies, some patterns are readily visible. First of all, if we accept *Labidodemas* at generic level, *Holothuria* is clearly paraphyletic. Second, the subgenera *Halodeima* and *Semperothuria* form a distinct clade which is positioned at the base of the [*Holothuria* (partim), *Labidodemas*] clade. This (*Halodeima*, *Semperothuria*) clade is characterised by species which have reduced table ossicles (fig. 6A,B), button-like rosettes (fig 2A), no true buttons (cfr. fig 2B), rugose rods and irregular plates (fig. 6C,D). The more derived [*Holothuria* (partim), *Labidodemas*] clade includes those species which generally have well developed and often intricate tables (fig. 6E,F), true buttons (fig. 2B), no button-like rosettes (cfr. fig.2A), less rugose rods and more regular plates (fig. 6G,H); it is here represented by the other holothurian subgenera as well as by all the *Labidodemas* spp.

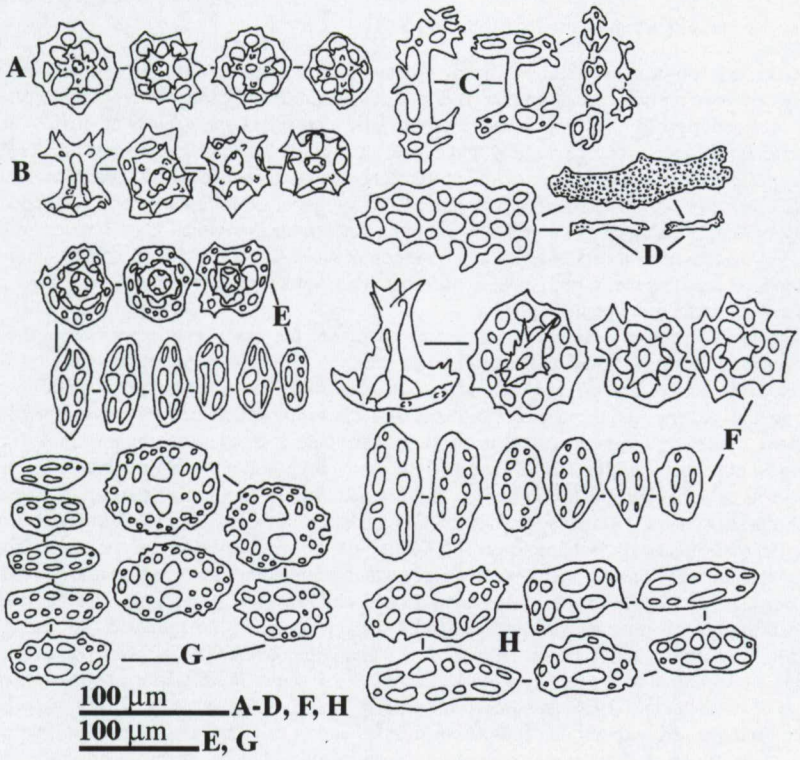

Figure 6 (on p. 152). Some representative ossicles as found in the *Holothuria, Labidodemas* clade. A. Tables of the body wall of *H. (Halodeima) atra* Jaeger, 1833; B. Tables of the body wall of *H. (Semperothuria) cinerascens* (Brandt, 1835); C. Rosettes and (pseudo)plates of the tube feet of *H. (H.) atra*; D. Rods and plates of the tube feet of *H. (S.) cinerascens*; E. Tables and buttons of the body wall of *H. (M.) leucospilota* Brandt, 1835; F. Tables and buttons of the body wall of *L. rugosum* (Ludwig, 1875); G. Buttons to plates of the tube feet of *H. (M.) leucospilota*; H. Buttons to plates of the tube feet of *L. rugosum*.

Contrary to Kerr *et al.* (submitted) we found no direct evidence that *Bohadschia* and *Pearsonothuria* are derived from within *Holothuria*. Instead, these genera clustered together with *Actinopyga* at the base of the Holothuriidae. Albeit our point of view is substantiated with moderate to high bootstrap support (61 % in the unweighted and 89 % in the weighted analysis), the Bremer support unfortunately proved rather low (1 and 1.9 for equal and successive weighting). Nevertheless, as the tree where all the investigated *Holothuria* subgenera, *Labidodemas*, *Bohadschia* and *Pearsonothuria* are constrained to one clade is not significantly longer than the most parsimonious one, we cannot deny that *Bohadschia* and *Pearsonothuria* could be closer to certain *Holothuria* subgenera than to *Actinopyga,* as suggested by Kerr *et al.* (submitted). However, such clustering would imply that: (i) species with regular tables and true buttons have given rise to species with complex rosettes and racquet-like pseudotables (*Pearsonothuria*) or to species with simple, unbranched solid grains to variously dichotomously branched rosettes (*Bohadschia*), and (ii) *Actinopyga* rosettes are analoguous to *Bohadschia* and *Pearsonothuria* rosettes. However, because *Actinopyga*, *Bohadschia* and *Pearsonothuria* share such features as a robust calcareous ring, rod-like rosettes, and absence of regular tables and buttons (cfr. Pearson 1914) we prefer to cling to our topology. Further evidence for this point of view comes from the observation that *Actinopyga* and *Pearsonothuria*, just like the outgroup, share the presence of the same type of rods in the musculature, the gonad and the cloaca (*Bohadschia* however lacks these in the gonad). *Bohadschia* and *Pearsonothuria* are further linked to each other by presenting the same type of Cuvierian tubules (Vanden Spiegel, 1993; Vanden Spiegel, pers. comm) and in having a superterminal to dorsal anus.

Toward a new classification of the Holothuriidae?

Nevertheless, the phylogeny obtained from molecular data (Kerr *et al.*, submitted) and the present phylogeny converge on two crucial points: (i) it requires a significantly longer tree to make *Holothuria* ([as currently defined by a.o. Rowe (1969)] monophyletic and (ii) *Labidodemas* is firmly nested within *Holothuria*. If we accept our phylogeny and if we downgrade *Labidodemas* to subgeneric level (as a subgenus of *Holothuria)*, amendment of the current classification reduces itself to nomenclatural changes. However, given the size of the genus *Holothuria* (18 subgenera comprising some 150 species) and the possibility of deeper paraphyly, we prefer to adopt an eclectic or Darwinian classification (a classification that is based on the criteria of similarity and common descent; see also Mayr 1982; Mayr & Bock 2002) and, as such, retain the generic rank of *Labidodemas*. This however, necessitates altering the classification of *Holothuria* to retain monophyletic genera.

Alas, as we remain currently largely in the dark in regards to the phylogenetic position of the type species of *Holothuria* [*Holothuria (Holothuria) tubulosa* Gmelin, 1790], we cannot unambiguously decide to which clade the name *Holothuria* will apply. On the other hand, if the basal position of the clade comprising the genera *Actinopyga, Bohadschia* and *Pearsonothuria* can be substantiated with further phylogenetic evidence, there is no reason to deny that clade a separate taxonomic rank (family?). It is interesting to note that Panning (1940) inherently came to the same conclusion when he proposed to treat *Actinopyga* as a subgenus of *Bohadschia.* As *Bohadschia* is the earliest generic name, the name Bohadschiidae seems most suitable. In fact, such emendation mirrors Gill's (1907a) suggestion to replace the name Holothuriidae with Bohadschiidae. As Gill's (1907a) reasons were nomenclatural (he attacked the validity of the name *Holothuria* and its derivatives) rather than taxonomic or systematic (he did not alter the diagnosis or classification in any way), the name Bohadschiidae remains available. The name Holothuriidae would then apply only to the clade wherein falls the type species, *H. tubulosa.* As such, it would be restricted to the current generic names *Holothuria* s.l. and *Labidodemas*. Within *Holothuria* s.l. then at least two clades are discernable. The first of these comprises the clade (*Halodeima, Semperothuria)* to which *Selenkothuria* Deichmann, 1958 and *Acanthotrapeza* Rowe, 1969 most probably also belong (both subgenera hold species with similar button-like rosettes and/or rods, never true buttons); while the second entails the remainder of the *Holothuria* subgenera and *Labidodemas*. Such a scenario is reminiscent of

Panning's (1935a) splitting of the subgenus *Holothuria s.s.* Hereby, he termed the group with rosettes *Abteilung A* (to which he in 1940 attributed the generic rank *Halodeima* Pearson, 1914) and the group with buttons *Abteilung B* or *Sporadipus* Brandt, 1835 (a name that has been conclusively rejected by Clark & Rowe, 1967). Thus, a further modification to the current classification possibly entails a re-appraisal of *Halodeima* Pearson, 1914 at generic rather than at subgeneric level as proposed by Rowe (1969). Panning's (1940) split of *Holothuria* s.s. into the genera *Microthele* Brandt, 1835 and *Holothuria* Linneaus, 1767 is, in the light of the present evidence, more problematic. Rowe (1969: 145) was correct to note that neither Panning (1929; 1940; 1944) nor Deichmann (1958) "recognized Brandt's (1835) original concept of *H. (Microthele)*" and that as such, this name cannot be attributed to the species for which Panning used this name. Rowe (1969) solved this problem by (i) recognising the original sense of *Microthele* and (ii) by describing a new subgenus (*Platyperona*) for the relevant species. However, given the incompleteness of the present phylogeny (not all current *Holothuria* subgenera and species have been investigated), we prefer not to discuss the intersubgeneric taxonomy of *Holothuria*. For now, it suffices to note that there seems to be a clade (*Microthele, Metriatyla, Cystipus*) that is characterised by more rugose button- and table-ossicles.

In conclusion, a nomeclatural revision of Holothuriidae will depend on further comparative taxonomic studies as well as on more detailed phylogenetic analysis before any of the changes proposed above can be solidified into a new classification. It is, however, clear that the latter, by necessity must incorporate many of the insights as expressed by previous specialists (Pearson, 1914; Panning, 1929-1944; Deichmann, 1958 and Rowe, 1969) as well as novel insights from morphological (present study) and molecular systematics (Kerr *et al.*, submitted).

Acknowledgments

We thank Drs F.W.E. Rowe and C. Massin for their encouraging discussions and comments on holothuroid taxonomy and their review of this manuscript. Dr. F. Bossuyt is further thanked for providing insights into phylogenetic analyses. This work would not have been possible without the kind help of many of our colleagues in different museums worldwide. It is thus with great pleasure that we thank Drs J.F. Bertrand (MCZ), Massachusetts; S. Halsey (NHM), London; G. Hendler (NHM LAC), Los Angeles; C. Ahearn (USNM), Washington, M.B. Best (RMNH), Leiden and A. Laguarda Figueras (ICML-UNAM), Mexico for sending us type and non-type material of several species; sincere thanks also to Drs H. Ruhberg and P. Stewie for welcoming one of us (YS) at the ZMH. Financial support to YS came from the Flemish Fund for Scientific Research (project number G.0086.96), the Ministry of the Flemish Community (project numbers BIL98/84 and BIL01/46) and the Research Council of the Free University of Brussels (travel grants to Kenya and the Republic of South Africa). Support to AMK came from the Lerner Gray Fund (AMNH), an Ernst Mayr Grant (MCZ) and The Falconwood Corporation. [Museum acronyms in Massin *et al.*, submitted]

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Chapter Five

Annotated checklist of the echinoderms from the Kiunga Marine National Reserve, Kenya
Part I: Echinoidea and Holothuroidea

64082

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ABSTRACT

The echinoderm fauna of the Kiunga Marine National Reserve, Kenya, is documented, based on the results of a field trip, and additional information from the literature. In this first paper, the Holothuroidea and Echinoidea are discussed. A total of 91 specimens representing 8 orders, 13 families, 19 genera and 37 species were collected. Five other species were not collected but were identified in the field. Six additional species are reported from literature only and are not discussed. Diagnostic characters of every species recorded are given, as well as an assessment of their abundance in the Kiunga Marine Reserve. *Clypeaster rarispinus, Phyllacanthus imperialis, Microcyphus rousseaui* (Echinoidea), , *Holothuria (Cystipus) rigida, Holothuria (Platyperona) difficilis, Labidodemas pertinax, Stichopus chloronotus* and *Stichopus cf. monotuberculatus* (Holothuroidea) are new records for Kenya. *Holothuria (Theelothuria) turriscelsa* is a new record for the Indian Ocean. This study stresses the importance of the Kiunga Marine National Reserve as a sanctuary in the conservation of the marine invertebrate fauna.

Introduction

Few basic studies have been undertaken to map the distribution of echinoderms in the western Indian Ocean. All information available for echinoderms of shallow-water of the Indo-West Pacific Ocean was reviewed by Clark & Rowe (1971). This work is now at least partly outdated; also, the scale with which the distributions were mapped is too coarse to support management of these important natural resources. Humphreys (1981) lists all species of echinoderms in the Watamu/Malindi area, and in parts of Tanzania. Richmond (1997) compiled a book on most fauna and flora groups of the seashores of eastern Africa, including a chapter on echinoderms (Rowe & Richmond, 1997). But again, geographical ranges are too broad for management purposes. Tortonese (1949, 1951, 1980) studied the echinoderms of the Somali coast. Obura *et al.* (1998) surveyed the Kiunga Marine Reserve, but unfortunately did not take any specimens; so their identifications must be treated with caution.

This expedition was a joint effort of the Free University of Brussels (Unit of Ecology & Systematics), WWF Kenya and Kenya Wildlife Service. Collecting was done by hand-picking at low tide, by snorkeling and by SCUBA diving up to depths of 31 m, from 3 to 12 May, 1999. Destructive sampling techniques like dredging were never used.

Analogous to Sloan *et al.* (1979), detailed taxonomic descriptions and geographical distributions are not included; instead we refer to major works (Clark & Rowe, 1971; Clark & Courtman-Stock, 1976; Rowe & Doty, 1977; Cherbonnier, 1988; Rowe & Gates, 1995; Massin, 1996a, 1999) from which the original descriptions and geographical distributions can be traced. A brief field description is included, as are important records for eastern Africa and the western Indian Ocean.

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Study region

The Kiunga Marine National Reserve was gazetted in 1979 as a Marine National Reserve and at 250 km^2 is the largest marine reserve in Kenya. It is part of the Bajuni Archipelago, which lies at the northernmost extremity of the Kenya coast, bordering Somalia. The seven islands of the archipelago are fringed with mangrove forests, surrounded by extensive seagrass beds and coral reefs. The area is important for biodiversity, and provides nesting sites for marine turtles and migratory birds (Obura *et al.*, 1998). Table 1 lists the names and coordinates of the different sampling sites within the Reserve, together with the depth ranges (see also figure 1).

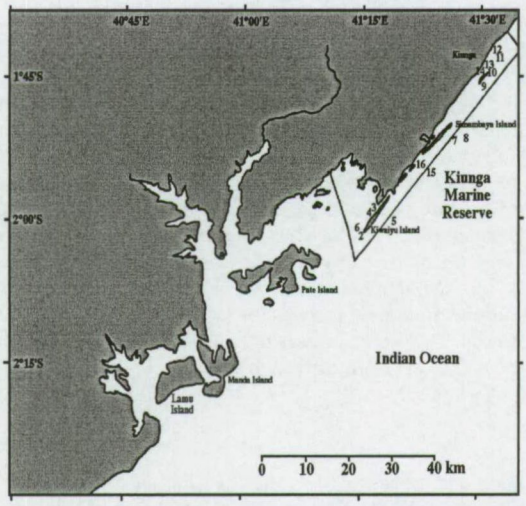

Figure 1. Map with observation and collection sites in the Kiunga Marine Reserve. (1) Mkomani; (2) Kilima Nungu; (3) Mike's Outer Reef; (4) Mike's Inner Reef; (5) Chongo cha Chano; (6) Shimo la Tewa; (7) Chongo cha Kui; (8) Kui; (9) Mwamba Mkuu; (10) Mlango wa Bomani; (11) Wreck; (12) Kaddhika; (13) Mwamba wa Boso; (14) Kiunga Camp; (15) Chongo cha Mvundeni; (16) Hindi.

TABLE 1. Names and coordinates of the different sampling and observation sites in the Kiunga Marine Reserve. Depths apply to the low water level.

DATE	SITE NAME	REGION	DEPTH RANGE (M)	LATITUDE	LONGITUDE
4 / 4 / 99	Mkomani	Kiwaiyu	1-4	01°57'42" S	41°18'02" E
4 / 4 / 99	Kilima Nungu	Kiwaiyu	4-8	02°02'40" S	41°15'55" E
5 / 4 / 99	Mike's Outer Reef	Kiwaiyu	1.5-3	01°59'39" S	41°17'28" E
5 / 4 / 99	Mike's Inner Reef	Kiwaiyu	5-8	01°59'40" S	41°17'28" E
6 / 4 / 99	Chongo cha Chano	Kiwaiyu	8-17	02°00'29" S	41°20'01" E
6 / 4 / 99	Shimo la Tewa	Kiwaiyu	3-7	02°02'35" S	41°14'47" E
7 / 4 / 99	Chongo cha Kui	Kui	12-21	01°52'02" S	41°26'55" E
7 / 4 / 99	Kui	Kui	1-4	01°49'29" S	41°26'43" E
8 / 4 / 99	Mwamba Mkuu	Kiunga	7-17	01°46'10" S	41°30'38" E
8 / 4 / 99	Mlango wa Bomani	Kiunga	1-5	01°44'37" S	41°31'09" E
9 / 4 / 99	Wreck	Ishakani	6-10	01°43'14" S	41°32'48" E
9 / 4 / 99	Kaddhika	Ishakani	1-3	01°43'04" S	41°32'28" E
9 / 4 / 99	Mwamba wa Boso	Kiunga	1-3	01°44'18" S	41°31'34" E
9 / 4 / 99	Kiunga Camp	Kiunga	1-8	01°45'14" S	41°30'35" E
10 / 4 / 99	Mwamba Mkuu	Kiunga	8-22	01°44'39" S	41°31'15" E
10 / 4 / 99	Kui	Kui	0.5-5	01°49'29" S	41°26'43" E
11 / 4 / 99	Chongo cha Mvundeni	Rubu	8-28	01°55'29" S	41°23'35" E
11 / 4 / 99	Hindi	Rubu	1-5	01°54'25" S	41°22'22" E
12 / 4 / 99	Chongo cha Chano	Kiwaiyu	11-31	02°00'35" S	41°19'58" E
12 / 4 / 99	Mike's Outer Reef	Kiwaiyu	1-4	01°59'39" S	41°17'29" E
12 / 4 / 99	Kilima Nungu	Kiwaiyu	4-8	02°02'40" S	41°15'55" E

Results

A total of 91 specimens representing 37 species were collected. An overview of the echinoids and holothurians from the Kiunga Marine Reserve (Obura *et al*, 1998; this study) compared to the echinoid and the holothurian fauna of Kenya (Levin, 1979: holothurians only; Humphreys, 1981) and Somalia (Tortonese, 1949–1951; 1951; 1980) is given in table 2. Several important 'historical papers' also describe echinoderms collected in the region of interest. These are not included in table 2, but are separately discussed in the systematic account. A species is considered to belong to the echinoderm fauna of the Kiunga Marine Reserve if it is reported by us or if it is reported from both Somalia and Kenya.
An indication of abundance in the Kiunga Marine Reserve is given in four categories:

- **Very rare:** only one or two specimens seen during the survey;
- **Rare:** spotted up to five specimens during the survey;
- **Common:** seen up to 20 specimens during the survey;
- **Abundant:** spotted more than 20 specimens during the survey.

Systematic account

Tables 3 and 4 list the different species with their collection site, depth range, abundance and collection number. This collection is deposited in the Royal Belgian Institute for Natural Sciences, in Brussels, Belgium. Most of the identifications are based on the key provided by Clark & Rowe (1971) for the echinoids and on the keys provided by Cherbonnier (1988) for the holothurians.

TABLE 2. Littoral Holothuroidea and Echinoidea from the Kiunga Marine Reserve and surrounding regions (recent records only): (1) Tortonese, 1980 (Somalia); (2) Tortonese, 1951 (Somalia); (3) Tortonese, 1949-51 (Somalia); (4) Levin, 1979 (Mombasa, Kenya) (5) Humphreys, 1981 (Kenya and adjacent regions); (6) Obura et al, 1998 (Kiunga Marine Reserve); (7) this study. ** denotes a new record for the Indian Ocean; * denotes a new record for Kenya.

CURRENT SPECIES NAME	1	2	3	4	5	6	7	
ECHINOIDEA								
IRREGULARIA								
Brissidae								
Brissus latecarinatus (Leske, 1778)					x			
Metalia sternalis (Lamarck, 1816)					x			
Clypeasteridae								
Clypeaster fervens Koehler, 1922					x			
Clypeaster rarispinus de Meijere, 1902					x		x	*
Clypeaster reticulatus (Linnaeus, 1758)					x			
Echinoneidae								
Echinoneus cyclostomus Leske, 1778	x				x			
Laganidae								
Laganum depressum Lesson in L. Agassiz, 1841	x	x			x		x	
Laganum joubini Koehler, 1922					x			
Schizasteridae								
Schizasterid sp.					x			
Spatangidae								
Maretia planulata (Lamarck, 1816)					x			
Scutellidae								
Echinodiscus bisperforatus Leske, 1778 cited as *Echinodiscus biforis* (Gmel.)					x		x	
REGULARIA								
Cidaridae								
Eucidaris metularia (Lamarck, 1816)	x				x			
Prionocidaris baculosa (Lamarck, 1816)					x			
Prionocidaris verticillata (Lamarck, 1816)					x			
Phyllacanthus imperialis (Lamarck, 1816)							x	*
Diadematidae								
Astropyga radiata (Leske, 1778)					x		x	
Diadema savignyi Michelin, 1845					x		x	
Diadema setosum (Leske, 1778)					x	x	x	
Echinothrix diadema (Linnaeus, 1758)	x				x	x	x	
Echinothrix calamaris (Pallas, 1774)		x			x		x	
Echinometridae								
Colobocentrotus atratus (Linnaeus, 1758)			x		x			

CURRENT SPECIES NAME	1	2	3	4	5	6	7	
Echinometra mathaei (de Blainville, 1825)	x	x			x	x	x	
cited as *E. mathaei violacea*			x					
Echinostrephus molaris (de Blainville, 1825)					x	x	x	
Heterocentrotus mammillatus (Linnaeus, 1758)					x		x	
Heterocentrotus trigonarius (Lamarck, 1816)			x		x			
Stomopneustidae								
Stomopneustes variolaris (Lamarck, 1816)	x	x			x	x	x	
Parasalenidae								
Parasalenia gratiosa A. Agassiz, 1863					x			
Temnopleuridae								
Microcyphus rousseaui L. Agassiz, 1846	x						x	*
Salmacis bicolor in Agassiz & Désor, 1846		x						
Toxopneustidae								
Toxopneustes pileolus (Lamarck, 1816)	x	x			x	x	x	
Tripneustes gratilla (Linnaeus, 1758)	x	x	x		x	x	x	
HOLOTHUROIDEA								
Holothuriidae								
Actinopyga echinites (Jaeger, 1833)	x						x	
cited as *A. plebeja*				x				
Actinopyga lecanora (Jaeger, 1833)				x				
Actinopyga mauritiana (Quoy & Gaimard, 1833)	x				x	x	x	
Actinopyga miliaris (Quoy & Gaimard, 1833)				x	x		x	
cited as *Actinopyga* sp.						x		
Actinopyga sp.					x			
Bohadschia atra Massin *et al*, 1999							x	
Bohadschia subrubra (Quoy & Gaimard, 1833)						x	x	
cited as *Bohadschia koellikeri* (Semper, 1868)					x			
Bohadschia vitiensis (Semper, 1868)						x		
Bohadschia marmorata Jaeger, 1833				x	x		x	
Holothuria (Acanthotrapeza) pyxis Selenka, 1867				x				
Holothuria (Cystipus) rigida (Selenka, 1867)							x	*
Holothuria (Halodeima) atra Jaeger, 1833	x				x	x	x	
Holothuria (Halodeima) edulis Lesson, 1830						x	x	
Holothuria (Lessonothuria) pardalis Selenka, 1867	x				x		x	
Holothuria (Mertensiothuria) leucospilota (Brandt, 1835)	x				x		x	
Holothuria (Metriatyla) scabra Jaeger, 1833					x	x	x	
Holothuria (Microthele) nobilis (Selenka, 1867)	x				x	x	x	
Holothuria (Platyperona) difficilis Semper, 1868							x	*
Holothuria (Platyperona) strigosa Selenka, 1867								
cited as *Holothuria (Thymiosycia) strigosa*	x							
Holothuria (Semperothuria) cinerascens (Brandt, 1835)	x			x	x		x	
Holothuria (Selenkothuria) erinaceus Semper, 1868	x							
Holothuria (Selenkothuria) parva Lampert, 1885	x					x		
Holothuria (Stauropora) fuscocinerea Jaeger, 1833					x		x	
Holothuria (Stauropora) pervicax Selenka, 1867	x				x			
Holothuria (Theelothuria) turriscelsa Cherbonnier, 1980							x	**
Holothuria (Thymiosycia) arenicola Semper, 1868	x						x	*
Holothuria (Thymiosycia) hilla Lesson, 1830	x				x		x	
Holothuria (Thymiosycia) impatiens (Forskål, 1775)	x				x		x	
Labidodemas rugosum (Ludwig, 1875)	x							
Labidodemas pertinax Ludwig, 1875							x	*
Labidodemas semperianum Selenka, 1867					x			
Stichopodidae								
Stichopus chloronotus Brandt, 1835							x	*
Stichopus herrmanni Semper, 1868							x	
cited as *Stichopus variegatus* Semper, 1868				x	x			
Stichopus monotuberculatus (Quoy & Gaimard, 1833)							x	*
cited as Stichodactylidae sp. 1						x		
Thelenota ananas (Jaeger, 1833)					x			
Phyllophoridae								
Afrocucumis africana (Semper, 1868)	x				x		x	
Chiridotidae								
Polycheira fusca (Quoy & Gaimard, 1833)								
cited as *Polycheira rufescens* (Brandt, 1835)	x							
Synaptidae								
Opheodesoma spectabilis Fischer, 1907								
cited as *Opheodesoma* sp. Prob. *O. spectabilis* Fischer, 1907					x			
Synapta maculata (Chamisso & Eysenhardt, 1821)					x		x	

ECHINOIDEA (Local Swahili name: urumba)

We collected 34 specimens, representing 14 species of Echinoidea. No specimens were collected for two species that were reliably identified in the field: *Astropyga radiata* and *Heterocentrotus mammillatus*. According to literature, four more species, *Colobocentrotus atratus, Echinoneus cyclostomus, Eucidaris*

metularia and *Heterocentrotus trigonarius* are expected in the studied region. This would bring the total echinoid fauna of the Kiunga Marine Reserve to 20 species; three of these are reported here for the first time from Kenya: *Clypeaster rarispinus, Phyllacanthus imperialis* and *Microcyphus rousseaui.*

Order Clypeasteroidea L. Agassiz & Desor, 1847
Family Clypeasteridae L. Agassiz, 1881
Genus *Clypeaster* Lamarck, 1801

TABLE 3. List of echinoids collected at the different localities in the Kiunga Marine Reserve. The number of specimens refers to the number of animals that were encountered during a 60-minute sampling period. i.t. stands for intertidal. Depths apply to the low water level.

SPECIES	SITE NAME	MIN-MAX DEPTH (M)	APPROX #	COLLECTION N°
IREGULARIA				
Clypeasteridae				
Clypeaster rarispinus	Mkomani	i.t.	No data	KKiun/9916
Laganidae				
Laganum depressum	Mkomani	i.t.	No data	KKiun/9917
Scutellidae				
Echinodiscus bisperforatus	Mkomani	i.t.	No data	KKiun/9915
REGULARIA				
Cidaridae				
Phyllacanthus imperialis	Mkomani	7	1	None
	Kilima Nungu	5	1	KKiun/9901
Diadematidae				
Astropyga radiata	Mlango Bomani	2	1	None
Diadema savignyi	Mkomani	i.t.	2	None
	Mwamba Mkuu	9	1	None
	Kaddhika	1	2	None
	Hindi	1	2	KKiun/9903
Diadema setosum	Shimo La Tewa	3-7	3	None
	Chongo Cha Kui	8	1	None
	Kui	3	1	KKiun/9902
Echinothrix calamaris	Kaddhika	2	1	KKiun/9905
Echinothrix diadema	Mwamba Mkuu	10-12	2	KKiun/9904
	Mlango wa Bomani	1-3	10	None
	Kaddhika	1-3	6	None
	Mwamba wa Boso	1-3	8	None
	Hindi	1-3	5	None
Echinometridae				
Echinometra mathaei	Mkomani	i.t.	10	KKiun/9913
	Kui	2-4	2	None
	Mwamba Mkuu	9-10	10	None
	Mlango wa Bomani	1-3	10	None
	Kaddhika	1-2	1	None
	Mwamba wa Boso	1	1	None
	Chongo cha Chano	10	1	None
Echinostrephus molaris	Mkomani	2	2	KKiun/9914
	Mwamba Mkuu	7-17	>100	None
	Mlango wa Bomani	2-4	>50	None
	Wreck	6-10	15	None
	Kiunga Camp	1-7	20	None
	Chongo cha Mvundeni	14-27	>30	None
	Chongo cha Chano	9-13	3	None
	Mike's Outer Reef	1-2	3	None
Heterocentrotus mammillatus	Mlango wa Bomani	2-5	1	None
Stomopneustidae				
Stomopneustes variolaris	Mkomani	1-2	>100	KKiun/9910
	Mlango wa Bomani	1-3	>50	None
	Kiunga Camp	1-7	>20	None
	Hindi	2	1	None
	Kilima Nungu	4-8	5	None
Temnopleuridae				
Microcyphus rousseaui	Kiunga Camp	7	1	KKiun/9906
	Chongo cha Mvuendi	17	1	KKiun/9907

SPECIES	SITE NAME	MIN-MAX DEPTH (M)	APPROX #	COLLECTION N°
Toxopneustidae				
Toxopneustes pileolus	Mlango wa Bomani	1-5	1	None
	Mwamba wa Boso	1-2	3	None
	Hindi	1	2	KKiun/9911
Tripneustes gratilla	Mlango wa Bomani	1-2	>50	KKiun/9912
	Kaddhika	1-2	2	None
	Mike's Outer Reef	2	1	KKiun/9908
	Hindi	1.5	1	KKiun/9909

Clypeaster rarispinus de Meijere, 1902. Pl. 1A
Material examined – KKiun/9916 (four specimens).
Taxonomic description – See Mortensen, 1948: 58–62, figure 43, pl. 6 figures 1–15, pl. 40 figures 4, 5, 8, 9, pl. 64 figures 11, 12, 14–17, 20 (as *Clypeaster (Leptoclypus) rarispinus*); Clark & Rowe, 1971: 160.
Field description – Relatively small species with lengths smaller than 100 mm; flattened and pentagonal body, only slightly raised centrally; five narrow petal areas reaching to about a third of the diameter, periproct hardly separated from the posterior edge; sutures of oral and aboral plates forming a dark reticulum.
Abundance in the Kiunga Marine Park – Probably *common*, although neither Obura *et al.* (1998) (KMR), nor Tortonese (1949, 1951, 1980) (southern Somalia) were able to find it.
Local distribution - Humphreys (1981) also failed to find it in Kenya, but dredged it at Tumbatu, Zanzibar Channel. The burrowing behaviour of this species makes it hard to find, so data on abundance are not reliable for now, and earlier workers might have easily missed it. It is reported here as a first record for Kenya. Russo (1932) and Tortonese (1936) report it from the Red Sea as *Clypeaster Audouin;* Tortonese (1955) from the Red Sea as *Clypeaster (Leptoclypus) rarispinus.* Price (1982) reports this species from the Arabian Gulf, SE Arabia, the Red Sea, the Gulf of Aqaba and the Gulf of Suez. Clark & Rowe (1971) list it as an Indo-Pacific species from East Africa (with the Red Sea) to the East Indies (see also Mortensen, 1948).

Family Laganide A. Agassiz, 1872
Genus *Laganum* Gray, 1825

Laganum depressum Lesson *in* L. Agassiz, 1841
Material examined – KKiun/9917 (seven specimens).
Taxonomic description – See Mortensen, 1948: 313-318, figure 197, pl. 52 figures 12, 14, pl. 53 figures 3, 4, 6–32, pl. 70, figure 20; Clark & Rowe, 1971: 162; figure 77, p. 162; pl. 25 figure 10.
Field description – Flattened, elliptical body with test length up to 40 mm, with rather thick margins and well developed petals reaching up to the thickened margin; five clearly visible pores; periproct nearer to the posterior edge than to the mouth.
Abundance in the Kiunga Marine Park – Probably *common.* Due to its burrowing behaviour this species is easily overlooked, so data on abundance are not reliable.
Local distribution - Humphreys (1981) found it earlier in Kenya (Watamu Marine Park, north Kilifi, Malindi), Tortonese (1951, 1980) in Somalia (unspecified and Sar Uanle, 20 km South of Kismayu). Ludwig (1899) was the first to report it from East Africa (Zanzibar). Clark & Rowe (1971) list it as an Indo-Pacific species from East Africa (with the Red Sea) to the Islands of the South-Pacific (see also Mortensen, 1948; Rowe and Richmond, 1997).

Family Scutellidae Gray, 1825
Genus *Echinodiscus* Leske, 1778

Echinodiscus bisperforatus Leske, 1778
Material examined – KKiun/9915 (one specimen). This sample was fragmented during transport to Belgium, our field description is completely similar to Mortensen's (1948).
Taxonomic description – See Mortensen, 1948: 406–411, figures 241a, 242a, b, pl. 58 figures 2, 6–8, pl. 71 figures 6–9, 18; Clark & Rowe, 1971: 162; pl. 25 figure 9.

Field description – Test length up to 130 mm, flattened body with posteriorly two distinct closed lunules in the posterior paired ambulacra, at least as long as the petals; body covered with fine spines, on the oral side forming a distinct pattern in the ambulacral areas.
Abundance in the Kiunga Marine Park – *Abundant*, however we collected only one specimen, which was unfortunately fragmented during transport. Not reported by Obura *et al.* (1998) from the Kiunga Marine Reserve; J. Church reports on the species as being abundant in the Kiunga Marine Reserve (pers. comm.).
Local distribution - Tortonese (1949, 1951, 1980) failed to find it in Somalia, he reported it earlier from the Red Sea (Tortonese, 1936). Later Price (1982) confirms that record by reporting it from the Red Sea, the Arabian Gulf, SE Arabia, and the Gulf of Suez; Ludwig (1899), Ruwa (1989) and Humphreys (1981) report it from Kenya (Lamu), making the species expected and abundant for the examined region. Lambert (1921–22) also reported it from East Africa (Madagascar) as *Tetrodiscus biforis*. *Echinodiscus bisperforatus* ranges geographically from East Africa (with the Red Sea) to the islands of the South Pacific (see also Mortensen, 1948; Clark & Rowe, 1971; Clark and Courtman-Stock, 1976; Rowe & Richmond, 1997).

Order Cidaroidea Duncan, 1899
Family Cidaridae Gray, 1825
Genus *Phyllacanthus* Brandt, 1835

Phyllacanthus imperialis (Lamarck, 1816). Pl. 1B
Material examined – KKiun/9901 (one specimen).
Taxonomic description – See Mortensen, 1928: 504–509, figure 163, pl. 54 figure 4, pl. 57 figure 3, pl. 74 figure 6, pl. 88 figure 4–10; Clark & Rowe, 1971: p. 151; figure 59 b, p. 150; pl. 23 figure 2.
Field description – Large cidaroid with test diameter up to 100 mm; red primary spines of approximately the same length as the horizontal diameter, smooth, white-grey banded, grooved at their tips; surrounded by short reddish spatulate secondary spines. Apical area 29–34 % of the horizontal diameter with a more or less dense covering of spinelets. Primary spines often with epizoic organisms. Nocturnal foraging behaviour. Naked test: pore-pairs in single series, sunken in a common furrow; apical system with exsert ocular plates and with numerous tubercles; peristomial pores in double rows, zig-zagging; genital pores not elevated.
Abundance in the Kiunga Marine Reserve – *Very rare*; not reported by Obura *et al.* (1998); we have seen this species twice during night dives in the Kiunga Marine Reserve (Mkomani and Kilima Nungu).
Local distribution - Reported from Zanzibar by Agassiz (1872, in Ludwig, 1899) as *Leiocidaris imperialis*. Humphreys (1981) didn't report it from Kenya; Tortonese (1949; 1951; 1980) failed to report it in Somalia, making this observation a new record for Kenya. Other important records include those by Hoffman (1874) as *Cidaris fustigera* and Mortensen (1931) from Madagascar (Tuléar and Nosy Bé); by Lambert (1921–22) as *Leiocidaris imperialis* from Réunion; by Sloan *et al.*, 1979 from Aldabra and by A.M. Clark (1984) from the Seychelles. A.M. Clark & Rowe (1971) list it as an Indo-Pacific species from East Africa (with the Red Sea) to the East Indies (see also H.L. Clark, 1925; Mortensen, 1928; Rowe & Richmond, 1997).

Order Aulodonta Jackson, 1912
Family Diadematidae Peters, 1855[1]
Genus *Astropyga* Gray, 1825

Astropyga radiata (Leske, 1778). Pl. 1C
Material examined – Since only one specimen was spotted in the Kiunga Marine Reserve (at Mlango wa Bomani) no sample was taken; identification in the field is certain (see also pl. 1C).
Taxonomic description – See Mortensen, 1940: 187–196, figures 111–115, pls. 8 figure 6, pl. 9 figures 6–9, pls. 10–12 figures 1–2, pl.12 figure 1, pl. 14 figures 1–3, pl. 15 figure 2, pl. 16 figure 1, pl. 17 figure 1, pl. 18 figure 1, pl. 20 figure 4, pl. 70 figures 1–3, 7, 13–17, pl. 71 figures 2, 4, 6; Clark & Rowe, 1971: p. 152; figure 63 a, p. 152; pl. 23 figure 3 (juvenile specimen).

[1] Mortensen (1940) states that Peters, 1855 and not Gray, 1835 (*in* Mortensen, 1940) or 1855 (in Mortensen, 1940) is the authority for the Diadematidae. This because Gray's paper of 1835 only speaks of the genera *Arbacia, Salenia, Echinus and Echinometra*; and because Gray's paper of 1855 speaks of the Diademadae [*sic*] (however with a correct description of the family in question). Peters, 1855 speaks of the Diadematiden (with a correct description of the family, however without using a scientific, Latinised name) and read his paper in 1853, *i.e.* well before Gray.

Field description – Large sea urchin, test diameter up to 180 mm. Test with intense red bands bordered by fluorescent blue spots; anus red-brown with white-red spots. Periproct flat or low conical. A large colour variation, from almost white to almost black, exists, but the red cross is always clearly visible. Primary spines black, finely ridged, long, easily breakable, filled with loose meshwork. Naked test: crenulate primary tubercles well developed over the total test surface; pore-pairs arranged in arcs, elongated genital plates.
Abundance in the Kiunga Marine Reserve – *Very rare,* but not observed by Obura *et al.* (1998)
Local distribution - Humphreys (1981) found a single test in the Watamu Marine Park, Tortonese (1949; 1951; 1980) failed to find it in Somalia. One of us (YS) found it earlier along the Kenyan coastline (in Gazi Bay and in Mombasa). The Kiunga Marine Reserve can however be considered as part of its range, since Price (1982) reports its presence from South East Arabia and several workers recorded it more to the South: Zanzibar (Agassiz, 1872; Pfeffer, 1896), Aldabra (Sloan *et al.*, 1979), Mozambique (Peters, 1854; Bell, 1884) and in the Seychelles (Bell, 1884; Clark, 1984). Its geographical range is the total tropical Indo-Pacific (with the Red Sea) up to Hawaii (see also Mortensen, 1940; Clark & Rowe, 1971; Clark & Courtman-Stock, 1976; Rowe & Richmond, 1997).

Genus *Diadema* Humphreys, 1797

Diadema savignyi Michelin, 1845
Material examined – KKiun/9903 (two specimens: one adult and one juvenile).
Taxonomic description – See Mortensen, 1940: 265–269, figures 136, 141b, 143, pl. 48 figure 1, pl. 49 figure 4, pl. 52 figures 1–2, pl. 53 figures 2–5, pl. 59 figure 1–12, pl. 60 figures 4–6, pl. 74 figures 10–14, 16, 19; Clark & Rowe, 1971: p. 153.
Field description – Small-bodied sea urchin (horizontal test diameter max 50 mm) with long (up to 100 mm), slender, fragile (hollow), finely ridged, black or grey primary spines, which can be white-banded (especially prominent in juveniles); no orange ring around tip of the anal cone, iridescent blue lines around the periproct and down the interambulacra; buccal plates spineless. Naked test: total surface with well-developed primary perforate and crenulate tubercles (decreasing in size towards the peristome); triplet of pore-pairs arranged in arcs for each primary tubercle; genital plates not longer then wide; length-breadth test ratio usually 4–5:1.
Abundance in the Kiunga Marine Reserve – *Common*, however not reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.
Local distribution - Documented as *well distributed* by Humphreys (1981) from Kenya (Watamu and Malindi Marine Park), however not reported from Somalia (Tortonese, 1949; 1951; 1980). Tortonese (1936) reports it as *Diadema Savignyi* from the Red Sea and Price (1982) reports it further South from South-East Arabia making the Kiunga Marine Reserve part of its range. Even more to the South an important local record is that by Décary (1924) as *Diadema Savignyi* from Madagascar. Clark & Rowe (1971) list it as a tropical Indo-Pacific species from East Africa (without the Red sea) to the Islands of the South Pacific, however not found on Hawaii (see also Mortensen, 1940; Clark & Courtman-Stock, 1976; Rowe & Richmond, 1997).

Diadema setosum (Leske, 1778)
Material examined – KKiun/9902 (one specimen).
Taxonomic description – See Mortensen, 1940: 256–264, figures 140, 141a, pls. 49 figures 1–2, pls. 50, 51, 52 figure 3, pl. 53 figure 1, pl. 54 figures 2–3, pl. 55 figure 1–6, pl. 56 figures 1–13, pl. 60 figures 1–2, pl. 61 figure 1, pl. 73 figures 1, 10–12, pl. 74 figures 15, 17, 18, 20; see Clark & Rowe, 1971: p. 153; figure 62, p. 152; figure 64 b, p. 153; pl. 24 figure 1.
Field description – Small-bodied sea urchin with approximately the same horizontal diameter as *D. savignyi*, with long (up to 100 mm), slender, fragile needle-sharp, black primary spines, which can be banded (especially prominent in juveniles); five white spots on interambulacra, a clear orange ring around the tip of the anal cone; buccal plates without spines. Naked test: very similar to *D. savignyi* but compound plates (pore-pairs no longer correspond to the number of pore triplets) already present in individuals of ca. 40 mm horizontal diameter (see also figures 140 and 143 in Mortensen, 1940).
Abundance in the Kiunga Marine Reserve – *Common*, also reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.

Local distribution - Reported by Humphreys (1981) from Mida Creek and from the Watamu Marine Park, Kenya; not found in Somalia by Tortonese (1949, 1951, 1980), but documented further north by Price (1981, 1982). Other important records include those by Peters (1854) from Mozambique; by Ludwig (1899) from Zanzibar (Ludwig, 1899 also lists older records from the region); by Haacke (1880) from Mauritius, and by Lambert (1921–22) as *Centrostephanus setosum* from Madagascar. Clark & Rowe (1971) list it as a tropical Indo-Pacific species from East Africa (with the Red Sea, see also Tortonese, 1936, 1955) to the Islands of the South Pacific, however not on Hawaii (see also Mortensen, 1940; Clark & Courtman-Stock, 1976; Rowe & Richmond, 1997).

Genus *Echinothrix* Peters, 1853

Echinothrix calamaris (Pallas, 1774)
Material examined – KKiun/9905 (one specimen).
Taxonomic description – See Mortensen, 1940: 285–290, figures 147–149, pl. 39 figure 1, pl. 40, pl. 41 figures 1–2, pl. 42 figures 1–5, pl. 43 figure 3, pl. 44 figures 2–10, pl. 46 figure 1, pl. 47 figures 1–3, 5, pl. 48 figure 3, pl. 71 figures 5–8; Clark & Rowe, 1971: 153; figure 63 b, p. 152; pl. 31 figure 17.
Field description – Small-bodied (horizontal test diameter up to 85 mm) very dark-green to black echinoid with aborally long, barbed, needle-like primary spines. Primary spines relatively firm, but with a large central cavity. Both the primary and the very fine secondary spines are often banded with green (especially prominent in juveniles); periproct spotted. Ambulacra bulging aborally with apically naked interambulacra. Naked test: usually greenish in colour; primary tubercles perforated and crenulated, similar over total test surface; genital plates approximately as long as wide.
Abundance in the Kiunga Marine Reserve – *Rare*, only observed in one locality (Kaddhika). Not reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.
Local distribution - Humphreys (1981) reports this species from several localities in Kenya, Tortonese (1949; 1951, 1980) failed to find it in the littoral waters of Somalia; Price (1982), however, reports this species from further afield in SE Arabia, the Red Sea (see also Tortonese, 1955), the Gulf of Aqaba and Suez. Other important historical records for the region include those by Ludwig (1899) as *Echinothrix Desori* from Zanzibar and by Lambert (1921-22) as *Diadema Frappieri* from Madagascar. Clark & Rowe (1971) list it as a tropical Indo-Pacific species from East Africa up to Hawaii (see also Mortensen, 1940; Clark & Courtman-Stock, 1976; Rowe and Richmond, 1997).

Echinothrix diadema (Linnaeus, 1758)
Material examined – KKiun/9904 (one specimen).
Taxonomic description – See Mortensen, 1940: 290–295, figures 150–152, pl. 43 figures 1–2, pl. 44 figure 1, pl. 45 figures 1–8, pl. 46, figures 2–4, pl. 47 figures 4, 6–7, pl. 48 figure 4, pl. 71 figures 1, 3; Clark & Rowe, 1971: 153; figure 64 a, p. 153; pl. 24 figure 2.
Field description – Large bodied (test diameter up to 140 mm) echinoid; all interambulacral plates covered with fine black backwardly-barbed primary spines, dark-reddish test. Ambulacra not distinctively bulging, aborally no naked ambulacral areas. Cavity in very brittle, medium-long (up to 80 mm) primary spines very small. Naked test: similar to *E. calamaris*, but mostly larger and never greenish, sometimes reddish.
Abundance in the Kiunga Marine Reserve – *Abundant*. Reported from the same locality by Obura *et al.* (1998).
Local distribution - Reported from Kenya by Humphreys (1981) in low numbers in Mida Creek, from southern Somalia (Gesira and Sar Uanle) by Tortonese (1980). Other important historical records for the region include those by Ludwig (1899) as *Echinothrix spinosissimum*; by Haacke (1880) *as E. turcarum* from Mauritius; and by Lambert (1921–22) as *Diadema turcarum* from Madagascar. Clark & Rowe (1971) list it as a tropical Indo-Pacific species from East Africa up to Hawaii (see also Mortensen, 1940; Rowe & Richmond, 1997).

Order Camarodonta Jackson, 1912
Family Echinometridae Gray, 1855
Genus *Echinometra* Gray, 1825

Echinometra mathaei (de Blainville, 1825)
Material examined – KKiun/9913 (six specimens).

Taxonomic description – See Mortensen, 1943b: 38–3931, figures 185–194, pl. 42 figures 1–10, pl. 47 figures 1–4, pl. 65 figures 16–26; Clark & Rowe, 1971: p. 157; figure 69 b, p. 156; pl. 23, figure 5.
Field description – Small sea urchin (test diameter up to ~ 65 mm) with a distinct oval body (when viewed from above) and a high colour variation (from green to brown to purple to black). Fairly long, slender, tapering, stout primary spines, often with a white band at their base. Naked test: oval in outline, with long axis of the test through ambulacrum 1 and interambulacrum 3, horizontal test diameter approximately equal to the height of the test; four pore pairs per arc aborally; primary tubercles imperforate; shallow gill slits.
Abundance in the Kiunga Marine Reserve – *Abundant*; together with *Stomopneustes variolaris* and *Echinostrephus molaris*, this species is the most abundant sea urchin in the Kiunga Marine Reserve (see also Obura *et al.*, 1998).
Local distribution - Humphreys (1981) comes to the same conclusion for the Watamu Marine Park and Kilifi. In southern Somalia Tortonese (1951, 1980) reports on large populations. Other important historical records for the region include those by Ludwig (1899) as *Echinometra lucunter* from Zanzibar; by Lambert (1921–22) as *Ellipsechinus lukunter* from Madagascar. Clark & Rowe (1971) list it as a tropical Indo-Pacific species (with the Red Sea, see also Tortonese, 1936, 1955) from East Africa up to Hawaii (see also Mortensen, 1943b; Clark & Courtman-Stock, 1976; Rowe & Richmond, 1997).

Genus *Echinostrephus* A. Agassiz, 1863

Echinostrephus molaris (de Blainville, 1825)
Material examined – KKiun/9914 (one specimen).
Taxonomic description – See Mortensen, 1943b: 311–316, figure 149a, b, figure 150 a, b, pl. 35 figures 1–10, pl. 58 figures 1, 2, 4, 9; Clark & Rowe, 1971: p. 157.
Field description – Small species with test diameter seldom larger than 30 mm. Test broadest at the flattened aboral side. Always in self-made deep rocky burrows, aboral side flat, with a vertically projecting tuft of long, easily breakable primary spines with variable colouration (whitish-blue to black). Naked test: shallow gill slits; test flattened aborally; invariably three pore-pairs in each arc.
Abundance in the Kiunga Marine Reserve – *Abundant,* also reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.
Local distribution - Previously reported from Kenya as *common* by Humphreys (1981); however never recorded from the Somalian coast; reported from the Red Sea, the Gulf of Aqaba and the Arabian Gulf but not from South East Arabia (Price, 1982). Further South Agassiz (1872, in Ludwig, 1899) lists records from Zanzibar and Mozambique; Bell (1903) from Zanzibar as *Echinostrephus molare*. Clark & Rowe (1971) list it as a tropical Indo-Pacific species from East Africa to the Islands of the South Pacific (see also Mortensen, 1943b; Clark & Courtman-Stock, 1976; Rowe & Richmond, 1997).

Genus *Heterocentrotus* Brandt, 1835

Heterocentrotus mammillatus (Linnaeus, 1758). Pl. 1D
Material examined – Due to its low population numbers (only few specimens have been seen by one of us, YS, over the total Kenyan coastline), no sample was collected. Moreover identification in the field is certain; picture D on pl. 1, taken at Mlango wa Bomani leaves no doubt over the identification.
Taxonomic description – See Mortensen 1943b: 409–420, figures 204, 205a, 206, 207a, b, 208a, 209, 210, pl. 51 figures 1–6, pl. 52 figures 6–8, pl. 66 figures 7, 9–20; Clark & Rowe, 1971: p. 158; figure 71 b, p. 153; pl. 23 figure 4.
Field description – Large species with horizontal test diameter up to 80 mm; test oval; massive primary spines are long (up to 100 mm at the ambital side), smooth, blunt and tapering, triangular in cross section, distally with transversal white banding; secondary spines distributed over the total test surface, whitish, short and with flattened tips. Naked test: 9–11 pore-pairs in each arc at the ambital region; primary ambulacral tubercles smaller above ambitus.
Abundance in the Kiunga Marine Reserve – *Very rare* to *Rare*, only observed once by us; not reported by Obura *et al.* (1998).
Local distribution - Tortonese (1949; 1951, 1980) failed to record it in Somalian waters; Humphreys (1981) reports it from Kenya (Ras Ngomeni); Price reports from SE Arabia, Red Sea (see also Tortonese, 1955) and the Gulf of Aqaba; Haacke (1880) from Mauritius. Given these records and the fact that *Heterocentrotus mammillatus* is nocturnal this species is probably more abundant than what is deduced from

our observations. A.M. Clark & Rowe (1971) list it as a tropical Indo-Pacific species from East Africa (with the Red Sea) up to Hawaii (see also Mortensen, 1943b; H.L. Clark, 1925; Rowe & Richmond, 1998).

Family Temnopleuridae A. Agassiz, 1872
Genus *Microcyphus* L. Agassiz, 1841

Microcyphus rousseaui L. Agassiz, 1846. Pl. 1E
Material examined – KKiun/9906 (one specimen); KKiun/9907 (one specimen).
Taxonomic description – See Mortensen, 1943a: 155–159, figure 84, pl. 12 figs 18–25, pl. 47 figs 18–20, 23–24; Clark & Rowe, 1971: p. 156; pl. 24 figure 6.
Field description – Relatively small species with horizontal test diameter rarely exceeding 50 mm. Naked, dark purple areas with a distinct whitish-pink zig-zag line; spines beige-brown with distinct darker brown bands. Apical system rounded. Naked test: each ambital and ambulacral plate with a distinct tubercle, which is indistinctly crenulate, the sutural pores are very small; five very distinct naked areas descending from the aboral side over almost the total test
Abundance in the Kiunga Marine Reserve – *Very rare,* only observed twice by us, not seen by Obura *et al.* (1998) in the Kiunga Marine Reserve.
Local distribution - First record for Kenya. Humphreys (1981) failed to find it in Kenya, but it was observed by Tortonese (1980) in southern Somalia (Gesira). Also found by Price (1982) in SE Arabia, the Red Sea and the Gulf of Aqaba. Further South, Lambert (1921–22) describes it as *Microcyphus Decaryi* from Madagascar, A.M. Clark & Rowe (1971) list it as a tropical Indian Ocean species restricted to East Africa and Madagascar, the Red Sea (see also Tortonese, 1936 as *Microcyphus maculatus*) and SE Arabia. Rowe & Richmond (1997) give as its distribution the Red Sea, the western Indian Ocean to the West Pacific Ocean (see also Mortensen, 1943a).

Family Toxopneustidae Trosschel, 1872
Genus *Toxopneustes* L. Agassiz, 1841

Toxopneustes pileolus (Lamarck, 1816)
Material examined – KKiun/9911 (one specimen).
Taxonomic description – See Mortensen, 1943a: 472–480, figures 240b, 293a, 294, 295a, 296, 297a, b, 298, pl. 26 figure 3, pl. 27 figures 1–4, pl. 28 figures 1, 2, pl. 29 figures 1–5, pl. 30 figures 1–4, pl. 31 figure 9, pl. 33 figures 5, 6, pl. 54 figures 1, 3–6, 8–10, 13–16, pl. 55 figure 13; Clark & Rowe, 1971: p. 156; figure 69, p. 156; pl. 24 figure 7; pl. 31 figure 15.
Field description – Large-bodied sea urchin with low test (horizontal diameter up to 150 mm; with very large, orange, globiferous pedicellariae (diameter up to 3 mm); very short (up to 20 mm) orange, finely-ridged longitudinal primary spines. Naked test: usually sunken towards the mouth; purple banded horizontally; every second ambulacral plate with a primary tubercle; oligoporous ambulacral plates.
Abundance in the Kiunga Marine Reserve – *Common.*
Local distribution - This species has been found by almost all the researchers that sampled in this region. A.M. Clark & Rowe (1971) list it as a tropical Indo-Pacific species from East Africa (without the Red Sea) to the Islands of the South Pacific (see also Mortensen, 1943a; A.M. Clark & Courtman-Stock, 1976). Rowe & Richmond (1997) include the Red Sea in the geographical distribution.

Genus *Tripneustes* L. Agassiz, 1741

Tripneustes gratilla (Linnaeus, 1758)
Material examined – KKiun/9908 (one specimen, juvenile); KKiun/9909 (one specimen, juvenile); KKiun/9912 (one specimen).
Taxonomic description – See Mortensen, 1943a: 500–508, figs 306, 307, pls 33 figures 1–3, pl. 34 figures 2–6, pl. 35 figures 3–4, pl. 37 figs 1–2, 4–10, pl. 38 figures 1–4, pl. 56 figure 11; Clark & Rowe, 1971: p. 156; figure 65 b, p. 153; pl. 24 figure 8; pl. 31 figure 16.
Field description – Large-bodied sea urchin (test diameter up to 120 mm) with high almost globular (up to 55 mm) test, with numerous small whitish primary spines in the interambulacral areas, and with 10 darker bands corresponding to the podia (not the pedicellaria which are much smaller). Naked test: only one in

three or four ambulacral plates with a primary tubercle; pore-pairs in horizontal arcs and spaced to form three distinct series.
Abundance in the Kiunga Marine Reserve – *Abundant.*
Local distribution - Reported by all the researchers that sampled in this region (see e.g. Bell, 1903 who reports it as *Hipponoe variegata* from Zanzibar or Lambert (1921–22) who reports it from Madagascar). A.M. Clark & Rowe (1971) list it as a tropical Indo-Pacific species from East Africa (with the Red Sea) up to Hawaii (see also Mortensen, 1943a; Tortonese, 1955; A.M. Clark & Courtman-Stock, 1976; Rowe and Richmond, 1997).
Remarks – Although this species is not harvested in the Kiunga Marine Reserve, nor in Kenya (as far as we know), it is suitable for human consumption. The large population numbers and the synchronised lunar reproductive cycle (Muthiga, pers. comm.), whereby the gonads grow large enough for harvesting once a month, make it a species with a high economic potential. We observed harvesting of this species in northern Kwazulu Natal (Bangha Nek), Republic of South Africa.

Order Stiridonta Jackson, 1912
Family Stomopneustidae Pomel, 1883
Genus *Stomopneustes* L. Agassiz, 1841

Stomopneustes variolaris (Lamarck, 1816)
Material examined – KKiun/9910 (three specimens).
Taxonomic description – See Mortensen, 1935: 507–512, figure 301, 302, pl. 71 figures 3–5, pl. 72 figs 1, 2, pl. 89 figures 16–26; Clark & Rowe, 1971: p. 153; figure 65a, p. 153; figure 66, p. 154; pl.23 figure 6.
Field description – Medium sized species (horizontal test diameter up to 80 mm); test round, with large (up to 80 mm long), solid, slightly tapering green-blue primary spines. Naked test: tubercles neither perforated nor crenulated; ambulacral plates doubly compound, at the ambitus one very large ambulacral tubercle corresponds to up to six arcs.
Abundance in the Kiunga Marine Reserve – *Abundant.* This species was present in large numbers in almost all the sampling sites, which is in agreement with the observations made by Obura *et al* (1998) in the same marine reserve.
Local distribution - Humphreys (1981) reports it as 'extremely numerous' in several locations along the Kenyan coast. Also reported by Tortonese (1980) from Sar Uanle (southern Somalia), although he doesn't describe abundance. Other important records for the region include those by Ludwig (1899) from Zanzibar and by Lambert (1921–22) from Madagascar. A.M. Clark & Rowe (1971) list it as a tropical Indo-Pacific species from East Africa (without the Red Sea) to the Islands of the South Pacific (see also Mortensen, 1935; A.M. Clark & Courtman-Stock, 1976). Rowe & Richmond (1997) also report its presence from the Red Sea. Haacke (1880) reported it from Mauritius.

HOLOTHUROIDEA (Local Swahili Name: majongo ya baharini)

We collected 57 specimens belonging to 23 different species of Holothuroidea. Samples of two more species were lost, due to inadequate preservation: *Bohadschia subrubra* and *Stichopus herrmanni.* According to literature, two more species—*Holothuria (Mertensiothuria) pervicax* and *Holothuria (Selenkothuria) parva*—are expected.
The holothurian fauna of the Kiunga Marine Reserve is now represented by 28 species. *Actinopyga echinites, Holothuria (Cystipus) rigida, Holothuria (Platyperona) difficilis, Labidodemas pertinax, Stichopus chloronotus* and *Stichopus cf. monotuberculatus* are new records for Kenya. *Holothuria (Theelothuria) turriscelsa* is a new record for the Indian Ocean.

Order Apodida Brandt, 1835
Family Synaptidae Burmeister, 1837
Subfamily Synaptinae Burmeister, 1837
Genus *Synapta* Escholtz, 1829

Synapta maculata (Chamisso & Eysenhardt, 1821)
Material examined – KKiun/9951 (one specimen).

Taxonomic description – See Cherbonnier, 1988: 251–252; figure 112, p. 253.
Field description – Very large species with a distinct vermiform body, reaching lengths up to 3,000 mm and widths up to 35 mm. Body colour dark green to brown with numerous transverse darker brown bands and radii with a longitudinal brown stripe. Mouth terminal surrounded by 15 feather-like tentacles. Anus terminal. Body wall smooth and thin, but very 'sticky' due to the numerous anchor spicules (visible with the naked eye when skin is held against the light) in the body tissue.

TABLE 4. List of holothurians collected at the different localities in Kiunga Marine Reserve. The number of specimens refers to the number of animals that were encountered during a 60-minute sampling period. i.t. stands for intertidal. Depths apply to the low water level.

SPECIES	SITE NAME	MIN-MAX DEPTH (M)	APPROX #	COLLECTION N°
APODIDA				
Synaptidae				
Synapta maculata	Kui	2	1	KKiun/9951
ASPIDOCHIROTIDA				
Holothuriidae				
Actinopyga echinites	Kui	1-4	4	KKiun/9922
	Kaddhika	2-4	2	None
	Chongo cha Chano	9-13	2	None
Actinopyga mauritiana	Kilima Nungu	4	1	None
	Mike's outer reef	1-3	25	KKiun/9921
	Kui	1-3	3	None
	Kaddhika	1-3	6	None
	Mwamba wa Boso	1-3	6	None
	Kui	1-2	1	None
	Hindi	2-4	4	None
Actinopyga miliaris	Kui	3	1	KKiun/9923
	Hindi	2	1	KKiun/9924
	Chongo cha Mvundeni	12	1	None
Bohadschia atra	Mkomani	1-4	4	KKiun/9927
	Hindi	2	1	KKiun/9928
	Chongo cha Chano	14	1	None
Bohadschia marmorata	Mike's Outer Reef	2-3	4	KKiun/9925
	Kui	1-4	2	KKiun/9926
Bohadschia subrubra	Kui	1-4	15	None
	Hindi	3	2	None
Holothuria (Cystipus) rigida	Kui	4	1	KKiun/9948
Holothuria (Halodeima) atra	Kilima Nungu	3-5	4	Kkiun/9929
	Chongo cha Chano	8-12	4	None
	Shimo la Tewa	3-4	2	None
	Mlango wa Bomani	1-4	10	KKiun/9930
	Wreck	6-9	3	None
	Mwamba wa Boso	1-5	10	None
	Mwamba Mkuu	12-20	5	None
Holothuria (Halodeima) edulis	Kilima Nungu	6	1	None
	Mike's inner reef	5-7	1	None
	Mwamba Mkuu	10-14	3	KKiun/9931
	Mlango Bomani	4	1	None
	Chongo cha Chano	10-20	2	None
	Kilima Nungu	6	1	None
Holothuria (Lessonothuria) pardalis	Kilima Nungu	4	1	KKiun/9934
	Mlango wa Bomani	1-4	1	KKiun/9935
	Kaddhika	4	1	KKiun/9936
	Kui	1-4	1	KKiun/9937
Holothuria (Mertensiothuria) leucospilota	Mkomani	2-4	5	KKiun/9932
	Mike's Inner Reef	7	1	None
	Mlango wa Bomani	1-2	2	KKiun/9933
	Hindi	1-3	4	None
Holothuria (Metriatyla) scabra	Kui	2	1	KKiun/9939
Holothuria (Microthele) nobilis	Chongo cha Kui	16-21	2	KKiun/9940
	Mwamba Mkuu	15-17	6	None
	Chongo cha Mvundeni	17-24	4	None
	Chongo cha Chano	18	1	None
Holothuria (Platyperona) difficilis	Kui	2	1	KKiun/9949

SPECIES	SITE NAME	MIN-MAX DEPTH (M)	APPROX #	COLLECTION N°
Holothuria (Semperothuria) cinerascens	Mlango wa Bomani	2	1	KKiun/9941
Holothuria (Stauropora) fuscocinera	Mike's Inner Reef	5	1	KKiun/9938
	Mike's Inner Reef	5	1	KKiun/9946
Holothuria (Theelothuria) turriscelsa	Kilima Nungu	5-7	2	KKiun/9947
Holothuria (Thymiosycia) arenicola	Mkomani	i.t.	1	KKiun/9945
Holothuria (Thymiosycia) hilla	Mlango wa Bomani	2	1	KKiun/9942
	Kaddhika	3	3	KKiun/9943
Holothuria (Thymiosycia) impatiens	Kui	0.5	4	KKiun/9944
Labidodemas pertinax	Mkomani	4	1	KKiun/9919
	Shimo la Tewa	7	1	None
	Mlango wa Bomani	1-4	2	KKiun/9920
	Kilima Nungu	5	1	None
Stichopodidae				
Stichopus herrmanni	Kui	1-4	2	None
	Hindi	3	1	None
Stichopus cf. monotuberculatus	Kilima Nungu	5-7	2	KKiun/9950
	Mike's Inner Reef	5-7	4	None
Stichopus chloronotus	Hindi	2	1	None
DENDROCHIROTIDA				
Phyllophoridae				
Afrocucumis africana	Kui	i.t.	5	KKiun/9918

Abundance in the Kiunga Marine Reserve – *Very rare.* Only a single specimen was found in a small seagrass bed (location Kui). Not reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.
Local distribution - Recorded in low numbers by Humphreys (1981) in Kenya (Mida Creek). Not found by Tortonese (1980) in Somalia. Other important local records include those by Lampert (1896) as *Synapta beselii* from Zanzibar; by Sloan *et al.* (1979) from Aldabra; and by Clark (1984) from the Seychelles. Massin (1999, figure 92: p. 109) shows an Indo-Pacific distribution from East Africa (with the Red Sea) to the Society Islands (Tahiti).

Order Aspidochirotida Grube, 1840
Family Holothuriidae Ludwig, 1894
Genus *Actinopyga* Bronn, 1860

Actinopyga echinites (Jaeger, 1833). Pl. 1F
Material examined – KKiun/9922 (four specimens).
Taxonomic description – See Cherbonnier, 1988: 31, 32; figure9, p.33.
Field description – Colour in life from light brown to chocolate brown, dorsally and ventrally, sometimes mottled with brown or black. Mouth ventral, with 20 brown peltate feeding tentacles. Anus terminal surrounded by five yellowish teeth. Trivium covered with numerous cylindrical podia, which are distributed distinctively in three ambulacral areas in smaller individuals, and scattered over the interambulacra in the largest individual. Bivium with fewer podia both in the radial and interradial areas.
Abundance in the Kiunga Marine Reserve – *Common,* although Obura *et al.* (1998) didn't report this very recognisable species in the Kiunga Marine Reserve.
Local distribution - Humphreys (1981) was unable to discern between *A. echinites* and *A. miliaris* he collected in Kenya (Mida Creek and Kibirijini Point). Levin (1979) reports this species (as *A. plebeja*) from Mombasa. Tortonese (1980) reports on two specimens from South Somalia (Sar Uanle, 20 km South of Kismayu). Other important records for eastern Africa/ western Indian Ocean include those by Lampert (1896) and Panning (1944) from Zanzibar; by Hughes & Gamble (1977) from Aldabra; by Lampert (1885), Ludwig (1899) and Clark (1984) from the Seychelles. Rowe & Doty (1977) summarise the geographical distribution as "general distribution from scattered localities throughout the tropical Indo-Pacific, but not on Hawaii".
Remarks – This species is well known by local seacucumber fishermen; they refer to it as 'iyongo wimbi' (like millet) which refers to the body colour and texture. In the Kiunga market it is sold for 1 KSh/fresh specimen. Obura *et al.* (1998) noted two species of *Actinopyga* in the Kiunga Marine Reserve: *A. mauritiana* and *Actinopyga* sp. While no collections were made by them, we can be quite sure that it is *A.*

echinites since this species is easily distinguished from the other two *Actinopyga* species found in the Kiunga Marine Reserve: *A. miliaris* which is uniform black, and *A. mauritiana* (which they did identify). Humphreys (1981) collected an *Actinopyga* in the Channel to Mida Creek and on a wave-cut platform at Kibirijini Point in Kenya, however he was unable to identify it to the species level.

Actinopyga mauritiana (Quoy & Gaimard, 1833)
Material examined – KKiun/9921 (one specimen).
Taxonomic description – See Cherbonnier, 1988: 16–18; figure 2 p. 19.
Field description – Species length up to 350 mm, width up to 85 mm. Colour very variable: dorsally chocolate brown with numerous conical papillae; ventrally white-grey to brown, densely covered with large cylindrical brown to green tube feet scattered over interambulacra and ambulacra. Bivium clearly distinguishable from trivium. Mouth ventral, surrounded by at least 25 short and stout, dark brown feeding tentacles which in turn are surrounded by a distinct collar of papillae. Anus terminal, guarded by five conspicuous teeth.
Abundance in the Kiunga Marine Reserve – *Abundant,* probably the most abundant species in the Reserve. Obura *et al.* (1998) found it in the Kiunga Marine Reserve.
Local distribution - Humphreys (1981) reports on specimens from Kenya (Big Tree Cave at the mouth of Mida Creek), and Tortonese (1980) from Somalia (Gesira, 18 km South of Kismayu). Other important records for eastern Africa/western Indian Ocean include those by Lampert (1896) from Zanzibar (as *Muelleria mauritiana*); by Lampert (1885) (as *Muelleria mauritiana*), Ludwig (1899) (as *Muelleria mauritiana*) and A.M. Clark (1984) from the Seychelles; by Quoy & Gaimard (1833) (as *Holothuria mauritiana,* in Mitsukuri, 1912); by Ludwig (1883) (as *Muelleria mauritiana*) from Mauritius and by Sloan *et al.* (1979) from Aldabra.
Remarks – This species is also well known by local seacucumber fishermen; they refer to it as 'iyongo bura'. In the Kiunga market it is sold for 5 KSh/fresh specimen.

Actinopyga miliaris (Quoy & Gaimard, 1833)
Material examined – KKiun/9923 (one specimen); KKiun/9924 (one specimen).
Taxonomic description – See Massin, 1996a: 12–13; figure 6, p. 13; Massin, 1999: 10–12; figures 5, p. 10.
Field description – Species length up to 400 mm, width up to 100 mm. Colour in life uniform dark brown dorsally and ventrally (although some specimens may show a slightly lighter colour ventrally). Mouth ventral surrounded by 16 firm brown tentacles. Anus terminal surrounded by five easily noticeable yellow-orange teeth. Five to eight rows of podia with the same colouration as the body wall on the ventro-lateral radii, 12–15 rows of podia on the ventro-median radius.
Abundance in the Kiunga Marine Reserve – *Rare*, only spotted in three locations (Kui, Kaddhika and Chongo Cha Chano). Not found by Obura *et al.* (1998) in the Kiunga Marine Reserve.
Local distribution - Humphreys (1981) found it only in one location on the Kenyan Coast (Mida Creek); Levin (1979) reports it from Mombasa; Tortonese (1949, 1951, 1980) didn't report it from Somalia; but Price (1982) found it in the Red Sea, the Gulf of Aqaba and in the Gulf of Suez. Other important records from eastern Africa/western Indian Ocean include those by Lampert (1885) from Zanzibar (as *Muelleria miliaris*); by Haacke (1880) and Ludwig (1883) from Mauritius (as *Muelleria miliaris*). Massin's (1999, figure 6: p. 11) distribution map shows an Indo-Pacific distribution from East Africa (with the Red Sea) to the Fiji Islands. The Kiunga Marine Reserve is now the most northern point along the East African coast.
Remarks – This species is known by local seacucumber fishermen although they fail to make a distinction with the other black species like *Holothuria atra, H. leucospilota* and *Bohadschia atra*; they refer to it as 'iyongo leusi' (black seacucumber). In the Kiunga markets fishermen get 1 KSh for a fresh specimen.

Genus *Bohadschia* Jaeger, 1833

Bohadschia atra Massin, Rasolofonirina, Conand & Samyn, 1999
Material examined – KKiun/9927 (three specimens); KKiun/9928 (one specimen).
Taxonomic description – See Massin *et al.*, 1999: 151–160; figure 1, p. 152; figure 2, p. 154; pl.1.B, D, p. 159.
Field description – Species up to 400 mm long and 150 mm wide. Deep brown to black bivium with numerous lighter brown to red spots. Trivium slightly lighter in colour, without red spots. Ventral podia scattered over radial and interradial areas, dorsal podia also scattered but less numerous. Mouth ventral,

surrounded by 18–20 black tentacles, anus dorsal. Cuvierian tubules present and very readily ejected in large quantities.
Abundance in the Kiunga Marine Reserve – *Common.* Minor range extension from Shariani (some 30 km north of Mombasa). Not reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.
Local distribution - *Bohadschia atra* Massin *et al.*, 1999 was recently described by one of us (YS in Massin *et al.*, 1999). That paper also discusses the distribution. The Kiunga Marine Reserve is now documented here as the most northern point of its range.

Bohadschia subrubra (Quoy & Gaimard, 1833) Pl.1G
Material examined – None, picture G on pl. 1 leaves no doubt over the identification.
Taxonomic description – See Massin *et al.*, 1999: 151–160; figure 3, p. 155; figure 4, p. 156; figure 5, p. 157; pl.1A, C, D, p. 159.
Field description – Species up to 350 mm long and 130 mm wide. Bivium brown to orange with unevenly distributed dark brown areas. Trivium white, with tiny black spots. Numerous ventral podia, white, very long, and scattered over the whole surface. Dorsal podia less numerous, scattered, white, so clearly visible against the orange background. Mouth ventral surrounded by 18 stout, white feeding tentacles. Anus dorsal, unguarded by anal teeth or papillae. Cuvierian tubules present and very readily ejected in large quantities.
Abundance in the Kiunga Marine Reserve – *Common.* Also reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.
Local distribution - Minor range extension from Shariani (some 30 km north of Mombasa). *Bohadschia subrubra* was recently redescribed (Massin *et al.*, 1999). That paper also discusses the distribution.
Remarks – Species well-known by the local fishermen, who refer to it as 'iyongo la tambi' (meaning spaghetti; referring to the readily ejected Cuvierian tubules); the other *Bohadschia* sp get the same common name. It has a limited commercial value. The specimens identified by Humphreys (1981) as *Bohadschia koellikeri,* were not seen by us. However, the description (p. 33) of the colour in life ("bold camouflage pattern in deep brown and beige, tube feet spread over surface give white dotted surface and often hold marine angiosperm leaves over the surface of the animal") is characteristic of *Bohadschia subrubra.* This species is quite common in the studied site, which is now considered to be the northern edge of its range.

Bohadschia marmorata Jaeger, 1833
Material examined – KKiun/9925 (three specimens); KKiun/9926 (two specimens).
Taxonomic description – See Cherbonnier, 1988: 36–38; fig 11, p. 37.
Field description – Large species up to 300 mm long and 100 mm wide. Body colour yellow-white ventrally and laterally, brownish dorsally, spotted by numerous small brown spots corresponding to conical podia. Dorsally, transversal banding is sometimes visible. Mouth ventral, surrounded by 15–20 light brown, relatively small tentacles which in turn are surrounded by a circle of brown podia; relatively large terminal anus surrounded by a brown line. Ventral tube feet spread in the ambulacral and the interambulacral zones. Bivium covered by conical tube feet surrounded at their base by a small brownish circle. Cuvierian tubules present.
Abundance in the Kiunga Marine Reserve – *Common.* First record for the Kiunga Marine Reserve.
Local distribution - Humphreys (1981) reports it from Kenya in the Mida Channel and throughout the Watamu Marine Park; Levin (1979) from Mombasa. Sloan *et al.* (1979) reports on the species from Aldabra; Clark (1984) from the Seychelles. Another important record for eastern Africa/western Indian Ocean is Haacke (1880) from Mauritius (as *Holothuria utrimquestigmosa).* It is reported throughout the shallow waters of the tropical zone of the Indo-Pacific.
Remarks - Obura *et al.* (1998) only observed one species of *Bohadschia,* which they identified as *Bohadschia vitiensis.* This species is listed and depicted in Richmond's book on the fauna and flora of eastern Africa (1997). However without microscopic examination of the spicules no differentiation with *Bohadschia marmorata* can be made (See also Massin, 1996a for a discussion). Therefore we would include *B. marmorata* in the fauna of Kiunga Marine Reserve, and (for now) not *B. vitiensis.*

Genus *Holothuria* Linnaeus, 1767
Subgenus *Cystipus* Haacke, 1880

Holothuria (Cystipus) rigida (Selenka, 1867) Pl. 1H
Material examined – KKiun/9948 (one specimen).

Taxonomic description – See Cherbonnier, 1988: 126–127 & 129; figure 51, p. 127.
Field description – Medium-sized species (125 mm long and 25 mm wide). Body colour white to yellow ventrally and somewhat lighter dorsally. Podia in trivium evenly distributed over the radial and interradial areas; conical podia in bivium distributed in three interradial areas. Anus terminal, surrounded by conical papillae, mouth ventral, with 20 small, yellow-brown tentacles.
Abundance in the Kiunga Marine Reserve – *Very rare*, only observed once. Not observed by Obura *et al.* (1998) in the Kiunga Marine Reserve.
Local distribution - First record for Kenya. Other important records from eastern Africa/western Indian Ocean include those by Selenka (1867) from Zanzibar (as *Stichopus rigidus*), by Haacke (1880) (as *Cystipus pleuripus*) and by Ludwig (1883) (as *Holothuria pleuripus*) from Mauritius, by Sloan *et al.* (1979) from Aldabra, by Clark (1984) from the Seychelles; by Cherbonnier (1988) from Iles Glorieuses.
Remarks – Selenka's (1867: p. 317) description (as *Stichopus rigidus*) says that *H. (Cystipus) rigida* contains few long tubules of Cuvier. In the single specimen we collected these are not visible.

Subgenus *Halodeima* Pearson, 1914

Holothuria (Halodeima) atra Jaeger, 1833
Material examined – KKiun/9929 (one specimen); KKiun/9930 (five specimens).
Taxonomic description – See Cherbonnier, 1988: 73–74; figure 28, p. 74.
Field description – Uniform black species with a cylindrical body, reaching sizes up to 300 mm long and 70 mm wide. Ventrally short, black, cylindrical podia scattered over the radial and interradial areas; dorsally short, black, conical tube feet over the total surface. Mouth ventral, surrounded by 20 short, black feeding tentacles. Anus terminal, unguarded. Cuvierian tubules always absent. Body wall often covered with fine sand.
Abundance in the Kiunga Marine Reserve – *Abundant.* Also reported in the Kiunga Marine Reserve by Obura *et al.* (1998).
Local distribution - Humphreys (1981) reports *H. atra* from the Watamu Marine Park, and Tortonese (1980) from Somalia (Sar Uanle, 20 km South of Kismayu). Massin's distribution map (1999; figure 13: p. 21) shows an Indo-Pacific distribution from the coast of East Africa (with the Red Sea) to the coast of western America.
Remarks – In the field, this species is easily confused with *H. leucospilota*, the other abundant black species. Table 5 lists some characters recognisable in the field.

Holothuria (Halodeima) edulis Lesson, 1830
Material examined – KKiun/9931 (one specimen).
Taxonomic description – See Cherbonnier, 1988: 75–77; figure 29, p. 76.
Field description – Species can be up to 300 m long and 50 mm wide. Body colour in life:

TABLE 5. Field characters to discern *Holothuria (Mertensiothuria) leucospilota* from *Holothuria (Halodeima) atra.*

Character	*H. atra*	*H. leucospilota*
Colour	Uniform black	Dark brown-red to black, ventral side sometimes lighter
Size	Up to 300 mm long	Often longer than 300 mm
Podia on bivium	Few, conical, radial and interradial areas	Few, conical, in 2 to 3 rows in the radial areas
Distribution of podia on trivium	Few, cylindrical, black, very short, in radial and interradial areas	Numerous, cylindrical, short but thick with brown sucking disc, in 4 to 5 rows in radial areas
Morphology of tentacles	20, short, black	20, long, dark brown to black
Habitat	Exposed on sand flats and in sea grass beds	Often partially concealed below coral block
Body covering	Often covered with fine sand, with bare patches	Not covered with sand
Tubules of Cuvier	Always absent	Always present
Red fluid	Release of red fluid after rubbing	No release of toxic red fluid after rubbing

large chocolate brown to dark-grey patches dorsally, salmon pink to red ventrally. Body elongated and slender; somewhat wrinkled. Mouth ventral surrounded by 20 yellow to light-pink tentacles. Anus terminal, unguarded by teeth or papillae, but bordered by a dark-pink circle. Trivium covered by short tube feet, scattered over both ambulacra and interambulacral areas. Bivium with few tube feet in total area. Cuvierian tubules absent.

Abundance in the Kiunga Marine Reserve – *Rare*, although also reported in Obura *et al.* (1998) in the Kiunga Marine Reserve.

Local distribution - Not observed along the Somalian coast by Tortonese (1949; 1951; 1980), nor by Humphreys (1981) along the Kenyan coastline. Other important records for eastern Africa include those by Ludwig (1875) from Zanzibar, by Cherbonnier (1988) from northern Madagascar (Nosy Bé). Massin (1999; figure 14: p. 22) shows an Indo-Pacific distribution from East Africa (with the Red Sea) to Tahiti.

Remarks – Although the name *H. edulis* suggests that this species is edible, in Kenya no real market exists for this low-valued species. The Kiunga fisherman do not have a common name for it.

Subgenus *Lessonothuria* Deichmann, 1958

Holothuria (Lessonothuria) pardalis Selenka, 1867

Material examined – KKiun/9934 (one specimen); KKiun/9935 (one specimen); KKiun/9936 (one specimen); KKiun/9937 (one specimen).

Taxonomic description – Cherbonnier, 1988: 117–119; figure 47, p. 118; Massin, 1999: 25–27; figure 18, p. 26.

Field description – Relatively small species, up to 100 mm long and 40 mm wide. Total body wall white-yellow, with two rows of conspicuous dark areas on the dorsal side and with innumerable small yellow areas giving the animal a speckled appearance. Rough bivium clearly separated from the smoother trivium. Bivium with small homogeneously spread papillae, more numerous at the posterior side; trivium with long cylindrical podia in the radial areas (two to four rows laterally; four to five rows in the median area), however with some spreading into the interambulacral areas. Mouth ventral, surrounded by 17 long 'dendritic' tentacles, surrounded at their base by long conical papillae. Anus terminal, surrounded by conical papillae. Cuvierian tubules absent

Abundance in the Kiunga Marine Reserve – *Rare*, possibly *common*. Not reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.

Local distribution - Humphreys (1981) reports it as abundant in the channel to Mida Creek, on the rock reefs near Big Tree Caves and in the Watamu Marine Park. Tortonese (1980) reports it abundant at Bender Mtoni (20 km South of Kismayu), Somalia. Other important records for eastern Africa include those by Selenka (1867) from Zanzibar (as *Holothuria subditiva);* by Haacke (1880) from Mauritius (as *Labidodemas punctulatum*); by Sloan *et al.* (1979) from Aldabra; by Clark (1984) from the Seychelles. Massin (1999, figure 19: p. 27) shows an Indo-Pacific distribution from East Africa (with the Red Sea) to the West coasts of central and North America.

Remarks – Since this species lives unexposed, hiding under coral blocks on coral debris and crustose algae, its abundance is possibly much larger then suggested here.

Subgenus *Mertensiothuria* Deichmann, 1958

Holothuria (Mertensiothuria) leucospilota (Brandt, 1835)

Material examined – KKiun/9932 (one specimen); KKiun/9933 (one specimen).

Taxonomic description – See Cherbonnier, 1988: 112–114; figure 45, p. 113; Massin, 1999: 27–30; figure 20, p. 29.

Field description – Relatively large cylindrical and elongate species, reaching lengths of over 300 mm. Its body wall is coloured in life uniform brown to reddish black, sometimes somewhat lighter ventrally. Ventral tube feet large, but relatively short, with brown to grey sucking disc, distributed in the radial areas with major scattering into the interradial areas. Soft, brown papillae in the radial areas of the dorsal side. Mouth ventral with 20 large, black tentacles. Anus terminal. Cuvierian tubules present.

Abundance in the Kiunga Marine Reserve – *Abundant*, although not reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.

Local distribution - Humphreys (1981) reports it from Mida Creek and the Watamu Marine Park; Tortonese (1980) reports it from Bender Mtoni, 20 km South of Kismayu. Other important records for eastern Africa include those by Selenka (1867) from Zanzibar as *H. vagabunda*; by Sloan *et al.* (1979) from

Aldabra; by A.M. Clark (1984) from the Seychelles. Massin (1999, figure 21: p. 29) shows an Indo-Pacific distribution from East Africa (with the Red Sea) to the West coasts of tropical America.

Subgenus *Metriatyla* Rowe, 1969

Holothuria (Metriatyla) scabra Jaeger, 1833
Material examined – KKiun/9939 (1 specimen).
Taxonomic description – See Cherbonnier, 1988: 135–137; figure 55, p. 136; Massin, 1999: 30–33; figure 22, p. 31.
Field description – Species can be up to 400 mm long and150 mm wide. Body colour dorsally grey with transverse narrow white bands; ventral side light-grey with numerous homogeneously distributed grey spots corresponding to the tube feet. Grey tube feet in trivium and bivium, spread over the ambulacral and interambulacral areas, in bivium less numerous. Papillae always dorsal, small, and black, surrounded by a narrow grey ring, sparsely distributed over all the bivium. Mouth ventral, surrounded by 20 grey tentacles; anus terminal. Cuvierian tubules absent.
Abundance in the Kiunga Marine Reserve – *Very rare*, also observed in the Kiunga Marine Reserve by Obura and his team (1998).
Local distribution - Humphreys (1981) reports it from Kenya (Malindi Marine Park, Mida Creek, Suda Island); Panning (1941) from Mombasa, and Somalia. Other important records for eastern Africa/western Indian Ocean include those by Selenka (1867) from Zanzibar as *Holothuria tigris;* by Haacke (1880, in Théel, 1886), Ludwig (1883) and Théel (1886) from Mauritius; and by Clark (1984) from the Seychelles. Massin (1999, figure 23: p. 32) shows an Indo-Pacific distribution from East Africa (with the Red Sea) to the Cook Islands.
Remarks – This species probably was abundant up to a few years ago, but extensive fishing caused a sharp decline in the abundance. An old synonym of *Holothuria scabra* Jaeger, 1833 is *Holothuria tigris* Selenka, 1867, the local fishermen refer to that old name in their language: they call this species 'iyongo tigri'. It has a high market value, of 20 KSh/fresh specimen.

Subgenus *Microthele* Brandt, 1835

Holothuria (Microthele) nobilis (Selenka, 1867)
Material examined – KKiun/9940 (two specimens).
Taxonomic description – See Cherbonnier, 1988: 142–144; figure 58, p. 143; Massin, 1999: 33–38; figure 24, p. 34; figure 25, p. 36; figure 26, p. 37.
Field description – Loaf-shaped body, with the dorsal side round and coloured grey to black, and ventral side flattened and uniform white to grey. Lateral four to eight large white-yellow 'teats' (*i.e.* conical projections) separate the trivium from the bivium. Grey tube feet with brown sucking disk scattered all over the ventral surface, black tube feet with brown sucking disk on dorsal side. Mouth ventral with 20 grey to dark brown, large feeding tentacles with brown spots on the stalk. Anus dorsal surrounded by five small white teeth. Body wall approximately 10 mm thick, often covered with sand. Cuvierian tubules present in both specimens.
Abundance in the Kiunga Marine Reserve – *Common.* Also reported from the Kiunga Marine Reserve by Obura *et al.* (1998).
Local distribution - Humphreys (1981) reports it from Kenya in the Watamu Marine Park and in Mida Channel. Other important records for eastern Africa include those by Panning (1941) from Somalia (unspecified locality); by Selenka (1867) and Semper (1869) from Zanzibar as *Muelleria nobilis*; by Sloan *et al.* (1979) from Aldabra; by Clark (1984) from the Seychelles. Massin (1999, figure 27: p. 38) shows an Indo-Pacific distribution from East Africa (with the Red Sea) to Easter Islands.

Subgenus Platyperona Rowe, 1969

Holothuria (Platyperona) difficilis Semper, 1868
Material examined – KKiun/9949 (one specimen).
Taxonomic description - See Cherbonnier, 1988: 99–101; figure 40, p. 102; Massin, 1999: 38–40; figure 28, p. 39.

Field description - Cylindrical body up to 120 mm in length (see Rowe, 1969), bivium variegated purple-brown, trivium slightly lighter and more uniform in colouration. Dorsal pedicels dark brown, surrounded at their base by a brown ring-like area, scarce in number, distributed over the total area, ventral tube feet more numerous, distributed mainly in the radial areas (especially posteriorly) in four to six rows, although some spreading into the interradial areas can occur. Anus terminal guarded by five small, brown, pointed teeth and numerous non-calcified papillae. Mouth ventral surrounded by 20 small but firm tentacles, green-brown in colouration. Body wall rough, relatively thin (2–3 mm). Large Cuvierian tubules present, however not readily ejected.
Abundance in the Kiunga Marine Reserve - *Very rare*. Not reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.
Local distribution - First record for Kenya. Previously important records for eastern Africa/western Indian Ocean were made by Haacke (1880) as *Muelleria pervula* and Ludwig (1883) as *Holothuria difficilis* in Mauritius; by Sloan *et al.* (1979) from Aldabra; by Clark (1984) from the Seychelles; by Cherbonnier (1988) from Madagascar. Massin (1999, figure 29: p. 40) shows an Indo-Pacific distribution from East Africa (with the Red Sea) to the West coasts of America.

Subgenus *Semperothuria* Deichmann, 1958

Holothuria (Semperothuria) cinerascens (Brandt, 1835)
Material examined – KKiun/9941 (one specimen).
Taxonomic description – See Cherbonnier, 1988: 70–72; figure 27, p. 72.
Field description – Medium sized species up to 120 mm in length and 40 mm in width. Red-brown to purple body colour, somewhat lighter ventrally. Yellow-brown tube feet scattered over the total ventral and dorsal surface. The dorsal tube feet are less numerous, short, and surrounded at their base by a yellow circle. Twenty large and branched red-purple tentacles around the ventral mouth. Anus dorsal, unguarded. Body wall soft and rather smooth. Cuvierian tubules always absent.
Abundance in the Kiunga Marine Reserve – *Very rare*. Not reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.
Local distribution - Reported from Kenya—Mida channel and Kibirijini point—by Humphreys (1981), and from Mombasa by Levin (1979). From southern Somalia—Bender Mtoni, 20 km South of Kismayu—by Tortonese (1980). Other important records for eastern Africa/western Indian Ocean include those by Lampert (1896) from Zanzibar; by Ludwig (1883) from Mauritius as *Holothuria pulchella;* by Sloan *et al.* (1979) from Aldabra; by Lampert (1885), Ludwig (1899) and by Clark (1984) from the Seychelles.
Remarks – It is possible that this species is more abundant than reported here, since its hiding behaviour under coral rocks makes it hard to find.

Subgenus *Stauropora* Rowe, 1969

Holothuria (Stauropora) fuscocinerea Jaeger, 1833
Material examined – KKiun/9938 (one specimen).
Taxonomic description – See Massin, 1999: 48–51; figure 38, p. 50.
Field description – Specimens can be up to 200 mm long and 50 mm wide. Bivium mottled green-grey with dark spots (white-tipped conical papillae distributed over the total surface; trivium grey-green with homogeneously distributed brown spots corresponding to cylindrical tube feet (with white sucking disc). Mouth ventral surrounded by 20 yellow-green stout tentacles, in turn surrounded by a collar of small yellow conical papillae. Anus dorsal surrounded by a dark purple ring. Cuvierian present, very thick, white and very readily ejected.
Abundance in the Kiunga Marine Reserve – *Very rare.* Only seen once during a night dive. Obura *et al.* (1998) failed to find it in the Kiunga Marine Reserve.
Local distribution - Humphreys (1981) recorded a single specimen in the Watamu Marine Park; Tortonese (1980) failed to find it in Somalia. Pearson (1913) reports it as a "not very common species with an Indo-Pacific distribution". Massin (1999, figure 39: p. 51) shows an Indo-Pacific distribution from East Africa (with the Red Sea) to the Gulf of California; quite a few records are now known.

Subgenus *Theelothuria* Deichmann, 1958

Holothuria (Theelothuria) turriscelsa Cherbonnier, 1980 Pl. 2A, B
Material examined – KKiun/9947 (two specimens).
Taxonomic description – See Cherbonnier, 1980: 644; figure 15 A–L, pl. 1E.
Field description – Relatively large species reaching lengths of about 250 mm and widths of about 75 mm. Well developed white to almost translucent Cuvierian tubules, which is very readily ejected (further disturbance results in the ejection of the situs viscerum). Colour yellow-green ventrally with numerous dark green spots corresponding to cylindrical brown tube feet with distinct white sucking discs; mottled dark green to yellow dorsally; the green patches correspond to the basis of the short, well-developed dark brown conical papillae; the smaller yellow spots bear shorter dark brown papillae. Bivium clearly separated from the flattened trivium. Mouth ventral surrounded by 19–20 large, yellow-green tentacles. Anus dorso-terminal, guarded by dark-brown conical papillae. Tube feet spread evenly over the ambulacra and interambulacra in the trivium; papillae in the bivium spread over the total surface. Body wall several mm thick.
Abundance in the Kiunga Marine Reserve – *Rare*. Not reported by Obura *et al.* (1998) in the Kiunga Marine Reserve.
Local distribution - This recently described species is reported here as a new species for the Indian Ocean. Up till now it was only known from four localities: Indonesia (Sulawesi) (Massin, 1999), Mariana Islands (Guam) (Kerr *et al.*, 1992), New Caledonia (Cherbonnier, 1980; Cherbonnier & Féral, 1984; Féral & Cherbonnier, 1986); and the Society Islands (Tahiti) (Cherbonnier & Féral, 1984) (see also distribution map Massin, 1999, figure 43: p. 55). One of us recorded it earlier in Kenya and Tanzania, Pemba Island (Samyn, pers. observation).
Remarks –This species was observed during a night dive in a single location. Due to its nocturnal habits, it is possible that this species is more common than reported here.

Subgenus Thymiosycia Pearson, 1914

Holothuria (Thymiosycia) arenicola Semper, 1868
Material examined – KKiun/9945 (one specimen).
Taxonomic description – See Cherbonnier, 1988: 82–84; figure 32, p. 83; Massin, 1996a: 27–30; figure19, p. 29.
Field description – Small burrowing species, up to 150 mm long and 25 mm wide. Body cylindrical, tapering at both ends. Colour grey to yellow with numerous tiny black spots ventrally; dorsally yellowish-grey with two rows of conspicuous brown areas lying in narrow and shallow longitudinal scars, and with numerous tiny black spots. Mouth terminal surrounded by 18 feeding tentacles. Large terminal anus guarded by five groups of four to five papillae. White cylindrical tube feet in trivium distributed in the radial areas, but with major spreading into the interradial area; in bivium spread evenly in the total area. Cuvierian tubules absent.
Abundance in the Kiunga Marine Reserve – *Very rare*. Not observed by Obura *et al.* (1998) from the Kiunga Marine Reserve.
Local distribution - First record for Kenya. Humphreys (1981) failed to find it in Kenya. It was however recorded from Somalia (Sar Uanle, 20 km South of Kismayu) by Tortonese (1980). Other important records for eastern Africa/western Indian Ocean include those by Sloan *et al.* (1979) from Aldabra; by Haacke (1880) from Mauritius; by Ludwig (1899) as *Holothuria maculata* and by Clark (1984) from the Seychelles; by Lampert (1885; 1896) and Ludwig (1899) as *Holothuria maculata* from Zanzibar; by Haacke (1880) and Ludwig (1883) as *Holothuria maculata* from Mauritius. Rowe & Doty (1977) and Massin (1996b) report on the distribution of *H. arenicola* as being tropical Indo-West Pacific (with the Red Sea).
Remarks – The burrowing behaviour of this species makes it very difficult to find: only an in- and outflow in the sand is visible, so abundance is possibly much larger than reported here.

Holothuria (Thymiosycia) hilla Lesson, 1830
Material examined – KKiun/9942 (one specimen); KKiun/9943 (three specimens).
Taxonomic description – See Cherbonnier, 1988: 85–87; figure 34, p. 88; Massin, 1999: 55–57.
Field description – Cylindrical body up to 150 mm long and 35 mm wide. Bivium chocolate brown with longitudinal rows of yellow pointed papillae; trivium slightly lighter with long cylindrical yellow tube feet

arranged in two to three rows in the lateral radial areas and in three to four rows in the median ambulacrum. Mouth ventral surrounded by 19 to 20 yellow tentacles. Anus terminal surrounded by small conical papillae. Body wall thin. Cuvierian tubules present but not readily ejected.

Abundance in the Kiunga Marine Reserve – *Common*, although not found by Obura *et al.* (1998) in the Kiunga Marine Reserve.

Local distribution - Previously reported from Kenya by Humphreys (1981) from Big Tree Caves in front of Mida Creek; from southern Somalia (Bender Mtoni) by Tortonese (1980). Other important records for eastern Africa include those by Selenka (1867) as *Stichopus gyrifer* and Ludwig (1899) as *Holothuria monacaria* from Zanzibar; by Haacke (1880) as *Labidodemas neglectum* and Ludwig (1883) as *Holothuria monacaria* from Mauritius; by Sloan *et al.* (1979) from Aldabra; by Ludwig (1899) as *Holothuria monacaria* and by Clark (1984) from the Seychelles. Massin (1999, figure 44: p. 56) shows an Indo-Pacific distribution from East Africa (with the Red Sea) to the Society Islands.

Holothuria (Thymiosycia) impatiens (Forsskål, 1775)

Material examined – KKiun/9944 (four specimens).

Taxonomic description – See Cherbonnier, 1988: 89–91; figure 35, p. 90.

Field description – Species reaching sizes up to approximately 120 mm in length and 30 mm in width. Trivium light brown with some lighter areas corresponding to the basis of the tube feet; bivium somewhat darker with dark brown areas more or less connected to form transverse bands. Mouth terminal, surrounded by 18 relatively small tentacles; anus terminal with five conical papillae. Thick Cuvierian tubules present but not readily ejected. Body wall only few mm thick and relatively smooth.

Abundance in the Kiunga Marine Reserve – *Rare*, found only in one location under boulders and coral heads over sandy gravel and coarse rubble. Not observed by Obura *et al.* (1998) from the Kiunga Marine Reserve.

Local distribution - Previously recorded from Kenya by Humphreys (1981) from Mida creek, Watamu Marine Park and Ras Ngomeni; from Sar Uanle (southern Somalia) by Tortonese (1980); from Aldabra by Sloan *et al.* (1979); and from the Seychelles by Clark (1984). Other important records for eastern Africa include those by Selenka (1867) and Ludwig (1899) from Zanzibar as *Holothuria botellus*; by Haacke (1880) and Ludwig (1883) from Mauritius; by Ludwig (1883) from Madagascar; by Lampert (1885) and Ludwig (1899) from the Seychelles. A.M. Clark & Rowe (1971) show an Indo-Pacific (with the Red Sea, see also tortonese, 1955) distribution.

Genus *Labidodemas* Selenka, 1867

Labidodemas pertinax Ludwig, 1875. Pl. 2D

Material examined – KKiun/9919 (one specimen); KKiun/9920 (two specimens).

Taxonomic description – See Cherbonnier, 1988: 51–53; figure 17, p. 52; Rowe & Gates, 1995: p. 304.

Field description – Uniform white dorsally with a pinkish shine ventrally. Mouth terminal, surrounded by a 5 mm wide dark purple to brown ring. Trivium with distinct radial areas containing long cylindrical yellow to brown tube feet (median ambulacrum in two rows); bivium with fewer short white conical tube feet spread over the ambulacral and interambulacral areas. Mouth terminal, surrounded by 15 to 20 small feeding tentacles. Anus terminal, sometimes surrounded by conical papillae. Skin thin but leathery.

Abundance in the Kiunga Marine Reserve – *Common*, although this species is rarely seen, due to its hiding behaviour. Not reported by Obura *et al.* (1998) from the Kiunga Marine Reserve.

Local Distribution – Two species of *Labidodemas* are known to occur in the Indian Ocean: *Labidodemas rugosum* and *Labidodemas pertinax* (Rowe, 1969). In eastern Africa *Labidodemas pertinax* is only known from a few localities: Iles Glorieuses (North of Madagascar) (Cherbonnier, 1988). However its range stretches further North towards the Arabian Gulf (Price, 1981) and the Red Sea (Price, 1982) and West via the Bay of Bengal, the East Indies, North Australia and the Philippines up to Hawaii (see Clark & Rowe, 1971 for distribution table).

Remarks - All the specimens were seen under coral boulders on sand gravel or on coarser coral rubble.

Family Stichopodidae Haeckel, 1886
Genus *Stichopus* Brandt, 1835

Stichopus chloronotus Brandt, 1835. Pl. 2D
Material examined – The specimen from the Kiunga Marine Reserve could not be preserved adequately and was discarded. The picture D on pl. 2 leaves no doubt over the identification.
Taxonomic description – See Cherbonnier, 1988: 146–147; figure 60, p. 149.
Field description – Medium sized species up to 150 mm long and up to 60 mm wide. The body colour of live specimens varies from dark green to black-brown. Trivium distinctively flattened, slightly lighter colour than bivium. The mouth is positioned ventrally and is surrounded by large dark green papillae and 16 to 20 white or grey (after preservation) peltate tentacles. Anus terminal. Relatively long dark green cylindrical tube feet cover the whole ventral side, posteriorly in four distinct rows. On the dorsal side two rows of large conical papillae of the same body colour but with yellow-orange distal ends. The bivium is separated from the trivium by a single row of these papillae. Skin smooth, 3 to 4 mm thick.
Abundance in the Kiunga Marine Reserve – *Very rare*, only recorded as a single specimen from a single locality (Hindi). Not reported by Obura *et al.* (1998) in the Kiunga Marine Reserve.
Local distribution - Not reported from Kenya by Humphreys (1981), nor by Tortonese (1949; 1951; 1980) from Somalia. It is here described for the first time from Kenya, although it is a well-known tropical Indo-Pacific (see Clark & Rowe, 1971: 178–179; Rowe & Doty, 1977) and Red Sea (Price, 1982) species ranging from East Africa to Hawaii. The most representative local records are those by Selenka (1867) who reports it from Zanzibar; by Haacke (1880) as *Stichopus cylindricus* and Ludwig (1883) as *Stichopus (Perideris) chloronotus* from Mauritius; by Sloan *et al.* (1979) from Aldabra; and by Clark (1984) from the Seychelles.

Stichopus herrmanni Semper, 1868. Pl. 2 E
Material examined – None from Kiunga, however picture E. on pl. 2 leaves no doubt over the identification.
Taxonomic description – See Rowe & Gates, 1995: 324; Massin, 1996a: 35–38; figure 24, p. 37; Massin, 1999: 63-65; figure 52, p. 64.
Field description – Large species, up to 250 mm long and to 65 mm wide. Body form is squarish, with a smooth surface. The colour of live animals is uniform bright olive-green dorsally and ventrally. Dorsal surface with large transverse scars. Mouth ventral with 16 to 18 greenish tentacles. Anus terminal, without anal teeth or papillae. On the flattened ventral side cylindrical podia positioned both on the ambulacra and the interambulacra. Conical, light green papillae with dark green stripes and yellow to orange distal tips, lateral and dorsal, for the latter side only in the ambulacral areas. Body wall from 3 to 5 mm thick, smooth.
Abundance in the Kiunga Marine Reserve – *Rare*. First record for the Kiunga Marine Reserve.
Local distribution - Recorded from Mombasa by Levin (1979) as *Stichopus variegatus*. It is a well-known Indo-Pacific species (Rowe & Gates, 1995). However, as Massin (1999) notes, its exact distribution is problematic due to confusion with *Stichopus monotuberculatus*.

Stichopus cf. *monotuberculatus* (Quoy & Gaimard, 1833). Pl. 2F, G, H
Material examined – KKiun/9950 (two specimens).
Taxonomic description – See Cherbonnier, 1952: 23–25, pl.3 figure 4, text–figure 8 a–t; Massin, 1996b: 163–164; figure 9, p. 165; figure 10, p. 166; pl. 1C, D.
Field description – Large species, in life up to 350 mm long and 80 mm wide. Colour in life: dorsal side from grey green to orange-brown with dark green to black patches, ventral side grey-green with numerous small dark patches. In alcohol the colours fade to light green with patches of light brown. Ventral side flattened, dorsal side swollen, giving the animal a squarish view in cross-section. Mouth ventral surrounded by 20 large tentacles surrounded in turn by a circle of large papillae. Anus terminal, without anal teeth or papillae. Large cylindrical, yellowish brown tube feet in trivium in ambulacral areas only. Large conical papillae distributed more or less randomly in bivium, but with a distinct fringe of 8–10 larger papillae laterally. Skin rather rough compared to the other *Stichopus* species found in the region.
Abundance in the Kiunga Marine Reserve – *Common*. observed at several localities in the Kiunga marine reserve, although not reported by Obura *et al.* (1998).
Local distribution - *Stichopus monotuberculatus* is reported here as a first record for Kenya. It was seen by one of us (YS) further South, Pemba Island, Tanzania. Neither Humphreys (1981), nor Tortonese (1949, 1951, 1980) found it in the immediate surroundings. It is however an expected species since, Massin's

distribution map (1996b, map 3, p. 174) shows an Indo-Pacific distribution from the Red sea and Madagascar to Eastern Islands, and from Japan to Australia.
Remarks - The specimens discussed here were only seen at night, although one of us (YS) observed a specimen at Pemba island (Tanzania) foraging during the day. It is with some hesitation that we refer this species to *S. monotuberculatus.* Although the spicules match the descriptions given by Cherbonnier (1952) and Massin (1996b), the colouration and the pattern of the body wall is somewhat different: the 'numerous white spots, often clumped toghether forming a whitish surface, and deep brown spots' (after Massin, 1996b) are largely absent from our specimens. Pl. 2F and G depict the largest specimen found in the Kiunga Marine Reserve. Pl. 2H shows the spicules found in the various body parts. More specimens of different sizes from different localities are needed to clarify the identity of our specimens.

Order Dendrochirotida Grube, 1840
Family Sclerodactylidae Panning, 1949
Subfamily Cladolabinae Heding & Panning, 1954
Genus *Afrocucumis* Deichmann, 1944

Afrocucumis africana (Semper, 1868)
Material examined – KKiun/9918 (four specimens).
Taxonomic description – See Cherbonnier, 1988: p. 218–220; figure 95, p. 219.
Field description – Small species, length up to 60 mm, width up to 10 mm, tapering at both ends. Total body surface homogeneous dark green to brown. Mouth and anus terminal. Mouth surrounded by 19 small dendritic tentacles. Tube feet long, cylindrical, of the same colour as the rest of the body, distributed ventrally and dorsally in the ambulacra.
Abundance in the Kiunga Marine Reserve – *Rare*, maybe *common.* Only observed in one locality in the reserve. Not reported from the Kiunga Marine Reserve by Obura *et al.* (1998).
Local distribution - It was previously recorded from southern Somalia (Gesira and Bender Mtoni) by Tortonese (1980) and from Mida Creek, Watamu Marine Park, and Kibirijini in Kenya by Humphreys (1981). Other important local records include those by Sloan *et al.* (1979) from Aldabra; by Clark (1984) from the Seychelles; by Ludwig (1887) as *Pseudocucumis theeli* from Zanzibar; and Heding and Panning (1954) as *Orcula cucumiformis* from Zanzibar. Massin (1999, figure 79: p. 96) shows an Indo-Pacific distribution from East Africa (excluding the Red Sea) to the Fiji Islands.
Remarks - Due to its small size and its burrowing behaviour this species is probably easily overlooked.

ACKNOWLEDGEMENTS

We wish to thank J. Church, WWF-project manager at the Kiunga Marine Reserve. She and her excellent team provided us with logistics and in-depth knowledge of the collection and observation sites within the Reserve. We also wish to thank D. Obura for his aid in preparing this expedition. M. Jangoux provided access to his extensive collection of reprints on echinoderms. Financial support came from the *Research Council* (OZR) of the Free University Brussels (VUB), and from the Flemish Fund for Scientific Research (FWO). Authorisation to study the Kenyan echinoderms came from the Office of the President through J.E. Ekirapa. The field assistance of Bruno Van Bogaert who helped with the collection of the specimens is greatly appreciated. This work would not have been possible without Dr C. Massin who kindly provided the necessary literature, checked the holothurian identifications and reviewed the earliest drafts.

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Plate 1. (A) *Clypeaster rarispinus* de Meijere, 1902; B. *Phyllacanthus imperialis* (Lamarck, 1816); C. *Astropyga radiata* (Leske, 1778); D. *Heterocentrotus mammillatus* (Linnaeus, 1758); E. *Microcyphus* rousseaui L. Agassia, 1846; F. *Actinopyga echinites* (Jaeger, 1833); G. *Bohadschia subrubra* (Quoy & Gaimard, 1833); H. *Holothuria (Cystipus) rigida* (Selenka, 1867). All pictures by Y. Samyn except A. F. Bossuyt; B. (J. Church) and D. (B. Van Bogaert).

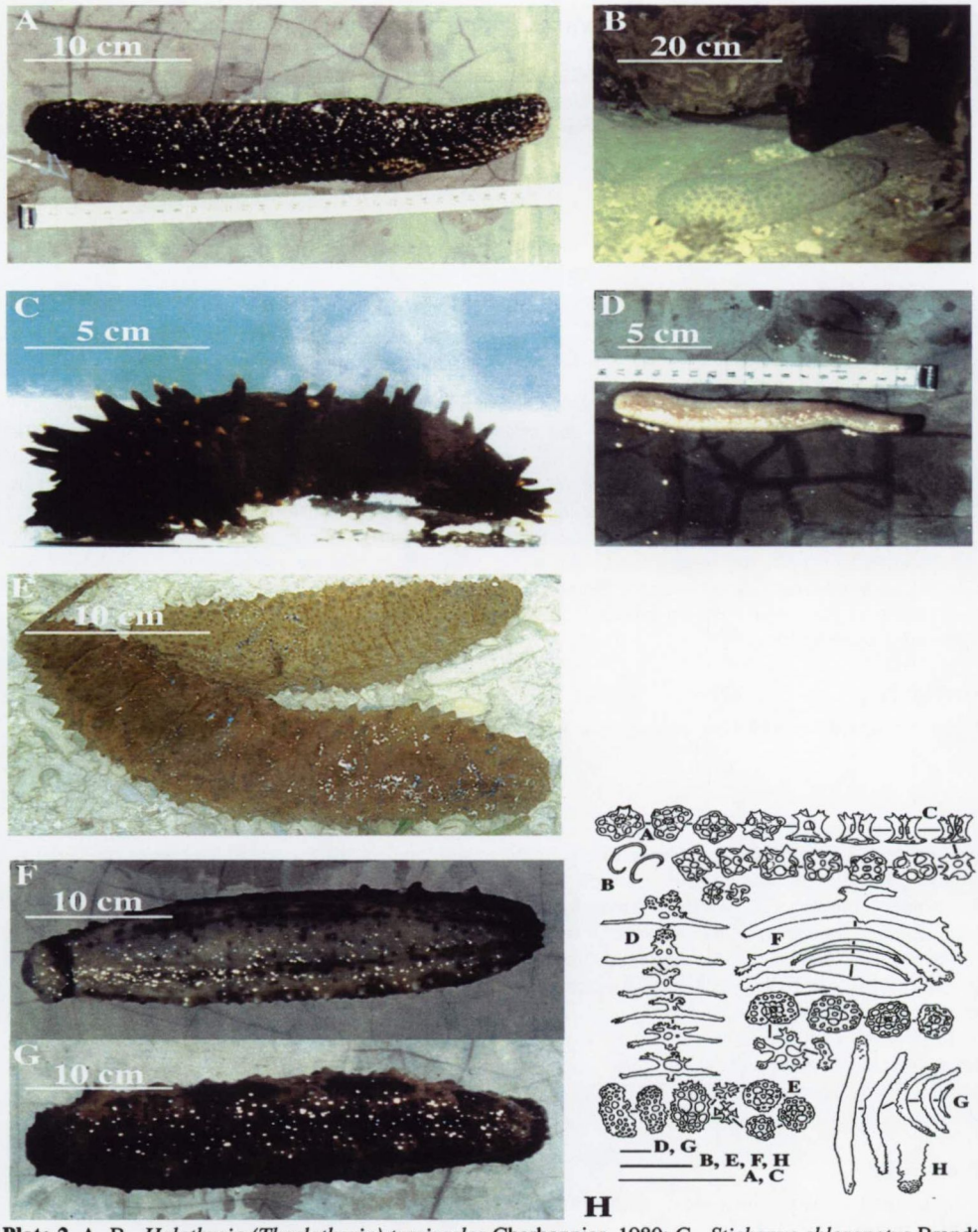

Plate 2. A, B. *Holothuria (Theelothuria) turriscelsa* Cherbonnier, 1980; C. *Stichopus chloronotus* Brandt, 1835; D. *Labidodemas pertinax* Ludwig, 1875; E. *Stichopus herrmanni* Semper, 1868; F. *Stichopus cf. monotuberculatus* (Quoy & Gaimard, 1833), ventral view; G. *Stichopus cf. monotuberculatus* (Quoy & Gaimard, 1833), dorsal view; H. *Stichopus cf. monotuberculatus* (Quoy & Gaimard, 1833): A. tables from the ventral body wall; B. C-shaped rods from the ventral body wall; C. tables and rosettes from the from the dorsal body wall; D. modified rods from the ventral body wall; E. plates, tables and X-shaped rods from the ventral tube feet; F. rods and tables from the dorsal papillae; G. rods from the tentacles; H. detail of the distal end of a rod from the tentacle. Scale bars are 100 μm. All pictures by Y. Samyn.

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Monograph of the Shallow-water Holothurioidea (Echinodermata) from Kenya and Pemba Island (Tanzania), with notes on the holothuroids from the western Indian Ocean

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ABSTRACT

A total of 225 specimens - representing three orders, four families, 12 genera, 44 species and one variety - collected in the shallow-waters of Kenya and Pemba Island (Tanzania) - are investigated. *Bohadschia cousteaui, B. similis, Holothuria (Metriatyla) albiventer, Pearsonothuria graeffei, Thelenota anax, Euapta godeffroyi, Opheodesoma grisea, O. spectabilis* and *Synaptula recta* are new records for Kenya and from Pemba Island (Tanzania). *H. (M.) timana* is a new record for the western Indian Ocean. Diagnostic characters and descriptions (including some brief notes on the ecology) are given for most species. Identification keys up to the species level are also included. The results are compared to the shallow-water holothuroid biodiversity of the western Indian Ocean. This study stresses the richness of the holothuroid biodiversity of Kenya and Pemba Island. The holothuroid fauna of Kenya (with Pemba Island) is now represented by 48 species.

Keywords

Echinodermata; Holothurioidea; new records; Western Indian Ocean; Kenya; Tanzania; zoogeography.

RÉSUMÉ

Un total de 225 spécimens - représentant trois ordres, quatre familles, 12 genres, 44 espèces et une variété – prélevés dans les eaux peu profondes du Kenya et de l'île de Pemba (Tanzanie) - sont examinés. *Bohadschia cousteaui, B. similis, Holothuria (Metriatyla) albiventer, Pearsonothuria graeffei, Thelenota anax, Euapta godeffroyi, Opheodesoma grisea, O. spectabilis* et *Synaptula recta* sont signalés pour la première fois au Kenya et à l'île de Pemba (Tanzania). *H. (M.) timana* est signalé pour la première fois dans les eaux de l'Océan Indien occidental. Les caractères distinctifs et les descriptions (ainsi que quelques notes sommaires sur l'écologie) sont donnés pour la majorité des espèces. Les clefs de détermination spécifique sont également incluses. Les résultats sont comparés et discutés par rapport à la biodiversité des holothuries des eaux peu profondes de l'Océan Indien occidental. Cette étude souligne la richesse de la biodiversité des holothuries du Kenya et de l'île de Pemba. La faune des holothuries du Kenya (avec l'île de Pemba) comprend actuellement 48 espèces

Mots-clefs

Echinodermata; Holothurioidea; nouvelles observations; Océan Indien ouest; Kenya; Tanzanie; zoogéographie.

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Introduction

Despite the fact that in the past two centuries many notable naturalists have turned their attention to the holothuroid fauna of the Indo-Pacific, the shallow-water holothuroid fauna of Kenya is only known from a handful of publications (LEVIN 1979; HUMPHREYS 1981), while that of Pemba Island (Tanzania) has never been the object of any study. Because, in recent years, several additions have been made to this fauna (MASSIN *et al.* 1999; SAMYN 2000; SAMYN & VANDEN BERGHE 2000; SAMYN *et al.* 2001; MASSIN *et al.* in press), it was thought desirable to draw an up-to-date annotated checklist of the shallow-water holothuroid fauna of Kenya (with Pemba Island). As such, this work forms the first attempt since more then 20 years to document and understand the holothuroid biodiversity in the shallow-waters (up to 50 m depth) of Kenya (with Pemba Island, Tanzania). Recent work of CHERBONNIER (1988) on the holothuroids of Madagascar, an important reference tool that provides detailed descriptions of no less then 122 species, and ROWE (*in* ROWE & RICHMOND 1997) on the echinoderms of eastern Africa, prooved to be of immense value towards this endeavour.

In order to get a better understanding of the holothuroid species richness of Kenya (with Pemba Island), the observed richness is also compared to that of the total western Indian Ocean. Assessing the species richness in the western Indian Ocean was possible by screening the bulk of the available literature. The monographic works of early workers like QUOY & GAIMARD (1833) on material collected by the *Astrolabe*, BRANDT (1835) on *Mertensio* material, SELENKA (1867; 1868), SEMPER (1868; 1869), LAMPERT (1885), FISHER

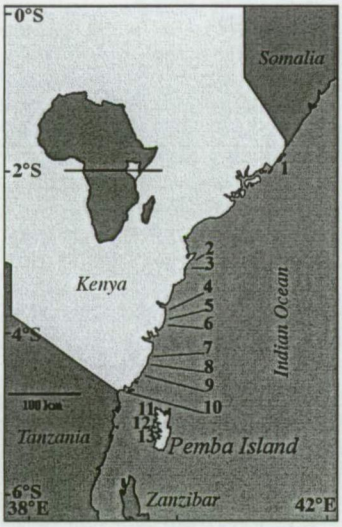
(1907), MITSIKURI (1912) and H.L. CLARK (1946) on Indo-Pacific material, BELL (1884) on material collected by the *H.M.S. Alert*, LUDWIG (1886) on specimens collected by the *Vettor Pisani*, THÉEL (1886) on *Challenger* material, LAMPERT (1889a, b) on *Gazelle* material, SLUITER (1901) on *Siboga* material, and the work of many other researchers on selected groups [LUDWIG (1875; 1887) on the Holothurioidea; H.L. CLARK (1908) on the Apodida; H.L. CLARK (1924) and HEDING (1928; 1929; 1931) on the Synaptidae; PANNING (1929-1935a-d) on *Holothuria*; PANNING (1949) on the Cucumariidae; HEDING & PANNING (1954) on the Phyllophoridae], regions [GRAY (1872), LUDWIG (1877 [1880]; 1886), HÉROUARD (1893), VANEY (1905); HELFER (1911, 1912, 1913), ERWE (1919), MORTENSEN (1926; 1937), TORTONESE (1936a, b; 1947; 1953a, b); A.M. CLARK (1952), CHERBONNIER (1954a, 1955, 1963, 1967) and JAMES & PEARSE (1969) on material from the Red Sea Region; HEDING (1940b) on material from the Persian Gulf; BRITTEN (1910); H.L. CLARK (1923), HEDING (1938), JOHN (1939), DEICHMANN (1944; 1948), CHERBONNIER (1952a; 1953b; 1954b; 1970a) on material from South Africa; HOFFMAN (1874), HAACKE (1880), LAMPERT (1896), LUDWIG (1899), PEARSON (1910, 1913, 1914a), PANNING (1941, 1944), CHERBONNIER (1953a); KALK (1858, 1959) and CHERBONNIER (1970b) on material from the Indian Ocean *sensu lato*] or museum collections [LUDWIG (1881) on Mertens-Brandt's species, LUDWIG (1882) on the collection in the Leyden Museum, LUDWIG (1883) on the collection in the Kieler Museum; KOEHLER & VANEY (1908) on the collection in the Indian Museum; HEDING (1931) on the collection in the Hamburg Museum; TORTONESE (1937-38) on the collection in the Torino Museum; PANNING (1951) on Rüppels collection; CHERBONNIER (1952b) on QUOY & GAIMARD'S species and JAMES (1969) on material deposited in the CMFRI collection], brought significant insights into the taxonomy and faunistics of the shallow-water holothuroids of the Indo-pacific Ocean. In the early seventies, CLARK & ROWE (1971) assembled all the available information into a comprehensive (and at that time very complete) monography. DANIEL & HALDER (1974) undertook a similar effort, but their work can hardly be called effective for taxonomic errors and other inconcistencies obstruct a clear understanding of the faunistical relationships. The present monograph incorporates the above taxonomic sources in addition to work that appeared after CLARK & ROWE's (1971) monograph or that was missed by these authors.

It is my strong belief that such an integrated effort was urgently needed for the commercially exploited holothuroids (see also PANNING 1944; CONAND & BYRNE 1993; CONAND 1997; 1998a, b; CONAND 2001; MARSHALL *et al.* 2001 for insights into holothuroid fisheries), as the current Kenyan sea cucumber fisheries are hardly regulated and stocks are in danger of getting depleted (SAMYN 2000; MARSHALL *et al* 2001). Further - as it can be shown that the current insufficient taxonomic documentation for the region and the problems associated with species identifications (SAMYN 2000) hamper understanding of the structure, function, history and future of the geographic range of this important biological and economical group - this work possibly can aid in directing future conservation efforts. This because, as argued before (SAMYN 2000; SAMYN & MASSIN 2002), taxonomic accuracy and systematic stability in combination with faunistics are the first steps towards true estimates of species richness in an area and to an understanding of the observed biodiversity. The present paper thus not only attempts to describe the shallow water holothuroid fauna of Kenya (with Pemba Island), but also tries to provide a stable systematic framework for the species discussed.

It is, however, obvious that an accurate description of the diversity and the distribution of the holothuroid fauna of a short stretch of coast like the Kenyan Coast only makes sense when one simultaneously considers the biogeographic regions to which the study area belongs. Thus, the taxonomic and biogeographic literature of the whole western Indian Ocean was screened and compared with that of Kenya. Hereby special care was taken to avoid the numereous taxonomic inconsistencies and erroneous or dubious distribution records that are hidden in the vast amount of available literature (see for instance DANIEL & HALDER 1974).

Study Sites

Kenya's coast, from Somalia in the North to Tanzania in the South, stretches over some 480 km, Pemba Island is located some 30 km South of Kenya and experiences the same physical and biological oceanographic conditions as the South of Kenya. Map 1 shows the different sites (Kenya: Kiunga Marine Reserve; Malindi Marine National Park and Reserve, Watamu Marine National Park and Reserve, Shariani, Kanamai, Mombasa Marine National Park and Reserve, Diani Marine Reserve, Gazi Bay, Shimoni Marine



National Park and Reserve and Vanga; Tanzania, Pemba Island: Fundu and Mesali) where collecting was done. Sampling was done in the inner and outer coral reefs, in the sea grass beds, but due to practical reasons not in the extensive mangrove forests that fringe the coastline under study.

MAP 1 - Collection and observation sites. 1. Kiunga Marine Reserve; 2. Malindi Marine Park & Reserve; 3. Watamu Marine Park & Reserve; 4. Shariani; 5. Kanamai; 6. Mombasa Marine Park & Reserve; 7. Diani Marine Reserve; 8. Gazi Bay; 9. Shimoni Marine Park; 10. Vanga; 11. Fundu North; 12. Fundu South; 13. Mesali.

Materials & Methods

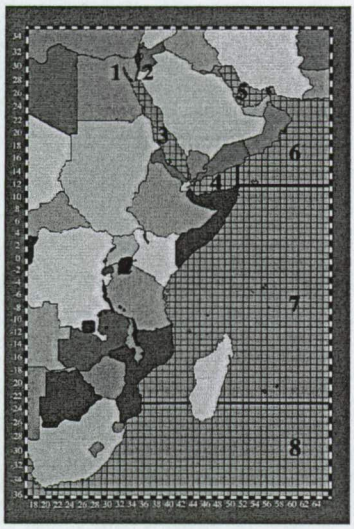
The specimens for the present study were collected during three seperate expeditions (July to August 1997, July to August 1998 and April 1999) to several sites along the Kenyan Coast and along the western coastline of Pemba Island. Collection was done by hand-picking at low tide, by snorkelling and by SCUBA diving up to depths of maximum 40 m. Fugetive (i.e. those partially concealed under hard substrate such as corals or rocks) and fossorial (i.e. those found burried more or less completely in the sandy substrate) species were recovered by lifting coral fragments and rocks and by selective digging into the sandy substrate. Systematical sieving of the substrate to uncover small infaunal forms was however not done. As such, the majority of the present collection consists of moderate to large sized individuals. As individuals generally had a rather scattered distribution over the reef, line and / or quadrate transects were not used in estimating density. Instead by using the Catch Per Unit Effort (CPUE), *i.e.* the number of observed individuals per species per diver per hour, an approximate estimate of abundancy in each sampling locality was obtained (see table 1).

Specimens were anaesthetized in 5 % magnesium chloride during 4 hours, transferred to 100 % buffered alcohol for 24 hours, and transferred to 70 % buffered alcohol for permanent storage. Of some specimens permanent preparations were made according to the method described by MASSIN (1999). Scaled ossicle illustrations were made by *camera lucida*. Part of this collection is deposited in the IRSNB (holothuroids from the Kiunga Marine Reserve), part of it in the MRAC.

All the species sampled during the present surveys are keyed and full descriptions are provided for the majority of them. For each species that is reported from the study area a list of synonyms and records (complementary with previous works) is given, whereby special attention was paid to the records from the shallow-waters of the western Indian Ocean[1].

In addition, species that belong to genera that are present in Kenya, but have *hitherto* not been reported from the study area, are mentionned in the text-tables under each genus (for the genus *Holothuria*, all the subgenera found in the WIO are treated in the main text). These, for now, non-Kenyan species are not incorporated in the identification keys, nor in the systematic account, but the geographical region, the exact locality (when known) and the reference wherein the record appeared are given. Moreover, species reported from the shallow-waters of the WIO but not belonging to genera found in Kenya are tabulated according to the following ten areas in the WIO: Gulf of Suez, Gulf of Aqaba, northern Red Sea, central Red Sea, southern Red Sea, Gulf of Aden, Persian Gulf, Arabian Sea, tropical WIO and southern WIO. The area

[1] "Shallow-waters of the western Indian Ocean" will be abbreviated as "WIO" from hereon.



tropical WIO was delibirately kept wide as preliminary analysis showed that it was rather uniform in species composition. Map 2 visualizes this arbitrary ten-fold division of the WIO.

Map 2 - The western Indian ocean as study area was divided in cells of one degree latitude/longitude and eight larger geographic areas were descerned herein: (1) Gulf of Suez, (2) Gulf of Aqaba, (3) Red Sea, (4) Gulf of Aden; (5) Persian Gulf, (6) Arabian Sea, (7) tropical WIO and (8) southern WIO.

To facilitate further studies on the biodiversity of the shallow-water holothuroids of the WIO, the whole area was divided into cells of one degree latitude/longitude. All records were fed into a *Filemaker Pro* database that allowed automated mapping with the freeware *imap*. Distribution in the WIO has been mapped for all the species known with certainity from Kenya (with Pemba Island, Tanzania).

Results

A total of 225 specimens distributed over three orders, four families, twelve genera and 44 species and one variety were collected. A list of the specimens collected at the different localities is given in table 1.

Table 1 - List of the holothurians collected at the different locations along the coast of Kenya and Pemba Island (Tanzania). CPUE stands for the Catch Per Unit Effort, the number of observed individuals per species per diver per hour. '?' Means that data could not be acquired, e.g. in those few cases were a specimen was bought from a sea cucumber fisherman.

Locality	Depth (m)	Systematics	CPUE	Collection number	Number of voucher specimens
		DENDROCHIROTIDA			
		Sclerodactylidae			
Kiunga	i.t.	*Afrocucumis africana* (SEMPER, 1868)	5	KKiun/9918	4
		ASPIDOCHIROTIDA			
		Holothuriidae			
Kanamai	1-2	*Actinopyga echinites* (JAEGER, 1833)	3	KKan/9715; KKan/9716; KKan/9724	1; 1; 1
Malindi	3		2	KMal/9888	1
Chale Island	2		2	KCi /9743	1
Vanga	3		3	KVan/9762	1
Kiunga	1-4		6	KKiun/9922	4
Fundu	8		1	none	0
Chale Island	2	*Actinopyga lecanora* (JAEGER, 1833)	1	KCi /9761	1
Mombasa	11		2	none	0
Fundu	12-14		3	TFun/9809; TFun/9810; TFun/9811	1; 1 1
Shariani	1-3	*Actinopyga mauritiana* (QUOY & GAIMARD, 1833)	2	none	0
Kanamai	1-2		4	KKan/9719; KKan/9720	1; 1
Mombasa	2-4		2	none	0

Chale Island	1-4		4	KCi/9744 ; KCi/9753; KCi/9754; KCi/9755	1; 1; 1; 1
Malindi	3-7		3	KMal/9885; KMal/9886; KMal/9887	1; 1; 1
Vanga	3		2	KVan/9763	1
Kiunga	1		4	KKiun/9921	1
Fundu	16-18	*Actinopyga miliaris* (QUOY & GAIMARD, 1833)	2	TFun/9822; TFun/9823	1; 1
Kiunga	2-3		2	KKiun/9923; KKiun/9924	1; 1
Mombasa	14		1	none	0
Malindi	8-12		2	none	0
Mesali	18		1	none	0
Fundu	12	*Bohadschia atra* MASSIN, RASOLOFONIRINA, CONAND & SAMYN, 1999	2	IRSNB, IG 28 628/Fun 90-91	2
Mombasa	2-10		3	IRSNB, IG 28 628/Mom12; IRSNB, IG 28 628/Mom 60-61	1; 2
Shariani	2-3		2	IRSNB, IG 28 628/Shar 11; KShar/9734;	1; 1; 1
Kiunga	1-4		4	KShar/9735	3; 1
Malindi	1-6		3	KKiun/9927; KKiun/9928	0
Watamu	6		1	none	0
				none	
Kanamai	2	*Bohadschia cousteaui* CHERBONNIER, 1954	1	KKan/9714	1
Fundu	10-14		2	TFun/9895; TFun/9896	1; 1
Kiunga	2-3	*Bohadschia marmorata* (JAEGER, 1833)	5	KKiun/9925; KKiun/9926	3; 2
Mombasa	4		1	None	0
Kanamai	1-3		3	None	0
Chale Island	3	*Bohadschia* cf. *similis* (SEMPER, 1868)	1	KCi/9742	1
Shariani	1	*Bohadschia subrubra* (QUOY & GAIMARD, 1833)	1	IRSNB, IG 28 628/Shar 10	1
Mombasa	14-18		4	IRSNB, IG 28 628/Mom 89-92-93-94	1; 1; 1; 1
Fundu	14		1	IRSNB, IG 28 628/Fun 7	1
Kiunga	?			none	0
Malindi	3		2	none	0
Watamu	12		1	none	0
Kanamai	1-2		3	none	0
Chale island	16		1	none	0
Shimoni	18		1	none	0
Vanga	?		?	none	0
Kiunga	1-4	*Labidodemas pertinax* (LUDWIG, 1875)	3	KKiun/9919; KKiun/9920	1; 2
Kiunga	4	*Holothuria (Cystipus) rigida* (SELENKA, 1867)	1	KKiun/9948	1
Chale Island	2	*Holothuria (Cystipus)* cf. *rigida* (SELENKA, 1867)	1	KCi/9760	1
Kanamai	1	*Holothuria (Halodeima) atra* JAEGER, 1833	+10	KKan/9705; KKan/9706; KKan/9707	1; 1; 1
Chale Island	2		3	KCi/9747; KCi/9748	1; 1
Shariani	2		1	KShar/9733	1
Mombasa	8		5	KMom/9825	1
Fundu	30		2	TFun/9826; TFun/9827	1; 1
Malindi	5		5	KMal/9883	1
Kiunga	1-4		6	KKiun/9929; KKiun/9930	1; 5
Vanga	2		2	none	0
Watamu	1-3		1	none	0
Fundu	18-22	*Holothuria (Halodeima) edulis* LESSON, 1830	2	TFun/9801; TFun/9802	1; 1
Kiunga	14		3	KKiun/9931	1
Watamu	20		2	none	0
Mombasa	21		3	none	0
Chale Island	15		1	none	0
Kiunga	2-4	*Holothuria (Lessonothuria) pardalis* SELENKA, 1867	5	KKiun/9934; KKiun/9935; KKiun/9936; KKiun/9937	1; 1; 1; 1
Mombasa	5		2	none	0
Mesali	21	*Holothuria (Lessonothuria) verrucosa* SELENKA, 1867	1	TMes/9899	1
Mombasa	5	*Holothuria (Mertensiothuria) hilla* LESSON, 1830	8	KMom/9857	1
Kisite	6		2	KKis/98102	1
Kiunga	2-3		5	KKiun/9942; KKiun/9943	1; 3
Mesali	10		1	none	0
Kanamai	1-2	*Holothuria (Mertensiothuria) leucospilota* (BRANDT, 1835)	6	KKan/9701; KKan/9702; KKan/9703; KKan/9704	1; 1; 1; 1
Mesali	3-5		8	TMes/9854; TMes/9855; TMes/9856	1; 1; 1
Kiunga	1-3		5	KKiun/9932; KKiun/9933	1; 1
Shariani	2		1	KShar/9741	1
Chale Island	1		3	none	0
Mombasa	1-4		3	none	0
Malindi	1-3		2	none	0
Watamu	1-3		4	none	0
Vanga	0-2	*Holothuria (Metriatyla) albiventer* SEMPER, 1868	4	KVan/9780; KVan/9781	1; 1
Chale Island	2-8	*Holothuria (Metriatyla) scabra* JAEGER, 1833	3	KCi/9756; KCi/9757;	1; 1;

				KCi/9758; KCi/9759 1; 1
Kanamai	1-3		2	KKan/9863; KKan/9864; 1; 1; KKan/9865 1
Vanga	2-3		8	KVan/9769; KVan/9770; 1; 1; KVan/9771; KVan/9772; 1; 1 KVan/9773 1
Kiunga	2		1	KKiun/9939 1
Malindi	8		1	none 0
Mesali	21	*Holothuria (Metriatyla) scabra* var. *versicolor* CONAND, 1986	1	TMes/9898 1
Kanamai	2	*Holothuria (Metriatyla) timana* LESSON, 1830	2	KKan/9717; KKan/9718 1; 1
Vanga	12		1	KVan/9774 1
Fundu	32	*Holothuria (Microthele) fuscopunctata* JAEGER, 1833	1	TFun/9806 1
Mombasa	16-18	*Holothuria (Microthele) nobilis* (SELENKA, 1867)	4	KMom/9845; KMom/9846 1; 1;
Kiunga	16-21		3	KKiun/9940 2
Malindi	12-20		3	none 0
Watamu	24		1	none 0
Shimoni	17		1	none 0
Fundu	19		2	TFun/9820; TFun/9821 1; 1
Vanga	15	*Holothuria (Microthele) nobilis* (SELENKA, 1867) *(sensu fuscogilva)*	1	KVan/9776 1
Kiunga	2	*Holothuria (Platyperona) difficilis* SEMPER, 1868	1	KKiun/9949 1
Malindi	1	*Holothuria (Selenkothuria) erinacea* SEMPER, 1868	5	KMal/9866; KMal/9867; 1; 1; KMal/9868; KMal/9869; 1; 1 KMal/9870; KMal/9872 1; 1
Malindi	0-2	*Holothuria (Semperothuria) cinerascens* (BRANDT, 1835)	3	KMal/9871 1
Mombasa	4		1	KMom/9859 1
Kiunga	1		1	KKiun/9941 1
Kanamai	1	*Holothuria (Stauropora) fuscocinerea* JAEGER, 1833	1	KKan/9730 1
Vanga	i.t		1	KVan/9777 1
Mombasa	3		1	KMom/9858 1
Fundu	28		3	TFun/9830 1
Kiunga	5		1	KKiun/9938; KKiun/9946 1; 1
Kananmai	2-3	*Holothuria (Stauropora) pervicax* SELENKA, 1867	2	KKan/9722; KKan/9723 1; 1
Malindi	13		1	none 0
Mombasa	12		1	none 0
Chale Island	2		1	none 0
Kiunga	5-7	*Holothuria (Theelothuria) turriscelsa* CHERBONNIER, 1980	2	KKiun/9947 2
Fundu	9-10		3	TFun/9815; TFun/9816 1; 1
Kiunga	i.t.	*Holothuria (Thymiosycia) arenicola* SEMPER, 1868	1	KKiun/9945 1
Mailindi	0-1		12	KMal/9875; KMal/9876; 1; 1; KMal/9877; KMal/9878; 1; 1 KMal/9879; KMal/9880 1; 1
Vanga	i.t.		1	KVan/9778 1
Mombasa	2		1	none 0
Fundu	10	*Holothuria (Thymiosycia) impatiens* (FORSKÅL, 1775)	2	TFun/9828; TFun/9829 1; 1
Kiunga	i.t.		3	KKiun/9944 4
Mesali	21		3	TMes/98100; TMes/98101 1; 1
Fundu	15-26	*Pearsonothuria graeffei* (SEMPER, 1868)	6	TFun/9803; TFun/9804; 1; 1; TFun/9805 1
Malindi	12		2	KMal/9764; KMal/9765 1; 1
Shimoni	16		1	KShim/9766 2
Mombasa	18-28		4	none 0
Mesali	23		6	none 0
		Stichopodidae		
Mombasa	2-12	*Stichopus chloronotus* BRANDT, 1835	10	KMom/9847; 1; 1; KMom/9848; 1; 1 KMom/9849; 1; 1
Kanamai	0-2		2	KMom/9850; 1; 1
Watamu	6		2	KMom/9851; KMom/9768 0 KKan/9728: KKan/9729 none
Mombasa	12	*Stichopus herrmanni* SEMPER, 1868	3	KMom/9852 1
Kanamai	2		2	KKan/9709 2
Vanga	4		1	KVan/9767 1
Watamu	3		1	none 0
Kiunga	3		2	none 0
Diani	1		1	none 0
Fundu	16-23	*Stichopus* cf. *monotuberculatus* (QUOY & GAIMARD, 1833)	3	TFun /9812; TFun/9813; 1; 1; TFun/9814 1
Kiunga	5-7		2	KKiun/9950 1
Kisite	19	*Thelenota ananas* (JAEGER, 1833)	2	KKis/9843 1
Mombasa	18-25		2	none 0
Vanga	?		?	none 0
Kisite	18-32	*Thelenota anax* H.L. CLARK, 1921	2	KKis/9841; KKis/9842 1; 1
		APODIDA		
		Synaptidae		
		Cladolabinae		

Fundu	14-16	*Euapta godeffroyi* (SEMPER, 1868)	3	TFun/9817; TFun/9818	1; 1
Fundu	12	*Opheodesoma* sp. (J. MÜLLER, 1850)	1	TFun/9819	1
Kanamai	1	*Opheodesoma grisea* (SEMPER, 1868)	2	KKan/9725; KKan/9726	1; 1
Kanamai	1-2	*Opheodesoma mauritiae* HEDING, 1928	2	KKan/9873; KKan/9874	1; 1
Fundu	10		1	TFun/99832	1
Kanamai	2	*Opheodesoma* cf. *mauritiae* HEDING, 1928	1	KKan/9731	1
Mesali	10	*Opheodesoma spectabilis* FISHER, 1907	1	TMes/9834	1
Kanamai	1	*Synapta maculata* (CHAMISSO & EYSENHARDT,	5	KKan/9712	1
Kiunga	2	1821)	1	KKiun/9951	1
Shariani	1-3		4	KShar/9736; KShar/9737; KShar/9738	1; 1; 1
Chale Island	1-2		4	KCi/9749; KCi/9750; KCi/9751	1; 1; 1
Mombasa	2		2	KMom/9862	1

Systematic account

Key to the orders and families of Kenya (with Pemba island)
(after Clark & Rowe 1971: 196)

1. Small to large body; tube feet and / or papillae present; body usually stout and muscular; ossicles: mostly tables, buttons, perforated plates, cups, rods or rosettes. **2**

1'. Tentacles pinnate; tube feet and / or papillae, anal papillae and respiratory trees absent; warty prominences often present; body usually vermiform; skin thin, often sticky to the touch; ossicles: anchors and anchor-plates in combination with granules . . . . . **Apodida (Synaptidae)**

2. Tentacles peltate or peltato-digitate; true introvert with associated retractor muscles absent . . . . . **Aspidochirotida** **3**

2'. Tentacles bushy or tree-shaped, much branched (dendritic); true introvert with retractor muscles present . . . . . **Dendrochirotida (Sclerodactylidae)**

3. Body cylindrical; gonads in single tuft to the left of the dorsal mesentery; ossicles in the body wall mainly tables, buttons and plates; S or C shaped rods always absent . . . . . **Holothuriidae**

3'. Body squarish in transverse view; gonads in two tufts, one on each side of the dorsal mesentery; ossicles in the tegument contain S and C shaped rods; buttons always absent . . . . . **Stichopodidae**

4. Ossicles in the tegument anchors and anchor-plates in combination with granules; tentacles pinnate . . . . . **Synaptidae**

Ordo Dendrochirotida GRUBE, 1840
Family Sclerodactylidae PANNING, 1949
Subfamily Cladolabinae HEDING & PANNING, 1949
Genus *Afrocucumis* DEICHMANN, 1944

Diagnosis - [Type species: *Cucumaria africana* SEMPER, 1868 by original designation] See HEDING & PANNING 1954:108.
Currently only two species are known in *Afrocucumis*: *Afrocucumis africana* (SEMPER, 1868) and *A. stracki* MASSIN, 1996. The first species has a wide Indo-Pacific distribution and is found in the shallow-waters of Kenya (with Pemba Island); the latter species is for now only known from its type locality (Ambon).

Afrocucumis africana (SEMPER, 1868)
(fig. 1A-C, fig. 51A)

Cucumaria africana SEMPER, 1868: 53, 270, pl. 15 fig. 16.
Pseudocucumis africana; DANIEL & HALDER 1974: 428.
Afrocucumis africana; THANDAR 1989c: 298; MUKHOPADHYAY 1991: 409; MASSIN 1999: 96 (synonymy and records before 1999), fig. 79 (distribution map), fig. 113c (colour picture); LANE *et al.* 2000: 490; SAMYN & VANDEN BERGHE 2000: 5 (tab.2), 18 (tab. 4), 32.

Status and location type - Holotype: unknown; syntypes: ZMB (three specimens) (ROWE, *in* ROWE & GATES 1995).

Type locality - Querimba Islands (northern Mozambique).

Material examined - KKiun/9918 (four specimens).

General description - Small species, reaching lengths up to 60 mm and widths up to 10 mm; tapering at both ends. Total body surface homogeneous dark green to brown. Mouth terminal, surrounded by 20 small tentacles, positioned in two crowns: 15 large tentacles in outer and five small tentacles in inner crown. Anus terminal, unguarded. Tube feet long, cylindrical, same colour as the rest of the body, distributed in the ambulacral areas only. Single Polian vesicle. Single stone canal. Calcareous ring long; interradial pieces pointed anteriorly; radial pieces sub rectangular, high, extended posteriorly by 4-5 calcareous fragments (see CHERBONNIER 1988: 219, fig. 95D).
Ossicles: Body wall with lenticular, rough-surfaced, perforated pieces, 100-300 µm across; and smaller smooth plates (fig. 1A). Tube feet with straight rods perforated distally, 125-190 µm long; and small perforated plates, 150-200 µm long (fig. 1B); endplate ca. 400 µm across. Tentacles with rods similar in size and shape to the ones from the tube feet (fig. 1C).

Diagnosis - See HEDING & PANNING 1954: 109, fig. 39.

Ecology - Only found intertidally, under coral blocks, on fine sand and coral debris; specimens firmly attached to the substratum to withstand surf.

Distribution in the study region - This species was only observed at Kui in the Kiunga Marine Reserve (See also SAMYN & VANDEN BERGHE 2000). HUMPHREYS (1981) reports this species from Kenya (Mida Creek, from the foreshore of Watamu Marine National Park and from Kibirijini).

Geographic distribution - Well known species from the tropical Indo-West Pacific Ocean (no records from the Red Sea nor from the Persian Gulf). The distribution map as drawn by MASSIN (1999: 96, fig. 79) gives the global distribution, but the following localities in the WIO have to be added: Kenya, Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000); Madagascar, Tuléar, St. Augustin and Nosy Lava (CHERBONNIER 1988). Figure 51A shows the known distribution in the WIO in detail.

Ordo Aspidochirotida GRUBE, 1840
Family Holothuriidae LUDWIG, 1894

Key to the genera of Kenya (with Pemba Island)
(after Rowe 1969: 126)

1. Ossicles: rods only, usually dichotomously branched or lobed (rosettes); tables, buttons and perforated plates always absent **2**

1'. Ossicles: tables nearly always present; buttons, rods, perforated plates and rosettes present or absent **3**

2. Anus guarded by 5 prominent calcified anal teeth; 20-30 tentacles ..... ***Actinopyga*** **BRONN, 1860**

2'. Anus not guarded by anal teeth, sometimes uncalcified papillae may be present around the anus; 20 tentacles ..... ***Bohadschia*** **JAEGER, 1833**

3. Calcareous ring with interradial plates almost as large as radial plates; body wall with small rosettes and knobbed pseudoplates; tentacles with complex rosettes and heavily branched rods ... . ***Pearsonothuria*** **LEVIN, KALININ & STONIK, 1984**

3' Calcareous ring with interradial plates always distinctly smaller as radial plates; body wall never with knobbed pseudoplates; tentacles with rods only, never rosettes **4**

4. Calcareous ring slender and ribbon-like; tube feet mostly confined to the ambulacral areas; ossicles: tables either with reduced disc and low spire ending in a spiny ring, or disc well developed and spinose, spire as high as the width of the disc, buttons present or absent..... ..... ***Labidodemas*** **SELENKA, 1867**

4'. Calcareous ring stout, never ribbon-like; tube feet of trivium (ventral side) more or less regularly arranged in the ambulacral areas; papillae and / or tube feet of bivium (dorsal side) more or less irregularly arranged in the ambulacral and interambulacral areas .... ***Holothuria*** **LINNAEUS, 1767**

Genus *Actinopyga* Bronn, 1860

Diagnosis (after ROWE 1969: 130) - [Type species: *Mülleria echinites* JAEGER, 1833 by subsequent designation].

Size from moderate up to very large (400 mm); stout body with thick and firm body wall, covered by small and numerous tube feet and papillae; mouth ventral, surrounded by 20-30 peltate tentacles; firm calcareous ring with the radial pieces about twice as large as the interradial pieces; anus dorsal, guarded by five prominent calcified papillae (anal teeth). Ossicles in body wall consist of dichotomously branched, smooth or spiny, rods; tentacles with rods, often spiny at the extremities; tube feet with rods and rosettes similar to the ones of the body wall; longitudinal muscles with rods similar to the ones from the body wall; tables, buttons, and S- or C-shaped rods absent in the latter tissue.

Fifteen species are currently recognized as being valid[2]: *Actinopyga agassizi* (SELENKA, 1867); *A. albonigra* CHERBONNIER & FÉRAL, 1984; *A. bacilla* CHERBONNIER, 1988; *A. bannwarthi* PANNING, 1944; *A. caroliniana* TAN TIU, 1981[3]; *A. crassa* PANNING, 1944; *A. echinites* (JAEGER, 1833); *A. flammea* CHERBONNIER, 1979; *A. lecanora* (JAEGER, 1833); *A. mauritiana* (QUOY & GAIMARD, 1833); *A. miliaris* (QUOY & GAIMARD, 1833); *A. obesa* (SELENKA, 1867); *A. palauensis* PANNING, 1944; *A. serratidens* PEARSON, 1903 and *A. spinea* CHERBONNIER, 1980. Four of these are found in the waters of Kenya (with Pemba Island); they are keyed hereunder.

Key to the species of Kenya (with Pemba island)

1. Anus not surrounded by a lighter zone; body colour variable. **2**

1'. Anus surrounded by a lighter zone; body colour green to brown, fairly uniform though some small yellowish patches may be present; ossicles range from rosettes in the ventral body wall to slender dichotomously branched rods in the dorsal body wall. . . . . ***A. lecanora* (JAEGER, 1833)**

2. Species always with more than 20 tentacles, usually 25; body colour variable but never uniform dark brown to black; dorsally usually chocolate brown with numerous conical papillae; ventrally white-grey to brown, densely covered with large brown to green tube feet scattered over interambulacral and ambulacral areas; bivium clearly distinguishable from trivium; ossicles: ventral body wall with smooth granules, stout rods, and rosettes; dorsal body wall with spiny rods and rosettes . . . . . ***A. mauritiana* (QUOY & GAIMARD, 1833)**

2'. Never more than 20 tentacles **3**

3. Tube feet on trivium distributed mainly in the ambulacral areas; body colour from light brown to dark green; ossicles: ventral body wall with branching rods and rosettes, granules always absent; dorsal body wall with rods with lateral extensions, spiny, sometimes X or Y shaped; dorsal pedicels with rosette-like ossicles . . . . . ***A. echinites* (JAEGER, 1833)**

3'. Tube feet on ventral surface spread into the interambulacral areas; body colour uniform, from dark brown to black; ossicles: similar rosettes in ventral and dorsal body wall, no rods nor granules present in the body wall . . . . . ***A. miliaris* (QUOY & GAIMARD, 1833)**

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[2] PEARSON (1914b) grouped the genera *Holothuria* LINNEAUS, 1758 and *Mülleria* JAEGER, 1833 SELENKA, 1867 in *Holothuria* sens. nov. wherein he discerned five ill-defined subgenera; one of them being *Actinopyga* BRONN, 1860 (= *Actinopyga* BRONN, 1860, partim; *Mülleria* JAEGER, 1833, partim). In that subgenus PEARSON (1914b) grouped eight species, one of these being *Holothuria (Actinopyga) formosa* (SELENKA, 1867). Based on MITSIKURI's (1912) observation that *formosa* is virtually identical to *Stichopus ananas* (JAEGER, 1833) (apart from the presence of anal teeth), H.L. CLARK (1921: 184) removed the species from *Actinopyga* and believed that it "very possibly belongs to *Thelenota*", BRANDT's (1835) subgeneric taxon (in *Holothuria*) he had raised to generic level to accommodate *T. ananas* (JAEGER, 1833) and *T. anax* H.L. CLARK, 1921 (see also Clark & Rowe 1967, for decision of authorship of *Thelenota*). PANNING (1944), upon examination of SELENKA's type, followed H.L. CLARK (1921) in recognizing that the ossicle assemblages of *formosa* and *ananas* are identical and that the type of *formosa* is in such a bad state that presence or absence of anal teeth could not be confirmed. The species was thus put to the synonymy of *T. ananas*. ROWE (pers. comm.) however feels that the species might be *T. anax* rather than *T. ananas*; if this should be the case then the older name *formosa* has priority over *anax*. Unfortunately, as the type material of *formosa* is currently unavailable (TROESTER, pers. comm.), ROWE's claim can here not be confirmed.

[3] The validity of *Actinopyga caroliniana* TAN TIU, 1981, needs to be ascerted by examining the type series (deposited in the University of San Carlos marine collection at the Science Complex), since the original description (TAN TIU 1981) is not distinctive enough to distinguish it from *A. echinites* (JAEGER, 1833) or *A. crassa* PANNING, 1944.

Actinopyga echinites (JAEGER, 1833)
(fig. 2A-E, fig. 51B, pl. 1A, B)

Muelleria echinites JAEGER, 1833: 17, pl. 3 fig.6.
Actinopyga echinites; DANIEL & HALDER 1974: 429; HUGHES & GAMBLE 1977: 355; SLOAN *et al.* 1979: 121; HUMPHREYS 1981: 32; TAN TIU 1981: 70, 102 pl. 12; PRICE 1982: 10; A.M. CLARK 1984:99; FÉRAL & CHERBONNIER 1986: 70, 71 (colour picture); CANNON & SILVER 1986: 20, figs 3a, 5a (colour drawing); CHERBONNIER 1988: 31 (synonymy); MUKHOPADHYAY 1991: 413; MARSH *et al.* 1993: 63; VANDENSPIEGEL & JANGOUX 1993: 43, fig 1A-B; MASSIN 1996a: 8, fig. 2A-B; ROWE & GATES 1995: 286; ROWE & RICHMOND 1997: 302, 303 (colour drawing); CONAND 1998b: 1167; CONAND 1999: 10, 12, 16, 39, pl. 1 (colour picture); LANE *et al.* 2000: 488; SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE 2000: 4 (tab. 2), 17 (tab. 4), 18; MARSHALL *et al.* 2001: 46 (tab. 29), 47, 53, 54, 58 (tab. 37).
Actinopyga plebeja (SELENKA, 1867); MACNAE & KALK, 1958: 130; 1962: 112; LEVIN 1979: 19; PRICE 1982: 10; CHERBONNIER, 1988: 28 (synonymy).
Actinopyga plegeja; KALK, 1959: 22 (*lapsus calami*).
Actinopyga echinites plebeja; DANIEL & HALDER, 1974: 422.

Status and location type - Status and data of whereabouts undetermined (ROWE, *in* ROWE & GATES 1995).

Type locality - Sulawesi (as Celebes), Indonesia.

Material examined - KKan/9715 (one specimen); KKan/9716 (one specimen); KKan/9724 (one specimen); KCi/9743 (one specimen); KVan/9762 (one specimen); KMal/9888 (one specimen); KKiun/9922 (four specimens).

General description - Medium sized species reaching lengths up to 300 mm and widths up to 65 mm. Colour in life from green to light brown, both on bivium and trivium (pl. 1A, B); bivium sometimes mottled with dark brown. Body wall up to 6 mm thick. Mouth ventral, surrounded by 20, large, brown tentacles. Anus terminal guarded by five calcified papillae. Trivium with numerous long, yellow to green tube feet, in smaller specimens distributed solely in the ambulacral areas, in larger individuals scattered into the interambulacral areas. Ventrally, tube feet absent in the first 10-15 mm posterior to the mouth. Bivium with fewer tube feet, both in radial and interradial areas. Radial areas of the bivium also bear few, large, yellow to green conical papillae. Cuvierian tubules not observable in preserved specimens, though in live specimens a pink to reddish tuft can be seen when the animal is squeezed for a couple of minutes (inset pl. 1B). One to two, long, Polian vesicles. One to three stone canals. Calcareous ring stout, radial piece almost twice as wide as the interradial pieces; radial pieces with wide anterior notch, interradial pieces toothed (see CHERBONNIER 1988: 33, fig. 9P).
Ossicles: Tentacles with rods, 135-375 µm long, straight or slightly arched, the larger ones spiny at the extremities (fig. 2A). Ventral body wall with straight and branching rods and rosettes (fig. 2C). Dorsal body wall with similar rods and rosettes, although more branched (fig. 2B). Ventral tube feet with smooth to spiny rods, often branching (fig 2D); some rosettes similar to those of the body wall also present. Dorsal tube feet present pseudo-plates (fig. 2E).

Diagnosis - See PANNING 1941: 5-7, figs 3, 4a-u; CHERBONNIER 1988: 31-32, fig. 9A-O.

Ecology - Only found in shallow water (up to 8 m); detritus feeder; almost invariably on hard coralline substrates browsing on sediment trapped in turf algae.

Distribution in the study region - Kiunga, Malindi, Kanamai, Chale Island, Vanga, Fundu (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - Tropical Indo-West Pacific Ocean (see also ROWE & DOTY 1977; ROWE & GATES 1995). *A. echinites* was also recorded from the Gulf of Suez, unspecified locality (PRICE 1982); Gulf of Aqaba, Faraun Island [A.M. CLARK 1952, as *A. miliaris* (QUOY & GAIMARD, 1833)]; Red Sea, unspecified locality (LUDWIG 1877 [1880], as *Mülleria miliaris* QUOY & GAIMARD, 1833; ERWE 1919, as *M. echinites* JÄGER, 1833; PANNING 1944, as *A. echinites plebeja* (SELENKA, 1867), and PRICE 1982, as *A. echinites* and as *A. plebeja*); Kenya, Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000), Malindi, Kanamai, Chale Island, Vanga (this work); and Tanzania, Fundu (this work). Figure 51B shows the known distribution in the WIO in detail.

Remarks - VANDENSPIEGEL & JANGOUX (1993) demonstrated that several species in the genus *Actinopyga* possess Cuvierian tubules (no more than ten tubules per individual) that are attached independently to the left respiratory tree near the cloaca. According to these authors, these tubules differ from those of other holothuroid genera in several ways: (i) they are never expelled; (ii) they cannot elongate or become sticky;

(iii) each of these tubules has three distinctive parts: (a) a smooth proximal half of the trunk, (b) a slightly rugged distal half of the trunk, and (c) highly ragged, elongated primary and secondary branches. It is remarkable that it is almost impossible to find these typical Cuvierian tubules in preserved material (pers. observ.; VANDENSPIEGEL pers. comm.). This type of Cuvierian tubules has thus far been reported in *A. echinites, A. mauritiana* (QUOY & GAIMARD, 1833), *A. miliaris* (QUOY & GAIMARD, 1833), and *A. agassizi* (SELENKA, 1867). We here confirm the presence of this type of Cuvierian tubules in *A. echinites* (see also inset plate 1B).

Actinopyga lecanora (JAEGER, 1833)
(fig. 3A-E, fig. 51C)

Muelleria lecanora JAEGER, 1833: 18, pl. 2 figs 2, 2b, pl. 3 fig. 8.
Actinopyga lecanora; DANIEL & HALDER 1974: 429; CONAND 1999: 12, 16, 39 pl. 1 (colour picture); MASSIN 1999: 8 (synonymy and records before 1999), fig. 4 (distribution map), fig. 110a (colour picture); LANE *et al.*, 2000: 488; SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE 2000: 4 (tab. 2).

Status and location type - Status and data of whereabouts undetermined (ROWE, *in* ROWE & GATES 1995).

Type locality - Sulawesi (as Celebes), Indonesia.

Material examined - KCi/9761 (one specimen); TFun/9809 (one specimen); TFun/9810 (one specimen); TFun/9811 (one specimen).

General description - Medium sized species: live specimens reaching lengths up to 250 mm and widths up to 85 mm. The four specimens examined measure 143 to 160 mm in length and 35 to 83 mm in width, after preservation. Colour in life similar to colour in alcohol: ventrally yellow to beige; dorsally beige, green or brown; 10 to 20 mm above the anus with a lighter zone with fine brownish lines. Body wall smooth, up to 8 mm thick. Mouth ventral, surrounded by 20 green to brown tentacles. Anus dorsal, surrounded by five yellowish anal teeth. Ventral tube feet long, in ambulacral areas only, in five to eight rows. Dorsal tube feet small, conical, scattered in interambulacral and ambulacral areas. Cuvierian tubules not observed in the preserved nor in the live specimens (see also remarks with *A. echinites*). Single Polian vesicle. Single stone canal. Calcareous ring stout, radial pieces twice as wide as the interradial pieces; radial pieces with narrow slit on their central anterior tooth (See MASSIN 1999: 9, fig. 3A).
Ossicles: Tentacles with massive rods up to 300 µm long, spiny at their extremities (fig. 3A). Dorsal body wall with slender dichotomously branched rods to rosettes, 25-30 µm long (fig 3B). Ventral body wall with similar rods and rosettes, 20-30 µm long (fig. 3C). Ventral tube feet with small rosettes, 20-35 µm long and branched rods, up to 60 µm long (fig. 3D). Dorsal papillae with rosettes similar to the ones from the body wall, rods, 65-90 µm long, and plate-like ossicles (fig. 3E).

Diagnosis - See JAEGER 1833: 18, pl. 2 figs 2, 2b, pl. 3 fig. 8; PANNING 1929 [1931]: 127, fig. 9a-c.

Ecology - Depth range from 0-23 m; detritus / deposit feeder on coral debris, occasionally in sea grass beds. The specimens from Fundu were found at night, attached to live coral.

Distribution in the study region - Chale Island; Fundu and Mombasa (see also LEVIN 1979).

Geographic distribution - Well known species from the tropical Indo-West Pacific. The distribution map as drawn by MASSIN (1999: 10, fig. 4) gives the global distribution, but the following localities in the WIO have to be added: northern Red Sea, Habban Dschidda (PANNING 1944, as *Actinopyga lecanora miliaris* (QUOY & GAIMARD, 1833)); Gulf of Aden, unspecified locality (DANIEL & HALDER 1974); Arabian Sea, unspecified locality (PRICE 1982); Kenya, Chale Island (this work); Tanzania, Fundu (this work), Zanzibar (PANNING 1941; PANNING 1944, as *A. lecanora lecanora;* DANIEL & HALDER 1974); Madagscar, Tuléar and Nosy Bé (CHERBONNIER 1988) and Mozambique, Maiyapa Bay (PEARSON 1910, as *Mülleria lecanora* JAEGER, 1833; see also THANDAR 1984). Figure 51C shows the known distribution in the WIO in detail.

Actinopyga mauritiana (QUOY & GAIMARD, 1833)
(fig. 4A-C, fig. 51D, pl. 1C, D)

Holothuria mauritiana QUOY & GAIMARD, 1833: 138 (see also CHERBONNIER 1952b: 41, fig. 16a-o).
Holothuria guamensis QUOY & GAIMARD, 1833: 137-138.
Microthele guamensis; CHERBONNIER 1952b: 40, pl. 2 fig1.

Actinopyga mauritiana; CHERBONNIER 1955: 139; MACNAE & KALK 1958: 34, 99, 107 (from THANDAR 1984); KALK 1959: 5, 22; JAMES 1969: 61; JAMES & PEARSE 1969: 103; DANIEL & HALDER 1974: 429; TORTONESE 1979: 316; HUMPHREYS 1981: 33; PRICE 1982: 10; CANNON & SILVER 1986: 20; SLOAN *et al.* 1979: 121; BRANCH & BRANCH 1981: 248 (from THANDAR 1984); A.M. CLARK 1984: 87, 99; CANNON & SILVER 1986: 20; FÉRAL & CHERBONNIER 1986: 72, 73 (colour picture); CHERBONNIER 1988: 16 (synonymy), fig. 2A-M; MUKHOPADHYAY 1991:403, 412; MARSH *et al.* 1993: 63; VANDENSPIEGEL & JANGOUX 1993: 43, figs 2, 3A-B, 4-18; ALLEN & STEENE 1994: 242 (colour picture; possibly not *A. mauritiana*); MASSIN 1996a: 11; ROWE & GATES 1995: 287; ROWE & RICHMOND 1997: 302, 303 (colour drawing); CONAND 1999: 10, 12, 16, 39, pl. 1 (colour picture), 16; LANE *et al.*, 2000: 488; SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE, 2000: 4 (tab. 2), 17 (tab. 4), 19; MARSHALL *et al.* 2001: 46 (tab. 29), 47, 53, 58 (tab. 37)..

Type location - Three syntypes in MNHNP (CHERBONNIER 1952b; ROWE, *in* ROWE & GATES 1995).

Type locality - Mauritius.

Material examined - KKan/9719 (one specimen); KKan/9720 (one specimen); KCi/9744 (one specimen); KCi/9753 (one specimen); KCi/9754 (one specimen); KCi/9755 (one specimen); KMal/9885 (one specimen); KMal/9886 (one specimen); KMal/9887 (one specimen); KVan/9763 (one specimen); KKiun/9921 (one specimen).

General description - Relatively large species: live specimens reaching lengths up to 350 mm and widths up to 100 mm; preserved specimens up to 30 % smaller. Colour very variable: dorsal side greenish to chocolate brown with numerous light-brown conical papillae, scattered evenly over the total bivium (body wall around the lateral papillae in the bivium is often light-brown to grey); ventral body wall white-grey to light brown, densely covered with long, light-brown to green, tube feet, scattered over the interambulacral and ambulacral areas. Bivium clearly separated from the somewhat flattened trivium. Thickness of body wall up to 10 mm. Mouth ventral, surrounded by (at least) 25 dark brown, stout, peltate tentacles, which in turn are surrounded by a distinct collar of brown papillae. Tentacle ampullae, 30-40 mm long. Anus small, terminal, guarded by five white anal teeth. Cuvierian tubules not observed in the preserved specimens (see also remark with *A. echinites*); visible as a small pinkish tuft in live specimens (SAMYN pers. observ.). Three Polian vesicles (two long; one short). Ten stone canals each ending in relatively large egg-shaped madreporic plate. Calcareous ring very stout, radial pieces almost three time as wide as the interradial pieces, interradial pieces almost as high as the radial pieces (See CHERBONNIER 1988: 19, fig. 2H).
Ossicles: Tentacles with large, rugose rods, 165-210 µm long (fig. 4A). Dorsal body wall with spiny rods, 55-90 µm long, and simple, very small rosettes, 20-45 µm long (fig. 4B). Ventral body wall with small grains, elongated grains and rods that can be spiny or smooth (fig 4C).

Diagnosis - See PANNING 1944: 5, figs 3, 4; CHERBONNIER 1952b: 41, fig. 16.

Ecology - Depth range: from 1 to 7 m (0-12 m according to LANE *et al.* 2000); detritus/deposit feeder in coral reef lagoon, on hard coral ruble substrate, also in sea grass beds.

Distribution in the study region - Shariani, Kanamai, Mombasa, Gazi Bay, Malindi, Vanga, Kiunga Marine Reserve (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - Well known species from the tropical Indo-west-central Pacific (ROWE, *in* ROWE & GATES 1995), with the Red Sea, but no records from the Persian Gulf. Figure 51D shows the known distribution in the WIO in detail.

Actinopyga miliaris (QUOY & GAIMARD, 1833)
(fig. 5A-E, fig. 51E, pl. 1E)

Holothuria miliaris QUOY & GAIMARD, 1833: 137 (see also CHERBONNIER 1952b: 39, pl. III fig. 3)
Actinopyga miliaris; KALK 1954: 112 (from THANDAR 1984); KALK 1958: 198, 238; DANIEL & HALDER 1974: 429; MUKHOPADHYAY 1991: 403; VANDENSPIEGEL & JANGOUX 1993: 43; CONAND 1999: 10, 12, 16, 39 pl. 1 (colour picture), 16; MASSIN 1999: 10 (synonymy and records before 1999), fig. 6 (distribution), fig. 110b (colour picture); LANE *et al.*, 2000: 488; SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE 2000: 4 (tab. 2), 17 (tab. 4), 19; MARSHALL *et al.* 2001: 46 (tab. 29), 47, 53, 58 (tab. 37).

Status and location type - Holotype lost, possibly in MNHNP (ROWE, *in* ROWE & GATES 1995).

Type locality - Vanikoro Islands (Solomon Islands).

Material examined - TFun/9822 (one specimen); TFun/9823 (one specimen); KKiun/9923 (one specimen); KKiun/9924 (one specimen).

General description - Large species reaching lengths up to 400 mm and widths up to 100 mm. Examined specimens, after preservation, 190 to 210 mm long and 50 to 70 mm wide. The smallest specimen auto eviscerated. Colour in life uniform dark brown to black (pl. 1E) (some specimens are slightly lighter ventrally); colours preserved in alcohol. Body wall soft to the touch, up to 8 mm thick. Mouth ventral surrounded by 16-20 firm, brown to black, tentacles. Anus terminal, surrounded by five, yellow to orange, anal teeth. Trivium with numerous black tube feet scattered over the radial and interradial areas. Bivium easily distinguishable from the trivium by the scarcity of evenly distributed pedicels on the former. Cuvierian tubules neither observed in life, nor in preserved specimens (see also remarks with *A. echinites*). One or two (then one long and one short) Polian vesicles. Single, very short, stone canal. Calcareous ring stout, radial pieces twice as broad as the interradial ones; radial pieces with three anterior teeth (see MASSIN 1999: 11, fig. 5a).

Ossicles: Tentacles with knobbed rods up to 260 µm long (fig. 5A). Dorsal and ventral body wall with rosettes and rods (fig. 5B, C). Ventral tube feet with similar but larger rods and rosettes (fig. 5D). Dorsal tube feet with very large (up to 370 µm long) rods and pseudo-plates (fig. 5E).

Diagnosis - See PANNING, 1929 [1931]: 127, fig. 10a-g.

Ecology - Depth range from 0 to 20 m; detritus/deposit feeder on sandy patches between coral heads. Forages actively during the day.

Distribution in the study region - Malindi, Mombasa, Fundu, Mesali, Kiunga (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - Well known species from the tropical Indo-West Pacific (with the Red Sea, no records from the Persian Gulf). The distribution map as drawn by MASSIN (1999: 11, fig. 6) gives the global distribution, but the following localities in the WIO have to be added: Gulf of Suez, Ras el Millan (HELFER 1912, as *Mülleria miliaris* QUOY & GAIMARD, 1833), Suez (MORTENSEN 1926) (see also PRICE 1982 for unspecified localities from the Gulf of Suez); Gulf of Aqaba, Aqaba (TORTONESE 1977) (see also PRICE 1982 for unspecified locality from the Gulf of Aqaba); Red Sea, unspecified locality (LAMPERT 1885, as *M. miliaris*; THÉEL 1886, as *M. miliaris*; MITSIKURI 1912, as *M. miliaris*; CLARK & ROWE 1971; PRICE 1982); Tanzania, Fundu and Mesali (this work); Mozambique, unspecified locality (LAMPERT 1885, as *M. miliaris*; THÉEL 1886, as *M. miliaris*; MITSIKURI 1912; H.L. CLARK 1923); southern Mozambique (KALK 1958). Figure 51E shows the known distribution in the WIO in detail.

Table two lists the other *Actinopyga* species that are known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record(s) appeared.

Current Species Name	Known WIO Distribution	Reference(s)
A. bacilla CHERBONNIER, 1988	Madagascar (Nosy Bé) only	CHERBONNIER 1988
A. bannwarthi PANNING, 1944 (see also discussion)	Gulf of Suez (Suez, Mersa Thlemel)	PANNING 1944; CHERBONNIER 1955; DANIEL & HALDER 1974; PRICE 1982?
	Gulf of Aqaba (Eilat, Aqaba)	CHERBONNIER 1963; 1967; TORTONESE 1977; PRICE 1982
	Red Sea (unspecified)	PANNING 1944; CLARK & ROWE 1971; PRICE 1982?
	Arabian Sea	PRICE 1982
	Gulf of Aden (Djibouti, Obok)	VANEY 1905[(1)]; CHERBONNIER 1955
	Seychelles (Aldabra)	SLOAN *et al.* 1979
	Madagascar (Nosy Bé, Fort Dauphin)	CHERBONNIER 1988
A. crassa PANNING, 1944	Arabian Sea	PRICE 1982
	Gulf of Aden (Djibouti)	CHERBONNIER 1955
	Madagascar (Nosy Bé, Fort Dauphin)	CHERBONNIER 1988
	Mozambique (Querimba Archipelago, Port Moresby)	PANNING 1944; THANDAR 1984
	Mascarene Islands (unspecified)	CLARK & ROWE 1971
A. obesa (SELENKA, 1867) (see also discussion)	Comores	CHERBONNIER 1988
	South Africa (KwaZulu-Natal)	pers. observ.
A. serratidens PEARSON, 1903	Gulf of Suez (Mersa Thlemel)	CHERBONNIER 1955; PRICE 1982
	Gulf of Aqaba (Eilat, Aqaba)	TORTONESE 1977; PRICE 1982; CHERBONNIER 1967
	Red Sea (Hurghada, Dahlak Kebir, Entedebirand Nocra, Djeddah)	PEARSON 1914a; MORTENSEN 1937; PANNING 1944; TORTONESE 1953a; CHERBONNIER 1967; TORTONESE 1979; PRICE 1982
	Madagascar (Nosy Bé)	CHERBONNIER 1988

Table 2 - Other species within the genus *Actinopyga* known to occur in the shallow-waters of the WIO. [(1)] Cited as *Mülleria lecanora* JÄGER

Genus *Bohadschia* JAEGER, 1833

Diagnosis (after ROWE, 1969: 129-130) - [Type species: *Bohadschia marmorata* JAEGER, 1833 by subsequent designation].
Size from moderate up to very large (450 mm); body stout, body wall variable in thickness and usually muscular; covered by small and numerous tube feet and papillae; mouth ventral surrounded by 20 peltate tentacles; calcareous ring very stout with the radial pieces twice as large as the interradial pieces and possessing a median anterior ampullary notch, interradial pieces with a short anterior median tooth-like projection; anus dorsal, without anal teeth though five groups of papillae may be present. Ossicles: tables, buttons, S- or C-shaped rods always absent; body wall with perforated and unperforated grains, tentacles and tube feet with rods; longitudinal muscles devoid of ossicles.
Eleven species are currently recognized as being valid: *Bohadschia argus* (JAEGER, 1833); *B. atra* MASSIN, RASOLOFONIRINA, CONAND & SAMYN, 1999; *B. cousteaui* CHERBONNIER, 1954; *B. maculisparsa* CHERBONNIER & FÉRAL, 1985; *B. marmorata* JAEGER, 1833; *B. mitsioensis* CHERBONNIER, 1988; *B. paradoxa* (SELENKA, 1867); *B. similis* (SEMPER, 1868); *B. steinitzi* CHERBONNIER, 1963; *B. subrubra* (QUOY & GAIMARD, 1833) and *B. vitiensis* (SEMPER, 1868). Five of these are found in the waters of Kenya (with Pemba Island); they are keyed hereunder.

Key to the species of Kenya (with Pemba island)

1. Bivium and trivium with a more or less uniform colouration, ranging from yellow-brown to black **2**

1'. Body not uniformly coloured: bivium brown to orange with unevenly distributed dark brown to black areas; trivium white, with tiny black spots between the tube feet; bivium clearly separated from the trivium by a brown line with dark brown triangular areas. . . . . ***B. subrubra* (QUOY & GAIMARD, 1833)**

2. Body colour ranging from yellow to light brown. **3**

2'. Body colour dark brown to black **4**

3. Body colour yellow-white ventrally and laterally, brownish dorsally, spotted by numerous small brown spots corresponding to the tube feet; body wall with grains (occasionally perforated) and rosettes; ventral and dorsal tube feet with bended, sometimes cruciform, rods. . . . . ***B. marmorata* JAEGER, 1833**

3'. Body colour uniform yellow to light brown ventrally; brownish with numerous dark patches corresponding to the papillae dorsally. Body wall with some perforated grains and numerous rosettes; ventral tube feet with grains, rosettes and simple rods; dorsal pedicels with simple rosettes . . . . . ***B. similis* (SEMPER, 1868)**

4. Deep brown to black bivium with numerous brown to red spots, surrounding black dorsal papillae; trivium slightly lighter in colour, without red spots; dorsal and ventral body wall with grains, granules, rosettes and rods; ventral tube feet with smooth rods and grains; dorsal papillae with rosettes; tentacles with spiny rods. . . . . ***B. atra* MASSIN *et al.*, 2000**

4'. Body colour uniform dark brown, slightly lighter ventrally; ventral body wall with imperforated grains, rods and simple rosettes; dorsal body wall with cross shaped rods and complex rosettes; ventral tube feet with smooth straight rods, sometimes perforated at their extremities, grains, and cross shaped rods; dorsal tube feet with long smooth or spiny rods, cross-shaped rods, and some small rosettes. . . . . ***B. cousteaui* CHERBONNIER, 1954**

Bohadschia atra MASSIN, RASOLOFONIRINA, CONAND & SAMYN, 1999
(fig. 6A-E, fig. 51F, pl. 1F)

Bohadschia atra MASSIN, RASOLOFONIRINA, CONAND & SAMYN, 1999: 151, figs 1A-J, 2A-E, Pl. 1B, D (colour pictures); SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE 2000: 4 (tab. 2), 17 (tab. 4), 20.
Bohadschia aff. *subrubra*; CONAND 1999: pl. 2 [colour picture with *B. subrubra* (top) and *B. atra* (bottom)].

Status and location type - Holotype: MNHNP, EcHh 7133; Paratypes: IRSNB, IG 28 628/Fun90-91 (two specimens).

Type locality - Mayotte (Comores).

Material examined - KShar/9734 (one specimen); KShar/9735 (one specimen); IRSNB IG 28 628/Fun90-91 (two specimens); IRSNB 28 628/Mom12 (one specimen); IRSNB IG 28 628/Shar11 (one specimen); IRSNB IG 28 628/Mom60-61 (two specimens); KKiun/9927 (three specimens); KKiun/9928 (one specimen).

GEneral description - Large species; living specimens up to 400 mm long and 150 mm wide, preserved specimens up to 25 % smaller. Bivium; deep brown to black with numerous brown to red spots, surrounding black dorsal papillae (pl. 1F). Trivium slightly lighter in colour, without red spots. Transverse brown-red bands may be visible in larger individuals. Body wall smooth, 2-5 mm thick Mouth ventral, surrounded by 18-20 black tentacles. Anus dorsal, unguarded. Ventral tube feet scattered over radial and interradial areas. Dorsal tube feet also scattered but, less numerous. Cuvierian tubules present and very readily ejected in large quantities. Single Polian vesicle. Single stone canal. Calcareous ring stout with radial pieces twice as large as the interradial pieces; radial pieces with an anterior median notch and two anterio-lateral holes, interradials with a pointed tooth (See MASSIN *et al.* 1999: 152, fig. 1).
Ossicles: Dorsal and ventral body wall with grains, granules, rosettes and rods (fig. 6A, B); morphology, size and abundance of each type dependent on the size of the specimen (see also MASSIN *et al.* 1999). Ventral tube feet with smooth rods, sometimes perforated at the extremities, and grains (fig. 6C). Dorsal papillae with rosettes (fig. 6D) and rods. Tentacles with spiny rods (fig. 6E).

Diagnosis - See MASSIN *et al.* 1999: 15, figs 1, 2; pl.1.B, D.

Ecology - *B. atra* dwells in shallow (up to 12 m depth) inner reefs, on sandy patches between coral heads and on the leeward-side of sea grass beds (mainly *Thalassodendron ciliata*). *B. atra* has been observed feeding on sand; faeces of *B. atra* also composed of sand, no rubble.

Distribution in the study region - Fundu, Kiunga (See also SAMYN & VANDEN BERGHE 2000), Malindi, Mombasa, Shariani, Watamu.

Geographic distribution - Species restricted to the western Indian Ocean; not recorded from the Red Sea, nor from the Persian Gulf (See also MASSIN *et al.* 1999). Figure 51F shows the known global distribution in detail.

Bohadschia cousteaui CHERBONNIER, 1954
(fig. 7A-F, fig. 51G, pl. 1G)

Bohadschia cousteaui CHERBONNIER, 1954a: 252 (see also CHERBONNIER 1955: 133, pl. 23 figs a-k); CHERBONNIER 1963: 5; CHERBONNIER 1967: 55; CLARK & ROWE 1971: 176; TORTONESE 1977: 275; PRICE 1982: 10; CHERBONNIER 1988: 44; SAMYN 2000: 15 (tab. 1).
Bohadschia consteani; DANIEL & HALDER 1974: 417 (*lapsus calami*).

Type location - MNHNP.

Type locality - Red Sea (Al Lith, Saudi Arabia).

Material examined - KKan/9714 (one specimen); TFun/9895 (one specimen); TFun/9896 (one specimen).

General description - The specimen from Kanamai (KKan/9714), recovered from the shelves of the Kenya Marine Fisheries and Research Institute, Mombasa, is in poor state for uncontrolled dissection has been performed on it. The specimen is 227 mm long and 77 mm wide. The two specimens from Fundu (TFun/9895-96) measure 224 x 60 and 186 x 56 mm. Body colour in alcohol is uniform dark brown, slightly lighter ventrally (pl. 1G). Body wall smooth to the touch, up to 5 mm thick. Mouth ventral surrounded by 15-20 brown stout tentacles. Anus large, subdorsal, unguarded by papillae. Tube feet on the ventral side short, brown, distributed without order over the ambulacral and interambulacral areas. Tube feet on the dorsal side similar, fewer in number, distributed over ambulacral and interambulacral areas. Cuvierian tubules abundant. Calcareous ring stout; radial pieces one and a half times broader than the interradial pieces (see CHERBONNIER 1988: 45, fig. 15K).
Ossicles: Ventral body wall with imperforated grains; rods and simple rosettes, up to 40 µm long (fig 7A). Dorsal body wall with cross-shaped rods, up to 45 µm long; and rosettes of a more complex nature, up to

30 µm long (fig 7B). Ventral tube feet with smooth, straight rods, sometimes perforated at their extremities, 50 to more than 200 µm long (fig. 7C); grains, and cross shaped rods (fig. 7D). Dorsal tube feet with long, smooth or spiny rods, up to 280 µm long; cross-shaped rods, 20-85 µm long; and some small rosettes of approximately 20 µm (fig. 7E). Tentacles with smooth or spiny rods, sometimes bifurcated, up to 260 µm long (fig. 7F).

Diagnosis - See CHERBONNIER 1988: 44, fig. 15 p. 45

Ecology - The Kanamai specimen was found intertidally, in a sea grass bed, on fine coralline sand. The specimens from Fundu were found on sandy patches, on coral rubble, ten to 14 m depth.

Distribution in the study region - Fundu, Kanamai.

Geographic distribution - Species for now only known from a handful of localities in the WIO: Gulf of Aqaba , Eilat, Aqaba (CHERBONNIER 1963; 1967; TORTONESE 1977; see also PRICE 1982); central Red Sea, Al Lith, Entedebir (CHERBONNIER 1954a; 1955, 1967; see also CLARK & ROWE 1971; DANIEL & HALDER 1974 as *B. consteani* CHERBONNIER (*lapsus calami*); PRICE 1982), Kenya, Kanamai (this work); Tanzania, Fundu (this work); Madagascar, Nosy Bé, Tuléar (CHERBONNIER 1988). Figure 51G shows the known global distribution in detail.

Bohadschia marmorata JAEGER, 1833
(fig. 8A-E, fig. 51H, pl. 1H)

Bohadschia marmorata JAEGER, 1833: 18, pl. 3 fig. 9.
Holothuria marmorata; DANIEL & HALDER 1974:428.
Holothuria (Bohadschia) marmorata; MORTENSEN 1937: 7; TORTONESE 1937-38: 180 (synonymy).
Bohadschia marmorata; TORTONESE 1936b: 11; LEVIN 1979: 19; SLOAN *et al.* 1979: 121; PRICE 1982: 10; HUMPHREYS 1981: 33; TAN TIU 1981: 69, 101 pl. 11; A.M. CLARK 1984: 87, 99; CANNON & SILVER 1986: 20, fig. 5d (colour drawing); CHERBONNIER 1988: 36, (synonymy); MUKHOPADHYAY 1991: 403, 412; MARSH *et al.* 1993: 63; ALLEN & STEENE 1994: 243 (colour picture, possibly not *B. marmorata*); ROWE & GATES 1995: 289; GOSLINER *et al.* 1996: 278 (colour picture); CONAND 1999: 12, 19, 20, 39; LANE *et al.* 2000: 488; SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 21; MARSHALL *et al.* 2001: 46 (tab. 29), 58 (tab. 37).
Bohadschia tenuissima SEMPER 1868; LEVIN 1979: 20; PRICE 1982: 10; CHERBONNIER 1967: 55; FÉRAL & CHERBONNIER 1986: 78, 79 (colour picture); CHERBONNIER 1988: 46 (synonymy); CONAND 1999: 10.

Status and location type - Status and data of whereabouts undetermined (ROWE, *in* ROWE & GATES 1995).

Type locality - Sulawesi (as Celebes), Indonesia.

Material examined - KKiun/9925 (three specimens); KKiun/9926 (two specimens).

General description - Large species; after preservation up to 300 mm long and 100 mm wide. Body colour yellow-white ventrally and laterally, brownish dorsally, spotted by numerous small brown spots corresponding to the tube feet. Transverse, dorsal banding is typical of the species (pl. 1H; see also GOSLINER *et al.* 1996: 278, colour picture), though not always clearly visible. Mouth ventral, surrounded by 20 light-brown, relatively small, tentacles that in term are surrounded by a circle of brown tube feet. Anus terminal, relatively large, surrounded by a brown line. Ventral tube feet spread in the ambulacral and the interambulacral zones. Bivium covered by conical tube feet surrounded at their base by a small brownish circle. Cuvierian tubules present. Calcareous ring stout, radial pieces two and a half times as wide as the interradial pieces; radial pieces with a large anteriorly placed central notch and two lateral attachment sites for the longitudinal muscles; interradial pieces with an anterior tooth and a shallow concave posterior side (See CHERBONNIER 1988: 37, fig. 11L).
Ossicles: Tentacles with rods, up to 220 µm long, spiny at the extremities (fig. 8A). Ventral body wall with grains of various forms that can be perforated (fig. 8B). Dorsal body wall with rosettes and perforated grains (fig. 8C). Ventral and dorsal tube feet with bended, sometimes cruciform, rods and few rosettes (fig. 8D, E).

Diagnosis - See JAEGER 1833: 18, pl. 3 fig. 9; CHERBONNIER 1988: 36-38, fig 11A-L.

Ecology - Depth ranges from 0 to 36 m (LANE *et al.* 2000); detritus/deposit feeder on sandy areas in patchy coral reefs. The specimens here examined had very fine dark (anoxic?) sand in their guts.

Distribution in the study region - Mombasa, Kanamai, Kiunga (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - Tropical Indo-west Pacific, except Hawaii (with the Red Sea, not recorded from the Persian Gulf) (see also ROWE & GATES 1995). Fig. 51H shows the known distribution in the WIO in detail.

Remarks - Transverse dorsal banding is often the only field characteristic that makes *B. marmorata* distinguishable from the congeneric species *B. similis*, *B. vitiensis*, *B. tenuissima*, *B. bivittata* and *B. koellikeri*. As ROWE (*in* ROWE & GATES 1995) already noted, the species in the genus *Bohadschia* are in need of critical review. The ossicles of the examined specimens (see fig. 8) closely resemble the ones of *B. marmorata* described in CHERBONNIER (1988). However, the different *Bohadschia* species show a great variation in their ossicles (MASSIN 1996a: 1999), and overlap often occurs between the different valid species. This prompted THÉEL (1886), PEARSON (1903) and KOEHLER & VANEY (1908) to unite several species under the name *H. tenuissima* SEMPER, 1868 and later (PEARSON 1913) under *H. vitiensis* SEMPER, 1868. ROWE (*in* ROWE & GATES 1995) also used a 'sweeping synonymy' [sic] wherein *B. bivittata* (MITSIKURI, 1912), *B. koellikeri* (SEMPER, 1868), *B. similis* (SEMPER, 1868), *B. tenuissima* (SEMPER, 1868) and *B. vitiensis* (SEMPER, 1868) are put as synonyms of *B. marmorata*. I, however, feel that the type material of these supposed synonyms (type material for SEMPER'S species in ZMH, for MITSIKURI'S species in TIU) needs further detailed study and that at least *B. vitiensis* and *B. similis* must for now be regarded as valid species (see also MASSIN 1996a; 1999). I agree however with ROWE (*in* ROWE & GATES 1995) that much more material from different regions is needed to clarify the status of the taxa in the *Bohadschia* complex.

Bohadschia cf. *similis* (SEMPER, 1868)
(fig. 9A-E, fig. 52A, pl. 2A)

Holothuria similis SEMPER, 1868: 85, 277, pls 25, 30 pl., fig. 18.
Bohadschia similis; MASSIN 1996a: 14: fig. 8A-E (synonymy before 1996); CONAND 1998b: 1173; CONAND 1999: 10; SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 488.

Status and location type - Holotype ZMH E.2640 (ROWE in ROWE & GATES 1995).

Type locality - Bohol (Philippines).

Material examined - KCi/9742 (one specimen).

General description - The single preserved specimen at our deposition is 140 mm long and 45 mm wide and was retrieved from the shelves of the Kenya Marine and Research Institute. It is in bad shaped due to uncontrolled dissection, whereby the calcareous ring was removed. The colour pattern in life is similar to the colour in alcohol (pl. 2A), although the latter is markedly lighter. Colouration in life: uniform yellow to light brown ventrally; brownish with numerous dark patches corresponding to the papillae dorsally. Mouth ventral, surrounded by 20 yellow to brown, short and small tentacles; surrounded at their base by a ring of small conical papillae. Anus large, dorsal. Brownish tube feet distributed over the radial and interradial areas ventrally. Dorsal papillae scattered over the total dorsal area. Cuvierian tubules present. Calcareous ring large with an anterior notch on the interradial pieces and with a single pointed tooth on the radial pieces (see MASSIN 1996a: 16, fig. 8A).
Ossicles: Ventral body wall with some perforated grains and numerous rosettes, 15 to 30 µm long (fig 9A). Dorsal body wall with rosettes of similar length (fig. 9B). Ventral tube feet with grains, rosettes and simple rods up to 65 µm in length (fig 9C). Dorsal papillae with simple rosettes (fig 9D). Tentacles with rods up to 230 µm long.

Diagnosis - See PANNING 1929 [1931]: 112, fig. 3d, e.

Ecology - The specimen was collected in a shallow sea grass bed of approximately 2 m depth. As the gut contents consist of fine sand we deduct that *B. similis* actively feeds on this substratum.

Distribution in the study region - Chale Island.

Geographic distribution - Ambon, Kenya, La Réunion, Mauritius, New Caledonia, Tahiti, the Philippines according to MASSIN (1996a), also known from the South China Sea according to LANE *et al* (2000). Fig. 52A shows the known distribution in the WIO in detail, whereby it should be noted that the record for Kenya is new and that the record from La Réunion could not be tracked down (CLARK & ROWE 1971 list it from the Mascarene Islands; unspecified locality in CONAND 1999).

Remarks - ROWE & DOTY (1977) and ROWE & GATES (1995) place *B. similis* as a junior synonym of *B. marmorata*, an opposite view to that of CHERBONNIER (1980, 1988), CHERBONNIER & FÉRAL (1984a), FÉRAL & CHERBONNIER (1986), CONAND (1989, 1998b), and MASSIN (1996a). As we have only a single specimen in our collection, intraspecific variation cannot be investigated now. Nevertheless, as the body wall of the specimen under investigation presents numerous rosettes together with few perforated grains and no imperforated grains; it has more affinity to *B. similis* then to *B. marmorata*. Moreover, the transverse banding, characteristic of *B. marmorata* was not visible in our specimen.

Bohadschia subrubra (QUOY & GAIMARD, 1833)
(fig. 10A-D, fig. 52B, pl. 2B)

Holothuria subrubra QUOY & GAIMARD, 1833: 136.
Bohadschia subrubra; MASSIN *et al.* 1999:155 (synonymy and records before 1999), figs. 3, 4, 5, pl. 1A,C, D (colour plate); CONAND 1999: 19, 20; SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE, 2000: 5 (tab. 2), 17 (tab. 4), 20; MARSHALL *et al.* 2001: 46 (tab. 29).
Bohadschia aff. *subrubra*; CONAND 1999: pl. 2 (colour picture with *B. subrubra* on top)
Bohadschia cf. *subrubra*; CONAND 1999: 12, 39.
?Holothuria kollikeri; DANIEL & HALDER 1974: 423 (*non H. koellikeri* SEMPER 1868) (*lapsus calami*).
?Bohadschia koellikeri; HUMPHREYS 1981: 33 (*non H. koellikeri* SEMPER 1868).

Status and location type - Faculty of Sciences Lyon (CHERBONNIER 1952b).

Type locality - Ile aux Cerfs (Mauritius).

Material examined - IRSNB IG 28 628/Shar10 (one specimen); IRSNB IG 28 628/Mom89-92-93-94 (four specimens); IRSNB IG 28 628/Fun7 (one specimen).

General description - Species up to 350 mm long and 130 mm wide. Bivium brown to orange with unevenly distributed dark brown to black areas. Trivium white, with tiny black spots between the tube feet (pl. 2B). Bivium clearly separated from the trivium by a brown line with dark brown triangular areas. Body wall smooth, 2-5 mm thick. Mouth ventral, surrounded by 18 stout, white tentacles. Anus dorsal, unguarded by anal teeth or papillae. Numerous ventral tube feet, white, very long, and scattered over the whole surface. Dorsal tube feet less numerous, scattered, white, clearly visible against the orange to brown dorsal body colour. Cuvierian tubules present, white, very readily ejected in large quantities. Single Polian vesicle. Single stone canal. Calcareous ring stout with radial pieces twice as high and wide as the interradial pieces; radial pieces with a deep central notch and two lateral hollows (see MASSIN *et al.* 1999: 155, fig. 3)
Ossicles: Body wall with rosettes (fig. 10B, C). Tube feet with rods, rosettes (fig. 10D) and a very large endplate (up to 450-500 µm across). Tentacles with large spiny rods (fig. 10A). (See also illustrations MASSIN *et al.* 1999).

Diagnosis - See MASSIN *et al.* 1999: 155, figs 3-5; pl.1.A, C.

Ecology - Found on sandy patches in patch reefs, also on coral rubble and sometimes on dead coral. Species often covers itself with pieces of algae and sea grass, and occasionally with shell fragments.

Distribution in the study region - Kiunga, Malindi, Watamu, Shariani, Kanamai, Mombasa, Chale Island, Shimoni, Vanga, Fundu.

Geographic distribution - Kenya, Kiunga, Sharianai, Kanamai, Mombasa, Chale Island, Malindi, Watamu, Vanga; Madagascar, Tuléar, Nosy Bé (MASSIN *et al.* 1999), Mauritius, Ile aux Cerfs (MASSIN *et al.* 1999); Republic of South Africa, Sodwana Bay and Bhanga Nek, KwaZulu-Natal (pers observ.), Tanzania, Pemba Island, Fundu North Reef (this work). Fig. 52B shows the known global distribution in detail.

Remarks - Although this species was only recently re-described (MASSIN *et al.* 1999), it is one of the most ubiquitous aspidochirotid holothurians to be found in the shallow reef waters of East and South-East Africa (ROWE *in* ROWE & RICHMOND 1997; pers. observ.). HUMPHREYS (1981) described *B. koellikeri* (SEMPER, 1868) from Kenya, but his description makes me believe (SAMYN & VANDEN BERGHE 2000) that this specimen is in fact *B. subrubra*. Unfortunately the voucher specimens could not be found in any of the three museums: MRAC (pers observ.), NHM (pers. observ.) and NMK (VANDEN BERGHE, pers. comm.) where HUMPHREYS deposited his samples.

Table three lists the other *Bohadschia* species that are known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record(s) appeared.

Current Species Name	Known WIO Distribution	Reference(s)
B. argus JAEGER, 1833	Tanzania	MARSHALL *et al.* 2001
(see also discussion)	Seychelles	LAMPERT 1885; MITSIKURI 1912; PANNING 1944
	Madagascar (Nosy Bé, Tuléar)	CHERBONNIER 1988; CONAND 1999
B. maculisparsa CHERBONNIER, 1980	SW Indian Ocean (unspecified)	CONAND 1999
(see also discussion)		
B. mitsioensis CHERBONNIER, 1988	Madagascar (Nosy Bé)	CHERBONNIER 1988
(see also discussion)		
B. steinitzi CHERBONNIER, 1963	Gulf of Aqaba (Eilat, Aqaba)	CHERBONNIER 1963; 1967; TORTONESE 1977; PRICE 1982
B. vitiensis (SEMPER, 1868)	Madagascar (Nosy Bé, Ile St. Marie, Tuléar)	CHERBONNIER 1988; CONAND 1999
	Eastern Africa	ROWE & RICHMOND 1997
	Kenya (Kiunga Marine Reserve)	OBURA *et al.* 1998
	Mauritius (Trou aux Biches, Riambel)	ARAKAKI & FAGOONEE 1996; CONAND 1999
	La Réunion	CONAND 1999
	Seychelles (Mahé: Ste. Anne Marine Park)	ARAKAKI & FAGOONEE 1996; CONAND 1999

Table 3 - **Other species within the genus *Bohadschia* known to occur in the shallow-waters of the WIO.**

Genus *Labidodemas* SELENKA, 1867

Diagnosis (retaken from MASSIN *et al.* submitted) - [Type species: *Labidodemas semperianum* SELENKA, 1867 by monotypy].
Size medium to moderate (100 to 200 mm long); body has two distinct morphotypes: vermiform or more cylindrical; ventral tube feet mainly in ambulacral areas, in one to four rows (sometimes also spread into the interambulacral areas); dorsal papillae and tube feet in ambulacral and often also in interambulacral areas, or altogether absent; anal papillae present or absent. Species fugitive or fossorial, with thin body wall and 20 terminally placed tentacles. Calcareous ring with massive radial pieces and narrow ribbon-like interradial pieces. Body wall ossicles variously developed tables, either with disc reduced and spire low, ending in a cluster of firm, often bifurcate, spines frequently longer than radius of table disc, or with disc well developed and with low to moderate spire ending in a cluster of firm spines or a wide, centrally perforated crown; buttons (when present), usually with rim smooth to slightly knobbed, some buttons spiny, often irregular and incompletely formed; minute, occasionally perforate, branching or curved rods. Tube feet ossicles similar to those of body wall, with in addition rounded plates apparently derived from buttons. Tentacles always with small, smooth to slightly spiny rods. Longitudinal muscles devoid of ossicles. Cuvierian tubules present only in the central East Pacific *L. americanum.*
Until recently four species were recognized as being valid: *Labidodemas americanum* DEICHMANN, 1958; *L. pertinax* (LUDWIG, 1875); *L. rugosum* (LUDWIG, 1875), *L. semperianum* SELENKA, 1867. A recent revision (MASSIN *et al.* submitted) of the genus resulted in several species new to science. Only *L. pertinax* is known to occur in the shallow-waters of Kenya as HUMPHREYS' (1981) voucher specimen of *L. semperianum* from Watamu proved to be *L. pertinax* (MASSIN *et al.* submitted).

Labidodemas pertinax (LUDWIG, 1875)
(fig. 11A-E, fig. 52C)

Holothuria pertinax LUDWIG, 1875: 24, pl. 7 fig. 50.
Labidodemas pertinax; MASSIN *et al.* submitted (synonymy and records before 2002).

Status and location type - Holotype ZMH E.2608.

Type locality - Samoa (as Navigator Islands).

Material examined - KKiun/9919 (one specimen); KKiun/9920 (two specimens); Kenya (Watamu), 20.viii.1969, coll. W. Humphreys, NHM 1979.2.5.229 (one specimen identified as *L. semperianum*). (see also MASSIN *et al.* submitted for a representative list of examined specimens coming from the complete distribution area).

General description - Small to medium-sized species; preserved specimens from 70 to 105 mm long and 7-14 mm wide. Body cylindrical, tapering, with mouth and anus terminal. Body colour in life similar as colour after preservation (pl. 2C): uniform white dorsally with a very faint yellow to pinkish shine ventrally; mouth surrounded by a 5 mm wide dark-purple to brown ring in the largest specimen (1 mm wide in the smallest specimens). Skin thin but rather gritty to the touch. Mouth surrounded by 20 (occasionally fewer), small, dirty white, tentacles. Trivium with long, cylindrical, yellow to brown tube feet in the radial areas (in two rows in the median ambulacrum); bivium with fewer, short, whitish tube feet spread over the ambulacral and interambulacral areas. Cuvierian tubules absent. Calcareous ring slender and ribbon-like with the radial pieces twice as wide as the interradial ones (see MASSIN *et al.* submitted).
Ossicles: Tentacles with simple, smooth rods, 25-50 µm long (fig 11A). Dorsal and ventral body wall with simple or branching rods up to 200 µm long, and stout tables with spinose disc and crown (fig 11B, C). Tables with disc 40-65 µm across, perforated by four central holes and occasionally some small peripheral holes (see CHERBONNIER 1988: 52, fig. 18A, B, D, H); rim of disc regularly spiny; height of spire lower then width of disc; spire with no or single cross beam ending in a crown with a wide central opening; diameter of crown 60-90 % of disc diameter. Rods more abundant in ventral than in dorsal body wall; the reverse for the tables. Ventral tube feet with rods similar to those of the body wall and some ill-formed tables (fig. 11E). Dorsal tube feet comprise the same ossicle-assemblage as that of the ventral tube feet (fig. 11D).

Diagnosis - See CHERBONNIER 1988: 51, fig. 18; MASSIN *et al.* submitted.

Ecology - Shallow water (only few meters deep); deposit/detritus feeder; hides under coral slabs in and on coarse coral debris.

Distribution in the study region - Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000).

Geographic distribution - Tropical Indo-Pacific Ocean from the East coast of Afrika (South Africa and Kenya) to Tahiti and from South Africa (KwaZulu-Natal) to China, however not recorded from the Red Sea and the Persian Gulf (see also global distribution map in MASSIN *et al.* submitted). Figure 52C shows the WIO distribution in detail.

Table four gives the other *Labidodemas* species that are known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record(s) appeared.

Current Species Name	Known WIO Distribution	Reference(s)
L.semperianum SELENKA, 1867	Gulf of Aqaba (Aqaba, Eilat)	TORTONESE 1977[(1)]; CHERBONNIER 1967[(1)]; PRICE 1982[(1)]
	Persian Gulf (Jurayd Islands)?	PRICE 1981; 1982
	Mauritius (Ile aux Cerfs, Albion, Blue Bay)?	ARAKAKI & FAGOONEE 1996
L. rugosum (LUDWIG, 1875)	Somalia (Gesira)	TORTONESE 1980
(see also discussion)	Seychelles (unspecified)	A.M. CLARK 1984
	Seychelles (Aldabra)	SLOAN *et al.* 1979
	Madagascar (Glorious Islands, Nosy Bé)	CHERBONNIER 1988
	South Africa (KwaZulu-Natal)	MASSIN *et al.* submitted

Table 4 - Other species within the genus *Labidodemas* known to occur in the shallow-waters of the WIO. The records of *L. semperianum* from Mauritius (ARAKAKI & FAGOONEE 1996) and the Persian Gulf (PRICE 1981; 1982) are uncertain and might be misidentified individuals of *L. pertinax* (MASSIN *et al.* submitted). [(1)] Cited as *Holothuria proceraspina* CHERBONNIER.

Genus *Holothuria* Linnaeus, 1767

Diagnosis (after ROWE, 1969: 133) - [Type species: *Holothuria tremula* LINNAEUS, 1767 by monotypy].
Size very variable from small to very large; body morphology very variable, from slender vermiform to thick cylindrical, sometimes with a distinct flattened trivium; covered by tube feet and papillae which can be distributed over the ambulacral and the interambulacral areas of the dorsal and ventral sides; mostly 20 tentacles; calcareous ring well developed with the radial pieces two to three times as long as the interradial pieces; mouth often ventral, though sometimes terminal; anus dorso-terminal mostly without calcified papillae but often guarded by anal papillae. Ossicles: mostly with well-developed tables (except in the subgenus *Selenkothuria* and some species of the subgenus *Theelothuria*); smooth, perforated rods and plates or spinose rods; buttons often present.

Key to the subgenera of Kenya (with Pemba island)
(after Rowe 1969: 126)

1. Tables said to be present in some species, but if so always reduced in form and sparsely distributed in the body wall; mostly perforated plates and rods only ..... ***Selenkothuria*** **DEICHMANN, 1958**

1'. Tables always present; usually well developed; alone or in combination with buttons, pseudobuttons, rods or rosettes **2**

2. Tables usually well developed; always in combination with buttons or pseudobuttons; never with rosettes or rods in the body wall **5**

2'. Tables variously developed; always in combination with rods or rosettes; never with buttons or pseudobuttons **3**

3. Tables in combination with rosettes only, never with rods in the body wall **4**

3'. Tables in combination with spinose rods, never with rosettes . ***Semperothuria*** **DEICHMANN, 1958**

4. Tables with reduced disc, spire as high as the disc diameter is wide (occasionally higher) and spire ending in a few spines forming a Maltese cross when viewed from above ..... ***Halodeima*** **PEARSON, 1914**

4'. Table with well developed spinose disc; it's rim often turned to give a 'cup and saucer' appearance to the table in lateral view ..... ***Acanthotrapeza*** **ROWE, 1969**

5. Table disc usually squarish or octogonal in outline, perforated by a large centrally placed cruciform hole and a variable number of regular peripheral holes; buttons present ..... ***Stauropora*** **ROWE, 1969**

5'. Tables variously developed, disc never perforated by a large centrally-placed cruciform hole ... **6**

6. Buttons of the body wall knobbed or rugose **7**

6'. Buttons of the body wall generally smooth **10**

7. Squat-or tack like tables usually present. **8**

7'. Tables never squat or tack-like, always very robust **9**

8. Tables squat-like; disc usually knobbed; buttons simple with large regularly or irregularly arranged knobs ..... ***Cystipus*** **HAACKE, 1880**

8'. Tack-like tables usually present; table disc spinose, slightly knobbed ..... ***Theelothuria*** **DEICHMANN, 1958**

9. Table disc smooth, spire variable in length terminating in a dense crown of spines; buttons mostly modified into hollow fenestrated ellipsoids, some simple knobbed buttons may also be present. .... ***Microthele*** **BRANDT, 1835**

9'. Buttons never modified into spheres; buttons simple with moderate-sized irregularly arranged knobs and 3-6 pairs of relatively large holes ..... ***Metriatyla*** **ROWE, 1969**

10. Table disc smooth, buttons smooth, regular in outline **11**

10'. Table disc spinose; buttons generally more irregular, often twisted **12**

11. Buttons without optical discontinuity ..... ***Thymiosycia*** **PEARSON, 1914**

11'. Buttons very thin; with optical discontinuity ..... ***Platyperona*** **ROWE, 1969**

12. Tables stellate; buttons twisted; longitudinal muscles without ossicles whatsoever ..... ***Lessonothuria*** **DEICHMANN, 1958**

12'. Tables poorly developed; buttons irregular, perforated by 3-6 pairs of holes; ventral tube feet with rods, buttons and wide plates; longitudinal muscles with rods, buttons and oblong rings ..... ***Mertensiothuria*** **DEICHMANN, 1958**

Subgenus *Acanthotrapeza* ROWE, 1969

Diagnosis - (See ROWE 1969: 138) [Type-species: *Holothuria pyxis* SELENKA, 1867 by original designation].

Four species are currently recognized as being valid: *Holothuria (Acanthotrapeza) coluber* SEMPER, 1868; *H. (A.) kubaryi* LUDWIG, 1875[4]; *H. (A.) pyxis* SELENKA, 1867 and *H. (A.) tripilata* MASSIN, 1987.

[4] F.W.E. ROWE (pers. comm.) remarks that *H. (A.) kubaryi* might be a synonym of *H. (Cystipus) rigida* (SELENKA, 1867).

Table five gives the only record (*H. (A.) pyxis*) within the subgenus *Acanthotrapeza* that is known to occur in the shallow-waters of the WIO. I hesitate in placing this species between the WIO records, because LEVIN's (1979) record from Mombasa (see also fig. 53C) is hard to verify since the mention of the species is without description and without drawings. Moreover, the species has not been recorded from the western side of the Indian Ocean (CLARK & ROWE 1971) prior to LEVIN's (1979) observation. For completeness, it must be noted that CONAND (1999) mentions *H. (A.) coluber* SEMPER, 1868 from the South East Indian Ocean. However, as the distribution map of MASSIN (1999: fig 12, p. 19) gives a rather narrow East Indo-West Pacific Ocean distribution for this species, it is not considered here.

Current Species Name	Known WIO Distribution	Reference
H. (Acanthotrapeza) pyxis SELENKA, 1867	Mombasa	LEVIN 1979

Table 5- *Holothuria (Acanthotrapeza) pyxis* SELENKA, 1867, the only species within *Acanthotrapeza* known to occur in the shallow-waters of the WIO.

Subgenus *Cystipus* Haacke, 1880

Diagnosis (after ROWE 1969: 155) - [Type-species: *Cystipus pleuripus* HAACKE, 1880 (= *Stichopus rigidus* SELENKA, 1867) by original designation]
Size variable, usually moderate, sometimes up to 200 mm long; body usually vermiform in shape; tube feet in the ventral area restrained more or less to the ambulacral areas; small papillae evenly distributed dorsally; mouth ventral, surrounded by twenty tentacles; calcareous ring well-developed with radial pieces about twice as long as the interradial pieces; anus terminal; body wall thin but rough to the touch. Ossicles: body wall presents tables with large, regularly knobbed disc and low spiny spire; buttons with four to six holes, regularly knobbed, often with a distinct knob at the median extremities of the buttons; ventral tube feet with elongated smooth buttons; dorsal papillae with centrally enlarged plates.
Eleven species are currently recognized as being valid: *Holothuria (Cystipus) cubana* LUDWIG, 1875; *H. (C.) dura* CHERBONNIER & FÉRAL, 1981; *H. (C.) inhabilis* SELENKA, 1867; *H. (C). jousseaumei* CHERBONNIER, 1955; *H. (C.) mammosa* CERBONNIER, 1988; *H. (C.) occidentalis* LUDWIG, 1875; *H. (C.) pseudofossor* DEICHMANN, 1930; *H. (C.) rigida* (SELENKA, 1867); *H. (C.) sucosa* ERWE, 1919; *H. (C.) sulcata* LUDWIG, 1875; *H. (C.) turrisimperfecta* CHERBONNIER, 1964.
It must, however, be stressed that this subgenus is in critical need of review. ROWE's (1969) notes on *H. rigida* (compared to *H. cubana, H. inhabilis, H. jousseaumei,* and *H. pseudofossor*), in combination with CHERBONNIER's observations (1988) on *H. rigida, H. cubana* and *H. inhabilis* might serve as a guide to establish synonyms in this ill-studied group. In this context, it is noteworthy that (i) *H. cubana, H. jousseaumei* and *H. rigida* are the only ones in *Cystipus* which present hollow fenestrated spheres, (ii) ROWE (1969, partially based on DEICHMANN 1958) suspects that *H. rigida* & *H. jousseaumei* and *H. pseudofossor* & *H. inhabilis* might be conspecific[5]; (iii) CHERBONNIER (1988) observed that SELENKA's (1867) description of *H. rigida* was based upon specimens originating from Zanzibar, Society Islands and Florida even as the ones from the latter locality are most probably conspecific with *H. cubana* (= *H. fossor* DEICHMANN, 1926 according to DEICHMANN 1958 and CHERBONNIER 1988); (iv) CHERBONNIER (1988) suspects that *H. inhabilis* from the Society and Hawaiian Islands are conspecific with *H. rigida.*

Holothuria (Cystipus) rigida (SELENKA, 1867)
(fig. 12A-E, fig. 52D, pl. 2C)

Stichopus rigidus SELENKA, 1867: 317, pl. 18, figs. 30-31 (*partim*).
Stichopus rigidus; DANIEL & HALDER 1974: 423.
Holothuria rigida; SEMPER 1868: 79; SEMPER 1869: 120; LAMPERT 1885: 76; THÉEL 1886: 231; DANIEL & HALDER 1974: 427; HICKMAN 1998: 55 (colour picture).
Cystipus rigidus HAACKE, 1880: 47.
Holothuria pleuripus; DANIEL & HALDER 1974: 423.
Holothuria (Cystipus) rigida; HUGHES & GAMBLE 1977: 355; SLOAN *et al.* 1979: 121; PRICE 1981: 9; TAN TIU 1981: 81, 109 pl.23; PRICE 1982: 10; PRICE 1983: 89; A.M. CLARK 1984: 99; CANNON & SILVER 1986: 22, figs 3e, 6b (colour drawing); PRICE & REID 1985: 4; FÉRAL & CHERBONNIER 1986: 80 (colour picture), 81; CHERBONNIER 1988: 126 (synonymy);

[5] Examination of *H. (C.) jousseaumei* specimens from the Seychelles deposited in the MRAC showed that the species is definitely valid.

MUKHOPADHYAY 1991: 413; ROWE & GATES 1995:290; LANE *et al.* 2000: 488; SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 21, pl. 1H (colour picture).
Holothuria (Cystipus) rigida?; ARAKAKI & FAGOONEE 1996: 122.

Status and location type - Lectotype MCZ 694 (ROWE & GATES 1995).

Type locality - Society Islands.

Material examined - KKiun/9948 (one specimen).

General Description - Medium sized species, 125 mm long and 25 mm wide after preservation. Body colour in life white to yellow ventrally and somewhat lighter dorsally (pl. 2C). Body wall thin but gritty to the touch. Mouth ventral, surrounded by 20 small, yellowish brown tentacles. Anus terminal, surrounded by conical papillae. Tube feet in trivium evenly distributed in radial and interradial areas; conical papillae in bivium in radial areas only. Cuvierian tubules absent. Calcareous ring with radial pieces twice the size of the interradials; radial plate with a large central notch anteriorly, interradial plate toothed anteriorly (see CHERBONNIER 1988: 127, fig. 51L)
Ossicles: Tentacles with spinose rods, up to 180 µm long (fig 12A). Ventral and dorsal body wall with similar tables and buttons (fig. 12B). Tables (fig.12B): disc knobbed at the periphery, perforated by up to 18 holes, up to 100 µm across; pillars short, united by no or a single cross beam, ending in a narrow crown of spines. Buttons (fig. 12C): knobbed regularly, often with a characteristic terminal knob at the median extremities. Ventral tube feet with elongated buttons and narrow plates (fig 12D) in addition to tables that are less developed as those from the body wall. Dorsal papillae with rods and rod-like plates up to 200 µm long (fig 12E).

Diagnosis - See CHERBONNIER 1988: 126-129, fig.51.

Ecology - Eulittoral species, in Kenya found in shallow water; H.L. CLARK (1946) reports *Holothuria rigida* from the Great Barrier Reef at depths of 20 m. Burrows under coral rubble.

Distribution in the study region - Kiunga Marine Reserve (See SAMYN & VANDEN BERGHE, 2000).

Geographic distribution - Indo Pacific Ocean, with the Red Sea and the Persian Gulf (CLARK & ROWE 1971; CHERBONNIER 1988). SELENKA (1867), SEMPER (1868), LAMPERT (1885) and THÉEL (1886) also reported the species from Florida; but these records are probably misidentified *H. (C.) cubana* LUDWIG, 1875. Figure 52D gives the kown WIO distribution in detail.

Remarks - H.L. CLARK (1946) noted that it was recognized long ago that several species [*i.e. H. rigida* (SELENKA, 1867) (based on SEMPER's (1868) figures) and *H. inhabilis* SELENKA, 1867] were included under SELENKA's types of *Stichopus rigidus* (see also DEICHMANN 1958: 321). In the original description of *Stichopus rigidus,* SELENKA (1867: 317) described Cuvierian tubules ('am Grunde des rechten Lungesbaumes Cuvier'sche Organe in Büscheln, deren Schläuche getheilt sind' [Sic.]), although it is not certain on which specimen(s) SELENKA based his description. It is interesting to note, that in the same paper, SELENKA (1867: 333) described *H. inhabilis* that apparently has no Cuvierian tubules ('Cuvier'sche Organe nicht gesehen' [Sic.]). In 1946, H.L. CLARK stated that the specific status of *H. inhabilis* and *H. rigida* may be open to question but that 'in my [his] opinion they are distinct and can be told apart by the tables, though each species may have atrophied or hypertrophied tables resembling those normal to the other [Sic.]', an opinion that subsequently was magnified by DEICHMANN (1958) who created the genus *Fossothuria* for *rigida* and the genus *Jaegerothuria* for *inhabilis*. ROWE (1969: 156, 157) emended this generic division and put *Fossothuria* and *Jaegerothuria* as synonyms of *Cystipus* HAACKE, 1880; a name available under the rules of the Code (A.M. CLARK & ROWE 1967). Even though ROWE (1969) puts a different taxonomic weight to the species, he kept them apart without to much doubt. In my interpretation of ROWE's writing, this division was mainly based on distribution (Indo-Pacific for *H. rigida*, while East Indies, Pacific and Panamic for *H. inhabilis*) rather than on morphological criteria. A different view to this problem came from CHERBONNIER (1988) who stated that SELENKA's (1867) type series included *H. rigida* specimens (with Indo-Pacific distribution) and *H. cubana* LUDWIG, 1875 (with eastern Atlantic distribution). In addition, CHERBONNIER (1988) put forward the hypothesis (without testing it) that *H. inhabilis* and *H. rigida* might be conspecific for SELENKA (1867) might have missed the presence of Cuvierian tubules in the former. The one specimen, currently at my disposition fits well with the available descriptions of *H. (C.) rigida*, even though I fail to report Cuvierian tubules.
In conclusion, it is clear that only an in depth examination of the type material of *H. inhabilis* (which, according to SELENKA'S description, does not present Cuvierian tubules) compared to the type material of

H. rigida will bring certainty to this matter. As up to-date, only *H. (C.) rigida* has been reported from the WIO, I believe a conservative attitude is best, and identify the present specimen as *H. (C.) rigida.*

Holothuria (Cystipus) cf. *rigida* (SELENKA, 1867)
(fig. 13A-J, pl. 2D)

Status and location type - See *H. (Cystipus) rigida.*

Type locality - See *H. (Cystipus) rigida.*

Material examined - KCi/9760 (one specimen).

General Description - The single specimen at our disposition is in very bad shape; completely eviscerated apart from the right respiratory tree that reaches almost to the buccal side of the animal. Calcareous ring and tentacles have been cut out. Medium sized species, 200 mm long and 54 mm wide after preservation. Body colour in life white dorsally and orange ventrally (pl. 2D); posterior side with a wide (3 cm) white ring. Body wall 3 mm thick, gritty to the touch. Mouth ventral, surrounded by 15(?) small tentacles, white at base, yellowish distally. Anus terminal, surrounded by five white uncalcified conical papillae. Tube feet in trivium distributed in radial areas; tube feet in bivium very sparsely spread without order over the total surface. Presence of Cuvierian tubules could not be ascerted as only the right respiratory tree remains). Number of Polian vesicle(s) and stone canal(s) not determinable. Calcareous ring similar as the one descriped for *H. (C.) rigida.*
Ossicles: Tentacles with spinose rods up to 200 µm long (fig 13A). Ventral and dorsal body wall with similar tables and buttons (fig. 13B-E). Tables numerous, rim of disc undulating to spiny, disc often knobbed at the edge, 60-75 µm across, perforated by four central and few peripheral holes, pillars short (no cross beam) ending in a spiny crown (fig. 13B, E). Buttons very numerous, three to five pairs of small holes, knobbed at the rim and in the center, 55-110 µm long; occasionally some unknobbed plate-like rods also present (fig. 13C, D). Dorsal tube feet with tables and buttons similar to the ones of the body wall, oblong or pear-shaped plates, 100-150 µm long (fig. 13G), and perforated rods, up to 210 µm long (fig. 13F). Ventral tube feet with buttons and tables similar to the ones from the body wall; rods, 115-220 µm long, curved to straight, with or without median thickening and perforations (fig. 13H) and plate-like buttons (fig.13J)

Diagnosis - See *H. (Cystipus) rigida.*

Ecology - Unknown.

Distribution in the study region - Chale Island only.

Geographic distribution - See *H. (Cystipus) rigida.*

Remarks - The gritty touch of the body wall, the absence of a collar of papillae around the base of the tentacles, the tables with knobbed disc and low spire and none to a single cross beam, and the immensity of large-size knobs on the buttons, perforated by three to five small holes, are characters reminiscent of the subgenus *Cystipus.* However, as we have only one, poorly preserved, specimen at our disposition, identification to the species level is difficult. The regular arrangement of the knobs on the buttons, the knobbed table discs and the low spire presented by the specimen under study, bears closest resemblance to *H. (C.) rigida.* However, it differs from the specimen described above by its colouration, the thickness of the body wall and the presence of pear-shaped plates in the dorsal tube feet (see also remarks with the previous species).

Table six gives the other species in the holothurian subgenus *Cystipus* that are known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known distribution in the WIO, while column three provides the reference wherein the record(s) appeared. DANIEL & HALDER (1974) put *H. (Cystipus) occidentalis* LUDWIG, 1875 between the species from the South-West Indian Ocean (locality mentionned is E. coast of Africa); however, I cannot agree with this locality for this species is known only from the Atlantic Ocean (see LUDWIG 1875; THÉEL 1886; DEICHMANN 1930; PANNING 1935d). It seems that DANIEL & HALDER (1974) have confused the ancient name "West Indies" (*i.e.* Carribean and the North Coast of South America) with West Indian. PRICE's (1982) record of *H. (C.) inhabilis* SELENKA, 1867 from South East Arabia is likewise not considered in the present study for this species is only known from the tropical, east and west central Pacific Ocean (ROWE &

GATES 1995). To add to the confusion CLARK & ROWE (1971) mention VANEY's (1905) paper for records from S.E. Arabia. However, VANEY (1905) dealt with the holothurians of Djibouti (côte Française des Somalis), whereby *H. (C.) inhabilis* was not mentionned.

Current Species Name	Known WIO Distribution	Reference(s)
H. (Cystipus) jousseaumei CHERBONNIER, 1954 (see also discussion)	Gulf of Aden (Djibouti)	CHERBONNIER 1954a; 1955
	Red Sea (Entedebir)	CHERBONNIER 1954a; 1955; 1967; DANIEL & HALDER 1974
	Gulf of Aqaba (Aqaba)	TORTONESE 1977
	Seychelles (Mahé)	MRAC record (pers. observ.)
	Madagascar (Nosy Bé)	CHERBONNIER 1988
H. (Cystipus) mammosa CHERBONNIER, 1988	Red Sea (Massaua, Entedebir Isl.)	TORTONESE 1936a[1]; CLARK & ROWE 1971
H. (Cystipus) sucosa Erwe, 1919 (see also discussion)	Gulf of Suez (Gimsay Bay, Tor)	HELFER 1912[2]; ERWE 1919; PRICE 1982
	Gulf of Aqaba (Dahab, Aqaba)	A.M. CLARK 1952; TORTONESE 1977; DANIEL & HALDER 1974; PRICE 1982

Table 6 - Other species within the holothurian subgenus *Cystipus* known to occur in the shallow-waters of the WIO. [1] Cited as *Holothuria ocellata* JÄGER; [2] as *Cucumaria hartmeyeri* HELFER.

Subgenus *Halodeima* PEARSON, 1914

Diagnosis (after ROWE 1969: 137-138) - [Type-species: *Holothuria atra* JAEGER, 1833 by original designation].
Size moderate to large, up to 350 mm long; body elongated, as good as cylindrical; tube feet distributed over the total body surface, more numerous on the ventral side than on the dorsal side, mostly not clearly arranged in rows; mouth ventral surrounded by twenty tentacles; calcareous ring stout, radial pieces up to three times the length of the interradial pieces; anus dorso-terminal. Ossicles consist of tables with reduced, sometimes spiny disc, moderate or high spire, forming a Maltese cross when viewed from above, rosettes, plates and pseudo-plates. Large flattened or spinose rods are never present in the body wall.
Eleven species are currently recognized as being valid: *Holothuria (Halodeima) atra* JAEGER, 1833; *H. (H.) chilensis* SEMPER, 1868; *H. (H.) edulis* LESSON, 1830; *H. (H.) floridana* POURTALÉS, 1851; *H. (H.) grisea* SELENKA, 1867; *H. (H.) kefersteinii* (SELENKA, 1867); *H. (H.) manningi* PAWSON, 1978; H. *(H.) mexicana* LUDWIG, 1874; *H. (H.) pulla* SELENKA, 1867, *H. (H.) signata* LUDWIG, 1875 and *H. (H.) stocki* CHERBONNIER, 1964. Two other species: *H. dicorona* HEDING, 1934 and *H. pseudoimitans* CHERBONNIER, 1951 are also listed under *Halodeima* (SMILEY & PAWSON unpublished manuscript), but the taxonomic position of these is *terra incognita* to me. *H. (H.) atra, H. (H.) edulis, H. (H.) floridana* and *H. (H.) pulla* are reported from the western Indian Ocean; but as the identification or the validity of the latter two species is doubtful only *H. (H.) atra* and *H. (H.) edulis* are keyed hereunder.

Key to the species of Kenya (with Pemba Island).

1. Body colour in life completely black. Tables: disc small; rim smooth, sometimes spiny; perforated by four central and four peripheral holes. Rosettes mostly incomplete, with two to four holes. Tube feet with tables with spire very reduced, simple rosettes and large pseudo-plates ..... ***Holothuria (Halodeima) atra* JAEGER, 1833**

1'. Body colour in life chocolate brown to dark-grey dorsally; salmon pink to red ventrally.. Tables: disc perforated by one central hole. Button-like rosettes, with up to ten holes. Tube feet without tables, with rods, large pseudobuttons and large perforated plates ..... ***Holothuria (Halodeima) edulis* LESSON, 1830**

Holothuria (Halodeima) atra JAEGER, 1833
(fig. 14A-D, fig. 52E, pl. 2E)

Holothuria atra JAEGER, 1833: 22; TORTONESE 1936b: 13; TORTONESE 1953a: 40; KALK 1954: 113 (from THANDAR 1984); KALK 1958: 216; MACNAE & KALK 1958: 43, 99, 101, 104, 107, 130 (from THANDAR 1984); KALK 1959: 5; MACNAE & KALK 1962: 108, 112, 118; CHERBONNIER 1963: 5; CHERBONNIER 1967: 56; DANIEL & HALDER 1974: 428; BRANCH & BRANCH 1981: 248 (from THANDAR 1984); HICKMAN 1998: 45 (colour plates); BRANCH *et al.* 1999: 204; CONAND 1999: 10, 12; MARSHALL *et al.* 2001: 46 (tab. 29), 47, 58 (tab. 37).
Holothuria atra ambonensis THÉEL, 1886; DANIEL & HALDER 1974: 423.

Halodeima atra; HEDING 1940a: 113; A.M. CLARK 1952: 204; CHERBONNIER 1979a: 861; CONAND 1999: 10, 12, 18, 39, pl. 2 (colour picture).

Holothuria (Halodeima) atra; MUKHOPADHYAY 1991: 404, 413; ARAKAKI & FAGOONEE 1996: 122; MASSIN 1999: 20 (synonymy and records before 1999), fig. 13 (distribution); SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 488; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 22, 23 (tab. 5).

Holothuria floridana; SELENKA 1867: 324 (non *H. floridana* POURTALES); DANIEL & HALDER 1974: 423 (non *H. floridana* POURTALES).

Status and location type - Status and whereabouts undetermined (ROWE & GATES 1995).

Type locality - Sulawesi (as Celebes), Indonesia.

Material examined - KKiun/9929 (one specimen); KKiun/9930 (five specimens); KKan/9705 (one specimen); KKan/9706 (one specimen); KKan/9707 (one specimen); KCi/9747 (one specimen); KCi/9748 (one specimen); KShar/9733 (one specimen); KMom/9825 (one specimen); KMal/9883 (one specimen); TFun/9826 (one specimen); TFun/9827 (one specimen).

General description - Body cylindrical, up to 300 mm long and 70 mm wide, after preservation. Body colouration after preservation similar to colour in life: uniform black (pl. 2E). Body wall relatively thin, smooth, often covered with fine sand, leaving bare some isolated patches. Mouth ventral, surrounded by 20 short, black tentacles. Anus terminal, unguarded. Ventral tube feet, short, black, distributed in radial and interradial areas; dorsal tube feet short, black, distributed over the total surface. Cuvierian tubules absent. Several stone canals (8-10) positionned in two clusters. Several Polian vesicles of which one or two are markedly longer. Calcareous ring stout with the radial pieces three times as long as the interradial pieces (see CHERBONNIER 1988: 74, fig. 28J).

Ossicles: Tentacles with simple rods (fig. 14A). Ventral and dorsal body wall with similar tables and rosettes. Tables from the ventral body wall with a larger, more spinose disc then tables from the dorsal body wall (fig. 14B, C). Table disc perforated by four central and four peripheral holes, with high spire ending in a Maltese cross (fig. 14B). Rosettes simple, more numerous in the dorsal then the ventral body wall, 20-25 µm long. (fig.14C). Tube feet with pseudo-plates, 75-100 µm long, and rosettes of similar size as those presented in the body wall (fig. 14D).

Diagnosis - See JAEGER 1833: 22; PANNING 1935a: 30, fig. 22a-f.

Ecology - *H. (H.) atra* can be found on sandy patches within the shallow reef flat or in seagrass beds; highest densities however on reef flats. MACNAE & KALK (1962) and ROWE & RICHMOND (1997) note that *H. (H.) atra* lives commensal with the polychaete *Gastrolepidia clavigera* (SCHMARDA).

Distribution in the study region - Found in large numbers in virtually all the localities visited, making it one of the most abundant holothurians from the study region.

Geographic distribution - Very well known species from the tropical and subtropical Indo-Pacific (with the Red Sea and the Persian Gulf). The distribution map as drawn by MASSIN (1999: 21, fig. 13) gives the global distrubution, but the following localities have to be added: Gulf of Suez (SEMPER 1868; 1869, as *Holothuria maxima* FORSKÅL, 1757; LAMPERT 1885, as *H. maxima*; CHERBONNIER 1955, as *Halodeima atra* JAEGER, 1833; PRICE 1982); Eritrea, Assab (LUDWIG 1886; MITSIKURI 1912), Dobar Island (TORTONESE 1936b), Nocra Island (TORTONESE 1953a), Harmil and Entedebir (CHERBONNIER 1967, as *Halodeima atra*); Gulf of Aden, Djibouti (CHERBONNIER 1955, as *Halodeima atra*); Madagascar, Ile St. Marie and Tuléar (CHERBONNIER 1988); La Réunion (CONAND 1999) and southern Mozambique, Inhaca (KALK 1958; THANDAR 1984; MRAC record pers. observ.). Fig. 52E shows the known distribution in the WIO in detail.

Holothuria (Halodeima) edulis LESSON, 1830
(fig. 15A-E, fig. 52F, pl. 2F)

Holothuria edulis LESSON, 1830: 125, pl. 46, fig. 2; MACNAE & KALK 1962: 108; DANIEL & HALDER 1974: 428; WEINBERG 1997: 245 (colour picture); CONAND 1999: 10, 12, 18, 39, pl. 2 (colour picture); MARSHALL *et al.* 2001: 46 (tab. 29), 47, 54.

Halodeima edulis; CHERBONNIER 1963: 5; CHERBONNIER 1979a: 861.

Holothuria (Halodeima) edulis; PRICE 1981: 9; MASSIN 1999: 21 (synonymy and records before 1999), figs. 14 (distribution), 110d (colour picture); SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 488; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 22.

Status and location type - Holotype, MNHNP (number not given) (ROWE & GATES, 1995).

Type locality - Moluccas Islands, Indonesia.

Material examined - TFun/9801 (one specimen); TFun/9802 (one specimen); KKiun/9931 (one specimen).

General description - Medium to large species; preserved specimens up to 300 mm long and 50 mm wide. Body elongated and slender; somewhat wrinkled in alcohol. Body colour in life: dorsally marked with large chocolate brown to dark-grey patches (pl. 2F); ventrally, salmon pink to red. Body colour in alcohol: grey-brown dorsally and grey-white ventrally. Body wall 3-5 mm thick, more rough to the touch then *H. (Halodeima) atra.* Mouth ventral, surrounded by 20 yellow to light-pink tentacles. Anus dorso-terminal, unguarded by teeth or papillae, fringed by a dark-pink circle. Trivium covered by short tube feet, scattered over both ambulacral and interambulacral areas. Bivium with few tube feet distributed over the total area. Cuvierian tubules absent. Calcareous ring with very large radial pieces, up to three times as wide as the pointed interradial pieces (see CHERBONNIER 1988: 76, fig. 29I).

Ossicles: Tentacles with well-developed rods, up to 180 µm long, spiny at the extremities (fig. 15A). Body wall with tables and button-like rosettes, similar in size and shape ventrally and dorsally (fig. 15B, C). Tables with disc strongly reduced, four pillars united by a single cross beam, pillars ending in four points each forming a Maltese cross (fig. 15B, C). Button-like rosettes, perforated by 4-10 uneven holes, 30-70 µm long, rim of rosettes irregular, (fig. 15B, C). Ventral tube feet with plates, 100-140 µm long, and rods (fig. 15D). Dorsal tube feet with large rods (fig. 15E).

Diagnosis - See PANNING 1935a: 30, fig. 36a-d.

Ecology - *H. (Halodeima) edulis* is found up to 29 m depth, on sand or coral rubble, often partially hidden under coral.

Distribution in the study region - Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000); Watamu; Mombasa; Gazi Bay; Fundu.

Geographic distribution - Similar to *H. (Halodeima) atra*, but not recorded on the eastern side of the Indo-Pacific barrier. For global distribution, see also map as drawn by MASSIN (1999: 22, fig. 14), but note that the following localities have to be added in the shallow-waters of the WIO: Gulf of Suez, Shab Mahmoud (CHERBONNIER 1955, as *Halodeima edulis* (LESSON, 1830)) (see also ERWE 1919; PRICE 1982 for unspecified localities from the Gulf of Suez); Gulf of Aqaba, Eilat (CHERBONNIER 1963; 1967, as *Halodeima edulis*), Aqaba (TORTONESE 1977; CHERBONNIER 1979a, as *Halodeima edulis*), Dahab (A.M. CLARK 1952; CHERBONNIER 1955; both as *Halodeima edulis*), Abu Zabad (A.M. CLARK 1952, as *Halodeima edulis*) (see also DANIEL & HALDER 1974; PRICE 1982 for unspecified localities from the Gulf of Aqaba); Eritrea, Entedebir (CHERBONNIER 1967, as *Halodeima edulis*); Kenya, Mombasa, Chale Island, Watamu Marine Park (this work), Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000); Tanzania, Fundu (this work); southern Mozambique, Inhaca (THANDAR 1984; MRAC record pers. observ.) and Madagascar, Tuléar (CHERBONNIER 1988). Figure 52F shows the known distribution in the WIO in detail.

Table seven gives another species within the subgenus *Halodeima* that is known to occur in the shallow waters of the WIO, but that for now has not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record appeared. It should however be noted that *H. (H.) pulla* seems to differ from *H. (H.) atra* only by having Cuvierian tubules. However, SELENKA'S (1867) description of the Cuvierian tubules [Cuvier'sche Organen blinddarmförmig, rothbraun] could as well refer to a part of the respiratory tree. Unfortunately, the type specimen of *H. (H.) pulla* is currently untraceable as the labels of the specimens in the collection of the ZMG have turned unreadable due to a flooding accident (HAUDE pers. comm.). *H. (H.) floridana* was reported from Zanzibar by SELENKA (1867) and by DANIEL & HALDER (1974); ROWE (1969) gives West Indian as distribution. THANDAR (1984) regards *H. (H.) floridana* as a synonym of *H. (H.) mexicana.* For the latter species ROWE (1969) again gives a West Indian distribution, while THANDAR (1984) states that it has a tropical West Atlantic distribution and that it would be best not to consider it as belonging to the fauna of eastern Africa. HENDLER *et al.* (1995) on the other hand list *H. floridana* as a valid species from the Carribean. Be as it may; as I have not seen type material of *H. mexicana* or *H. floridana*, I am not in a position to judge on the status of these species, but I believe the specimens from Zanzibar are nothing but misidentified individuals of *H. atra.*

Current Species Name	Known WIO Distribution	Reference(s)
H. (Halodeima) pulla SELENKA, 1867	Indo-Pacific (unspecified) East coast of Africa (unspecified) ?Mozambique	PANNING 1944 DANIEL & HALDER 1974 LAMPERT 1885[1]; BELL 1884; THANDAR 1984

Table 7 - *Holothuria (Halodeima) pulla* SELENKA, 1867, the third species within *Halodeima* known to occur in the shallow-waters of the WIO. The validity of this species remains however debatable (synonym of *H. (Halodeima) atra*?). Cited as [1] *Holothuria aethiops* BRANDT.

Subgenus *Holothuria* LINNAEUS, 1767

Diagnosis - (see Rowe 1969: 133) [Type-species: *Holothuria tubulosa* GMELIN, 1790; validated opinion 80, 1924: 17-18]

Eight species are currently recognized as being valid: *Holothuria (Holothuria) caparti* CHERBONNIER, 1965; *H. (H.) dakarensis* PANNING, 1939; *H. (H.) fungosa* HELFER, 1912; *H. (H.) helleri* VON MARENELLER, 1877; *H. (H.) mammata* GRUBE, 1840; *H. (H.) massaspicula* CHERBONNIER, 1954; *H. (H.) stellati* DELLE CHIAJE, 1823; *H. (H.) tubulosa* GMELIN, 1790. ROWE (pers. comm.) suspects that *H. (H.) massaspicula* is a junior synonym of *H. (H.) fungosa*; as I have not been able to study any of these species, I refrain from commenting on this point of view.

Table eight gives the only records within the subgenus *Holothuria* that are known to occur in the shallow-waters of the WIO, but have *hitherto* not been reported in Kenya (with Pemba Island). Column two gives the known distribution in the WIO, while column three provides the reference wherein the record appeared. The subgenus is here included for completeness only.

Current Species Name	Known WIO Distribution	Reference(s)
H. (Holothuria) fungosa HELFER, 1912	Gulf of Suez (Um el Jerman)	HELFER 1912; ERWE 1919; DANIEL & HALDER 1974; PRICE 1982
H. (Holothuria) massaspicula CHERBONNIER, 1954	Red Sea (unspecified) Gulf of Suez (Suez)	ERWE 1919[1]; DANIEL & HALDER 1974 CHERBONNIER 1954a; 1955; PRICE 1982

Table 8 - Other species within the holothurian subgenus *Holothuria* known to occur in the WIO. The validity of *H. (H.) massaspicula* remains however debatable (synonym of *H. (H.) fungosa*?). Cited as [1] *Holothuria tubulosa* GMELIN.

Subgenus *Lessonothuria* DEICHMANN, 1958

Diagnosis - (after ROWE, 1969: 149) [Type species: *Holothuria pardalis* SELENKA, 1867 by original designation]

Small to moderate species, cylindrical body reaching lengths up to 150 mm; tube feet and papillae more or less irregularly arranged in both trivium and bivium; 17-30 tentacles fringed by a collar of conical papillae; anus terminal, mostly guarded by some kind of papillae; calcareous ring relatively well developed with the radial pieces about twice as long as the interradial pieces. Ossicles comprise tables with smooth or toothed disc, spire of moderate height, ending in a narrow spiny ring; smooth buttons and pseudobuttons abundantly present.

Ten species are currently recognized as being valid: *Holothuria (Lessonothuria) cavans* MASSIN, 1996; *H. (L.) cumulus* CLARK, 1921; *H. (L.) duoturricula* CHERBONNIER, 1988; *H. (L.) glandifera* CHERBONNIER, 1955; *H. (L.) hawaiiensis* FISHER, 1907; *H. (L.) insignis* LUDWIG, 1875; *H. (L.) lineata* LUDWIG, 1875; *H. (L.) multipilula* L. YULIN, 1975; *H. (L.) pardalis* SELENKA, 1867 and *H. (L.) verrucosa* SELENKA, 1867. Only *H. (L.) pardalis* and *H. (L.) verrucosa* are present in Kenya (with Pemba Island), they are keyed hereunder.

Key to the species of Kenya (with Pemba island).

1. 17-20 Tentacles. Buttons and pseudobuttons of the body wall rather regular, smooth, perforated by four to ten holes.. ..... ***Holothuria (Lessonothuria) pardalis* SELENKA, 1867**

2. More than 20 Tentacles. Buttons and pseudobuttons very irregular, often knobbed, perforated by two to five pairs of holes often reduced to one row of holes. . . . . ***Holothuria (Lessonothuria) verrucosa* SELENKA, 1867**

Holothuria (Lessonothuria) pardalis SELENKA, 1867
(fig. 16A-F, fig. 52G, pl. 2G)

Holothuria pardalis SELENKA, 1867: 336, pl. 19 fig. 85 (partim); PEARSON 1910: 179 (non *H. lineata* LUDWIG); KALK 1958: 212; JAMES & PEARSE 1969: 106; DANIEL & HALDER 1974: 428; HUGHES & GAMBLE 1977: 335, 336, 337, 338, 355; HICKMAN 1998: 48 (colour plates).

Holothuria (Lessonothuria) pardalis; MUKHOPADHYAY 1991: 404; MASSIN 1999: 25 (synonymy and records before 1999), fig. 19 (distribution); SAMYN 2000: 15, tab. 1; LANE *et al.* 2000: 488; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 23.

Status and location type - SELENKA (1867) did not select a holotype in the series he had before him, ROWE (*in* ROWE & GATES 1995) could not establish presence of any of SELENKA's specimens in Germany, thus decided to select a specimen from the MCZ (N°677 partim; includes six specimens which are *H. (Lessonothuria) lineata*) as lectotype; as paralectotypes the four specimens belonging to vial MCZ 676 were chosen. These specimens now define *H. (L.) pardalis* SELENKA, 1867.

Type locality - Hawaiian Islands.

Material examined - KKiun/9934 (one specimen); KKiun/9935 (one specimen); KKiun/9936 (one specimen); KKiun/9937 (one specimen).

General description - Small to moderate species, up to 100 mm long and 40 mm wide after preservation; cylindrical in shape. Dorsal body wall white-yellow, with two rows of conspicuous dark areas and with copious small yellow areas giving the animal a speckled appearance (pl. 2G); ventral side lighter in colouration. Body wall only few mm thick. Rough bivium clearly separated from the smoother trivium. Mouth ventral to terminal, surrounded by 17-20 tentacles, fringed at their base by long conical papillae. Anus terminal, surrounded by conical papillae. Bivium with small homogeneously spread papillae, that are more numerous at the posterior side. Trivium with long tube feet in the radial areas (two to three rows laterally; four to five rows in the median area), however with some spreading into the interambulacral areas. Cuvierian tubules absent. Two Polian vesicles. Single stone canal. Calcareous ring slender with radial pieces three times as wide as the interradial pieces, the radial plates have a deep anterior notch (see MASSIN 1999: 26, fig. 18a).

Ossicles: Ventral and dorsal body wall with similar tables and buttons (fig 16A-D). Tables: rim of disc smooth, undulating or toothed, 50-80 µm across, perforated by four, large central holes and four to twelve peripheral holes; spire low to high, narrow, ending in a small spiny crown. Buttons 40-70 µm long, smooth, with three to ten holes (fig 16A-D). Ventral tube feet with large plates up to 150 µm long (fig. 16E, F), in addition to tables and buttons similar to those of the body wall (fig. 16G). In the dorsal papillae large rods perforated at the extremities and plates, buttons and tables similar to those of the ventral tube feet (fig. 16H, J). Tentacles with rods up to 180 µm (fig. 16K)

Diagnosis - See PANNING 1935d: 3, fig. 106a-x.

Ecology - Species known from shallow water; hiding its total body under coral debris and under dead coral blocks.

Distribution in the study region - Mombasa, Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000); Mombasa.

Geographic Distribution - Very well known species from the tropical and subtropical Indo-Pacific Ocean with the Red Sea (and possibly the Persian Gulf) as is shown on the global distribution map drawn by MASSIN (1999: 27, fig. 19). In the shallow-waters of the WIO the following localities have to be added to this map: Gulf of Suez, Tor (HELFER 1912; CHERBONNIER 1967), Ras el Millan (HELFER 1913, as *Holothuria tenuicornis* HELFER, 1913), Shab Suleim (CHERBONNIER 1955), Wadi el Dom (JAMES 1969; JAMES & PEARSE 1969) (see also ERWE 1919; CHERBONNIER 1955; DANIEL & HALDER 1974; PRICE 1982 for unspecified localities from the Gulf of Suez); Gulf of Aqaba, Graa (A.M. CLARK 1952), Aqaba (TORTONESE 1977; 1979), Dahab (A.M. CLARK 1952) (see also DANIEL & HALDER 1974; PRICE 1982 for unspecified localities from the Gulf of Aqaba); Saudi Arabia, Abulat Island (CHERBONNIER 1955), Jeddah (TORTONESE 1979); Eritrea, Mitsiwa Island (LUDWIG 1886), Ras Benas, Massaua (TORTONESE 1936a), Entedebir (CHERBONNIER 1967); Djibouti (VANEY 1905; CHERBONNIER 1955) (see also SEMPER 1868;

1869; LUDWIG 1877 [1880]; LAMPERT 1885; THÉEL 1886; MITSIKURI 1912; CLARK & ROWE 1971; DANIEL & HALDER 1974; PRICE 1982 for unspecified records from the Red Sea); Persian Gulf? (DANIEL & HALDER 1974); Kenya, Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000); Mozambique, Inhaca (MRAC records, pers. observ.; see also KALK 1958; THANDAR 1984); Madagascar, Antisarana, Fort Dauphin, Tuléar (CHERBONNIER 1988); Republic of South Africa, Sodwana Bay (SAMYN pers. observ.). Figure 52G gives the known WIO distribution in detail.

Remarks - *Holothuria insignis* was described by LUDWIG in 1875 [and recognised as such by LAMPERT (1885) and THÉEL (1886)], but later LUDWIG (1887; see also 1877 [1880]; 1883) listed *H. insignis* LUDWIG, 1875 (together with *H. lineata* LUDWIG, 1875 and *H. peregrina* LUDWIG, 1875) as synonyms of *H. pardalis* SELENKA, 1867, however, without providing a satisfactory explanation for this judgment. LUDWIG'S judgement was partially followed by SLUITER (1889, from PANNING 1951) who put *H. insignis* as a variety of *H. pardalis*. Then again, HÉROUARD (1893) respected LUDWIG's (1887) decision and identified a specimen from the Red Sea as *H. pardalis*, even though he noted that the specimen under study corresponded very well with that of LUDWIG's (1875) *H. insignis*. LAMPERT (1896) (and later HELFER 1912; MITSUKURI 1912; PEARSON 1913; ERWE 1919; PANNING 1935d; H.L. CLARK 1938 and CHERBONNIER 1951a) also followed LUDWIG and continued to see *H. insignis* as the junior synonym of *H. pardalis*. Nevertheless, LAMPERT deserves the credit of noting that buttons with a single row of holes are typical of *H. insignis*, while buttons with a double row of holes are characteristic for *H. pardalis*. However, his observation that both types of buttons can occur in the same individual restrained him from reviving *H. insignis* as a valid species. In a brave attempt to resolve this issue, ROWE (*in* ROWE & GATES 1995) examined the type series of *H. (L.) pardalis* (MCZ 677) and concluded that six specimens are referable to *H. (L.) lineata* [which thus was resurected as a valid species (see also THÉEL 1886; PEARSON 1910)], but at the same time (after examination of extant type specimens and extensive museum collections), he (*in* ROWE & GATES 1995) respected LUDWIG'S (1887) judgement that *H. peregrina* and *H. insignis* are junior synonyms of *H. pardalis*. ROWE's decision is contrary to the viewpoint of HEDING (1934), PANNING (1951) and more recently THANDAR (1984) and MASSIN (pers. comm.) who argued that *H. (L.) insignis* should be regarded as a valid species (*H. peregrina* on the other hand, and here everyone *does* agree, remains in the synonymy of *H. pardalis*). Examination of material from the Republic of South Africa (KwaZulu-Natal) allowed me to substantiate the hypothesis that *H. insignis* is indeed a valid species. From these observations it is now clear that HÉROUARD's (1893) specimen is *H. (L.) insignis* rather then *H. (L.) pardalis*. As a consequence *H. (L.) insignis* is here reported for the first time from the Red Sea [PANNING's (1951) record is the second] and LAMPERT's (1896) record most probably is the first record from East Africa (Zanzibar).
Regarding the status of *Holothuria subditiva,* LUDWIG (1887) disagreed with THÉEL (1886) in that SELENKA's (1867) species is also a synonym of *H. pardalis*. Today, the status of *H. subditiva* remains unresolved. SELENKA's (1867) brief description lets me suspect that several species are present in his type series: while his figure (SELENKA 1867: pl. 19, fig. 87) and part of his description of the ossicle assemblage ('Die glatten schnallenförmigen Gebilde der Bindfaserschicht sind 0.04-0.06 Mm. Lang, in den Fusswandungen ein weiniger grösser' [*Sic.*]) is reminiscent of *H. (Thymiosycia) arenicola* SEMPER, 1868, SELENKA also mentioned that the ossicles are reminiscent of those found in *H. pardalis*. SELENKA's statement that Cuvierian tubules are present in *H. subditiva* necessitates yet another species, SMILEY & PAWSON (±1991, unpublished manuscript) believe that this third species might be *H. (Semperothuria) surinamensis* LUDWIG, 1875. As the type material of SELENKA (1867) is currently unavailable (TROESTER, pers. comm.), I am unfortunately not in the position to reject or defend SMILEY & PAWSON's judgement.

Holothuria (Lessonothuria) verrucosa SELENKA, 1867
(fig. 17A-H, fig. 52H)

Holothuria verrucosa SELENKA, 1867: 338, pl. 19, fig. 88; LUDWIG 1882:136; DANIEL & HALDER 1974: 427.
Holothuria collaris HAACKE, 1880; DANIEL & HALDER 1974: 423.
Holothuria immobilis SEMPER, 1868; LUDWIG 1883: 172; CHERBONNIER 1967: 56; DANIEL & HALDER 1974: 423.
Holothuria (Lessonothuria) verrucosa; SLOAN *et al.* 1979: 122; A.M. CLARK 1984: 99; CANNON & SILVER 1986: 22; FÉRAL & CHERBONNIER 1986: 82 (colour picture), 83; CHERBONNIER 1988: 121 (synonymy).

Status and location type - Holotype MCZ (ROWE & GATES, 1995).

Type locality - Hawaiian Islands (as Sandwich Islands).

Material examined - TMes/9899 (one specimen).

General description - The only specimen at our disposition measures 118 mm in length and 22 mm in width, after preservation; it is completely eviscerated apart from the anterior part of the gut and the right respiratory tree. Dorsal body wall variegated brown-beige with some irregular dark-brown blotches and numerous small yellowish dots giving the animal a speckled appearance; ventral body wall yellowish with two longitudinal brown lines. Mouth ventral, surrounded by 21 small, beige (spotted with brown on the stalk) tentacles, surrounded at the base by a simple ring of whitish papillae. Anus terminal surrounded by non-calcified papillae that are positioned in groups of three to four. Tube feet distributed in longitudinal lines in the radial and interradial areas, dorsally less numerously the ventrally. Cuvierian tubules not observed. Calcareous ring very small, with high, well-sculpted radial and short interradial pieces (see CHERBONNIER 1988: 122, fig. 49M). Longitudinal muscles well developed, wide and bifid but very thin.
Ossicles: Tentacles with narrow straight to slightly curved rods that can be slightly spiny at the extremities, 45-125 µm long (fig. 17A). Ventral and dorsal body wall with numerous irregular buttons, pseudobuttons and tables (fig. 17B, C). Tables with disc 60-75 µm across, rim of disc spiny, perforated by four central holes and five to eight peripheral holes, four pillars united by no or a single cross beam terminating in a small crown of eight to ten spines (fig. 17B). Buttons and pseudobuttons very irregular in outline, perforated by two to eight holes, sometimes knobbed, 45-75 µm long and 15-25 µm wide (fig. 17C). Dorsal tube feet with tables similar to the ones from the body wall, though disc up to 85 µm across (fig. 17D); buttons and pseudobuttons longer than those from the body wall (fig. 17E) and smooth rods, curved, often perforated by a small number of holes at the distal extremities, 80-225 µm long (fig. 17F). Ventral tube feet with tables and pseudobuttons similar to the ones from the body wall (fig. 17G); and plate-like rods, perforated mainly at the extremities, 85-145 µm long (fig. 17H).

Diagnosis - See CHERBONNIER 1988: 121, fig. 49A-M; present note (see also remarks).

Ecology - The only specimen was found on coarse coralline sand, at a depth of 21 m.

Distribution in the study region - Only found at Mesali Reef, Pemba Island, Tanzania.

Geographic distribution - Tropical Indo-West Pacific, from Kenya to Hawaii and from China to New Caledonia (MASSIN 1996a; see also CHERBONNIER & FÉRAL 1984a). Also reported from Eritrea, Um Aabak and Nocra Island. (CHERBONNIER 1967), but not from the Persian Gulf. Figure 52H gives the known distribution in the WIO in detail.

Remarks - *H. (L.) verrucosa* has been reported from a number of localities in East Africa (see fig.55D), and has recently been found by CHERBONNIER (1988) from Madagascar (Nosy Bé), hence this species is also expected to occur in Kenya. However, it is with some hesitation that this single specimen was identified as *H. (L.) verrucosa* as two observations do not fit completely with CHERBONNIER'S (1988) description. First: tables with six pillars cannot be found in our specimen; and second, the large plates that CHERBONNIER (1988) described of the tube feet of his specimens are absent in our specimen. However, SELENKA'S (1867) concise and not too accurate description does not exclude my specimen, as SELENKA (1867) stated that the tube feet contain spiny rods *or* perforated plates ['in allen Fusswandungen, nahe dem Endscheibchen, zahlreiche gedornte oder zu durchlöcherten Platten ausgebreitete Stützstäbe']. Unfortunately, SELENKA (1867) never gave the dimensions of the specimens he described, so without examination of the type-series it is impossible to state if presence or absence of plates in the tube feet is size dependent. In the same regard, it should be noted that MASSIN (1996a) also failed to describe the wide plates in the ventral tube feet of a juvenile of *H. (L.) verrucosa*, and that the plates depicted in CHERBONNIER & FÉRAL, 1984a) are only 125 µm long, while those described in CHERBONNIER (1980) and CHERBONNIER (1988) range from 250 to 500 µm.

Table nine lists the other species within the subgenus *Lessonothuria* that are known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known distribution in the shallow-waters of the WIO, while column three provides the reference(s) wherein the record appeared.
KALK (1959) and MACNAE & KALK (1958, from THANDAR 1984; 1962) are the only authors who mention *H. cumulus* H.L. CLARK, 1921 from the western Indian Ocean (Mozambique); however, even though THANDAR (1984) states that the identification of some of these specimens was done by CHERBONNIER, it seems very unlikely that *H. (L.) cumulus* is found in the western Indian Ocean for H.L. CLARK (1921; 1946) and ROWE & GATES (1995) mention it only from northern Australia (Mer, Murray Islands). The

taxonomy of *H. cumulus* deserves a few additional comments. ROWE (1969, see also ROWE & GATES 1995) suggested that *H. cumulus* might belong to the subgenus *Lessonothuria* (possibly because H.L. CLARK (1921) himseld noted that it is not impossible that *H. cumulus* is a young *H. pardalis*); in 1984, THANDAR suggested that *H. cumulus* might be very close to *H. (Thymiosycia) truncata* LAMPERT, 1885 [= *H. (T.) impatiens* FORSKÅL, 1775 according to ROWE & GATES (1995)] and *H. (Thymiosycia) arenicola* BRANDT, 1835 for the buttons of the body wall are regular and smooth and the tables of the body wall have a round, smooth disc. H.L. CLARK (1921) however, noted that the pedicels of *H. cumulus* present straight or curved rods, a character typical of *Lessonothuria* and not of *Thymiosycia*. The latter subgenus is characterised by tube feet that present rods with the central and distal part widened and perforated by relatively large holes. MASSIN & TOMASICK (1996) however, after examination of the type species, regard *H. cumulus* as a valid species and put it in *Lessonothuria*. After examination of the ossicle assemblage of the type specimen (type specimen in MCZ; preparations of the ossicles in IRSNB), I agree with the latter judgment.

Current Species Name	Known WIO Distribution	Reference(s)
H. (Lessonothuria) duoturricula CHERBONNIER, 1988	Madagascar (Nosy Bé)	CHERBONNIER 1988
H. (Lessonothuria) hawaiiensis Fisher, 1907	Red Sea (Aqaba)	CHERBONNIER 1979a
	Madagascar (Tuléar)	Cherbonnier 1988
H. (Lessonothuria) lineata LUDWIG, 1875	Red Sea (Kosseir)	LUDWIG 1880; LAMPERT 1885; THÉEL 1886
(see also discussion)	Mauritius (Reef Fouquets)	HAACKE 1880[(1)]; LUDWIG 1883; LAMPERT 1885; THÉEL 1886
	Arabian Sea	DANIEL & HALDER 1974
	South West Indian Ocean	DANIEL & HALDER 1974

Table 9 - Other species within the holothurian subgenus *Lessonothuria* known to occur in shallow-waters of the western Indian Ocean. The records of DANIEL & HALDER (1974) for *H. (L.) lineata* could not be verified for they only appear in a list. Cited as [(1)] *Labidodemas punctulatum* HAACKE.

Subgenus *Mertensiothuria* Deichmann, 1958

DIAGNOSIS (See SAMYN & MASSIN in press) [Type species: *Stichopus leucospilota* BRANDT, 1833 by original designation]

A recent revision of this subgenus retained only six valid species (SAMYN & MASSIN in press): *H. (M.) albofusca* CHERBONNIER, 1988; *H. (M.) aphanes* LAMPERT, 1885; *H. (M.) fuscorubra* THÉEL, 1886; *H. (M.) hilla* LESSON, 1830; *H. (M.) leucospilota* (BRANDT, 1835) and *H. (M.) papillifera* HEDING *in* MORTSENSEN, 1938. Two of these (*Holothuria hilla* and *Holothuria aphanes*) were transferred from the subgenus *Thymiosycia* to *Mertensiothuria*, while four other species formerly referred to *Mertensiothuria* (*H. arenacava* SAMYN, MASSIN & MUTHIGA, 2001, *H. artensis* CHERBONNIER & FÉRAL, 1984, *H. exilis* KOEHLER & VANEY, 1908 and *H. platei* LUDWIG, 1898) were removed from *Mertensiothuria* and temporarily not allocated to a given subgenus (SAMYN & MASSIN in press). Three of these species are present in the littoral waters of Kenya (with Pemba Island), a key to all the *Mertensiothuria* species can be found in SAMYN & MASSIN (in press).

Holothuria (Mertensiothuria) hilla LESSON, 1830
(fig. 53A)

Holothuria hilla LESSON, 1830; 226, pl. 78; MACNAE & KALK 1958: 36, 42, 99, 107, 117, 130 (from THANDAR 1984); KALK 1958: 213, 214, 338; KALK 1959: 7, 22; MACNAE & KALK 1962: 104, 112, 115; BRANCH & BRANCH 1981: 249 (from THANDAR 1984); WEINBERG 1997: 246 (colour picture); HICKMAN 1998: 47 (colour plates); CONAND 1999: 10, 12, 21.
Holothuria monacaria; DANIEL & HALDER 1974: 428.
Holothuria macleari; DANIEL & HALDER 1974: 423.
Holothuria fusco-punctata; DANIEL & HALDER 1974: 417.
Holothuria (Thymiosycia) hilla; MUKHOPADHYAY 1991: 407; MASSIN 1999: 55, figs. 44, 111d (colour plate) (synonyms and records before 1999); LANE *et al.*, 2000: 489.
Holothuria (Mertensiothuria) hilla; SAMYN & MASSIN in press (synonymy and records before 2002, colour plate).

Status and location type - Holotype; MNHNP EcHh542.

Type locality - Society Islands (Borabora).

Material examined - KKiun/9942 (one specimen); KKiun/9943 (three specimens); KMom/9857 (one specimen); KKis/98102 (one specimen)

General description - See SAMYN & MASSIN in press.

Diagnosis - See SAMYN & MASSIN in press.

Ecology - See SAMYN & MASSIN in press. MACNAE & KALK (1962) noted that specimens from Inhaca might also live in muddy sand; a behaviour not observed in Kenya.

Distribution in the study region - Kiunga Marine Reserve, Mombasa Marine Park, Kisite Marine Park, Mesali.

Geographic distribution - MASSIN (1999: 56, fig. 44) gives the known global distribution but the following localities have to be added: Gulf of Suez (ERWE 1919, as *Holothuria monacaria* (LESSON, 1830); PANNING 1951, as *H. monacaria*; PRICE 1982, as *H. (Thymiosycia) hilla*); Eritrea, Entedebir (CHERBONNIER 1967), Noccra Island (TORTONESE 1953a; CHERBONNIER 1967), Ingal (TORTONESE 1936b, as *H. monacaria*); Kenya, Mombasa, Kisite Marine Park (this work); Tanzania, Mesali (this work); southern Mozambique (KALK 1958; THANDAR 1984); Republic of South Africa, Sodwana Bay (SAMYN pers. observ.); Madagascar, Tuléar (CHERBONNIER 1988, as *H. (T.) hilla*); La Réunion (CONAND 1999, as *H. (T.) hilla*). Fig. 53 A gives the known WIO distribution in detail.

Remarks - Although *H. (M.) hilla* is a well-known, easy identifiable species from the tropical Indo-Pacific, its taxonomic position was only changed recently (SAMYN & MASSIN in press). The species is now placed in the subgenus *Mertensiothuria* for the presence of C-shape ossicles, rings and small smooth buttons in the longitudinal muscles is diagnostic to this subgenus. Moreover, the form and distribution of the other in the different body parts (especially the large plates in the tube feet) agrees better with the diagnosis of *Mertensiothuria* than of the subgenus *Thymiosycia* in which it was formerly placed. It is further most remarkable that the huge (reaching lengths of approximately 2 m), Caribbean coral reef inhabiting species, *H. (T.) thomasi* PAWSON & CAYCEDO, 1980, has ossicles that are almost identical to the ones of *H. (M.) hilla*. Investigation the holotype of *H. thomasi* leaves however no doubt that it is a valid species within the holothurian subgenus *Thymiosycia.*

Holothuria (Mertensiothuria) leucospilota (BRANDT, 1835)
(fig. 53B)

Stichopus (Gymnochirota) leucospilota BRANDT, 1835: 51.
Holothuria vagabunda SELENKA 1867; EYRE & STEPHENSON 1938: 43; STEPHENSON 1944: 277, 306, 348 (from THANDAR 1984)
Holothuria leucospilota; MACNAE & KALK 1958: 205, 238 (from THANDAR 1984); BRANCH & BRANCH 1981: 248 (from THANDAR 1984); HICKMAN 1998: 49 (colour plates); CONAND 1999: 10, 12, 21, 39; MARSHALL *et al.* 2001: 46 (tab. 29).
Holothuria (Mertensiothuria) leucospilota; ARAKAKI & FAGOONEE 1996: 122; SAMYN & MASSIN in press (synonymy and records before 2002).

Type - *Holothuria leucospilota* BRANDT, 1835.

Status and location type - Neotype, NHM 1968.7.3.105-6 (SAMYN & MASSIN in press).

Type locality - Solomon Islands.

Material examined - KKan/9701 (one specimen); KKan/9702 (one specimen); KKan/9703 (one specimen); KKan/9704 (one specimen); KShar/9741 (one specimen); TMes/9954 (one specimen); TMes/9955 (one specimen); TMes/9956 (one specimen); KKiun/9932 (one specimen); KKiun/9933 (one specimen).

General description - See SAMYN & MASSIN in press.

Diagnosis - See SAMYN & MASSIN in press.

Ecology - See SAMYN & MASSIN in press.

Distribution in the study region - *H. leucospilota* is perhaps the most common sea cucumber in the region, it was found on virtually every sampling locality (in shallow waters), sometimes with a density of 5 / m^2.

Geographic distribution - Tropical and subtropical Indo-Pacific Ocean (with the Red Sea and the Arabian Gulf) (see also distribution map MASSIN 1999: 29, fig. 21). The following locations have to be added to MASSIN's (1999) distributionmap: Gulf of Suez, Suez (CHERBONNIER 1955, as *Holothuria vagabunda*

SELENKA, 1867) (see also ERWE, 1919, as *H. vagabunda*; CHERBONNIER 1955, as *H. vagabunda*; PRICE 1982 for unspecified records from the Gulf of Suez); Gulf of Aqaba, Aqaba (TORTONESE 1977) (see also DANIEL & HALDER 1974, as *H. vagabunda*; PRICE 1982 for unspecified records from the Gulf of Aqaba); Eritrea, Assab (LUDWIG 1886, as *Holothuria lagoena* HAACKE, 1880), Massaua (TORTONESE 1936b), Nocra Island (TORTONESE 1953a), Entedebir (CHERBONNIER 1967, as *H. vagabunda*); Yemen, Derom Island (CHERBONNIER 1963; 1967, as *H. vagabunda*); Persian Gulf, Jez Shit War (HEDING 1940b, as *H. vagabunda*), Damman Channel (PRICE 1981; 1983), Jurayd Island (PRICE 1983) (see also KOEKLER & VANEY 1908, as *H. vagabunda* and PRICE 1982 for unspecified records from the Persian Gulf); Kenya, Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000), Malindi, Shariani, Kanamai, Mombasa, Chale Island (this work); Tanzania, Mesali (this work); Madagascar, Madirokely, Antisarana, Nosy Lava, Tuléar, Fort Dauphin (CHERBONNIER 1988); Mozambique, Inhaca (KALK 1958; THANDAR 1984; MRAC records pers. observ.); Republic of South Africa, Sodwana Bay (pers. observ.), Transkei (THANDAR 1984); Réunion (CONAND 1999). Fig. 53B gives the known WIO distribution in detail.

Table ten lists the other species within the subgenus *Mertensiothuria* that are known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known distribution in the WIO, while column three provides the references wherein the record appeared.

Current Species Name	Known WIO Distribution	Reference(s)
H. (Mertensiothuria) albofusca CHERBONNIER, 1988	Madagascar (Nosy Bé; Tuléar)	CHERBONNIER 1988
	Republic South Africa (KwaZulu-Natal)	Pers. observ.; THANDAR pers comm.
H. (Mertensiothuria) aphanes LAMPERT, 1885	Gulf of Aqaba (Aqaba)	TORTONESE 1977; PRICE 1982
	Gulf of Suez (unspecified)	PRICE 1982
	Red Sea (Kosseir)	LAMPERT 1885; THÉEL 1886; PRICE 1982
	Gulf of Aden (Djibouti)	CHERBONNIER 1955: DANIEL & HALDER 1974
	Arabian Sea	PRICE 1982
H. (Mertensiothuria) fuscorubra THÉEL, 1886 (see also discussion)	Persian Gulf (Bahrein)	HEDING 1940b[1]; PRICE 1982[2]
	Indo-Pacific (not specified)	PEARSON 1913; ROWE & RICHMOND 1997
	Mozambique (Inhaca)	MRAC record, pers. observ.
H. (Mertensiothuria) papillifera HEDING *in* MORTENSEN, 1938 (see also discussion)	Red Sea (Hurghada)	SAMYN & MASSIN in press
	Zanzibar	MRAC record, pers. observ.[3]

Table 10 - Other species within the holothurian subgenus *Mertensiothuria* known to occur in the shallow-waters of the WIO. Cited [1] as *Holothuria pardalis* SELENKA; [2] as *Holothuria (Lessonothuria) glandifera* CHERBONNIER; [3] as *Holothuria impatiens*(FORSKÅL).

Subgenus *Metriatyla* ROWE, 1969

Diagnosis (See ROWE 1969: 160) [Type species: *Holothuria scabra* JAEGER, 1833 by original designation] Eleven species are currently recognized as being valid: *H. (M.) albiventer* SEMPER, 1868; *H. (M.) brauni* HELFER, 1911; *H. (M.) conica* H.L. CLARK, 1938; *H. (M.) fuligina* CHERBONNIER, 1988; *H. (M.) horrida* MASSIN, 1987; *H. (M.) martensi* SEMPER, 1868; *H. (M.) ocellata* JAEGER, 1833; *H. (M.) scabra* JAEGER, 1833; *H. (M.) submersa* SLUITER, 1901; *H. (M.) timana* LESSON, 1830 and *H. (M.) tortonesei* CHERBONNIER, 1979. In addition, one variety [*H. (M.) scabra* var. *versicolor* (CONAND, 1986)] has been described, but no consensus has been reached over its validity. Three of these and the variety *versicolor* are found in the waters of Kenya (with Pemba Island); they are keyed hereunder.

Key to the species of Kenya (with Pemba island).

1. Distinct rows of conical extensions on ventral and dorsal body wall. . . . . ***Holothuria (Metriatyla) albiventer* SEMPER, 1868**

1'. No distinct rows of conical extensions on ventral and dorsal body wall. **2**

2. Colouration of body wall very variable: dorsally ranging from brownish-green to greyish to black, with black and white spots or patches, transverse white band may also be present. Ossicles of dorsal tube feet with plates.

a. Found in waters less than 10 m deep. . . . . ***H. (Metriatyla) scabra* JAEGER, 1833**

b. Found in waters deeper than 20 m ..... ***H. (Metriatyla) scabra* var. *versicolor*** **(CONAND, 1986)**

2'. Colouration of the body wall: dorsally brownish, ventrally white-yellow. Ossicles of dorsal tube feet without plates ..... ***Holothuria (Metriatyla) timana*** **LESSON, 1830**

Holothuria (Metriatyla) albiventer SEMPER, 1868
(fig. 18A-E, fig. 53C, pl. 2H)

Holothuria albiventer SEMPER, 1868: 83, pl. 30 fig 14, pl. 35 fig. 5; CHERBONNIER 1963: 5; CHERBONNIER 1967: 56; JAMES 1969: 62; JAMES & PEARSE 1969: 108; DANIEL & HALDER 1974: 428.
Holothuria (Metriatyla) albiventer; PRICE 1982: 11; CANNON & SILVER 1986: 23; CHERBONNIER 1988:129 (synonymy before 1988); ROWE & GATES 1995: 293; LANE *et al.* 2000: 489.
Holothuria (Metriatyla) sp. cf. *albiventer*; MARSH *et al.* 1993: 64.

Status and location type - Syntypes, whereabouts undetermined (?ZMH) ((ROWE & GATES 1995).

Type locality - Bohol (Philippines).

Material examined - KVan/9780 (one specimen); KVan97/81 (one specimen).

General description - Two specimens measuring in alcohol 37 x 13 mm and 64 x 20 mm respectively. The largest specimen, found on the shelves of the Kenya Marine Fisheries and Research Institute (Mombasa), is devoid of its calcareous ring and intestines. The smaller specimen eviscerated on collection, but is well preserved. Colour in alcohol similar to colour in life (pl. 2H): ventral side greyish with large, whitish, conical extensions, each of them bearing a whitish grey podium; dorsal side variegated white-grey with conical extensions similar in shape, but not in size and colouration, to the ones on the trivium, each of the extensions bears a whitish podium. Body wall up to 3 mm thick, inner side with conspicuous dark brown to black spots. Mouth ventral, surrounded by 20 small beige tentacles, surrounded at their base by a ring of small papillae of the same colouration as the body wall. Anus terminal, surrounded by some papillae. Tube feet on the bivium and trivium more or less arranged in rows. Presence or absence of Cuvierian tubules could not be asserted. Single Polian vesicle. Single stone canal. Calcareous ring relatively stout, with the radial pieces twice as wide as the interradial pieces; radial plate with a deep anterior notch and a scalloped posterior side (see CHERBONNIER 1988: 128, fig. 52H)

Ossicles: Tentacles with rods ranging from 55 to 335 µm in length, sometimes slightly spiny (fig. 18A). of the ventral and dorsal body wall consist of numerous, similar tables and buttons (fig. 18B, C). Buttons from 45 to 95 µm long; rim of button smooth but irregular; perforated by three to four (occasionally five) regular holes; knobbed medianly by two to three knobs and peripherically by some knobs (fig. 18B,C). Tables with disc 100 to 120 µm across, rim of disc undulating, smooth, perforated by four to six central holes and up to 15 peripheral holes; four to six pillars ending in a spiny crown which often is not perforated (fig. 18B, C). Ventral tube feet with plate-like rods and some tables (fig. 18D); rods 85 to 215 µm long; widened centrally, with two to four irregular holes; tables similar to the ones in the body wall, but slightly smaller and rim of disc occasionally knobbed. Dorsal papillae with rods similar in size to the ones in the ventral tube feet, but with perforations over the total length (fig. 18E).

Diagnosis - See SEMPER 1868: 67, 248, 277, pl. 30, fig. 14.

Ecology - Generally found intertidally and in shallow waters (up to 2 m), but ROWE (*in* ROWE & GATES 1995) reports it up to 36 m deep. This species is always found on sand.

Distribution in the study region - Vanga only.

Geographic distribution - Well known species from the tropical Indo-west Pacific Ocean (see also CHERBONNIER 1988; ROWE & GATES 1995), also reported from the Red Sea (SEMPER 1868, 1869; LAMPERT 1885; THÉEL 1886; HÉROUARD 1893; LAMPERT 1896; ERWE 1919; CHERBONNIER 1955, 1967; JAMES 1969; JAMES & PEARSE 1969; CLARK & ROWE 1971; DANIEL & HALDER 1974; PRICE 1982), but not from the Persian Gulf. Figure 53C shows the known distribution in the WIO in detail. The records reported here are new to the Kenyan fauna.

Remarks - The presence of Cuvierian tubules in the present specimens could not be asserted due to the eviscerated state. Nevertheless, CHERBONNIER's description (1988) ('Trés gros tubes de Cuvier blanc laiteux' [Sic.]) leaves no doubt on their presence.

Holothuria (Metriatyla) scabra JAEGER, 1833
(fig. 19A-E, fig. 53D, pl. 3A)

Holothuria scabra JAEGER, 1833: 23; CHERBONNIER 1952a: 504; KALK 1954: 113 (from THANDAR 1984); DAY & MORGANS 1956: 274, 278 (from THANDAR 1984); KALK 1959: 22; MACNAE & KALK 1958: 43, 99, 101, 107, 117, 130 (from THANDAR 1984); MACNAE & KALK 1962: 105, 112, 119; BRANCH & BRANCH 1981: 248 (from THANDAR 1984); DAY 1974a: 192 (from THANDAR 1984); DAY 1974b: 54, 59, 94 (from THANDAR 1984); DANIEL & HALDER 1974: 429; BRANCH *et al.* 1999: 204; CONAND 1999: 10, 12, 15, 24, 39, pl. 1 (colour picture); MARSHALL *et al.* 2001: 45, 46 (tab. 29), 47, 50, 53, 54, 58 (tab. 37), 59, 61.

Holothuria (Metriatyla) scabra; MASSIN 1999: 30 (synonymy and records before 1999), figs. 22a-l, 23, 110 f (colour picture); MASSIN *et al.* 2000: 77, figs. 1-14; SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 488; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 24; HAMEL *et al.* 2001: 129-223.

Holothuria tigris SELENKA, 1867: 333, pl. 19, figs 70-72.

Status and location type - Status and whereabouts undetermined (ROWE & GATES 1995).

Type locality - Sulawesi (as Celebes), Indonesia.

Material examined - KVan/9769 (one specimen); KVan/9770 (one specimen); KVan/9771 (one specimen); KVan/9772 (one specimen); KVan/9773 (one specimens); KCi/9756 (one specimen); KCi/9757 (one specimen); KCi/9758 (one specimen); KCi/9759 (one specimen); KKan/9863 (one specimen); KKan/9864 (one specimen); KKan/9865 (one specimen); KKiun/9939 (one specimen).

General description - 13 specimens measuring in alcohol from 50 to 160 mm in length and from 18 to 98 mm in width. The specimens from Chale Island are very contracted due to immediate transfer to formalin, three of them eviscerated. Colour in alcohol is the same as the colour in life (pl. 3A): ventral side white-grey with numerous grey spots, dorsally grey with black spots and patches, in the largest specimen white transverse bands and patches are visible. Body strongly contracted with deep transverse folds running from bivium through trivium. Thickness body wall up to 15 mm; the dorsal side being markedly thicker than the ventral side. Mouth ventral surrounded by 15-20 relatively small grey tentacles with distinct dark spots and a white base, surrounded by a ring of modified papillae with white-grey dots. Anus terminal. Grey tube feet on bivium and trivium, in radial and interradial areas. Bivium also with dark-grey conical papillae surrounded at the base by a light grey band. Lateral papillae without grey at the base. Cuvierian tubules absent. Single long Polian vesicle. Single stone canal. Ring of numerous white Tiedemann's bodies. Calcareous ring high; radial pieces twice as broad as the interradial pieces; radial pieces with deep anterior notch; interradial pieces with abrupt anterior tooth (see MASSIN 1999: 31, fig. 22a).

Ossicles: Tentacles with rods ranging from 80 µm to 260 µm in length (fig 19A). Dorsal body wall with tables, buttons and rods. Tables with disc on average 80 µm across, perforated by one to four central and eight to ten peripheral holes, rim of disc undulating; spire low, ending in a simple spiny crown (fig. 19B). Buttons smooth to knobbed, perforated by three to six evenly distributed regular holes (fig. 19C). Ventral body wall with similar ossicles (fig. 19D), but smaller buttons more numerous. Tube feet with buttons and tables (fig. 19E) similar to those of the body wall.

Diagnosis - See CHERBONNIER 1988: 135-137, fig. 55, p. 136 (see also MASSIN *et al.* 2000 for a detailed description of the ossicle change with age).

Ecology - Shallow water species (up to 10 m), often found in sea-grass beds, occasionally in coral gardens.

Distribution in the study region - Kanamai, Chale Island, Vanga, Malindi, Kiunga.

Geographic distribution - Very well known species from the tropical and sub-tropical Indo-west Pacific Ocean, also recorded from the Red Sea, but not from the Persian Gulf. The distribution map as drawn by MASSIN (1999: 32, fig. 23) gives the global distribution, but the following localities in the shallow-waters of the WIO have to be added: Gulf of Suez? (PRICE 1982); Saudi Arabia, Jeddah (TORTONESE 1979); Djibouti (CHERBONNIER 1955); Kenya, Kiunga Marine RESERVE (SAMYN & VANDEN BERGHE 2000), Kanamai, Chale Island, Vanga (this work); Mozambique, Beira (PANNING 1944), southern coast (H.L. CLARK 1923; THANDAR 1984); Madagascar, Mitsio Island, Ile St. Marie, Tuléar (CHERBONNIER 1988). A long list of localities were *H. scabra* has ever been reported is provided by HAMEL *et al.* (2001). Figure 53D shows the known distribution in the WIO in detail.

Remarks - MASSIN *et al.* (2000) clearly demonstrated that the ossicles of *H. (M.) scabra* vary significantly with size; specimens shorter then 30 mm show typical juvenile characters: tables with tall spire and several cross beams (spire and number of cross beams lowers with increasing body size) and no to slightly nodose

buttons. The present specimens neatly show the adult ossicles: nodose buttons in combination with tables with disc with an undulating rim, perforated by four central holes and one circle of ten to twelve peripheral holes.

Holothuria (Metriatyla) scabra var. *versicolor* (CONAND, 1986)
(fig. 20A-E, fig. 53E)

Holothuria (Metriatyla) scabra var. *versicolor* (CONAND, 1986): 19; CONAND 1999: 10, 12, 15, 39, pl. 1 (colour picture).

Status and location type - See *H. (M.) scabra.*

Type locality - See *H. (M.) scabra*; the variety *versicolor* was described from New Caledonia.

Material examined - TMes/9898 (one specimen).

General description - The single specimen at our disposition measures 72 mm in length and 22 mm in width, after preservation. Unfortunately, upon capture the specimen eviscerated; only the left respiratory tree and the anterior part of the gut remains. Colour in life similar to colour in alcohol: dorsal body wall beige to brown with eight, dark brown, large blotches and numerous dark tiny dots corresponding to the tube feet; ventral body wall uniform dirty yellow. Body wall only 1-2 mm thick, relatively rough to the touch. Mouth ventral, surrounded by 15 short, brown tentacles, surrounded at their base by conical papillae. Anus terminal, large. Dorsal tube feet homogeneously distributed over the total surface. Ventral tube feet restricted more or less to the ambulacral areas. Polian vesicle(s) not observed. Single narrow stone canal. Cuvierian tubules absent.
Ossicles: Tentacles with spiny rods, occasionally with some perforations, 70-305 µm long (fig. 20A). Ventral and dorsal body wall with nodose buttons, tables and rods (fig. 20B-F). Table discs 70-120 µm across, perforated by one to four large central holes and numerous smaller peripheral holes, positioned in one or several concentric circles; rim of disc undulating to spiny; four short pillars united by one cross beam ending in a spiny crown (fig. 20C, E). Buttons slightly to very nodose, 50-70 µm long, perforated 3-6 pairs of holes (fig. 20B, F). Rods relatively rare, distally branching, occasionally with some knobs, 100-140 µm long (fig. 20D). Ventral tube feet with perforated rods, 165-215 µm long (fig. 20G), in addition to buttons and tables similar to the ones from the body wall. Dorsal tube feet with rods, perforated rods and plates (fig. 20H), in addition to buttons similar to the ones from the body wall.

Diagnosis - See *H. (M.) scabra* in combination with CONAND 1986: 19; 1998: 1180.

Ecology - The specimen was found at 21 m depth in a healthy coral reef, on coarse coralline sand.

Distribution in the study region - Only observed at Mesali reef, Pemba Island, Tanzania.

Geographic distribution - IN 1998, CONAND stated that *H. scabra* var. *versicolor* has a widespread tropical Pacific distribution (excluding coral reef islands); in 1999 she added Madagascar (exact location unspecified) to the distribution. The present record is the new to Kenya. Figure 53E shows the known distribution in the WIO in detail.

Remarks - The ossicle assemblage of the specimen under study agrees with that of a typical *H. (M.) scabra* (see also CONAND 1998b; MASSIN 1999). In 1986, CONAND proposed the variety *H. (M.) scabra versicolor* in order to substantiate the differences in colour pattern, biometric relations, reproduction and ecology between *H. (M.) scabra* var. *versicolor* and *H. (M.) scabra*. According to CONAND (1986), the bivium of *H. (M.) scabra* var. *versicolor* can have all the intermediates between light beige and black and some individuals are speckled with moderate to large black areas; *H. (M.) scabra* on the other hand, presents a bivium that is light to dark gray and shows transverse whitish bands and small black spots. In this context it must, however, be stressed that the colour pattern of *H. (M.) scabra*, as observed by several authors (FÉRAL & CHERBONNIER 1986; CONAND 1989; MASSIN 1999; HAMEL *et al.* 2001) is so variable that it can hardly serve as a criterion to distinguish the two forms. Of greater importance is perhaps the observation that *H. (M.) scabra* var. *versicolor* is generally larger and heavier then *H. (M.) scabra* (CONAND 1986; HAMEL *et al.* 2001). From an ecological point of view, CONAND (1998b) noted that *H. (M.) scabra* var. *versicolor* is generally found in waters deeper than 20 m, while *H. (M.) scabra* is rarely found in water of more than 10 m. In terms of reproduction, the differences between *H. (M.) scabra* and *H. (M.) scabra* var. *versicolor* (*scabra* showing two peaks of sexual maturation *per annum*, while only one maturation *per annum* for *versicolor*), as presented by CONAND (1986), seem inconclusive to me, a finding sustained by CONAND's

(1986) personnal observation that interannual variation most probably exists in the New Caledonia population of *H. (M.) scabra*.
As only a single specimen is available in the present collection, it is imprudent to discuss the taxonomic status of *H. (M.) scabra* var. *versicolor*, but in the light of the evidence of the observed convergences in ossicle morphology of other *Holothuria* species (e.g. *H. (T.) thomasi* versus *H. (M.) hilla*; see remarks with the latter species); more samples from different areas might warrant it a specific status, but it is more likely that *H. (M.) scabra* var. *versicolor* is nothing but a colour-variant of *H. (M.) scabra*.

Holothuria (Metriatyla) timana LESSON, 1830
(fig. 21A-E, fig. 53F, pl. 3B)

Holothuria timana LESSON, 1830: 118, pl. 43.
Holothuria (Metriatyla) timana; ROWE & GATES 1995: 295 (synonymy, partim).
Holothuria aculeata SEMPER, 1868: 84, pls 24, 30 fig. 19; CHERBONNIER 1951b (1re note): 298.

Status and location type - Holotype lost (ROWE & GATES 1995).

Type locality - Waigiou Island, Offack Bay (South Pacific).

Material examined - KKan/9717 (one specimen); KKan/9718 (one specimen), KVan/9774 (one specimen).

General description - Three specimens measuring 155-209 mm in length and 68-94 mm in width, after preservation. Body colour in alcohol is preserved: ventrally and laterally yellow-white; dorsally brownish, spotted with numerous small brown spots corresponding to the tube feet (pl. 3B). Largest specimen with deep transverse furrows over the total body; the two smaller specimens only moderately contracted. Thickness of body wall, after preservation, up to 10 mm ventrally and up to 15 mm dorsally. Mouth ventral, surrounded by 20 light-brown, relatively small tentacles, surrounded at their base by a circle of brown tube feet. Anus terminal, relatively large, surrounded by a brown line. Ventral tube feet spread in the ambulacral and the interambulacral zones. Bivium covered by tube feet surrounded at their base by a small brownish circle. Cuvierian tubules absent. Gonad white and very developed. Single Polian vesicle. Tentacle ampullae up to 4 cm long. Longitudinal muscles bifid and well developed. Calcareous ring stout with large radial and small straight interradial pieces.
Ossicles: Tentacles present stout rods, 115-295 µm long, slightly spiny at the extremities (fig. 21A). Ventral and dorsal body wall with similar buttons and tables (fig 21B-E). Buttons occasionally smooth, but generally knobbed medially and peripherically, 40-70 µm long, perforated by six to eight regular holes (fig. 21B, E). Tables: disc on average 80 µm across, rim of disc smooth to undulating, low spire with single cross beam ending in simple spiny crown (fig. 21C, D). Ventral tube feet with plates up to 140 µm long and perforated rods, 60-120 µm long (fig. 21F). Dorsal tube feet with similar but simpler rods up to 100 µm long (fig. 21G).

Diagnosis - CHERBONNIER 1951b: 396 (from ROWE & GATES 1995).

Ecology - *H. (M.) timana* is a typical shallow water species, it has never been recorded deeper then 6 m. In Kenya it can be found during the day in shallow sea-grass beds, on sand or on fine coral rubble. Gut content is composed of a sand-rubble mixture.

Distribution in the study region - Kanamai and Vanga.

Geographic distribution - CLARK & ROWE (1971) record it (as *Holothuria (Metriatyla) aculeata* SEMPER, 1868) from the East Indies and the Philippine Islands. ROWE & GATES (1995) list it as a tropical, east Indo-west Pacific species. As *H. tigris* SELENKA, 1867 (from Zanzibar) clearly is a synonym of *H. scabra* JAEGER, 1833 and not of *H. timana* as ROWE & GATES (1995) suspected, the present records are to be considered as new to the western Indian Ocean [compare SELENKA's (1867) pl. 19 fig. 70 with figs 53E, F in the present work].

Table eleven lists the other species within the subgenus *Metriatyla* that are known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record for East Africa appeared.

Current Species Name	Known WIO Distribution	Reference(s)
H. (Metriatyla) brauni HELFER, 1911	Gulf of Suez (Suez)	HELFER 1911; PRICE 1982
	Red Sea (Safaga)	Pers. observ.
H. (Metriatyla) fuligina CHERBONNIER, 1988	Madagascar (Tuléar)	CHERBONNIER 1988
	Republic of South Africa (Bangha Nek)	Pers. observ.
H. (Metriatyla) horrida MASSIN, 1987 (see also discussion)	Madagascar (Tuléar)	CHERBONNIER 1988[1]
H. (Metriatyla) martensi SEMPER, 1868	Gulf of Aqaba (Aqaba)	CHERBONNIER 1979a; PRICE 1982
	Gulf of Aden (Djibouti)	CHERBONNIER 1955
	Mozambique (Pekawi)	PEARSON 1910; THANDAR 1984
	Madagascar (Antisarane, Tuléar)	CHERBONNIER 1988
	Arabian Sea?	PRICE 1982
H. (Metriatyla) ocellata JAEGER, 1833	Gulf of Suez?	PRICE 1982
	Red Sea (Massaua)	CHERBONNIER 1963[2]; ERWE 1919; PRICE 1982[2] DANIEL & HALDER 1974[2]
	Arabian Sea?	PEARSON 1913
	Seychelles (unspecified)	DANIEL & HALDER 1974
	South West Indian Ocean?	
H. (Metriatyla) tortonesei CHERBONNIER 1979	Red Sea (Jeddah)	CHERBONNIER 1979b; PRICE 1982

Table 11 - Other species within the holothurian subgenus *Metriatyla* known to occur in the shallow-waters of the WIO. Cited [1] as *Holothuria (Metriatyla)* sp. [2] as *Holothuria kurti* LUDWIG (non LAMPERT).

Subgenus *Microthele* BRANDT, 1835

Diagnosis (after ROWE 1969: 162) [Type species: *Holothuria (Microthele) maculata* BRANDT, 1835 (= *Muelleria nobilis* SELENKA, 1867) by subsequent designation].
Large, massive species reaching lengths of over 600 mm and widths up to 200 mm; body wall very thick, up to 12 mm; pedicels in ventral and dorsal area distributed over the ambulacral and interambulacral areas; mouth ventral, surrounded by twenty tentacles; anus dorsal, often surrounded by five anal teeth; calcareous ring massive, with radial and interradial pieces squarish, radial pieces twice as long as the pointed interradial pieces. Ossicles comprise well developed tables and buttons; tables with squarish, unknobbed disc, spire of moderate height, united by a single cross beam, terminating in a massive spiny crown; buttons heavily knobbed, perforated by up to ten holes, often modified into fenestrated ellipsoids.
Only three species are currently recognized as being valid: *Holothuria (Microthele) fuscopunctata* JAEGER, 1833; *H. (M.) nobilis* (SELENKA, 1867) and *H. (M.) whitmaei* BELL, 1887. The first two species are reported from the littoral waters of Kenya (with Pemba Island) and are keyed hereunder.

Key to the species of Kenya (with Pemba island).

1. Bivium grey to black with in between some white-cream areas; laterally a row of five to six prominent large papillae (commonly referred to as *teats*) present. . . . . ***H. (M.) nobilis* (SELENKA, 1867)**

1'. Bivium yellow to light brown with numerous brown areas around the tube feet; laterally teats absent. . . . . ***H. (M.) fuscopunctata* JAEGER, 1833**

Holothuria (Microthele) fuscopunctata JAEGER, 1833
(fig. 22A-E, fig. 53G, pl. 3C)

Holothuria fuscopunctata JAEGER, 1833: 23; CONAND 1998b: 1182; CONAND 1999: 10, 12, 19, 39, pl. 1 (colour picture); MARSHALL *et al.* 2001: 46 (tab. 29), 47.
Holothuria (Microthele) fuscopunctata; CHERBONNIER 1980: 623 (synonymy before 1980); FÉRAL & CHERBONNIER 1986: 88, 89 (colour picture); CHERBONNIER 1988: 144 (synonymy); ALLEN & STEENE 1994: 244 (colour plate); GOSLINER *et al.* 1996: 280 (colour plate); SAMYN 2000: 15 (tab.1); LANE *et al.* 2000: 489.
Holothuria (Microthele) fusco-punctata; MARSH *et al* 1993: 64.

Type - *Holothuria fuscopunctata* JAEGER, 1833.

Status and location type - Status and whereabouts undetermined according to ROWE (*in* ROWE & GATES 1995), who thus disregards CHERBONNIER's (1980) proposal to regard the specimen deposited in RMNH and described by LUDWIG (1882) as neotype. I see no reason to disdain CHERBONNIER's stabilizing decision.

Type locality - Sulawesi (Indonesia).

Material examined - TFun/9806 (one specimen).

General description - Large, massive species. The single specimen at our disposition measures 380 x 132 mm, after preservation. Dorsal side rounded with deep transverse scars; ventral side flattened. Body colour in alcohol similar as colouration life: dorsal body wall yellow to light brown with numerous darker brown spots corresponding to tube feet which are scattered over the ambulacral and interambulacral areas (pl. 3C); ventral body wall faint yellow with numerous brown tube feet distributed over the total surface. Body wall up to 10 mm thick, smooth to the touch. Mouth ventral, surrounded by twenty stout, uniform brown tentacles. Anus dorsal, wide, brown, unguarded by papillae. Cuvierian tubules absent. Calcareous ring with radial pieces twice as wide as the interradial pieces; radial and interradial pieces about the same height; radial pieces with shallow anterior notch; interradial pieces with anterior tooth (see also CHERBONNIER 1988: 145, fig. 59P).

Ossicles: Tentacles with straight rods, 30-150 µm long, slightly spiny, imperforated; the smaller ones occasionally curved, not spiny (fig. 22A). Dorsal and ventral body wall with numerous tables and ellipsoids (fig. 22B, C); ventral side present in addition some smooth to slightly knobbed buttons (fig. 22B). Tables with disc small, 35-55 µm across; rim irregular, spiny; disc perforated by four large central holes and few peripheral ones; four pillars united by a single cross beam ending in a moderately spiny crown (often incomplete) with a large central opening (fig. 22B,C). Ellipsoids very numerous; perforated 4-6 pairs of holes (fig. 22B, C); occasionally simple buttons which can be either smooth or slightly knobbed, with three to four pares of holes (fig. 22B). Dorsal and ventral tube feet with spiny plates and branching rods (fig. 22 D, E).

Diagnosis - See CHERBONNIER 1980: 623-626, fig. 5.

Ecology - The single specimen was found on the western side of Pemba Island (Fundu) on a large sand flat next to the reef slope at 32 m depth, three more specimens were seen at the same locality. CONAND (1998b) and FÉRAL and CHERBONNIER (1986) note that in New Caledonia this species can also be seen in shallow sea-grass beds and from 5 to 20 m depth, always on clear coralline sand. CHERBONNIER (1988) found his specimens in the shallow sea grass beds of Nosy Bé. CONAND (1998b) further remarks the low potential fecundity and late sexual maturity of this species.

Distribution in the study region - Only found on one location, Fundu, where it was known to live by our local divemaster.

Geographic distribution - Tropical Indo-west Pacific Ocean (ROWE & GATES 1995). Figure 53G gives the only records from WIO: Madagascar, Nosy Bé (CHERBONNIER 1988; but see also CONAND 1999 for an unspecified locality in Madagascar); Tanzania, Fundu (MARSHALL *et al.* 2001; this work).

Holothuria (Microthele) nobilis (SELENKA, 1867)
(figs 23A-K, 24A-B, 25A-C, fig. 53H, pl. 3D)

Muelleria nobilis SELENKA, 1867: 313, pl. 17 figs 13-15.
Holothuria nobilis; CONAND 1999: 8, 9, 10, 12, 13, 39, pl. 1 (colour picture); MARSHALL *et al.* 2001: 46 (tab. 29), 47, 50, 53, 54, 58 (tab. 37).
Holothuria (Microthele) nobilis; HUGHES & GAMBLE 1977: 355; CHERBONNIER 1979a: 861; MUKHOPADHYAY 1991: 406; ARAKAKI & FAGOONEE 1996: 122; MASSIN 1999: 33 (synonymy and records before 1999),110 g, h (colour plates) SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 488; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 25.
Microthele nobilis; CLARK 1952: 204; JAMES & PEARSE 1969: 103; CHERBONNIER 1963: 5; DANIEL & HALDER 1974: 427.
Holothuria (Microthele) fuscogilva CHERBONNIER 1980: 628, fig. 7A-L, pl. I,C.
Holothuria fuscogilva; CONAND 1999: 10, 12, 13, 39, pl. 1 (colour picture); MARSHALL *et al.* 2001: 46 (tab. 29), 47, 58 (tab. 37).

Status and location type - Lectotype MCZ 819 (ROWE & GATES, 1995).

Type locality - Zanzibar.

Material examined - Specimens *sensu 'nobilis'* KMom/9845-46 (two specimens); KKiun/9940 (two specimens); specimens *sensu 'fuscogilva'* KVan/9776 (one specimen); TFun/9820 (one specimen); TFun/9821 (one specimen).

General description - Large, massive species; the specimens at our disposition range from 180-250 mm in length and from 80-120 mm in width, after preservation. Colour in life similar to colour in alcohol

(although slightly faded): dorsal side grey to black, with in between some brownish areas (pl. 3D); ventral side flattened, uniform white to grey with a few black spots. Large lateral papillae, the so called *teats*, separate the trivium from the bivium. Body wall approximately 10 mm thick, often covered with sand. Mouth ventral, surrounded by twenty large white tentacles with brown spots on the stalk. Anus dorsal surrounded by five small white anal teeth. Grey tube feet with brown sucking disk scattered all over the ambulacral and interambulacral areas of the trivium; dark brown to black tube feet with brown sucking disk and few minute, blackish papillae spread scarcely over the ambulacral and interambulacral areas of bivium. Calcareous ring with very large radial pieces with conspicous anterior notch; interradial pieces narrow, pointed anteriorly (see also MASSIN 1999: 34, fig. 24a). Cuvierian tubules present in the Mombasa specimens, but not found in one of the specimens from Kiunga. Single Polian vesicle, single stone canal. Pearlfish were present in the eviscerate of some specimens; two species could be discerned *Encheliophis mourlani* (PETIT, 1934) and *E. homei* (RICHARDSON, 1844) (PARMENTIER, pers. comm.).

Ossicles: Tentacles with straight or slightly curved rods, 50-650 µm long, spiny at the extremities, occasionally with distal perforations (fig. 23A); tables reduced to the disc with some knobs, 40-60 µm across (fig. 23B); tables reduced to the disc without knobs, 40-65 µm across (fig 23C). Ventral and dorsal body wall present tables and ellipsoids. Tables: table disc 55-85 µm across; rim of disc smooth to slightly undulating, perforated by four large central holes and four to twelve peripheral holes; four pillars forming a short spire united by a single cross beam ending in a dense crown of spines; central hole of the crown sometimes obscured by spines (fig 23D). Ellipsoids: very numerous; 55-90 µm long; knobbed; six to ten pairs of holes (fig. 23E); in general dorsal ellipsoids more complex than the ventral ones (fig. 23F). Smooth to slightly knobbed buttons present in the ventral body wall of some specimens, 70-110 µm long (fig. 23G). Ventral tube feet present some tables of similar size and shape as those found in the body wall; buttons 60-100 µm long; similar to those found in the body wall; smooth to slightly knobbed perforated elongated plates, 100-125 µm long (fig. 23H); irregular long plates derived from rods, 150-350 µm long (fig. 23I), and large multiperforated plates, 130-180 µm long and 65-140 µm wide (fig. 23K); endplate ± 600 µm across. Dorsal tube feet with rods, elongated plates, buttons and tables; their dimenions comparable to those found in the ventral tube feet (fig. 24A). Dorsal papillae present elongated regular plates 140-200 µm long (fig. 24B), in addition to tables and ellipsoids similar to those in the body wall.

Diagnosis - See MASSIN 1999: 33-38, figs 24, 26, 27.

Ecology - *H. (Microthele) nobilis* is typically found at greater depths (up to 45 m) in the outer reef, on sand flats and on detritus piles.

Distribution in the study region - Kiunga Marine Reserve, Mombasa, Malindi, Watamu, Shimoni, Vanga, Fundu (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - Well-known species throughout the tropical and subtropical Indo-Pacific Ocean; also reported from the Red Sea. The distribution map as drawn by MASSIN (1999: 38, fig 27) gives the global distribution, but the following localities have to be added: Gulf of Suez, Suez (PANNING 1944); Gulf of Aqaba, Eilat (CHERBONNIER 1963; 1967, both as *Microthele nobilis* (SELENKA, 1867)), Aqaba (TORTONESE 1977; CHERBONNIER 1979a) (see also PRICE 1982 for unspecified record from the Gulf of Aqaba); Arabian Sea, unspecified locality (DANIEL & HALDER 1974, as *Microthele nobilis*); Kenya, Kiunga Marine Reseve (SAMYN & VANDEN BERGHE 2000), Malindi; Mombasa, Shimoni, Vanga (this work); Tanzania, Fundu (this work); Madagascar, Tuléar (CHERBONNIER 1988); Mozambique Channel (CHERBONNIER 1988); Mozambique, Beira and Port Amelia (PANNING 1944, as *Microthele nobilis*); La Réunion (CONAND 1999); Republic of South Africa, Banhga Nek and Sodwana Bay (SAMYN pers. observ.). Figure 53H shows the known distribution in the WIO in detail.

Remarks - ROWE (in ROWE & GATES 1995), after examination of extant type specimens, was the first to regard *H. (M.) fuscogilva* as a junior synonym of *H. (M.) nobilis*. Later MASSIN (1999) analysed four specimens from Sulawesi and conclusively showed that *H. (M.) nobilis* is a highly variable species in terms of body colour and ossicles. His analysis showed that the differences employed by CHERBONNIER (1980) to distinguish the two forms of *teatfish* are artefacts. The specimens collected in Kenya allow testing of this hypothesis as we have three specimens *sensu fuscogilva* and five specimens *sensu nobilis*. All specimens were collected in similar habitats, *i.e.* between 10-30 m deep, on coarse sand between dead and live coral.

Table 12 lists the characters that CHERBONNIER (1980) used to distinguish the two forms of teatfish. According to CHERBONNIER (1980), *H. (M.) fuscogilva* has a beige to greyish brown colouration, lacks Cuvierian tubules, and presents ossicles which differ from those found in *H. (M.) nobilis* in having tables

with a larger more spiny crown, a disc which can be knobbed (tables from the dorsal body wall) and button-like ossicles which consist of simple rugose buttons together with rugose ellipsoids in the ventral body wall, while the dorsal body wall presents rugose ellipsoids only, *H. (M.) nobilis* on the other hand has a grey to black colouration with the lateral teats whitish, always presents Cuvierian tubules and presents ossicles which differ to those of *H. (M.) fuscogilva* in having much smaller rods, plates and pseudo-plates in the tentacles; only ellipsoids (in stead of ellipsoids and rugose buttons for *H. (M.) fuscogilva)* in the ventral body wall; and in addition to plates also presents large spiny rods in the ventral tube feet. CHERBONNIER (1980) also noted that the two species occur in a different habitat; *H. (M.) nobilis* can be found from 0-30 m deep, *H. (M.) fuscogilva* has a narrower depth range of 10-20 m; *H. (M.) nobilis* feeds on coarser sediment and dead coral while *H. (M.) fuscogilva* has only fine sand in its intestine.

Character	*H. (M.) nobilis*	*H. (M.) fuscogilva*
Colour pattern		
• trivium	black	very light chestnut brown
• bivium	black with some light brown to grey patches	yellow to chocolate brown with beige blotches
Tube feet - ventral		
• distribution	numerous, in radial and interradial areas	numerous, in radial and interradial areas
• colour	overall colour not specified; yellowish sucking discs	dark yellow; brown sucking disc
• size	thin, short, cylindrical	short, cylindrical
• size endplate	680-700 µm across	600-610 µm across
Tube feet - dorsal		
• distribution	few; in radial and interradial areas	Few; in the brown blotches
• colour	Blackish; yellowish sucking disc	grey to white
• size	Short; cylindrical	very small
• size endplate	210-220 µm across	420-450 µm across
Papillae - dorsal		
• distribution	not specified	not specified
• colour	not specified	whitish
• size	not specified	not specified
Papillae - lateral		
• distribution	ten conical extensions on each side	five to six conical extensions each side
• colour	not specified	surrounded by a black ring
• size	very small	very small
Mouth		
1. position	ventral	ventral
2. number of tentacles	20	20
• colour of tentacles	yellow to grey	light chestnut-brown
• circle of papillae	in double circle, long, chestnut brown	long, yellow
Anus		
1. position	not specified	terminal
2. anal teeth	present as strong rectangular teeth	present as strong rectangular teeth
• circle of papillae	present; short, conical, yellowish	not specified
Calcareous ring		
• size radial pieces (R), interradial pieces (IR)	R twice as large as IR; R and IR about the same height	R twice as large as IR; R and IR about the same height
• size radial pieces (R), interradial pieces (IR)	R with central notch and two lateral indents, posterior side scalloped IR with anterior tooth	R with central notch and two lateral indents, posterior side scalloped IR with anterior tooth, posterior somewhat scalloped
Tentacle ampullae		
• number	20	20
• size	1/5 of body length	1/4-1/5 of body length
• colour	black at the tips (contenant une bouillie noirâtre [Sic.])	not specified
Polian vesicle		
• number	two	one
• size	one large, one small	1/5 of body length
Stone canal	single, very short	single; very short (2 mm)
Madreporic plate	large, spheric	large
Gonad	single tuft of simple, fine, long tubes	single tuft of simple, fine, long tubes
Longitudinal muscles	large with curled edges	large with curled edges
Respiratory trees	not specified	highly branched, reaching up to the calcareous ring

Cuvierian tubules	numerous	absent
Spicules - tentacles		
• shape	arched, spiny rods; pseudo-plates; small slightly knobbed plates; plates with relief	rods, spiny at the extrimities
• size	rods up to 125 µm long; pseudo-plates up to 120 µm long; small slightly knobbed plates 55-70 µm long; plates with relief ± 75 µm long	rods up to 700 µm
Spicules - ventral body wall		
• shape tables	disc with more or less rounded rim, unknobbed; four central holes; 12-16 peripheric holes; spire: 4-6 (exceptionally) pillars; single cross-beam; spiny crown	disc irregular with more or less rounded rim; unknobbed; four central holes; 10-15 peripheric holes; spire: 4 pillars; single cross beam; spiny crown
• size tables	disc up to 70 µm across	disc up to 70 µm across
• shape buttons	fenestrated ellipsoids, knobbed	simple buttons with rim irregular, four to five pairs of holes; slightly knobbed fenestrated ellipsoids
• size buttons	longer (65-100 µm) than wide (35-40 µm)	simple buttons: 65-80 µm long, 35-40 mm wide; ellipsoids: 65-75 µm long, 35-40 µm wide
Spicules - dorsal body wall		
• shape tables	same as ventral body wall	disc irregular with more or less rounded rim; knobbed disc; perforated by four central holes and +15 peripheric ones; four to six pillars; single cross beam; spiny, massive crown
• size tables	same as ventral body wall	disc up to 100 µm across
• shape buttons	fenestrated ellipsoids, knobbed	ellipsoids only, always knobbed
• size buttons	ellipsoids: 65-75 µm long, 40-50 µm wide	ellipsoids: 65-75 µm long, 35-40 µm wide
Spicules - ventral tube feet		
• shape	large plates with irregular rim and spiny rods	large plates with irregular rim
• size	plates 195 µm long, 95 µm wide; rods up to 250 µm long	plates up to 165 µm long and 85 µm wide
Spicules - dorsal tube feet	dissimilar to those of the ventral tube feet	same as ventral tube feet
• shape	large plates, rim irregular	same as ventral tube feet
• size	plates up to 250 µm long	same as ventral tube feet
Spicules - lateral papillae		
• shape	not specified	not specified
• size	not specified	not specified
Spicules - dorsal papillae		
• shape	not specified	not specified
• size	not specified	not specified
Habitat	0-30 m; currents not specified; on coral rubble and on dead corals, close to sand substrate	10-20 m; high currents; not abundant on loose sediments

Table 12 - Diagnostic characters allowing to separate *H. (M.) nobilis* from *H. (M.) fuscogilva* according to CHERBONNIER (1980).

The present analysis confirms the high variability as noted by ROWE (*in* ROWE & GATES 1995) and MASSIN (1999). The two colour forms of teatfish can easily be distinguished in our samples: the *nobilis* forms invariably present a grey to black dorsal side, with in between some brownish areas and a flattened, uniform white to grey with a few black spots ventral side; the *fuscogilva* forms are greyish-brown dorsally, grey to dirty white with tiny brown spots near the large lateral teats laterally, and greyish-brown ventrally. In terms of presence of Cuvierian tubules, in two out of five, and one out of three specimens of *nobilis* and *fuscogilva* respectively Cuvierian tubules can be found, which illustrates that Cuvierian tubules are not always easy to observe in preserved specimens rather than that they are absent or present in the two colour forms. In terms of ossicles some discrepancies between the ossicles can be found, although it seems that these differences are intra-rather then interspecific. The teatfish *sensu H. (M.) nobilis* always present pseudo-plates and small knobbed plates (fig. 23C, D) in their tentacles, whereas teatfish *sensu H. (M.) fuscogilva* only presents rods of approximately the same size and shape, although it could be argued that the rods in the latter form are more complex at the extremities (fig. 25A). The body wall ossicles in teatfish *sensu fuscogilva* and *sensu nobilis* are very alike: the tables are alike in the two forms (fig. 23D versus fig. 25B); two specimens in the *fuscogilva* group present, in addition to rugose ellipsoids, numerous smooth to slightly rugose buttons in the ventral body wall (fig. 25C), while the third specimen in that same group

presents no smooth buttons whatsoever; two specimens in the *nobilis* group alo present some smooth buttons (fig. 23G). The tables, plates and rods presented in the tube feet of the *fuscogilva* specimens are similar to those presented in the *nobilis* specimens.
Thus, the present study seems to further support that *H. (M.) fuscogilva* should be regarded as junior synonym of *H. (M.) nobilis* (ROWE, *in* ROWE & GATES 1995; MASSIN 1999). However, CONAND (1981, 1993) investigated the population and reproductive biology of both forms in New Caledonia and discovered that the white teatfish (*H. (M.) fuscogilva*) reproduces in the warm season, while the black teatfish[6] (*H. (M.) nobilis)* reproduces in the cold season. Although CONAND's results are quite conclusive it can be argued that she mixed up the two forms as she indicates that the black form varies in colour with age. Moreover, MORTENSEN (1938; see also CONAND 1980) found that *H. (M.) nobilis* individuals from the Red Sea reproduce during the warm rather then during the cold season. REICHENBACH (1999) analysed the reproductive cycle of *H. (M.) fuscogilva* thriving in the Maldives and found that onset of spawning started in December and that the majority of mature individuals are found from December to March, though mature individuals are present throughout the year. To add to the complexity, a recent study by RAMOFAFIA *et al.* (2000) demonstrates that the white teatfish thriving in the Solomon Islands has mature gametes in August and that spawning occurs from August to October. RAMOFAFIA *et al.* (2000) state that temperature changes can hardly affect timing of the reproductivc cycle as temperature fluctuations in the Solomon Islands are minimal. It could be incidental, but the spawning period of *H. (M.) fuscogilva* reported by RAMOFAFIA *et al.* (2000) coincides neatly with that of *H. (M.) nobilis* reported by CONAND (1981) in New Caledonia. Adding to that suspicion is the fact that RAMOFAFIA *et al.* (2000) named the white teatfish *H. fuscogilva* (SELENKA, 1867) rather than *H. (M.) fuscogilva* CHERBONNIER, 1980.
Clearly more material from different localities needs to be examined in a statistical way in order to unambiguously the possible synonymous nature of *H. (M.) nobilis* and *H. (M.) fuscogilva.* For now, I agree with ROWE (in ROWE & GATES 1995) and MASSIN (1999) in keeping *H. (M.) fuscogilva* CHERBONNIER, 1988 as junior synonym of *H. (M.) nobilis* (SELENKA, 1867).
In addition to the reservations given above, ROWE (pers. comm.) added the following supportive arguments: "SELENKA (1867: 313) described two colour forms – a mottled form (=*H. nobilis*) from Zanzibar [type locality according to Rowe (*in* ROWE & GATES 1995)] and a black form (=*Holothuria whitmaei* BELL, 1887) from Samoa [type locality according to ROWE (*in* ROWE & GATES 1995)]. As well as reproductive diffrences I [F.W.E. ROWE] also think the two differ in shape, an observation that helps justify two species: *H. nobilis* and *H. whitmaei*".

Table 13 gives another species within the subgenus *Microthele* that is known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record for East Africa appeared.

Current Species Name	Known WIO Distribution	Reference(s)
Holothuria (Microthele) whitmaei BELL, 1887 (see also discussion)	western Indian Ocean (unspecified)	ROWE, *in* ROWE & RICHMOND 1997

Table 13 - *Holothuria (Microthele) whitmaei* BELL, 1887, the third species within *Microthele* thought to occur in the shallow-waters of the WIO.

Subgenus *Platyperona* ROWE, 1969

Diagnosis (See ROWE 1969: 144) [Type species: *Holothuria discrepans* SEMPER, 1868 by original designation]
Currently eight species are regarded as being valid[7]: *Holothuria (Platyperona) crosnieri* CHERBONNIER, 1988; *H. (P.) difficilis* SEMPER, 1868; *H. (P.) excellens* LUDWIG, 1875; *H. (P.) insolita* CHERBONNIER,

[6] ROWE (pers. comm.) believes the black teatfish might be *H. (M.) whitmaei* BELL, 1887.
[7] It is tempting to list *Mülleria aegyptiana* HELFER, 1912 as another valid species in this subgenus; however it is best treated as a synonym of *H. difficilis*. Indeed, HELFER (1912: 330) himself noted that "Diese neue Form steht der *Mülleria parvula* SELENKA sehr nahe" and PANNING (1929 [1931]) observed that the ossicle assemblage of *aegyptiana* is very close to that of *H. difficilis* (this judgement is here respected). As *H. parvula* is considered a Carribbean species

1988; *H. (P.) parvula* (SELENKA, 1867); *H. (P.) rowei* PAWSON & GUST, 1981; *H. (P.) samoana* LUDWIG, 1875; *H. (P.) sanctori* DELLE CHIAJE, 1823. It must be noted that CHERBONNIER (1988) proposed to place *H. strigosa* SELENKA, 1867 under *Platyperona* rather then under *Thymiosycia*. In another paper (SAMYN & MASSIN submitted) this hypothesis will be discussed in detail. Only *H. (P.) difficilis* is found in the littoral waters of Kenya (with Pemba Island).

Holothuria (Platyperona) difficilis SEMPER, 1868
(fig. 26 A-C, fig. 54A)

Holothuria difficilis SEMPER, 1868: 92, pl. 30 fig. 21; KALK 1959: 5, 22; DANIEL & HALDER 1974: 426; HICKMAN 1998: 43 (colour plates, possibly not *H. difficilis*).
Microthele difficilis; JAMES 1961: 61; JAMES & PEARSE 1969: 104; CHERBONNIER 1967: 56, 57; DANIEL & HALDER 1974: 417.
Holothuria (Platyperona) difficilis; MUKHOPADHYAY 1991: 406, 412; MASSIN 1999: 38 (synonymy and records before 1999); fig. 29 (distribution); SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 488; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 25.
Mülleria aegyptiana HELFER, 1912: 330, figs 9-16
Actinopyga aegyptiana; DANIEL & HALDER 1974: 417.
Holothuria aegyptiana; PRICE 1982: 11.
Mülleria parvula; LUDWIG 1899: 557; HELFER 1912: 330; ERWE 1919: 180, 187 [non *H. (P.) parvula* (SELENKA, 1867)].
Actinopyga parvula; FISHER 1907: 647, pl. 67 fig. 2; DANIEL & HALDER 1974: 426 [non *H. (P.) parvula* (SELENKA, 1867)].
Argiodia parvula; PEARSON 1914a: 173, 177, pl. 28 fig. 4; 1914b: 170 [non *H. (P.) parvula* (SELENKA, 1867)].

Status and location type - Holotype ZMH E.2546.

Type locality - Samoa (Navigator Islands).

Material examined - KKiun/9949 (one specimen).

Description - Medium sized species; the single specimen at our disposition measures 86 x 24 mm, after preservation. Body colour in alcohol similar to colour in life: bivium variegated purple-brown, trivium slightly lighter and more uniform in colouration. Body wall rough to the touch, 2-3 mm thick. Mouth ventral surrounded by 20 small, but firm, green-brown tentacles. Anus terminal guarded by five minute, brown, pointed calcified papillae. Ventral tube feet numerous, distributed mainly in the radial areas (especially posteriorly), in four to six rows, although some spreading into the interradial areas occurs. Dorsal papillae few, coloured dark brown, surrounded at their base by a brown ring-like area, distributed in the ambulacral and interambulacral areas. Cuvierian tubules well developed and very numerous, however they were not ejected upon collection. Single, large, club-shaped, Polian vesicle. Stone canal not observed. Tentacle ampullae relatively short, 20 in number. Calcareous ring with radial pieces slightly wider than the interradial ones, the latter ones with a distinct anterior tooth (see MASSIN 1999: 39, fig. 28a).
Ossicles: Tentacles with curved, spiny rods, 130-350 µm long (fig. 26D). Dorsal and ventral body wall with similar tables and buttons (fig. 26A, B). Tables with rim of disc smooth; disc 30-80 µm across, perforated by four central and eight to ten peripheral holes; four pillars forming a short spire united by a single cross beam that ends in a small spinose crown (fig. 26A). Buttons regular, rim smooth, 80-140 µm long; thin, oval, with three to six pairs holes and with a median longitudinal line (fig. 26B). Tube feet with elongated plates, up to 250 µm long; and perforated plates, 110-130 µm long and 70-100 µm wide (fig. 26C).

Diagnosis - See MASSIN 1999: 38-40, figs 28, 29.

Ecology - Our single specimen was found under a block of dead coral, hidden between coral debris.

Distribution in the study region - Kiunga Marine Reserve only (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - The distribution map as drawn by MASSIN (1999: 40, fig. 29) gives a tropical and subtropical Indo-Pacific (with the Red Sea) distribution. However, the following localities in the WIO have to be added: Gulf of Suez, unspecified locality (PRICE 1982); Gulf of Aqaba, Abu Zabad and Dahab (A.M. CLARK 1952, as *Microthele difficilis*), Eilat (CHERBONNIER 1967, as *Microthele difficilis* (SEMPER, 1868)), Aqaba (TORTONESE 1977; CHERBONNIER 1979a, as *Holothuria (Stauropora) difficilis*) (see also DANIEL & HALDER 1974 and PRICE 1982 for unspecified records in the Gulf of Aqaba); Saudi Arabia,

(type locality Florida) devoid of Cuvierian tubules (SELENKA 1867; see also ROWE 1969), *M. aegyptiana* (type locality Gulf of Suez) cannot be a synonym of it. In turn, the WIO records of *H. parvula* are most probably nothing but misidentified *H. difficilis*.

Jeddah (TORTONESE 1979); Eritrea, Entedebir (CHERBONNIER 1967, as *M. difficilis*) (see also CLARK & ROWE 1971; PRICE 1982 for unspecified records in the Red Sea); Kenya, Kiunga Marine RESERVE (SAMYN & VANDEN BERGHE 2000); northern Mozambique (THANDAR 1984), Mozambique Island (KALK 1959; THANDAR 1984) (see also H.L. CLARK 1923 for unspecified record of Mozambique); Republic of South Africa, Durban (THANDAR 1984); Madagascar, Tuléar, Fort Dauphin and Nosy Manitsy (CHERBONNIER 1988). Figure 54A shows the known distribution in the WIO in detail.
Table 14 lists the other species within the subgenus *Platyperona* that are known are occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record appeared.

Current Species Name	Known WIO Distribution	Reference(s)
H. (Platyperona) crosnieri CHERBONNIER, 1988	Madagascar (Tuléar)	CHERBONNIER 1988
H. (Platyperona) excellens LUDWIG, 1875	Madagascar (Nosy Bé)	CHERBONNIER 1988; CONAND 1999
H. (Platyperona) insolita CHERBONNIER, 1988	Madagascar (Tuléar)	CHERBONNIER 1988
H. (Platyperona) samoana LUDWIG, 1875	Red Sea (unspecified)	LAMPERT 1885
	Gulf of Aden?	DANIEL & HALDER 1974
	Madagascar (Glorious Isl, Nosy Bé, Tuléar)	CHERBONNIER 1988[1]
	Mauritius (Flic en Flac)	ARAKAKI & FAGOONEE 1996[2]

Table 14 - Other species within the subgenus *Platyperona* known to occur in the shallow-waters of the WIO. Cited [1] as *Holothuria (Platyperona) altimensis* H.L. CLARK; [2] as *Holothuria (Thyrmiosycia) altaturricula* CHERBONNIER & FÉRAL.

Subgenus *Roweothuria* THANDAR, 1988

Diagnosis (See THANDAR 1988: 48) [Type species: *Holothuria arguinensis* KOEHLER & VANEY, 1908 by original designation].
Currently three species are regarded as being valid: *Holothuria (Roweothuria) arguinensis* KOEHLER & VANEY, 1908; *H. (R.) poli* DELLE CHIAJE, 1823; *H. (R.) vemae* THANDAR, 1988.
H. (Roweothuria) poli is the only species known from the shallow waters of the western Indian Ocean, Gulf of Suez (CHERBONNIER 1955; JAMES 1969; JAMES & PEARSE 1969; PRICE 1982). The subgenus is here included for completeness only. It is not found in Kenya (with Pemba Island).

Subgenus *Selenkothuria* DEICHMANN, 1958

Diagnosis (after ROWE, 1969: 135) [Type species: *Holothuria lubrica* SELENKA, 1867 by original designation].
Size moderate to large (up to 200 mm); body with flattened ventral 'sole' and arched dorsal side, body wall smooth to the touch, relatively thin (1-4 mm); papillae small, scattered over the radial and interradial areas of the bivium; tube feet distributed in three distinct rows on the trivium; 20 relatively large pelto-dendritic tentacles around the ventro-terminal mouth; calcareous ring with radial pieces up to three times as long as the interradial pieces, the latter usually with the outer surface slightly concave; anus terminal guarded by anal papillae. Ossicles: body wall: rugose, spinose or perforated rods, occasionally in combination with tables; tube feet: few rods similar to those of the body wall.
Currently eleven species[8] are regarded as being valid: *Holothuria (Selenkothuria) bacilla* CHERBONNIER, 1988; *H. (S.) erinacea* SEMPER, 1868; *H. (S.) glaberrima* SELENKA, 1867; *H. (S.) lubrica* SELENKA, 1867; *H. (S.) mactanensis* TAN TIU, 1981; *H. (S.) moebii* LUDWIG, 1883; *H. (S.) parva* LAMPERT, 1885; *H. (S.) portovallartensis* CASO, 1954; *H. (S.) sinica* LIAO, 1980; *H. (S.) theeli* DEICHMANN, 1938 and *H. (S.) vittalonga* CHERBONNIER, 1988. Only *H. (S.) erinacea* is found in the shallow waters of Kenya.

[8] *H. (S.) spinea* CHERBONNIER, 1988, known only from the holotype currently is also listed as a valid species in the subgenus *Selenkothuria*. However, the presence of rare tables in combination with spinose rods does not completely fit with the diagnosis of *Selenkothuria*. ROWE (pers. comm.) believes the presence of tables is due to contamination. Only detailed investigation of the type will prove if ROWE's statement is correct or if the species must be allocated to another subgenus (*Semperothuria*?)

Holothuria (Selenkothuria) erinacea SEMPER, 1868
(fig. 27 A-E, 54B)

Holothuria erinacea SEMPER, 1868: 91, pl. 30 (23-24).
Holothuria (Selenkothuria) erinaceus; KALK 1959: 7, 22; CANNON & SILVER 1986: 24, figs 7c, 4d (colour drawing); CHERBONNIER 1988: 60 (synonymy); SAMYN & VANDEN BERGHE 2000: 5 (tab. 2).
Holothuria (Selenkothuria) erinacea; ROWE & GATES 1995: 297; LANE *et al.* 2000: 488.
Holothuria marenzelleri LUDWIG, 1883: 167.
? *Halodeima lubrica* var. *marenzelleri*; PANNING 1944: 65.

Status and location type - Syntypes ZMH E.2551 (ROWE & GATES 1995).

Type locality - Fiji (ROWE & GATES 1995).

Material examined - KMal/9866 (one specimen); KMal/9867 (one specimen); KMal/9868 (one specimen); KMal/9869 (one specimen); KMal/9870 (one specimen); KMal/9872 (one specimen).

General description - Medium sized species; the specimens at our disposition range from 57-107 mm in length and from 13-80 mm in width, after preservation. Colour in life similar to colour after preservation: bivium beige to Bordeaux-red with some darker patches, near the anus beige speckled with brown; trivium markedly lighter in colouration with two conspicuous dark brown longitudinal bands. Bivium arched, well separated from flattened trivium. Body wall smooth to the touch; 2-4 mm thick. Mouth ventral, surrounded by 17-20 peltato-digitate tentacles. Anus terminal, surrounded by five groups of six to nine, long, non-calcified papillae. Ventral tube feet, uniform yellowish to beige, large and long, numerous, distributed more or less in rows on the radial areas (more or less absent posteriorly). Dorsal papillae short, uniform beige, sparsely distributed over the total surface. Cuvierian tubules present, very short and thin. Single short Polian vesicle. Single, long and straight stone canal. Tentacle ampullae short. Longitudinal muscles well developed, bifid. Calcareous ring with long and straight radial pieces twice as wide as the shorter anteriorly pointed interradial pieces (see CHERBONNIER 1988: 61, fig. 22F).
Ossicles: Tentacles present spinose rods, 75-125 µm long, distal extremities widened and very rugose (fig. 27A). Body wall with rods only (no buttons, no tables). Dorsal body wall with rods, 63-117 µm long; rim spiny; occasionally perforated by some holes (fig. 27B). Ventral body wall with similar but less spiny rods, 58-75 mm long (fig. 27C). Ventral tube feet with very few rods similar in size and shape to those of the ventral body wall (fig. 27D); endplate 400-425 µm across. Dorsal papillae with rods similar to those of the tentacles (fig. 27E).

Diagnosis - See SEMPER 1868: 91, pl. 30 figs 23, 24.

Ecology - Found mostly intertidally, but up to 5 m deep; under or between coral slabs over coarse to fine sand; firmly attached with the ventral side to the hard substratum.

Distribution in the study region - Only found at the Malindi Marine Park.

Geographic distribution - Tropical Indo-west Pacific Ocean (ROWE & GATES 1995), not recorded from the Red Sea nor the Persian Gulf. Figure 54B shows the known distribution in the WIO in detail.

Remarks - Although the species has been found in Somalia (TORTONESE 1980); northern Mozambique (KALK 1959; THANDAR 1984); Republic of South Africa, Durban area (THANDAR 1984) and Madagascar, Tuléar (CHERBONNIER 1988) it is the first record for Kenya.

Table 15 gives the other species within the subgenus *Selenkothuria* that are known to occur in the shallow waters of the WIO, but have for now not been reported from Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record appeared. DANIEL & HALDER (1974) list *H. (Selenkothuria) glaberrima* SELENKA, 1867 as a South West Indian Ocean species. However, the occurrence of this species in the shallow-waters of the WIO is considered improbable for the species is up till now only known from the Pacific Ocean (see MALUF 1988), as KOEHLER & VANEY's (1908) record from the Bay of Bengal must be referred to *H. (S.) erinacea* according to CHERBONNIER (1988). In this regard it must also be noted that ROWE's (1969) mention of *H. (S.) glaberrima* from the West Indies refers to the ancient locality "West Indies", *i.e.* the Carribean and the North Coast of South America. Similarly, DANIEL & HALDER (1974) list *Holothuria lubrica* SELENKA, 1867 as a West Indian Ocean species (Arabian Sea included with doubt); records they copied from LUDWIG 1899 and/or PANNING 1944 [cited as *H. lubrica* var. *marenzelleri* (LUDWIG), here referred to the synonymy of *H. erinacea*]. However, as *H. lubrica* is known to be restricted to the eastern Pacific (DEICHMANN 1958;

ROWE 1969), LUDWIG's (1899) record is obviously a misidentification; most probably it is *H. (Selenkothuria) parva* KRAUSS *in* LAMPERT, 1885.

Currrent Species Name	Known WIO Distribution	Reference(s)
H. (Selenkothuria) bacilla CHERBONNIER, 1988	Madagascar (Nosy Bé, Tuléar)	CHERBONNIER 1988
H. (Selenkothuria) moebii LUDWIG, 1883	Arabian Sea (Vizhingam)	JAMES 1969
(see also discussion)	Mauritius	THÉEL 1886; MITSIKURI 1912; DEICHMANN 1958
	Seychelles (Aldabra)	SLOAN *et al.* 1979; A.M. CLARK 1984
	East Coast of Africa?	DANIEL & HALDER 1974
H. (Selenkothuria) parva KRAUSS *in* LAMPERT, 1885	Red Sea (unspecified)	CHERBONNIER 1955; PRICE 1982
	Gulf of Aden (Djibouti, Obok)	CHERBONNIER 1955
	Persian Gulf (Bushire, Qism Tavila)	HEDING 1940b; PRICE 1982; KOEHLER & VANEY 1908
	Gulf of Oman (Muscat)	PRICE & REID 1985
	Arabian Sea (unspecified)	CLARK & ROWE 1971; DANIEL & HALDER 1974 [1]; PRICE 1982
	Somalia (Bender Mtoni)	TORTONESE 1980
	Zanzibar	LUDWIG, 1899 [2]; MITSIKURI 1912
	Tanzania (Ras Muhesa, Pangani)	MARSHALL *et al.* 2001; LAMPERT 1896; MITSIKURI 1912
	Comores	CHERBONNIER 1988
	Seychelles (Aldabra)	SLOAN *et al.* 1979; A.M. CLARK 1984
	Madagascar (Antisarana, Nosy Bé, Tuléar)	CLARK & ROWE 1971; CHERBONNIER 1988
	Mozambique (North and South Coast)	KALK 1959; THANDAR 1984
	South Africa (KwaZulu-Natal; Transkei)	LAMPERT 1885; THÉEL 1886; MITSIKURI 1912; DEICHMANN 1948; CHERBONNIER 1952a; THANDAR 1977[3]; 1984
	West Indian Ocean (unspecified)	ROWE *in* ROWE & RICHMOND 1997; DANIEL & HALDER 1974 [4]
H. (Selenkothuria) spinea CHERBONNIER, 1988	Madagascar (Nosy Bé)	CHERBONNIER 1988
H. (Selenkothuria) vittalonga CHERBONNIER, 1988	Madagascar (Tuléar)	CHERBONNIER 1988

Table 15 - Other species within the holothurian subgenus *Selenkothuria* known to occur in the shallow-waters of the WIO. Cited as [1] *Holothuria parva* and as *H. lubrica* SELENKA; [2] *H. lubrica;* [3] *H. (Selenkothuria) perrieri* THANDAR; [4] *Holothuria parva* and as *H. lubrica.*

Subgenus *Semperothuria* DEICHMANN, 1958

Diagnosis (after ROWE 1969: 135) [Type species: *Holothuria languens* SELENKA, 1867 by original designation].

Size moderate to large (200 mm); slender and cylindrical body with relatively thin (1-4 mm), smooth body wall; covered by numerous tube feet, mostly in the ambulacral areas of the trivium and by less numerous papillae all over the bivium; 20 (sometimes 22) relatively large tentacles surrounding ventral to terminal mouth; calcareous ring with radial pieces one-and-a-half to three times as long as the interradial pieces and with an undulating posterior side; anus terminal sometimes surrounded by anal papillae. Ossicles of body wall comprise tables in combination with rods (buttons and rosettes always absent); tables with disc reduced, spire longer than disc diameter, four pillars of spire united by single cross beam ending in a crown of spines forming a single or double Maltese cross when viewed from above; rods massive and spinose. Ossicles of tube feet: with large perforated plates in addition to tables and rods similar to those of the body wall.

Currently seven species are regarded as being valid: *Holothuria (Semperothuria) cinerascens* (BRANDT, 1835); *H. (S.) flavomaculata* SEMPER, 1868; *H. (S.) granosa* CHERBONNIER, 1988; *H. (S.) imitans* LUDWIG, 1875; *H. (S.) languens* SELENKA, 1867; *H. (S.) pseudoimitans* CHERBONNIER, 1951; *H. (S.) surinamensis* LUDWIG, 1875.

Only *H. (S.) cinerascens* is found in the shallow waters of Kenya (with Pemba island).

Holothuria (Semperothuria) cinerascens (BRANDT, 1835)
(fig. 28 A-D, fig 54C, pl. 3E)

Stichopus (Gymnochirota) cinerascens BRANDT, 1835: 51.
Holothuria pulchella SELENKA, 1867: 329, pl. 18 figs 61, 62; DANIEL & HALDER 1974: 427.
Holothuria cinerascens; EYRE & STEPHENSON 1938: 38, 43; EYRE *et al.* 1938: 105; STEPHENSON 1944: 277, 306, 348; DEICHMANN 1948: 339; MACNAE & KALK 1958: 34, 99, 107, 120, 130 (from THANDAR 1984); KALK 1958: 198, 238; KALK 1959: 22; MACNAE 1962: 208; DANIEL & HALDER 1974: 428; DAY 1974a: 192; JACKSON 1976: 15; TORTONESE 1977: 275; BRANCH

& BRANCH 1981: 248 (from THANDAR 1984); BRANCH *et al.* 1999: 204, 205 (colour picture); CONAND 1999: 9, 10, 12, 21, 39; MARSHALL *et al.* 2001: 46 (tab. 29).

Holothuria (Semperothuria) cenerascens; MUKHOPADHYAY 1991: 412 (*lapsus calami*).

Holothuria (Semperothuria) cinerascens; LEVIN 1979: 21; HUMPHREYS 1981: 35; PRICE 1982: 11; A.M. CLARK 1984: 90, 99; MUKHOPADHYAY 1991: 406; MASSIN 1996b: 155 (synonomy before 1996), pl. 1A (colour plate); SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 488; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 26.

Status and location type - Status and whereabouts undetermined (ROWE & GATES 1995).

Type locality - 'inter lapides in insulis Boninsimensibus' (NW Pacific) (BRANDT 1835, *in* ROWE & GATES 1995).

Material examined - KMom/9859 (one specimen); KMal/9871 (one specimen); KKiun/9941 (one specimen).

General description - Three specimens ranging from 107-131 mm in length, and from 24-40 mm in width, after preservation. Colour in alcohol fainter, but similar to the colour in live: ventral side uniform dark red to brown; dorsal side uniform dark red to brown, however with some lighter yellow to orange conical extensions (pl. 3E). Mouth terminal; surrounded by 20 well developed; variegated orange-red-brown, bushy tentacles; surrounded dorsally by few small conical papillae. Anus terminal; surrounded by thin and soft papillae in groups of two to three. Tube feet on trivium very numerous; cylindrical, light chestnut brown with end plate somewhat darker, distributed evenly over the ambulacral and the interambulacral areas. Tube feet on bivium also numerous, but fewer in number than on the trivium; same colouration and shape, though at their base sometimes surrounded by a ring of lighter colouration; distributed over the ambulacral and interambulacral areas. Tentacle ampullae very long (up to half the body length); yellowish; spotted with brown. One to several long stone canals, with the madreporic plate elongated. Several Polian vesicles; one very large (up to one third of body length). Gonad whitish, consisting of a simple tuft of tubules. Cuvierian tubules absent. Body wall smooth to the touch; up to five mm thick. Longitudinal muscles well developed; bifid. Calcareous ring with radial pieces almost as wide as the interradial ones, radial pieces with an anterior central depression, interradial ones anteriorly toothed in such a way that the pieces become triangular (see also CHERBONNIER 1988: 71, fig. 27D).

Ossicles: Dorsal and ventral body wall with similar tables and rods (fig. 28A, C). Tables more numerous in dorsal than ventral body wall, however slightly larger and stouter in the dorsal body wall. Disc of table in dorsal body wall 40-55 µm across, rim of disc smooth, sometimes slightly spinose, perforated by four large central and in most cases no peripheral holes; spire very stout, pillars united by a single cross beam ending in a large crown forming a spiny Maltese cross when seen from above; crown almost as wide as the disc (fig. 28A). Disc of tables of ventral body wall 35-55 µm across, spire somewhat lower than in the tables of the dorsal body wall (fig. 28C). Rods of dorsal body wall very spinose, 65-100 µm long (fig. 28B). Rods of ventral body wall comparable in size and shape, but less spinose (fig. 28D). Dorsal tube feet (fig. 28E) with perforated plates, up to 120 µm long; massive, up to 165 µm long, extremely rugose rods which can bifurcate at the edges, to small, slender rods only 15 µm long. Ventral tube feet (fig. 28F) with similar rods, though generally smaller and less rugose. Tentacles with rods (fig. 28G), 60 to 140 µm long, finely rugose at the sides.

Diagnosis - See PANNING 1935a: 37, fig. 32.

Ecology - This species thrives preferentially in shallow to intertidal pools, encrusts itself often with coral debris and sand, and firmly attaches itself between coral slabs.

Distribution in the study region - Only found at Malindi, Mombasa and the Kiunga Marine Reserve (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - Well known species from the Indo-west-central Pacific Ocean (ROWE & GATES 1995). The distribution map as drawn by MASSIN (1996b: 174, map 2) gives the global distribution, but the following localities in the WIO have to be added: Gulf of Aqaba, Abu Zabad (A.M. CLARK 1952, as *Halodeima cinerascens*), Aqaba (TORTONESE 1977) (see also DANIEL & HALDER 1974 and PRICE 1982 for unspecified records from the Gulf of Aqaba); northern Red Sea, Egypt (LAMPERT 1885), Kosseir (MITSIKURI 1912); Djibouti (CHERBONNIER 1955 as *Halodeima cinerascens*); South Yemen, Soccotra (LEVIN 1979); Arabian Sea, unspecified locality (CLARK & ROWE 1971; PRICE 1982; DANIEL & HALDER 1974 as *Holothuria pulchella* SELENKA, 1867); Somalia, Bender Mtoni (TORTONESE 1980); Kenya, Kiunga (SAMYN & VANDEN BERGHE 2000), Kibirijini Point and Mida Creek (HUMPHREYS 1981), Mombasa (LEVIN 1979; this work); Seychelles, Mahé (LUDWIG 1899; MRAC records) (see also LAMPERT 1885;

FISHER 1907; MITSIKURI 1912; PEARSON 1913; DANIEL & HALDER 1974; A.M. CLARK 1984); Mozambique, North coast (KALK 1959; THANDAR 1984), South coast (KALK 1958; THANDAR 1984); Madagascar, Fort Dauphin, Ile St. Marie, St. Augustin, Tuléar (CHERBONNIER 1988); La Réunion (CONAND 1999); Republic of South Africa, KwaZulu-Natal (H.L. CLARK, 1923; DEICHMANN 1948; DANIEL & HALDER 1974; THANDAR 1984; this work), Transkei (THANDAR 1984). Figure 54C shows the known distribution in the WIO in detail.

Remarks - Although we only observed this species in three localities we expect it along the total Kenyan Coast, wherever a suitable habitat is present. Our findings complement those by LEVIN (1979) and HUMPHREYS (1981) (see also SAMYN & VANDEN BERGHE 2000). THANDAR (1984) urges for a study on the intraspecific variation of this species, for he noted that the ossicles FISHER (1907) described in his Hawaii specimens are significantly larger than the ones presented in specimens not from Hawaii (table disc up to 86 µm for FISHER'S specimens compared to 40 µm for the specimens from Kenya and the rest of the world; rods up to 300 µm for FISHER'S specimens compared to 165-215 µm for the rest of the world). MASSIN (1996b) on the other hand, described a collection of nine specimens from Easter Island, whereby he notes that the variation between specimens from Madagascar (CHERBONNIER 1988), the Red Sea (CHERBONNIER 1955) and Hawaii (FISHER 1907) is acceptable to regard the Hawaii specimens as geographic variants of *H. (S.) cinerascens*. The three East African specimens discussed here, can however not shed light on this issue, since the variation presented here corresponds to the variation as described by others than FISHER (1907) (CHERBONNIER 1955, 1988; THANDAR 1984; MASSIN 1996b). Undoubtedly only examination of FISHER's specimens will settle the matter, but it is not improbable that THANDAR's (1984) observations on the size of the ossicles are nothing but results of erroneous measurements done by FISHER (1907) (interestinly FISHER's measurements are more or less the double of those made by subsequent authors). For now, even though I have never seen specimens from that region, I feel quite confident that the specimens from Hawaii are true *H. cinerascens*.

Table 16 gives the other species within the subgenus *Semperothuria* that are known to occur in the shallow waters of the WIO, but have for now not been reported from Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record appeared.

Currrent Species Name	Known WIO Distribution	Reference(s)
H. (Semperothuria) granosa CHERBONNIER, 1988	Madagascar (Fort Dauphin)	CHERBONNIER 1988
H. (Semperothuria) flavomaculata SEMPER, 1868	Red Sea (Entedebir, Nocra Island, Um Aabak)	CHERBONNIER 1967; TORTONESE 1953a; PRICE 1982
	Seychelles (Mahé)	LUDWIG 1899; DANIEL & HALDER 1974; MRAC record, pers. observ.
	Madagascar (Nosy Bé; Tuléar)	CHERBONNIER 1988
	West Indian Ocean to W. Pacific Ocean (with Red Sea)	ROWE *in* ROWE & RICHMOND 1997

Table 16 - Other species within the holothurian subgenus *Semperothuria* known to occur in the shallow-waters of the WIO.

Subgenus *Stauropora* ROWE, 1969

Diagnosis (See ROWE 1969: 140) [Type species: *Holothuria discrepans* SEMPER, 1868 by original designation]

Currently eight species are regarded as being valid: *Holothuria (Stauropora) annulifera* FISHER, 1907; *H. (St.) discrepans* SEMPER, 1868; *H. (St.) dofleini* AUGUSTIN, 1908; *H. (St.) fuscocinerea* JAEGER, 1833; *H. (St.) modesta* LUDWIG, 1875; *H. (St.) olivacea* LUDWIG, 1888; *H. (St.) pervicax* SELENKA, 1867.

Two of these are reported from the littoral waters of Kenya (with Pemba Island) and are keyed hereunder.

Key to the species of Kenya (with Pemba Island).

1. Bivium light brown with several transverse dark brown to black bands; all over bivium sparsely distributed conical, yellow extension, each bearing a brownish papilla. Ossicles of the body wall with pseudobuttons..... ***Holothuria (Stauropora) pervicax* SELENKA, 1867**

1'. Bivium mottled green-gray with dark spots that correspond to conical white-tipped papillae. Ossicles of the body wall with true, but irregular buttons..... ***Holothuria (Stauropora) fuscocinerea* JAEGER, 1833**

Holothuria (Stauropora) fuscocinerea JAEGER, 1833
(fig. 29A-J, fig. 54D)

Holothuria fuscocinerea JAEGER, 1833: 22; HICKMAN 1998: 50 (colour plates); DANIEL & HALDER 1974: 428.
Holothuria curiosa LUDWIG, 1875: 34, pl. 7, fig. 29; CHERBONNIER 1963: 5; DANIEL & HALDER 1974: 426; CHERBONNIER 1967:56.
Holothuria (Mertensiothuria) fuscocinerea; MUKHOPADHYAY 1991: 405, 413.
Holothuria (Mertensiothuria) fusco-cinerea; MUKHOPADHYAY 1991: 412 (*lapsus calami*).
Holothuria (Stauropora) fuscocinerea; MASSIN 1999: 48 (synonomy and records before 1999), fig. 111c (colour picture); SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 488; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab.. 4), 26.

Status and location type - Status and whereabouts undetermined (ROWE & GATES 1995).

Type locality - Java, Sulawesi (Indonesia).

Material examined - KKan/9730 (one specimen); KVan/9777 (one specimen); KMom/9858 (one specimen); TFun/9830 (one specimen); KKiun/9938 (one specimen); KKiun/9946 (one specimen)

General description - Moderate to large species, specimens up to 200 mm long and 50 mm wide, after preservation. Body colour in life similar to colour in alcohol: bivium mottled green-grey with dark spots (white-tipped conical papillae distributed in the ambulacral and interambulacral areas); trivium grey-green with homogeneously distributed brown spots corresponding to cylindrical tube feet (with white sucking disc). Body wall smooth to the touch, thin. Mouth ventral surrounded by 20 yellow-green stout tentacles, base of the tentacles surrounded by a collar of small yellow conical papillae. Anus dorsal surrounded by a dark purple ring. Cuvierian tubules present, very thick, white and very readily ejected. Single Polian vesicle. Single stone canal. Calcareous ring stout, compoused of massive radial pieces having a deep, narrow anterior notch (from MASSIN 1999: 49, fig. 38a, p. 50).
Ossicles: Tentacles present curved rods, 50-400 mm long, slightly rugose at the extremities (fig. 29A). Dorsal and ventral body wall with poorly developed tables and buttons (fig 29B, C). Tables: rim of disc round and smooth, 25-35 µm across, disc perforated by three to four large central holes and two to six small peripheral holes, spire low, consisting of four pillars, sometimes ending in an incomplete crown, tables sometimes without spire (fig. 29B). Buttons 25-40 µm long, rim smooth but often irregular, one to three pairs of holes (fig. 29C). Ventral tube feet with irregular, perforated rods, up to 235 µm long (fig. 29D); large perforated plates, 100-155 µm long (fig. 29E); buttons, up to 70 µm long (fig. 29F) and poorly developed tables with spire reduced to knobs and disc 45-60 µm across (fig. 29G) Dorsal papillae with rods, perforated at the extremities, up to 300 µm long (fig. 29H), and some large tables with spire reduced to knobs (fig. 29J).

Diagnosis - See DEICHMANN 1958: 300, pl. 3 figs 13-23.

Ecology - Eulittoral, up to depths of about 8 m. Nocturnal, on coarse sand and on anoxic fine sand.

Distribution in the study region - Kanamai, Vanga, Mombasa; Kiunga Marine Reserve (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - Well known tropical, Indo-west Pacific species according to ROWE & GATES 1995, but the global distribution map as drawn by MASSIN's (1999: 51 fig 39) also shows subtropical records (Xisha Islands, Gulf of California, southern East Australia, New Caledonia). To the latter map the following localities in the WIO have to be added: Madagascar, Tuléar (CHERBONNIER 1988) and the Seychelles (DANIEL & HALDER 1974). Figure 54D shows the known distribution in the WIO in detail.

Holothuria (Stauropora) pervicax SELENKA, 1867
(fig. 30A-D, fig. 54E, pl. 3F)

Holothuria pervicax SELENKA, 1867: 327, pl. 18 fig. 54; MACNAE & KALK 1958: 42, 43, 99, 107, 117, 130; (from THANDAR 1984); MACNAE & KALK 1962: 104, 108, 112, 115; KALK 1959: 4, 22; DANIEL & HALDER 1974: 427; TORTONESE 1977: 275; BRANCH & BRANCH 1981: 248; CONAND 1999: 10, 12.
Holothuria curiosa pervicax; DANIEL & HALDER 1974: 417
Holothuria curiosa var. *pervicax*; A.M. CLARK 1952: 204.
Holothuria fusco-cinerea var. *pervicax*; PANNING 1944: 73.
Holothuria mammiculata HAACKE 1880: 46, 48.
Holothuria mamiculata; DANIEL & HALDER 1974: 423 (*lapsus calami*).
Holothuria (Mertensiothuria) pervicax; LEVIN 1979: 21; SLOAN *et al.* 1979: 122; HUMPHREYS 1981: 34; PRICE 1982:11; A.M. CLARK 1984: 99; CANNON & SILVER 1986: 23, fig. 6h; FÉRAL & CHERBONNIER 1986: 84 (colour picture), 85; CANNON & SILVER 1986: 23, fig. 6h; CHERBONNIER 1988: 107 (synonomy); MUKHOPADHYAY 1991: 405; ROWE & RICHMOND 1997: 304, 305 (colour drawing).
Holothuria (Stauropora) pervicax; MARSH *et al.* 1993: 64; ROWE & GATES 1995: 300 (synonymy); SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 488; SAMYN & VANDENBERGHE 2000: 5 (tab. 2).

Status and location type - Lectotype and paralectotypes MCZ 1424 (ROWE & GATES 1995).

Type locality - Zanzibar.

Material examined - KKan/9722 (one specimen); KKan/9723 (one specimen).

General description - Small to moderate species; the specimens at our disposition are eviscerated and strongly contracted due to inadequate preservation; size 115 x 21 mm and 26 x 15 mm, after preservation. Colour in alcohol same as colour in life, though somewhat faded: dorsal side light brown with four to six dark-brown, transverse bands (pl. 3F). All over the bivium sparsely distributed, large, yellowish extensions, each bearing a small and slender, brownish conical papillae, surrounded at its base by a dark brown ring. Ventral side light yellow, covered by numerous long cylindrical tube feet with similar colouration; tube feet distributed more or less evenly over the total surface. Mouth ventral, surrounded by 20 large, yellowish (spotted with brown) tentacles. Anus terminal, large, surrounded by a wide dark brown ring. Five groups of small white papillae surround the anal opening. Twenty short tentacle ampullae. Single, long Polian vesicle (one third of body length). Single stone canal ending in a circular madreporic plate. Longitudinal muscles well developed, bifid. Cuvierian tubules well developed and readily ejected. Calcareous ring small with the radial pieces twice as wide and long as the interradial pieces (see also CHERBONNIER 1988: 109, fig. 43H).
Ossicles: Tentacles with rods, 150-375 µm long, the large ones, originating from the stalk, slightly spinose at the extremities; the small ones, derived from the crown, smooth (fig. 30A). Dorsal and ventral body wall present similar tables and pseudobuttons (fig. 30B, C). Tables: rim of disc undulating, 30-40 µm across, perforated by four central holes and one to three smaller peripheral holes; spire, if present, low, consists of four (sometimes only three) pillars united by a single cross beam, ending in a small, poorly formed crown (fig. 30B, C). Pseudobuttons of the dorsal body wall, 40-55 µm long (fig. 30B). Pseudobuttons of the ventral body wall 25-35 µm long, with some perforations (fig. 30C). Ventral tube feet with rods perforated laterally and at the extremities, 160-200 µm long, giving rise to irregular plates and elongated buttons, 35-140 µm long (fig. 30D). Dorsal papillae with simple to more complex rods, the later similar to those in the ventral tube feet, giving rise to irregular perforated plates which can reach lengths of 190 µm (fig. 30E).

Diagnosis - See CHERBONNIER and FÉRAL 1984a: 685-687, fig. 12.

Ecology - In East Africa we observed this species between coral blocks on fine coralline sand; 20 m deep, but also in shallow, 2 m deep, water on coarse coral rubble overgrown with algae. In New-Caledonia, CHERBONNIER & FÉRAL (1984a) report depths up to 55 m and state that *H. (S.) pervicax* can thrive in colonies.

Distribution in the study region - Malindi, Kanamai, Mombasa, Chale Island.

Geographic distribution - Well-known tropical and subtropical Indo-west-Pacific (also recorded from the Red Sea, but not from the Persian Gulf) (CHERBONNIER & FÉRAL 1984a; CHERBONNIER 1988; ROWE & GATES 1995). Malindi, Kanamai, Mombasa and Chale Islands are new records for Kenya (this work); those from Sodwana Bay and Umkomaas are new records for the Republic of South Africa (pers. observ.). Figure 54E shows the known distribution in the WIO in detail.

Table 17 lists the other species within the subgenus *Stauropora* that are known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record appeared.

Currrent Species Name	Known WIO Distribution	Reference(s)
Holothuria (Stauropora) dofleinii AUGUSTIN, 1908	WIO, East Africa (unspecified)	ROWE *in* ROWE & RICHMOND 1997
	Mozambique (Tunghi Bay)	PEARSON 1910; 1913; DANIEL & HALDER 1974
	Zanzibar	PEARSON 1910; 1913; DANIEL & HALDER 1974
H. (Stauropora) modesta LUDWIG, 1875	Red Sea (Kosseir)	LAMPERT 1885; PRICE 1982
	Arabian Sea?	DANIEL & HALDER 1974
Holothuria (Stauropora) olivacea LUDWIG, 1888 (see also discussion)	Red Sea (Dissei Island)	TORTONESE 1953a[(1)]; PRICE 1982[(1)]
	Madagascar (Nosy Bé, Antsakoaba, Tuléar)	CHERBONNIER 1988

Table 17 - Other species within the holothurian subgenus *Stauropora* known to occur in the shallow-waters of the WIO. Cited as [(1)] *Holothuria fusco-olivacea* FISHER or *H. fuscoolivacea* FISHER.

Subgenus *Theelothuria* DEICHMANN, 1958

Diagnosis (after ROWE 1969: 157) [Type species: *Holothuria princeps* SELENKA, 1867 by original designation]

Size moderate to large (250 mm) with trivium distinctly flattened and bivium arched; tube feet irregularly arranged on the ventral surface; large wart-like papillae spread without order over the dorsal surface; mouth ventral, surrounded by 18-20 tentacles, with a collar of papillae at the base of the tentacles; anus terminal, anal papillae usually present; body wall can be up to 6,5 mm thick, gritty to the touch; calcareous ring stout, radial pieces with rounded anterior notch and large posterior bifurcations, radial pieces up to twice as long as the interradial pieces. Ossicles: body wall comprise well developed tables with spinose rim, short to high spire terminating in a small cluster of spines; some tables with perfectly smooth spire tapering to a pointed apex giving the table a tack-like appearance; and buttons that are few in number, simple to very nodulous, often irregular, perforated by numerous holes.

Currently fourteen species are regarded as being valid: *Holothuria (Theelothuria) aspertita* CHERBONNIER & FÉRAL, 1981; *H. (T.) foresti* CHERBONNIER & FÉRAL, 1981; *H. (T.) hamata* PEARSON, 1913; *H. (T.) klunzingeri* LAMPERT, 1885; *H. (T.) maculosa* PEARSON, 1913; *H. (T.) michaelseni* ERWE, 1913; *H. (T.) notabilis* LUDWIG, 1875; *H. (T.) paraprinceps* DEICHMANN, 1938; *H. (T.) princeps* SELENKA, 1867; *H. (T.) spinifera* THÉEL, 1886; *H. (T.) squamifera* SEMPER, 1868; *H. (T.) turriscelsa* CHERBONNIER, 1980 and *H. (T.) viridia* CHERBONNIER, 1980. Only *H. (T.) turriscelsa* CHERBONNIER, 1980 has been reported from the shallow-waters of Kenya (with Pemba Island). The records of MARSHALL *et al.* 2001 of *H. (T.) spinifera* are unconfirmable as no taxonomic description of this species is included in the latter's work. However, as MARSHALL *et al.* 2001 (p. 50) report the species as one of the four most wanted species in the trading business, it must be abundantly present in Kenyan waters and thus our extensive sampling effort should have exposed at least some individuals. Hence, it is here argued that MARSHALL *et al.*'s (2001) records undoubtedly are misidentifications and therefore the species most possibly does not belong to the Kenya fauna.

Holothuria (Theelothuria) turriscelsa CHERBONNIER, 1980.
(fig. 31A-G, fig. 54F)

Holothuria (Theelothuria) turriscelsa CHERBONNIER, 1980: 644, fig. 15A-L, pl.I E; MASSIN 1999: 53 (synonomy and records before 1999); SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 27, pl. 2A, B (colour pictures).

Status and location type - Holotype, PMNH.

Type locality - New Caledonia.

Material examined - TFun/9813 (one specimen); TFun/915 (one specimen); KKiun/9947 (two specimens).

General description - The specimens at our disposition range from 155 to 200 mm in length and from 28 to 54 mm in width, after preservation. Body colour in life similar to colour in alcohol: yellow-green ventrally with numerous dark green to brown spots corresponding to the tube feet with white sucking discs;

mottled dark green to yellow dorsally; the green patches correspond to the basis of the short, well developed dark brown conical papillae; the smaller yellow spots bear shorter dark brown papillae. Bivium clearly separated from the flattened trivium. Body wall several mm thick. Mouth ventral surrounded by 20 large, yellow to green tentacles. Anus dorso-terminal, guarded by dark-brown conical papillae. Tube feet spread evenly over the ambulacral and interambulacral areas of the trivium; papillae in the bivium spread over the total surface. Well developed white to almost translucent Cuvierian tubules, which were very readily ejected upon collection. Single club-shaped Polian vesicle. Single, segmented stone canal ending in an oval madreporic plate. MASSIN (1999) describes the calcareous ring as "stout composed of massive radial pieces characterized by a deep rounded anterior notch and two large posterior points; interradial pieces with a small anterior median tooth [Sic.]" (see also MASSIN 1999: 54, fig. 42a)

Ossicles: Tentacles with rods, 150-625 µm long, the longest rods are spined over the total surface; the smaller rods only moderately spined (fig. 31A). Ventral and dorsal body wall with tables, some knobbed buttons and ellipsoids (fig. 31B, C). Tables with rim of disc spinose, disc 65-80 µm across, disc perforated by four large central holes and numerous small peripheral holes which in the larger tables are arranged in concentric circles, spire relatively long consist of four pillars, united by a one to several cross beams and ends in a narrow spiny crown (fig. 31B). Ellipsoids with nodules on the lateral and median side, approximately 65 µm long, often irregular in outline (fig. 31C). Dorsal papillae with tables similar to those of the body wall, perforated plates and numerous rods (fig. 31D), no buttons nor ellipsoids. Ventral tube feet with tables similar to those in the body wall (fig. 31E); rods up to 400 µm long, perforated in the lateral extensions (fig. 31F); large perforated plates, 130-200 µm long (fig. 31G); ellipsoids and some knobbed buttons similar to those of the tube feet.

Diagnosis - See CHERBONNIER 1980: 644-646, fig. 15.

Ecology - Strictly nocturnal species. *H. turriscelsa* was found on sandy patches between coral slabs. When disturbed numerous Cuvierian tubules are very readily ejected.

Distribution in the study region - Fundu (Pemba Island); Kiunga Marine Reserve.

Geographic distribution - Tropical Indo-west Pacific (not recorded from the Red Sea nor from the Persian Gulf) (see also SAMYN & VANDENBERGHE 2000). Figure 54F shows the known distribution in the WIO in detail.

Table 18 lists the other species within the holothurian subgenus *Theelothuria* that are known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record appeared.

Current Species Name	Known WIO Distribution	Reference(s)
H. (Theelothuria) hamata PEARSON, 1913	Gulf of Suez (Al Sayadh; Suez)	CHERBONNIER 1955; PEARSON 1913; DANIEL & HALDER 1974; PRICE 1982
	Seychelles (Aldabra[9])	SLOAN *et al.* 1979
H. (Theelothuria) klunzingeri LAMPERT, 1885	Gulf of Suez (unspecified)	CHERBONNIER 1955; PRICE 1982
	Red Sea (Beilul, Assab, Kosseir)	LAMPERT 1885; LUDWIG 1886; THÉEL 1886
	Gulf of Aden?	DANIEL & HALDER 1974
H. (Theelothuria) maculosa PEARSON, 1913	Madagascar (Nosy Bé; Tuléar)	CHERBONNIER 1988
	Seychelles (Aldabra)	PEARSON 1913; DANIEL & HALDER 1974; HUGHES & GAMBLE 1977; SLOAN *et al.* 1979; A.M. CLARK 1984
	Mozambique (Inhaca)	SLOAN et al. 1979?; CHERBONNIER 1988; MRAC records, pers. observ
	West Indian Ocean to West Pacific Ocean	ROWE & RICHMOND 1997
H. (Theelothuria) notabilis LUDWIG, 1874	Mozambique (South coast)	THANDAR 1984?
	South Africa (KwaZulu-Natal)	pers. observ.
H. (Theelothuria) spinifera THÉEL, 1886	Gulf of Suez (Sheikh Riyah)	CHERBONNIER 1955; PRICE 1982
	Red Sea (Hurghada)	MORTENSEN 1937; CLARK & ROWE 1971; PRICE 1982
	Persian Gulf (Kharg)	HEDING 1940b; PRICE 1982
	Kenya?	MARSHALL *et al.* 2001
	Tanzania?	MARSHALL *et al.* 2001
	Seychelles (Mahé)	MRAC record, pers. observ.
H. (Theelothuria) squamifera SEMPER, 1868	Gulf of Aqaba (Aqaba)	CHERBONNIER 1979a; PRICE 1982
	Gulf of Suez (Suez Bay)	CHERBONNIER 1955; PRICE 1982

[9] SLOAN *et al.* (1979) report on two specimens that they label *Holothuria (Theelothuria)* sp. cf. *H. hamata* PEARSON 1913. It remains to be investigated whether these specimens are indeed *H. (T.) hamata.*

	Red Sea (Kosseir) Gulf of Aden?	LAMPERT 1885 DANIEL & HALDER 1974

Table 18 - Other species within the holothurian subgenus *Theelothuria* known to occur in the shallow-waters of the WIO.

Subgenus *Thymiosycia* PEARSON, 1914

Diagnosis (after ROWE, 1969:145) [Type species: *Holothuria impatiens* FORSKÅL, 1775 by original designation].

Small to moderate species with cylindrical to vermiform body reaching lengths up to 350 mm; tube feet and papillae arranged more or less irregularly over the dorsal and ventral surface, though occasionally restricted to the ambulacral areas; mouth terminal, surrounded by 18-20 tentacles, surrounded by collar of papillae around the base; anus terminal mostly guarded by some kind of anal pedicels; body wall soft, thin, sometimes gritty to the touch; calcareous ring stout, radial pieces up to three times the length of the interradial pieces. Ossicles comprise stout tables with flattened disc, rim smooth, circular to squarish in outline, four pillars forming a spire of moderate height ending in a cluster of small spines; buttons with three to four pairs of holes, mostly regular in outline.

Currently thirteen species are recognised as being valid: *Holothuria (Thymiosycia) arenicola* SEMPER, 1868; *H. (T.) conusalba* CHERBONNIER & FÉRAL, 1984; *H. (T.) decorata* VON MARENZELLER, 1882; H. *(T.) gracilis* SEMPER, 1868; *H. (T.) hartmeyeri* ERWE, 1913; *H. (T.) impatiens* (FORSKÅL, 1775); *H. (T.) milloti* CHERBONNIER, 1988; *H. (T.) marginata* SLUITER, 1901; *H. (T.) minax* THÉEL 1886; *H. (T.) remollescens* LAMPERT, 1885; *H. (T.) strigosa* SELENKA, 1867; *H. (T.) thomasi* PAWSON & CAYCEDO, 1980; *H. (T.) truncata* LAMPERT, 1885. It must however be stressed that this subgenus is in urgent need of revision and that it cannot be excluded that several of these species will prove to be synonyms or will need to be allocated to a different subgenus (SAMYN, MASSIN & ROWE in prep.). This observation is further evidenced by a recent revision of the subgenus *Mertensiothuria* (SAMYN & MASSIN in press) in which *H. aphanes* LAMPERT 1885 and *H. hilla* LESSON, 1830 were transferred form *Thymiosycia* to *Mertensiothuria.* ROWE (*in* ROWE & GATES 1995) further referred the recently described *H. (T.) altaturricula* CHERBONNIER & FÉRAL, 1984 to the synonymy of *H. (P.) samoana* LUDWIG, 1874, *H. macroperona* H.L. CLARK, 1938 to the synomy of *H. (T.) hartmeyeri* ERWE, 1913, *H. truncata* LAMPERT, 1885 and the different colour forms of *H. impatiens* (*H. impatiens* var. *concolor* H.L CLARK, 1921; *H. impatiens* var. *pulchra* H.L. CLARK, 1921; *H. impatiens* var. *lutea* H.L. CLARK, 1921; *H. impatiens* var. *bicolor* H.L. CLARK, 1921) to the synonymy of *H. (T.) impatiens* (FORSKÅL, 1775). In my opinion ROWE's decision on *H. (T.) truncata* needs reconsideration for the tables depicted by CHERBONNIER (1974) have a spinier crown as those normally found in *H. (T.) impatiens*. Even so, *H. (T.) milloti* needs careful re-examination, for it most probably is but a synonym of *H. arenicola* (SAMYN, MASSIN & ROWE in prep.).

Only *H. (T.) arenicola* and *H. (T.) impatiens* have been reported from the shallow-waters of Kenya (with Pemba Island), they are keyed hereunder.

Key to the species of Kenya (with Pemba Island).

1. Bivium yellow to beige with a row of dark brown spots on each ambulacral area. Cuvierian tubules absent ..... ***Holothuria (Thymiosycia) arenicola* SEMPER, 1868**

1'. Bivium beige with irregular brown to dark brown blotches. Cuvierian tubules present ..... ***Holothuria (Thymiosycia) impatiens* (FORSKÅL, 1775)**

Holothuria (Thymiosycia) arenicola SEMPER, 1868
(fig. 32A-E, fig. 54G)

Holothuria arenicola SEMPER, 1868: 81, pls. 20, 30 fig. 13, 35 fig. 4; TORTONESE 1936a: 234; PANNING 1944: 69; TORTONESE 1953a: 44; MACNAE & KALK 1962: 108, 112; CHERBONNIER 1967: 56; JAMES 1969: 61; JAMES & PEARSE 1969: 105; DANIEL & HALDER 1974: 426; HICKMAN 1998: 44 (colour pictures); CONAND 1999: 12, 21, 39.

Sporadipus (Acolopos) maculatus BRANDT 1835: 46.

Holothuria maculata; DANIEL & HALDER 1974: 428.

Actinopyga maculata; DANIEL & HALDER 1974: 426.

Holothuria boutani HÉROUARD 1893: 132, pl. 7 fig. A.
Holothuria arenicola var. *boutani*; CHERBONNIER 1955: 153.
Holothuria fusco-punctata; VANEY 1905: 187; DANIEL & HALDER 1974: 417.
Holothuria (Thymiosycia) arenicola; SLOAN *et al.* 1979: 123; PRICE 1981: 9; PRICE 1982: 11; A.M. CLARK 1984: 99; CANNON & SILVER 1986: 25; CHERBONNIER 1988: 82 (synonymy); MUKHOPADHYAY 1991: 408; ROWE & GATES 1995: 301; ROWE & RICHMOND 1997: 304; James 1999: 15; SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 27.

Status and location type - Syntype ZMH E. 2508 (ROWE & GATES 1995).

Type locality - Viti Levu, Fiji (ROWE & GATES 1995).

Material examined - KKiun/9945 (one specimen); KMal/9875 (one specimen); KMal/9876 (one specimen); KMal/9877 (one specimen); KMal/9878 (one specimen); KMal/9879 (one specimen); KMal/9880 (one specimen); KVan/9778 (one specimen).

General description - Relatively small species, ranging from 80-125 mm in length and from 15-40 mm in width, after preservation. Colour in alcohol similar to the colour in life: whitish-grey to yellow ventrally and yellow to beige with a row of dark brown spots on each ambulacral area dorsally; some specimens are more orange with at the anterior and posterior end a white area; the dorsal blotches can fuse together and form an irregular line. Mouth terminal surrounded by 20 small, brownish tentacles. Anus terminal, surrounded by non-calcified papillae. Body wall is only a few mm thick, gritty to the touch. Ventral tube feet, wide but short, distributed over the ambulacral and interambulacral areas. Dorsal tube feet smaller, distributed over the total surface. Cuvierian tubules absent. Tentacle ampullae short. Single Polian vesicle. Single stone canal ending in a narrow madreporic plate.
Ossicles: Tentacles with rods, 70-135 µm long, the smallest smooth, the larger ones spiny at the extremities (fig. 32A). Ventral and dorsal body wall with the same type of tables and buttons (fig. 32B, C). Tables with rim of disc circular or squarish, disc 40-60 µm across, perforated by four central holes and four to eight peripheral holes, spire moderately long consists of four pillars united by a single cross beam and ending in a rather narrow spiny crown (fig. 32B). Buttons smooth, rim usually rather regular, three to five pairs of holes, 55-90 µm long (fig. 32C). Ventral tube feet with buttons, 50-100 µm long, and elongated plates, 100-180 µm long (fig. 32D). Dorsal tube feet with similar elongated plates as the ones in the ventral tube feet, though the outline is generally more irregular (fig. 32E), and few reduced tables (fig. 32F). Anal papillae with elongated plates similar to the ones of the tube feet and tables similar to the ones of the body wall (fig. 32G)

Diagnosis - See SEMPER 1868: 81, pls 20, 30 fig 13.

Ecology - In Kenya, *H. (T.) arenicola* invariably digs its body in the sand, hereby preferentially hiding under coral or sandstone slabs; its presence is only betrayed by a mound in the sand, at the summit of which characteristic holothurian faeces can be found (see also MACNAE & KALK 1962: 108). In Kenya, *H. arenicola* was only observed in the intertidal zone, but ROWE (*in* ROWE & GATES 1995) reports depths up to 30 m.

Distribution in the study region - Kiunga Marine Reserve, Malindi.

Geographic distribution - Tropical Indo-West Pacific Ocean (with the Red Sea, without the Persian Gulf) (MASSIN 1996a). Figure 54G shows the known distribution in the WIO in detail.

Holothuria (Thymiosycia) impatiens (FORSKÅL, 1775)
(fig. 33A-E, fig. 54H, pl. 3G)

Fistularia impatiens FORSKÅL, 1775: 121, pl. 39B
Holothuria botellus SELENKA 1867: 335, pl. 19 figs 82-84; DANIEL & HALDER 1974: 423
Holothuria impatiens; TORTONESE 1936a: 234; TORTONESE 1937-38; 191; HEDING 1940b: 121; CHERBONNIER 1955: 148; A.M. CLARK 1952: 204; KALK 1959: 22 (non *H. cumulus* H.L. CLARK 1921); MACNAE & KALK 1962: 108, 112; CHERBONNIER 1963: 5; CHERBONNIER 1967; JAMES 1969: 61; JAMES & PEARSE 1969: 105; DANIEL & HALDER 1974: 428; HICKMAN 1998: 45 (colour pictures); CONAND 1999: 10, 21, 39; MARSHALL *et al.* 2001: 46 (tab. 29).
Holothuria (Thymiosycia) impatiens; PRICE 1981: 9; MUKHOPADHYAY 1991: 407; MASSIN 1999: 57 (synonomy and records before 1999), fig. 111e (colour plate); SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 489; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 18 (tab. 4), 28.

Status and location type - Status and whereabouts undetermined (ROWE & GATES 1995).

Type locality - Red Sea (ROWE & GATES 1995).

Material examined - TFun/9828 (one specimen); TFun/9829 (one specimen); KKiun/9944 (four specimens); TMes/98100 (one specimen); TMes/98101 (one specimen).

General description - The size of the collected specimens varies from 13x73 to 30x260 mm, after preservation. Body colour in life similar to that in alcohol. Dorsal body wall beige with brown to dark brown blotches (pl. 3G), ventral side uniform beige. Mouth ventral surrounded by 20 tentacles with a ring of minute conical papillae at the base. Anus terminal. Body wall thin, rough to touch. Tube feet presented on conical elevation of the body wall (especially in the specimens from Fundu), sparsely distributed in both ambulacral and interambulacral areas, visible as narrow yellowish tubes. Respiratory trees short (one third of body length). Muscles bifid and wide. Single Polian vesicle, short (one seventh of body length). Single stone canal ending in simple madreporic plate. Gonad with long, beige tubules. Cuvierian tubules present, white, long and thick.

Ossicles: Tentacles with curved rods, 75-350 µm long, spiny at the extremities (fig. 33A). Ventral and dorsal body wall with similar tables and buttons (fig. 33B, C, D, E). Tables 80-90 µm across, rim of disc smooth, rounded to squarish in outline, perforated by four central and up to eight, relatively large peripheral holes; spire consists of four short pillars, united by a single cross beam, ending in a spiny crown with large central hole (fig. 33B,D). Buttons 60-100 µm long, smooth, with three to four pairs of holes, irregular, sometimes with median longitudinal ridge (fig. 33C, E). Ventral and dorsal tube feet with tables similar to those of the body wall, long buttons, and rods, perforated distally and laterally, 175-270 µm long (fig. 33F, G).

Diagnosis - See PANNING 1935c: 86, fig. 72a-u.

Ecology - Usually well concealed among rocks, more rarely in sand. Our specimens were found from 0 to10 m deep; LANE *et al.* (2000) report a bathymetric range from 0 to 30 m.

Distribution in the study region - Kiunga Marine Reserve; Mombasa, Fundu; Mesali (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - Circum-tropical and abundant throughout the Indo-Pacific (with the Red Sea and the Persian Gulf); it is also known from the Mediterranean Sea (TORTONESE 1953b). The distribution map as drawn by MASSIN (1999: 58, fig. 45) gives the global distribution, but the following localities have to be added to the WIO: Gulf of Suez, Suez (SEMPER 1868; 1869; HÉROUARD 1893; MITSIKURI 1912; CHERBONNIER 1955), Taufic (MORTENSEN 1926); Adabiya Point (JAMES 1969; JAMES & PEARSE 1969) (see also GRAY 1872; ERWE 1919; DANIEL & HALDER 1974; PRICE 1982 for unspecified records from the Gulf of Suez); Gulf of Aqaba, Aqaba (TORTONESE 1977), Dahab (A.M. CLARK 1952) (see also DANIEL & HALDER 1974 and PRICE 1982 for unspecified records from the Gulf of Aqaba); Saudi Arabia, Abulat Island., Lith (CHERBONNIER 1955), Jeddah (TORTONESE 1979); Eritrea, Entedebir (CHERBONNIER 1967), Perim Island. (LUDWIG 1886), Massaua (TORTONESE 1936a; CHERBONNIER 1963), Dissei & Nocra Islands (TORTONESE 1953a) (see also TORTONESE 1937-38 for unspecified record from Eritrea); Djibouti (VANEY 1905; CHERBONNIER 1955); Gulf of Aden (DANIEL & HALDER 1974); Persian Gulf, Farur (HEDING 1940b), Arabian Sea (CLARK & ROWE 1971); Kenya, Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000), Mombasa (this work); Tanzania, Fundu and Mesali (this work); northern Mozambique (KALK 1959, as *H. impatiens* and as *H. cumulus*; THANDAR 1984, including specimens identified as *H. (?Lessonothuria) cumulus*), Juan de Nova (LUDWIG 1899; MITSIKURI 1912); southern Mozambique (THANDAR 1984, as *H. (?Lessonothuria) cumulus*; MRAC record pers. observ.); Republic of South Africa, Banhga Nek and Sodwana Bay (pers. observ.) Madagascar, Antsakoaba, Fort Dauphin, St. Augustin, Tuléar (CHERBONNIER 1988). Figure 54H shows the known distribution in the WIO in detail.

Remarks - The specimens from Kiunga (from 13x33 to 20x72 mm) are distinctly smaller then those from Fundu (from 25x250 to 30x260 mm); the former present a body morphology which at first sight seems different from that presented by the specimens from Fundu: (1) the tube feet in the Kiunga specimens are presented on lower conical elevations, (2) the colouration of the Kiunga specimens is more uniform beige interspersed with brownish blotches which occasionally form transverse bands. Ossicle morphology, however, shows no variation in the specimens from both localities (see also MASSIN 1996a; 1999).

Table 19 lists the other species within the subgenus *Thymiosycia* that are known to occur in the shallow waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record for East Africa appeared.

Current Species Name	Known WIO Distribution	Reference(s)
H. (Thymiosycia) decorata VON MARENZELLER, 1882	Mauritius	LAMPERT 1885; THÉEL 1886
	East Coast of Africa (unspecified)	DANIEL & HALDER 1974
H. (Thymiosycia) gracilis SEMPER, 1868	Zanzibar	LAMPERT 1885
	Madagascar (Nosy Bé)	CHERBONNIER 1988
H. (Thymiosycia) milloti CHERBONNIER, 1988	Glorious Island	CHERBONNIER 1988
H. (Thymiosycia) remollescens LAMPERT, 1885	Red Sea (Kosseir)	LAMPERT 1885; THÉEL 1886; PRICE 1982
	Arabian Sea?	DANIEL & HALDER 1974
	Seychelles (Aldabra)	SLOAN *et al.* 1979; A.M. CLARK 1984
	South West Indian Ocean	DANIEL & HALDER 1974
H. (Thymiosycia) strigosa SELENKA, 1867	Gulf of Suez (Suez)	HÉROUARD 1893 [1]; PRICE 1982
	Red Sea (unspecified)	LUDWIG 1877 [1880]; LAMPERT 1885; PRICE 1982
	South Yemen (Soccotra)	LEVIN 1979
	Zanzibar	SELENKA 1867; LAMPERT 1885; SEMPER 1868, 1869
	Somalia (Sar Uanle)	TORTONESE 1980
	Madagascar (St. Augustin)	CHERBONNIER 1988
	Arabian Sea?	DANIEL & HALDER 1974
	South West Indian Ocean	DANIEL & HALDER 1974

Table 19 - Other species within the holothurian subgenus *Thymiosycia* known to occur in the shallow-waters of the WIO. Cited as [1] *Holothuria boutani* HÉROUARD.

Genus *Pearsonothuria* LEVIN, KALIN & STONINK, 1984.

Diagnosis [Type species: *Holothuria graeffei* SEMPER, 1868 by monotypy].
Moderate to large species with cylindrical body reaching lengths up to 350 mm. Tube feet of the trivium in ambulacral areas only. Papillae of the bivium few in number, distributed in longitudinal lines. Mouth ventral, surrounded by 20 tentacles with very specific colouration: black with a white edge. Calcareous ring stout, with the radial pieces almost undistinguishable from the interradial pieces. Ossicles comprise small rosettes that can look like perforated plates and knobbed pseudo-tables. Tentacles with rosettes only.
Pearsonothuria graeffei is present in the shallow-waters of Kenya and Pemba Island.

Pearsonothuria graeffei (SEMPER, 1868)
(fig. 34A-C, fig. 55A, pl. 3H)

Holothuria graeffei SEMPER, 1868: 78, pl. 30(9) [as *Holothuria gräffei*].
Bohadschia drachi CHERBONNIER 1954a: 253; CHERBONNIER 1955: 134; DANIEL & HALDER: 417.
Bohadschia graeffei; ARAKAKI & FAGOONEE 1996: 122.
Pearsonothuria (Bohadschia) graeffei; WEINBERG 1997: 248 (colour picture).
Pearosonothuria graeffei; ; MARSHALL *et al.* 2001: 47 (*lapsus calami*).
Pearsonothuria graeffei; MASSIN 1999: 62 (synonomy and records before 1999), fig. 111g, h (colour plates); CONAND 1999: 12, 21, 39, pl. 2 (colour picture); SAMYN 2000: 15 (tab. 1); LANE *et al.* 2000: 489; MARSHALL *et al.* 2001: 46 (tab. 29).

Status and location type - ZMB, ZMG, ZMH E.2696 (ROWE & GATES 1995).

Type locality - Fiji (Viti Island) (MASSIN 1999).

Material examined - KMal/9764 (one specimen); KMal/9765 (one specimen); KShim/9766 (one specimen); TFun/9803(one specimen); TFun/9804 (one specimen); TFun/9805 (one specimen).

General description - Specimens ranging from 150 to 347 mm in length and from 28 to 42 mm in width, after preservation. Body colour in life pale cream with numerous small brown specklings and with brown patches (pl. 3H). Body elongated and slender, dorsally somewhat rounded, ventrally slightly flattened. Bivium with two or more longitudinal folds an numerous transverse folds reaching into the trivium. Mouth ventral surrounded by 23-28 black tentacles (brown in alcohol) with white edge, of which two or three are distinctly smaller. Anus terminal, relatively large, no anal papillae. Body wall 2-3 mm thick, smooth to the touch. Trivium with three distinct longitudinal bands of large brownish tube feet with dark brown sucking disk, in four to seven rows on the median ambulacral area, in two to three rows on the lateral ambulacral areas. Bivium with small, low papillae scattered over total dorsal surface. Single very large Polian vesicle. Respiratory trees well developped, reaching to calcareous ring. Cuvierian tubules abundantly present, but usually not ejected upon disturbance. Very massive calcareous ring, with the radial pieces almost undistinguishable from the interradial pieces.

Ossicles: Tentacles with rods which can form rosettes (fig. 34A); Ventral and dorsal body wall with the same type of knobbed pseudo-tables and small rosettes (fig. 34B). Ventral and dorsal tube feet with small, very complex rosettes that resemble those from the body wall (fig. 34C)

Diagnosis - See CHERBONNIER 1988: 49-51, fig. 17A-F.

Ecology - *Pearsonothuria graeffei* was always observed feeding on coral substrate. Although no conclusive quantitative measurements were taken, the population-size on the West coast of Pemba was markedly greater after the 1998 El Nino then before.

Distribution in the study region - Mombasa, Shimoni, Malindi, Fundu and Mesali.

Geographic distribution - Well known species from the tropical Indo-west Pacific (with the Red Sea, without the Persian Gulf). The global distribution map as drawn by (MASSIN 1999: 63) gives the global distribution, however the following localities have to be added to the WIO: Gulf of Aqaba, Aqaba (CHERBONNIER 1979a; PRICE 1982, both as *Bohadschia drachi* CHERBONNIER 1954); Saudi Arabia, Abulat Island.(CHERBONNIER 1954a; 1955, as *B. drachi*), Jeddah (TORTONESE 1979, as *B. graeffei*); Eritrea, Nocra Island (TORTONESE 1953a, as *Bohadschia graeffei* (SEMPER, 1868)) (see also DANIEL & HALDER 1974 and PRICE 1982 for unspecified records for the Red Sea); Kenya, Malindi, Mombasa, Shimoni (this work); Tanzania, Fundu and Mesali (this work; see also MARSHALL *et al.* 2001 for an unspecified record from Tanzania); Madagascar; Tuléar (CHERBONNIER 1988; see also CONAND 1999 for an unspecified record from Madagascar); Mauritius (ARAKAKI & FAGOONEE 1996, as *Bohadschia graeffei*). Figure 55A shows the known distribution in the WIO in detail.

Family Stichopodidae HAECKEL, 1896

Key to the Genera of Kenya (with Pemba island)

1. Moderate to large species; body colour in life greenish; well developed papillae on the radial areas of bivium; ossicles of body wall consist of well developed tables, numerous rosettes, branched rods, C and S shaped rods ..... ***Stichopus* BRANDT, 1835**

1'. Large species; body colour grey to red; very large, sometimes branching papillae on bivium; ossicles of body wall seldomnly with poorly developed tables, miliary granules, dichotomously branched rods, C or S-shaped rods never present ..... ***Thelenota* H.L. CLARK, 1921**

Genus *Stichopus* BRANDT, 1835

Diagnosis [Type-species: *Stichopus (Perideris) chloronotus* BRANDT, 1835 by subsequent designation (H.L. CLARK 1933)]

Size from moderate to large (300 mm); body firm, quadrangular in section; flattened trivium; ambulacral areas of bivium covered by papillae of different sizes; trivium with numerous tube feet in the radial areas only; calcareous ring well developed with the radial pieces two to three times as large as the interradial pieces; mouth ventral surrounded by 20 tentacles; anus terminal, unguarded; Cuvierian tubules absent. Ossicles in body wall consist of tables, C-or S-shaped rods and rosettes, holothuriid buttons in four spp.; tentacles with curved rods; tube feet with tables, large perforated plates and rods with median perforated extension.

Currently some 20 species are recognised as being valid (MASSIN pers. comm; ROWE unpublished manuscript)[10]: *Stichopus badionotus* SELENKA, 1867 (usually placed in *Isostichopus*); *S. californicus* (STIMPSON, 1857); *S. chloronotus* BRANDT, 1835; *S. ellipes* H.L. CLARK, 1938; *S. flaccus* LIAO, 1980; *S. fuscus* LUDWIG, 1875; *S. herrmanni* SEMPER, 1868; *S. horrens* SELENKA, 1867; *S. johnsoni* THÉEL, 1886; S.

[10] ROWE (pers. comm.) noted that *Stichopus anapinusus* (LAMPERT, 1885) and *S. paradoxus* LAMPERT, 1885 are not recognisable and that they could as well be *Holothuria* spp; *Eostichopus arnesoni* CUTRESS & MILLER, 1982 could also belong to *Stichopus*; *S. flaccus* LIAO 1980 could be a synonym of *S. naso* SEMPER, 1868 and *S. mollis* (HUTTON, 1872) probably must be transferred to *Neostichopus* DEICHMANN, 1948.

leucothele (LAMBERT, 1986); *S. ludwigi* ERWE, 1913; *S. macroparentheses* H.L. CLARK, 1922; *S. mollis* (HUTTON, 1872); *S. monotuberculatus* (QUOY & GAIMARD, 1833); *S. naso* SEMPER, 1868; *S. noctivagus* CHERBONNIER, 1980; *S. parvimensis* (H.L. CLARK, 1913); *S. pseudohorrens* CHERBONNIER, 1967; *S. quadrifasciatus* MASSIN, 1999 and *S. vastus* SLUITER, 1888. It is surprising that only three of these species were found in the shallow-waters of Kenya (with Pemba Island), they are keyed hereunder.

It must be stressed that the genus *Stichopus* is in very critical need of review. ROWE (pers. comm.) not only argues that a new genus possibly must be created for those species that have holothuriid-like buttons [*i.e. S. californicus* (STIMPSON, 1857), *S. leucothele* (LAMPERT, 1896), *S. johnsoni* THÉEL, 1886 and *S. parvimensis* (H.L. CLARK, 1913)]; but also that several species most probably need to be transferred to other genera (see also footnote). However, as the *Stichopus* spp. from Kenya (with Pemba Island) do not pose identification and classification problems, further discussion of the taxonomy of *Stichopus* falls outside the scope of the present monograph.

Key to the Species of Kenya (with Pemba island)

1. Bivium without conspicuous double rows of large papillae. Ossicles of the body wall comprise numerous tables, C-or S-shaped ossicles, in addition to rosettes **2**

1'. Bivium with two conspicuous double dorsal rows of large papillae and two lateral rows of papillae. Ossicles of the body wall comprise numerous tables and C-shaped ossicles, never rosettes ..... ***Stichopus chloronotus* BRANDT, 1835**

2. Bivium more or less bright olive-green with numerous brownish spots, trivium slightly lighter. .... ***Stichopus herrmanni* SEMPER, 1868**

2'. Bivium yellow to brown with brown-grey areas (especially in the larger specimens), trivium yellow to brown. Bivium clearly distinguishable from trivium due to the presence of a lateral fringe of large papillae..... ***Stichopus monotuberculatus* (QUOY & GAIMARD, 1833)**

Stichopus chloronotus BRANDT, 1835
(fig. 35A-F, fig. 55B, pl. 4A)

Stichopus (Perideris) chloronotos BRANDT, 1835: 50.
Stichopus coronpus; PRICE 1971: 166 (*lapsus calami*?).
Stichopus cylindricus HAACKE 1880: 47; DANIEL & HALDER 1974: 423.
Stichopus chloronatus; DANIEL & HALDER 1974: 429 (*lapsus calami*).
Stichopus chlorontus; ARAKAMI & FAGOONEE 1996: 121 (*lapsus calami*).
Stichopus chloronotus; CHERBONNIER 1967: 57; SLOAN *et al.* 1979: 123; PRICE 1982: 11; A.M. CLARK 1984: 87, 99; FÉRAL & CHERBONNIER 1986: 94 (colour picture), 95; CANNON & SILVER 1986: 27, figs 4h, 7h (colour drawing); THANDAR 1987a: 280; CHERBONNIER, 1988: 146 (synonymy); MUKHOPADHYAY 1991: 408; ALLEN & STEENE 1994: 245 (colour picture); MASSIN 1996a: 34; GOSLINER *et al.* 1996: 281 (colour picture); ROWE & RICHMOND: 306, 307 (colour drawing); CONAND 1999: 10, 12, 39, pl. 2; SAMYN 2000: 15 (tab. 1), SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 18 (tab. 4), 30, pl. 2C; MARSHALL *et al.* 2001: 46 (tab. 29), 58 (tab. 37), 59.

Status and location type - Holotype (probable); whereabouts undetermined (ROWE & GATES 1995).

Type locality - Insula Lugunor and Guam (as Guahan) (ROWE & GATES 1995).

Material examined - KMom/9768 (one specimen); KKan/9728 (one specimen); KKan/9729 (one specimen); KMom/9847 (one specimen); KMom/9848 (one specimen); KMom/9849 (one specimen); KMom/9850 (one specimen); KMom/9851 (one specimen).

General description - Specimens ranging from 85 to 145 mm in length and from 24 to 40 mm in width, after preservation. Live specimens approximately 20 % larger. Body colour of live specimens is dark green to brown (pl. 4A); preserved specimens faint brown to whitish; ventral side slightly lighter in colour. Mouth ventral, surrounded by large dark green papillae and 19-20 white to grey (after preservation) tentacles. Anus terminal surrounded by five large papillae. Body wall smooth, 2-4 mm thick. Ventral tube feet, long, dark green, spread over the radial and interradial areas, posteriorly in four distinct rows. Dorsal side with two rows of large, conical, yellow to orange papillae; laterally, single row of similar papillae. Tentacle ampullae short. Single to two Polian vesicles large. Single to three stone canals. Calcareous ring stout, radial pieces with small concave depression posteriorly and four tooth-like extensions anteriorly (after CHERBONNIER 1988: 149, fig. 60 O).

Ossicles: Tentacles with rods, 90-265 µm long, sometimes slightly bifurcated, knobbed distally; and spiny edged plates, perforated by a variable number of holes (fig. 35A). Ventral and dorsal body wall with similar tables and C-shaped rods (fig. 35B), rosettes always absent; tables, 40-45 µm across, perforated by four central holes and a variable number of peripheric openings, single cross beam ending in simple, sometimes spiny crown; C-shaped rods 30-50 µm long. Tube feet with irregularly perforated plates, up to 250 µm long (fig. 35D); tables, 35-45 µm across (fig. 51E); and spiny rods, 285-470 µm long, some of them with enlarged median part, pierced by uneven holes (fig. 35F). Dorsal papillae filled with C-shaped rods, 45-65 µm long, occasionally irregular; tables similar though slightly larger than the ones from the body wall (fig. 35C); and perforated plates at the top of the papillae.

Diagnosis - See CHERBONNIER, 1988: 146: fig. 60 A-O.

Ecology - Shallow water (2-12 m), on sand between coral patches, in seagrass beds. ROWE (*in* ROWE & GATES 1995) report depths from 0-20 m.

Distribution in the study region - Kanamai, Mobasa Marine National Park and Reserve, Watamu Marine National Park.

Geographic distribution - Well known species from the tropical, Indo-west-central Pacific (with the Red Sea, without the Persian Gulf) (CHERBONNIER 1988; ROWE & GATES 1995). CHERBONNIER (1988) lists it from the Persian Gulf, probably based on HEDING's (1940a) record. However, this record stems from the Seychelles (Mahé) and not from the Persian Gulf. Figure 55B shows the known distribution in the WIO in detail.

Remarks - This species was recently reported as new to the Kenyan fauna (SAMYN & VANDEN BERGHE 2000), in the present work the following localities are added: Watamu, Kanamai, Mombasa.

Stichopus herrmanni SEMPER, 1868
(fig. 36A-L, fig. 55C, pl. 4B)

Stichopus variegatus Herrmanni SEMPER, 1868: 73, pl. 17, pl. 30, fig. 2.
Stichopus variegatus; THANDAR 1987a (synonymy): 281; GOSLINER *et al.* 1996: 281 (colour picture); CONAND 1999: 10, 12, 20, 39, pl. 2 (colour picture) ; MARSHALL *et al.* 2001: 46 (tab. 29), 53, 54, 58 (tab. 37).
? Stichopus variegatus; MUKHOPADHYAY 1991: 409; ARAKAKI & FAGOONEE 1996: 121.
Stichopus hermanii; MARSHALL *et al.* 2001: 47 (*lapsus calami*).
Stichopus herrmanni; MASSIN 1999: 63 (synonymy and records before 1999); SAMYN 2000: 15 (tab. 1), fig. 1 (colour picture); SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 18 (tab. 4), 31, pl. 2E.

Status and location type - Syntypes whereabouts undetermined (ROWE & GATES 1995).

Type locality - Philippines and Samoa (ROWE & GATES 1995).

Material examined - KKan/9709 (two specimens); KMom/9852 (one specimen); KVan/9767 (one specimen).

General description - Specimens ranging from 110 to 267 mm in length and from 30 to 64 mm in width, after preservation.The specimen collected in Vanga is in very poor state; preserved animals with deep transverse folds. Colour of live animals bright olive-green with numerous brownish spots dorsally (pl. 4B), slightly lighter ventrally; in alcohol uniform light green to nearly white. Mouth ventral with 16-18 greenish tentacles. Anus terminal, unguarded by anal teeth or papillae. Body wall, smooth, 3-5 mm thick. Flattened ventral side with cylindrical tube feet spread over ambulacral and partially also the interambulacral areas. Dorsal side with conical light green papillae with dark green stripes and yellow to orange distal tips, spread without alignment over ambulacral and interambulacral areas. Single Polian vesicle. Calcareous ring relatively small but firm; radial pieces more then twice as wide as interradial pieces; radial piece with two short posterior projections and shallow anterior notch; interradial pieces with single anterior tooth (from MASSIN 1999: 64, fig. 52a).
Ossicles: Tentacles with curved rods, 75-500 µm long, spiny at the extremities (fig. 36A, B). Ventral and dorsal body wall present tables, rosettes and C-shaped rods (fig. 36C, D, E). C-shaped bodies very numerous, 75-110 µm long (fig. 36C). Rosettes very numerous, 20-45 µm long (fig. 36D). Tables with disc 25-45 µm across, disc rounded, perforated by four central and four to eight peripheral holes, spire short, four pillars united by single cross beam, ending in narrow, often spined crown (fig. 36E). Dorsal papillae with rods up to 200 µm long (fig. 36F); C-or S-shaped bodies, similar in size and shape as those from the body wall (fig. 36G); and tables up to twice the size as those from the body wall (fig. 36H). Ventral tube

feet present rods, up to 335 µm long, with median part often enlarged and perforated (fig. 36J); perforated plates, irregular in outline, up to 235 µm long (fig. 36K); and few tables with poorly developed crown, similar in size as the ones from the body wall (fig. 36L).

Diagnosis - See MASSIN 1999: 63-65, fig. 52.

Ecology - In seagrass beds, grazing on sand and detritus piles; 2-12 m depth.

Distribution in the study region - Kiunga Marine Reserve; Watamu; Kanamai; Mombasa; Diani and Vanga (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - Probably tropical, Indo-west Pacific Ocean (with the Red Sea and the Persian Gulf) (ROWE & GATES 1995; MASSIN 1999). Figure 55B shows the known distribution in the WIO if we take the records identified as *Stichopus variegatus* by CHERBONNIER (1967) from the Gulf of Aqaba; ERWE (1919) from the Gulf of Suez; HEDING (1940b) from the Persian Gulf; LAMPERT (1885), TORTONESE (1936a; 1953a), JAMES (1969), JAMES & PEARSE (1969) and CLARK & ROWE's (1971) from the Red Sea; CLARK & ROWE (1971) from the Arabian Sea; LUDWIG (1887) and LAMPERT (1896) from Zanzibar; PEARSON (1910) and THANDAR (1987a) from Mozambique; THANDAR (1987a) from Natal; PANNING (1944) and CONAND (1999) from Madagascar; SLOAN *et al.* (1979), ARAKAKI & FAGOONEE (1996) and CONAND (1999) from the Seychelles; LUDWIG (1883), LAMPERT (1885), THÉEL (1886) and CONAND (1999) from Mauritius; CONAND (1999) from La Réunion, to be *S. herrmanni* (see also remarks hereunder). HAACKE's (1880; see also DANIEL & HALDER 1974) record of *Stichopus naso* SEMPER, 1868 from Mauritius is most probably also *S. herrmanni* (or *S. monotuberculatus* (QUOY & GAIMARD, 1833)), as *S. naso* is known as a tropical, east Indo-west Pacific Ocean species (ROWE & GATES 1995).

Remarks - ROWE (*in* ROWE & GATES 1995) and later MASSIN (1999) showed that the specimens identified as *S. variegatus* SEMPER, 1868, the senior synonym of *S. horrens* SELENKA, 1867, are or *S. herrmanni* or *S. monotuberculatus* (QUOY & GAIMARD, 1833). Hence the distribution map of this ubiquitous species remains largely unknown. Nevertheless, fig. 55C attempts to visualise the known distribution in the WIO.
This species was previously reported from Kenya, Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000); in the present work the following localities are added: Watamu, Kanamai, Mombasa., Diani, Vanga.

Stichopus cf. *monotuberculatus* (QUOY & GAIMARD, 1833)
(fig. 37A-K, fig. 55D, pl. 4C)

Holothuria monotuberculata QUOY & GAIMARD, 1833: 131, pl. 432, fig. 1.
Stichopus unituberculatus; SELENKA 1867: 320.
Holothuria lutea QUOY & GAIMARD 1833: 130 [see also CHERBONNIER 1952b: 21].
Stichopus luteus; LAMPERT 1885: 109; THÉEL 1886: 197.
Stichopus monotuberculatus; CHERBONNIER 1955: 161; JAMES 1969: 61; CHERBONNIER 1967: 57; JAMES 1969: 61; JAMES & PEARSE 1969: 102; TORTONESE 1977: 275; PRICE 1982: 11; MASSIN 1996b: 163 (synonymy); ROWE & RICHMOND 1997: 306.
Stichopus cf. *monotuberculatus*; SAMYN 2000: 15 (tab. 1); SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 18 (tab. 4), 31, Pl 2E.

Status and location type - Holotype probably in MNHNP (ROWE & GATES 1995).

Type locality - Port Louis, Mauritius (ROWE & GATES 1995).

Material examined - TFun/9812 (one specimen); TFun/9813 (one specimen); Tfun/9814 (one specimen); KKiun/9950 (one specimen).

General description - Specimens from 130 to 232 mm in length and from 25 to 55 mm in width, after preservation. Colour in alcohol: yellow to brown ventrally, yellow to brown with brown-grey areas (especially in the larger specimens) dorsally (pl. 4C). Bivium clearly distinguishable from trivium due to the presence of a lateral fringe of large papillae. Mouth ventral surrounded by 16-18 large yellow-brown tentacles with whitish stalk, surrounded at their base by large papillae. Anus terminal. Body wall up to 3 mm thick. Ventral tube feet, numerous, large and long, in four to five rows on the lateral radii and in eight to ten rows on the median radius. Bivium with some short papillae. Single, large Polian vesicle. Calcareous ring relatively small for the size of the specimens, radial pieces high; interradial pieces with elongated anterior tooth (see also MASSIN 1996b: 165, fig. 9A).
Ossicles: Ventral body wall presents tables and C-shaped bodies (fig. 33A,B); tables with rim of disc smooth and outline squarish, 30-45 µm across, perforated by four large central holes and three to six peripheral holes, spire short, four pillars united by single cross beam ending in a wide, spiny crown (fig. 37A); C-shaped bodies rare, up to 85 µm long (fig. 37B). Dorsal body wall with tables of similar size and

shape as those from the ventral body wall and with rosette-like rods (fig. 37C). Ventral tube feet with spiny rods, 250-415 µm long, with enlarged median process, unevenly perforated (fig. 37D); spiny plates 85-100 µm long; X-shaped rods; and tables with rounded but spiny disc (fig. 37E). Dorsal papillae with tables, rim of disc round but irregular, disc 45-70 µm across, perforated by four large central holes and up to 20 smaller peripheral holes (fig. 37F); some perforated rods which can be X-shaped (fig. 37G); and numerous large, 135-350 µm long, rods, that often have an enlarged median process (fig. 37H). Tentacles present rods, 140-650 µm long, straight to C-shaped, spiny at the extremities (fig. 37J, K).

Diagnosis - See MASSIN 1996b: 163-164; fig. 9, 10, pl. 1.C, D.

Ecology - In the Kiunga Marine Reserve two specimens were observed at night, foraging on sandy substrate between live coral; the specimens from Pemba Island were found during the day; depth ranges from 5 to 23 m in the study region. MASSIN's (1996b) ecological observations on Easter Island, state occurence from intertidal pools up to depths of 45 m.

Distribution in the study region - Kiunga Marine Reserve; Fundu (see also SAMYN & VANDEN BERGHE 2000).

Geographic distribution - The species seems to have a tropical Indo-west Pacific Ocean (with the Red Sea and the Persian Gulf), but as ROWE (*in* ROWE & GATES 1995) and MASSIN (1996b; 1999) have noted, there is some confusion with *S. herrmanni* and *S. horrens* when it comes to drawing the distribution map. MASSIN's (1996b: 174, map 3) distribution map has to be completed with the following records: Gulf of Suez, Wadi el Dom (JAMES 1969; JAMES & PEARSE 1969) (see also CHERBONNIER 1955; PRICE 1982 for unspecified localities in the Gulf of Suez); Gulf of Aqaba, Eilat (CHERBONNIER 1963; 1967), Aqaba (TORTONESE 1977) (see also PRICE 1982 for unspecified locality in the Gulf of Aqaba); Red Sea, Entedebir (CHERBONNIER 1967); Arabian Sea (PRICE 1982); Kenya, Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000); Tanzania, Fundu (this work); Mauritius (QUOY & GAIMARD 1833, as *Holothuria monotuberculata* QUOY & GAIMARD, 1833; SELENKA 1867, as *S. unituberculatus* QUOY & GAIMARD, 1833; LAMPERT 1885 and THEÉL 1886, both as *S. luteus* QUOY & GAIMARD, 1833; CHERBONNIER 1952b); Mascarene Islands (CLARK & ROWE 1971). Figure 55D shows the suspected WIO distribution in detail.

Table 20 lists the other species within the genus *Stichopus* that are known to occur in the shallow-waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record appeared.

Current Species Name	Known WIO Distribution	Reference(s)
Stichopus horrens SELENKA, 1867	Mozambique (Inhaca)	MRAC records, pers. observ.
	Madagascar (Nosy Bé)	CHERBONNIER 1988
	Seychelles (Aldabra)	SLOAN *et al.* 1979
	La Réunion	CHERBONNIER 1988
	Mauritius	ARAKAKI & FAGOONEE 1996
	West Indian Ocean to West Pacific Ocean, with the Red Sea	ROWE & RICHMOND 1997
Stichopus pseudohorrens CHERBONNIER, 1967	Gulf of Aqaba (Aqaba, Eilat)	CHERBONNIER 1967; TORTONESE 1977; CHERBONNIER 1979a; PRICE 1982

Table 20 - Other species within the genus *Stichopus* known to occur in the shallow-waters of the WIO.

Genus *Thelenota* H.L. CLARK, 1921

Diagnosis (See H.L. CLARK 1921:183) [Type species: *Trepang ananas* JAEGER, 1833 by original designation].

Currently three species are regarded as being valid: *Thelenota ananas* (JAEGER, 1833); *T. anax* H.L. CLARK, 1921 and *Thelenota rubralineata* MASSIN & LANE, 1991[11]. The first two species are present in the shallow-waters of Kenya; they are keyed hereunder.

[11] WEINBERG (1997) calls upon all recreational and non-recreational divers to report spottings of *T. rubralineata* MASSIN & LANE, 1991 in the WIO. To my knowledge, since then, this eye-catching species has not been reported in the WIO.

Key to the Species of Kenya (with Pemba Island).

1. Bivium bears prominent di-to quadrichotomously branched warts. Ossicles consist of pseudotables and large, more or less spiny; X-shaped plates; no grains ..... ***T. ananas* (JAEGER, 1833)**

1'. Bivium with conical warts, never branched in structure. Ossicles never in the form of pseudotables; numerous very small grains and smooth X-shaped plates ..... ***T. anax* H.L. CLARK, 1921**

Thelenota ananas (JAEGER, 1833)
(fig. 38A-E, fig. 55E, pl. 4D)

Trepang ananas JAEGER, 1833: 24, pl. 3 fig. 1.
Actinopyga formosa SELENKA 1867: 314, pl. 17 fig. 19a,b,c; DANIEL & HALDER 1974: 422.
Thelenota ananas; MUKHOPADHYAY 1991: 409; ARAKAKI & FAGOONEE 1996: 122; WEINBERG 1997: 249 (colour picture); MASSIN 1999:77 (synonymy and records before 1999); CONAND 1999: 10, 12, 18, 39, pl. 2 (colour picture); MARSHALL *et al.* 2001: 46 (tab. 29), 47, 50, 53, 54, 58 (tab. 37).
Thelenota ananas?; ARAKAKI & FAGOONEE 1996: 122.

Status and location type - Status and whereabouts undetermined (ROWE & GATES 1995).

Type locality - Sulawesi (Indonesia) (ROWE & GATES 1995).

Material examined - KKis/9843 (one specimen).

General description - Large species, squarish in cross-section. The single specimen measures 362x100 mm, after preservation. Colour in life, uniform orange-red (pl. 4D); colour in alcohol slightly faded. Mouth ventral, surrounded by 20 dark-orange tentacles. Anus terminal, unguarded. Thickness of body wall varies between 7 (anteriorly) and 10 mm (posteriorly). Bivium with prominent di-to quadrichotomously branched orange-red extensions which end in papillae ('cockscomb papillae'); interspersed between these large extensions, smaller brownish papillae can be found. Trivium densely covered by numerous long and thick reddish tube feet; ambulacral and interambulacral areas not discernable. Single large Polian vesicle. Single short stone canal. Gonad single, poorly developed. Calcareous ring relatively small with large radial and short interradial pieces.
Ossicles: Tentacles present large plates, 135 µm long and 95 µm wide (fig. 38A) and some smaller rods. Dorsal body wall with branched rods which are slightly spined, 40-80 µm long (fig. 38B). Ventral body wall with similar, though smooth plates (fig. 38C). Dorsal papillae with branched rods similar to the ones from the body wall and with slightly curved, spined rods, up to 155 µm long (fig. 38D). Ventral tube feet present large plates, 75-135 µm long and rods similar to the ones in the dorsal papillae (fig. 38E).

Diagnosis - See CHERBONNIER & FÉRAL 1984b: 829, fig. 62A-S

Ecology - In Kenya, always seen in deeper water, never found above ten m depth; feeding on detritus piles and coarse sand. MASSIN (pers. comm.) notes that in Papua New Guinea, this species is common in 1-2 m deep water, in the lagoon.

Distribution in the study region - Kisite, Mombasa Vanga.

Geographic distribution - Well-known species from the tropical, Indo-west Pacific Ocean (not recorded from the Red Sea nor from the Persian Gulf). The distribution map as drawn by MASSIN (1999: 77, fig. 62; see also LANE 1999: 20, fig. 2), gives the global distribution. Figure 55E shows the known distribution in the WIO in detail, whereby the record of ARAKAKI & FAGOONEE (1996) from the Seychelles, Mahé, must be treated with caution for these authors marked it with a question mark.

Thelenota anax H.L. CLARK, 1921
(fig. 39A-C, fig. 55F, pl. 4E)

Thelenota anax H.L. CLARK, 1921: 185, pl. 18 fig. 3
Thelenota anax; WEINBERG 1997: 248 (colour picture); MASSIN 1999: 78 (synonymy and records before 1999); CONAND 1999: 12, 19, 39, pl. 2 (colour picture); SAMYN 2000: 15, tab. 1; MARSHALL *et al.* 2001: 46 (tab. 29).
? Thelenota sp. 1.; ARAKAKI & FAGOONEE 1996: 122.
? Thelenota sp. 2.; ARAKAKI & FAGOONEE 1996: 122.

Status and location type - Holotype; MCZ 1068 (ROWE & GATES 1995).

Type locality - Mer, Murray Islands, Torres Strait, Queensland (Australia) (H.L. CLARK 1921).

Material examined - KKis/9841 (one specimen); KKis/9842 (one specimen).

General description - Preserved specimens measure 360 x 90 mm and 450 x 75 mm.; live specimens can reach the dimensions of the arm of an adult man. Markedly square in cross section. Body colour of live specimens grey-brownish dappled with dark-red; preserved specimens uniformly grey. Mouth ventral. Anus dorsal. Body wall up to 20 mm thick, very smooth to the touch. Dorsal body wall lacks large 'cockscomb' papillae as on *T. ananas*, but presents short papillae and very short tube feet. Ventral body wall flattened, uniformly covered with numerous fine and long tube feet. Bivium separated from trivium by row of large papillae which can be fused. Polian vesicles numerous. Calcareous ring relatively small; radial pieces twice as wide as interradial pieces and with two posterior extensions; radial pieces with short anterior tooth (see also MASSIN 1999: 79: fig. 63a).
Ossicles: Tentacles present spiny perforated plates, 80-100 µm long, and branched rods, 70-125 µm long (fig. 39A); Ventral and dorsal body wall with dichotomously branched rods, 70-100 µm long (fig. 39B), pseudotables and an almost infinite number of miliary granules only few µm across (not illustrated). Ventral tube feet with rods, 70-100 µm long, and large perforated plates, up to 275 µm long (fig. 39C).

Diagnosis - See CHERBONNIER 1988: 156-158, fig.64.

Ecology - Species restricted to 15-45 m depth; invariably found grazing on coarse sand.

Distribution in the study region - Kisite.

Geographic distribution - Tropical Indo-West Pacific species (not recorded from the Red Sea nor from the Persian Gulf). The distribution map as drawn by MASSIN (1999: 80, fig. 64; see also LANE 1999: 20, fig. 2), gives the global distribution, but the following have to be added: southern Mozambique (THANDAR 1987a); Seychelles, Aldabra (SLOAN *et al.* 1979); Mauritius (CONAND 1999). The present record is new to Kenya. Figure 55F shows the known distribution in the WIO in detail.

Remarks - *T. anax* is one of the high-value trepang species (prickly redfish), probably overharvested by fishermen. Hence local geographic distribution possibly was much larger then reported here.
The records of ARAKAKI & FAGOONEE (1996, as *Thelenota* sp. 1 and *Thelenota* sp. 2) from Mauritius, most probably are *T. anax* for these authors recognised *T. ananas* as a distinct species in the same paper.

Ordo APODIDA Brandt, 1835

Family Synaptidae Burmeister, 1837

Subfamily Rynkatorpinae Smirnov, 1989

Key to the Genera of Kenya (with Pemba Island) (after Clark & Rowe 1971: 207)

1. Stock of anchor irregularly branched; cartilaginous ring usually not present **2**
1'. Stock of anchor unbranched; cartilaginous ring commonly present **3**
2. Anchor-plates not abruptly contracted at posterior end but with a large central hole on each side; calacreous ring without conspicuous anterior projections ..... ***Euapta* ØSTERGREN, 1898**
2'. Anchor-plates abruptly contracted posteriorly, thus lacking a large smooth hole on each side of the bridge; calcareous ring with conspicuous anterior projections ..... ***Opheodesoma* FISHER, 1907**
3. Ossicles very large, anchors up to 1 mm or more; anchor-plates up to 650 µm long, subrectangular or irregular, broad posteriorly with numerous smooth holes ..... ***Synapta* ESCHSCHOLTZ, 1829**
3'. Ossicles never particularly large, anchors rarely exceeding 400 µm or anchor-plates 300 µm in length, anchor-plates rounded anteriorly and narrowing posteriorly, with a few holes and these generally regularly arranged and toothed ..... ***Synaptula* Ørsted, 1849**

Genus *Euapta* ØSTERGREN, 1898

Diagnosis (See FISHER 1907: 721) [Type species: *Synapta godeffroyi* SEMPER, 1868 by subsequent designation]

Six species are currently regarded as being valid: *Euapta godeffroyi* SEMPER, 1868; *E. lappa* (MÜLLER, 1850); *E. magna* HEDING, 1928; *E. polii* (LUDWIG, 1894); *E. tahitiensis* CHERBONNIER, 1955 and *E. tobagoensis* HEDING, 1928. In addition, *Opheodesoma sinevirga* CHERBONNIER, 1988 is here transferred to the genus *Euapta* for the structure of the anchor-plates are typical of the latter genus; *i.e.* they have a anchor-plates that are not abruptly contracted at posterior end, but with a large hole on each side.
Only *E. godeffroyi* is found in the shallow-waters of Pemba Island

Euapta godeffroyi (SEMPER, 1868)
(fig. 40A-E, fig. 55G)

Synapta Godeffroyi SEMPER, 1868; 231, pl. 39 fig. 13.
Euapta godeffroyi; CHERBONNIER 1967: 57; DANIEL & HALDER 1974: 423; TORTONESE 1977: 275; MUKHOPADHYAY 1991: 410; WEINBERG 1997: 250 (colour picture); MASSIN 1999: 100 (synonymy and records before 1999); LANE *et al.* 200:492.

Status and location type - Syntype: ZMH E. 2950 (ROWE & GATES 1995).

Type locality - Samoa (Navigator Islands) (ROWE & GATES 1995).

Material examined - TFun/9817 (one specimen); TFun/9818 (one specimen).

General description - Medium sized species; size from 110-260 mm in length and from 8-20 mm in width, after preservation. Body cylindrical, sticky to the touch. Body colour in life: whitish-yellow with numerous transverse dark brown bands and five conspicuous, narrow, brown longitudinal lines in the radial areas. Colour in alcohol fades to uniform beige with some brown blotches and traces of the longitudinal lines (especially visible at the anterior end). 14-15 feather-like tentacles that bear 20 or more pairs of digits, united by a web. Polian vesicles very thin, numerous. Stone canal not observed. Gonad branched. Cartilaginous ring wanting. Calcareous ring faint greenish, narrow; two interradial pieces alternating with one radial piece that is perforated anteriorly by a minute hole allowing passage for the nerve.
Ossicles: Body wall presents numerous miliary granules, few anchors and anchor-plates (fig. 40A-C, E). Anchors: arms smooth; vertex armed with four to six nodules; stock branched and granulous at the extremities; 300-315 x 170 µm (fig. 40B). Anchor-plates: oval in outline, *i.e.* without contracted posterior side; seven large serrated (fig. 40A) or smooth (fig. 40E) holes; two smooth articular holes and three small, smooth, posterior holes; bridge well developed, undulating to slightly angular, occasionaly perforated by small, smooth, holes; 200-225 µm long and 145-160 µm wide. Tentacles present spiny rods with bifurcating extremities, 150-225 µm long and occasionaly some smooth rods (fig. 40D) in addition to miliary granules exactely like the ones of the body wall.

Diagnosis - See SEMPER 1868: 230, pl. 39 fig. 13; see also MASSIN 1996b: 164-167, fig. 11, p. 168.

Ecology - *E. godeffroyi* was found at night in a healthy reef; bathymetric range 0-77 m (LANE *et al.*, 2000).

Distribution in the study region - Fundu.

Geographic distribution - Well-known species from the tropical Indo-West-central Pacific Ocean (with the Red Sea, not recorded from the Persian Gulf). The distribution map as drawn by MASSIN (1996b: 174, map 3; 1999: 102, fig. 85) gives the global distribution, but the following localities have to be added: Gulf of Aqaba, Eilat (CHERBONNIER 1967), Aqaba (TORTONESE 1977) (see also PRICE 1982 for unspecified record from the Gulf of Aqaba); Madagascar, Tuléar (CHERBONNIER 1988) and Tanzania, Fundu. (this work). Figure 55G shows the known distribution in the WIO in detail.

Remarks - MASSIN (1999) noted that *E. godeffroyi* is assumed to be common (a fact reflected in his distribution map); however only few records are known from the East African coast, *i.e.* Zanzibar, Aldabra, Madagascar, Mauritius and S. Africa. The present record is the first for Tanzania. Due to its nocturnal habit, the species was possibly overlooked in previous studies; and most probably also belongs to the Kenyan fauna as it was previously found in the northern (Seychelles: Aldabra) and the southern western Indian Ocean (Zanzibar, Madagascar, Mauritius, South Africa).
Malformed anchor-plates are supposed to be characteristic for this species (HEDING 1928: 138, fig. 10.1). Despite the fact that such anchor-plate were not found in the two specimens under study, the shape of the calcareous ring and the rods from the tentacles leave no doubt over its identity.

Table 21 gives the only other species within the genus *Euapta* that is known to occur in the shallow waters of the WIO, but has for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the reference wherein the record appeared.

Current Species Name	Known WIO Distribution	Reference(s)
E. sinevirga (CHERBONNIER, 1988)	Madagascar (Tuléar)	CHERBONNIER 1988

Table 21 - *Euapta sinevirga* (CHERBONNIER, 1988), the second species within *Euapta* known to occur in the shallow-waters of the WIO. ROWE's (pers. comm.) observation that this species belongs to *Euapta* rather than to *Opheodesoma* is here confirmed.

Genus *Opheodesoma* FISHER, 1907

Diagnosis [Type species: *Opheodesoma spectabilis* FISHER, 1907 by original designation]
Moderate to large species, vermiform body reaching lengths up to 1m or more in life; 15 pinnate large tentacles with numerous tentacular digits; body wall very thin, sticky to the touch; calcareous ring with conspicuous anterior projections, two interradial pieces for each radial piece; stone canals very numerous and short. Ossicles of the body wall comprise anchors, anchor-plates and miliary granules; of the tentacle miliary granules and sometimes rods; anchors with stock branched and spiny, arms smooth with vertex variously knobbed; anchor-plates quadrangular, abruptly contracted posteriorly thus lacking a large smooth hole on each side of the bridge.
Ten species are currently regarded as being valid: *Opheodesoma africana* HEDING, 1931; *O. australiensis* HEDING, 1931; *O. clarki* HEDING, 1928; *O. glabra* (SEMPER, 1868); *O. grisea* (SEMPER, 1868); *O. lineata* HEDING, 1928; *O. kamaranensis* A.M. CLARK, 1951; *O. mauritiae* HEDING, 1928; *O. serpentina* (J. MÜLLER, 1850) and *O. spectabilis* FISHER, 1907. Five of these are found in the shallow-waters of Kenya (with Pemba Island), they are keyed hereunder.

Key to the species of Kenya (with Pemba Island)

1. Web between the tentacle digits absent **2**
1'. Shallow web between the tentacle digits present ..... ***Opheodesoma glabra* (SEMPER, 1868)**
2. Tentacle and oral disc contain ossicles **3**
2'. Tentacles and oral disc without ossicles apart from some highly fragmented miliary granules ..... ***Opheodesoma grisea* (SEMPER, 1868)**
3. Calcareous ring greenish **4**
3'. Calcareous ring white; tentacles present rods in addition to miliary granules..... ***Opheodesoma mauritiae* HEDING, 1928**
4. Tentacles present miliary granules only..... ***Opheodesoma spectabilis* FISHER, 1907**
4'. Tentacles present few rods in addition to miliary granules ..... ***Opheodesoma* sp.**

Opheodesoma glabra (SEMPER, 1868)
(fig. 41 A-E, fig. 55H)

Synapta glabra SEMPER, 1868: 12, pl. 2 (colour drawing), pl. 4, fig. 8; Ludwig 1881: 577; THÉEL 1886: 10, 20; SLUITER 1894: 105.
Euapta glabra; SLUITER 1901: 123.
Opheodesoma glabra; H.L. CLARK 1908: 74; ?H.L. CLARK 1921: 159; H.L. CLARK 1924: 465; HEDING 1928:123; H.L. CLARK 1946: 448; CLARK & ROWE 1971: 184 (distribution table); TAN TIU 1981: 63; CANNON & SILVER 1986: 41; ROWE & GATES 1995: 333; LANE *et al.* 2000: 492.

Status and location type - Holotype whereabouts undetermined (?ZMH E. 5075) (ROWE & GATES 1995).

Type locality - 'Canal von Lapinig', Bohol (Phillippines) (ROWE & GATES 1995).

Material examined - KKan/9782 (two specimens).

General description - Small to moderate species reaching lengths of about 200 mm in life; 90-145 mm long and 4-5 mm wide after preservation. Body colouration in life: dorsal body wall variegated yellow-green to brown with transvere irregular bands, ventral body wall lighter, whithout transverse bands; colour

after preservation much lighter: dorsal body wall greyish with some greenish irregular blotches, ventral body wall uniform grey, white spots due to large heaps of miliary granules visible over the total body wall. Tentacles 15, yellow, each with ±25 pairs of digits, united by a shallow web. On the oral disc, at the base of each tentacle two minute, brown eye-spots. Calcareous ring low, white, radial pieces peforated for the nerve. Stone-canals minute, numerous. Polian vesicles at least as numerous, short. Cartilaginous ring thin, without slits, extending posteriorly for about the same length as the calcareous ring.

Ossicles: Body wall with anchors, anchor-plates and numerous miliary granules (fig. 41A); same size and shape at the anterior and posterior side of an individual; variation with size of the individual not apparent. Anchors: 235-265 µm long and 140-165 µm wide; arms smooth, vertex with some minute, irregular, knobs; stock branched and granulous (fig. 41A). Anchor-plates: quadrangular, 185-200 µm long and 155-170 µm wide; seven serrated holes; posterior part with three to six small, smooth holes; bridge convex, slightly undulating, occasionaly perforated (fig. 41B). Miliary granules 15-20 µm across (fig. 41C, F). Tentacles with miliary granules similar in size and shape as those of the body wall, in addition to very few rods, approximately 75 µm long with rounded extremities (fig. 41D, G). Oral disc with miliary granules similar in size and shape to those in the tentacles, in addition to rods of the same size and shape as those from the tentacles (fig. 41E).

Diagnosis - See H.L. CLARK 1924: 465-466, pl. 2 figs 7-9.

Ecology - H.L. CLARK (1946) noted that nothing is as yet recorded as to habitat or habits of this species. Since then, ROWE & GATES (1995) note that it is a benthic, inshore, detritus and deposit feeder and LANE *et al.* 2000 report on a bathymetric range of 0-20 m. The two specimens were found at the base of sea-grass in the lower eulittoral of the seagrass platform of Kanamai; during daytime they were actively sweeping their tentacles on the fine sand surrounding the sea grass *Thalassodendron cilliatum* (FORSKAAL, 1757).

Distribution in the study region - Kanamai.

Geographic distribution - Tropical Indo-west Pacific Ocean (no recorded from the Red Sea nor from the Arabian Gulf) (CLARK & ROWE 1971). The present record is the only one known for the WIO (see fig. 55H).

Remarks - Only four species within the genus *Opheodesoma* present a distinct web between the digits of the tentacles (HEDING 1928; 1931): *O. australiensis* HEDING, 1931; *O. clarki* HEDING, 1928, *O. glabra* (SEMPER, 1868) and *O. spectabilis* FISHER, 1907. HEDING (1928) used length:width proportion to distinguish the last three species. His table is repeated below (table 22) and completed with information on *O. spectabilis* FISHER, 1907 and *O. australiensis* (CHERBONNIER 1980). From this table (comparison of species with tentacle digits webbed) it is clear that the two specimens under study fit best with the description of *O. glabra* given by HEDING (1928). The only difference of significance is that the specimens under study (length from 90-145 mm) present few rods in the tentacles, while HEDING (1928) did not report these in the single specimen (length 450 mm) he studied. Hence, it is with some hesitation that I identified the present specimens as *O. glabra.*

Species	Web	Anchors			Anchor plates			Tentacles	Oral disc
		Length	Width	W:L	Length	Width	W:L		
O. australiensis	+	320-340	230-250	0.72-0.74	230-250	180-210	0.78-0.84	MG + few R	MG + few R
O. clarki	+	150-250	90-150	0.55-0.60	150-200	140-180	0.90-0.93	MG + R	MG + R
O. glabra	+	270-280	160-170	0.60-0.66	180-240	140-180	0.76-0.81	MG + few R	MG + R
O. spectabilis	+	150-130	185-200	0.66-0.74	220-250	180-185	0.74-0.81	MG	MG+R
KKan/9782	+	235-265	140-165	0.60-0.62	185-200	155-170	0.83-0.85	MG + few R	MG + R
O. mauritiae	-	285-305	175-200	0.61-0.65	220-235	160-180	0.73-0.77	MG+R	MG+R
O. serpentina	-	270	170	0.63	200	170	0.85	MG + R	MG + R
TFun/9819	-	385-435	260-300	0.68-0.69	265-325	205-240	0.74-0.77	MG + R	R

Table 22 - Overview of the *Opheodesoma* species with web between the tentacle digits and with miliary granules (MG) and rods (R) in both the tentacles and the oral disc. MG represents miliary granules; R represents rods. The two specimens belonging to KKan/9782 best fit with *O. glabra*, while the two specimens belonging to TFun/9819 best with *O. mauritiae* or O. *serpentina.*

Prior to the present study *O. glabra* was only known from the Philippines, the Dutch Indies, Fiji Islands, the South China Sea and Northern Australia (see H.L. CLARK 1946; CLARK & ROWE 1971; ROWE & GATES 1995; LANE *et al.* 2000). The presence of *O. glabra* on the East Coast of Africa extends the range of distribution considerably.

Opheodesoma grisea (SEMPER, 1868)
(fig. 42A-E, fig. 56A)

Synapta grisea SEMPER, 1868: 11, pl. 4 figs 6-7.
Euapta grisea; DANIEL & HALDER 1974: 420.
Ophiodesoma grisea; MACNAE & KALK 1962: 111 (*lapsus calami*).
Ophendesoma grisea; MUKHOPADHYAY 1991: 410 (*lapsus calami*).
Opheodesoma grisea; MASSIN 1999: 102 (synonymy and records before 1999); LANE *et al.* 2000: 492.

Status and location type - Status and whereabouts undetermined (?ZMH E. 5075) (ROWE & GATES 1995).

Type locality - Bohol (Phillippines) (ROWE & GATES 1995).

Material examined - KKan/9725 (one specimen); KKan/9726 (one specimen).

General description - Moderate sized species that can reach a length of up to 400 mm in life; 160 and 310 mm long after preservation. Body colour in life similar to colour after preservation: ventral and dorsal side variegated brownish-green with five narrow, longitudinal, cream coloured longitudinal bands; ventral side generally lighter. Tentacles 15, feather-like, with numerous pairs of digits not united by a web. Numerous long Polian vesicles. Numerous short stone canals. Calcareous ring with a minute tinge of green; two interradial pieces for each radial piece; posterior side of the pieces undulating; interradial pieces with a long pointed tooth and radial pieces peforated anteriorly. Cartilagenous ring as high as the calcareous ring.

Ossicles: Body wall presents anchors, anchor-plates and few miliary granules (fig. 42A-C). Anchors: 285-325 µm long and 195-225 µm wide; stock regularly branched and spinose; arms smooth, vertex with some irregular small knobs (fig. 42A). Anchor-plates: quadrangular in outline; 240-255 µm long and 165-175 µm wide; seven serrated holes; narrow posterior part with three to eight smooth holes; bridge smooth (fig. 42B). Miliary granules, 15-20 µm across (fig. 42C). Tentacles with highly fragmented miliary granules only (fig. 42D).

Diagnosis - See H.L. CLARK 1924: 466-467, pl. 2 figs 1-3.

Ecology - The two specimens were found in a shallow-water, 1 m deep at low tide, in seagrass bed; both specimens were actively sweeping their tentacles over the sand surface. LANE *et al.* 2000 give a bathymetric range of 0-36 m.

Distribution in the study region - Kanamai.

Geographic distribution - Well-known species from the Indo-west Pacific (with the Red Sea, without the Arabian Gulf). The distribution map as drawn by MASSIN (1999: 104, fig. 77) gives the global distribution, but the following localities have to be added: Gulf of Aqaba, Aqaba (TORTONESE 1977, as *O. griseum*) (see also PRICE 1982 for unspecified record from the Gulf of Aqaba); Arabian Sea (PRICE 1982; DANIEL & HALDER 1974, as *Euapta grisea*); Mozambique, Tunghi Bay (PEARSON 1910, as *Synapta grisae* SEMPER, 1868), Inhaca (MRAC record pers observ.); Madagascar, Fort Dauphin (CHERBONNIER 1988); and Kenya (present study). Figure 56A shows the known distribution in the WIO in detail.

Remarks - These two specimens were identified as *O. grisea* even if one of the distinctive characters of the species – presence of rods in the oral disc but not in the tentacles – could not be confirmed. However, as the body morphology, the structure of the calcareous ring and the size of the ossicles agree well with previous descriptions of *O. grisea* (CHERBONNIER 1988; MASSIN 1996b; 1999), I feel justified in my identification. In this viewpoint it must nevertheless be noted that some species in the genus *Polyplectana* H.L. CLARK, 1908 [*Polyplectana kefersteini* (SELENKA, 1867) and *P. nigra* (SEMPER, 1868)] are known to lack ossicles in the tentacles (see MASSIN 1999: 106, 108). However, the present specimens can hardly be referred to *Polyplectana* as the structure of the calcareous ring and the spicule morphology (unbranched stock of the anchor, ovate anchor-plates) is totally different to the ones described here; even so the number of tentacles in *Polyplectana* typically is 25 [although for *P. kefersteini* it has been noted that the number of tentacles varies from 16 to 27 (HEDING 1928; CHERBONNIER & FÉRAL 1984b; MASSIN 1999)]; and the shape of the

miliary granules in *Polyplectana* (branched or curved rods) does not agree with what is reported from the specimens under study.
These two poorly preserved specimens represent the first records for Kenya (Kanamai). *O. grisea* was previously reported from the western Indian Ocean in Zanzibar (H.L. CLARK 1924) and in Madagascar.(CHERBONNIER 1988).

Opheodesoma mauritiae HEDING, 1928
(fig. 43A-D, fig. 56B)

Opheodesoma mauritiae HEDING, 1928: 130, text figs 4(1), 6(14-17), 7 (4, 10); CHERBONNIER 1952a: 497, pl. 47, figs. 1-18; MACNAE and KALK 1958: 43, 130 (from THANDAR 1984); KALK 1959: 22; MACNAE & KALK 1962: 111; CLARK & ROWE 1971: 186; DANIEL & HALDER 1974: 423.
Opheodesoma africana HEDING, 1931; 645, fig. 2 (2, 6-11).
Synapta serpentina LAMPERT 1896: 64 (non J. MÜLLER 1850 = *O. serpentina)*

Status and location type - ZMUC (?).

Type locality - Mauritius.

Material examined - KKan/9873 (one specimen); KKan/9874 (one specimen); TFun/9832 (one specimen)

General description - Moderate sized species reaching lengths of about 600 mm in life; from 190 to 270 mm long after preservation. Body colour after preservation: ventral side more or less uniform greyish, dorsal side darker variegated brownish-grey with three narrow, longitudinal, brownish longitudinal bands. Tentacles 15, feather-like, with numerous pairs of digits not united by a web. Numerous long Polian vesicles. Numerous short stone canals. Calcareous ring white in colouration; anterior processes of radial pieces not more than one third of the height of the calcareous ring. Cartilagenous ring higher than calcareous ring.
Ossicles: Body wall presents anchors, anchor-plates and numerous miliary granules (fig. 43A-C). Anchors 285-305 µm long and 175-200 µm wide; stock regularly branched and spinose, occasionaly perforated by a small hole; arms smooth, vertex with some irregular small knobs (fig. 43A). Anchor-plates: quadrangular in outline; 220-235 µm long and 160-180 µm wide; seven serrated holes; narrow posterior part with three to six smooth holes; bridge straight (fig. 43B). Miliary granules very numerous, 17-22 µm across (fig. 43C). Tentacles and oral disc with miliary granules similar to those of the body wall and rods with rounded or slightly spinose extremities, 70-115 µm long (fig. 43D).

Diagnosis - See CHERBONNIER 1952a: 497-498, pl. 47 figs 1-18.

Distribution in the study region - Kanamai, Fundu.

Geographic distribution - Western Indian Ocean (no records from the Red Sea nor from the Persian Gulf). Figure 56B shows the known distribution in the WIO in detail.

Remarks - This specimen bears very close similarity to *O. serpentina* described below. However, the anchors and anchor-plates are distinctively smaller. The present records are new to Kenya (Kanamai) and Tanzania (Fundu).

Opheodesoma cf. *mauritiae* HEDING, 1928
(fig. 44A-D, pl. 4F)

Status and location type - See *O. mauritiae.*

Type locality - See *O. mauritiae.*

Material examined - KKan/9731 (one specimen).

General Description - The single specimen at our disposition is strongly contracted; 71 x 8 mm after preservation. Gross body morphology similar to that of *O. mauritiae.*

Ossicles: Body wall presents anchors, anchor-plates and miliary granules (fig. 44A, B) similar, but slightly smaller to those presented by the other specimens of *O. mauritiae*. Oral disc presents miliary granules and rods (fig. 44C) similar in size and shape as those from *O. mauritiae*. Tentacles present miliary granules only (fig. 44D)

Diagnosis - See *O. mauritiae.*

Distribution in the study region - Kanamai only.

Geographic distribution - See *O. mauritiae.*

Remarks - Although the overall body morphology and the shape of the ossicles agrees well with *O. mauritiae*, I dare not identify it as such for two differences are apparent. *Primo*, the tentacles of *O. mauritiae* present rods and miliary granules (fig. 43D), while those of the present specimen present miliary granules only (fig. 44D). *Secundo,* the anchor and anchor-plates of *O. mauritiae* are markedly smaller than those of the present specimen (anchors: 285-305 µm long and 175-200 µm wide in *O. mauritiae* versus 330-360 µm long and 205-225 µm wide in *O.* cf. *mauritiae*, anchor-plates: 220-235 µm long and 160-180 µm wide in *O. mauritiae* versus 265-280 µm long and 185-205 µm wide in *O.* cf. *mauritiae*). Even thought is a well known fact that the size of the ossicles in many apodids changes with body size (MASSIN 1999), increase of size of ossicles with decreasing body size has not been reported. These two differences bring the specimen close to another *Opheodesoma* known to occur in the western Indian Ocean: *O. spectabilis* FISHER, 1907. However, the latter species was reported only once from the East African coast (CHERBONNIER 1974), at a depth of 25 m. Other specimens of *O. spectabilis* have been found in the tropical Pacific Ocean, always at depths exceeding 20 m (CLARK & ROWE 1971; LANE *et al.* 2000).

Opheodesoma sp.
(fig. 45A-D, fig. 56C, pl. 4G)

Material examined - TFun/9819 (one specimen).

Description - The single specimen at my disposition is 510 mm long and on average 25 mm wide. Life colouration is uniform dark-brown to black with conspicuous white tentacles; after preservation body colouration dark chocolate-brown overall, although slightly lighter ventrally, posterior side of the tentacles chocolate brown, anterior side whitish, digits somewhat more yellow Tentacles 15, with over 25 pairs of digits, not webbed together. Stout calcareous ring, greenish in colouration, with two interradial pieces alternating with one radial piece; posterior margin undulating; radial pieces with a large quadrangular hole for the nerve; anterior tooth of the interradial pieces not more than one third of the length of the calcareous ring. Polian vesicles numerous. Stone canals numerous and very short. Cartilaginous ring well developed, slighhtly higher than the calcareous ring; pierced by small holes just below the calcareous ring.
Ossicles: Body wall presents anchors, anchor-plates and numerous miliary granules (fig. 45A-C). Anchors: 385-435 µm long and 260-300 µm wide; stock regularly branched and spinose; arms smooth; vertex with some irregular small knobs (fig. 45A). Anchor-plates: more or less quadrangular in outline; 265-325 mm long and 205- 240 µm wide; seven serrated holes; narrow posterior part with three to eight smooth holes; bridge straight (fig. 45B). Miliary granules, 15-20 µm across (fig. 45C). Tentacles with miliary granules, 16-23 µm across (fig. 45D) and few rods with the ends a little swollen (fig. 45E). Oral disc with rods, 80-120 µm long, rounded or slightly spinose at the extrimities (fig. 45F)

Ecology - The single specimen was found at night, 12 m deep, the posterior part of the body was hiding under a large coral slab. The animal seemed to be actively feeding on the mucus attached to live coral.

Distribution in the study region - Fundu only.

Geographic distribution - Unknown,

Remarks - To my knowledge, only five species within the genus *Opheodesoma* have miliary granules and rods in both the tentacles and the oral disc: *O. australiensis* HEDING, 1931; *O. clarki* HEDING 1928; *O. glabra* (SEMPER, 1868) *O. mauritiae* HEDING, 1928 and *O. serpentina* J. MÜLLER, 1850. The first three species are characterized by having a distinct web between the tentacle digits while the latter species does not present this character.
As shown in table 22, the specimen under study fits best with *O. serpentina* or *O. mauritiae*. However, as the colouration of the specimen, the dimensions of the ossicles and the absence of miliary granules in the oral disc does not fit with the above two species, it cannot be assigned to it. As I have only one specimen at my disposition I refrain from creating a new species. Fig. 56C gives the WIO distribution for *O. sperpentina* with the present specimen included.

Opheodesoma spectabilis FISHER, 1907
(fig. 46A-D, fig. 56D)

Opheodesoma spectabilis FISHER, 1907: 723, pl. 66, pl. 80, fig. 1a-d, pl. 81 fig 2.
Opheodesoma spectabilis; CLARK 1908: 75; H.L. CLARK 1924: 467; HEDING 1928: 120; CLARK & ROWE 1971: 186; CHERBONNIER 1974; 1445 (synonymy); FÉRAL & CHERBONNIER 1986: 104 (colour picture), 105; LANE *et al.* 2000: 492; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2).
Opheodesoma sp. prob. *O. spectabilis*; HUMPHREYS 1981: 36.

Status and location type - Most probably type material exists in the Smithsonian Institute.

Type locality - Pearl Harbour, Hawaii Islands.

Material examined - TMes/9834 (one specimen).

General description - Moderate sized species reaching lengths of about 450 mm in life; 290 mm long and 21 mm wide after preservation. Body colour after preservation: ventral side more or less uniform white, dorsal side white grey with numerous transverse greyish bands. Tentacles 15, white-cream in clouration, feather-like, with numerous pairs of digits not united by a web. Numerous long Polian vesicles. Numerous short stone canals. Calcareous ring greenish with anterior processes less then one third of the height of the calcereous ring. Cartilagenous higher as the calcareous ring, with openings in its below the calcareous ring.
Ossicles: Body wall presents anchors, anchor-plates and miliary granules (fig. 46A, B). Anchors 440-455 µm long and 270-280 µm wide; stock regularly branched and spinose; arms smooth, vertex with some irregular small knobs (fig. 46A). Anchor-plates: quadrangular in outline; 300-310 µm long and 225-235 µm wide; 7 serrated holes; narrow posterior part with 4-7 smooth holes; bridge straight (fig. 46B). Miliary granules very numerous. Tentacles with miliary granules only; these are similar to those of the body wall (fig. 46C). Oral disc with rods only, rounded or slightly spinose extrimities, 80-100 µm long (fig. 46D).

Diagnosis - See FISHER 1907: 723, pl. 66, pl. 80, fig. 1a-d, pl. 81 fig 2; CHERBONNIER 1974: 1445-1447, text fig. 1A-H.

Ecology - The specimen was found during a night-dive, actively sweeping its tentacles over fine coralline sand between coral boulders, 10 m depth. LANE *et al.* (2000) state that this species lives at depths exceeding 20 m; CHERBONNIER's (1974) record was found at 25 m depth. It is noteworthy that *O. spectabilis* is reported as the host of the pontoniid shrimp *Periclimenes imperator* BRUCE, 1967 (CHERBONNIER 1974).

Distribution in the study region - Mesali only.

Geographic distribution - Tropical Indo-west Pacific (no records from the Red Sea nor from the Persian Gulf). In the WIO only known from a few localities: Tanzania, Zanzibar (CHERBONNIER 1974), Mesali (this work); Kenya, Ras Ngomeni (HUMPHREYS 1981, as *Opheodesoma* sp. prob. *O. spectabilis*). Figure 56D shows the known WIO distribution in detail.

Remarks - H.L. CLARK (1924) examined 29 specimens of *O. spectabilis* from Pearl Harbor, Oahu, Hawaiian Islands and noted that large differences exist between young and old specimens. Two variations with size are apparent: (1) the development of the cartilagenous ring: "in general, it (the calcareous ring) may be said to be wanting in very small specimens and heavy in those that are full grown [sic]"; and (2) the size of the calcareous deposits increases with increasing body length (table 23).

Length body wall (in mm)	Average length anchor ossicle (in µm)
40	232
100	295
160-200	326
More than 200	Often exceeding 400

Table 23 – Intraspecific variation in *O. spectabilis* FISHER, 1907 as observed by H.L. CLARK (1924). Note that the length of the ossicles increases with increasing body length.

The length of the specimen under study (290 mm long) falls in the last category and its ossicle dimensions agree with H.L. CLARK's (1924) observations. To further confirm the identification, it can be noted that absence of rods in the tentacles and presence of smooth to slightly knobbed rods in the oral disc agrees with *O. spectabilis* (CHERBONNIER 1974).

Up to now, CHERBONNIER (1974) was the only researcher to document *O. spectabilis* with certainity from E. Africa, Zanzibar (see also distribution table CLARK & ROWE 1971: 186). It should however be noted that HUMPHREYS (1981) reported on *Opheodesoma* sp. prob. *spectabilis* from Ras Ngomeni (near Malindi, Kenya). Hereby, he stated that, if his identification is correct, his record is a range extension from the western Pacific, thus ignoring CHERBONNIER's (1974) record. Unfortunately I failed to locate HUMPHREYS (1981) voucher specimen in the MRAC or NHM.

Table 24 lists the other species within the genus *Opheodesoma* that is known to occur in the shallow waters of the WIO, but has for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record appeared.

Current Species Name	Known WIO Distribution	Reference(s)
O. kamaranensis A.M. CLARK, 1951	Red Sea (Kamaran Islands)	A.M. CLARK 1951; DANIEL & HALDER 1974 PRICE 1982

Table 24 - *O. kamaranensis* A.M. CLARK, 1951 is the only other species within the genus *Opheodesoma* known to occur in the shallow-waters of the WIO.

Genus *Synapta* ESCHSCHOLTZ, 1829

Diagnosis [Type species: *Synapta mammillosa* ESCHSCHOLTZ, 1829 (=*Holothuria maculata* CHAMISSO & EYSENHARDT, 1821) by subsequent designation].
CLARK (1908) believed the genus *Synapta* to be monotypic, but HEDING (1928; 1929; 1931) consitently included *S. oceanica* (LESSON, 1839) as a second valid species and recognised two varieties of *S. maculata*: *S. maculata* var. *sundaensis* HEDING, 1928 and *S. maculata* var. *Andrea* HEDING, 1928. The latter varieties are now regarded as true synonyms of *S. maculata*; the status of *S. oceanica* remains debatable.

Synapta maculata (CHAMISSO & EYSENHARDT, 1821)
(fig. 47A-G, fig. 56E)

Holothuria maculata CHAMISSO & EYSENHARDT, 1821: 235, pl. 25.
Chondrocloea beselli JÄGER, 1833; DANIEL & HALDER 1974: 427.
Synapta beselli; DANIEL & HALDER 1974: 429.
Synapta oceanica (LESSON, 1830): 99; MACNAE & KALK 1958: 43, 69, 75, 99, 107, 117, 130 (from THANDAR 1984); MACNAE & KALK 1962: 111, 118; KALK 1959: 22; BRANCH & BRANCH 1981: 247 (from THANDAR 1984).
Synapta maculata; DANIEL & HALDER 1974: 418; HUGHES & GAMBLE 1977: 355; MUKHOPADHYAY 1991: 410, 412; ARAKAKI & FAGOONEE 1996: 122; BRANCH *et al.* 1999: 202, 203 (colour picture); MASSIN 1999: 108 (synonymy and records before 1999); LANE *et al.* 2000: 492; SAMYN & VANDEN BERGHE 2000: 5 (tab. 2), 17 (tab. 4), 18.

Status and location Type - Status and whereabouts undetermined (ROWE & GATES 1995).

Type locality - Marshall Islands (as 'Ad Insulas Radack') (ROWE & GATES 1995).

Material examined - KKan/9712 (one specimen); KShar/9736 (one specimen); KShar/9737 (one specimen); KShar/9738 (one specimen); KCi/9749 (one specimen); KCi/9750 (one specimen); KCi/9751 (one specimen); KKiun/9951 (one specimen); KMom/9862 (one specimen).

General description - Large species; live specimens attain two to three meters in length by 3-5 cm in diameter; observed specimens range from 90 to1170 mm in length and from 8 to 35 mm in width, after preservation. Colour in life more or less retained after preservation: body olive-green with five olive-brown stripes and numerous white spots, tentacles similar in colouration but with some fine white stripes instead of white spots. Mouth terminal, surrounded by 15 tentacles, each of them with 30-40 pairs of digits that are not united by a web. Anus terminal, small. Single to two stone canals ending in a circular madreporic plate. Gonad long, branched. Calcareous ring weakly developed, composed of radial and interradial pieces of the same size; radial pieces perforated for the nerve, posterior part of the pieces undulating, anterior part of the pieces pointed. Cartilaginous ring huge, almost completely envelopping the calcareous ring. Polian vesicles numerous and long.
Ossicles: Body wall with anchors, anchor-plates and miliary granules (fig. 47A-G). Anchors 750-950 µm long and 575-740 µm wide; stock unbranched but finely toothed (fig. 47C); arms smooth, some minute

knobs positioned on the vertex or in little groups on each side of the vertex. Anchor-plates 600-715 µm long and in the articular end 375-400 µm wide; articular end typically 25-30 % wider than the anterior end; bridge usually well developed (broken in some anchor-plates), irregular, occasionaly with more or less prominent spines; central hole in the anchor-plates usually with a fine meshwork; anterior side of the plate with numerous small holes; posterior side with larger holes (fig. 47B, F). Miliary granules are simple rosettes of irregular shape, 15-25 µm across (fig. 47D, G). Tentacles with numerous miliary granules similar in size and shape as those found in the body wall; suporting rods always absent.

Diagnosis - See HEDING 1928: 113, fig. 2 (1-10).

Ecology - In seagrass beds, feeding on organic material attached to the leaves of sea grasses and algae, or sweeping the sandy substrate. LANE *et al.* 2000 report a bathymethric range of 0-25 m. In Kenya never seen deeper than 5 m. MACNAE & KALK (1962) report the pontoniid shrimp *Periclimenes rex* KEMP on *S. maculata* (as *S. oceanica*).

Distribution in the study region - Seagrass beds along the coast, very large population in Kanamai.

Geographic distribution - Tropical, Indo-west Pacific Ocean (with the Red Sea, without the Persian Gulf). The distribution map as drawn by MASSIN (1999: 109, fig. 92) gives the global distribution, but the following localities have to be added: Gulf of Aqaba, Aqaba (TORTONESE 1977), Um Nageila (A.M. CLARK 1952; DANIEL & HALDER 1974) (see also PRICE 1982 for unspecified record from the Gulf of Aqaba); Saudi Arabia, Jeddah (TORTONESE 1979); Djibouti (CHERBONNIER 1955); Kenya, Kiunga Marine Reserve (SAMYN & VANDEN BERGHE 2000), Shariani, Kanamai, Mombasa, Chale Island (this work); Madagascar, Tuléar, Ile St. Marie, Antsakoabe (CHERBONNIER 1988), Figure 56E shows the known distribution in the WIO in detail.

Remarks - *Synapta maculata* is a well-known species from the western Indian Ocean and was reported by numerous workers under its junior synonym *Synapta Beselli* JAEGER, 1833 (see CLARK & ROWE 1971).
THANDAR (1984) believes that two fragments of body wall collected along the coast of Mozambique are referable to *S. oceanica*, for the observed colouration pattern (dirty greyish yellow with five darker longitudinal lines in the radial areas) is similar to that described by HEDING (1929) for *S. oceanica.* MACNAE & KALK (1958) reported the latter species from Mozambique. As I have not seen these or HEDING's voucher specimens, I am not in the position to debate the taxonomic status of *S. oceanica*, but nevertheless, after examination of several individuals of *S. maculata* from Kenya and the Seychelles, I remain extremely sceptical about the validity of *S. oceanica* that to me fits into the intraspecific variation of *S. maculata.*

Genus *Synaptula* ÖRSTED, 1849

Diagnosis (after HEDING, 1928: 154) [Type species: *Synaptula vivipara* ÖRSTED, 1849 (= *Synaptula hydriformis* LESUEUR, 1824) by monotypy; see also ROWE & GATES 1995: 336]
Small to moderate species, vermiform bodies reaching lengths up to 800 mm in life; usually 10 or 13 tentacles (occasionaly 12 or 15), each with 4-30 pairs of digits (digit number increases with age), web between digits present or absent; body wall very thin, sticky to the touch; calcareous ring fine with one or two interradial pieces for each radial piece, that are always perforated; cartilaginous ring present, development from very faint and translucent to voluminous, often perforated close to the ring canal; 3-50 Polian vesicles; one to several stone canals; gonad distinctly branched (except in *S. hydriformis* and *S. indivisa*). Ossicles: body wall present anchors, anchor-plates and miliary granules (except in *S. aspera*); tentacles present miliary granules only (except in *S. hydriformis* which also presents some rods); anchors with stock unbranched and slightly spiny, arms smooth, vertex with some quadrangular teeth; anchor-plates rounded anteriorly and narrowing posteriorly; anchors and anchor-plates in posterior body end often a little larger than those in the anterior body end; miliary granules generally rosettes, but sometimes circles of 'minute granules'.
Currently 29 species are regarded as being valid: *Synaptula alba* HEDING, 1928, *S. albolineata* HEDING, 1928; *S. aspera* (SLUITER, 1901); *S. ater* HEDING, 1928; *S. bandae* HEDING, 1928; *S. denticulata* HEDING, 1928; *S. hydriformis* (LESUEUR, 1824); *S. indivisa* (SEMPER, 1868); *S. jolensis* HEDING, 1928; *S. lactea*

(SLUITER, 1887)[12]; *S. lamperti* HEDING, 1928; *S. macra* (H.L. CLARK, 1938)[13]; *S. maculata* (SLUITER, 1888); *S. madreporica* HEDING, 1928; *S. media* CHERBONNIER & FÉRAL, 1984; *S. minima* HEDING, 1928; *S. mortenseni* HEDING, 1929; *S. neirensis* HEDING, 1928; *S. nigra* (SEMPER, 1868); *S. psara* (SLUITER, 1887); *S. reciprocans* (FORSKÅL, 1775); *S. recta* (SEMPER, 1868); *S. reticulata* (SEMPER, 1868); *S. rosetta* HEDING, 1928; *S. spinifera* MASSIN & TOMASICK, 1996; *S. tualensis* HEDING, 1928; *S. varians* (NAIR, 1946); *S. violacea* HEDING, 1928; *S. virgata* (SLUITER, 1901) and *S. vittata* (FORSKÅL, 1775).

Even though HEDING'S contributions (1928; 1929; 1931) brought significant insights into this important genus, careful examination of his type material (in ZM), in comparison with other museum and new material, most probably will reveal the synonymous nature of several of the above species (ROWE *in* ROWE & GATES 1995; see also footnotes). This because (i) HEDING described a number of species based on single specimens and often fragmented material (ROWE *in* ROWE & GATES 1995), and (ii) it is known for several *Synaptula* spp. that several characters (size of anchors and anchor plates, presence of a long spine on the anchor-plate bridge, number of tentacles and number of tentacular digits) vary with size of the species (MASSIN 1999). In zoogeographic respect it is interesting to note that HEDING (1928) thought that all *Synaptula* species (apart from *S. hydriformis*) were restricted to the Malay Archipelago. It is however now known[14] that several species extend into the western Indian Ocean and the Red Sea[15]: Table 26 shows that several *Synaptula* spp. have been recorded in the Gulf of Suez, Gulf of Aqaba, Red Sea and eastern Africa; no *Synaptula* sp. has apparently reached the Persian Gulf.

Synaptula recta (SEMPER, 1868)
(fig. 48A-F, fig. 56F, pl. 4H)

Synapta recta SEMPER, 1868: 14, pl. 4 figs 2-3, pl. 5 fig. 18, pl. 8 fig. 2.
Chondrocloea recta; DANIEL & HALDER 1974: 429.
Synaptula recta; TORTONESE 1936a: 241; TORTONESE 1953a; 46; MUKHOPADHYAY 1991: 411, 413; MASSIN 1999: 116 (synonymy), fig 102 (distribution), 114b,c (colour pictures); LANE *et al.* 2000: 492.

Status and location type - Status and whereabouts undetermined (ROWE & GATES 1995).

Type locality - Bohol (Philippines).

Material examined - TMes/9833 (one specimen); TMes/9835 (one specimen); TMes/9836 (one specimen); TMes/9837 (one specimen); TMes/9838 (one specimen); TMes/9839 (one specimen); TMes/9840 (one specimen).

General description - Moderate to large species reaching lengths up to 800 mm in life; observed specimens 120-470 mm long and 4-17 mm wide after preservation. Body colour in life variable: from uniform beige-brown with slightly darker tentacles to uniform dark red with orange to brown tentacles. Body colour after preservation faded to greyish, slightly lighter ventrally. Tentacles 13 (12 in TMes/9836); digits united by a very shallow web, number of digits variable, but commonly 15-25 pairs (abberant numbers seem to results from bad preservation). In well-preserved specimens, heaps of miliary granules forming white transverse bands in the tentacles can be seen. Huge cartilaginous ring, perforated at the base, completely masks the calcareous ring. Numerous (15-23) Polian vesicles of at least two sizes. Gonads well developed and branched several times. Intestinal loop not observed. Calcareous ring consists of two interradial pieces for each radial piece, radial and interradial pieces of the same size with the radial pieces perforated for the nerve.

Ossicles: Body wall with anchors, anchor-plates and miliary granules (fig. 48A-F). Anchors of anterior and posterior side of the same shape: stock unbranched, finely dented at the periphery, arms smooth and a few tooth on the vertex (fig. 48B, E). Anchor size significantly larger posteriorly (fig. 48B) than anteriorly (fig.

[12] ROWE (*in* ROWE & GATES, 1995) notes that the relationship between *Synaptula reticulata* (SEMPER, 1868), *Synaptula lactea* (SLUITER, 1887) and *Synaptula lamperti* HEDING, 1928 needs further investigation.

[13] ROWE (*in* ROWE & GATES, 1995) notes that *Synaptula macra* (H.L. CLARK, 1938) 'almost certainly will prove to be a large form of *Synaptula recta* (SEMPER, 1868) when sufficient material has been compared' [sic].

[14] TORTONESE (1936a) even went so far to note the following 'Tutte queste Sinapte [here referring to *Synaptula*] sono littorale ed abitano la regione indo-pacifica, ad eccezione di una (*S. hydriformis* (LESS.)) vivente nel mar delle Antille', a statement which is not substantiated by our present state of knowledge on the distribution of *Synaptula.*

[15] H.L. CLARK (1908: 132) provides a map with the global distribution of the genus *Synaptula*; three distinct regions are drawn: (i) the Red sea and East Africa (up to equator), (ii) central Indonesia / northern Australia and (iii) the Carribean area.

48E) (280.7 ± 19.6 μm versus 310.5 ± 19.5 μm; n = 120; t-value = -13.39). Anchor-plates of posterior (fig. 48A) and anterior (fig. 48D) side of the same shape: six serrated holes and three smooth articular holes (central one occasionally slightly serrated), bridge slightly knobbed to spiny; posterior holes one to six, average of 3.2 ± 0.8 (n= 120) on the posterior anchor-plates and three to seven, average of 3.95 ± 1.2 (n=120) on the anterior ones. Miliary granules (fig. 48C, F), 15-25 μm across, from rosettes to dissociated grains. In the tentacles miliary granules only, somewhat larger than in the body wall, 25-45 μm across, mostly as rosettes (fig. 48G).

Diagnosis - See HEDING 1928: 167, figs16 (4-6), 17 (3-8), 17.

Ecology - *S. recta* specimens were found on sponges (beige to red forms) and on a sandy bottom (beige form) between two coral slabs. LANE *et al.* 2000 give a bathymetric range of 0-20 m; our deepest specimen was found at 35 m depth.

Distribution in the study region - Mesali.

Geographic distribution - First record for the East African coast. Previous African records were only known from the Gulf of Aqaba (TORTONESE 1977; PRICE 1982), Red Sea (TORTONESE 1936a; 1953a; 1979; A.M. CLARK 1952; CLARK & ROWE 1971; PRICE 1982) and Gulf of Aden (H.L. CLARK 1908). Overall, this species has a tropical Indo-west Pacific Ocean (without the Persian Gulf) distribution as evident from the distribution map as drawn by MASSIN (1999: 116, fig. 100). However, DANIEL & HALDER's (1974 as *Chondrocloea recta* (SEMPER, 1868)) unverifiable records from Somalia (? *lapsus* for French Somalia = Djibouti?) and Zanzibar possibly have to be added. Figure 56F shows the known distribution in the WIO in detail.

Remarks - It was already noted above that the genus *Synaptula* is in critical need of review. A first morphological examination of the collected specimens on a morphological level (body colouration, structure of the calcareous and cartilageneous ring, number of tentacles, number of digits on these tentacles,...) revealed some variation. However, factor analysis of the ossicle assemblage of each specimen of *S. recta* (maximum length and width of 20 anterior & 20 posterior anchors, 20 anterior & 20 posterior anchor-plates and the number of posterior holes in these anchor-plates), pointed in the direction of one (or maybe two; see *S.* cf. *recta* below) species (fig. 49).

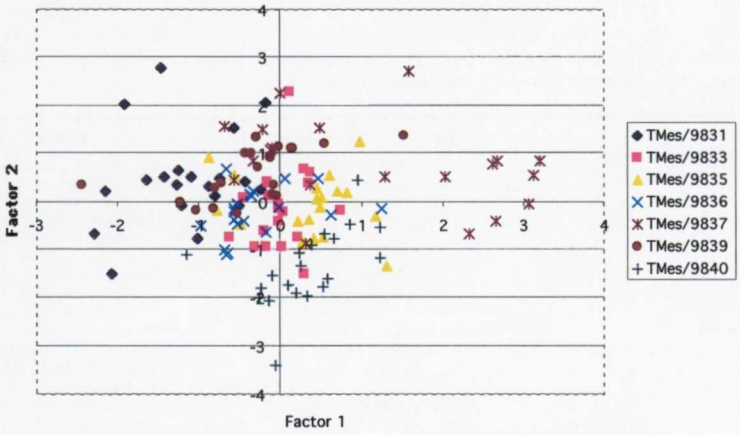

FIG. 49 – Factor analysis performed on the ossicle assemblage of the collected *Synaptula* specimens, with factor 1 explaining 36.17 % of the variation and factor 2 explaining 16.53 % of the variation. The observed variation thus seems to be intra-rather than interspecific.

Synaptula cf. *recta* (SEMPER, 1868)
(fig. 50 A-F, pl. 4J)

Status and location type - Status and whereabouts undetermined (ROWE & GATES 1995)

Type locality - Bohol (Phillipines).

Material examined - TFun/9831 (one specimen).

General description - See *S. recta*.

Diagnosis - See *S. recta*.

Ecology - The single specimen was found under live hard coral, on coralline sand.

Distribution in the study region - Mesali.

Geographic distribution - See *S. recta*.

Remarks - While fig. 49 shows that the present specimen largely falls within the cluster of *S. recta*, I hesitate in identifying it as such for the specimen differs in several aspects: (i) the body wall does not have the warty body wall extensions typical of *S. recta* (see pl. 4H versus pl. 4J); (ii) the live specimen was light beige rather then dark-beige to brownish red, the preserved specimen is clear white while the others are faint gray; (iii) the cartilageneous ring has regular, narrow slits rather then irregular holes as observed in the other specimens; an (iv) the dimensions of the ossicles are significantly different in size (not in shape) to those found in a *Synaptula recta* specimen of similar dimensions (table 25). Nevertheless, as I have only one specimen at my disposition, it is unwise to put it under another name until more material from the same region becomes available.

Ossicle	TMes/9831 (L=150 mm)	TMes/9835 (L=160 mm)	Significance
Length AP $_{(anterior)}$	187.67 ± 10.6 µm (n=20)	210.00 ± 11.7 µm (n=20)	*** (t=-5.23)
Width AP $_{(anterior)}$	145.67 ± 8.1 µm (n=20)	164.67 ± 7.8 µm (n=20)	*** (t=-6.27)
Length AP $_{(posterior)}$	211.50 ± 10.6 µm (n=20)	224.33 ± 7.8 µm (n=20)	*** (t=-4.45)
Width AP $_{(posterior)}$	171.67 ± 8.8 µm (n=20)	180.17 ± 8.2 µm (n=20)	** (t=-3.51)
# Posterior holes $_{(anterior)}$	4.85 ± 1.1 (n=20)	4.70 ± 1.3 (n=20)	NS
# Posterior holes $_{(posterior)}$	3.50 ± 1.0 (n=20)	3.20 ± 0.7 (n=20)	NS
Length A $_{(anterior)}$	267.50 ± 16.3 µm (n=20)	281.00 ± 15.4 µm (n=20)	** (t=-2.92)
Length A $_{(posterior)}$	311.33 ± 15.9 µm (n=20)	313.67 ± 9.2 µm (n=20)	NS

Table 25 - Pairwise comparison between a specimen of *Synaptula recta* and the specimen temporarily identified as *Synaptula* cf. *recta* of similar length. Significance is assessed through a two-tailed (paired) t-test; levels of signifigance:*** = $P < 0.001$; ** = $P < 0.01$; NS: not significant; n: number of ossicles measured; AP: anchor plate; A: anchor.

Table 26 lists the other species within the genus *Synaptula* that are known to occur in the shallow waters of the WIO, but have for now not been reported in Kenya (with Pemba Island). Column two gives the known WIO distribution, while column three provides the references wherein the record(s) appeared.

Current Species Name	Known WIO Distribution	Reference(s)
S. reciprocans (Forskål, 1775)	Gulf of Suez (Suez, Great Lake Amer, Lake	Selenka 1867; Semper 1868; 1869;
(see also discussion)	Timash, Great Bitter Lake, fontaine de Moise,	Forskål, 1775; Gray 1872; Lampert 1885;
	Wadi el Dom, Ismaila)	Théél 1886; Hérouard 1893;
		Mortsensen 1926; Heding 1928;
		Cherbonnier 1955; James 1969;
		James & Pearse 1969;
		daniel & Halder 1974; Price 1882
	Gulf of Aqaba (Aqaba)	Cherbonnier 1979a; Price 1982
	Red Sea (Entedebir, Abulat Island, Disei Island,	de Blainville 1821; Selenka 1867;
	Dur Chella, Hurghada, Jeddah, Noccra Island,	Tortonese 1936a; 1937-38; 1953a; 1977;
	Shek Said)	Mortensen 1937; Cherbonnier 1955; 1967;
		James 1969; James & Pearse 1969;
		Daniel & Halder 1974; Price 1982
	Gulf of Aden (Djibouti)	Vaney 1905; Cherbonnier 1955
	Arabian Sea	Daniel & Halder 1974; Price 1982
	Somalia?	Daniel & Halder 1974
	Madagascar (Nosy Komba and Mitsio Island)	Cherbonnier 1988
S. mortenseni Heding, 1929	Madagascar (Tuléar)	Cherbonnier 1988
(see also discussion)	Zanzibar	Heding 1929
S. nigra (Semper, 1868)	Gulf of Suez	H.L. Clark 1908
	Red Sea (Kosseir, Bay Margabla, Assab)	Lampert 1885; Ludwig 1886;
		H.L. Clark 1908
	Gulf of Aden?	Daniel & Halder 1974
S. vittata (Forskål, 1775)	Gulf of Suez	Gray 1872; Daniel & Halder 1974
	Red Sea	Daniel & Halder 1974

Table 26 - Other species within the genus *Synaptula* known to occur in the shallow-waters of the WIO.

Discussion

The (urgent) need to assess native levels of shallow-water holothuroid biodiversity in Kenya

During my first trip to Kenya (back in 1995) I noticed that large numbers of different species of holothuroids were collected *en masse* in several locations along the Kenyan Coast (e.g. Gazi Bay, Kanamai). At that time, I was surprised that nobody could tell me what species were fished and what the impact of such harvesting was on the fragile seagrass and coral reef ecosystem. Back in those days, little did I know that almost no checklists existed for the sea cucumber or bêche-de-mer resources of Kenya, and in fact of all East Africa. These observations prompted me to submit a project for describing and mapping the holothuroid biodiversity of the shallow-waters of Kenya. Later on, during a recreational dive trip to the western side of Pemba Island, I observed the very rich and apparently pristine underwater fauna of these coral gardens. As the holothuroid fauna of Pemba Island had not been the object of any study, I chose to include it in detail in the present paper.

During three sampling expeditions (from 1997 to 1999), I observed that in some locations holothuroid stocks were reaching depletion due to extensive harvesting for the bêche-de-mer industry, an observation which is apparantly shared by the sea cucumber fishermen (MARSHALL *et al.* 2001). However, to date, conservation and management of the Kenyan holothuroid fauna is still in its infancy; one of the main reasons probably results from the fact that the Kenyan Government lacks accurate species lists. For now, the Kenya Government addressed the problem of resource exploitation by gazetting marine reserves and parks. Marine parks being fully protected areas (no exploitation allowed), while marine reserves are only partially protected (fishing by traditional means is allowed). In addition the Kenyan authorities, through *The Fisheries Act 1991,* imposes collectors and traders in bêche-de-mer to hold a license, but as an extensive interview amongst holothuroid fishermen revealed, few fishermen hold such a license and many of them believe that the buyers and/or middlemen are the ones for whom this rule applies (MARSHALL *et al.* 2001).

Estimating the Kenyan holothuroid richness – How complete is the present checklist?

In order to develop a rational program to conserve as many species as possible we need to have an idea of the total number and distribution of the species in the area (MAY 1992; SAMYN 2000; DOPHLIN & QUICKE 2001). A rough prediction of the species richness of Kenya (with Pemba Island) can be obtained by plotting the cumulative number of species reported from the area against the sampling effort; the species accumulation curve that fits to the data predicts the final number of species (the asymptote) that exist in the area (fig. 57). This approximation reveals a number somewhere around 50; a number not far from what is reported here.

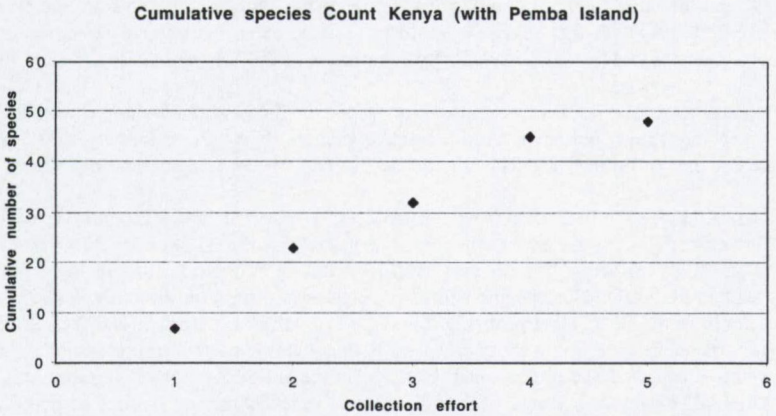

FIG. 57 - Estimating *holothuroid* species richness from Kenya (with Pemba Island) by constructing a cumulative count. 1 Denotes the cumulative count after PANNING (1941); 2 gives the known species after the former and LEVIN (1979); 3 after the former and HUMPHREYS (1981); 4 the former and the 1997 survey; 5 after the former and the 1998 survey; 6 after the former and the 1999 survey.

It can be argued that the observed discrepancy is due to the patchiness of the sampling effort and the sampling efficiency. This can be tested by looking for species that have been reported from the immediate North (Somalia) and from the immediate South (Tanzania) of Kenya, but not from Kenya. In such a way it is revealed that only three species – *H. (S.) parva* LAMPERT, 1885, *H. (P.) strigosa* SELENKA, 1867 and *Polycheira fusca* (QUOY & GAIMARD, 1833) – are missing in the present checklist (see fig. 58).

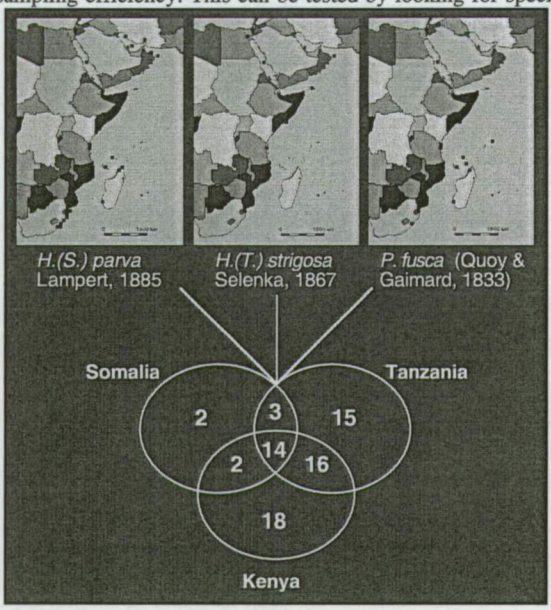

FIG. 58 - Gap analysis of the Somalian and the Tanzanian shallow-water Holothurioidea. Of the 17 species that are reported from both Somalia and Tanzania, only three [*Holothuria (Selenkothuria) parva* LAMPERT, 1885; *Holothuria (Thymiosycia) strigosa* SELENKA, 1867 and *Polycheira fusca* (QUOY & GAIMARD, 1833)] have not been found in Kenya.

However, as the sampling effort, sampling efficiency and taxonomic effort in Tanzania and especially in Somalia can hardly be called sufficient, it was thought desirable to examine at the broader geographic scale of the western Indian Ocean. This way several species that are potentially present in Kenya can be found; these species are listed in the different text tables included under each genus or subgenus. Some of these[16] need some additional comments in terms of distribution and expected occurrence in Kenya.

- *Actinopyga bannwarthi* PANNING, 1944. This species is reported from the Red Sea (up to Djibouti), the Seychelles and Madagascar (see table 2). The records from the Seychelles and Madagascar must however be treated with caution as the former was reported as *Actinopyga* sp. cf. *A. bannwarthi* (SLOAN *et al.* 1979) and the latter might not be *A. bannwarthi* for the ossicles reported from the dorsal body wall (CHERBONNIER 1988: 17, fig. 1E, F, G, K) differ to some extent with those depicted in the original decription (PANNING 1944: 54, fig. 22k-r). Its occurrence in the Kenyan shallow waters thus remains doubtful.
- *Actinopyga obesa* (SELENKA, 1867). The most northern record in the western Indian Ocean is Ile Mayotte (Comores), wherefrom it is known from a single specimen. It is further known from South Africa (pers. observ.), the Phillipines and Hawaii. Its occurrence in the Kenyan shallow waters is improbable.
- *Bohadschia argus* JAEGER, 1833. In East Africa this species is reported with certainity from the Seychelles and Madagascar (PANNING 1944 states that *B. argus* is distributed between 30°N & 20°S and between 50°E & 140°W). Recently, it has also been reported along the coastline of the African continent (MARSHALL *et al.* 2001). This species with its conspicuous circles on the body wall can be identified without doubt in the field. Most probably, the record of MARSHALL *et al.* (2001) is *B. atra* rather than *B. argus*. Its occurrence in the Kenyan waters is thus extremely doubtful, especially since questioning of several recreational and professional divers (with the aid of the pictures in GOSLINER *et al.* 1996 and WEINBERG 1997) on the presence of this ubiquitous species yielded no positive response.

[16] While the text-tables give the distribution in the WIO, it was thought wise to discuss the possibility of occurrence in Kenya in more detail. However, species of which it is obvious that they are restricted to a certain area (for instance all records of the species stem from the Red Sea) are here not further discussed. On the other hand records that are problematic (possibilty of misidentification) are more thoroughly analyzed.

- *Bohadschia maculisparsa* CHERBONNIER & FÉRAL, 1984. CONAND (1999) is the only one to report this species from the Indian Ocean. Most probably, CONAND's recording is *B. marmorata* rather then *B. maculisparsa* as the latter species is known only from the holotype (New Caledonia).
- *Bohadschia mitsioensis* CHERBONNIER, 1988. This species is only known from the holotype and the paratype, both specimens from North-western Madagascar (Mitsio Island). CHERBONNIER (1988) himself expresses his doubts on the validity of this species. The ossicle assemblage as shown in CHERBONNIER (1988) makes me believe that it is a colour variety of *B. marmorata* rather then a valid species.
- *Labidodemas rugosum* (LUDWIG, 1875). This species undoubtedly can also thrive in the Kenyan waters; however the burrowing behavior of *Labidodemas* spp. makes them difficult to find. Global distribution maps of all *Labidodemas* spp. can be found in MASSIN *et al.* (submitted).
- *Holothuria (Cystipus) jousseaumei* CHERBONNIER, 1954. Prior to the present study, this species was only known from the Red Sea (see table 6); the finding of a voucher specimen from the Seychelles in the MRAC, expands the distribution considerably, making its presence in the Kenyan waters probable.
- *Holothuria (Cystipus) sucosa* ERWE, 1919. Endemic species to the Red Sea (see table 6). As most records are derived from secondary sources, it is difficult to ascertain the validity of the species.
- *Holothuria (Lessonothuria) lineata* LUDWIG, 1875. ROWE (*in* ROWE & GATES 1995) resurected this species from the synonymy of *H. (L.) pardalis* SELENKA, 1867. It remains to be investigated if the specimens from Mauritius are indeed *H. lineata* or rather, as I suspect, misidentified individuals of *H. pardalis*.
- *Holothuria (Mertensiothuria) fuscorubra* THÉEL, 1886. This species has long been regarded as a synonym of *H. (M.) leucospilota* but was recently resurected as a valid species (SAMYN & MASSIN in press). If the vast amount of voucher specimens of *H. leucospilota* could be re-examined, undoubtedly the distribution of *H. fuscorubra* would be more detailed, making it very possible that the species belongs to the Kenyan fauna.
- *Holothuria (Mertensiothuria) papillifera* HEDING *in* MORTENSEN, 1938. Prior to the present study, this species was only known from the Red Sea (SAMYN & MASSIN in press); the finding of a voucher specimen [identified as *Holothuria (Thymiosycia) impatiens* (FORSKÅL, 1775)] from Tanzania (Dar Es Salaam) in the MRAC, expands the distribution considerably, making its presence in the Kenyan waters very probable.
- *Holothuria (Metriatyla) horrida* MASSIN, 1987. The recognition that CHERBONNIER's (1988) *Holothuria (Metriatyla)* sp. shows almost no differences with the recently described *H. (Metriatyla) horrida* expands the distribution from Indonesia to Madagascar. It remains uncertain if this rare species also thrives in Kenya.
- *Holothuria (Microthele) whitmaei* BELL, 1887. The only record of this species from the WIO is that of ROWE & RICHMOND (1997). As these authors made their book by drawing on other sources, it is strange that the species figures in their work for I failed to find a publication dealing with the holothuroids of the WIO that mentions this species. Its occurrence in the shallow-waters of the WIO seems improbable even if ROWE & GATES (1995) state that it is distributed through the tropical, Indo-west Pacific Ocean.
- *Holothuria (Selenkothuria) moebii* LUDWIG, 1883. It remains most uncertain if this species with a wide Indo-west Pacific distribution has indeed reached the East Coast of Africa as claimed by DANIEL & HALDER (1974). DEICHMANN (1958) gives a distribution from Mauritius to Japan.
- *Holothuria (Semperothuria) flavomaculata* SEMPER, 1868. This well-known, easily recognisable and widely distributed species has strangely enough never been found along the East African coast (but see CHERBONNIER 1988: 69). The MRAC record from the Seychelles and the records from Madagascar (see table 16) for now indicate the most western localities in the Indian Ocean, but I believe it is only a matter of time before this species will be found along the East African coast.
- *Holothuria (Stauropora) olivacea* LUDWIG, 1888. CHERBONNIER's (1988) recent finding of of this species in Madagascar indicate that this Indo-west-central Pacific species possibly also thrives along the East African coasts.
- *Holothuria (Theelothuria) hamata* PEARSON, 1913. The recent findings of this species at the North coast of Australia (ROWE & GATES 1995) indicate that this species most probably is distributed throughout the tropical Indian Ocean (with the Red Sea) and that SLOAN *et al.*'s (1979) record from the Seychelles (Aldabra) is probable; presence in Kenya is thus also possible.

- *Holothuria (Theelothuria) maculosa* PEARSON, 1913. Difficult to state if this species will ever be found in Kenya; for now this species is known only from the Seychelles (Aldabra), Madagascar and Inhaca (CHERBONNIER 1988).
- *Holothuria (Theelothuria) notabilis* LUDWIG, 1874. ROWE (*in* ROWE & GATES 1995) gives the tropical Indo-Malayan region as the distribution area. The discovery of *H. notabilis* on the KwaZulu-Natal coast, expands its distribution considerably. Whether this species is present in Kenya seems to depend on the dispersion route taken by the species. If it traversed the Indian Ocean with the South Equatorial Current and arrived in North-East South Africa with the Mozambique and the Agulhas Current, presence in Kenya is also likely. If, on the other hand it split of with the Madagascar current (the current that flows the eastern Madagascar coast) and from there reached South Africa with the Agulhas Current, presence in Kenya is unlikely. Pointing the most probable hypothesis is at present difficult, and will depend on future explorations along the Mozambique Channel.
- *Holothuria (Thymiosycia) gracilis* SEMPER, 1868. This species is rather ill-known, with the sparse distribution records spread over the Indo-West Pacific (CLARK & ROWE 1971; CHERBONNIER 1988; LANE *et al.* 2000), but as it has been found in Zanzibar (LAMPERT 1885), presence in Kenya is also very probable.
- *Stichopus horrens* SELENKA, 1867. The confusion of *Stichopus variegatus* SEMPER, 1868 (junior synonym of *S. horrens*) with *S. monotuberculatus* (QUOY & GAIMARD, 1833) and *S. herrmanni* SEMPER, 1868 makes it difficult to discuss the distribution of this species. Nevertheless, as the species is known from the North and the south of Kenya, it most probably also belongs to the Kenyan fauna.
- *Stichopus pseudohorrens* CHERBONNIER, 1967. CONAND (1999: 10) is the only one who lists the species from the Indian Ocean, all the other records in the WIO are from the Gulf of Aqaba (see table 20). FÉRAL & CHERBONNIER (1986) report the species also from New Caledonia and LANE *et al.* (2000) from the South China Sea. The record of LANE *et al.* (2000) cannot be judged for the paper does not give descriptions, the record of FÉRAL & CHERBONNIER (1986) on the other hand differs from CHERBONNIER's (1967) original description in several ways, hence their species might be another (new?) species. During a recreational dive at Pemba Island (Fundu) I was able to photograph a *Stichopus* sp. (fig. 59) which morphologically corresponds to CHERBONNIER's (1967) description of *S. pseudohorrens*. Unfortunately, at that time I lacked a collecting permit so no voucher specimen could be taken; later, I never found the species again. I hesitate to identify it as *Stichopus pseudohorrens*, but given CONAND's (1999) record from the Indian ocean (no exact locality given), it is likely that this species has to be added to the Kenyan fauna as well. For now, until a voucher specimen is available, I refrain from doing so.



FIG. 59 - *Stichopus* sp. as photographed at Pemba Island (Fundu) most probably represents *S. pseudohorrens* CHERBONNIER, 1967.

- *Synaptula mortenseni* HEDING, 1929. Species known only from Zanzibar (Heding 1929) and Madagascar (CHERBONNIER 1988); most probably it can also be found in Kenya.
- *Synaptula reciprocans* (FORSKÅL, 1775). This species has been reported from the Red Sea by an impressive number of authors (see table 23). But, as CHERBONNIER (1988) was the only one to report it from the Indian Ocean (Madagascar, Nosy Komba and Mitsio Island), his voucher specimens need careful re-examination to check their validity. In fact, as this genus is in critical need of review, it is almost impossible to comment on the zoogeography of this group.

In addition, a large number of species that do not fall under genera (or even families and orders) known from Kenya can be found in the shallow waters of the WIO. These are grouped in table 27, whereby the eight arbitrary chosen geographic regions correspond with those specified in map 2. As most of these species are ill-known to me, I will (for now) refrain from commenting on their taxonomy, but nevertheless will flag (with footnotes and question marks) those species that are improbable in terms of occurrence

(depth, geographic locality), validity or systematic position. The exact locality of collection of each of the mentioned species can be found in the accompanying references.

TAXON	CITED AS	REFERENCE(S)	1	2	3	4	5	6	7	8
APODIDA										
Chiridotidae ÖSTERGREN, 1907										
Chiridota durbanensis THANDAR, 1996	*Chiridota durbanensis* THANDAR	THANDAR 1996								x
Chiridota eximia HAACKE, 1880	*Chiridota eximia* HAACKE	HAACKE 1880; LAMPERT 1885; THÉEL 1886; DANIEL & HALDER 1974							x	
Chiridota rigida SEMPER, 1868	*Chiridota rigida* SEMPER	THANDAR & ROWE 1989							x	x
Chiridota stuhlmanni LAMPERT, 1896	*Chiridota stuhlmanni* LAMPERT	LAMPERT 1896; H.L. CLARK 1908; HEDING 1931; CHERBONNIER 1967; TORTONESE 1977; SLOAN *et al.* 1979; PRICE 1982; A.M. CLARK 1984; CHERBONNIER 1988	x						x	x
Chiridota violacea PETERS *in* J. MÜLLER, 1850	*Chiridota violacea* (J. MÜLLER)	CLARK & ROWE 1971; SLOAN *et al.* 1979; A.M. CLARK 1984; CHERBONNIER 1988							x	x
	Chiridota violacea PETERS	MÜLLER 1850; SELENKA 1867; SEMPER 1868; BELL 1884; LAMPERT 1885; DANIEL & HALDER 1974							x	
	Chiridota violacea PETERS *in* MÜLLER	THÉEL 1886							x	
	Chiridota violacea	H.L. CLARK 1908; HUGHES & GAMBLE 1977	x						x	
Polycheira fusca (QUOY & GAIMARD, 1833)	*Polycheira fusca* (QUOY & GAIMARD, 1833)	CHERBONNIER 1988							x	x
	Chiridota rufescence BRANDT	DANIEL & HALDER 1974		x					x	
	Chiridota rufescens BRANDT	LAMPERT 1896; LUDWIG 1899							x	
	Polycheira rufescens (BRANDT)	HEDING 1929; CLARK & ROWE 1971; SLOAN *et al.* 1979; TORTONESE 1980; A.M. CLARK 1984; THANDAR 1989a							x	x
	Polycheira rufescens CLARK	HEDING 1931							x	
Trochodota mira CHERBONNIER, 1988	*Trochodota mira* CHERBONNIER	CHERBONNIER 1988								x
Trochodota vivipara CHERBONNIER, 1988	*Trochodota vivipara* CHERBONNIER	CHERBONNIER 1988							x	x
Synaptidae BURMEISTER, 1837										
Anapta gracilis SEMPER, 1868	*Anapta gracilis* SEMPER	CLARK & ROWE 1971							x	
Labidoplax mortenseni HEDING, 1931	*Labidoplax* sp	MORTENSEN 1926	x							
	Labidoplax mortenseni HEDING	HEDING 1931	x							
Leptosynapta chela MORTENSEN, 1926	*Leptosynapta chela* MORTENSEN	MORTENSEN 1926; CLARK & ROWE 1971; PRICE 1981; 1982; 1983	x		x		x	x		
Leptosynapta geyserensis CHERBONNIER, 1988	*Leptosynapta geyserensis* CHERBONNIER	CHERBONNIER 1988							x	
? *Leptosynapta inhaerens* (O. F. MÜLLER, 1776)[17]	*Synapta inhaerens* O. F. MÜLLER	LAMPERT 1885			x					
	Synapta inharens O.F. MÜLLER	DANIEL & HALDER 1974			x	x				
Leptosynapta knysnaensis (CHERBONNIER, 1952)	*Epitomapta knysnaensis* CHERBONNIER	CHERBONNIER 1952a; DANIEL & HALDER 1974								x
	Epitomapta sp.	CHERBONNIER 1954b								x
	Leptosynapta ancaracuta CHERBONNIER	DANIEL & HALDER 1974								x
	Leptosynapta ancoracuta CHERBONNIER	CHERBONNIER 1954b								x
	Leptosynapta knysnaensis (CHERBONNIER)	THANDAR & ROWE 1989								x
	Leptosynapta sp.	CHERBONNIER 1954b								x
Leptosynapta naiga THANDAR & ROWE, 1989	*Leptosynapta naiga* THANDAR & ROWE	THANDAR & ROWE 1989								x
Leptosynapta oblonga CHERBONNIER, 1988	*Leptosynapta oblonga* CHERBONNIER	CHERBONNIER 1988							x	
Leptosynapta pustulosa CHERBONNIER, 1970	*Leptosynapta pustulosa* CHERBONNIER	CHERBONNIER 1970a								x
Leptosynapta tantula CHERBONNIER, 1988	*Leptosynapta tantula* CHERBONNIER	CHERBONNIER 1988								x
Oestergrenia spatula THANDAR & ROWE, 1989	*Oestergrenia spatula* THANDAR & ROWE	THANDAR & ROWE 1989							x	x
Patinapta crosslandi HEDING 1928	*Patinapta crosslandi* HEDING	HEDING 1929; TORTONESE 1936a; 1937-38; DEICHMANN 1948; CLARK & ROWE 1971; DANIEL & HALDER 1974; PRICE 1982; CHERBONNIER 1988; THANDAR 1989a		x					x	x
	Patinapta crosslandii HEDING	HEDING 1931							x	
Patinapta dumasi CHERBONNIER, 1954	*Patinapta dumasi* CHERBONNIER	CHERBONNIER 1954a; 1955; CHERBONNIER 1967; JAMES 1969; JAMES & PEARSE 1969; DANIEL & HALDER 1974; PRICE 1982	x		x					
	Leptosynapta steinitzi CHERBONNIER	CHERBONNIER 1967; PRICE 1982			x					
Patinapta ooplax (VON MARENZELLER, 1881)	*Patinapta ooplax* (VON MARENZELLER)	CLARK & ROWE 1971; CHERBONNIER 1988							x	x
	Synapta ooplax V. MARENZELLER	LAMPERT 1896; LUDWIG 1899							x	
	Leptosynapta ooplax	H.L. CLARK 1908							x	

[17] The records of LAMPERT (1885) and DANIEL & HALDER (1974) need confirmation. This species, together with *Holothuria (Roweothuria) poli* DELLE CHIAJE, 1823 and *H. (Thymiosycia) impatiens* (FORSKÅL, 1775), are the only ones, known with certitude, to be present in both the Mediterranean Sea and the WIO (TORTONESE 1953b).

Patinapta vaughani CHERBONNIER, 1953	*Patinapta vaughani* CHERBONNIER	CHERBONNIER 1953a						x
Polyplectana kefersteini (SELENKA, 1867)	*Polyplectana kefersteini* (SELENKA)	TORTONESE 1977; SLOAN *et al.* 1979; PRICE 1982; A.M. CLARK 1984; ARAKAKI & FAGOONEE 1996; MASSIN unpublished	x	x				x x
	Polyplectana kefersteinii	H.L. CLARK 1908		x				
	Synapta kefersteinii SELENKA	LAMPERT 1885; DANIEL & HALDER 1974		x	x			
	Synaptula kefersteinii (SELENKA)	FISHER 1907				x		
Protankyra autopista (VON MARENZELLER, 1881)	*Protankyra autopista* (MARENZELLER)	TORTONESE 1977; PRICE 1982	x					
Protankyra magnihamula HEDING, 1928	*Protankyra magnihamula* HEDING	HEDING 1940b; PRICE 1982, 1983				x		
Protankyra picardi CHERBONNIER, 1988	*Protankyra picardi* CHERBONNIER	CHERBONNIER 1988						x
Protankyra pseudodigitata (SEMPER, 1868)	*Protankyra pseudodigitata* (SEMPER)	HEDING 1928; HEDING 1940b; CHERBONNIER 1955; PRICE 1982; 1983	x			x		
	Protankyra sp.	MORTENSEN 1926	x					
ASPIDOCHIROTIDA								
Stichopodidae HAECKEL, 1896								
Neostichopus grammatus (H.L. CLARK, 1923)	*Neostichopus grammatus* (H.L. CLARK)	DEICHMANN 1948; THANDAR 1987a; CHERBONNIER 1988; pers. observ.						x
	Neostichopus grammata (H.L. CLARK)	DANIEL & HALDER 1974						x
	Holothuria grammata HL CLARK	H.L. CLARK 1923						x
Synallactidae LUDWIG, 1894								
? *Synallactes mollis* CHERBONNIER, 1952[18]	*Synallactes mollis* CHERBONNIER	DANIEL & HALDER 1974						x
? *Synallactes viridilimus* CHERBONNIER, 1952[19]	*Synallactes viridilimus* CHERBONNIER	DANIEL & HALDER 1974						x
DENDROCHIROTIDA								
Cucumariidae LUDWIG, 1894								
Actinocucumis typica LUDWIG, 1875	*Actinocucumis typicus* LUDWIG	DANIEL & HALDER 1974					x	
Aslia forbesi (BELL)	*Cucumaria forbesi* BELL	DANIEL & HALDER 1974					x	
Aslia spyridiphora (H.L. CLARK, 1923)	*Aslia spyridiphora* (H.L. CLARK)	THANDAR 1991						x
	Cucumaria spyridiphora H.L. CLARK	H.L. CLARK 1923; DEICHMANN 1948; DANIEL & HALDER 1974						x
Athyone exila CHERBONNIER, 1988	*Athyone exila* CHERBONNIER	CHERBONNIER 1988						x
Athyone maculisparsa CHERBONNIER, 1988	*Athyone maculisparsa* CHERBONNIER	CHERBONNIER 1988						x
? *Cercodemas anceps* SELENKA, 1867[20]	*Pentacta tuberculosus* (QUOY & GAIMARD)	DANIEL & HALDER 1974					x	x
? *Colochirus colloradiatus* HAACKE, 1880[21]	*Colochirus colloradiatus* HAACKE	HAACKE 1880; LAMPERT 1885; THÉEL 1886					x	
? *Colochirus propinquus* HAACKE, 1880[22]	*Colochirus propinquus* HAACKE	HAACKE 1880; LAMPERT 1885					x	
Colochirus quadrangularis TROSCHEL, 1846	*Colochirus tristis* LUDWIG	LUDWIG 1875; LAMPERT 1885; THÉEL 1886; PANNING 1949					x	
	Cucumaria tristis LUDWIG	DANIEL & HALDER 1974					x	
	Pentacta quadrangularis (LESSON)	DANIEL & HALDER 1974						x
Cucumella decaryi CHERBONNIER, 1988	*Cucumella decaryi* CHERBONNIER	CHERBONNIER 1988						x
Koehleria unica CHERBONNIER, 1988	*Koehleria unica* CHERBONNIER	CHERBONNIER 1988; pers. observ.						x
Leptopentacta javanicus (SLUITER, 1881)	*Leptopentacta javanicus* (SLUITER)	CLARK & ROWE 1971; PRICE 1982					x	
Neocucumis kilburni RAJPAL & THANDAR, 1998	*Neocucumis kilburni* RAJPAL & THANDAR	RAJPAL & THANDAR 1998						x
Ocnus (?) *amiculus* CHERBONNIER, 1988	*Ocnus amiculus* CHERBONNIER	CHERBONNIER 1988						x
Ocnus (?) *corbulus* (CHERBONNIER, 1953)	*Cucumaria corbula* CHERBONNIER	CHERBONNIER 1953b; DANIEL & HALDER 1974						x
	Ocnus corbulus (CHERBONNIER)	THANDAR 1991						x
Ocnus(?) *cylindricus* SEMPER, 1867[23]	*Cucumaria cylindrica* SEMPER	SEMPER 1868					x	
? *Ocnus planci* (BRANDT, 1835)[24]	*Cucumaria planci* BRANDT	THÉEL 1886; DANIEL & HALDER 1974					x	

[18] From DANIEL & HALDER's (1974) list, it cannot be judged if this species occurs in shallow-water (up to 50 m). As this is most probably not the case, CHERBONNIER (1952) reports a depth of 200 fths, this species is best omitted in future analyses of the shallow-water holothuroids of the WIO.

[19] Idem as footnote 18; CHERBONNIER (1952) reports a depth of 290 fths for this species.

[20] ROWE (*in* ROWE & GATES 1995: 271) re-established the genus *Cercodemas* SELENKA, 1867 from the synonymy of *Pentacta* GOLDFUSS, 1820, because his comparative studies revealed that the type species – *C. anceps* SELENKA, 1867 – and others included in *Cercodemas*, *Colochirus* TROSCHEL, 1846 and *Plesiocolochirus* CHERBONNIER, 1946 do not correspond with the diagnosis of *Pentacta* [type species *P. doliolum* (PALLAS, 1766)] as supposed by H.L. CLARK (1946). The records of DANIEL & HALDER [1974, as *P. tuberculosus* (QUOY & GAIMARD, 1833) which are considered senior synonyms by ROWE (pers. comm)] must be treated with care as the known distribution of *C. anceps* is the tropical east-Indo-west Pacific Ocean (ROWE & GATES 1995).

[21] As this species has not been found since it's original description, its validity is dubious, and thus best omitted in future analyses.

[22] Idem as footnote 21.

[23] Idem as footnote 21, but see also footnote 24.

[24] It is doubtful that the European species *Ocnus planci* (BRANDT, 1835) is present in the WIO; ROWE (pers. comm.) notes that the present record "surely must be a misidentification which is best omitted from the present list". However, as only examination of the voucher specimen will allow correct identification, it is here temporarily retained. Recently, O'LOUGHLIN & ALCOCK (2000) re-assigned several New Zealand and Australian cucumariid species, previously

Ocnus (?) *tantulus* CHERBONNIER, 1988	*Ocnus tantulus* CHERBONNIER	CHERBONNIER 1988						x
Orbithyone megapodia H.L. CLARK, 1938	*Orbythyone megapodia*	HUGHES & GAMBLE 1977; SLOAN *et al.* 1979					x	
Parathyone incurva CHERBONNIER, 1988	*Parathyone incurva* CHERBONNIER	CHERBONNIER 1988					x	
Pawsonellus africanus THANDAR, 1986	*Pawsonellus africanus* THANDAR	THANDAR 1986; 1991; pers. observ.						x
Pentacta capensis (THÉEL, 1886)	*Cucumaria capensis* THÉEL	THÉEL 1886; LUDWIG 1887						x
	Psolus capensis	DANIEL & HALDER 1974						x
Pentacta doliolum (PALLAS, 1766)	*Pentacta doliolum* (PALLAS)	DEICHMANN 1948; DANIEL & HALDER 1974; PRICE 1982; THANDAR 1991	x					x
	Colochirus doliolum (PALLAS)	THÉEL 1886; HELFER 1912; MITSIKURI 1912	x					x
	Cucumaria discolor THÉEL	THÉEL 1886; H.L. CLARK 1923; DANIEL & HALDER 1974					x	x
	Cucumaria doliolum PALLAS	SEMPER 1868						x
	Cucumaria posthuma	THÉEL 1886						x
	Holothuria doliolum LAMK.	DE BLAINVILLE 1821						x
Pentacta minuta MACNAE & KALK, 1958 (non LUDWIG, 1875)[25]	*Colochirus minutus* ((MACNAE & KALK, 1958 (non LUDWIG))	THANDAR 1991						x
Pentacta ? pusilla (HELFER, 1912)[26]	*Pentacta pusilla* (HELFER)	PRICE 1982	x					
	Colochirus pusillus HELFER	HELFER 1912	x					
	Pentacta pusillus HELFER	DANIEL & HALDER 1974	x					
Pentacta tesselara CHERBONNIER, 1970	*Pentacta tesselara* CHERBONNIER	CHERBONNIER 1970a; THANDAR 1991						x
	Unidentified MRAC record	pers. observ.						x
Pentacta verrucula CHERBONNIER, 1988	*Pentacta verrucula* CHERBONNIER	CHERBONNIER 1988						x
Plesiocolochirus armatus (VON MARENZELLER, 1881)	*Pentacta loeppenthini* (HEDING)	PRICE 1982; 1983			x			
	Colochirus löppenthini HEDING	HEDING 1940b			x			
Plesiocolochirus dispar (LAMPERT, 1889)	*Pentacta dispar* (LAMPERT)	PRICE 1982; CHERBONNIER 1988					x	x x
	Pentacta gravieri (VANEY)	CHERBONNIER 1955; DANIEL & HALDER 1974		x			?	
	Colochirus Gravieri VANEY	VANEY 1905		x				
Pseudocnella insolens (THÉEL, 1886)	*Cucumaria sykion*	DEICHMANN 1948						x
	Cucumaria insolens THÉEL	THÉEL 1886; H.L. CLARK 1923; CHERBONNIER 1952a; DANIEL & HALDER 1974					x	x
	Semperia insolens (THÉEL)	LUDWIG 1887						x
	Pseudocnella insolens (THÉEL)	THANDAR 1987b; 1991						x
Pseudocnella sinorbis (CHERBONNIER, 1952)	*Cucumaria sykion*	DEICHMANN 1948						x
	Cucumaria sinorbis CHERBONNIER	DANIEL & HALDER 1974						x
	Pseudocnella sinorbis (CHERBONNIER)	THANDAR 1987b; 1991						x
Pseudocnella sykion (LAMPERT, 1885)	*Pseudocnella sykion* (LAMPERT)	THANDAR 1987b; 1991; pers. observ.						x
	Cucumaria jageri LAMPERT	LAMPERT 1885; THÉEL 1886; DANIEL & HALDER 1974						x
	Cucumaria sykion (LAMPERT)	THÉEL 1886; H.L. CLARK 1923; DEICHMANN 1948; CHERBONNIER 1952a; KALK 1958; DANIEL & HALDER 1974						x
	Semperia sykion LAMPERT	LAMPERT 1885						x
Pseudocnus echinatus VON MARENZELLER, 1881	*Pseudocnus echinatus* (V. MARENZELLER)	CHERBONNIER 1963; PRICE 1982		x				
Pseudocolochirus violaceus (THÉEL, 1886)	*Pseudocolochirus violaceus* (THÉEL)	PEARSON 1910; CHERBONNIER 1988; THANDAR 1991					x	x
	Pseudocolochirus bicolor CHERBONNIER	CHERBONNIER 1970b						x
Roweia frauenfeldi (LUDWIG, 1882)	*Roweia frauenfeldi* (LUDWIG)	THANDAR 1985; 1991						x
	Cucumaria deichmanni CHERBONNIER	DANIEL & HALDER 1974						x
	Cucumaria frauenfeldi LUDWIG	LUDWIG 1882; THÉEL 1886; H.L. CLARK 1923; JOHN 1939; DEICHMANN 1948; CHERBONNIER 1952a						x
	Cucumaria posthuma LAMPERT	LAMPERT 1885; DANIEL & HALDER 1974					x	x
	Cucumaria webbi THANDAR	THANDAR 1977						x
	Phyllophorus Frauenfeldi LUDWIG	LUDWIG 1875; 1880; LAMPERT 1885; THÉEL 1886; HÉROUARD 1893; DANIEL & HALDER 1974	x	x				

assigned to *Ocnus* FORBES & GOODSIR *in* FORBES, 1841, to other genera. The latter authors (2000: 2) regard *Ocnus* as "a European genus with diagnostic characters inapplicable to the New Zealand and Australian species". Similarily, the other *Ocnus* spp. here reported on, possibly must be allocated to other genera. For now, until comparative analysis of the voucher specimens is possible, they are retained in this genus.

[25] THANDAR (1991) draws on CHERBONNIER's expertise for keeping *Colochirus minutus* MACNAE & KALK, 1958 (non LUDWIG) (identified by CHERBONNIER) separate from *P. tesselara* CHERBONNIER, 1970. THANDAR's (1991) judgment to retain it as a valid species in *Pentacta* is here respected.

[26] The systematic position of this ill-known species (only known from the 6 mm long holotype) is most uncertain and almost certainly this species cannot be classified under *Pentacta*. In future analyses, it is best omitted, unless examination of its type assigns it to its correct systematic position (which cannot be determined from the poor original description).

Roweia stephensoni (JOHN, 1939)	*Roweia stephensoni* (JOHN)	THANDAR 1985; 1991						x
	Cucumaria frauenfeldi LUDWIG	H.L. CLARK 1923						x
	Cucumaria stephensoni JOHN	JOHN 1939; DEICHMANN 1948; CHERBONNIER 1953b; DANIEL & HALDER 1974						x
Staurothyone rosacea (SEMPER, 1869)	*Staurothyone rosacea* (SEMPER)	PRICE 1982				x		
	Thyone (Stolus) rosacea SEMPER	SEMPER 1869			x			
	Thyone rosacea SEMPER	LAMPERT 1885; THÉEL 1886; SEMPER 1868; DANIEL & HALDER 1974			x	x		
Trachythyone crucifera (SEMPER, 1869)	*Trachythyone crucifera* (SEMPER)	PRICE 1982; A.M. CLARK 1984; CHERBONNIER 1988; THANDAR 1991; pers. observ.	x			x	x	x
	Cucumaria crucifera SEMPER	SEMPER 1868; 1869; LAMPERT 1885; 1896; THÉEL 1886; LUDWIG 1887; 1899; DEICHMANN 1948; KALK 1958; DANIEL & HALDER 1974			x		x	x
	Unidentified MRAC record	pers. observ.						x
Trachythyone glaberrima (SEMPER, 1869)	*Cucumaria glaberrima* SEMPER	SEMPER 1869; LUDWIG 1883; LAMPERT 1885; THÉEL 1886; DANIEL & HALDER, 1974			x			
	Paracucumaria glaberrima (SEMPER)	PRICE 1982				x		
	Trachythyone dollfusi CHERBONNIER	CHERBONNIER 1954a; 1955; DANIEL & HALDER 1974; PRICE 1982	x					
Trachythyone improvisa (LUDWIG, 1875)	*Cucumaria improvisa* LUDWIG	LUDWIG 1875; LAMPERT 1885; THÉEL 1886; H.L. CLARK 1923; DEICHMANN 1948; DANIEL & HALDER 1974					x	x
	Trachythyone improvisa (LUDWIG)	THANDAR 1991						x
Trachythyone rigidapeda (CHERBONNIER, 1952)	*Cucumaria rigidapeda* CHERBONNIER	CHERBONNIER 1952a; DANIEL & HALDER 1974						x
Phyllophoridae OESTERGREN, 1907								
Globosita murrea CHERBONNIER, 1988	*Globosita murrea* CHERBONNIER	CHERBONNIER 1988						x
Havelockia ferali CHERBONNIER, 1988	*Havelockia ferali* CHERBONNIER	CHERBONNIER 1988					x	x
Havelockia festina (KOEHLER & VANEY, 1908)	*Thyone festina* KOEHLER & VANEY	KOEHLER & VANEY 1908; DANIEL & HALDER 1974; PRICE 1982, 1983				x		
Havelockia transitoria (VANEY, 1905)	*Havelockia transitoria* (VANEY)	PRICE 1982				x		
	Athyone transitoria (VANEY)	CHERBONNIER 1955			x			
	Athyone transitoria CHERBONIER non VANEY	PRICE 1982				x		
	Cucumaria transitera VANEY	DANIEL & HALDER 1974			x		x	
	Cucumaria transitoria VANEY	VANEY 1905			x			
Havelockia turrispinea CHERBONNIER, 1988	*Havelockia turrispinea* CHERBONNIER	CHERBONNIER 1988					x	
? *Havelockia venustella* (HEDING & PANNING, 1954)[27]	*Thyone venustella*	DANIEL & HALDER 1974					x	
Havelockia versicolor (SEMPER, 1868)	*Havelockia versicolor* (SEMPER)	THANDAR 1989c						x
	Thyone mirabilis	KALK 1958						x
Hemithyone semperi (BELL, 1884)	*Hemithyone semperi* (BELL)	CHERBONNIER 1988					x	
	Cucumaria semperi BELL	PEARSON 1910; DANIEL & HALDER 1974					x	
Lipotrapeza ambigua CHERBONNIER, 1988	*Lipotrapeza ambigua* CHERBONNIER	CHERBONNIER 1988						x
Lipotrapeza incurva CHERBONNIER, 1988	*Lipotrapeza incurva* CHERBONNIER	CHERBONNIER 1988						x
Lipotrapeza ventripes (JOSHUA & GREED, 1915)	*Lipotrapeza ventripes* (JOSHUA & GREED)	CHERBONNIER 1988						x
Neothyonidium arthroprocessum THANDAR, 1989	*Neothyonidium arthroprocessum* THANDAR 1989	THANDAR 1989b; 1990; 1996; pers. observ.						x
Neothyonidium dissimilis CHERBONNIER, 1988	*Neothyonidium dissimilis* CHERBONNIER	CHERBONNIER 1988						x
Neothyonidium? sp nov.[28]		pers. observ.						x
Phyllophorus (Phyllonovus) anomalia CHERBONNIER, 1988	*Phyllophorus (Phyllonovus) anomalia* CHERBONNIER	CHERBONNIER 1988						x
Phyllophorus (Phyllophorella) calypsoi CHERBONNIER, 1954	*Phyllophorus calypsoi* CHERBONNIER	CHERBONNIER 1954a; 1955; DANIEL & HALDER 1974	x		x			
	Phyllophorus (Phyllophorella) calypsoi CHERBONNIER	PRICE 1982		x				
Phyllophorus (Phyllophorella) contractura CHERBONNIER, 1988	*Phyllophorus (Phyllophorella) contractura* CHERBONNIER	CHERBONNIER 1988						x
Phyllophorus (Phyllophorella) rosetta THANDAR, 1994	*Phyllophorus (Phyllophorella) rosetta* THANDAR	THANDAR 1994						x
Phyllophorus (Phyllophorella) spiculata CHANG, 1935	*Phyllophorus parvipedes* H.L. CLARK	DANIEL & HALDER 1974				x		
Phyllophorus (Urodemella) brocki LUDWIG, 1888	*Phyllophorus (Urodemella) brocki* LUDWIG	CHERBONNIER 1988					x	x
Phyllophorus (Urodemella) oculus CHERBONNIER, 1988	*Phyllophorus (Urodemella) oculus* CHERBONNIER	CHERBONNIER 1988					x	

[27] Even though DANIEL & HALDER (1974) do not give the depth of occurrence for this species, it is safe to state that it is no shallow-water species. In future analyses it is thus best omitted.

[28] A new phyllophorid species is currently being described, it has most affinity with *Neothyonidium* DEICHMANN, 1938.

Phyllophorus (Urodemella) tenuis HAACKE, 1880	*Phyllophorus tenuis* HAACKE	HAACKE 1880; LUDWIG 1883; LAMPERT 1885; DANIEL & HALDER 1974						x	
Selenkiella paradoxa CHERBONNIER, 1970	*Selenkiella paradoxa* CHERBONNIER	CHERBONNIER 1970a; 1988; THANDAR 1990							x
Stolus buccalis (STIMPSON, 1856)	*Stolus buccalis* (STIMPSON)	CLARK & ROWE 1971; PRICE 1982; 1983; CHERBONNIER 1988; THANDAR 1990; pers. observ.	x		x	x	x	x	
	Stolus sacellus SELENKA	SEMPER 1968; 1869; HEDING 1940b; CHERBONNIER 1955; 1967	x	x	x		x		
	Thyone sacella SELENKA	SELENKA 1867; THÉEL 1886			x		x		
	Thyone sacellus SELENKA	LAMPERT 1885; VANEY 1905; MITSIKURI 1912; H.L. CLARK 1923; KALK 1958; DANIEL & HALDER 1974			x	x	x	x	
	Unidentified MRAC record	pers. observ.							x
Thorsonia fusiformis HEDING, 1940	*Thorsonia fusiformis* HEDING	HEDING 1940b; PRICE 1982; 1983				x			
Thyone aurea (QUOY & GAIMARD, 1833)	*Thyone aurea* (QUOY & GAIMARD)	SEMPER 1868; LAMPERT 1885; THÉEL 1886; H.L. CLARK 1923; DANIEL & HALDER 1974; THANDAR 1990							x
	Thyone proceracorona CHERBONNIER	DANIEL & HALDER 1974							x
	Thyone turrissolida CHERBONNIER	CHERBONNIER 1954b							x
	Thyone turrisoolida CHERBONNIER	DANIEL & HALDER 1974							x
Thyone avenusta CHERBONNIER, 1970	*Thyone avenusta* CHERBONNIER	CHERBONNIER 1970a; 1988; THANDAR 1990							x
Thyone carens CHERBONNIER, 1988	*Thyone carens* CHERBONNIER	CHERBONNIER 1988						x	x
Thyone comata CHERBONNIER, 1988	*Thyone comata* CHERBONNIER	CHERBONNIER 1988						x	x
Thyone crebrapodia CHERBONNIER, 1988	*Thyone crebrapodia* CHERBONNIER	CHERBONNIER 1988							x
Thyone curvata LAMPERT, 1885	*Thyone curvata* LAMPERT	LAMPERT 1885; THÉEL 1886; DANIEL & HALDER 1974						x	x
Thyone dura KOEHLER & VANEY, 1908	*Thyone dura* KOEHLER & VANEY	KOEHLER & VANEY 1908; HEDING 1940b; PRICE 1982				x	x		
	Thyone sp. ? *T. dura* KOEHLER & VANEY	PRICE 1983				x			
Thyone guillei CHERBONNIER, 1988	*Thyone guillei* CHERBONNIER	CHERBONNIER 1988							x
Thyone hirta CHERBONNIER, 1970	*Thyone hirta* CHERBONNIER	CHERBONNIER 1970a; THANDAR 1990							x
Thyone imperfecta (CHERBONNIER, 1970)	*Havelockia imperfecta* CHERBONNIER	CHERBONNIER 1970a							x
	Thyone imperfecta (CHERBONNIER)	THANDAR 1990							x
Thyone infusca CHERBONNIER, 1954	*Thyone infusca* CHERBONNIER	CHERBONNIER 1954b; DANIEL & HALDER 1974; THANDAR 1990							x
Thyone longicornis CHERBONNIER, 1988	*Thyone longicornis* CHERBONNIER	CHERBONNIER 1988							x
Thyone propinqua CHERBONNIER, 1970	*Thyone propinqua* CHERBONNIER	CHERBONNIER 1970a; THANDAR 1990							x
Thyone quadriperforata CHERBONNIER, 1954	*Thyone quadriperforata* CHERBONNIER	DANIEL & HALDER 1974	x						
	Thyone sp. ? *T. quadruperforata* CHERBONNIER	PRICE 1982					x		
	Thyone (?) *quadriperforata* CHERBONNIER	CHERBONNIER 1954a; 1955		x					
Thyone sineturra CHERBONNIER, 1988	*Thyone sineturra* CHERBONNIER	CHERBONNIER 1988							x
Thyone vadosa CHERBONNIER, 1988	*Thyone vadosa* CHERBONNIER	CHERBONNIER 1988							x
Thyone venusta SELENKA, 1868	*Thyone venusta* SELENKA	SELENKA 1868; 1869; LAMPERT 1885; ERWE 1919; DANIEL & HALDER 1974; PRICE 1982; THANDAR 1990; pers. observ.	x	x					x
Thyonidiella exigua CHERBONNIER, 1988	*Thyonidiella exigua* CHERBONNIER	CHERBONNIER 1988							x
Thyonidiella oceana HEDING & PANNING, 1954	*Thyonidiella oceana* HEDING & PANNING	HEDING & PANNING 1954; DANIEL & HALDER 1974; CHERBONNIER 1988						x	x
Thyonina articulata (VANEY, 1908)	*Thyonina articulata* (VANEY)	THANDAR 1990							x
Psolidae PERRIER, 1902									
Psolidium ornatum (Ed. PERRIER, 1893)	*Psolidium (Georisia) ornatum* (PERRIER)	PERRIER 1893						x	
	Psolidium ornatum (Ed. PERRIER)	CHERBONNIER 1988						x	
? *Psolus agulhasicus* LUDWIG & HEDING, 1935[29]	*Psolus agulhasicus*	DANIEL & HALDER 1974							x
? *Psolus appendiculatus* (DE BLAINVILLE, 1821)[30]	*Psolus appendiculatus* BLAINVILLE	SELENKA 1867; LAMPERT 1885; THÉEL 1886						x	
	?*Psolus appendiculatus* BLAINVILLE	SEMPER 1868						x	
	Psolus appendiculata PHILIPPI	DANIEL & HALDER 1974						x	
	Holothuria appendiculata DE BLAINV.	DE BLAINVILLE 1821						x	
? *Psolus imperfectus* H.L. CLARK, 1923[31]	*Psolus imperfectus*	DANIEL & HALDER 1974							x
Rhopalodinidae R. PERRIER, 1902									
Rhopalodinaria gigantea CHERBONNIER, 1970	*Rhopalodinaria gigantea* CHERBONNIER	CHERBONNIER 1970a; THANDAR 2001							x
Rhopalodinaria minuta CHERBONNIER, 1970	*Rhopalodinaria minuta* CHERBONNIER	CHERBONNIER 1970a; THANDAR 2001							x
Sclerodactylidae PANNING, 1949									
Cladolabes aciculus (SEMPER, 1868)	*Cladolabes aciculus* (SEMPER)	HEDING & PANNING 1954						x	
	Pseudocucumis acicula SEMPER	HAACKE 1880; THÉEL 1886; LAMPERT 1885; DANIEL & HALDER 1974						x	x

[29] Idem as footnote 27.
[30] Idem as footnote 21.
[31] Idem as footnote 27.

		1885; DANIEL & HALDER 1974							
	Unidentified MRAC record	pers. observ.							x
Cladolabes bifurcatus (DEICHMANN, 1944)	*Cladolabes bifurcatus* (DEICHMANN)	CHERBONNIER 1988; THANDAR 1989c; pers. observ.							x
	Urodemas bifurcatum DEICHMANN	DEICHMANN 1944; DANIEL & HALDER 1974							x
Cladolabes pichoni CHERBONNIER, 1988	*Cladolabes pichoni* CHERBONNIER	CHERBONNIER 1988							x
Ohshimella ehrenbergi (SELENKA, 1868)	*Ohshimella ehrenbergi* (SELENKA)	CHERBONNIER 1967; JAMES 1969; JAMES & PEARSE 1969; CLARK & ROWE 1971; DANIEL & HALDER 1974; PRICE 1981; 1982; 1983; CHERBONNIER 1988; THANDAR 1989c; pers. observ.	x	x	x		x	x	x
	Ohshimella ehrenbergii (SELENKA)	HEDING & PANNING 1954			x				
	Phyllophorus ehrenbergi SELENKA	VANEY 1905; DANIEL & HALDER 1974			x	x			
	Phyllophorus ehrenbergii (SELENKA)	SEMPER 1868; 1869; LAMPERT 1885; THÉEL 1886; ERWE 1919; CHERBONNIER 1955	x		x	x			
	Phyllophorus frauenfeldi	H.L. CLARK 1923							x
	Phyllophorus gracilis (SELENKA)	SEMPER 1868; 1869; ERWE 1919	x		x				
	Phyllophorus gracile SELENKA	LAMPERT 1885; THÉEL 1886; DANIEL & HALDER 1974			x				
	Phyllophorus sp.nov.	SEMPER 1868			x				
	Cucumaria turbinata HUTTON	PEARSON 1910; DANIEL & HALDER 1974						x	x
	Unidentified MRAC record	pers. observ.							x
	Urodemas ehrenbergii SELENKA	SELENKA 1868			x				
	Urodemas gracile SELENKA	SELENKA 1868			x				
	Orcula torrense HELFER	HELFER 1913	x						
Ohshimella mauritiensis HEDING & PANNING, 1954	*Ohshimella mauritiensis* HEDING & PANNING	HEDING & PANNING 1954; DANIEL & HALDER 1974; MASSIN unpubl						x	x
Sclerothyone velligera (LUDWIG & HEDING, 1935)[32]	*Pentamera velligera*	DANIEL & HALDER 1974							x
MOLPADIIDA									
Caudinidae (HEDING, 1931)									
Acaudina leucoprocta (H.L. CLARK, 1938)	*Acaudina irania* (HEDING)	PRICE 1982; 1983				x			
	Aphelodactyla irania H.L. CLARK	HEDING 1940b				x			

Table 27 - Species of the shallow-waters of the WIO that do not belong to genera found in Kenya. For locations 1 to 8 see map 2 and table 28; the question marks refer to uncertainties in terms of occurrence (misidentifications, location, depth) or systematic status.

From the above data-sets several superficial observations can easily be made. The Kenyan holothuroid fauna can be called rich in terms of species richness (near 50 species), but it is equally obvious that the majority of these species belongs to the order Aspidochirotida (81.3 %) and to a lesser extent to the Apodida (16.7 %). The observation that only 2.1 % (represented by only one species: *Afrocucumis africana*) of the reported species belongs to the order Dendrochirotida is striking. Table 28 shows the taxonomic composition (at the level of the order) for the eight defined areas in the WIO

	1	2	3	4	5	6	7	8	
	Gulf of Suez	Gulf of Aqaba	Red Sea	Gulf of Aden	Persian Gulf	Arabian Sea	Tropical WIO	Southern WIO	Kenya
Apodida	14.6 % (7 spp)	22.5 % (9 spp)	20.3 % (15 spp)	15.8 % (6 spp)	14.8 % (4 spp)	9.3 % (4 spp)	17.0 % (23 spp)	14.5 % (22 spp)	16.7 % (8 spp)
Adjusted	-	-	*19.4 %*	-	*15.4 %*	*9.5 %*	*17.8 %*	*15.1 %*	-
Aspidochirotida	72.9 % (35 spp)	72.5 % (29 spp)	66.2 % (49 spp)	60.5 % (23 spp)	59.3 % (16 spp)	67.4 % (29 spp)	60.7 % (82 spp)	40.1 % (61 spp)	81.3 % (39 spp)
Adjusted	-	-	*66.7 %*	-	*61.5 %*	*69 %*	*62.0 %*	*41.8 %*	-
Dendrochirotida	12.5 % (6 spp)	5 % (2 spp)	13.5 % (10 spp)	23.7 % (9 spp)	22.2 % (6 spp)	23.3 % (10 spp)	22.2 % (30 spp)	45.4 % (69 spp)	2.1 % (1 spp)
Adjusted	-	-	*13.9 %*	-	*23.1 %*	*21.4 %*	*20.2 %*	*43.2*	-
Molpadida	0 % (0 spp)	0 % (0 spp)	0 % (0 spp)	0 % (0 spp)	3.7 % (1 spp)	0 % (0 spp)	0 % (0 spp)	0 % (0 spp)	0 % (0 spp)
Adjusted	-	-	-	-	*0 %*	-	-	-	-
Species richness	48 spp	40 spp	74 spp	38 spp	27 spp	43 spp	135 spp	152 spp	48 spp
Adjusted	-	-	*72 spp*	-	*26 spp*	*42 spp*	*129 spp*	*146 spp*	-

[32] Idem as footnote 27.

Table 28 (previous page) - Taxonomic composition at the level of the order (%) of the eight arbitrary regions in the WIO compared to Kenya (see also map 2). The adjusted values take into account those species that can be omitted due to improbable horizontal (geographical distribution) or vertical distribution (depth exceeding 50 m).

The reason for the low number of dendrochirotids needs further investigation, especially since a plot of the taxonomic composition (at the level of the order) in a 10° circumtropical belt shows that this situation holds for the Somalian side and not for the Tanzanin side (fig. 60). In this regard, it is interesting to note that Levin (1999: 104, fig. 6.3 A, B), upon an analysis of 39 lists of holothuroids inhabiting different parts of the World Ocean, uncovered a similar latitudinal zonation of species community in the meridian direction. Massin (1999) on the other hand, upon a study of the tropical reef-dwelling fauna of the Spermonde Archipelago (South-West Sulawesi, Indonesia), found that only ±57 % (32 out of 56 spp) of the recovered species are aspidochirotids, ±18 % are dendrochirotids (10 spp.) and 25 % are apodids (14 spp). Thus, *de novo* sampling along the sandy coastline of Somalia must be carried out to reveal if this is a truthful situation or conversely an artefact of undersampling.

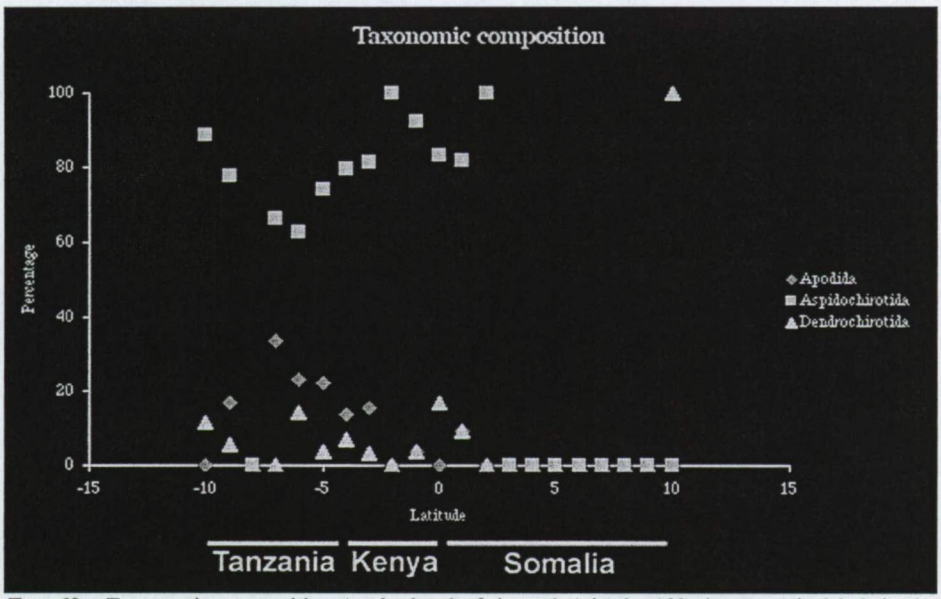

FIG. 60 - Taxonomic composition (at the level of the order) in the 10° circumtropical belt in the WIO reveals that dendrochirotids are underrepresented throughout the tropical WIO (the 100 % at 10°N represents only a single species).

Future research – understanding the factors that control the holothuroid biodiveristy of the WIO

In order to really understand the zoogeography of the present day holothuroid biodiversity of the WIO, it is not sufficient to inventor the species richness in the different areas, but it is of equal importance to understand how, when and why the present day distributions appear like they are. In order to do so, we must not only get insight in the descriptive (faunistics, phylogeography and biocoenotic zoogeography), but also in the causal (historical and ecological) zoogeography. Therefore, future work (in preparation) will have to put geological history, physical and biological oceanography in perspective to the present day distribution. Once this analysis is done, we will be able to construct a transdisciplinary, integrative holistic, heuristic and balanced framework that makes conservation scientifically correct and exploitation sustainable.

Acknowledgments

It is with great pleasure that I thank the Drs C. Massin, F.W.E Rowe and A.S. Thandar for sharing their extensive knowledge on the Holothuroidea with me and for critically reviewing the early versions of the manuscript; two anonymous referees are also thanked for critical commenting on the manuscript; Dr. N. Ameziane Cominardi (MNHNP), Paris, for the loan of type and non type material of several *Holothuria* species; Dr. S. Halsey (NHM), London, for welcoming me at her museum and for the loan of type and non type material of several *Holothuria* and *Labidodemas* species; Dr. C. Ahearn (SI) for the loan of type material of *H. (Thymiosycia) thomasi*; Dr. D. VandenSpiegel (MRAC), Tervuren, for welcoming me at his museum and for the loan of specimens from the Seycelles and Inhaca; Dr. H. Ruhberg (ZMH), Hamburg, for welcoming me at her museum. Financial support came from the Flemish Fund for Scientific Research (project number G.0086.96), from the Research Council of the Free University Brussels and from the Flemish Community [Bilateral (international) scientific and technological cooperation; projects BIL98/84 and BIL01/46]. Clearance to work on the echinoderm fauna of Kenya came from the Office of the President through Mr. J.E. Ekirapa. Kenya Wildlife Services, WWF Kenya and KwaZulu-Natal Nature Conservation Service provide field support.
This work would not have been possible without the kind assistance of I. Tallon, who not only carefully constructed the framework of the *Filemaker Pro 5.5* database, but who also assisted in the automated plotting of the distributionrecords. The latter exercise was made easy thanks to the excellent freeware *imap* developed at the Lab of Plant Systematics at the K.U.Leuven (**http://www.kuleuven.ac.be/bio/sys/imap/**).

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Appendix

Museum acronyms

NHM	Natural History Museum, London, England
IRSNB	Institut Royal des Sciences Naturelles, Brussels, Belgium
IM	Indian Museum, Calcutta, India
MCZ	Museum of Comparative Zoology. Harvard University Cambridge, Massachusetts, USA
MGH	Museum Goddefroyi, Hamburg (now in ZMH), Germany
MNHNP	Muséum National d'Histoire Naturelle, Paris, France
MRAC	Muséum Royal de l'Afrique central, Tervuren, Belgium
RMNH	Nationaal Natuurhistorisch Museum, Leiden, Netherlands
TIU	University of Tokyo, Tokyo, Japan
ZM	Zoological Museum, Copenhagen, Denmark
ZMB	Museum für Naturkunde an der Universität Humboldt zu Berlin, Berlin, Germany
ZMH	Zoologisches Museum für Hamburg, Hamburg, Germany

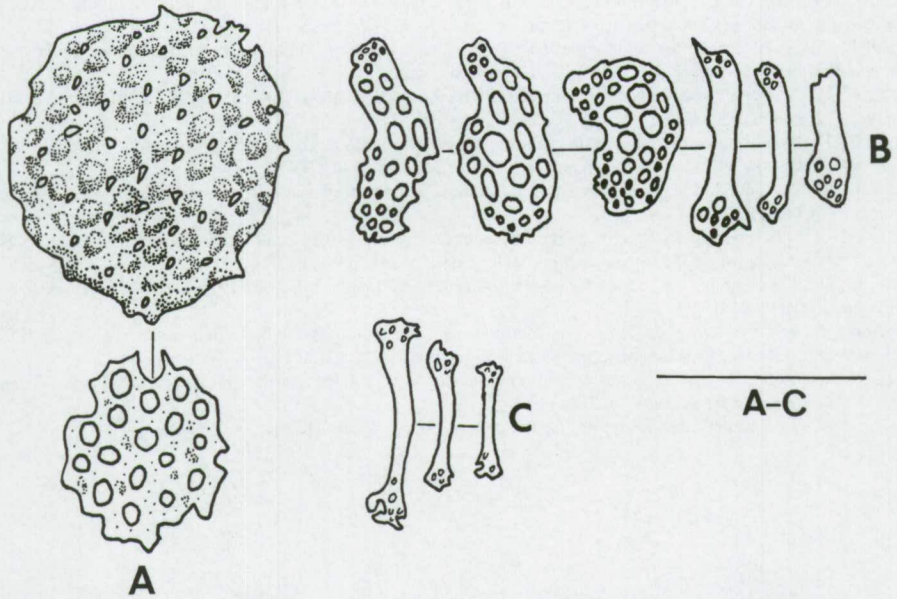


Figure 1. *Afrocucumis africana* (SEMPER, 1868). (A) Lenticular and developing plate of dorsal body wall; (B) Perforated rods and plates of tube feet; (C) Rods of tentacles. Scale bar A-C represents 100 µm.

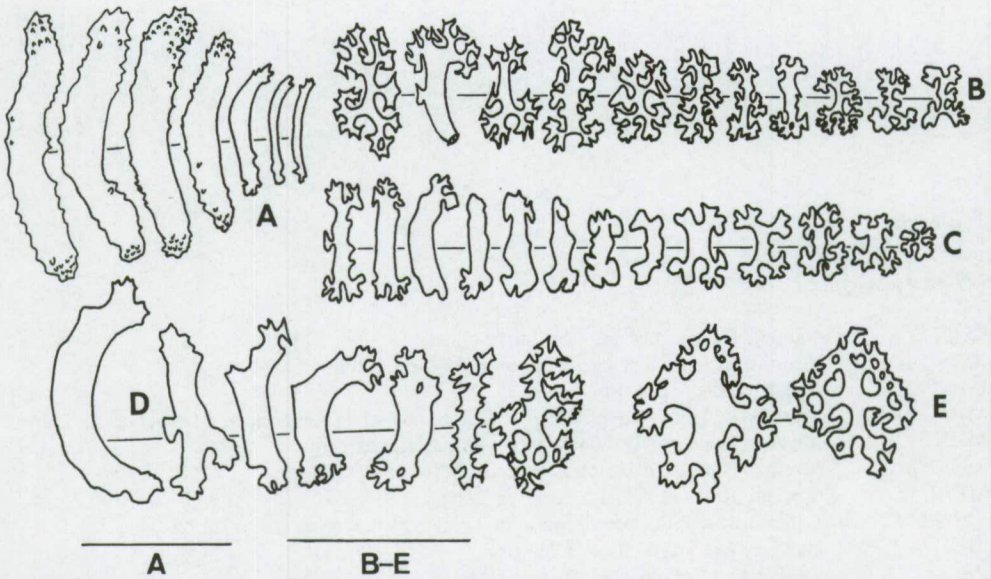


Figure 2. *Actinopyga echinites* (JAEGER, 1833). (A) Rods of tentacles; (B) Rods and rosettes of dorsal body wall; (C) Rods and rosettes of ventral body wall; (D) Rods and branched rods of ventral tube feet; (E) Pseudo-plates of dorsal papillae. Scale bar A represents 200 µm; scale bar B-E represents 100 µm.

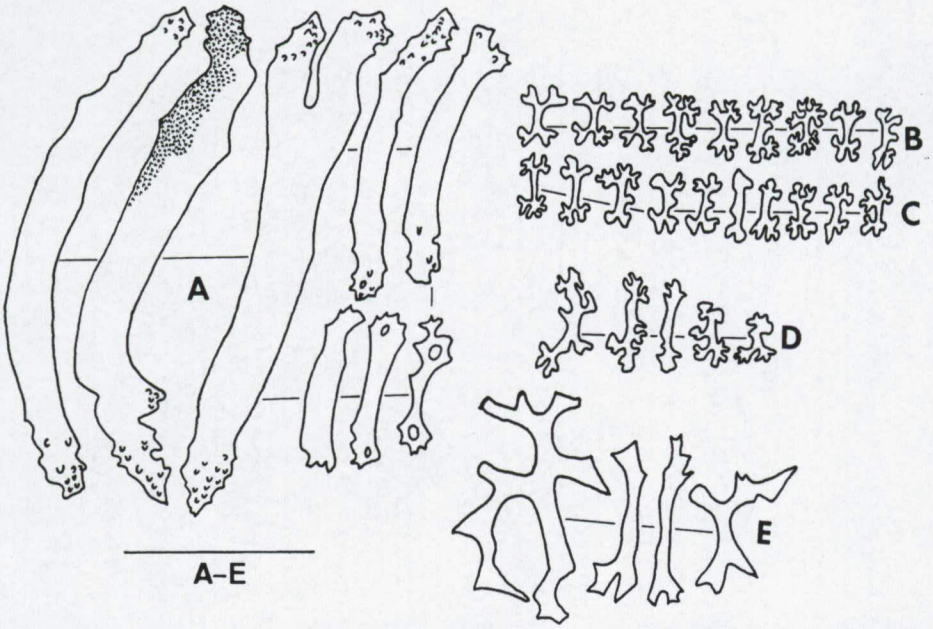


Figure 3. *Actinopyga lecanora* (JAEGER, 1833). (A) Rods of tentacle; (B) Rosettes of dorsal body wall; (C) Rosettes of ventral body wall; (D) Rosettes of ventral tube feet; (E) Rods of dorsal pedicels. Scale bar A-E represents 100 µm.

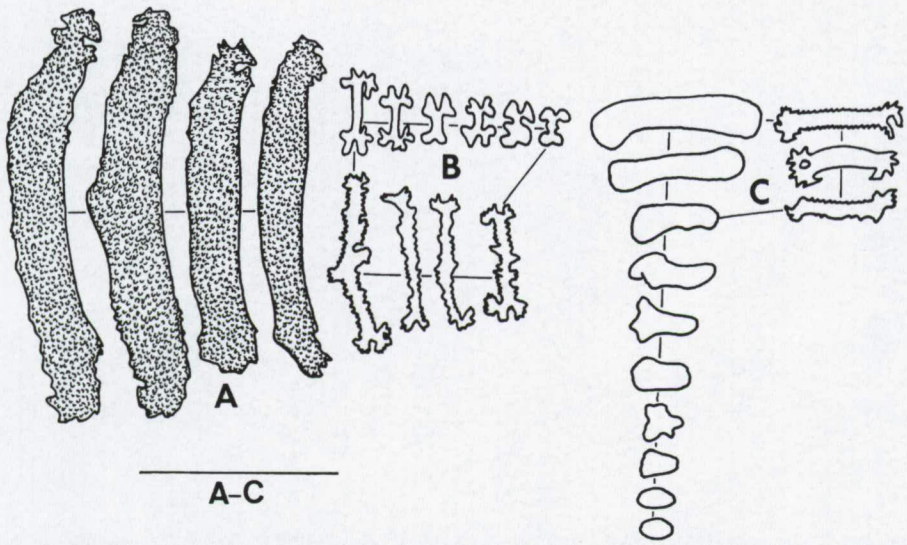


Figure 4. *Actinopyga mauritiana* (QUOY & GAIMARD, 1833). (A) Rods of tentacle; (B) Rosettes and rods of dorsal body wall; (C) Grains and rods of ventral body wall. Scale bar A-C represents 100 µm.

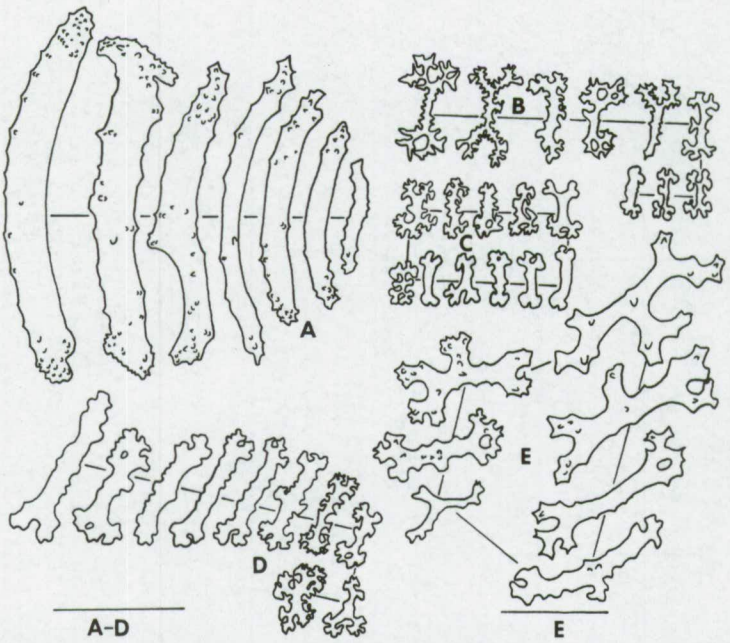


Figure 5. *Actinopyga miliaris* (QUOY & GAIMARD, 1833). (A) Rods of tentacle; (B) Rosettes and rods of dorsal body wall; (C) Rosettes and rods of ventral body wall; (D) Rods of ventral tube feet; (E) Rods of dorsal tube feet. Scale bar A-D represents 100 μm; scale bar E represents 200 μm.

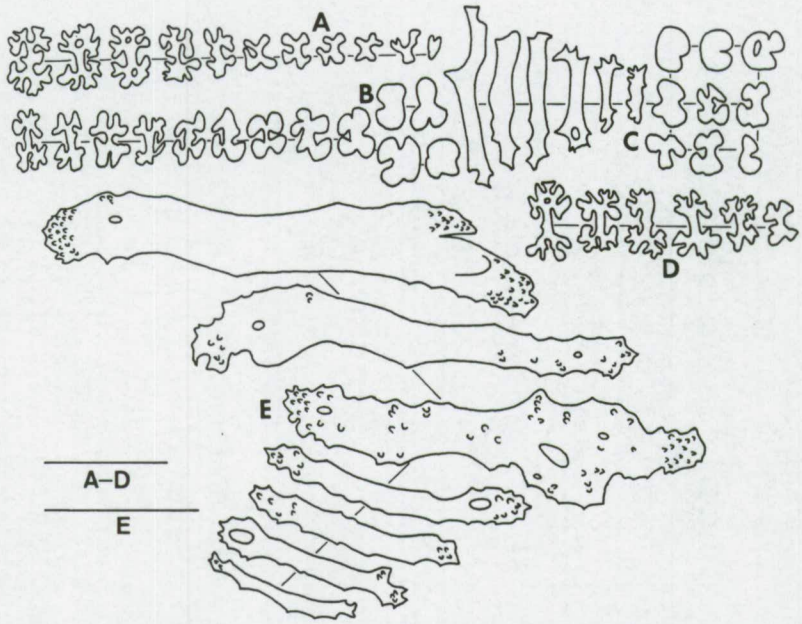


Figure 6. *Bohadschia atra* MASSIN, RASOLOFONIRINA, CONAND & SAMYN, 1999. (A) Rosettes and grains of dorsal body wall; (B) Rosettes and grains of ventral body wall; (C) Rods and grains of ventral tube feet; (D) Rosettes of dorsal papillae; (E) Rods of tentacle. Scale bar A-D represents 50 μm; scale bar E represents 100 μm.

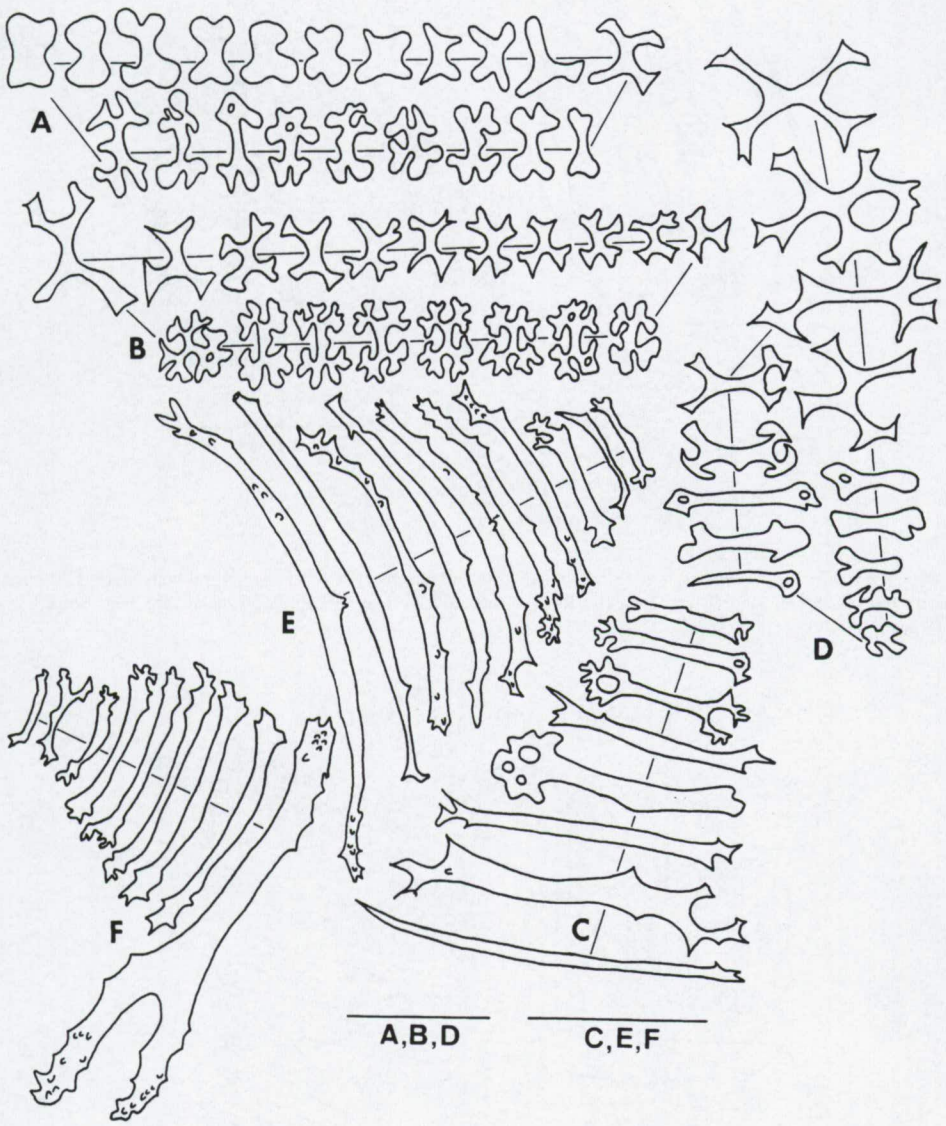


Figure 7. *Bohadschia cousteaui* CHERBONNIER, 1954. (A) grains rods and rosettes of ventral body wall; (B) Cross-shaped rods and rosettes of dorsal body wall; (C) Rods of ventral tube feet; (D) Grains and cross-shaped rods of ventral tube feet; (E) Rods and rosettes of dorsal pedicels; (F) Rods of tentacles. Scale bar A, B, D represents 50 μm; scale bar C, E, F represents 100 μm.

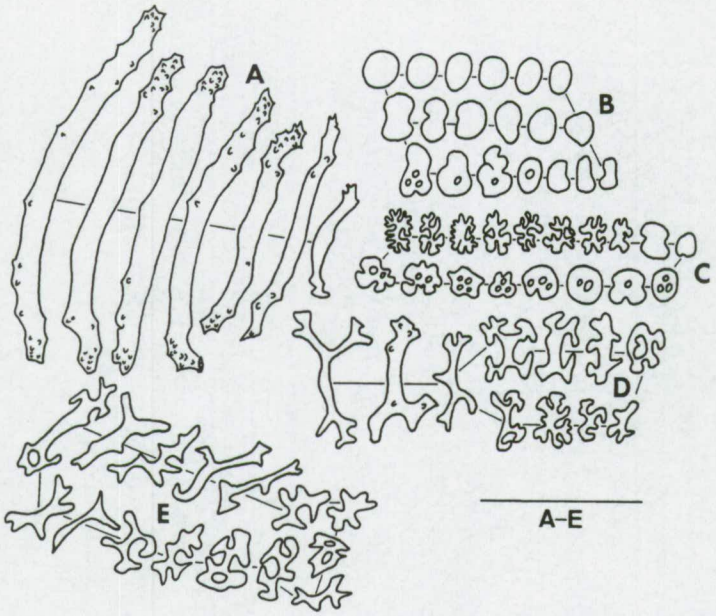


Figure 8. *Bohadschia marmorata* JAEGER, 1833. (A) Rods of tentacles; (B) Grains of ventral body wall; (C) Perforated grains and rosettes of ventral tube feet; (D) Rods of ventral tube feet; (E) Rods of dorsal tube feet. Scale bar A-E represents 100 µm.

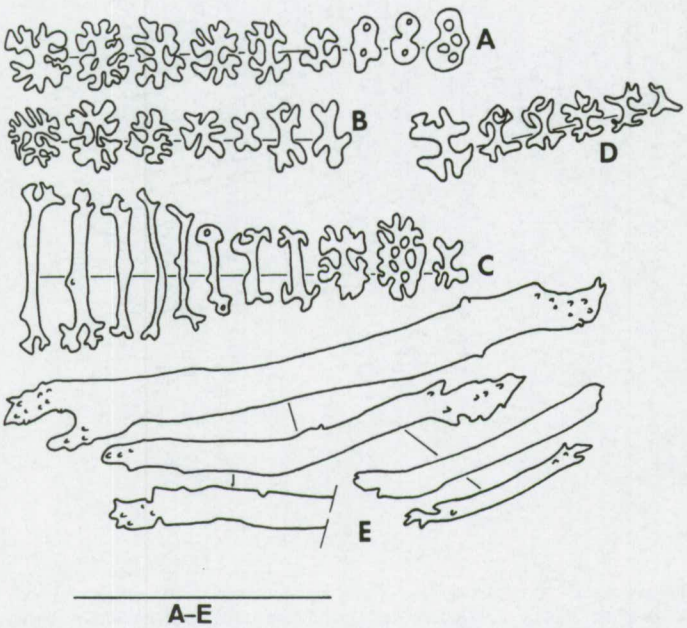


Figure 9. *Bohadschia* cf. *similis* (SEMPER, 1868). (A) Rosettes of ventral body wall; (B) Rosettes of dorsal body wall; (C) Grains, rods and rosettes of ventral tube feet; (D) Simple rosettes of dorsal pedicels; (E) Large rods of tentacle. Scale bar A-E represents 100 µm.

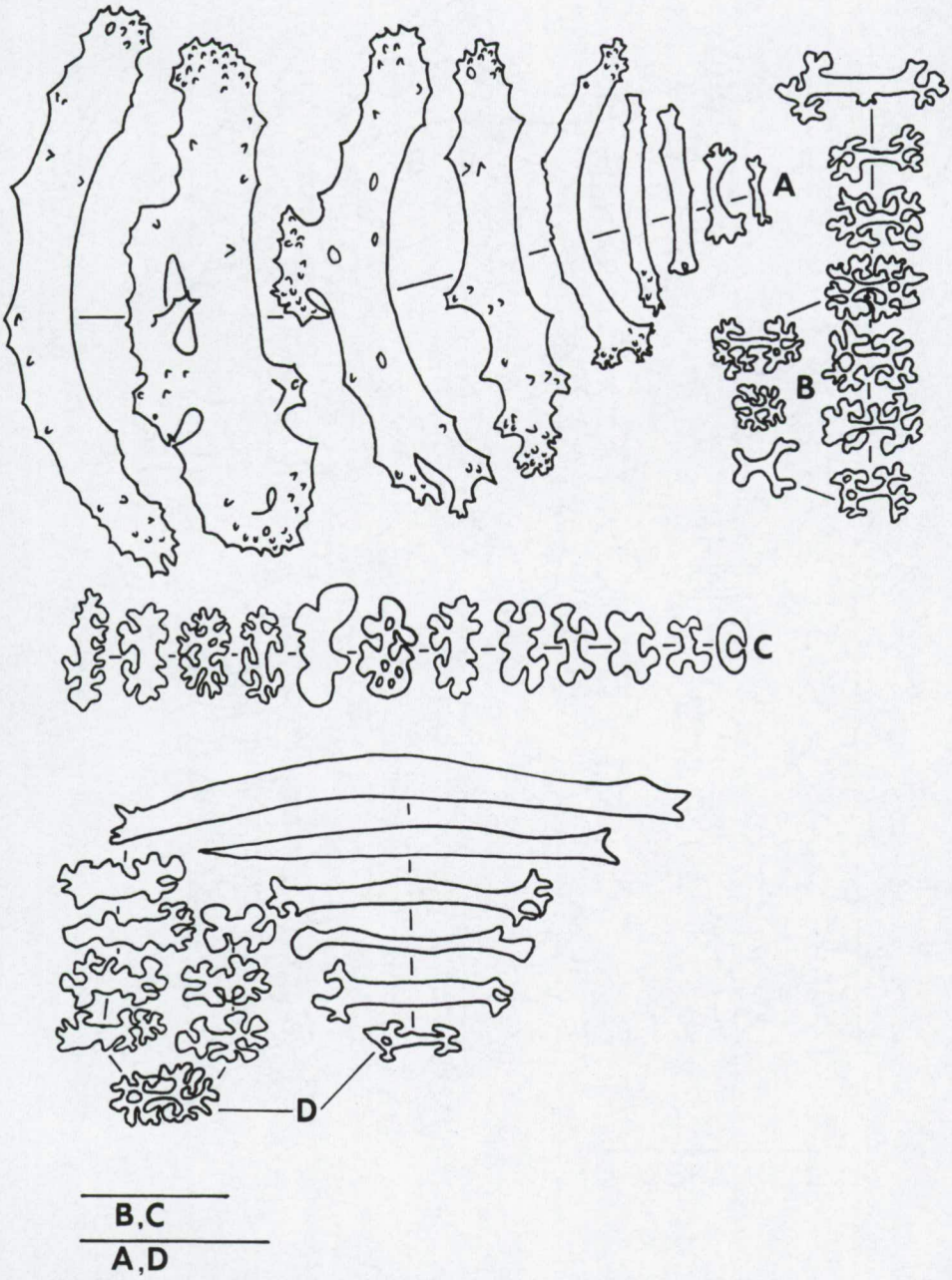


Figure 10. *Bohadschia subrubra* (QUOY & GAIMARD, 1833) (A) Rods of tentacles; (B) Rosettes of dorsal body wall; (C) Rosettes of ventral body wall; (D) Rods and rosettes of ventral tube feet. Scale bar B, C represents 100 μm; scale bar A, D represents 50 μm.

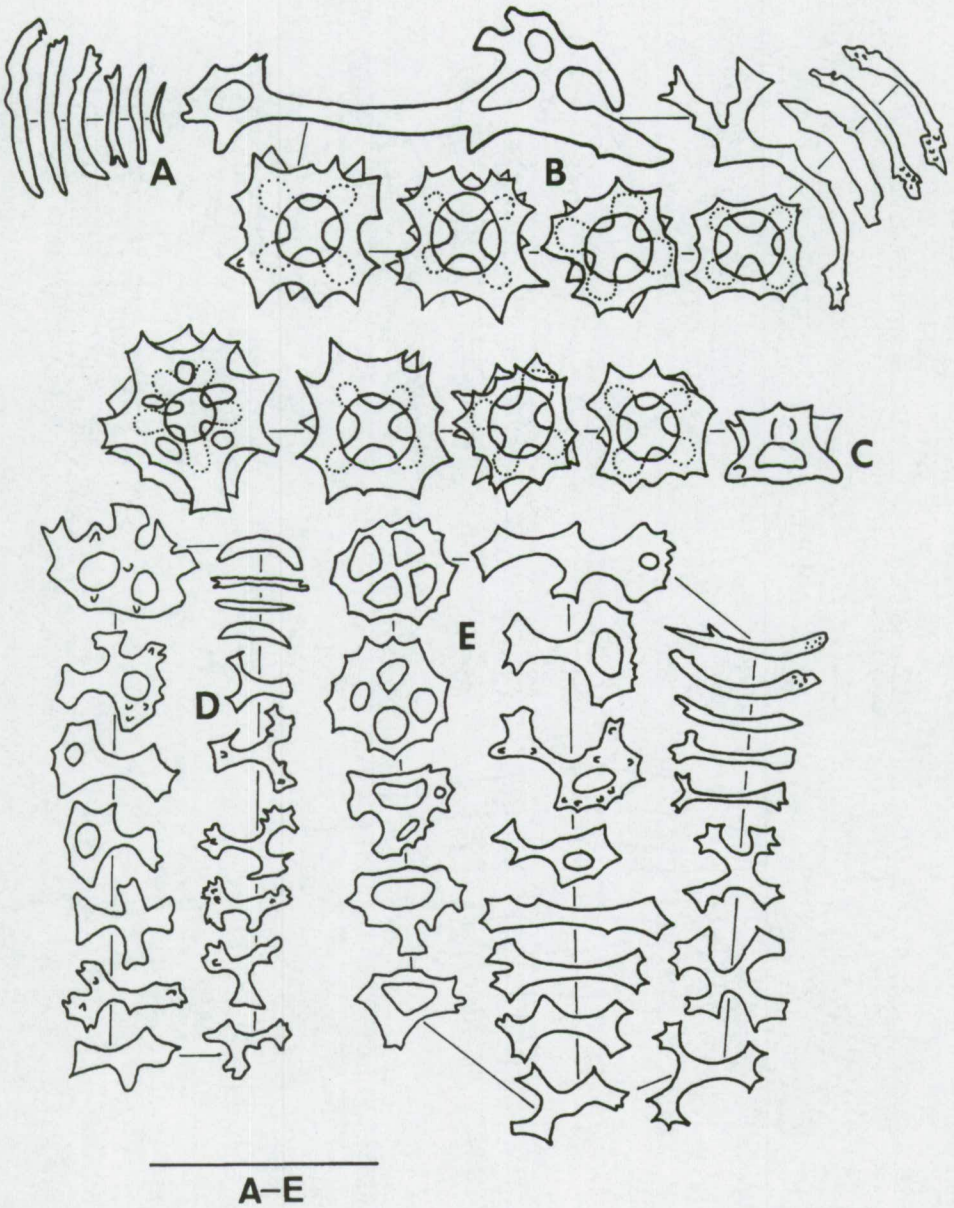


Figure 11. *Labidodemas pertinax* LUDWIG, 1875. (A) Rods of tentacles; (B) Tables and rods of dorsal body wall; (C) Tables of ventral body wall; (D) Rods of dorsal tube feet; (E) Plates and rods of ventral tube feet. Scale bar A- E represents 100 μm.

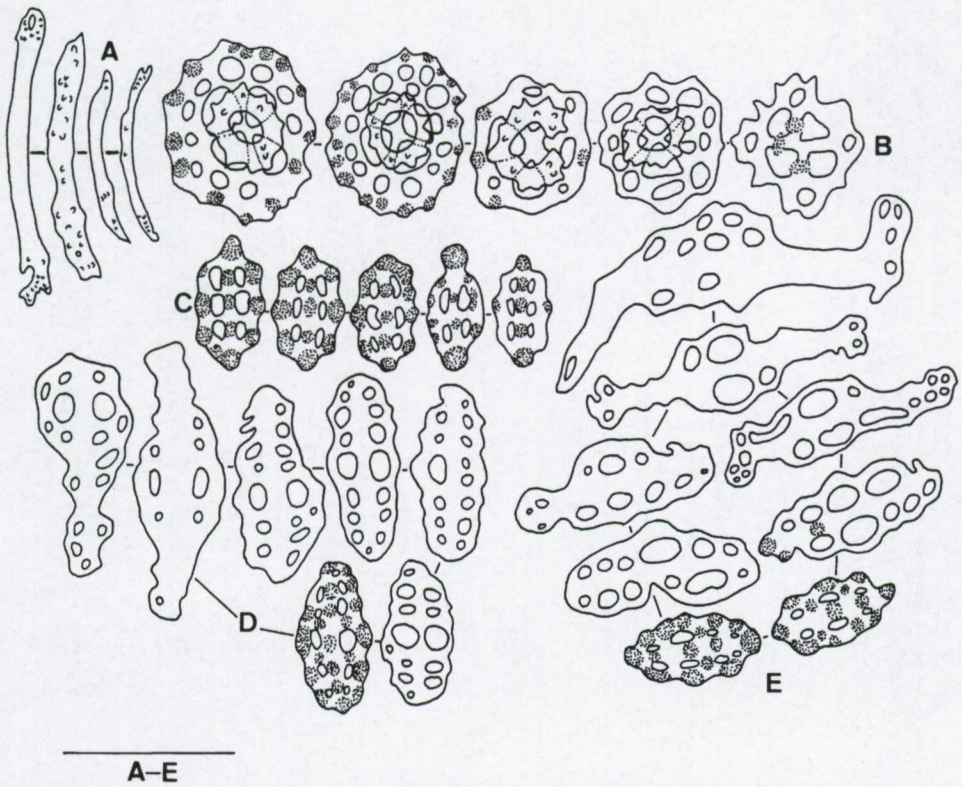


Figure 12. *Holothuria (Cystipus) rigida* (SELENKA, 1867). (A) Rods of tentacles; (B) Tables of body wall; (C) Buttons of body wall; (D) Buttons and narrow plates of ventral tube feet; (E) Buttons and plate-like rods of dorsal papillae. Scale bar A-E represents 100 µm.

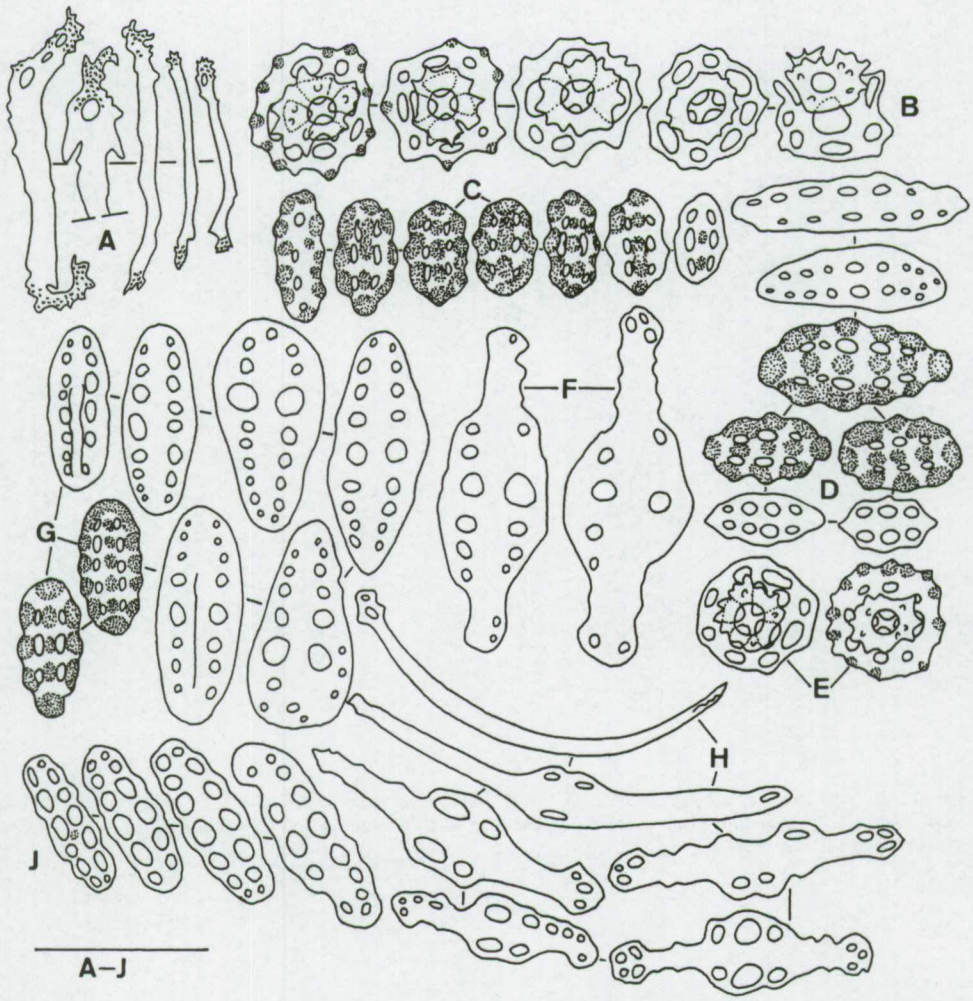


Figure 13. *Holothuria (Cystipus)* cf. *rigida* (Selenka, 1867). (A) Rods of tenatcles; (B) Tables of ventral body wall; (C) Buttons of ventral body wall; (D) Buttons of dorsal body wall; (E) Tables of dorsal body wall; (F) Perforated rods of dorsal tube feet; (G) Plates and buttons of dorsal tube feet; (H) Rods of ventral tube feet; (J) Buttons of ventral tube feet. Scale bar A-J represents 100 μm.

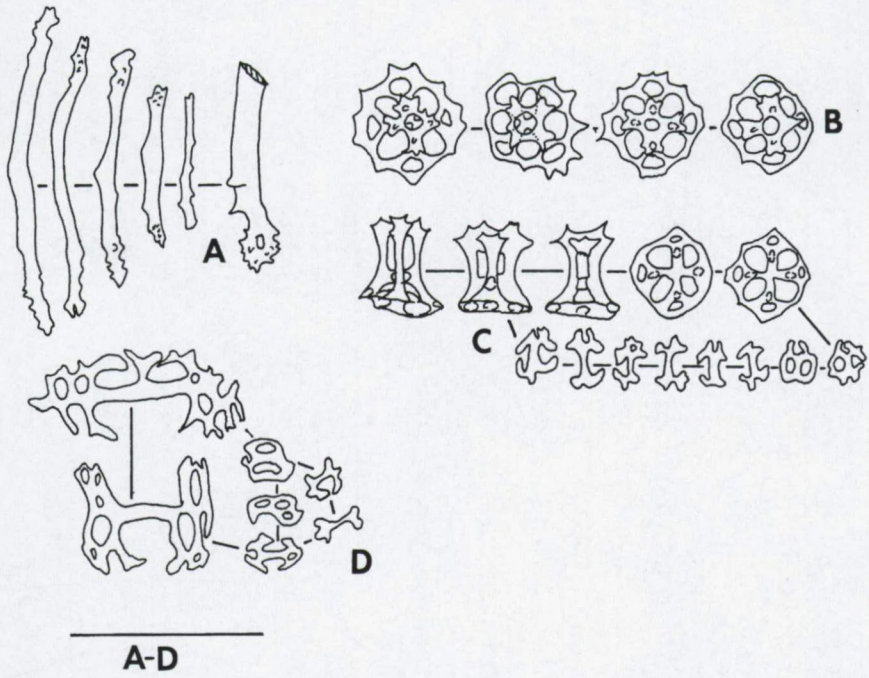


Figure 14. *Holothuria (Halodeima) atra* JAEGER, 1833. (A) Rods of tentacles; (B) Tables of ventral body wall; (C) Tables and rosettes of dorsal body wall; (D) Pseudo-plates and rosettes of tube feet. Scale bar A-D represents 100 μm.

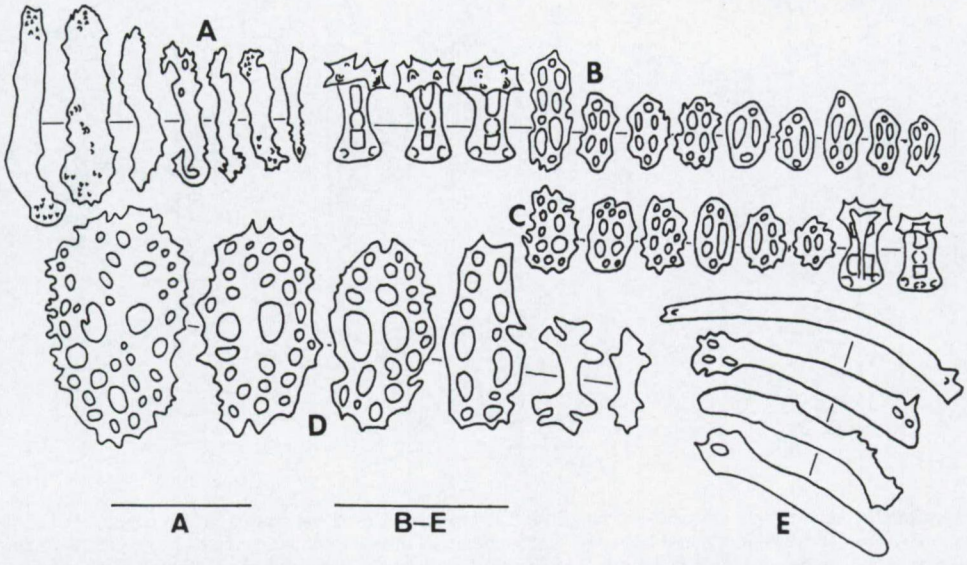


Figure 15. *Holothuria (Halodeima) edulis* LESSON, 1830. (A) Rods of tentacles; (B) Buttons and tables of dorsal body wall; (C) Buttons and tables of ventral body wall; (D) Plates and rods of ventral tube feet; (E) Rods of dorsal tube feet. Scale bar A represents 200 μm; scale bar B-E represents 100 μm

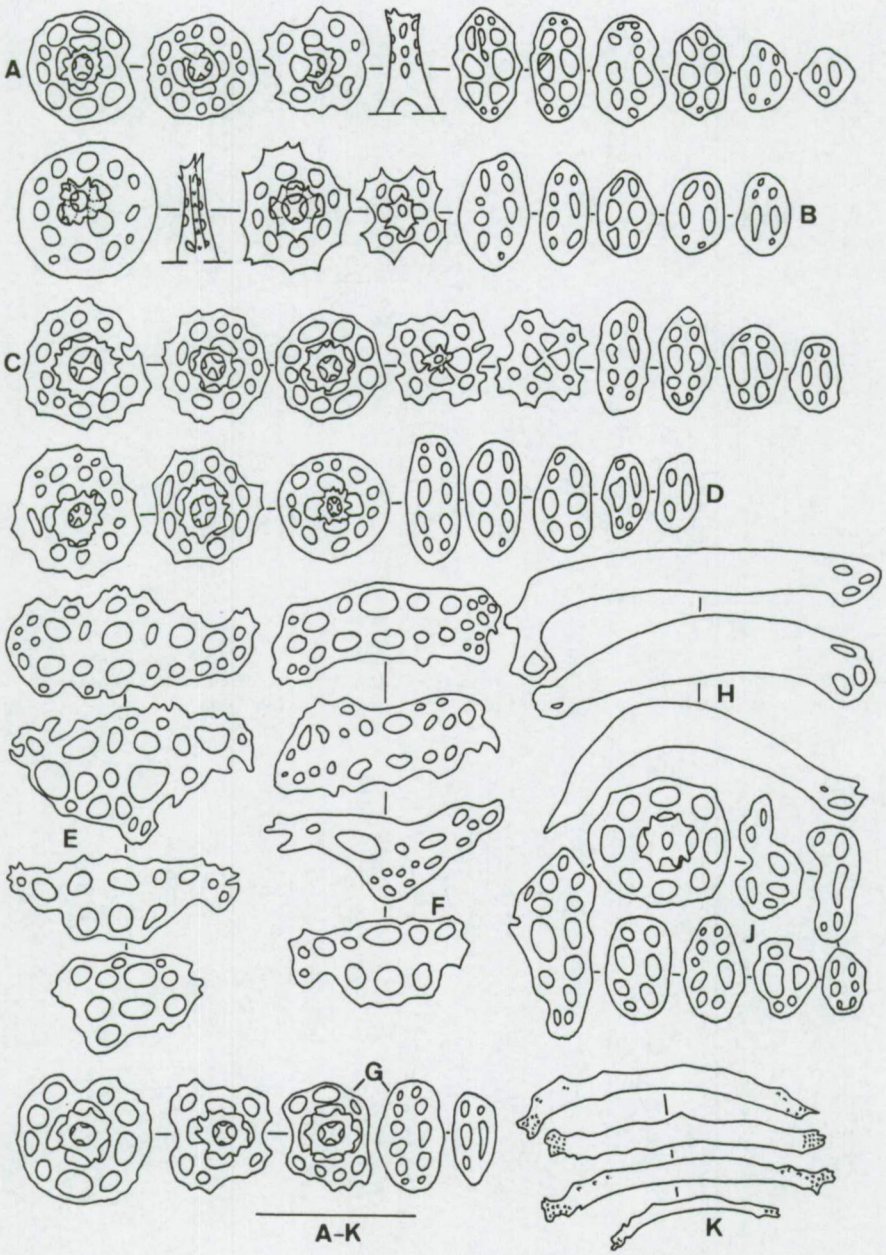


Figure 16. *Holothuria (Lessonothuria) pardalis* SELENKA, 1867. (A) Tables and buttons of dorsal body wall (L=50 mm); (B) Tables and buttons of dorsal body wall (L=85 mm); (C) Tables and buttons of ventral body wall (L=50 mm); (D) Tables and buttons of ventral body wall (L=85 mm); (E) Perforated plates of ventral tube feet (L=50 mm); (F) Perforated plates of ventral tube feet (L=85 mm); (G) Tables and buttons of ventral tube feet (L=50 mm); (H) Rods of dorsal papillae (L=50 mm); (J) Tables, plates and buttons of dorsal papillae (L=50 mm); K. Rods of tentacles (L=85 mm). Scale bar A-K represents 100 μm.

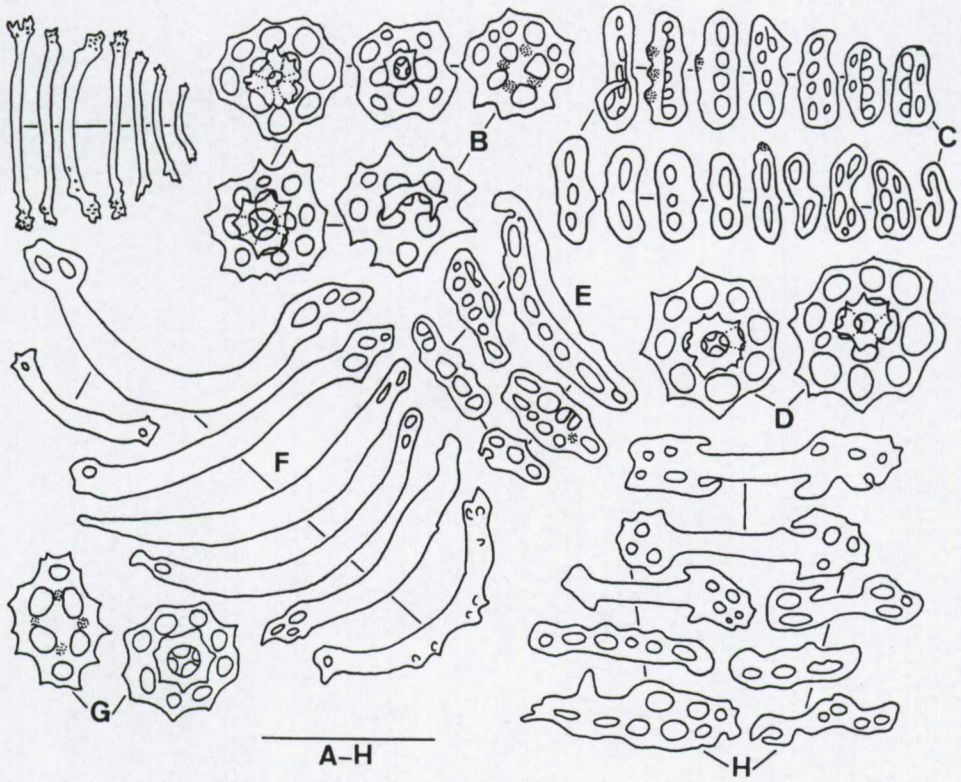


Figure 17. *Holothuria (Lessonothuria) verrucosa* SELENKA, 1867. (A) rods of tentacles; (B) Tables of body wall; (C) Buttons and pseudobuttons of body wall; (D) Tables of dorsal tube feet; (E) Pseudobuttons of dorsal tube feet; (F) Rods of dorsal tube feet; (G) Tables of ventral tube feet; (H) Plates and rods of ventral tube feet. Scale bar A-H represents 100 μm.

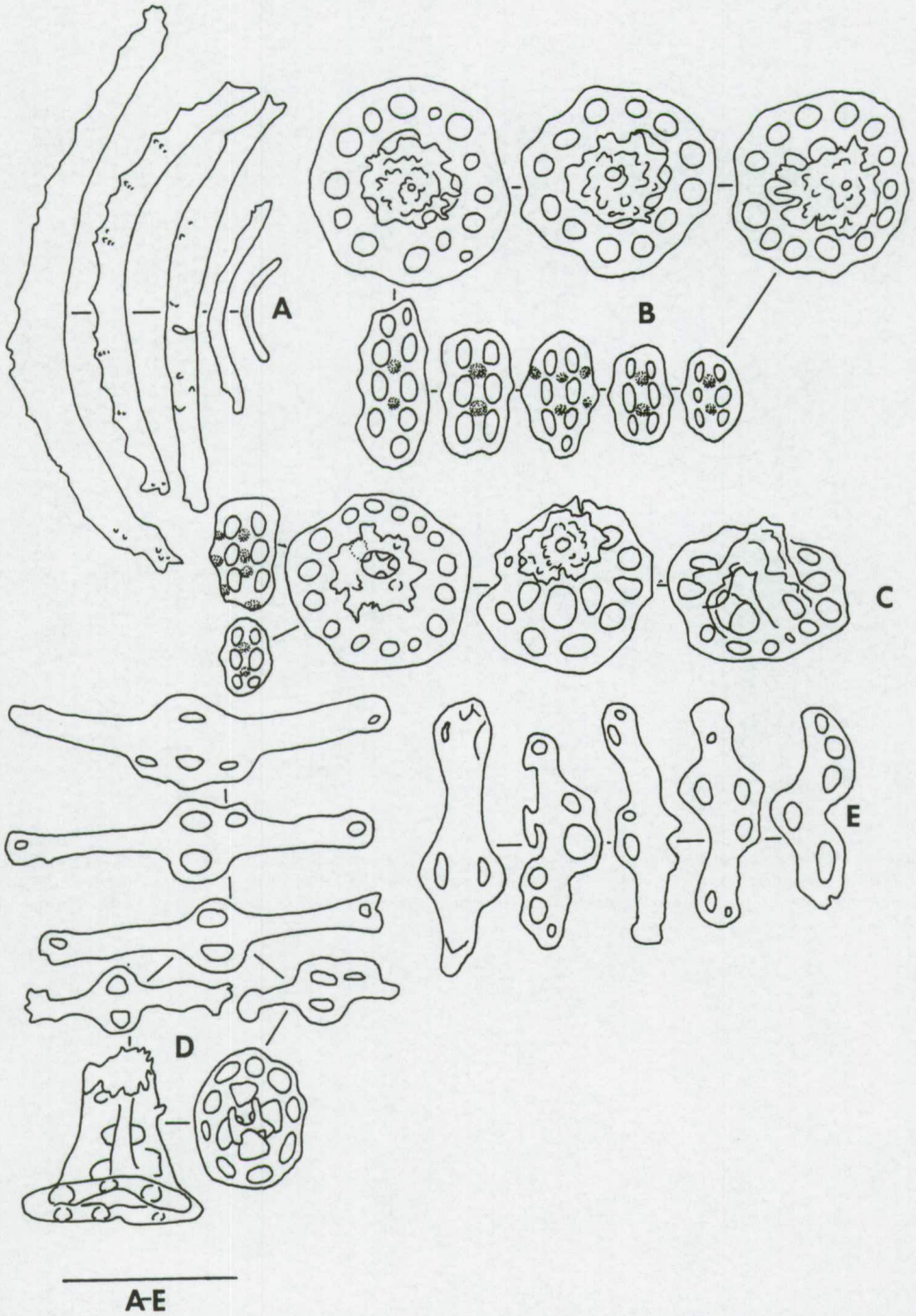


Figure 18. *Holothuria (Metriatyla) albiventer* SEMPER, 1868. (A) Rods of tentacles; (B) Tables and buttons of ventral body wall; (C) Tables and buttons of dorsal body wall; (D) Rods and tables of ventral tube feet; (E) Plate-like rods of dorsal papillae. Scale bar A-E represents 100 μm.

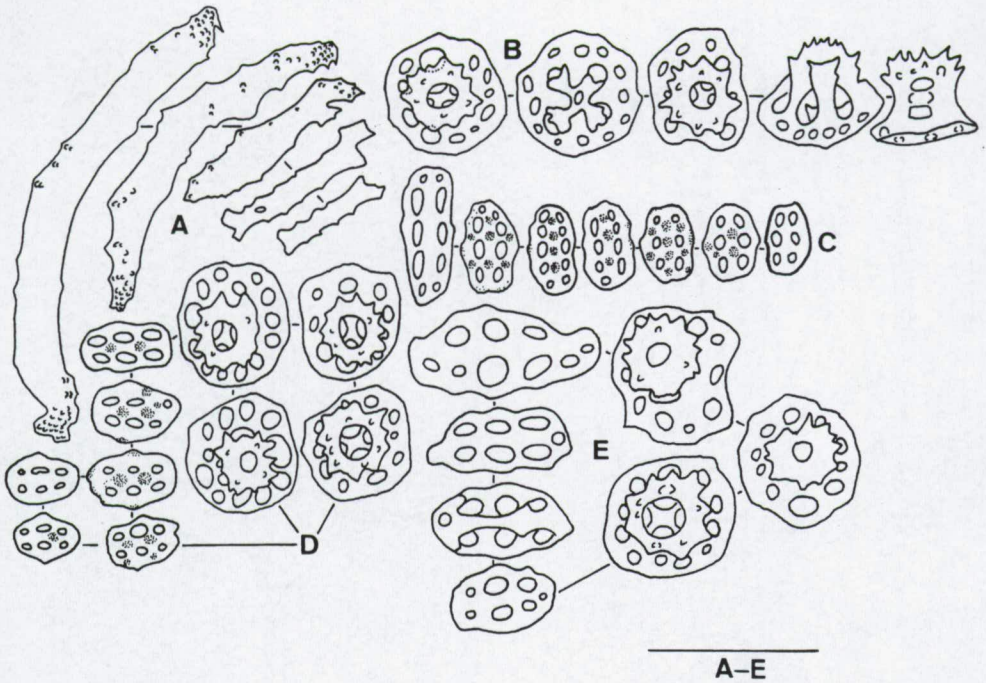


Figure 19. *Holothuria (Metriatyla) scabra* JAEGER, 1833. (A) Rods of tentacles; (B) Tables of dorsal body wall; (C) Buttons of dorsal body wall; (D) Tables and buttons of ventral body wall; (E) Buttons and tables of tube feet. Scale bar A-E represents 100 μm.

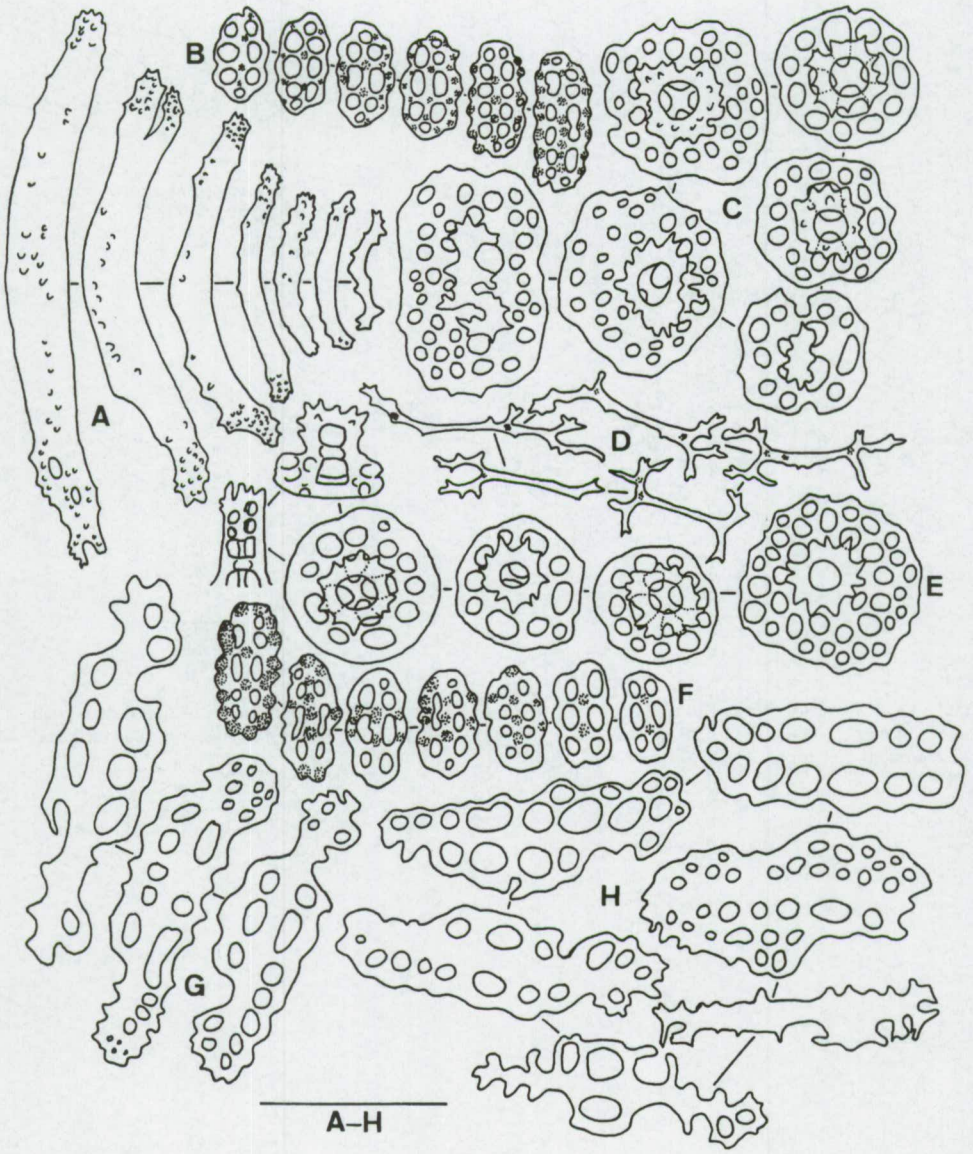


Figure 20. *Holothuria (Metriatyla) scabra* var. *versicolour* (CONAND, 1986). (A) Rods of tentacles; (B) Buttons of dorsal body wall; (C) Tables of dorsal body wall; (D) Rods of ventral body wall; (E) Tables of ventral body wall; (F) Buttons of ventral body wall; (G) Plates of ventral tube feet; (H) Plates of dorsal tube feet. Scale bar A-H represents 100 µm.

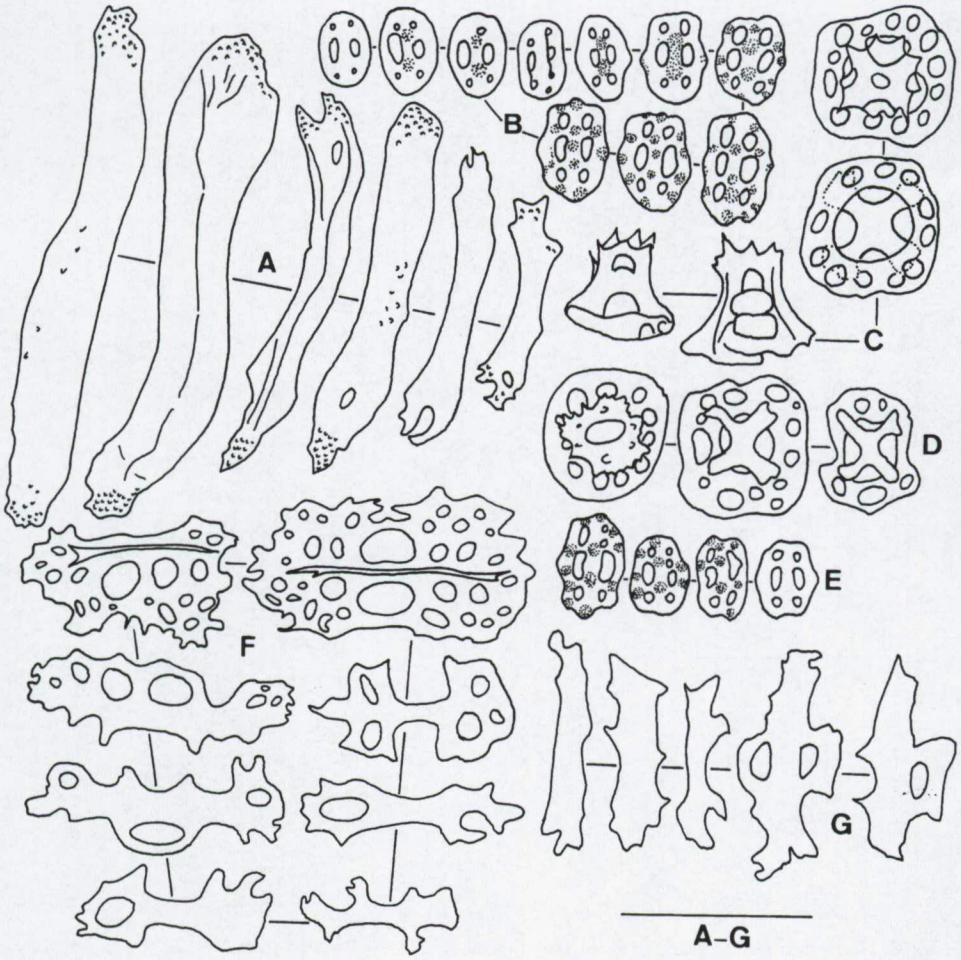


Figure 21. *Holothuria (Metriatyla) timana* LESSON, 1830. (A) Rods of tentacles; (B) Buttons of dorsal body wall; (C) Tables of dorsal body wall; (D) Tables of ventral body wall; (E) Buttons of ventral body wall; (F) Tables and rods of ventral tube feet; (G) Rods of dorsal tube feet. Scale bar A-G represents 100 μm.

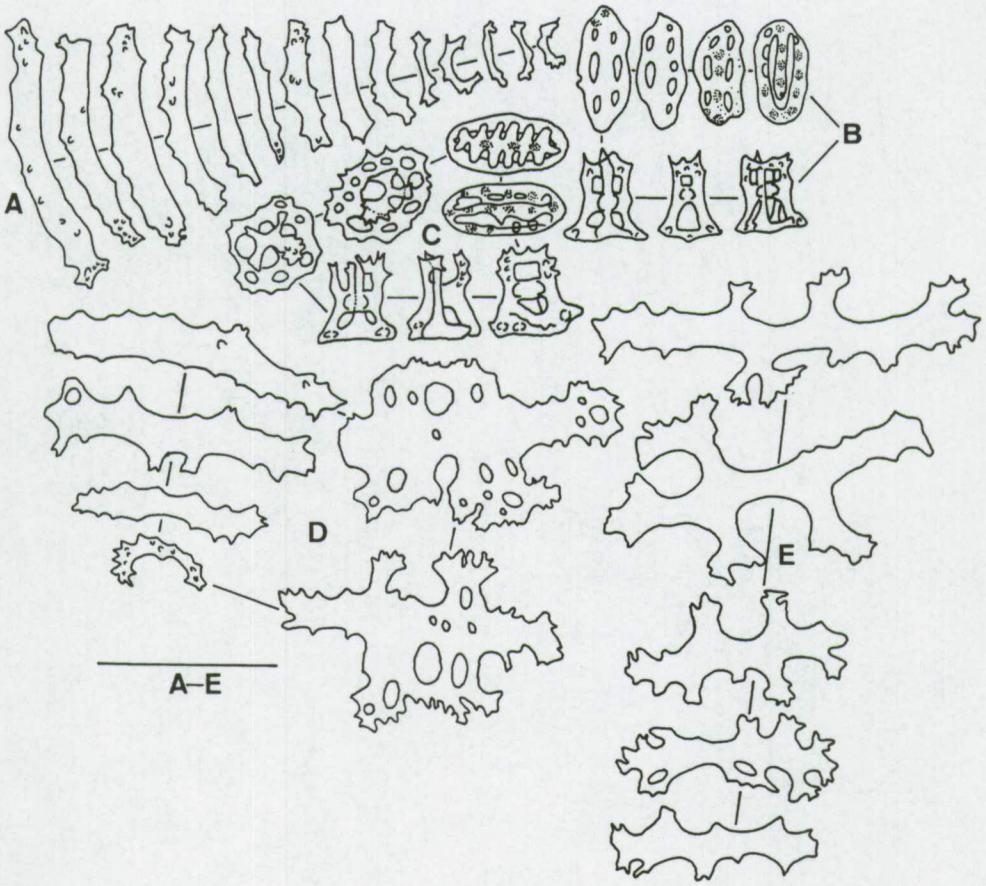


Figure 22. *Holothuria (Microthele) fuscopunctata* JAEGER, 1833. (A) Rods of tentacles; (B) Tables, buttons and ellipsoids of ventral body wall; (C) Tables and ellipsoid buttons of dorsal body wall; (D) Plates and rods of dorsal tube feet; (E) Modified rods of ventral tube feet. Scale bar A-E represents 100 μm.

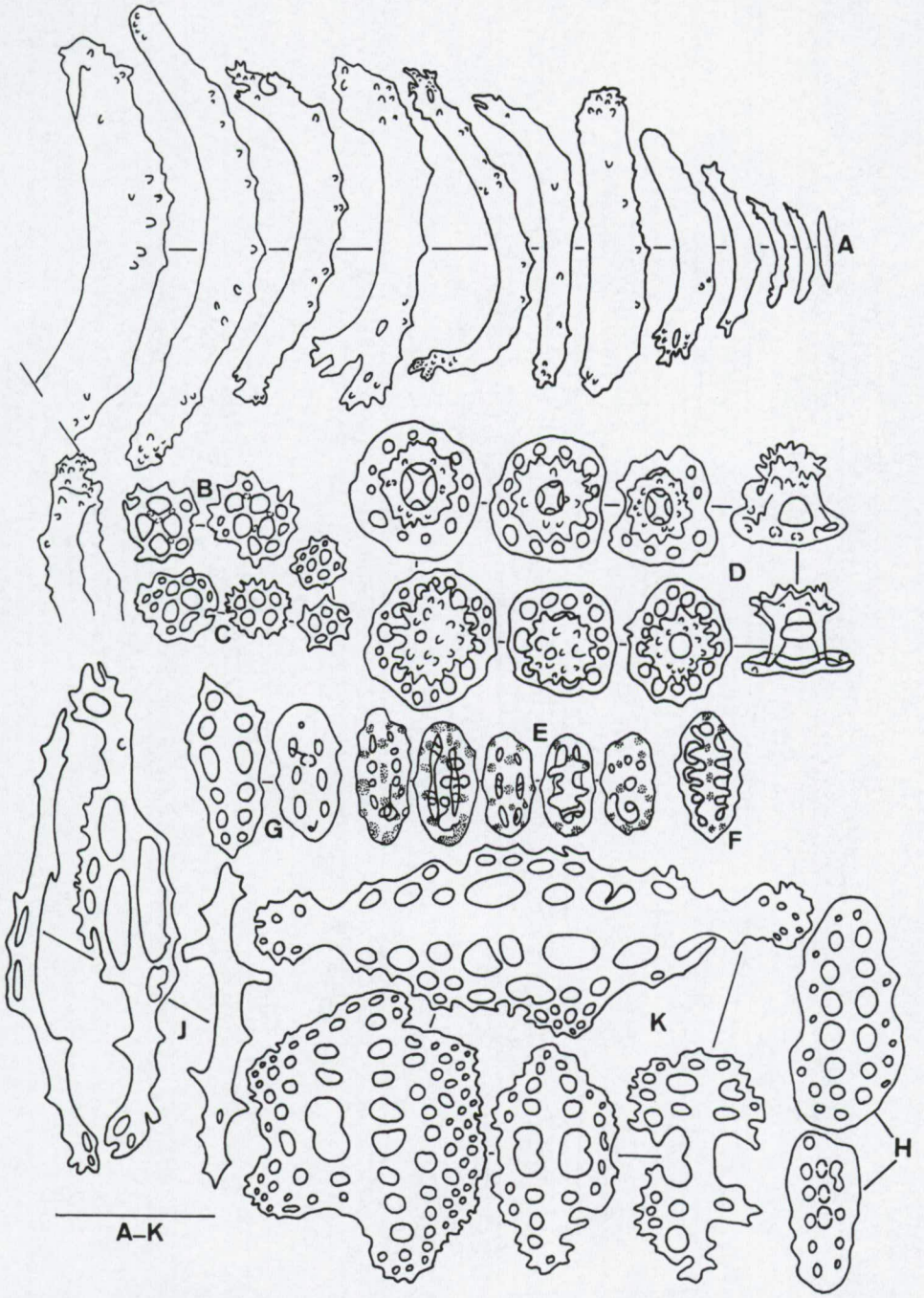


Figure 23. *Holothuria (Microthele) nobilis* (SELENKA, 1867). (A) Rods of tentacles; (B) Tables (reduced to the disc with some knobs) of tentacles; (C) Tables (reduced to disc without knobs) of tentacles; (D) Tables of body wall; (E) Rugose ellipsoids of body wall; (F) Complex rugose ellpsoid of dorsal body wall; (G) Smooth to slightly knobbed buttons of ventral body wall; (H) Smooth to slightly knobbed elongated plates of ventral tube feet; (J) Rod-like plates of ventral tube feet; K. Large multiperforated plates of tube feet. Scale bar A-K represents 100 μm.

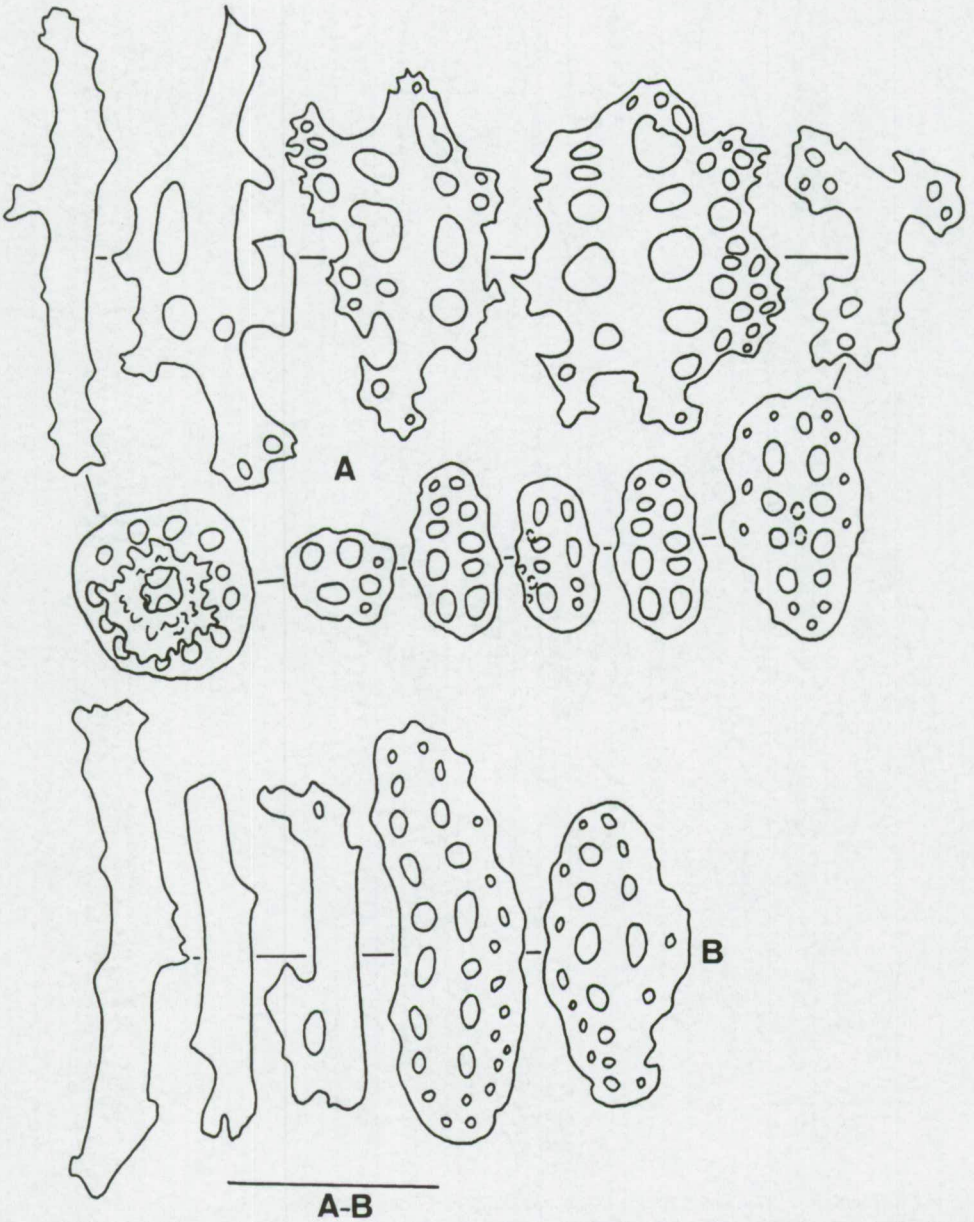


Figure 24. *Holothuria (Microthele) nobilis* (SELENKA, 1867). (A) Rod-like plates, multiperforated plates, buttons and table of ventral tube feet; (B) Rods and elongated plates of dorsal papillae. Scale bar A, B represents 100 μm.

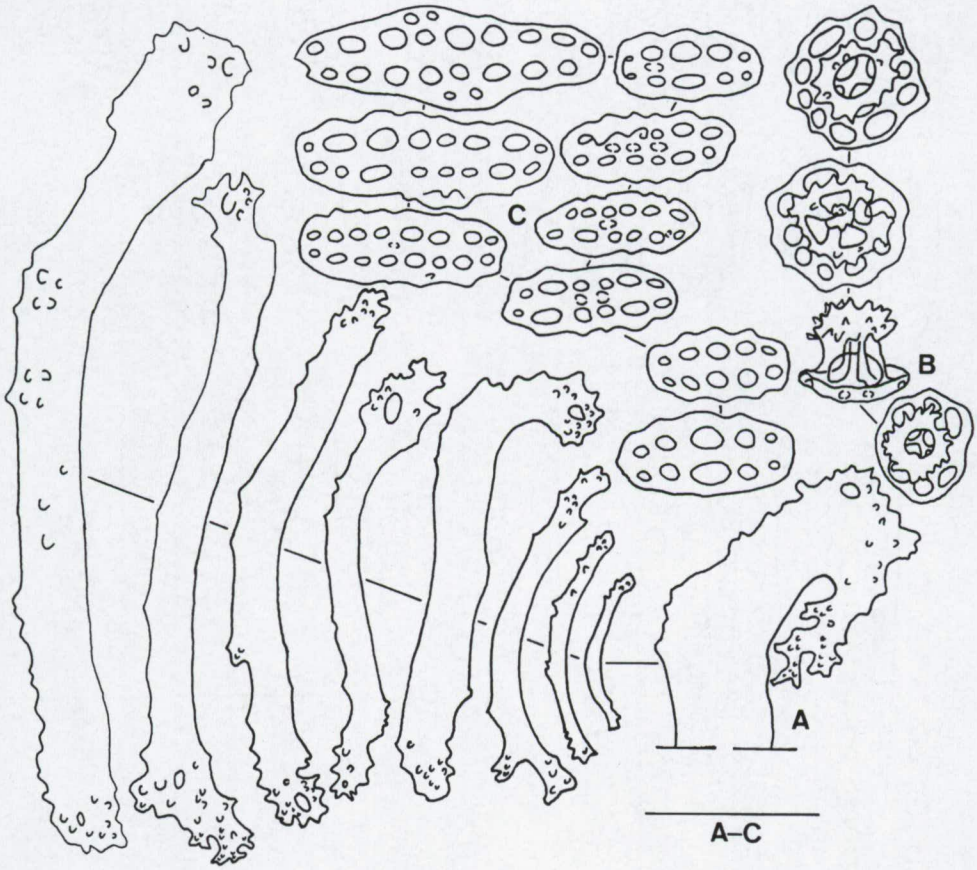


Figure 25. *Holothuria (Microthele) nobilis* (SELENKA, 1867). (A) Rods of tentacles; (B) Tables of body wall; (C) Smooth to slightly rugose buttons and plates of ventral body wall. Scale bar A-C represents 100 μm.

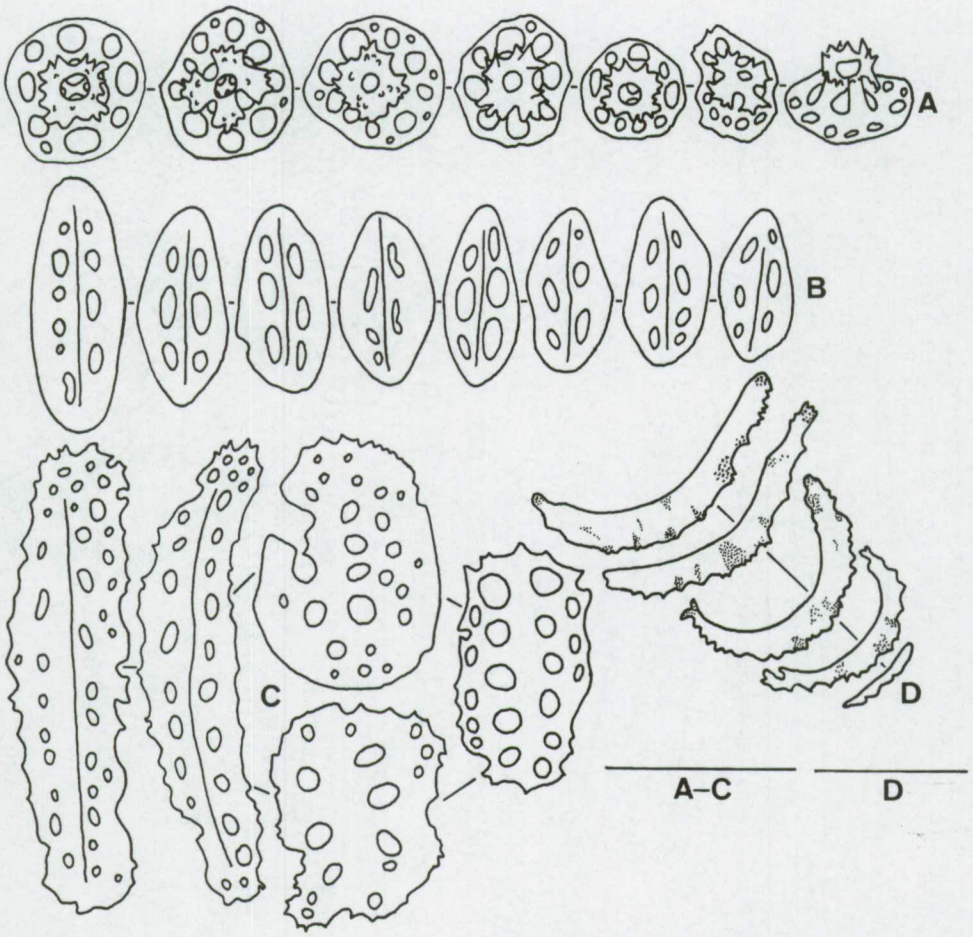


Figure 26. *Holothuria (Platyperona) difficilis* SEMPER, 1868. (A) Tables of body wall; (B) Buttons of body wall; (C) Perforated plates of ventral tube feet; (D) Rods of tentacles. Scale bar A-C represents 100 µm; scale bar D represents 200 µm.

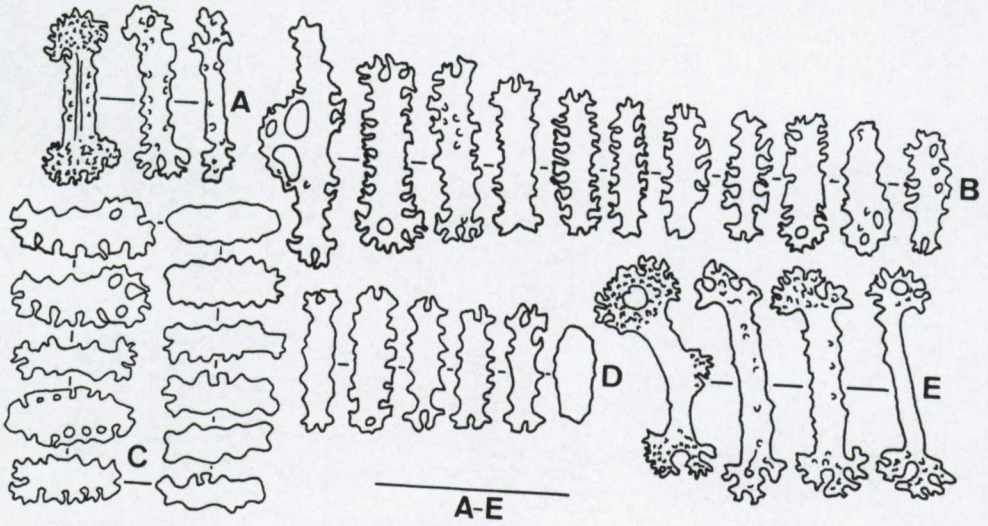


Figure 27. *Holothuria (Selenkothuria) erinacea* SEMPER, 1868. (A) Rods of tentacles; (B) Rods of dorsal body wall; (C) Rods of ventral body wall; (D) Rods of ventral tube feet; (E) Rods of dorsal papillae. Scale bar A-E represents 100 μm.

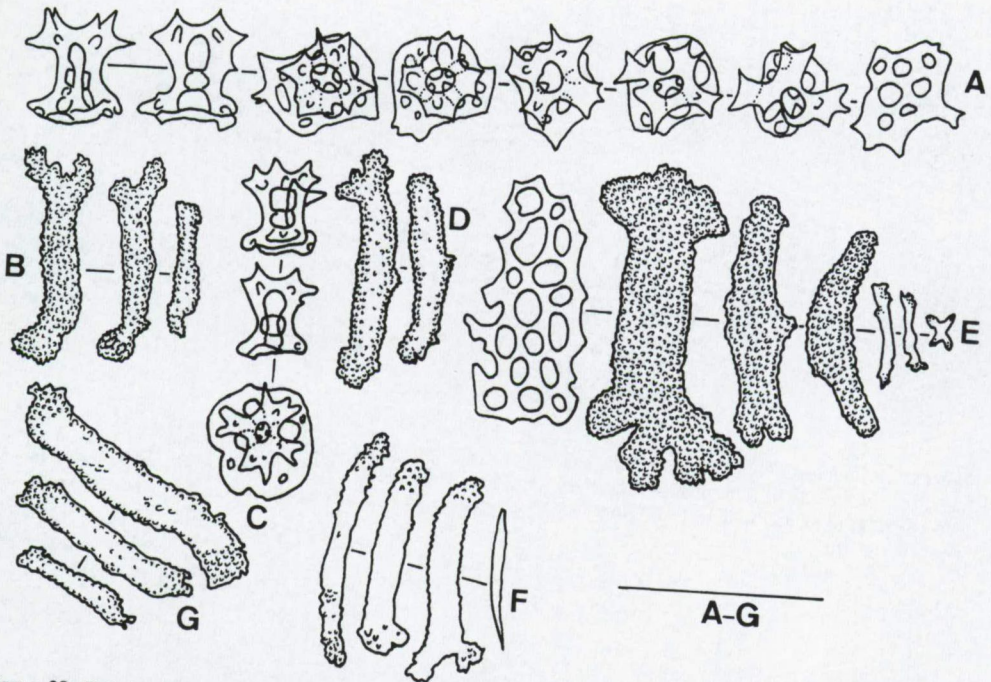


Figure 28. *Holothuria (Semperothuria) cinerascens* (BRANDT, 1835). (A) Tables of dorsal body wall; (B) Rods of dorsal body wall; (C) Tables of ventral body wall; (D) Rods of ventral body wall; (E) Plate and rods of dorsal tube feet; (F) Rods of ventral tube feet; (G) Rods of tentacles. Scale bar A-G represents 100 μm.

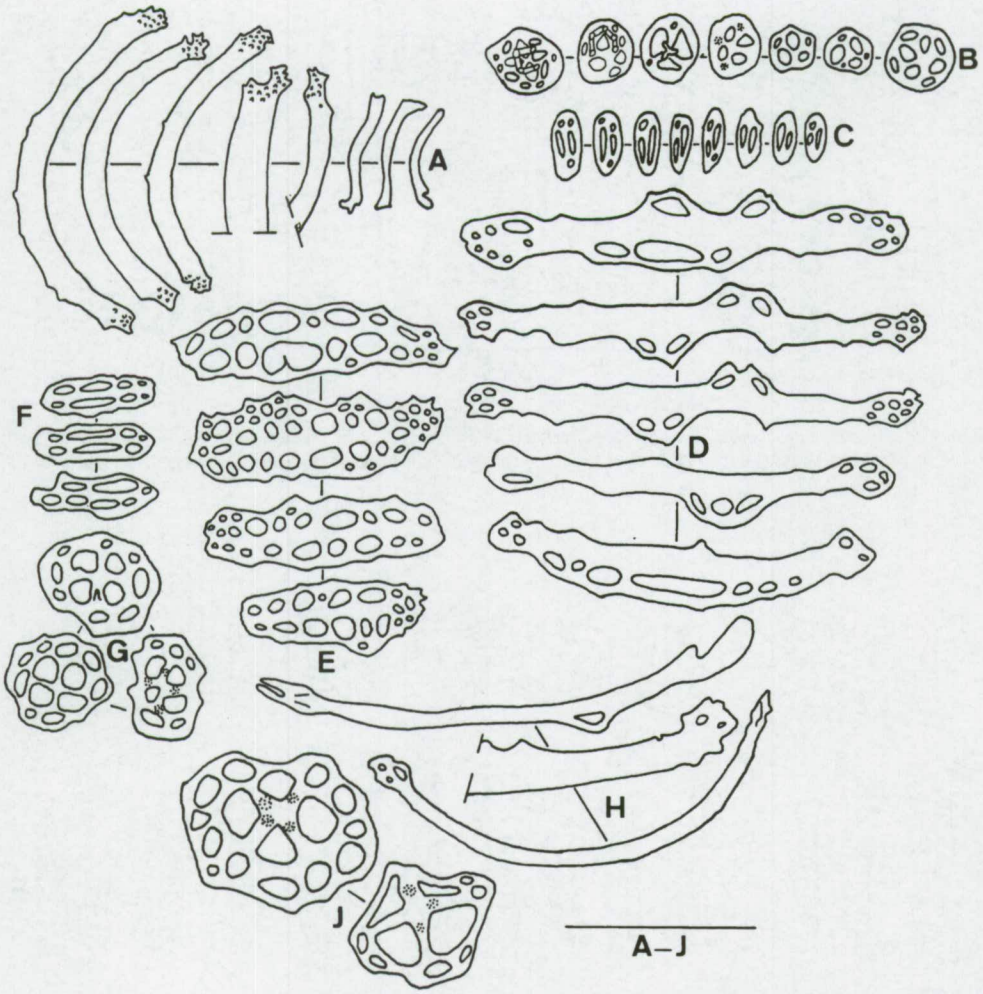


Figure 29. *Holothuria (Stauropora) fuscocinerea* JAEGER, 1833. (A) Rods of tentacles; (B) Tables of body wall; (C) Buttons of body wall; (D) Rods of ventral tube feet; (E) Plates of ventral tube feet; (F) Buttons of ventral tube feet; (G) Reduced tables of ventral tube feet; (H) Rods of dorsal papillae; (J) Reduced tables of dorsal papillae. Scale bar A-J represents 100 μm.

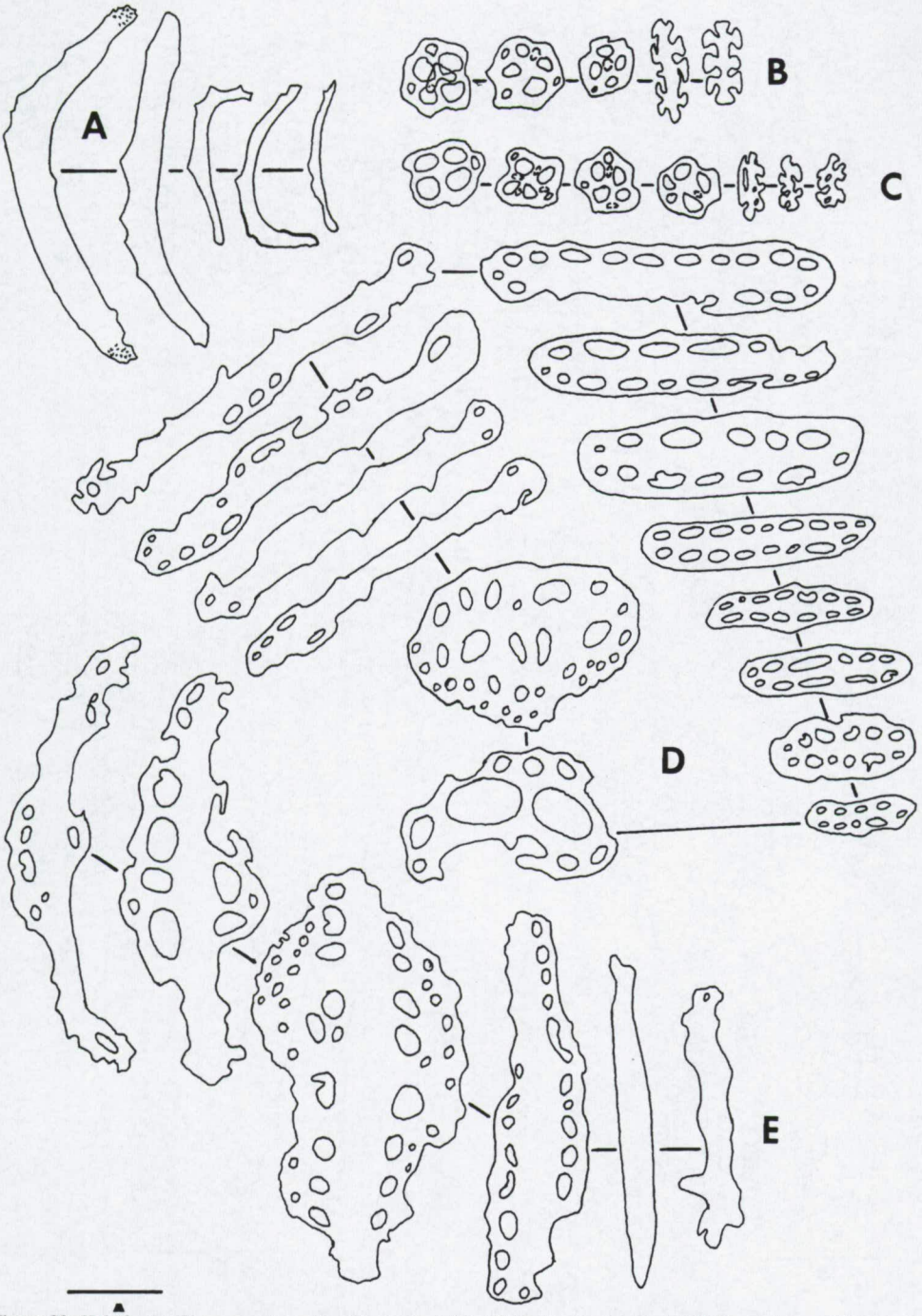


Figure 30. *Holothuria (Stauropora) pervicax* SELENKA, 1867. (A) Rods of tentacles; (B) Tables and pseudo-buttons of dorsal body wall; (C) Tables and pseudo-buttons of ventral body wall; (D) Rods, plates and buttons of ventral tube feet; (E) Rods and plates of dorsal papillae. Scale bars A and B-E represent 100 μm.

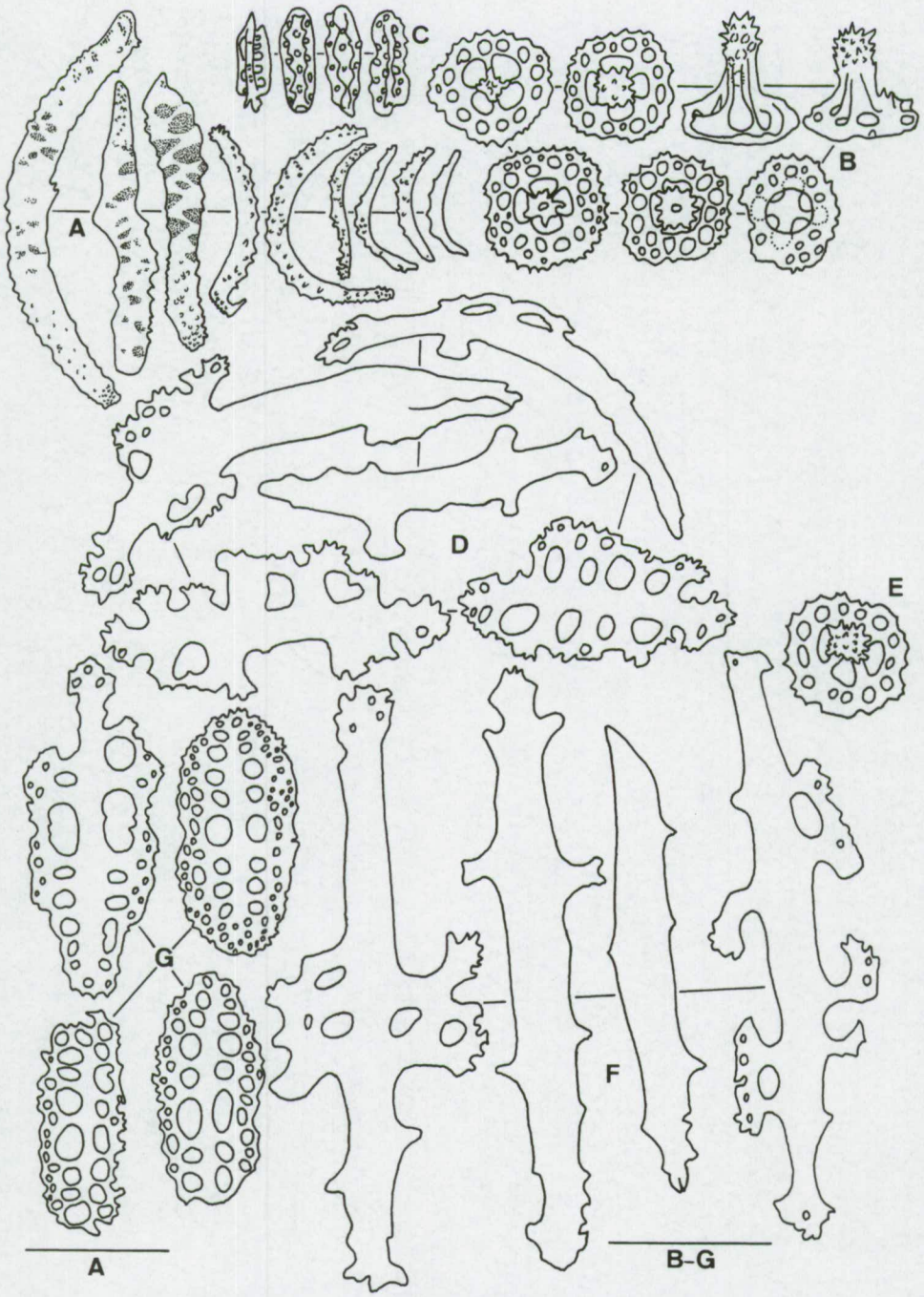


Figure 31. *Holothuria (Theelothuria) turriscelsa* CHERBONNIER, 1980. (A) Rods of tentacles; (B) Tables of body wall; (C) Ellipsoids of body wall; (D) Rods and plates of dorsal papillae; (E) Table of ventral tube feet; (F) Rods of ventral tube feet; (G) Plate of ventral tube feet. Scale bar A represents 200 μm; scale bar B-G represents 100 μm.

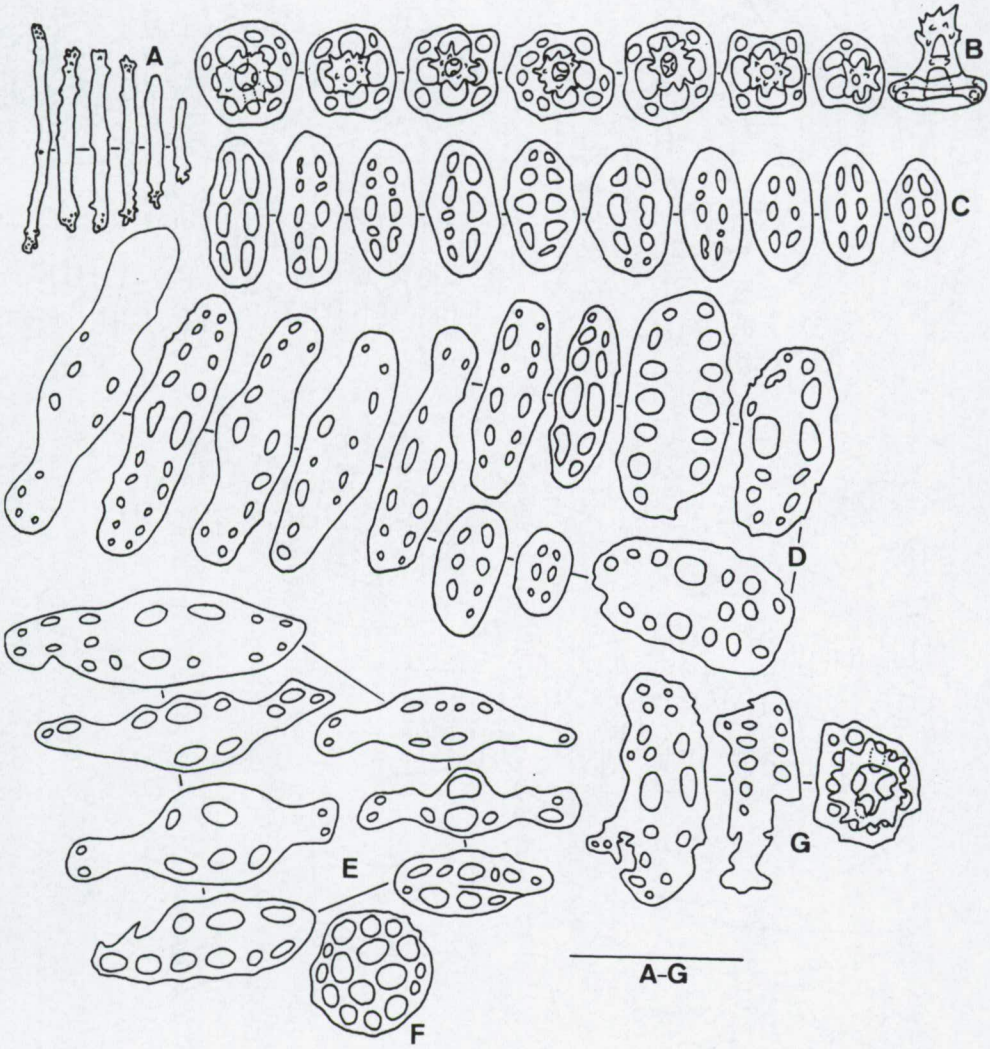


Figure 32. *Holothuria (Thymiosycia) arenicola* SEMPER, 1868. (A) Rods of tentacles; (B) Tables of body wall; (C) Buttons of body wall; (D) Elongated plates and buttons of ventral tube feet; (E) Rod like plates of dorsal tube feet; (F) Reduced table of dorsal tube feet; (G) Rod-like plates and table of anal papillae. Scale bar A-G represents 100 µm.

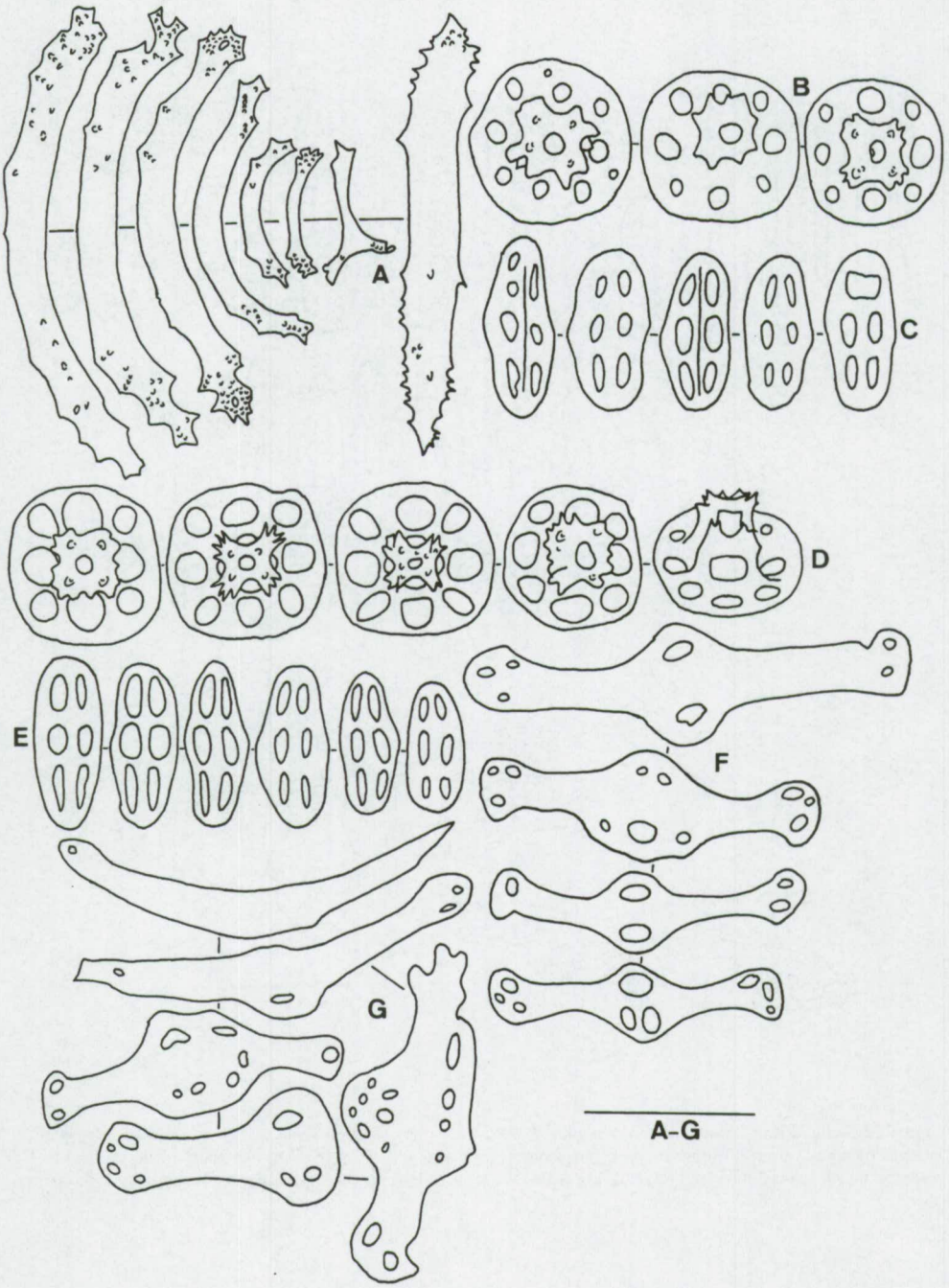


Figure 33. *Holothuria (Thymiosycia) impatiens* (FORSKÅL, 1775). (A) Rods of tentacles; (B) Tables of dorsal body wall; (C) Buttons of dorsal body wall; (D) Tables of ventral body wall. (E) Buttons of ventral body wall; (F) Rods of ventral tube feet; (G) Rods of dorsal tube feet. Scale bar A-G represents 100 µm.

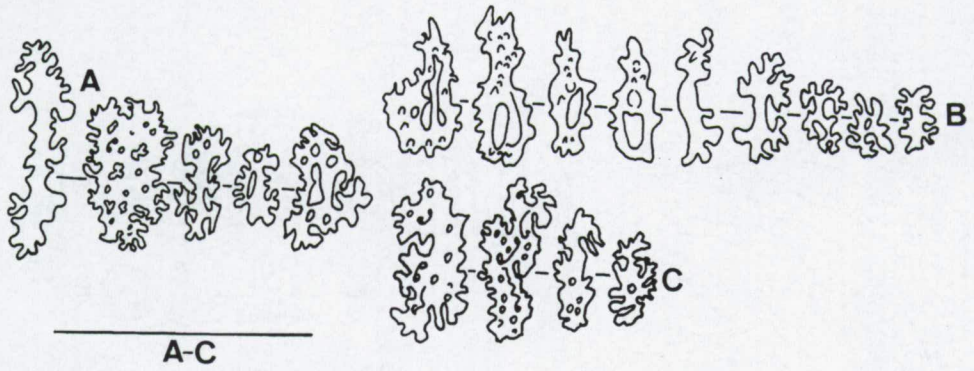


Figure 34. *Pearsonothuria graeffei* (SEMPER, 1868). (A) Rosettes of tentacles; (B) Pseudo-tables and rosettes of body wall; (C) Rosettes of tube feet. Scale bar A-C represents 100 μm.

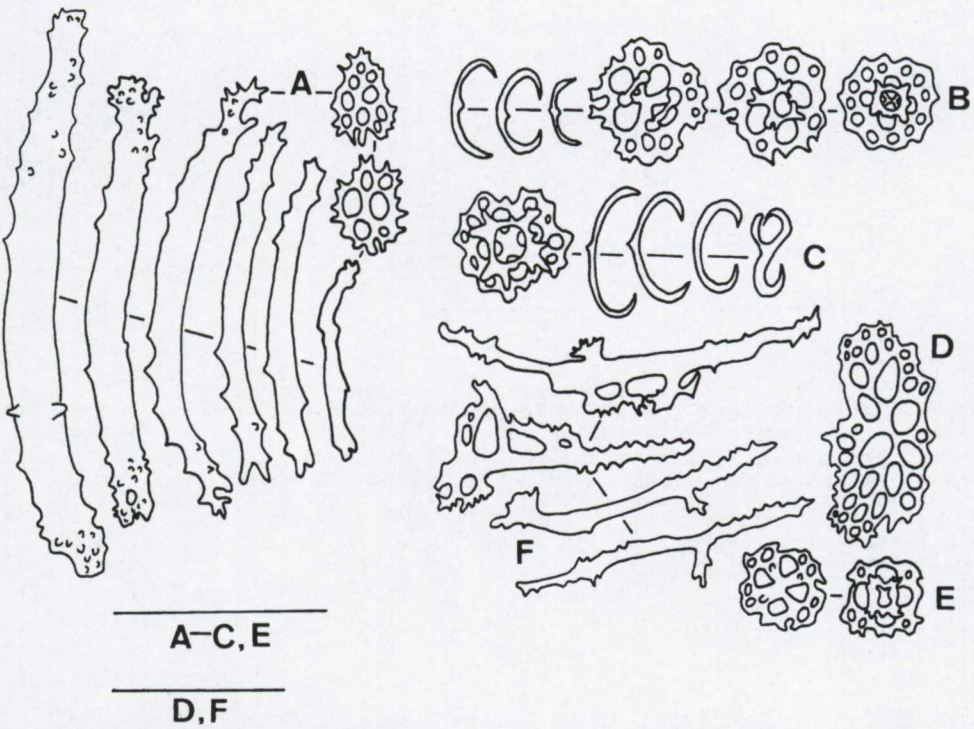


Figure 35. *Stichopus chloronotus* BRANDT, 1835. (A) Rods and plates of tentacles; (B) Tables and C-shaped rods of body wall; (C) Tables and C-shaped rods of dorsal papillae; (D) Perforated plate of ventral tube feet; (E) Tables of ventral tube feet; (F) Rods of ventral tube feet. Scale bar A-C, E represents 100 μm; scale bar D, F represents 200 μm.

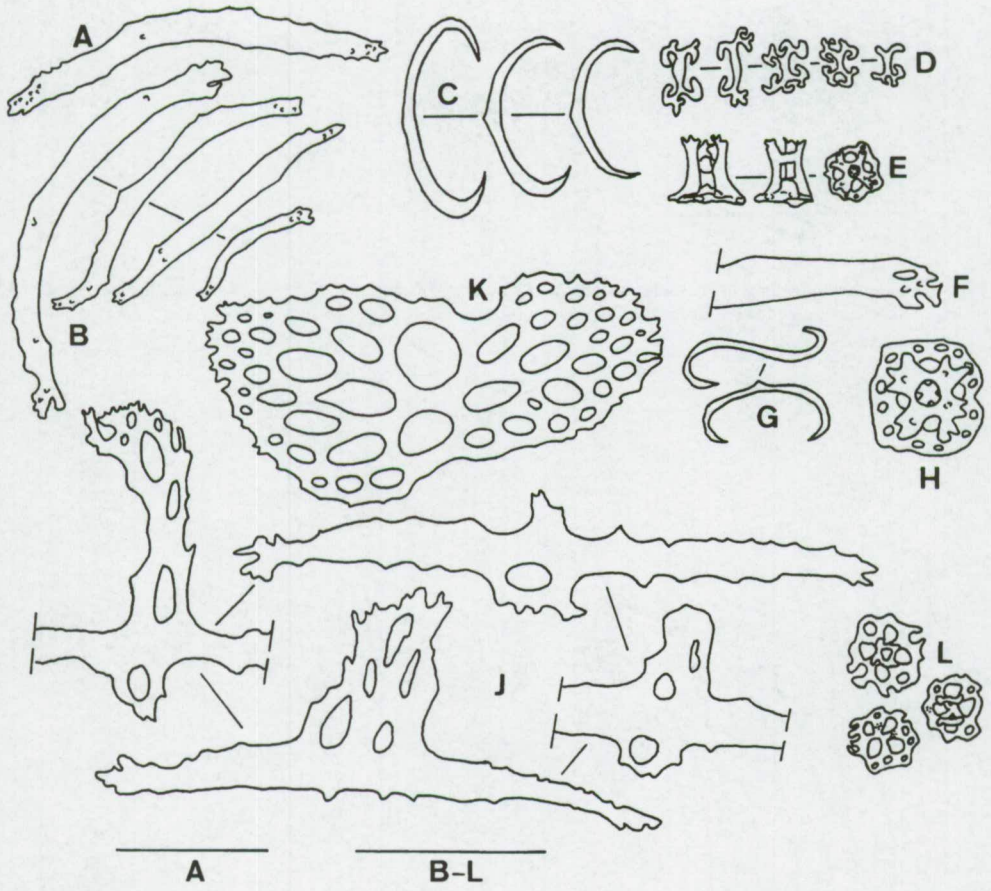


Figure 36. *Stichopus herrmanni* SEMPER, 1868. (A) Large rod of tentacles; (B) Rods of tentacles; (C) C-shaped bodies of body wall; (D) Rosettes of body wall; (E) Tables of body wall; (F) Rod of dorsal papillae; (G) C-and S-shaped bodies of dorsal papillae; (H) Table of dorsal papillae; (J) Rods of ventral tube feet; (K) Perforated plate of ventral tube feet; (L) Tables of ventral tube feet. Scale bar A represents 200 μm; scale bar B-L represents 100 μm.

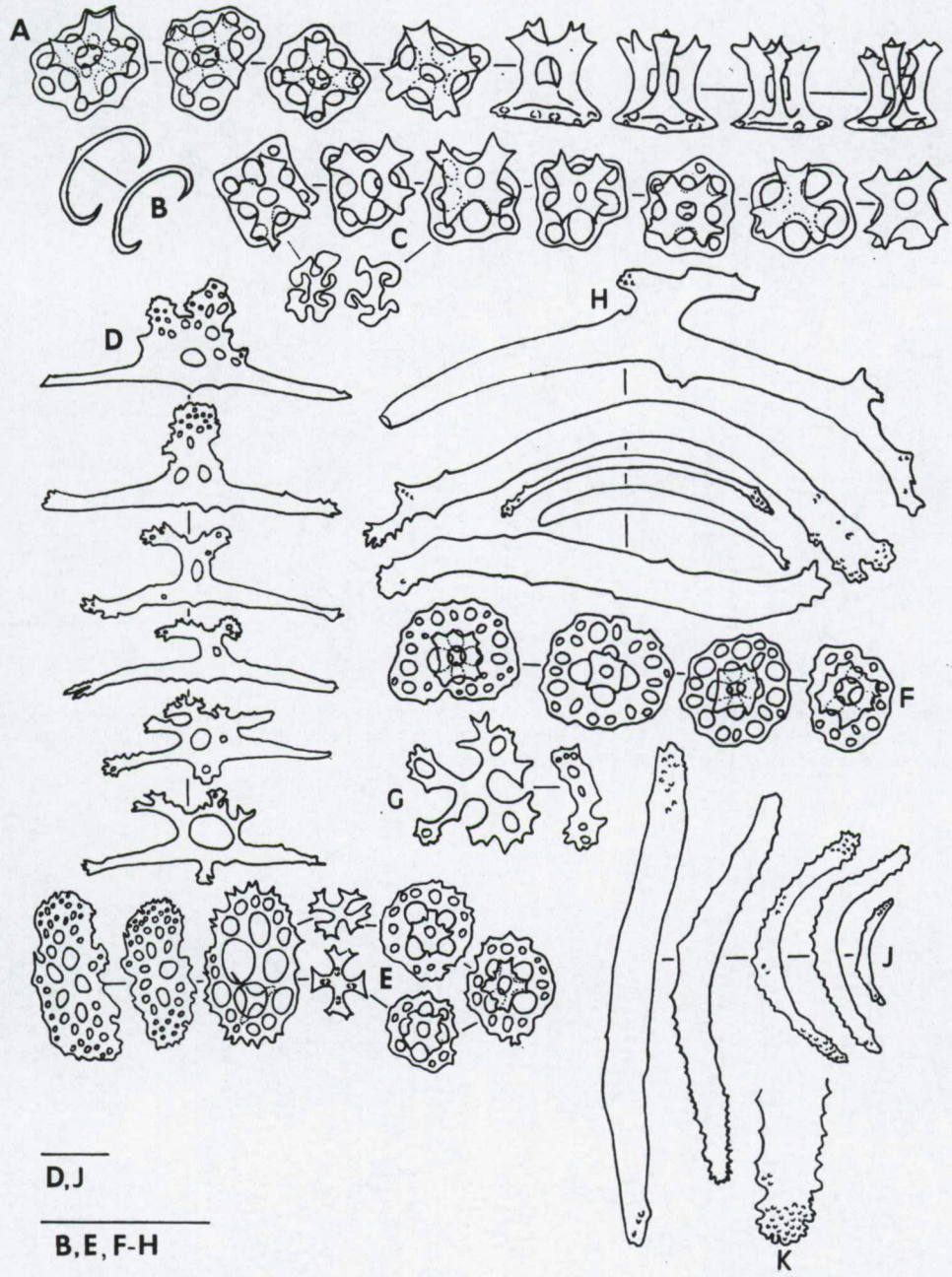


Figure 37. *Stichopus monotuberculatus* (QUOY & GAIMARD, 1833). (A) Tables of ventral body wall; (B) C-shaped rods of ventral body wall; (C) Tables and rosette-like rods of dorsal body wall; (D) Rods of ventral tube feet; (E) Plates and tables of ventral tube feet; (F) Tables of dorsal papillae; (G) Table fragment and small rod of dorsal papillae; (H) Rods of dorsal papillae; (J) Rods of tentacles; (K) Detail of rod of tentacle. All scale bars represent 100 μm.

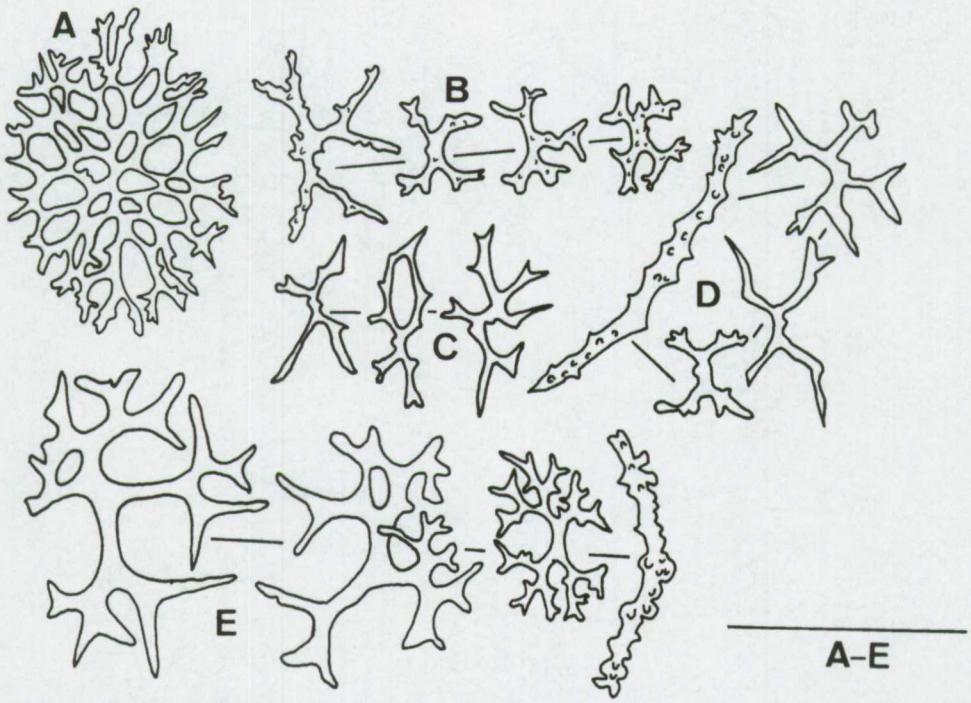


Figure 38. *Thelenota ananas* (JAEGER, 1833). (A) Perforated plate of tentacle; (B) Branched rods of dorsal body wall; (C) Branched rods of ventral body wall; (D) Branched and unbranched rods of dorsal papillae; (E) Branched and unbranched rods of ventral tube feet. Scale bar A-E represents 100 µm.

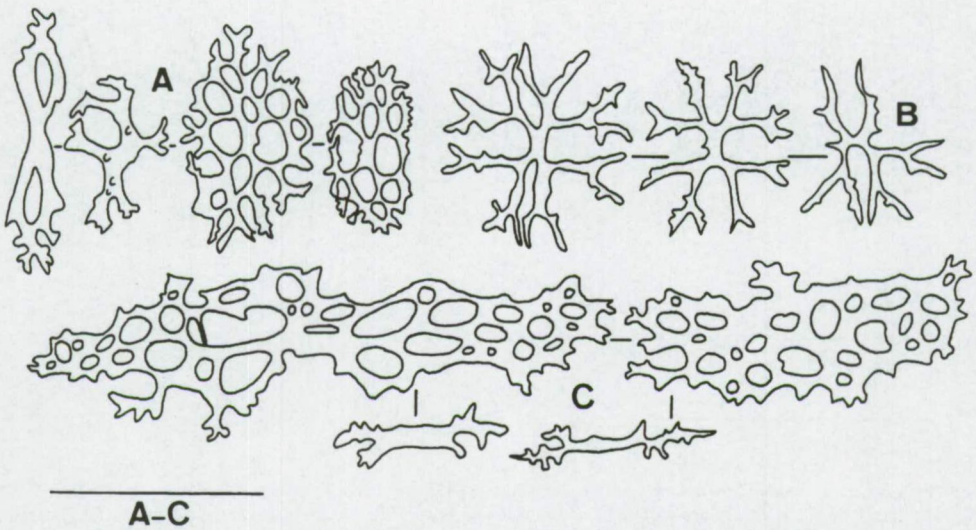


Figure 39. *Thelenota anax* H.L. Clark, 1921. (A) Rods and perforated plates of tentacles; (B) Rods of body wall; (C) Rods and perforated plates of ventral tube feet. Scale bar A-C represents 100 µm.

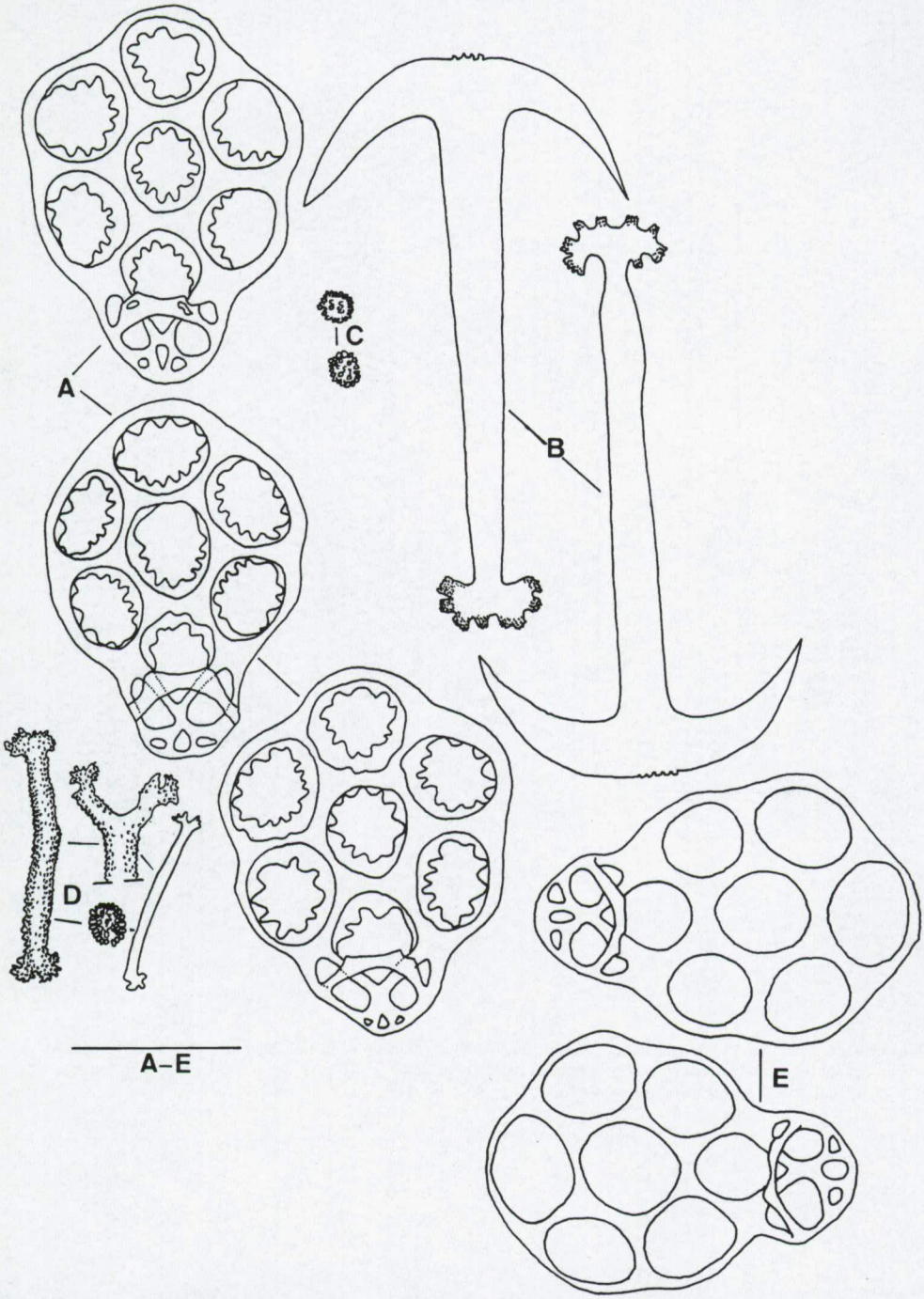


Figure 40. *Euapta godeffroyi* (SEMPER, 1868). (A) Anchor-plates with serrated holes of body wall; (B) Anchors of body wall; (C) Miliary granules of body wall; (D) Rods and miliary granule of tentacles; (E) Anchor-plates with smooth holes of body wall. Scale bar A-E represents 100 μm.

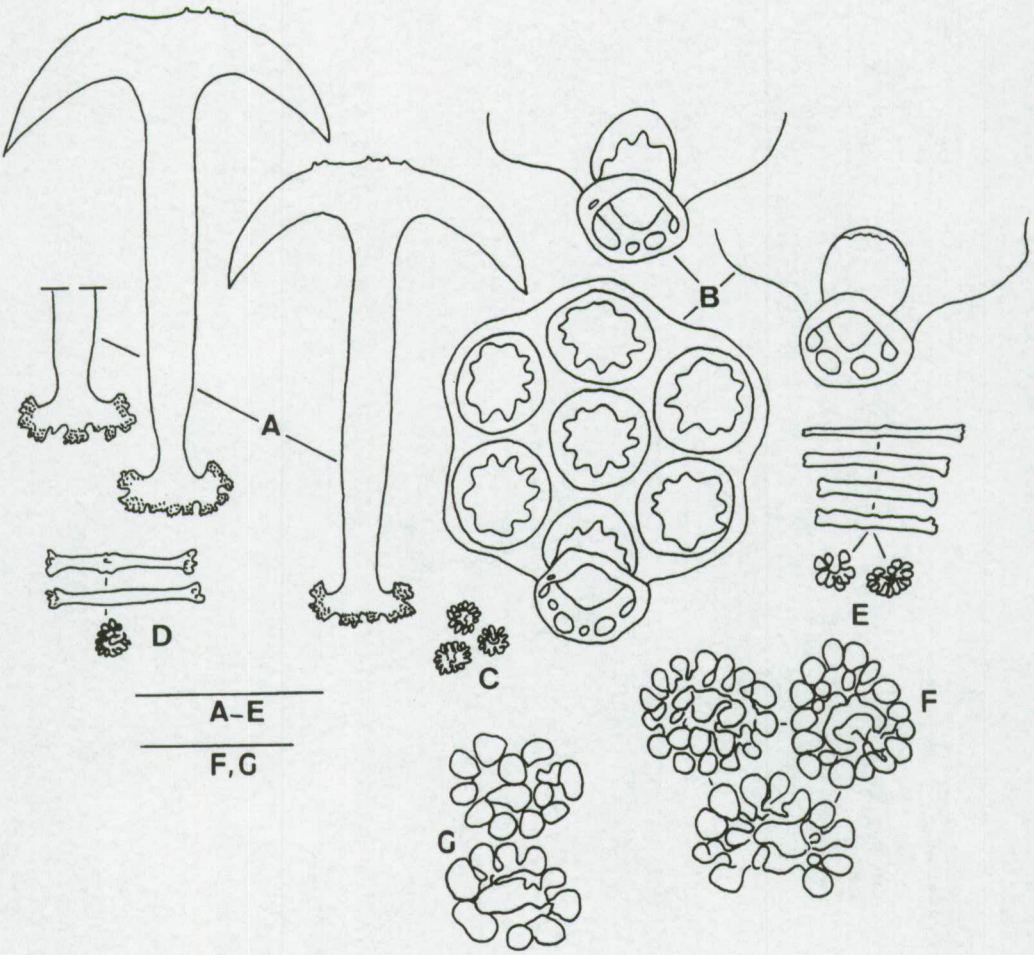


Figure 41. *Opheodesoma glabra* (SEMPER, 1868). (A) Anchors of body wall; (B) Anchor-plates of body wall; (C & F) Miliary granules of body wall; (D & G) Miliary granule and rods of tentacle; (E & G) Milary granules and rods of oral disc. Scale bar A-E represents 100 µm; scale bar F, G represents 20 µm.

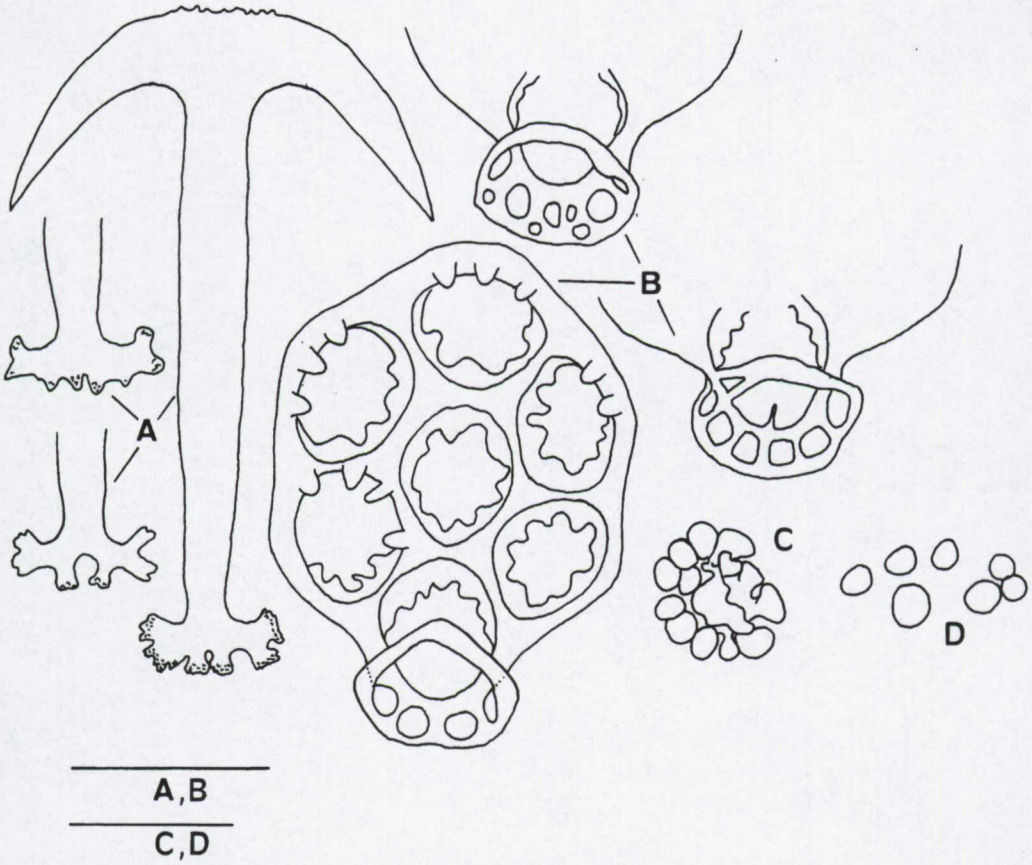


Figure 42. *Opheodesoma grisea* (SEMPER, 1868). (A) Anchor of body wall; (B) Anchor-plates of body wall; (C) Miliary granule of body wall, (D) Fragmented miliary granules of tentacles. Scale bar A & B represents 100 µm; scale bar D, E represents 20 µm.

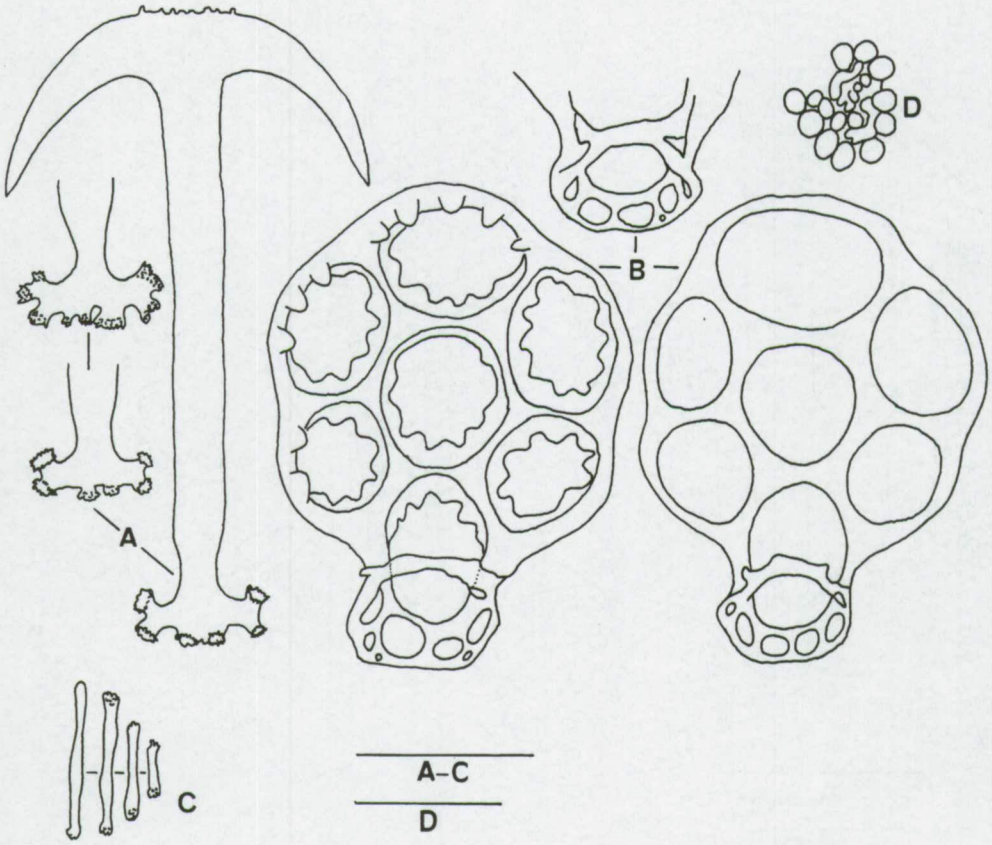


Figure 43. *Opheodesoma* cf. *mauritiae* HEDING, 1928. (A) Anchors of body wall; (B) Anchor-plates of body wall; (C) Rods of oral disc; (D) Miliary granule of tentacles. Scale bar A-C represents 100 µm; scale bar D represents 20 µm.

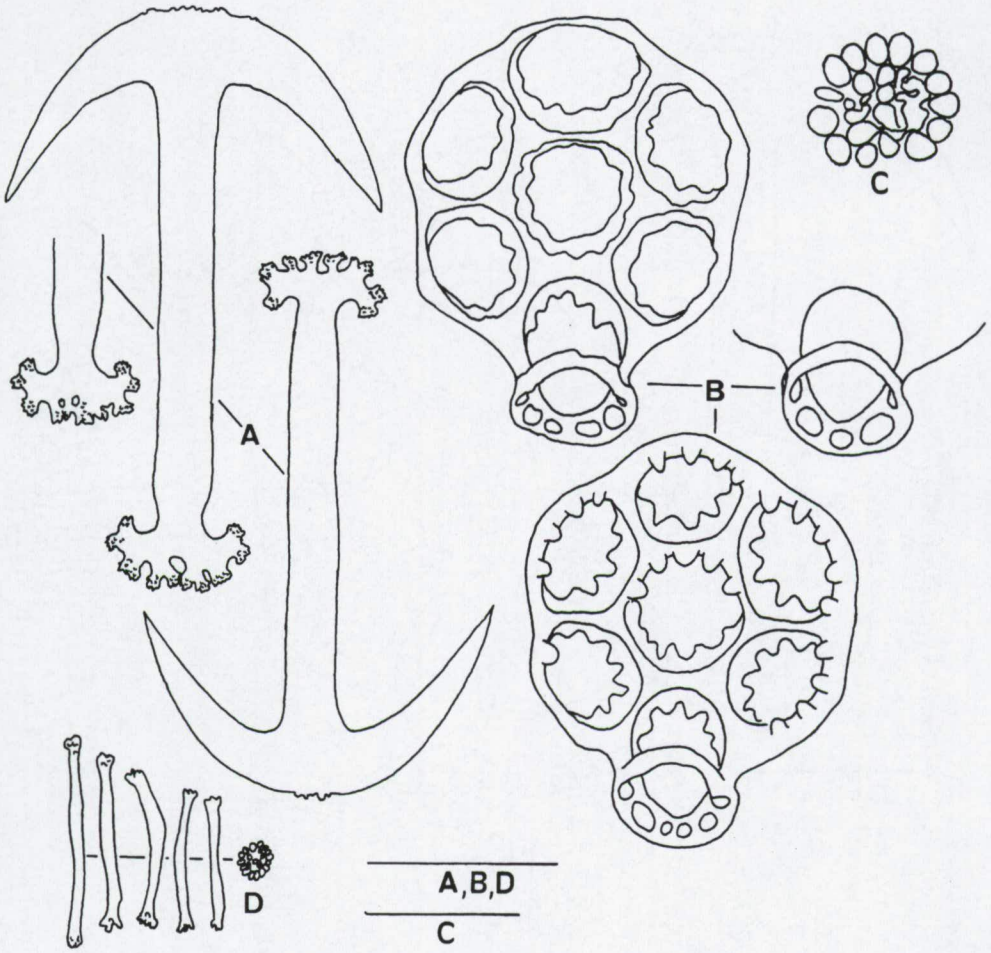


Figure 44. *Opheodesoma* cf. *mauritiae* HEDING, 1928. (A) Anchors of body wall; (B) Anchor-plates of body wall; (C) Miliary granules of body wall; (D) Miliary granules and rods of tentacles and oral dis(C) Scale bar A, B, D represents 100 µm; scale bar C represents 20 µm.

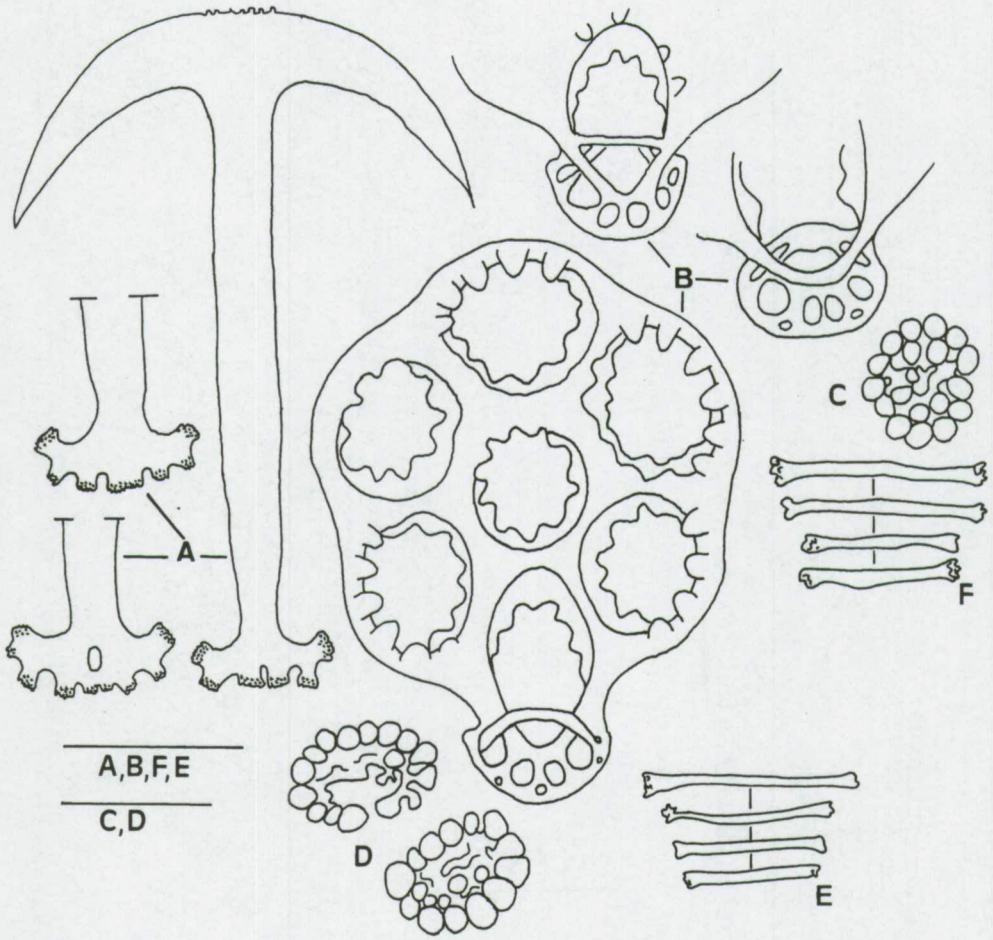


Figure 45. *Opheodesoma* sp. (A) Anchors of body wall; (B) Anchor-plates of body wall; (C) Miliary granule of body wall; (D) Miliary granule of tentacle; (E) Rods of tentacle; (F) Rods of oral disc. Scale bar A, B, F, E represents 100 μm; scale bar C, D represents 20 μm.

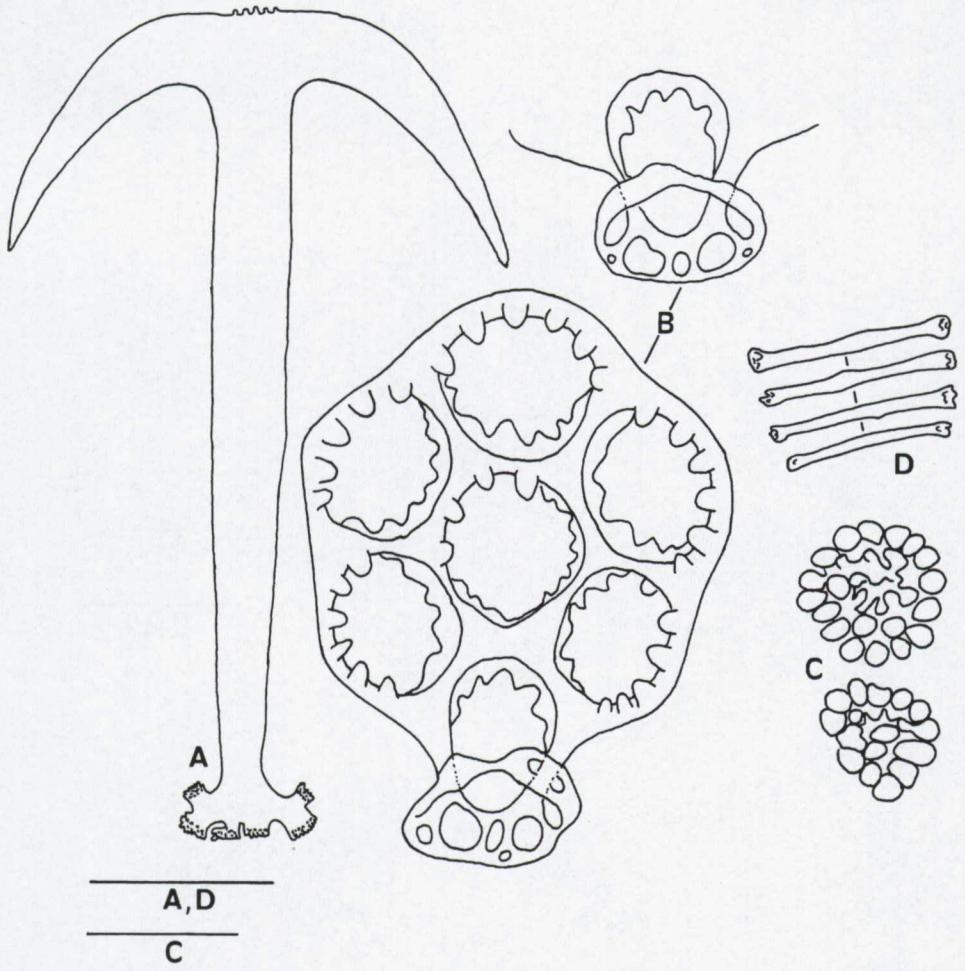


Figure 46. *Opheodesoma spectabilis* FISHER, 1907. (A) Anchor of body wall; (B) Anchor-plate of body wall; (C) Miliary granule of tentacle; (D) Rods of oral disc. Scale bar A, B, D represents 100 µm; scale bar C represents 20 µm.

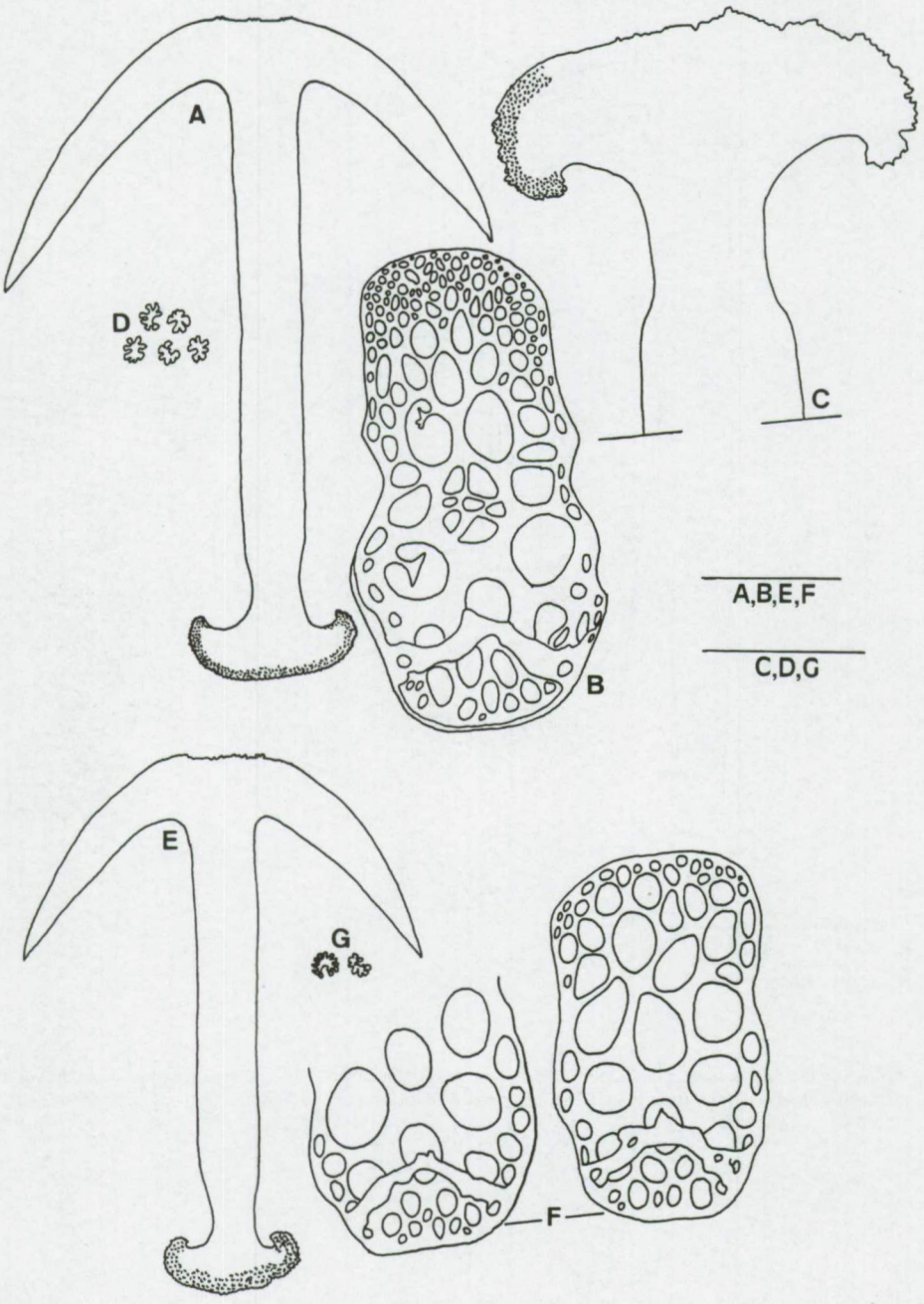


Figure 47. *Synapta maculata* (CHAMISSO & EYSENHARDT, 1821). (A) Anchor of body wall (L=600mm); (B) Anchor-plate of body wall (L=600mm); (C) Detail of stock of anchor (L=600mm); (D) Miliary granules of body wall (L=600mm); (E) Anchor of body wall (L=87mm); (F) Anchor-plates of body wall (L=87 mm); (G) Miliary granules of body wall (L=87 mm). Scale bar A, B, E, F represents 200 µm; scale bar C, D, G represents 100 µm.

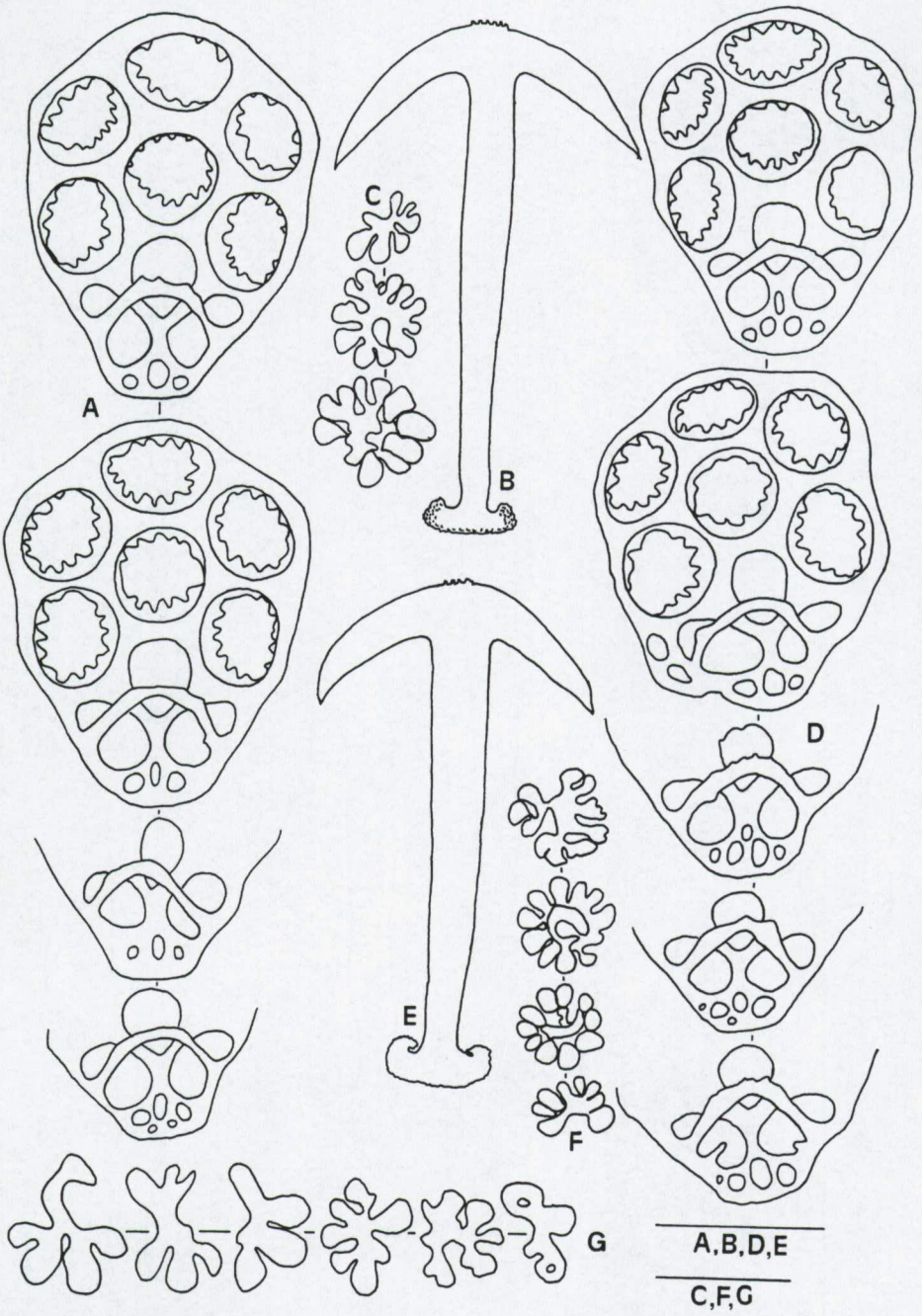


Figure 48. *Synaptula recta* (SEMPER, 1868). (A) Anchor-plates of posterior body wall; (B) Anchor of posterior body wall; (C) Miliary granules of posterior body wall; (D) Anchor-plates of anterior body wall; (E) Anchor of anterior body wall; (F) Miliary granules of anterior body wall; (G) Miliary granules of tentacles. Scale bar A, B, D represents 100 μm; scale bar C, F, G represents 50 μm.

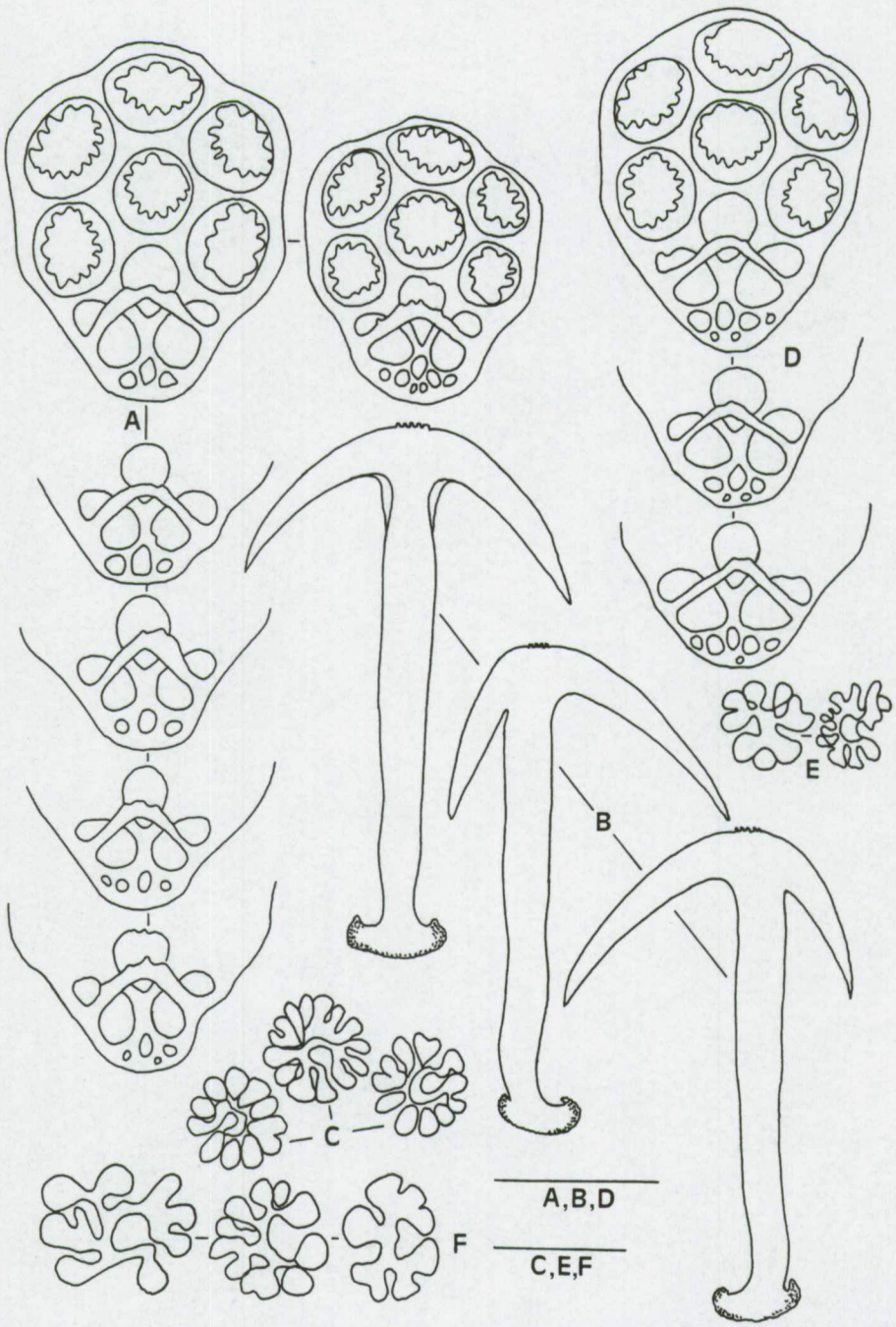


Figure 50. *Synaptula* cf. *recta* (SEMPER, 1868). (A) Anchor-plates of posterior body wall; (B) Anchors of posterior body wall; (C) Miliary granules of posterior body wall; (D) Anchor-plates of anterior body wall; (E) Miliary granules of anterior body wall; (F) Miliary granules of tentacle. Scale bar A, B, D represents 100 μm; scale bar C, E, F represents 50 μm.

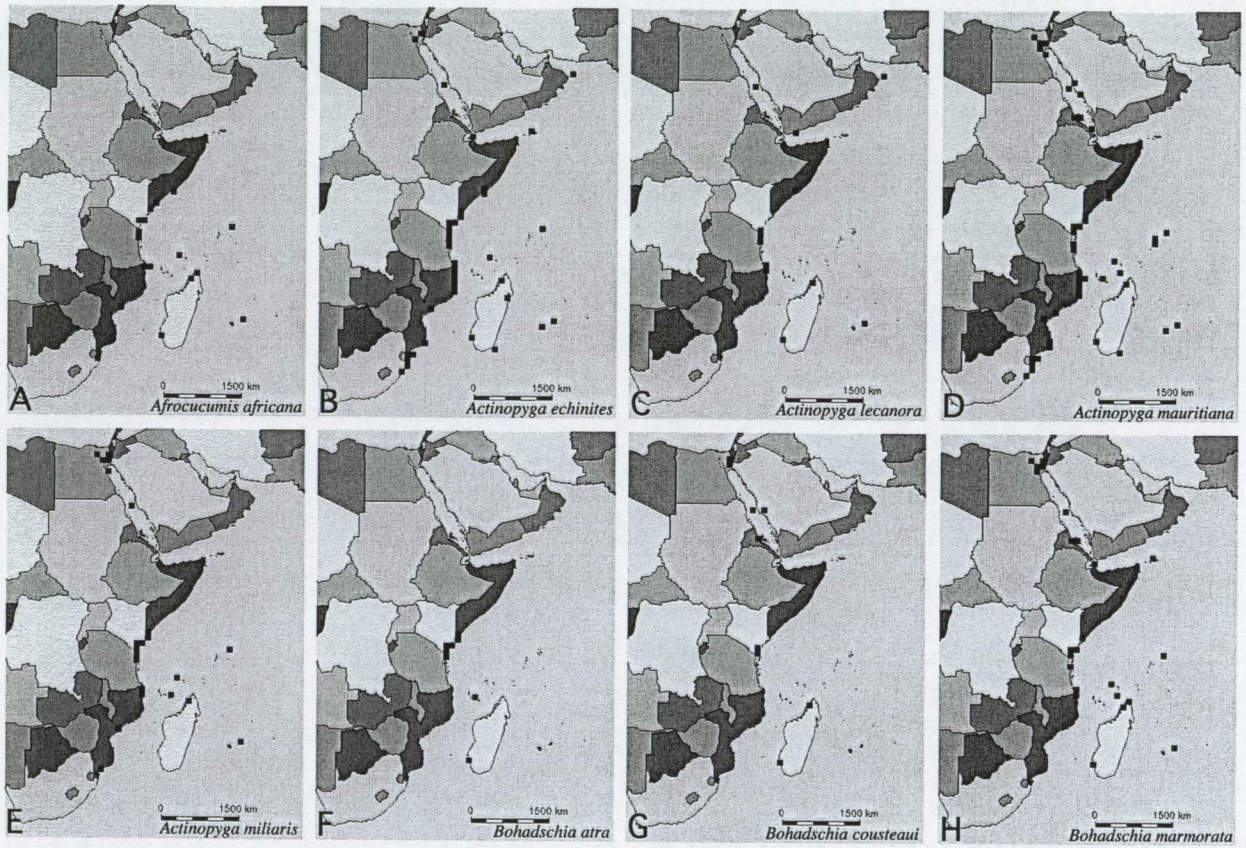


Figure 51. WIO distribution of shallow-water holothurians known from Kenya and/or Pemba Island. (A) *Afrocucumis africana* (SEMPER, 1868); (B) *Actinopyga echinites* (JAEGER, 1833); (C) *Actinopyga lecanora* (JAEGER, 1833); (D) *Actinopyga mauritiana* (QUOY & GAIMARD, 1833); (E) *Actinopyga miliaris* (QUOY & GAIMARD, 1833); (F) *Bohadschia atra* MASSIN, RASOLOFONIRINA, CONAND & SAMYN, 1999; (G) *Bohadschia cousteaui* CHERBONNIER, 1954; (H) *Bohadschia marmorata* (JAEGER, 1833).

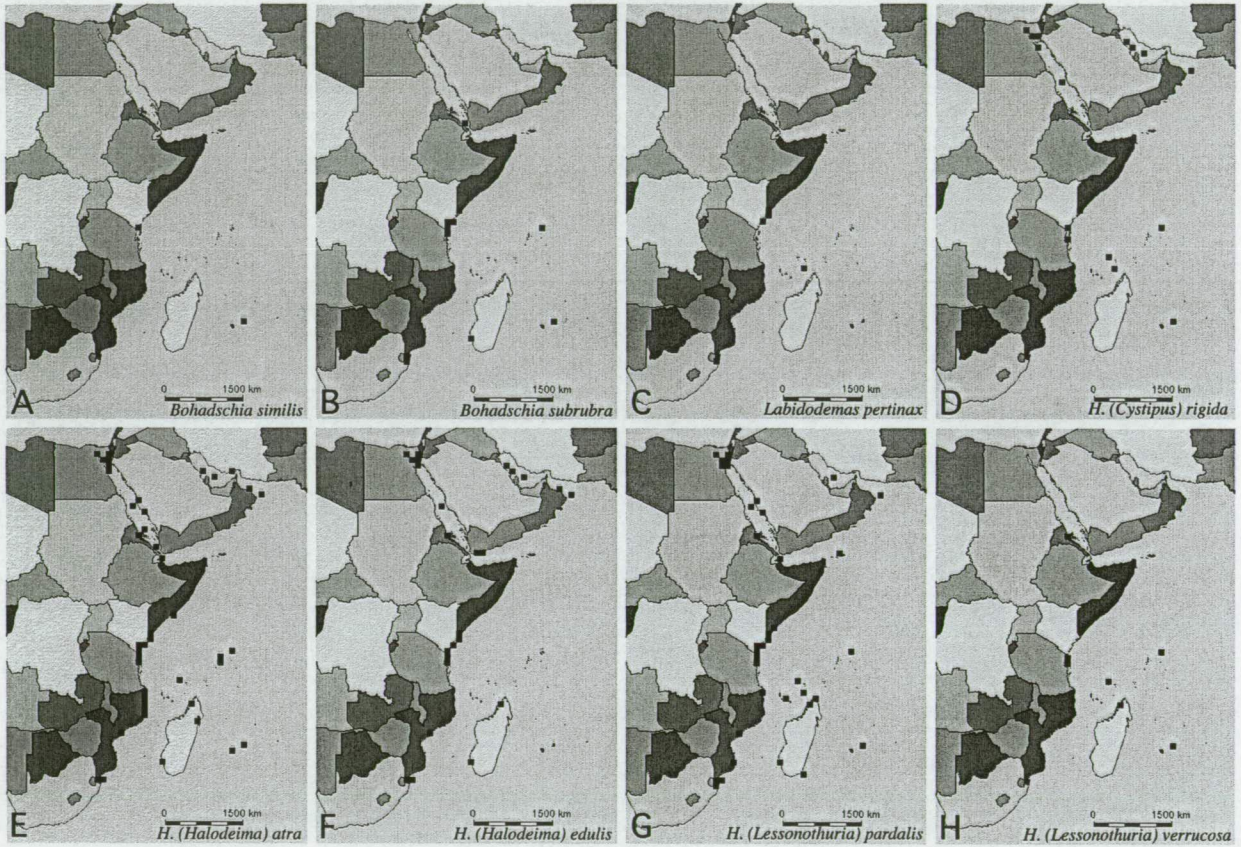


Figure 52. WIO distribution of shallow-water holothurians from Kenya and/or Pemba Island. (A) *Bohadschia* cf. *similis* (SEMPER, 1868); (B) *Bohadschia subrubra* (QUOY & GAIMARD, 1833); (C) *Labidodemas pertinax* (LUDWIG, 1875); (D) *Holothuria (Cystipus) rigida* (SELENKA, 1867); (E) *Holothuria (Halodeima) atra* JAEGER, 1833; (F) *Holothuria (Halodeima) edulis* LESSON, 1830; (G) *Holothuria (Lessonothuria) pardalis* SELENKA, 1867; (H) *Holothuria (Lessonothuria) verrucosa* SELENKA, 1867.

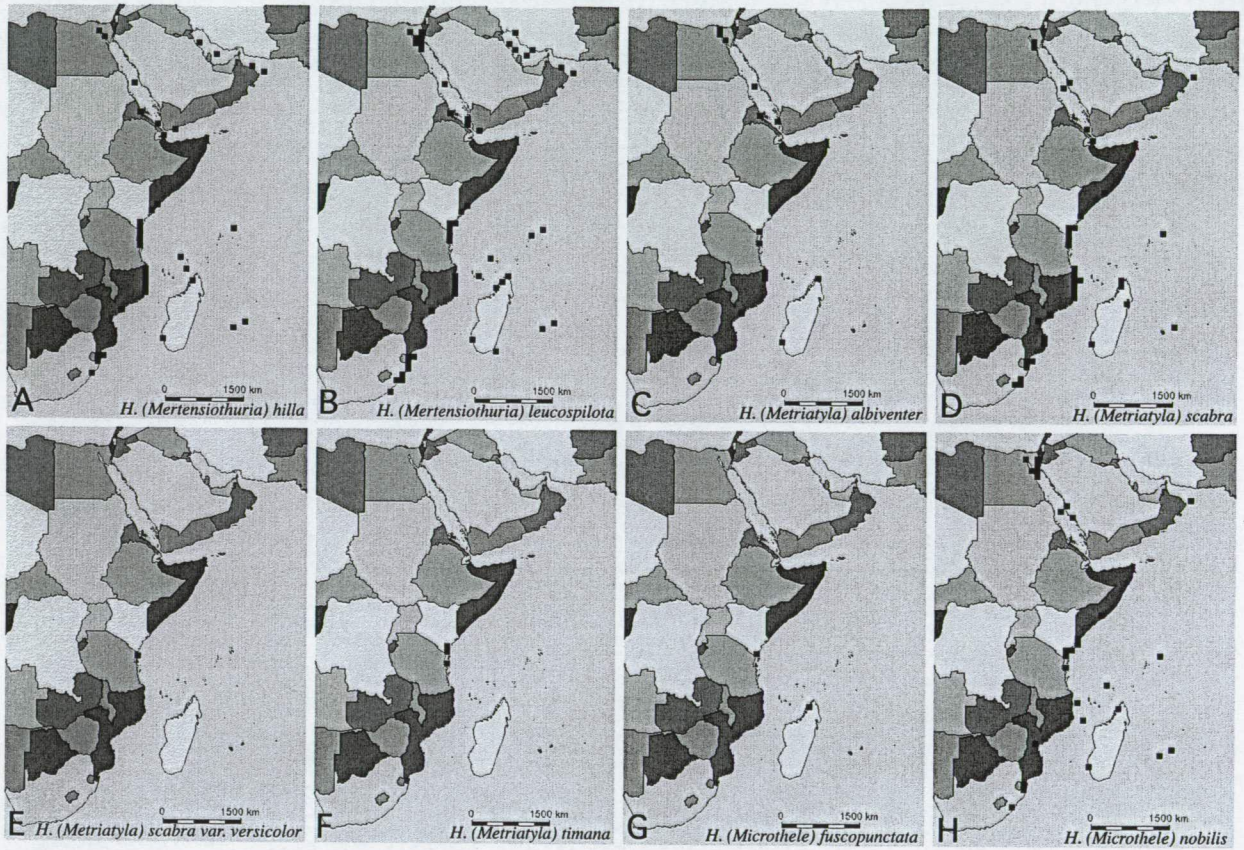


Figure 53. WIO distribution of shallow-water holothurians from Kenya and/or Pemba Island. (A) *Holothuria (Mertensiothuria) hilla* LESSON, 1830; (B) *Holothuria (Mertensiothuria) leucospilota* (BRANDT, 1835); (C) *Holothuria (Metriatyla) albiventer* SEMPER, 1868; (D) *Holothuria (Metriatyla) scabra* JAEGER, 1833; (E) *Holothuria (Metriatyla) scabra* var. *versicolor* (Conand, 1986); (F) *Holothuria (Metriatyla) timana* LESSON, 1830; (G) *Holothuria (Microthele) fuscopunctata* JAEGER, 1833; (H) *Holothuria (Microthele) nobilis* (SELENKA, 1867).

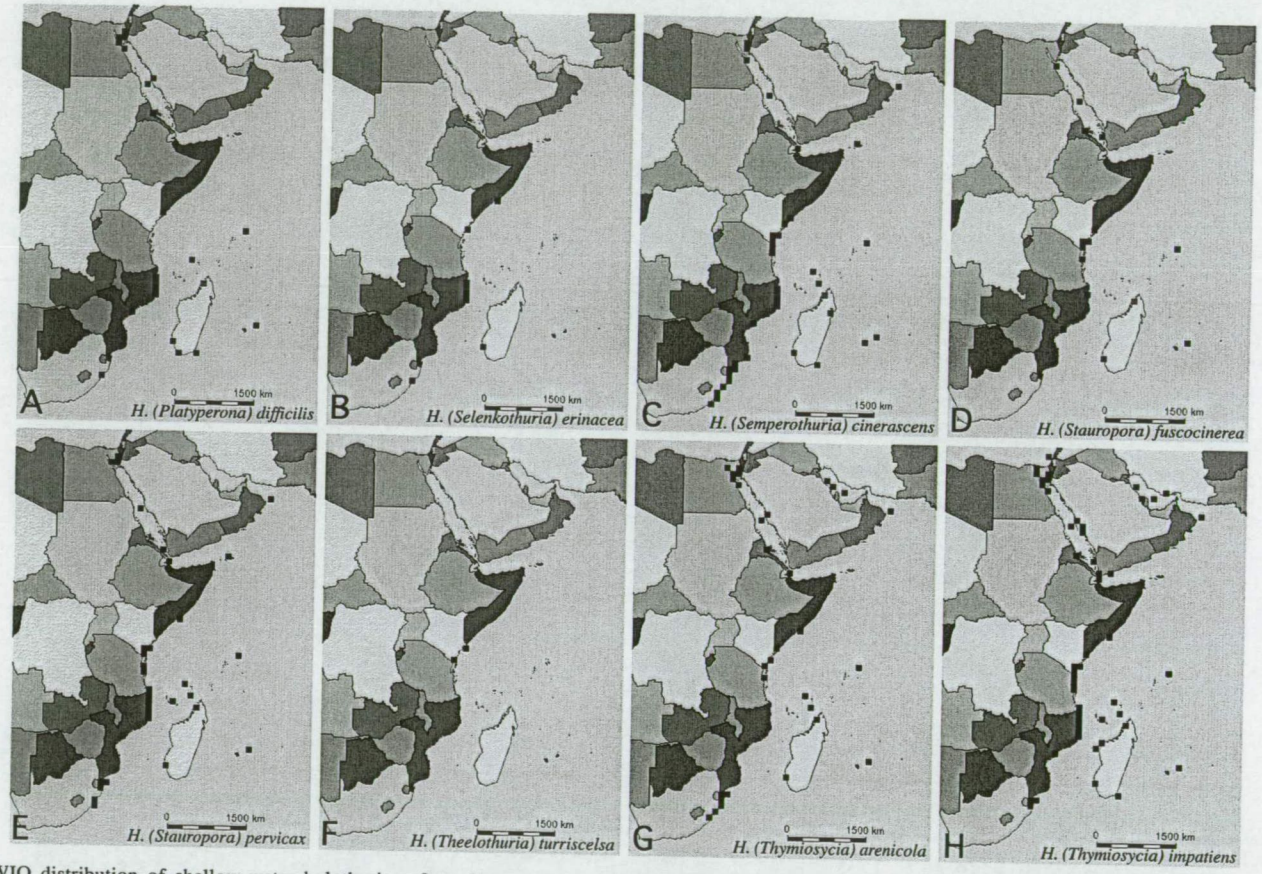


Figure 54. WIO distribution of shallow-water holothurians from Kenya and/or Pemba Island. (A) *Holothuria (Platyperona) difficilis* SEMPER, 1868; (B) *Holothuria (Selenkothuria) erinacea* SEMPER, 1868; (C) *Holothuria (Semperothuria) cinerascens* (BRANDT, 1835); (D) *Holothuria (Stauropora) fuscocinerea* JAEGER, 1833; (E) *Holothuria (Stauropora) pervicax* SELENKA, 1867); (F) *Holothuria (Theelothuria) turriscelsa* CHERBONNIER, 1980; (G). *Holothuria (Thymiosycia) arenicola* SEMPER, 1868; (H) *Holothuria (Thymiosycia) impatiens* (FORSKÅL, 1775).

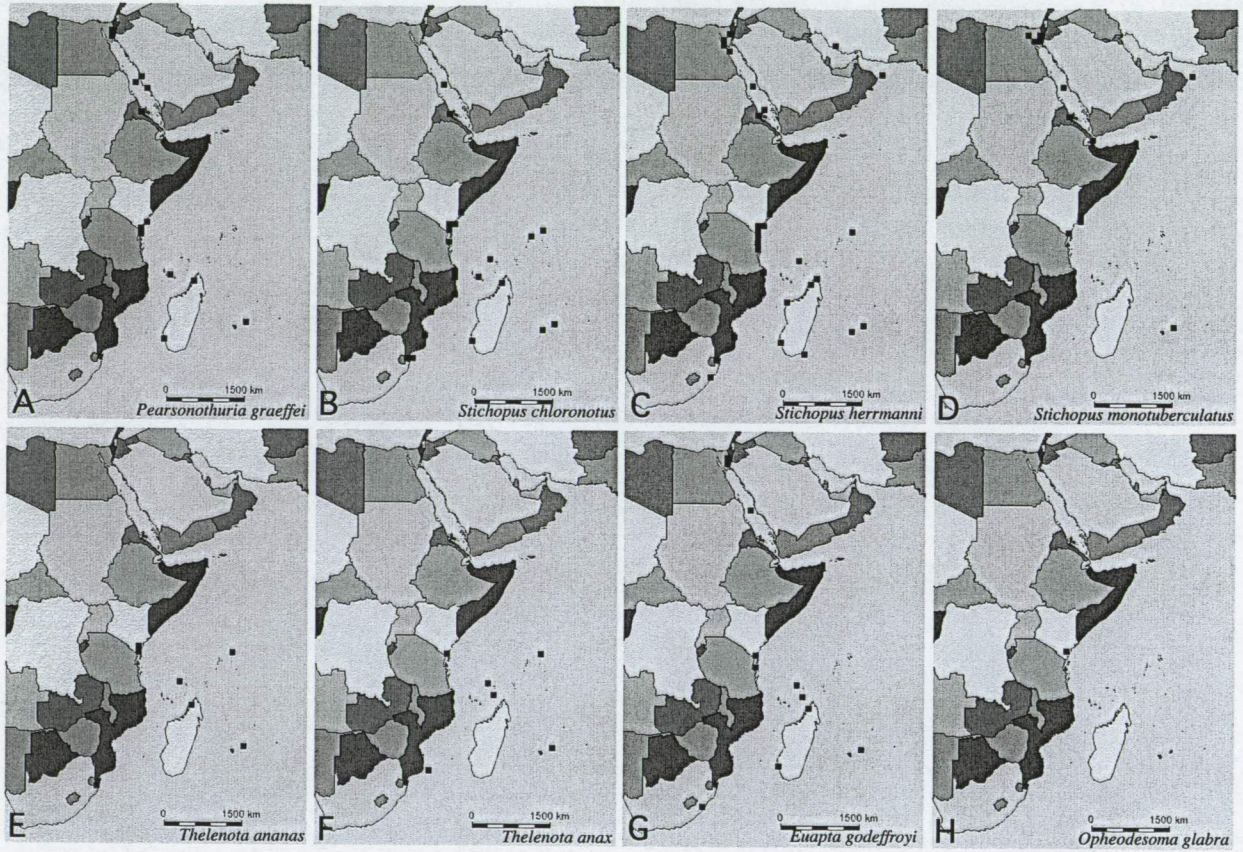


Figure 55. WIO distribution of shallow-water holothurians from Kenya and/or Pemba Island. (A) *Pearsonothuria graeffei* (SEMPER, 1868); (B) *Stichopus chloronotus* BRANDT, 1835; (C) *Stichopus herrmanni* SEMPER, 1868; (D) *Stichopus* cf. *monotuberculatus* (QUOY & GAIMARD, 1833); (E) *Thelenota ananas* (JAEGER, 1833); (F) *Thelenota anax* H.L. CLARK, 1921; (G) *Euapta godeffroyi* (SEMPER, 1868); (H) *Opheodesoma glabra* (SEMPER, 1868).

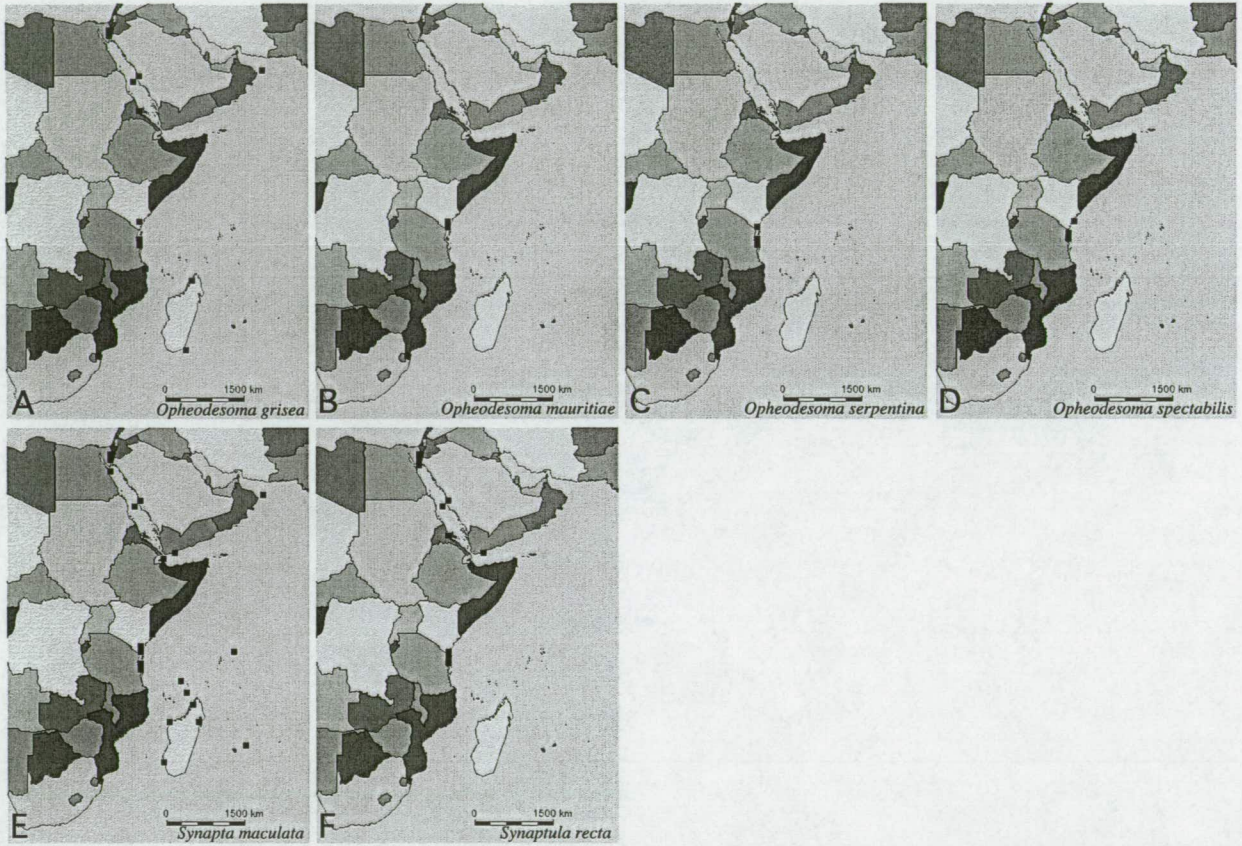


Figure 56. WIO distribution of shallow-water holothurians from Kenya and/or Pemba Island. (A) *Opheodesoma grisea* (SEMPER, 1868); (B) *Opheodesoma mauritiae* HEDING, 1928; (C) *Opheodesoma* cf. *serpentina* (J. MÜLLER, 1850); (D) *Opheodesoma spectabilis* FISHER, 1907; (E) *Synapta maculata* (CHAMISSO & EYSENHARDT, 1821); (F) *Synaptula recta* (SEMPER, 1868)

Plate 1

A. Ventral view of *Actinopyga echinites* (JAEGER, 1833).

B. *In situ* dorsal view of *Actinopyga echinites* (JAEGER, 1833), arrow on inset picture shows the Cuvierian tubules.

C. *In situ* dorsal view of *Actinopyga mauritiana* (QUOY & GAIMARD, 1833).

D. Ventral view of *Actinopyga mauritiana* (QUOY & GAIMARD, 1833).

E. Dorso-terminal view of *Actinopyga miliaris* (QUOY & GAIMARD, 1833).

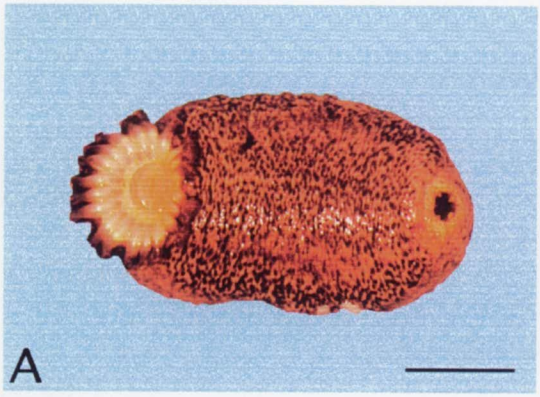
F. Dorsal view of *Bohadschia atra* MASSIN, RASOLOFONIRINA, CONAND & SAMYN, 1999.

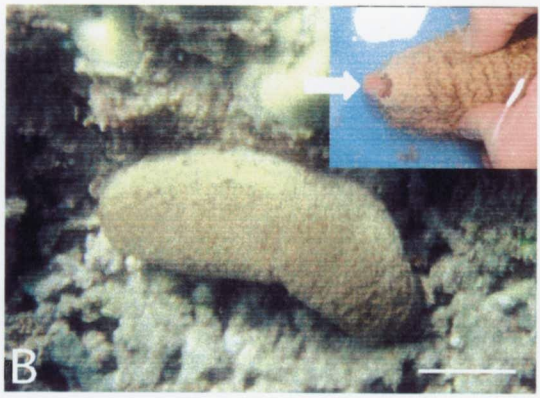
G. Dorsal view of *Bohadschia cousteaui* CHERBONNIER, 1954.

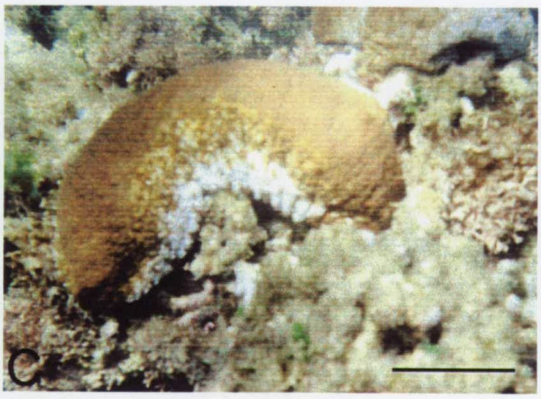
H. Dorsal view of *Bohadschia marmorata* (JAEGER, 1833).

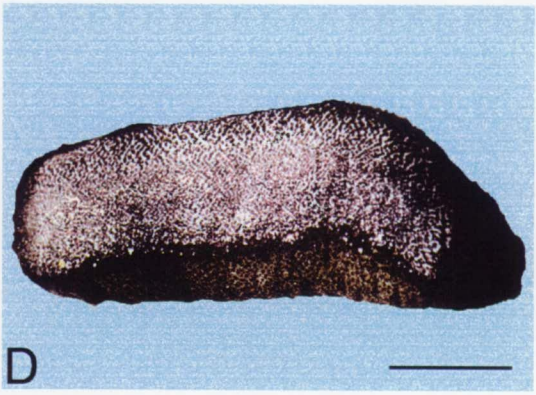
Scale bar A-D, G & H = 5 cm; E = 3 cm; F = 10 cm. All pictures by the author.

Plate 1

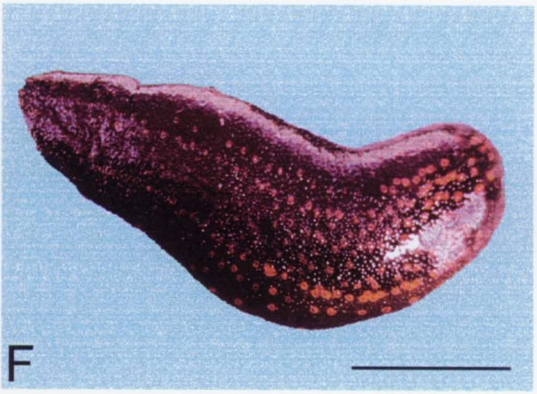


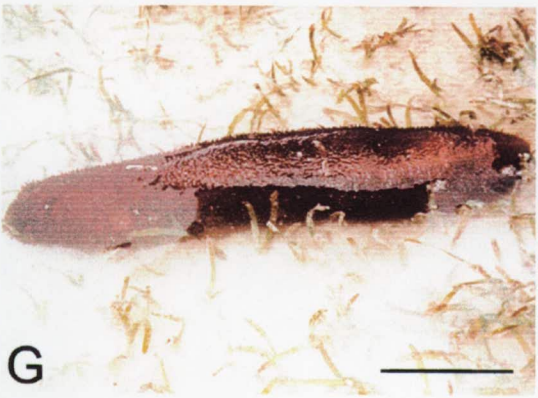












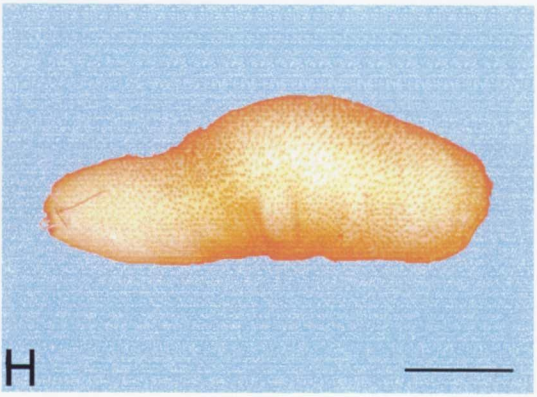


Plate 2

A. Dorsal view of *Bohadschia* cf. *similis* (SEMPER, 1868).

B. Lateral view of *Bohadschia subrubra* (QUOY & GAIMARD, 1833); top left inset picture shows the animal in situ, the anus with surrounding papillae and the pontoniid commensal shrimp *Periclimenes imperator* BRUCE, 1967.

C. Dorsal view of *Holothuria (Cystipus) rigida* (SELENKA, 1867).

D. Ventral view of *Holothuria (Cystipus)* cf. *rigida* (SELENKA, 1867).

E. Dorsal view of *H. (H.) atra* JAEGER, 1833.

F. Dorsal *in situ* view of *Holothuria (Halodeima) edulis* LESSON, 1830.

G. Dorsal view of *Holothuria (Lessonothuria) pardalis* SELENKA, 1867.

H. Dorsal view of *Holothuria (Metriatyla) albiventer* SEMPER, 1868.

Scale bar A, B, E, F & G = 5 cm; C, D & H = 2 cm. All pictures by the author.

Plate 2

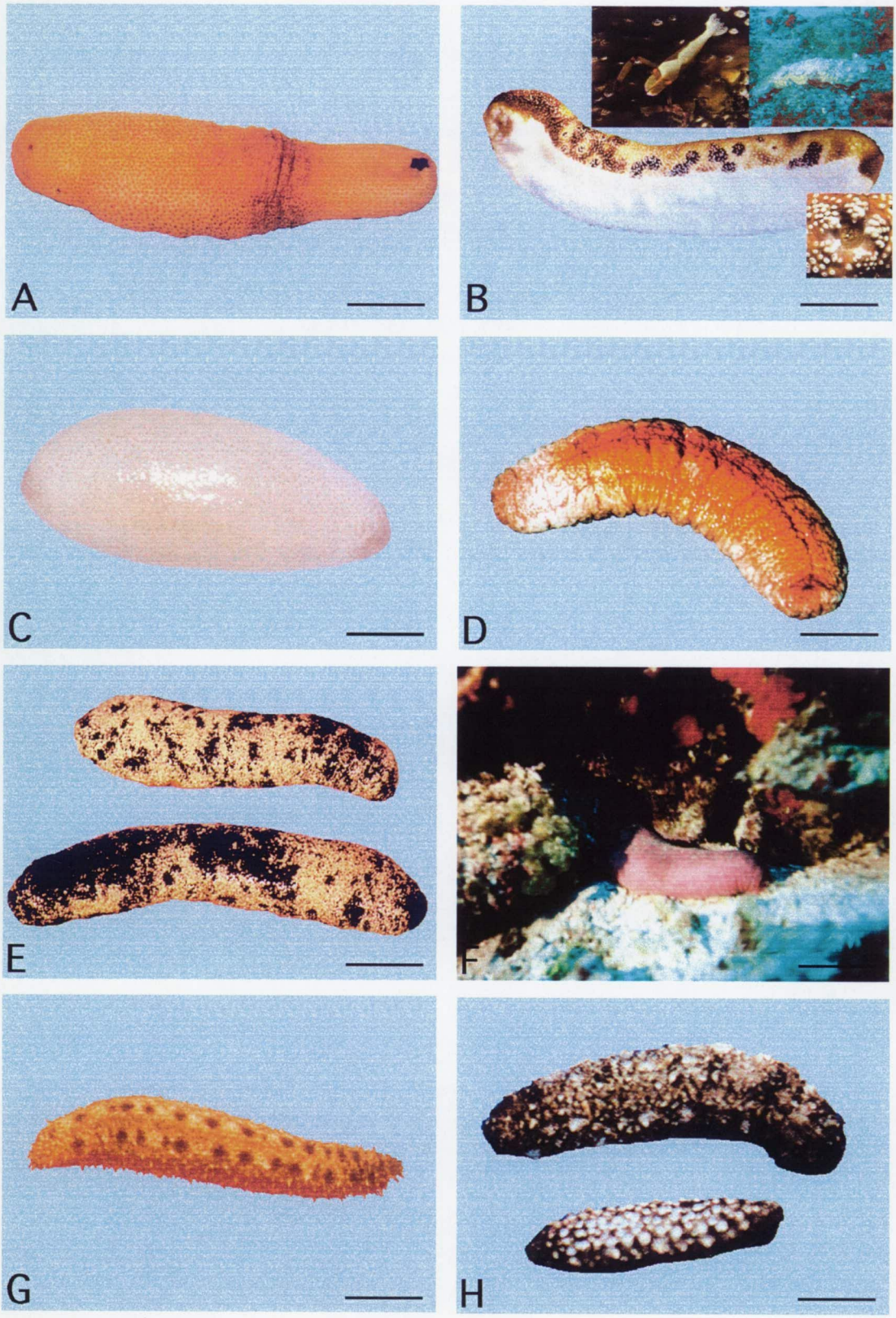


Plate 3

A. Dorsal view of *Holothuria (Metriatyla) scabra* JAEGER, 1833.

B. Dorsal view of *Holothuria (Metriatyla) timana* LESSON, 1830.

C. Dorsal view of *Holothuria (Microthele) fuscopunctata* JAEGER, 1833.

D. Dorsal view of *Holothuria (Microthele) nobilis* (SELENKA, 1867), inset picture shows the species *in situ*.

E. Dorsal view of *Holothuria (Semperothuria) cinerascens* (BRANDT, 1835).

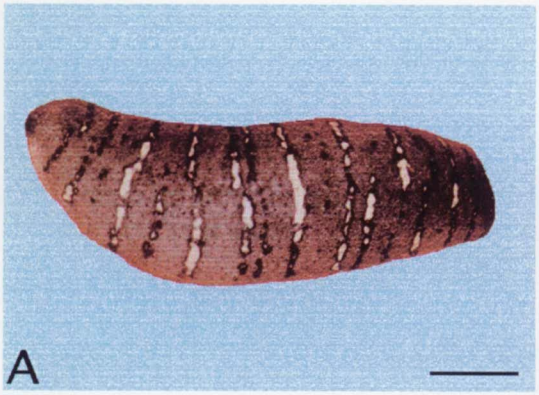
F. Dorsal view of *Holothuria (Stauropora) pervicax* SELENKA, 1867.

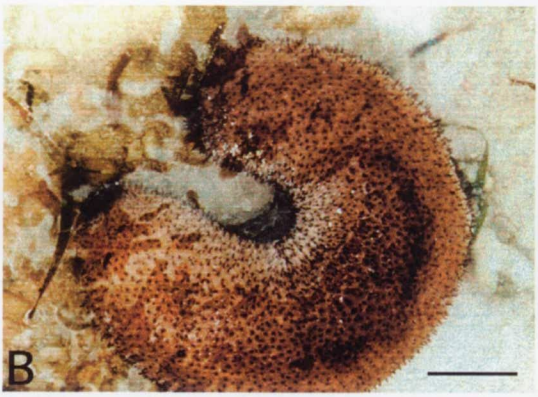
G. Dorsal view of *Holothuria (Thymiosycia) impatiens* (Forskål, 1775).

H. *Pearsonothuria graeffei* (SEMPER, 1868) grazing on mucus of live hard coral.

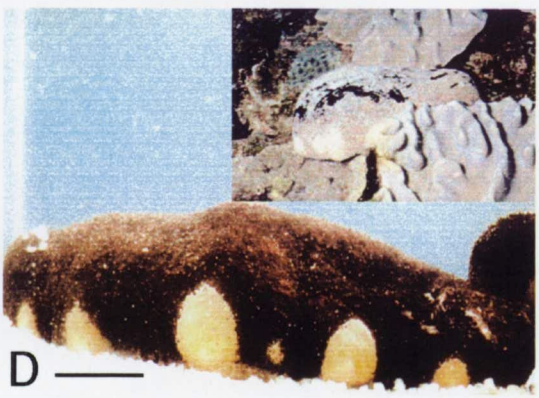
Scale bar A, B, H = 5 cm; C, D, G = 7 cm; E, F = 3 cm. All pictures by author, except inset with D and H by B. Van Bogaert.

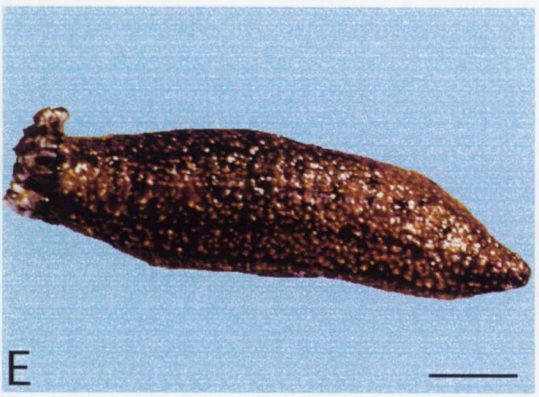
Plate 3

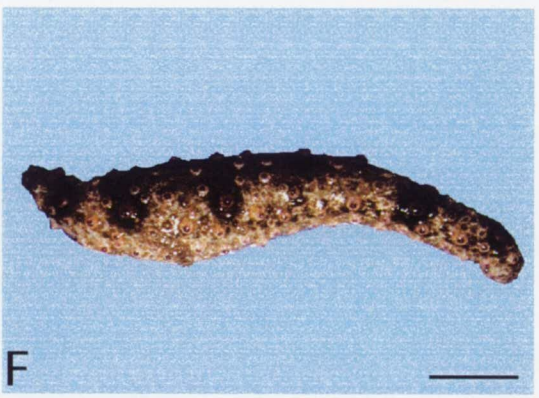














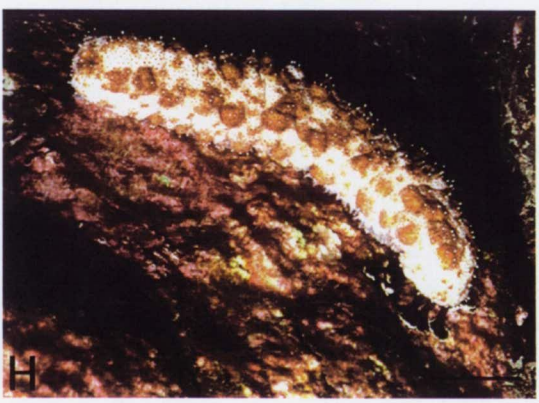


Plate 4

A. *Stichopus chloronotus* BRANDT, 1835.

B. *In situ* dorsal view of *Stichopus herrmanni* SEMPER, 1868.

C. Dorsal view of *Stichopus* cf. *monotuberculatus* (QUOY & GAIMARD, 1833).

D. *In situ* dorsal view of *Thelenota ananas* (JAEGER, 1833).

E. *In situ* dorsal view of *Thelenota anax* H.L. CLARK, 1921.

F. View of *Opheodesoma mauritiae* HEDING, 1928.

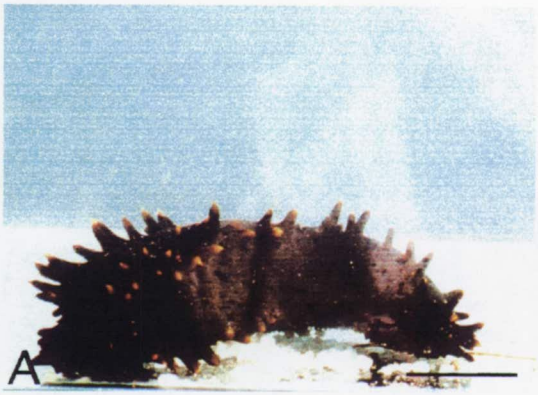
G. View of *Opheodesoma* sp. (J.MÜLLER, 1850).

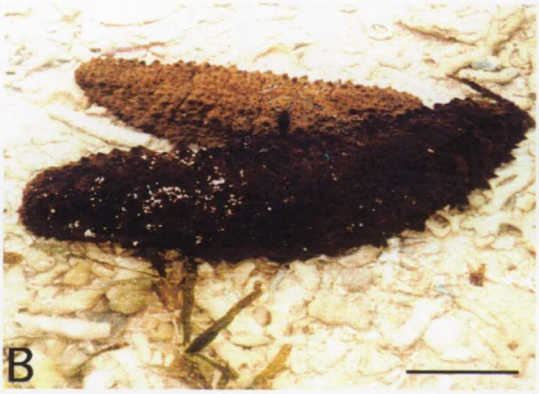
H. View of *Synaptula recta* (SEMPER, 1868).

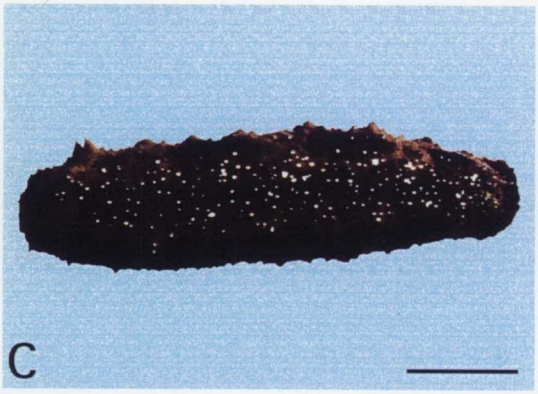
I. View of *Synaptulai cf. recta* (SEMPER, 1868).

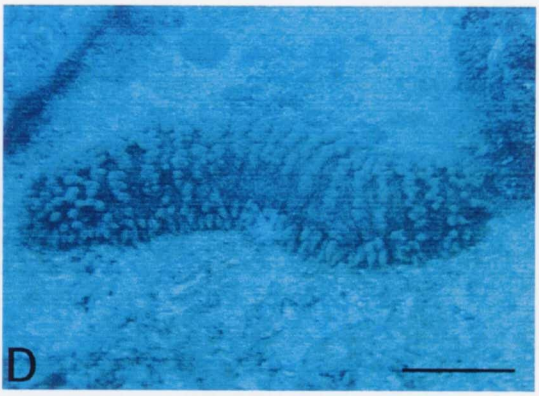
Scale bar A-C = 5 cm; D = 8 cm; E = 10 cm; F-J = 3 cm. All pictures by the author except D and E by B. Van Bogaert.

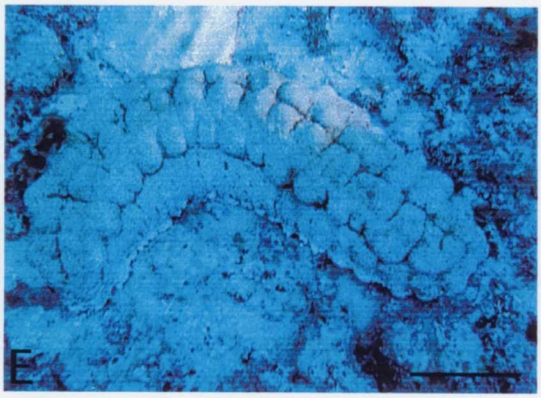
Plate 4



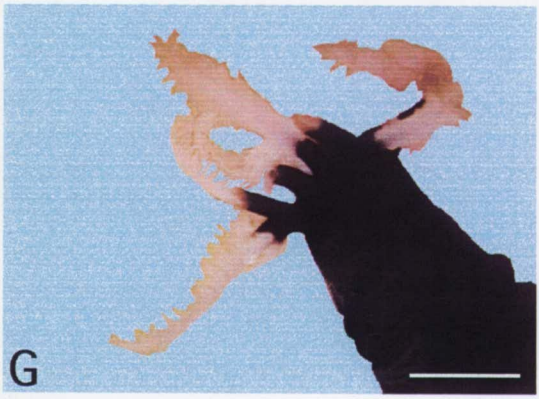
















Chapter Six

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Towards an understanding of the shallow-water echinoderm biodiversity of KwaZulu-Natal, Republic of South Africa

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ABSTRACT

Prior to this study, 130 shallow-water (*i.e.* less then 50 m deep) species of echinoderms were reported from the subtropical (26°S/32°E - 30°S/30°E) east coast of South Africa. The Indo-Pacific and the endemic components of this fauna made up 93 % of the species, while the circumtropical, the Atlantic and the cosmopolitan components represented only 7 % of the echinoderm fauna. A current study in the KwaZulu-Natal province has added some 39 % of new records (excluding the Crinoidea) to the echinoderm fauna of this province, changing its endemic component from 26 to 21 %, the Indo-Pacific component from 68 to 73 % with the other components remaining more or less stable. Total echinoderm species distribution of KwaZulu-Natal was analyzed with the second Kulczynski coefficient, a measurement of similarity between two bioassociational areas. This analysis reveals that while the faunistic components of KwaZulu-Natal seem rather homogeneous, the area in the region of St. Lucia Bay appears to be characterized by a high species turn-over.

Introduction

The province of KwaZulu-Natal, on the east coast of South Africa, is well known to harbour a mixture of tropical, subtropical and southern African endemic echinoderms. An understanding of this southern african marine region is of paramount importance in allowing us to determine the southern extent of the tropical province further north, the structure of the general Indo-West Pacific region, the origin of the southern African marine fauna, the development of a secondary evolutionary area in the shallow West Indian Ocean, and the transition between the southern African subtropical province and the warm temperate province further south.

Despite several comprehensive efforts by various workers (H.L. Clark 1923; Mortensen 1933, Deichmann 1948; Cherbonnier 1952; Clark & Courtman-Stock 1976 and Thandar 1989a), it is regrettable that the southern African echinoderm biodiversity and biogeography remain poorly investigated. Clark & Courtman-Stock's (1976) authoritative guide compiled all the available information for the echinoderms of southern Africa (excluding the holothuroids), while the zoogeographic paper by Thandar (1989a) summarised this effort with inclusion of the Holothuroidea and A.M. Clark's (1977) further additions to the fauna. Thandar (1989a) recorded no less then 407 species of echinoderms in the waters (both shallow and deep) south of the tropic of Capricorn. These comprised 17 crinoids, 99 asteroids, 124 ophiuroids, 59 echinoids and 108 holothuroids. The distribution pattern of continental shelf species (those occurring in waters less than 200 meters deep) obtained from this dataset, largely supported the division of Day (1967) in recognizing four more or less discrete faunistic provinces in the southern Africa marine region. These are: (1) the tropical Mozambique-Madagascar Province reaching Delagoa Bay; (2) the warm subtropical Natal Province south of Delagoa Bay to Bashee River; (3) the temperate Cape-South West African Province south of Port St. Johns to Walvis Bay; and (4) the CapeSouth West African Province north of Walvis Bay.

The main aim of the current investigation was to re-evaluate the echinoderm biodiversity of southern Africa by *de novo* collections of shallow-water (*i.e.* not deeper than 50 m) echinoderms along the poorly investigated coastline of KwaZulu-Natal. The results of this effort not only yielded significant new insights into the taxonomy and systematics of the echinoderms (mainly in the Holothuroidea, Samyn & Massin in press; Massin *et al.* in prep.), but also allowed re-evaluation of the hypothesis that KwaZulu-Natal is an important transitional zone between the tropical Indian Ocean and the cooler temperate South African south

coast (Thandar 1989a). In this context, different latitude and longitude squares of one degree were compared with each other using the second Kulczynski coefficient, which measures the percentage similarity between two bioassociational areas (Price 1982). The second Kulczynski coefficient (KC) is given by the following formula:

$$KC = 1/2[s/(s+u)+s/(s+v)]x100$$

where s is the number of species common to area A and area B; u is the number of species found in area A and absent from area B and, v is the number of species found in area B but absent in area A. This index of similarity has the advantage that it takes into account the disproportionate number of species reported from the different areas (Price 1982).
The Crinoidea resulting from these collections are not included since they still need to be identified.

Study region

The area considered in the present study is the warm subtropical KwaZulu-Natal Province on the north-east coast of South Africa, stretching from the southern border of Mozambique, just north of Kosi Bay, to Port Edward (Fig. 1). Sampling was done from Bhanga Nek to Palm Beach.

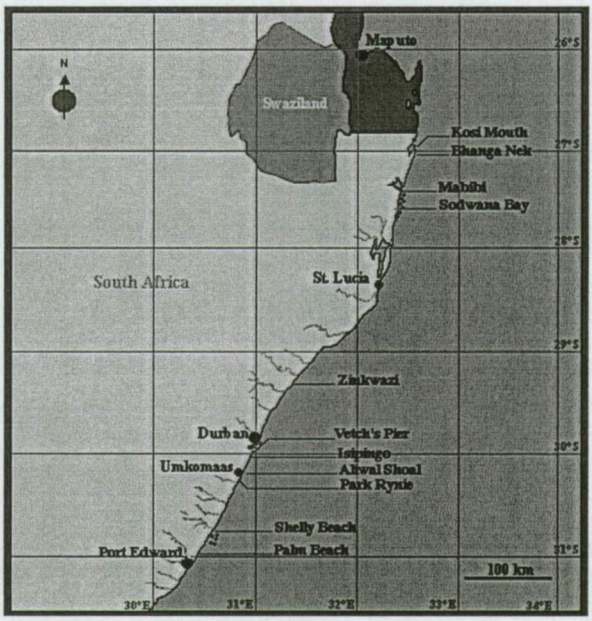

Figure 1. Map of the KwaZulu-Natal coastline indicating sampling sites (on right of map).

Materials and methods

Specimen acquisition and preservation

All the specimens in the present study were collected by hand-picking while skin-diving in intertidal pools or by SCUBA-diving up to depths of 45 m, from 2.VIII.1999 to 21.VIII.1999, 13.VII.2000 to 30.VII.2000, and 4.II.2001 to 13.II.2001. Notes on specific depth, substrate and ecology were made *in situ* for every specimen collected. Holothurian specimens were anaesthesized in 5 % magnesium chloride during 4 hours, transferred to 100 % buffered alcohol for 24 hours, and finally to 70 % buffered alcohol for permanent storage. Asteroids, echinoids and ophiuroids were anaesthesized in fresh water, transferred to 100 % buffered alcohol for 24 hours, transferred to 70 % buffered alcohol for transport and then dried for permanent storage.

Presentation of data

It was thought desirable to express distribution of echinoderms along the coast of KwaZulu-Natal in terms of latitude and longitude degree squares of one degree - a system designed by Day (1967) and later adopted by Clark & Courtman-Stock (1976) and Thandar (1989a) - as this allows easy comparison with previous distribution records.

Results

Biodiversity reconsidered

Table 1 lists the different sampling localities (see also Fig. 1) with the respective sampling effort.

Table 1. Sampling sites, depth ranges and duration of sampling times along the KwaZulu-Natal coastline

Locality	Depth range (m)	Sampling time (minutes)
South Coast		
Palm Beach	intertidal	95
Shelly Beach		
Uvongo Rocks	18-22	37
Orange Rocks	±18	48
Protea Bank	30-36	90
BoBoyi Reef	16-18	46
Broker Reef	±25	29
Old River Bed	intertidal	10
Various localities	8-16	102
Park Rynie	intertidal	60
Aliwal Shoal	12-26	432
Isipingo	intertidal	60
Central KwaZulu-Natal		
Vetch's Pier	3-5	72
Zinkwazi	intertidal	105
North Coast		
Sodwana Bay		
Adlam's Rock	intertidal	35
Diep Gat	8-10	51
1/4 Mile Reef	10-14	138
2 Mile Reef	8-36	711
5 Mile Reef	19	11
7 Mile Reef	18-24	85
9 Mile Reef	6-18	83
Mabibi	14-21	107
Bhanga Nek		
Linckia Reef	30-34	20
Sexton Reef	20-21	38
Tiger Reef	± 16	63

Prior to our sampling 130 species of echinoderms were known with certainty from KwaZulu-Natal, in waters less than 50 m deep (Clark & Courtman-Stock 1976; Thandar 1977, 1984, 1985, 1986, 1987a,b, 1989a-c, 1990, 1991, 1994, 1996; Thandar & Rowe 1989; Rajpal & Thandar 1998). After our study this number has risen by just over 39 %, to 181 species. Figure 2 shows that the main increase is found within the Ophiuroidea (+56.1%) and the Asteroidea (+53.8%), while the Holothuroidea (+24.4%) and the Echinoidea (+21.0%), as they were better known, increased less significantly.

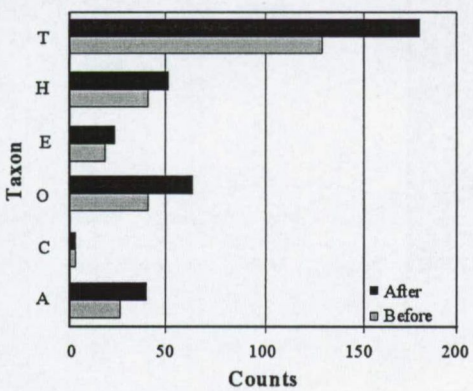

Figure 2. Species counts for the different classes of echinoderms before and after the present study. A - Asteroidea, C - Crinoidea, E - Echinoidea, O - Ophiouroidea , H - Holothuroidea and T - Total (A+C+O+E+H).

Biodiversity re-examined

As our sampling effort resulted in a significant increase in species richness for KwaZulu-Natal, it was thought desirable to plot the faunistic composition before and after the present study (Fig. 3).

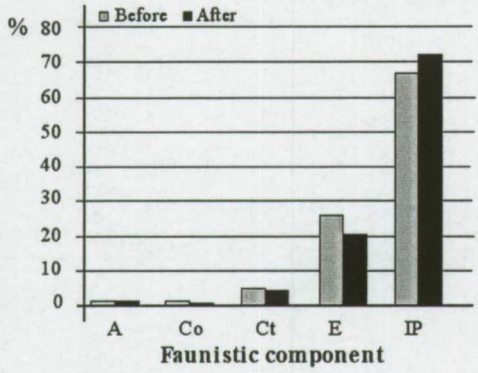

Figure 3. Faunistic components per class, prior to and after the present study. A-Atlantic, Co-Cosmopolitan, Ct-Circumtropical, E-Endemic, IP-Indo-Pacific.

From this figure it is clear that the Indo-Pacific component rises (+5.2%) to the same extent as the endemic component drops (-5.15%), while the other components vary only slightly as almost no additional species belonging to these components were found.

The hypothesis that KwaZulu-Natal is a transitional zone between the tropical Indian Ocean and the cooler temperate waters to the south is tested by calculating the faunistic similarity (expressed as the second Kulczynski coefficient) between the different latitude and longitude squares of one degree.

In the present analysis we used five areas (A-E), which we compared with each other: A represents latitude/longitude squares 30/30 & 30/31, B represents 29/31 & 29/32; C represents 26/31 & 26/32; D represents 27/32 & 27/33 and E represents 26/32 & 26/33 (Fig. 4).

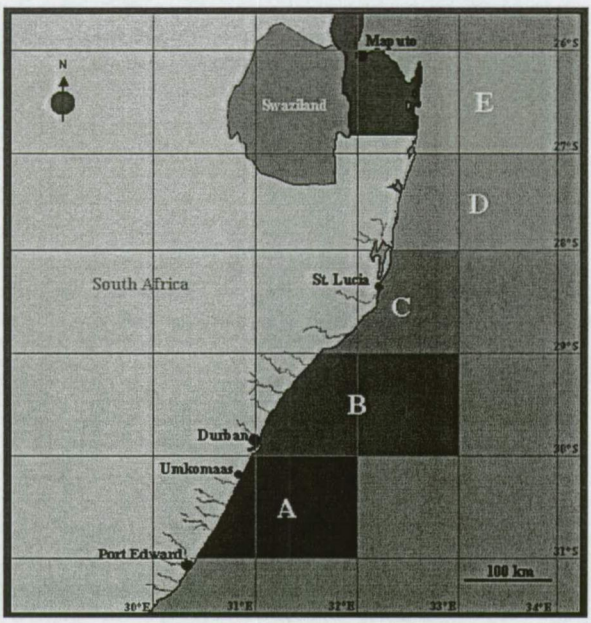

Figure 4. Map of the KwaZulu-Natal coastline indicating the combinations of latitude/longitude squares of one degree.

This cross-wise comparison of faunistic similarity yields a matrix (Tab. 2) with a confusing interpretation. For instance if area A (the most southern part of KwaZulu-Natal) is compared with the adjoining area B, a Kulczynski coefficient (KCij) of 48.1 is found; similarly the KC_{AC}, KC_{AD} and KC_{AE} remain high (42.5 to 47.9), indicating that the five areas have a large faunistic similarity. However, the results KC_{BC}=38.7, KC_{BD}=24.5 and KC_{CD}=28.9 seem to indicate that there is a large species turn-over at the top of area C (area opposite to St. Lucia Bay), which contradicts the large overall faunistic similarity.

Table 2. Kulczynski coefficient as calculated between the different areas (intertidal and shallow-water records combined). The numbers between brackets represent species counts in the different areas.

KC	A (82)	B (59)	C (21)	D (98)	E (132)
A	-				
B	48.1	-			
C	47.9	38.7	-		
D	47.0	24.5	28.9	-	
E	42.5	40.5	41.4	51.6	-

In an attempt to resolve this ambiguity we separated the intertidal from the shallow-water species. From the dataset with the intertidal species only (Tab. 3) we observe similar patterns: KC_{AB}, KC_{AC} and KC_{AD} remain high (from 41.3 to 50.1), KC_{BC} and KC_{CD} are also high (39.0 and 35.7 respectively), while KC_{BD} is exceptionally low (10.4). However, very disproportionate numbers of species in the different areas certainly cloud the indices as indicated by KC_{AE} and KC_{DE} (28.6 and 26.8 respectively).

Table 3. Kulczynski coefficient as calculated between the different areas (intertidal records only). The numbers between brackets represent species counts in the different areas.

KC	A (25)	B (25)	C (14)	D (6)	E (83)
A	-				
B	48.0	-			
C	50.1	39.0	-		
D	41.3	10.4	35.7	-	
E	28.6	44.2	41.7	26.8	-

The dataset with the intertidal species excluded (Tab. 4), shows similar trends and again seems to indicate that area C (area opposite to St. Lucia Bay) has a high species turnover.

Table 4. Kulczynski coefficient as calculated between the different areas (shallow-water records only). The numbers between brackets represent species counts in the different areas.

KC	A (64)	B (44)	C (4)	D (93)	E (64)
A	-				
B	32.6	-			
C	39.8	40.9	-		
D	46.2	21.1	13.0	-	
E	34.4	19.2	13.3	46.2	-

Discussion

Biodiversity reconsidered

Our addition of some 39 % new records to the shallow-water fauna of KwaZulu-Natal indicates the importance of drawing up a comprehensive checklist of all echinoderms in this region of the South African coastline. To date no complete checklist exists for the shallow-water echinoderms of this stretch of coast. The one given by Clark & Courtman-Stock (1976) was incomplete as it excluded the holothuroids, a deficiency now compounded with the discovery of numerous new records. It is not surprising that most of these latter additions are extensions of range from the tropical Indo-West Pacific, as previous knowledge pointed in the same direction (Clark & Courtman-Stock 1976, Clark 1977, Thandar 1989a). With the addition of numerous new records to the southern African region the percentage of endemics recorded by Thandar (1989a) drops significantly but what is noteworthy is that the degree of endemism in the subtropical province of KwaZulu-Natal increases. This is borne out by the fact that prior to our study only

23.5 % (8 of 34 species) southern African endemics were restricted to KwaZulu-Natal. With the discovery in KwaZulu-Natal of four more, yet undescribed new species, increases this figure of endemism to 31.6 % (12 of 38 species).

Biodiversity re-appraised

Interpretation of the local faunistics of the KwaZulu-Natal region is not easy. While, on the one hand, the present analyses indicate that faunal similarity across the different areas is large, on the other hand, existing and present data indicate that there is apparently a large species turn-over in the area opposite St. Lucia Bay, an area referred to as the Natal Bight. The low number of species reported from this area clouds the observed pattern of species diversity north and south of this region. In this preliminary phase of our investigations we are not in a position to conclusively state whether the low diversity here is an artefact due to the low sampling efforts conducted in this region (in the recent expeditions, it was logistically impossible to sample in the St. Lucia Marine Reserve), or whether it is a reflection of the environmental conditions that are known to persist here (Natal Bight). We do note that it is generally conceded that the distribution of the KwaZulu-Natal biota is under the controlling effect of the south-bound warm Agulhas current as evidenced by numerous workers (MacNae 1962, Thandar 1989a, Bolton et al. 2002 and many more). In this respect it is interesting to note that the Agulhas current runs close to the coast in northern KwaZulu-Natal, but as it reaches Cape St. Lucia it moves offshore, due to the widening of the continental shelf in the Natal Bight. Here, the change in the topography induces upwellings and lowering of the water temperature. In addition, the shallower shelf and the increased river discharges in this area induce high levels of turbidity. These changes in physical factors might influence the distribution of many local species dramatically, thus lowering species density.

Biodiversity awaited

In a recently accepted extension of the current project we intend focusing on the physical and biological conditions of the St. Lucia Marine Reserve in order to resolve the duality in the echinoderm distribution pattern of the KwaZulu-Natal coast.

Conclusions

The addition of some 39% new records clearly demonstrates that the shallow-water echinoderm fauna of KwaZulu-Natal was hitherto poorly known and that collecting with the aid of SCUBA yields good results. As the majority of the KwaZulu-Natal echinoderms have an Indo-Pacific character, it is certain that the southern African east coast echinoderms moved in from the north and north-east under the influence of the Agulhas current and perhaps also the East Madagascar current (Thandar 1989a).
At this preliminary phase, it remains impossible to state whether the low resolution in our faunistic analyses is the result of under-sampling of the St. Lucia Marine Reserve or a natural phenomenon linked to the oceanographic conditions that persist in this region. For now, the working hypothesis that the south-east African echinoderm fauna is Indo-Pacific in origin and that its high endemicity may be a reflection of active speciation in this part of the west Indian Ocean is upheld.

Acknowledgments

It is with pleasure that we thank Dr. C. Massin of the Royal Belgian Institute of Natural Sciences, Brussels, for his help in the identification of some holothurians; Drs B. Elliot and J. Harris of the KZN Nature Conservation Service for logistic support; P. Timm of Triton Divers, Sodwana Bay, for taking us to some of the more interesting spots along the KwaZulu-Natal coast and I. Tallon & E. VandenBerghe for their help during collections. I. Tallon's help with the creation of the database is greatly appreciated. The comments of two anonymous referees are greatly appreciated
The Flemish Fund for Scientific Research (project number G.0086.96), and the Research Council of the VUB made this research financially possible.

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Biodiversity studies on seaweeds and echinoderms in the transition between temperate southern Africa and the tropical western Indian Ocean

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ABSTRACT

A three-year project has increased by more than 30 % the number of seaweed and echinoderm species recorded off KwaZulu-Natal, and included some new to science? It demonstrates that we do not need to go to abyssal depths to make a significant and novel contribution to our knowledge of marine biodiversity.

A final workshop for this inter-institutional collaborative project, funded by the Flemish Government and the National Research Foundation, was held at the University of Ghent, Belgium on 31st August 2001. The project has been underway since 1999, enabling biologists from the Universities of Cape Town and Durban-Westville, and Marine and Coastal Management to collaborate with those working in Belgium on seaweeds (University of Ghent, UG) and echinoderms (Free University of Brussels, VUB) of the tropical Indian Ocean.

Joint work has involved detailed collecting in Kwazulu-Natal, concentrating on the poorly investigated subtidal. The extent of this collecting is clear from the facts that: (1) the echinoderm biologists accomplished approximately 42 hours of subtidal observations per diver, hereby obtaining some 725 specimens and (2) a biogeographical seaweed analysis presented (F. Leliaert) utilised information from 3447 annotated specimens. After an introduction that emphasized the importance of KZN as an overlap between temperate and tropical regions of the western Indian Ocean (Coppejans), there followed a summary of previous knowledge of marine biogeographical patterns in the region (Bolton). There is much confusion in the literature as to whether the KZN marine biota is best described as subtropical, a mixture of temperate and tropical, tropical, or various combinations of the three. Biogeographical boundaries have been drawn at a number of different parts of the coast.

In a preliminary biogeographical analysis (Samyn), the echinoderm fauna of KZN is revealed as primarily Indo-Pacific (72.9 %), although with a considerable number of southern African endemics (21.0 %). The data suggest a region of change around St. Lucia, although as this particular part of the coastline is not well sampled strong conclusions cannot be made at this stage. Distribution data of 440 species of seaweeds, distributed from Tsitsikamma on the south coast to the extreme north of KZN was compiled (Leliaert). A detailed analysis was carried out only on the 270 intertidal species in this dataset, as the subtidal data is too discontinuous at this stage. The major change in the flora occurs between the St. Lucia and Sodwana regions, with a less ,marked region of change. between the Transkei and southern KZN coasts. To stimulate discussion on possible explanations for these patterns, recent literature on inshore oceanography of KZN was presented (Anderson). The Agulhas current has a powerful controlling effect on the KZN coastal biota. The current runs close to the coast in northern KZN (Maputaland), but begins to move offshore around Cape St Lucia, where in the Natal Bight the continental shelf widens. Here, topographically-induced upwelling lowers the water temperature. The shallower shelf and increased river run-off also result in higher levels of turbidity inshore. These changes in physical factors may explain the biogeographical importance of the Cape St Lucia region. A detailed understanding of the causes of distribution patterns of the inshore biota is hampered by the lack of relevant temperature data along the KZN coast.

The recorded shallow-water (less than 50 m deep) echinoderm fauna of KZN comprised around 130 definitely valid species before the project, although the majority of these were only known from single collections (Thandar). As with some other groups such as polychaetes; only a temperate and a tropical

biogeographical region have been recognized, with a boundary along the Transkei coast. In the course of the project 51 species have been added to the echinoderm fauna of the region, an increase of almost 30% (Samyn). Most of the additions belong to the tropical Indo-West-Pacific component, although they include at least three species of seacucumber and presumably one species of brittlestar new to science. It is also noteworthy that several genera belonging to different echinoderm classes are here reported for the first time for southern Africa. In this respect, some of the new findings in the family Holothuriidae (Holothuroidea: Aspidochirotida) are bearing the palm. For instance, the genus *Labidodemas* which comprised up till now only four species was hithertho unknown from southern Africa, while in the course of this project two known species and one new species to science have been reported, allowing a worldwide revision of the genus. Similar efforts are undertaken for the holothurian genera *Actinopyga* and *Holothuria* and for the genus *Ophiocoma* (Ophiuroidea: Ophiocomidae). The recorded flora of red algae (Rhodophyta) for KZN has been similarly increased by 30%, from 221 to 289 species (De Clerck). Among the 68 new records, the majority are again Indo-West-Pacific tropical species, with a few pan-tropical species. A few species have disjunct distributions in the Indian Ocean, and these tend to be deeper subtidal species, suggesting that the gaps are due to insufficient collections. New records of species described from Australia are not uncommon, but there are very few species which appear to be endemic to northern KZN/southern Mozambique. A new genus of the red algal family Ceramiaceae will be submitted for publication; based on these collections (De Clerck). Detailed studies of the taxonomy of certain red algal groups were presented, including *Plocamium* (Engledow, UG), and molecular systematic studies on the Gelidiaceae (Tronchin, UCT) and the Gracilariaceae (Iyer, UCT). A number of new species and new records will eventually be published from these studies: For the green algae (Chlorophyta; Leliaert), 23 of the species found were new records for KZN (38% increase), including 17 new records for South Africa. The flora now includes 11 species of *Cladophora* (previously 3), and 11 species of *Caulerpa*.

A further presentation introduced the Flanders Marine Data and Information Centre (Vanden Berghe, Flanders Marine Institute) who will contribute GIS and other expertise to a proposed extension of the current project. A clear understanding of biogeographical boundaries is necessary to investigate potential effects of global warming; and further studies are planned to concentrate on the Cape St Lucia marine boundary. These would include the documenting the inshore temperature regime at a number of sites, describing the subtidal marine vegetation and the echinoderm biodiversity in this overlap, as well as producing guides to the seaweeds and echinoderms of Kwazulu-Natal.

We are greatful to Drs Jean Harris and B. Elliot and their colleagues at KZN Wildlife, for their invaluable logistical support.

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Zoogeography of the shallow-water holothuroids of the western Indian Ocean

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ABSTRACT

Aim Determination of the zoogeography of the shallow-water holothuroids of the western Indian Ocean. To what extent do differences in species' ability to disperse across potential barriers shape that pattern?

Location Shallow-waters (50 m isobaths) of the western Indian Ocean, the area ranging from Suez to Cape Town and from the coastline of East Africa up to 65° East.

Methods Cluster analysis on several β-diversity coefficients; parsimony analyses of endemicity.

Results The shallow-water holothuroid fauna of the western Indian Ocean is highly diverse and part of the larger Indo-Pacific and the South African biogeographic provinces. The western Indian Ocean is however best split into several biogeographic units. To the north, we found some evidence that the northern Red Sea holothuroid fauna differs from the southern Red Sea fauna, the latter bears closest affinity with South-East Arabia and the Persian Gulf and thus the biogeographic barrier of Bab-el-Mandab nowadays seems to be of minor significance. The important cold upwelling at the east coast of Somalia forms an effective barrier for holothuroids and especially those with lecitotrophic (short-lived) larvae. The circumtropical biogeographical pattern was not well-resolved, but important taxonomic turnovers suggest that it is composed of several distinct subprovinces. The biogeography of the western Indian Ocean is best explained with (i) species' dispersion ability, (ii) the prevalent current patterns and (iii) recent geological history. As a by-product of this research we demonstrate that Rapoport's rule does not hold for the shallow-water holothuroid fauna in the here studied latitudinal gradient.

Main conclusions The shallow-water biota of the western Indian Ocean (WIO) were generally believed to belong to the tropical Indo-West Pacific and in the far South (Cape area) to the South African biogeographic Province. This study analysed this simple biogeographic model and concluded that the western Indian Ocean best be split in (at least) three biogeographic realms. Conspicuous differences in dispersion abilities of the three dominant orders are identified as the shaping factors. As a serendipitous find, we found that Rapoport's rule does not hold in the western Indian Ocean.

Keywords

Echinodermata, Holothuroidea, western Indian Ocean, β- and γ-diversity, PAE, dispersion capacity, latitudinal and longitudinal diversity gradients

Introduction

For several centuries, shallow-water holothuroids (mainly those belonging to the order Aspidochirotida) have been fished to feed the sea cucumber or *beche-de-mer* trade in the Far-East (Conand and Byrne, 1993; Conand, 1997; 1998a, b; 2001; Marshall *et al.*, 2001). However, the last decades, in love with the ever-increasing market demand, have witnessed relentless overharvesting in many consuming countries and noted that harvesting has partially shifted to non-consuming countries of the western Indian Ocean (Samyn, 2000; Marshall, *et al* 2001). Although biologists are only starting to grasp the functional roles of these invertebrates, they fear that the present exploitation-rate might alter biodiversity and redundancy of ecosystems to the point of no return. Conservationists thus urge to control and regulate holothuroid

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fisheries, but their efforts are bound to fail due to lack of qualitative and quantitative measurements of the biodiversity of this non-charismatic taxon. Until recently, such lack of information applied especially to the tropical East coast of Africa for which only a handful of taxonomic and/or faunistical publications have appeared during the last two decades (Clark, 1984; Cherbonnier, 1988; Arakaki & Fagoonee, 1996; Rowe & Richmond, 1997). However, as our team has in recent years intensively sampled along the tropical coasts of Kenya and Pemba Island (Tanzania) and along the subtropical coast of KwaZulu-Natal (Republic of South Africa), we were able to re-evaluate local fauna's (Samyn, 2000; Samyn & Vanden Berghe, 2000; Bolton *et al.*, 2001; Samyn & Thandar, 2003; Samyn, in press), describe several new taxa (Massin *et al.*, 1999; Samyn *et al.*, 2001; Massin *et al.*, in press; Samyn & Thandar, in press), revise some supraspecific taxa (Samyn & Massin, in press; Massin *et al.*, in press) and detail some of the patterns of nested relationships among certain clades (Kerr *et al.*, submitted; Samyn *et al.*, in preparation). An analysis of the large-scale patterns of holothuroid species richness has however never been performed in the western Indian Ocean. Nevertheless, as convincingly argued elsewhere (a.o. O'Hara *et al.*, 2000; Purvis & Hector, 2000), insight into this component of biodiversity can greatly enhance our understanding of the history of regional biota, can paint the red triangles on the green background of ecological studies and can provide a potential scaffold for future conservation initiatives. The present study is the first attempt to analyse the distribution of the shallow-water holothuroids from the western Indian Ocean. The spadework for this analysis was laid down in the monograph of Samyn (in press), which is here transformed into a presence / absence dataset for several *a priori* defined operational geographic units.

Geology and oceanography of the western Indian Ocean

The shallow-water biota of the western Indian Ocean (WIO) are generally believed to belong to the tropical Indo-West Pacific biogeographic province and to the South African Province (Briggs, 1974; Adey & Steneck, 2001). It is well documented that the Indian Ocean was formed some 185 to 180 mya by the Ferrar volcanism along the coast of present southern Mozambique (Courtillot *et al.*, 1999). This volcanism caused the drifting away of Australia and Antarctica to the east and south respectively, while Africa (still linked with Madagascar, the Seychelles and India) moved north. By the late Cretaceous (± 95 mya), spreading in the Mascarene Basin pushed India (still linked with the Seychelles) rapidly (15 $cmyr^{-1}$) to the north, leaving Madagascar behind. Later (60-65 mya) India drifted apart from the Seychelles, the latter have since then retained their position. The pre-Cambrian granitic boulders of the northern islands evidence the historical association of the Seychelles with Africa. On the other hand, the southern Seychelles are made of fossilised coral of much younger Pleistocene origin (1.64 million to 10.000 years old); these are placed on top of the once active volcanoes of the Réunion plume. The more eastern Islands of the WIO (La Réunion, Mauritius, Rodriguez Island; all placed on the Mascarene Ridge), also thank their existence to such relatively young (± 15 mya up until now for La Réunion) volcanic activity. Here again, the top of the (by now) submerged volcanoes is covered with Pleistocene coralline sediments. Similar volcanic activity took place in the Mozambique Channel (±15 mya) and formed the Comoros Islands (Mayotte being the oldest). Yet another geological origin is to be assigned to the three main islands that fringe the Tanzanian coast (Pemba Island, Zanzibar and Mafia Island). Pemba Island, surrounded by relatively deep water (> 200m), is believed to have broken away from the continent through seafloor spreading in the Pemba rift some 10 mya. Zanzibar and Mafia Island on the other hand are believed to be Pleistocene inshore reefs that are now separated from the mainland by shallow (< 50m) waters. The geological origin of the Red Sea (and afterwards the Gulf of Aden) nowadays is interpreted in terms of two distinct phases of seafloor spreading (one between 30 and 15 mya and one that continues to occur since about 5 my) along the East African rift (Omar & Steckler, 1995; Courtillot *et al.*, 1999). The northern part of the Red Sea holds the Gulf of Suez and the Gulf of Aqaba; the former is recognised as an abandoned rift basin with less than 100-meter water depths, while the latter is a young (spreading since 5 my), rapidly subsiding wrench basin with maximum water depth of 1850 meters. The Persian Gulf is a sedimentary basin with shallow water (depth on average only some 30 m); it is thought to be a remnant of the Tethys Sea.

The reality of the Pleistocene, with its glaciations, significant land rises and lowering of the sea level [according to some recent calculations, 20 ky BP the sea level declined with some 130 m (Cutler *et al.*, 2003)], thus readily explains the occurrence of fossilised coral reefs along most of the African continental shelf (the Red Sea included) (fig. 1A). In the southern hemisphere, at the mouth of the Zambezi river (Mozambique), that pattern is brusquely disrupted. While north of the Zambezi estuary the general settings are very similar to those of tropical East Africa; south of that point the coastline consists of low coastal

plains that form vast sand beaches and dunes (fig. 1B). South of the Zambezi estuary, coral growth is severely inhibited by the vast amounts of sediments that are discharged by the Zambezi River.

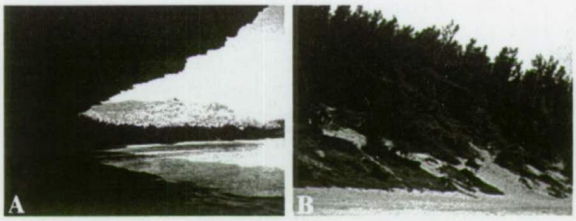

Fig. 1. (A) By wave action undercut fossilised coral deposits of Pleistocene origin can be found along large parts of the East African coastline (here at the Kiunga Reserve in northern Kenya); (B) South of the Zambezi Estuary the coastline forms vast stretches of sand beaches that are fringed by high dunes (here Sodwana Bay in South Africa).

Coral outcrops (patch reefs) re-appear in southern Mozambique and more or less flourish around Inhaca and the northern parts of KwaZulu-Natal (South Africa). Still, it must be stressed that the coral growth around this regions is limited and not on top of Pleistocene coralline deposits. As such, these deposits are best seen as sabelariid reefs rather than as true coral reefs. In the northern hemisphere, Pleistocene coralline deposits (and coral growth in general) are absent in the 1000 km of Somalian coastline south of Soccotra. Here, the seasonal cold upwelling during the southeast monsoon obstructs coral growth and reef formation (Glynn, 1993; Kemp, 1998).

The eustatic sea level changes in the Pleistocene are generally assumed to have had a major impact on the distribution of marine organisms (amongst many others Adey & Steneck, 2001). For instance, it is believed that the Pleistocene drop in sea level has emptied the (very shallow) Persian Gulf completely (Price, 1982 and references therein) and that today's Persian Gulf biota are obligate post-Pleistocene immigrants from the larger Indo-Pacific or recently speciated species thereof. Similarly, the shallow (±100 m) and narrow passage to the Red Sea (Bab-el-Mandab) is thought to have dried at some time in the Pleistocene (Price, 1982; Kemp, 1998), isolating the Red Sea from the Indian Ocean and thus again possibly promoting active speciation within the Red Sea.

Next to the geological processes, past and present oceanic current patterns (cfr. fig. 11) are undoubtedly the other thick fingers in the pie when it comes to the distribution of holothuroids, marine organisms with free-living larvae. These current patterns are (at least partially) under the influence of the prevailing wind patterns, which change according to the monsoon seasons, the morphology of the continental shelf and the Coriolis force (McClanahan, 1988). The permanently west flowing South Equatorial Current (SEC) traverses the Indian Ocean and is partially diverted south along the eastern Madagascar coast were it becomes the Madagascar current (MaC). Upon reaching the continent at ±10°S (southern Tanzania), the SEC splits into the northward flowing East African Coastal Current (EACC) and the southward flowing Mozambique Current (MoC). During the south-east Monsoon (April to October), the northwards flowing EACC flows along the Somali coast (forming the Somali Current; SoC) with a mean velocity of four to five knots (occasionally reaching seven knots); it leaves the continent at the Gulf of Aden and passes South Arabia before joining the Indian Monsoon Current (IMC) that turns eastward in the Arabian Sea. During that time, increasing offshore winds north of the equator cause cold-water upwellings along the Indian Ocean coast of Somalia, with water temperatures as low as 13°C (Currie *et al.*, 1973 in Kemp, 1998). During the northeast monsoon (from November to March), the northeast Monsoon Current (NEMC) flows westward across the Arabian Sea, from India to southern Arabia. The northern winds of the northeast monsoon slow the northerly water movement of the SoC and eventually reverse the movement, forming the Somali Counter Current (SoCC), which off flushes from the continent approximately at Malindi in Kenya (±4°S). The SoCC joins the EACC and generates the east flowing Equatorial Counter Current (ECC). Where the MoC and MaC unite internal currents and eddies are generated within the Mozambique Channel. These perhaps transport larvae from the western coast of Madagascar to the Mozambique coast. Eventually the MoC joins completely with the MaC and the warm and southward flowing Agulhas Current (AC) is formed. The AC flows south with a high-velocity and with a strong stability in its trajectory brought about by the very narrow and steep continental shelf along the East coast of southern Africa (Lutjeharms *et al.*, 2000). The southbound AC washes the eastern shores of South Africa up to Cape Agulhas (±36°S) where it retroflects towards the Indian Ocean. Between Cape Agulhas and the Cape Peninsula, the interaction of the AC and the cold Benguela Current (BC) sweeping from the West coast of South Africa and the prevailing trade winds cause important upwellings that result in important temperature fluctuations.

Materials and methods

Study area

The western Indian Ocean (as WIO from hereon) is here defined as the area ranging from Suez to Cape Town and from the coastline of East Africa up to 65° East. In order to comprehend the faunistics of the WIO in a standardized way, the study area was divided into cells of one-degree latitude and longitude (fig. 2). These cells were simultaneously assigned to eight coarser operational geographic units (OGU from hereon) (terminology from De Grave, 2001), which were delimited on the basis of published faunistical borders (Thandar, 1989; Kemp, 1998; Proches & Marshall, 2002; Samyn & Thandar, 2003) and tectonic ridges (Santini & Winterbottom, 2002).

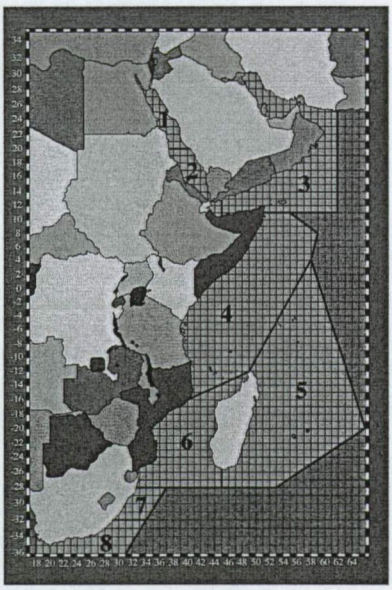

Fig. 2. The WIO with the demarcation of the OGU's. 1. northern Red Sea (NRS) inclusive of the Gulfs of Suez and Aqaba, bounded at 20°N; 2. southern Red Sea (SRS), delimited to the east at 45°E; 3. Arab Basin (AB), inclusive of the Persian Gulf and the Island of Soccotra, bounded to the south at 11°N and to the east by the boundary between Iran and Pakistan; 4. Somali Basin (SB), inclusive of the Comores, bounded to the northeast by the Carlsberg ridge, to the south by the Comores and to the southwest by Madagascar; 5. Mascarene Plateau (MP), bounded to the south at 28°S; 6. Mozambique Channel (MC), bounded to the south at 28°S; 7. Natal Province (NP), subtropical area delimited to the south at 32°S; 8. Cape Province (CP), delimited to the west at the Cape. The gridded cells are one longitudinal degree wide and one latitudinal degree long (±12500 km^2 each); the shaded cells represent cells that fall outside our OGU definition; no records were scored in these cells.

Data acquisition

Shallow-water (*i.e.* not deeper than the 50 m isobaths) holothuroid distribution data for the WIO were obtained from the monograph of Samyn (in press), whereby the provided distributions were transformed into a presence / absence dataset for each OGU and for each one degree lat/long cell therein. Uncertain species, as flagged by the above author (*i.e. Cercodemas anceps, Colochirus colloradiatus, C. propinquus, Holothuria (Lessonothuria) glandifera, Leptosynapta inhaerens, Ocnus cylindricus, O. planci, Pentacta pusilla* and *Psolus appendiculatus*), were omitted from the analyses. As already noted by Samyn (in press), some records are so broadly defined in terms of location (*e.g.* location given as "Red Sea") that they cannot be attributed to discrete one-degree lat/long cells. For such records we constructed one or several aggregation cells in each OGU; these conglomerate cells were only used in the "coarse grain" (inter-OGU relationships) analyses whereas in the "fine-grain" (at the level of the one degree cells) analyses they were discarded. The resulting dataset holds 235 species that belong to 63 genera, 12 families and four orders. Distribution records cover a total of 117 one-degree cells (eight of which being aggregation cells) (see appendix for complete dataset).

Zoogeographical analyses

The zoogeographic value and the relation between the eight *a priori* selected OGU's were tested by performing cluster analyses with several β-diversity coefficients as well as with parsimony analyses of endemicity (PAE) (Rosen, 1988). The utilised β-diversity coefficients are the Dice or Sorensen, the Jaccard and the first & second Kulczynski similarity coefficients (see Magurran, 1988 and Price, 1982 for details).

PAE were run under the heuristic search algorithm (10^6 replicates), using *Paup** (Swofford, 2002). By adding a hypothetical OGU outgroup - with all species coded as absent, implying that all cells were initially empty (Lundberg rooting) and that presences are new arrivals or new speciations - we were able to deduce historical OGU-relationships and make inferences on the direction of colonisations. As explained by Cracraft (1991; see also De Grave, 2001) this assumptive scenario is the only possibility when no fossil record is available. The robustness of the nodes in the PAE topology was investigated by bootstrapping with replicates encompassing 1000 data sets and with Bremer support indices (*i.e.* the number of additional records needed to collapse an internal branch). We applied Wagner and Dollo parsimony to the dataset; the first allows the analysis to run unordered (taxa are allowed to colonise an OGU, disappear and re-colonise as many times as necessary), the second orders the colonisation events (taxa can colonize an OGU only once, but can be lost independently in each OGU). As explained by De Grave (2001), Wagner parsimony thus allows inferences on long-distance dispersion, whilst Dollo-dispersion can only handle short-distance dispersion.

Understanding the zoogeographic provinces

As the dominant families in the present dataset have different life history strategies we investigated if these can be held responsible for the observed zoogeographical pattern. Indeed, species belonging to the aspidochirotid families Holothuriidae and Stichopodidae and to the apodid family Synaptidae are characterised by an indirect development. Hereby the gastrula first develops into an auricularia, which undergoes metamorphosis to the doliolaria stage before settlement (Smiley *et al.*, 1991; Sewell & McEuen, 2002). On the other hand, species belonging to the dendrochirotid families and the apodid family Chiridotidae typically undergo direct development whereby the gastrula develops directly into the doliolaria larva (*i.e.* there is no auricularia stage) (Smiley *et al.*, 1991; Sewell & McEuen, 2002). We analysed if these two opposing life histories are determinant for the zoogeographical patterns by determining the dispersion capacity of the three dominant orders and of the two opposing life history strategies. This was done by constructing cumulative curves for species number against range size, the latter expressed as the number of cells within a species' extent of occurrence (Roberts *et al.* 2002). If life history (and therefore dispersion capacity) is indeed ruling the zoogeography, then it should, at least partially, reflect the species turnover as observed across latitudinal and longitudinal gradients. We thus also investigated how the taxonomic composition (at the level of the order) behaves across latitudes and longitudes. Moreover, we examined how the different orders contribute to each OGU by relating the total species richness to the number of species within each order. By calculating the bootstrapped 95% confidence limits (as computed by random allocation of each order to local sites from the total WIO species pool) we determined if the contributions of each order to each OGU falls within the bounds of what is predictable were the WIO a homogeneous region (see also Bellwood & Hughes, 2001).

Results

Describing biodiversity

Of Samyn's (in press) dataset, 235 species - belonging to 63 genera, 12 families and four orders - were retained. In total 117 one-degree cells (thus nearly 1.5 10^6 km^2) were scored to harbour holothuroid species. We assessed the completeness of this dataset by constructing a species accumulation curve for the WIO (fig. 3). The absence of an asymptote shows that with each additional sampling expedition new records continue to be found although the velocity of discovery is diminishing. The punctuated leap of species numbers in the late nineteen eighties is best seen as a more gradual accumulation of species, because this punctuated leap corresponds with Cherbonnier's (1988) monograph on Malagasy holothuroids, a major work that spans more than a century of sampling. The last additions can largely be credited to *de novo* sampling in Kenya and KwaZulu-Natal. The success of the last additions undoubtedly is related to the usage of SCUBA-gear.

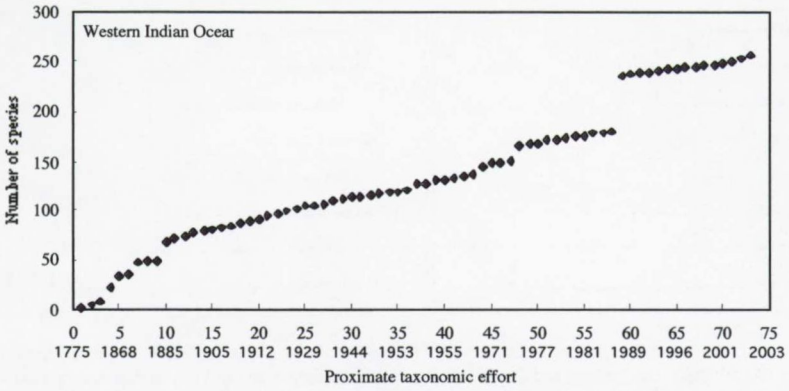

Fig. 3. Species accumulation curves for the complete WIO. Proximate taxonomic effort is ordered chronologically whereby the publication date of each fifth paper is also indicated (note that the series is linear in regard to effort and not in regard to publication date).

Plotting the species richness in each cell reveals a patchwork wherein one can hardly discern a pattern (fig. 4). While the Red Sea (note that the majority of available cells have not been investigated), tropical East Africa (Kenya, northern Tanzania, the Seychelles and northern Mozambique), relatively isolated parts of Madagascar (Nosy Be, Tuléar and to a lesser extent Fort Dauphin), Mauritius and subtropical Eastern southern Africa (KwaZulu-Natal and the Cape) can be called rich in species, south-east Arabia (including the Persian Gulf), the Gulf of Aden, the Somali coast, the central coast of Mozambique and large parts of eastern south Africa appear poor.

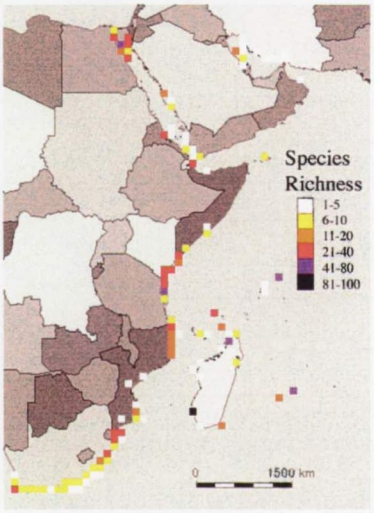

Fig. 4. Descriptive map of the sampled cells in the WIO. Each square represents a cell of one-degree latitude and longitude.

Zoogeography

Cluster analyses based on the Dice (or Sorensen), the Jaccard and the first Kulczynski coefficients all gave back the same topology (fig. 5A), the dendrogram calculated on the second Kulczinski coefficient gave a topology that differed only in the position of the MC (abbreviations of OGU's are given in the legend of fig. 2) (fig. 5B). The NRS and SRS, together with the AB have the highest faunistical similarity, whatever the employed β-diversity index. To a lesser extent this also applies to the MP and the SB. Further the CP clearly always came out as being different from the rest of the WIO (similarity coefficients equal 0.1 irrespective of the β-diversity coefficient utilised). The NP is further shown to act as the transition zone between the Cape Province and the rest of the WIO.

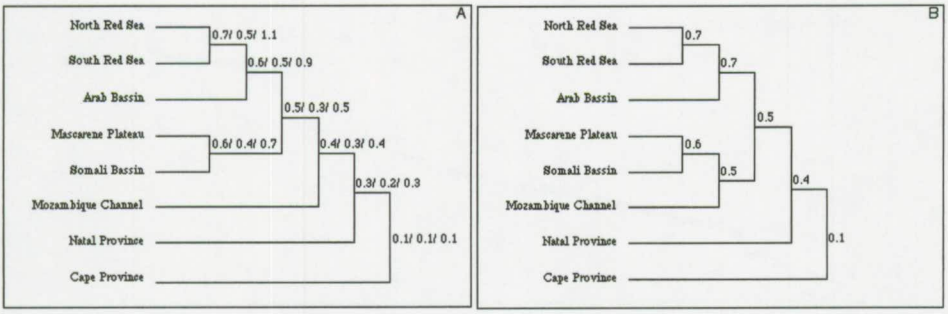

Fig. 5. Dendrogram using average linkage (between OGU's) produced by clustering with commonly used β diversity indices such as (A) the Dice, the Jaccard and the first Kulczynski coefficient and (B) the second Kulczynski coefficient. Numbers are the respective similarity coefficients.

Parsimony analysis - performed with *Paup** (Swofford, 2002) under the heuristic search mode with random addition sequence with 10^6 replicates and with all species weighted equally - on the 235 taxa in the dataset, revealed that only 113 of them are distributed in a parsimony informative way (*i.e.* shared by two or more OGU's but not all OGU's together; or in other words OGU autapomorphies and OGU symplesiomorphies excluded). Parsimony analysis of endemicity under Wagner parsimony gave back a single most parsimonious area cladogram with a tree length of 201 steps, a consistency index (CI) of 0.562 and a retention index (RI) of 0.567 (fig. 6A). PAE under Dollo parsimony generated two most parsimonious trees with tree length 240, CI=0.471 and RI=0.74 (fig. 5B for the strict consensus view).

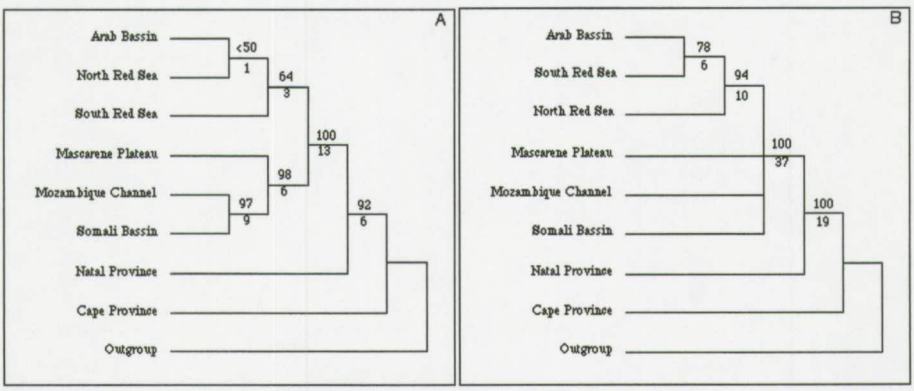

Fig. 6. OGU cladograms: (A) Single most parsimonious cladogram as obtained under Wagner parsimony; (B) strict consensus tree of the two most parsimonious cladograms as obtained under the Dollo parsimony. Numbers above branches represent bootstrap percentage; numbers below branches represents Bremer support. The outgroup is coded as all species absent from each cell.

Both the PAE under Dollo (dispersion obstructed) and the PAE under Wagner parsimony (dispersion permitted) present the CP and the NP as basal clades. Also, the (NRS, SRS, AB) branch returns as a derived clade from the tropical OGU (MP, MC, SB) branch. Dollo and Wagner parsimony however differed from each other in the position of the SRS and in the relation between MP, MC and SB. Under the Wagner parsimony the SRS is placed as sister area to the (AB, NRS) clade whereas under the Dollo parsimony the NRS is sister to the (AB, SRS) clade. Another difference between both parsimony approaches entails the relationships between the tropical OGU's, which returned as unresolved under the Dollo criterion whereas under the Wagner criterion the clade (MP,(MC,SB)) was uncovered. Bootstrap percentages and Bremer supports for and within the - by Wagner parsimony obtained - (SRS(NRS,AB)) clade proved very low (bootstrap support = 64 %; Bremer support = 3). On the other hand, the ((AB,SRS)NRS) clade as obtained with Dollo parsimony received high support for both indices (bootstrap

support = 94 %; Bremer support = 10). The bootstrap and Bremer support for the - by Wagner parsimony obtained - (MP(MC,SB)) clade is also high (bootstrap support = 98 %; Bremer support = 6). The latter topology was not uncovered under the Dollo parsimony although it must be stressed that the support for the (tropical OGU, Red Sea, AB) clade was very high, both under Wagner (bootstrap support = 100%; Bremer support = 6) and Dollo parsimony (bootstrap support = 100%; Bremer support = 37).

Given the differences between Dollo and Wagner parsimony we further explored the link between life history strategy and zoogeography. Thus, we plotted the geographical spreading of the three orders across the latitudinal and the longitudinal gradient of the WIO (figs 7 and 8). These plots reveal that species turnover between OGU's is largely governed by a taxic turnover at the level of the order. This applies especially to the ratio of aspidochirotids to dendrochirotids over the latitudinal gradient and is especially visible around 32° S., where the transition between the CP and the NP is located. Similar inversive trends, although smaller in amplitude, transpire around 29° S (transition between NP and MC), around 15° S (transition between MC and SB), around 6-7°S (within the SB and the MP), around the equator (within the SB and the MP), around 10° N (transition between SB and AB) and around 20° N (± transition between SRS and NRS). The trend line of the apodid/aspidochirotid proportion is less obvious to interpret, but changes at around 18°S (transition between MC and SB), around 8°S (within the SB and MP) and around 10°S (transition between SB and AB). No firm extrapolations can be made for the east coast of Somalia (1 to 11°N), for this regions is too poorly investigated; the only study being that of Tortonese (1980). At higher northern latitudes, the simultaneous rise of apodids and (although less pronounced) dendrochirotids also needs mentioning as it roughly (± 20° N) corresponds to the border between the North and South Red Sea.

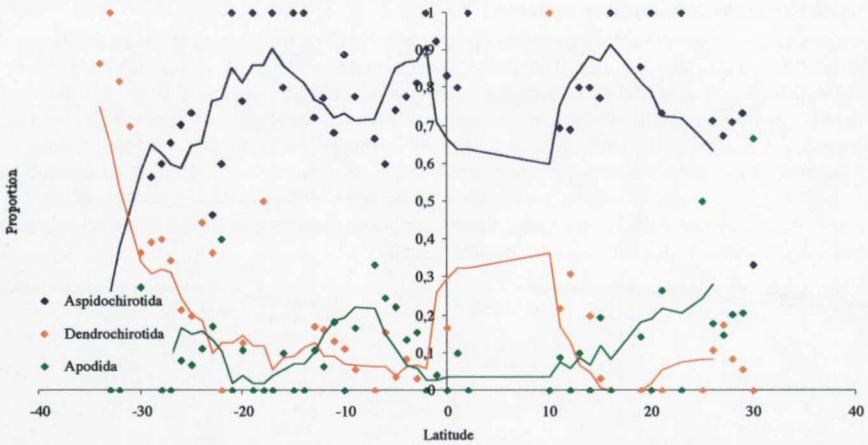

Fig. 7. Proportional contributions of the dominant orders across the investigated latitudinal gradient. Negative latitudes represent southern latitudes; positive values are northern latitudes. The curves represent the moving average (with period five).

Similar trends can be observed along the longitudinal gradient (fig. 8). Again the most obvious taxonomic turnover occurs in the CP / NP transition (around 30 to 32 °E). Also noteworthy is the minor shift around 45 °E [both the transition between AB and SRS and between MP and MC/SB(partim)].

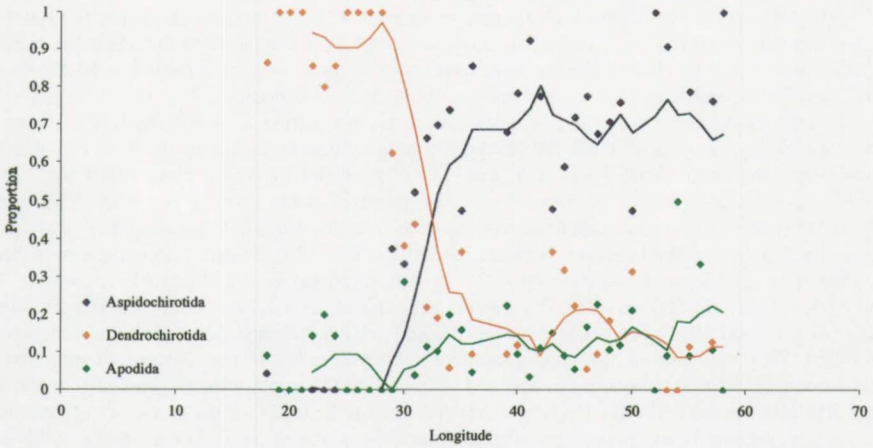

Fig. 8. Proportional contributions of the dominant orders across the investigated longitudinal gradient. Longitudes represent degrees East. The curves represent the moving average (with period five).

Understanding the zoogeographical patterns

The correspondence between life history strategy and range size of the dominant orders is clearly visible from the plot of range size vs. the cumulative species richness (fig. 9). Dendrochirotids (with their lecitotrophic doliolaria and direct development) reach the asymptotic range size after 23 cells, while the aspidochirotids (with their planctotrophic auricularia and indirect development) reach this saturation point only after 45 cells; apodids (with both types of development), are generally positioned somewhat in between but reach their asymptotic range size at 18 cells (at 10 cells for the lecitotrophic Chiridotidae). By splitting up on the basis of the life history rather than at the level of the orders, the above pattern was made even more visible; species with lecitotrophic larvae are range restricted after 23 cells, while those with planctotrophic larvae reach this saturation only after 45 cells.

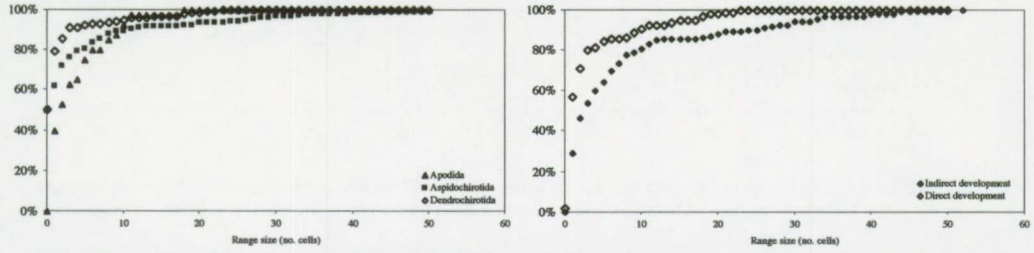

Fig. 9. Dispersion capacity (number of cells occupied) vs. cumulative species richness: (left) for the three dominant orders; (right) for holothuroids with lecitotrophic (Dendrochirotida and the apodid family Chiridotidae) and planctotrophic larvae (Aspidochirotida and the apodid family Synaptidae).

The significance of life history traits is further analysed by calculating the proportional contribution of the three dominant orders across the species richness of all sampled locations in the WIO. Our results show that the contribution of the orders varies considerably for each OGU and that moreover these values do not fall within the bounds predicted by random allocation of species to local sites from the global species pool (bootstrapped 95% confidence limits based on 235 iterations determines the theoretical confidence funnel) (fig. 10). More specifically, in the Red Sea, Somali Basin, Mascarene Plateau and to a lesser extent also the Mozambique Channel, the proportion of aspidochirotids is markedly higher than what is predicted by random allocation were the WIO homogenous. Conversely, more dendrochirotids as expected are found in

the Cape Province and to a lesser extent also the Natal Province. For the apodids the pattern largely matches the expected one.

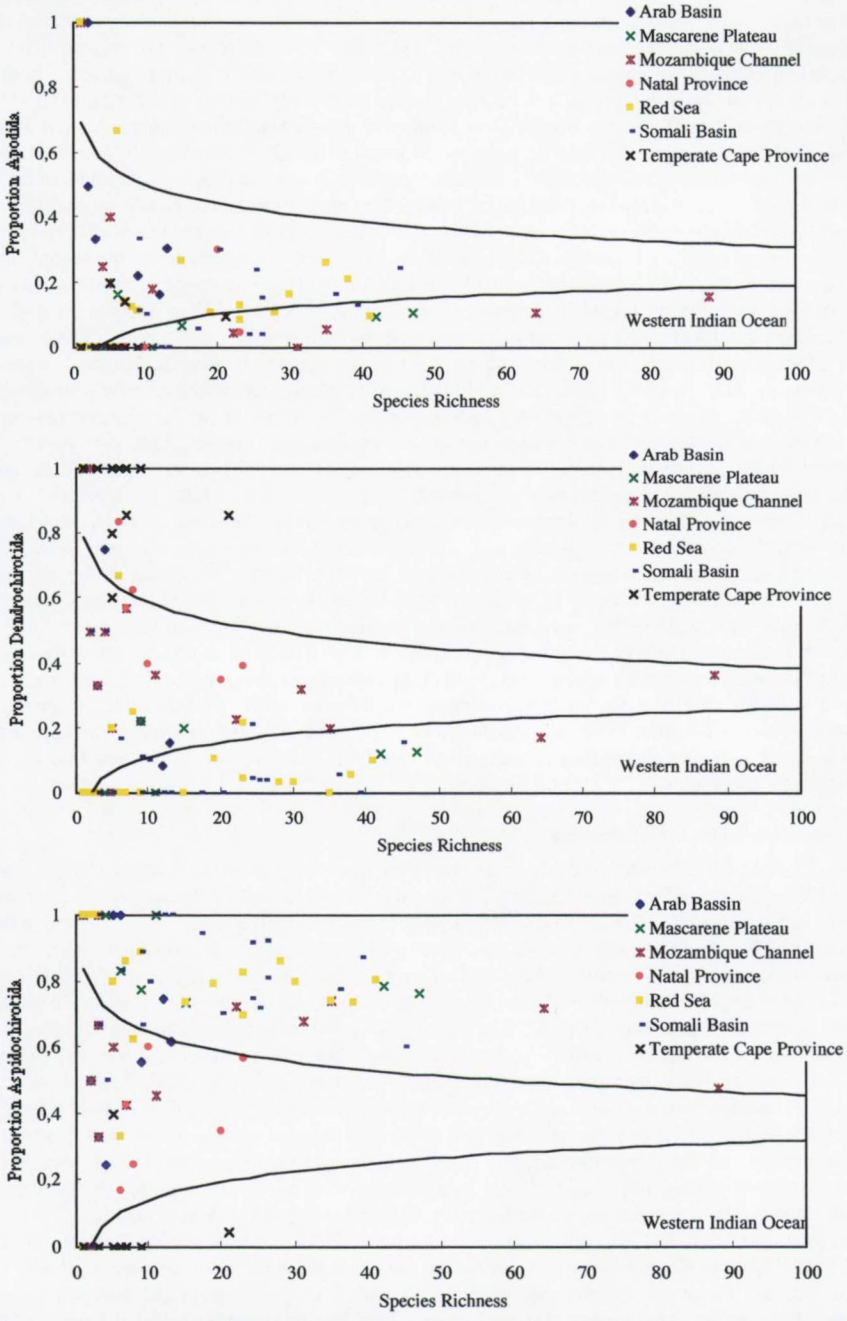

Fig. 10. Contribution of the three dominant orders to the total species pool of each OGU (northern and southern Red Sea are here lumped for clarity) across the range of total species richnesses. Solid lines represent the 95% confidence limits based on random selection of species from the total species pool.

Discussion

Quality of the dataset

A major problem for a study like the present one is that one needs a dataset that is rigid both in quantity (number of taxa, representative sampling efforts) and in quality (correct taxonomy and location of records). Unfortunately these parameters are hard to control and (more often than not) will require a formidable sampling, taxonomic and systematic effort (see also Vecchione *et al.*, 2000). Such is conclusively shown by figure 3: each additional sampling in a WIO area continues to bring additional records, even today. For instance, Samyn (in press) roughly doubled the number of Kenyan holothuroids and Samyn & Thandar (2003) were able to add nearly 25 % to the holothuroid fauna of KwaZulu-Natal (even though this is one of the best-studied stretches of coast along the African continent). Moreover, analyses of endemicity patterns (unpublished data) have revealed that the faunal lists as here employed underestimate rare species. On the other hand, even though the present dataset is based on an extensively researched taxonomic and systematic foundry (Samyn, in press), we cannot, with absolute certainty, exclude that some of the records later will have to be omitted. Such can be exemplified with Cherbonnier's (1988) monograph on the holothuroids of Madagascar, an *opus* that is generally accepted as the standard for East Africa. Despite its *grandeur* in temporal and geographical scope (it spans more than a century of sampling and covers a considerable part of larger Madagascar), more than a third (45 on 122) of the species treated in this work were new to science. However, in 40 % of the cases (18 on 45) these descriptions were based on only a single specimen and in ± 16 % of the cases (7 on 45) on only two specimens. Therefore, it can be expected that several of these newly created species will turn out to be but synonyms of existing species. This observation is further strengthened by the fact that: (i) many of these specimens are remarkably small, thus not excluding the possibility that they are but juveniles of already established species of which the intraspecific variation is inadequately known; (ii) some of them are obviously erroneously classified and thus have not been compared with their natural sister-species (e.g. *Opheodesoma sinevirga* Cherbonnier, 1988 obviously belongs to the genus *Euapta*). Moreover, as most of these new species have since then not been found again (Massin, pers comm.), the plausibility of synonymity has to remain in the back of our heads. Nevertheless, until we, or colleague taxonomists, have accumulated convincing proof for such lumping, we *must* retain them as valid. Simultaneously, the contrasting situation also has to be borne in mind. Indeed, some supposedly well-known species increasingly reveal themselves as cryptic species. Such was recently discovered to be the case in *Labidodemas semperianum* Selenka, 1867 (Massin *et al.*, in press) and in *Holothuria arenicola* Semper, 1868 (unpublished data). Undoubtedly, comprehension (and prediction) of such crypticness will to a large extend depend on our understanding of the factors that explain the zoogeographical distributions.

Baring nested inter-OGU relationships

Patterns of biodiversity have been actively researched ever since the pioneering work of Darwin (1859) and Wallace (1860). Gaston (2000) recently sketched the state of the art in this discipline and concluded that lately there has been a shift of focus from local to geographic scale and a move from descriptive to causal biogeography. The present study follows that trend and investigates the inter-OGU relationships by hierarchical clustering of β-diversity indices and by performing parsimony analyses of endemicity. Both analytical zoogeographical methods basically measure the same thing, namely that if two OGU's share the same species, they are more closely related than those OGU's that do not share the same species. However, whereas similarity coefficients quantify the faunistical similarity between the fauna's of any two existing OGU's and thus provide a measure of current species turnover (β-diversity), PAE allows recovery of historical relationships between the biota of any two OGU's (Rosen, 1988; De Grave, 2001). PAE has the additional advantage that it can operate with two parsimony options (Wagner and Dollo) which allows differential gauging of the dispersion capacity (long- and short-range respectively). PAE, which does not require an *a priori* phylogeny, thus basically acts as an analogue of true cladistic biogeography (the discipline that searches for the correspondence between phylogenies and area relationships). It must, however, be stressed that PAE can only act as a surrogate of cladistic biogeography. Despite this, PAE are for now, until robust phylogenetic hypotheses for the majority of holothuroids become available, the only option to decipher historical interactions. As our two analytical zoogeographical methods measure the relationship between any two bioassociational units, it can hardly surprise us that the main differences between the two approaches are found in the crown topologies rather than in the overall topology.

A first important observation comes from the area-dendrograms obtained through clustering with similarity coefficients (fig. 5). Hereby we, by large, prefer the topology as obtained with the second Kulczynski coefficient (fig. 5B) because this coefficient is known to behave more robust under circumstances were disproportionate number of samples are acting (Price, 1982 and references therein; Samyn & Thandar, 2003). This clustering learns that species turnover is lowest (largest similarity coefficients) within and between the (NRS, SRS, AB) and the (SB, MP and MC) branches. On the other hand, species turnover is at its largest at the southern extreme, *i.e* at the boundary between CP and NP. The intermediate position of the NP between the (NRS,SRS,AB,MC,SB,MP) and the CP once again proves that it acts as a bleeding zone between the Indo-Pacific and the South African Province (see also Thandar, 1989; Samyn & Thandar, 2003). The parsimony-based analyses provide complementary insights into the biogeographical evolution of the concerned taxa. Dollo and Wagner parsimony exposed some important differences (whereby it must be stressed that disparity does not necessarily favour one scenario over another). For instance Dollo parsimony returned ((AB,SRS),NRS) whilst Wagner gave back ((AB,NRS),SRS) as topology for the Red Sea, Arab Basin region. Dollo parsimony (dispersion restricted) thus indicates that the SRS has more affinity with the AB, while Wagner parsimony (dispersion allowed) reveals that taxa from the AB can reach the NRS. These observations in combination with the similarity coefficients indicate that the narrow and shallow passage between the Red Sea and the Gulf of Aden, the zoogeographic barrier of the Bab-el-Mandab (Briggs 1974; Price 1982), is (at least nowadays) of minor significance in the dispersion of shallow-water holothuroids. This observation is in agreement with Kemp's (1998) postulate on the biogeography of the chaetodontid fish from the Soccotra Archipelago. The hypothesis that the North and South Red Sea fauna's are separated by a zoogeographic barrier around 20° N (Kemp, 1998 and references therein) is harder to prove given the paucity of distribution data from the central part of the Red Sea (see fig. 4). Nevertheless, figure seven, indicates that at roughly that latitude, quite a few aspidochirotids are replaced by apodids and to a lesser extent dendrochirotids. Closer examination indicates that the majority of these apodids belong to the family Synaptidae that have the ability to disperse over longer distances, thanks to their planctotrophic larvae. This explains why our PAE under Wagner parsimony (dispersion not constricted) put the Arab Basin and the North Red Sea in one clade. In fact, the reality of long-range dispersion of Indo-Pacific species through the Red Sea is evidenced by the Lessepsian migrations of *Holothuria impatiens* (Forskål, 1775), *Holothuria poli* Delle Chiaje, 1823 and *Leptosynapta inharens* (O.F. Müller, 1776) (Tortonese, 1953) and by the fact that the majority of holothuroids at the most northern extreme of the Red Sea (the Gulfs of Aqaba and Suez) belong to the aspidochirotids (Samyn, in press) and the apodids (again mainly the Synaptidae). Further, as indicated by figure 6B, the Arab Basin and the southern Red Sea are intimately connected. However, whether this region has to be seen as a distinct biogeographical region [an extension from the centre of endemism in Oman (Randall & Hoover, 1995)], as postulated by Kemp (1998), can here not be decided, for the simple reason that we lack detailed holothuroid species lists from most of southeast Arabia.

The relationships between the circumtropical OGU's (Mascarene plateau, Somali Basin and the Mozambique Channel) returned different for every analysis. The similarity coefficients teach us that the Mascarene Plateau (roughly composed of the Seychelles, Mauritius, Réunion and the eastern side of Madagascar) and the Somali Basin are always positioned in the same cluster; the Mozambique Channel is according to the second Kulczynski coefficient most similar to that cluster (fig. 5B). Here the PAE returned a fully resolved picture only under Wagner parsimony; under Dollo parsimony two most parsimonious trees were recovered [*i.e.* (CP,(NP,(MC,(SB,(MP,(NRS,(SRS,AB))))))) and (CP,(NP,(MP,(SB,MC),(NRS,(SRS,AB))))))]. Potential reasons for such ambiguity are plentiful, but the most straightforward one can readily be read from figure seven, which shows that at several latitudes important order turnovers occur within the Somali Basin and the Mascarene Plateau (one from 18 to 8°S; one from 8 to 1°S and one from 1°S to 10°N), which thus possibly hold several as yet unrecognised biogeographic units. Undoubtedly, *de novo* sampling in these regions (e.g. the poorly known Comores, Mafia Island, Somali Coast) can reveal if these observations are truth or artefact. Be it as it may, it is clear that the circumtropical OGU's are to a large extent connected to each other.

Now rests the question on the causality of the observed patterns. It is generally assumed (Bakus, 1973) that dendrochirotids are considered to inhabit temperate rather than tropical waters, while for aspidochirotids the reverse situation exists. The reason for this has been attributed to the feeding habit of the orders (Bakus, 1973 and many others): dendrochirotids being suspension-feeders (and thus by large preferring colder, richer water), whereas aspidochirotids and apodids (family Synaptidae, not Chiridotidae which are burrowing) are epibenthic deposit feeders (preferring warmer waters were they act as "vacuum cleaners").

Levin (1999), however, disregarded the above explanation and claimed that the low density of dendrochirotids in the tropics has to be attributed to (i) an absence of attachment sites; (ii) weak wave action and high sedimentation and (iii) competitive exclusion by aspidochirotids. We do not want to go into too much detail, but it is long known (Darwin, 1845) that coral reefs flourish in a large circumtropical belt (Stoddart & Young, 1971). These biogenic constructs fabricate the wanted attachment sites, are not seldom subject to strong wave action (e.g. atolls) and are found exactly at these locations where there's hardly any sedimentation.

Given the above-sketched patterns, it is now clear that important taxonomic turnovers occur within the latitudinal and longitudinal gradient of the WIO, which thus by far is the homogeneous area as has long been thought (Briggs, 1974). As shown by figure eight, their exists a considerable discrepancy in dispersion capacity between the species with planctotrophic and the species with lecitotrophic larvae. By combining this dispersion capacity with the prevalent currents (fig. 11) and the geological history we can now arrive at an integrated picture.

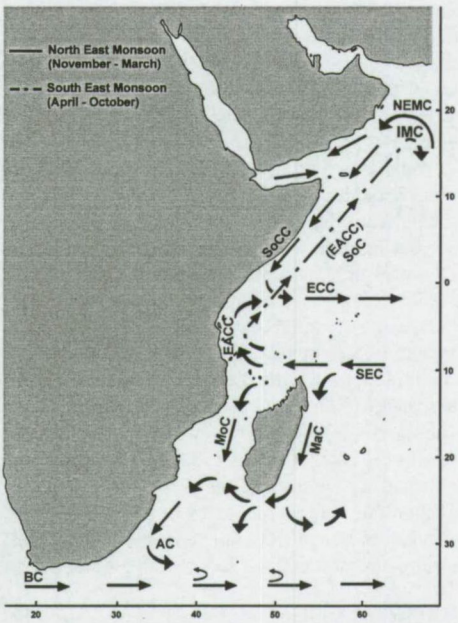

Fig. 11. Prevailing currents in the western Indian Ocean (abbreviations of the currents in introduction).

Bellwood & Hughes (2001), Roberts *et al.* (2002) and many others have conclusively shown that within the Indo-Pacific, species richnesses peak in the East Indies triangle (EIT). Away from this local zenith, species numbers rapidly tail off towards the eastern Pacific and the western Indian Ocean. An almost uncountable number of hypotheses have been put forward to explain this pattern, but (as any scholarly textbook will tell) they come in three main breeds: (i) centre of origin and dispersion; (ii) centre of accumulation and (iii) centre of survival. Whatever the correct explanation is for the origin of the EIT, it seems clear that nowadays the WIO fauna is - through the SEC and NEMC - to a lesser or larger extent connected with the EIT. Such connectivity is supported by the fact that most of the shallow-water WIO holothuroids are clearly related to some Indo-Pacific species and that most of the WIO genera are shared with other areas in the WIO (Thandar, 1989). By analysing the current patterns within the WIO (see fig. 11) in conjection with the dispersion capacity, the recent (crown clades in the PAE) biogeographic units can be largely explained. In the PAE, the Red Sea/Arab Basin is derived from the western Indian Ocean *sensu stricto*. In the Red Sea / Arab Basin region species can come in from the East (carried by the NEMC) and from the South (with the SoC). The paucity of stepping stones along the northern Arabian Sea and the cold upwelling along the East Coast of Somalia act as a filter for species with limited dispersion capacity and as such explain why the proportion of dendrochirotids is lower as expected in this region (cfr. fig. 10). A similar situation exists in the circumtropical OGU's MP, MC and SB where disproportionate high ratios of aspidochirotids/dendrochirotids are found (cfr. fig. 10); here again only those species with long-lived larvae

seem to have survived the journey across the Indian Ocean. Towards the more southern OGU's the proportion of species with lecitotrophic larvae increases steadily. This cannot (at least not to the same extent) be explained through the same dispersion mechanism (*i.e.* coming from the EIT) for these communities are dispersion limited. Rather, as can be deduced from the PAE, these fauna's are the oldest (although we cannot substantiate this with hard evidence such as fossils), and thus are best seen as relicts of historical distributions. However, the fact that the fauna's of southern Australia, New Zealand, Antarctica and South America show no clear relationships with the WIO fauna indicates that it are not Mesozoic and early Cenozoic plate-tectonics that shaped the distribution pattern (Thandar, 1989; see also De Grave, 2001). Nevertheless, assigning a relict status to the CP / NP fauna is in (partial) agreement with Santini & Winterbottom's (2002) vicariant scenario. These authors give evidence that part of the Indo-Pacific fauna (inclusive of the EIT) has originated from ancient lineages within the western Indian Ocean. We cannot agree with Santini & Winterbottom's (2002) decision to place the Red Sea/Arab Basin as the cradle of the WIO fauna, for we found that this area was the most derived in our PAE analyses. Rather we believe that the (geologically recent) Pleistocene glacial swings have not only led to the closure of the Red Sea at the Bab-el-Mandab and to the complete evaporation of the Persian Gulf, but also to some rather extensive species range shifts that have trapped species in refugia such as the Red Sea and the southern WIO. Roy *et al* (1998) have demonstrated for Atlantic and eastern Pacific prosobranch gastropods, those post-Pleistocene latitudinal diversity gradients are significantly correlated with average sea surface temperature. If the latter is true for the WIO as well, then it becomes clear why the low temperature loving, suspension-feeding dendrochirotids are doing so well at high southern latitudes and why they are doing so poorly in the Red Sea/Arab Basin biogeographic unit. It thus seems that in the former area they have become so well established (and to a large degree isolated) that they now constitute an active evolutionary centre with a high level of endemism (unpublished data), while in the latter they have been competitively excluded by the better adapted high temperature-loving, epibenthic aspidochirotids.

Rapoport's rule

The present study also had one serendipitous find: the latitudinal gradient of the species community in the meridian direction. This distribution clearly shows that, in a narrow circumtropical band, the majority of the holothuroid fauna belongs to the order Aspidochirotida (see also Samyn, in press). Previously, Levin (1999) has recovered the same pattern for the holothuroids of the World Ocean. This pattern is contradictory to the rule that dictates that species' range sizes decrease towards lower latitudes, *i.e.* Rapoport's rule (Gaston *et al.*, 1998). We found conclusive evidence that aspidochirotids have the largest dispersion capacity (and thus range size) amongst shallow-water holothuroids (fig. 8). Our observations are again in agreement with those of Roy *et al.* (1998) who - upon a study of the geographic ranges of nearly 4000 species of marine prosobranch gastropods living on the shelves of the western Atlantic and eastern Pacific Ocean - found that the median latitudinal ranges of species are greater, not in high but in low low latitudes. Gaston *et al* (1998) revised the latitudinal species gradients and concluded that Rapoport's rule is equivocal. If valid at all, so continued the latter authors, then only on local scale and only at higher latitudes. As we have only analysed a latitudinal range of 64° (30°N to 34 °S) we cannot falsify the latter statement. Nevertheless, the present study adds to the evidence that in the circumtropical belt, Rapoport's rule cannot be upheld and thus most probably deserves its epitaph (Gaston *et al.* 1998).

Conclusions

Describing and understanding the patterns of biodiversity always involves gross abstractions because these patterns are subject to a correlate of causal parameters (physical variables such as area, depth, temperature and geological history as well as biological variables such as productivity, dispersion capacity, extinction and speciation) that operate at different scales. The present study provided the first description and a tentative understanding of the biodiversity patterns as revealed by shallow-water holothuroids of the WIO. The WIO can roughly be divided in three larger biogeographic realms: the Red Sea and associated Arab Basin, an asymmetrical circumtropical region stretching from the horn of Africa to southern Mozambique and the temperate Cape province. The subtropical Natal Basin acts as the bleeding zone between the tropical and temperate provinces. The main causality of this pattern is the dispersion capacity.

Acknowledgments

It is with great pleasure that we thank Drs C. Massin (Royal Belgian Institute of natural Sciences, Belgium) and F.W.E. Rowe (Australian Museum) for their thorough criticism on the dataset. We also want to express our gratitude to Dr N. Koedam (Free University Brussels, Belgium) for his constructive criticism on the first draft of this manuscript. Dr. E. Vanden Berghe is greatly acknowledged for writing the macro that calculates the bootstrapped confidence limits.

Financial support for travel grants to Kenya and the Republic of South Africa came from the Flemish Fund for Scientific Research (project number G.0086.96), the Ministry of the Flemish Community (project number BIL98/84 and BIL01/46) and the Research Council of the Free University of Brussels

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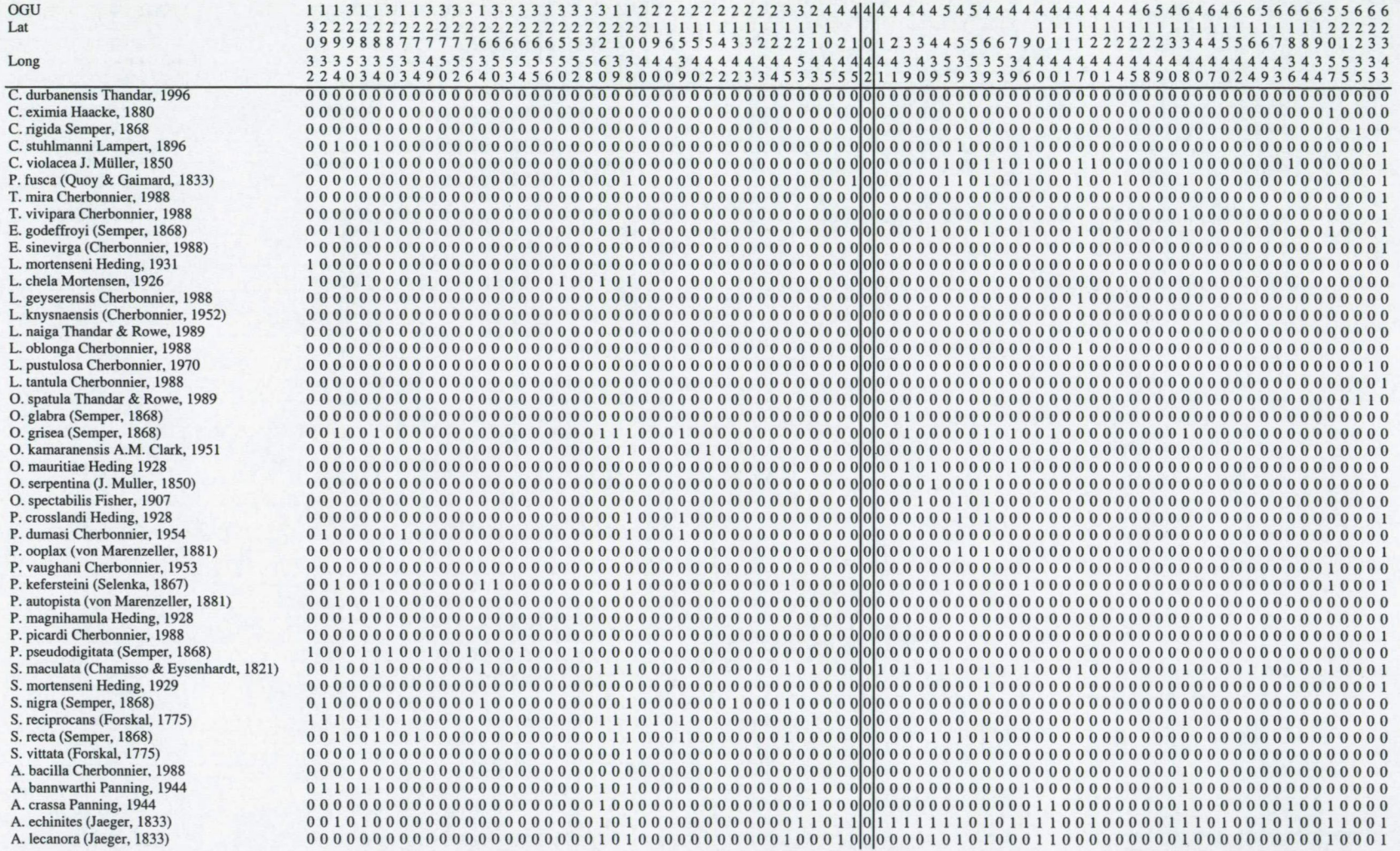
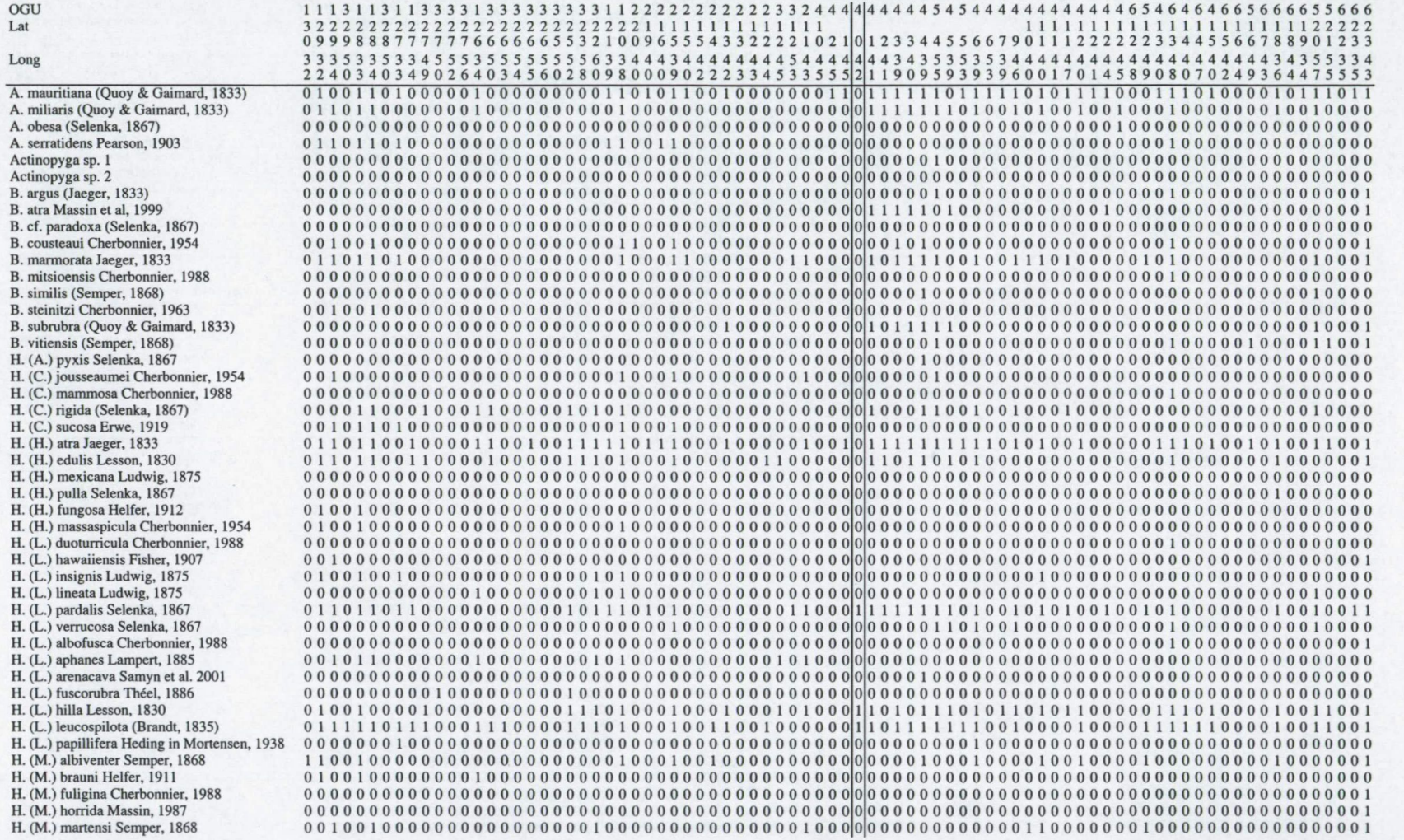
Appendix. Matrix with presence/absence scorings over the one degree cells that hold records. Left from verticale line: northern hemisphere cells; right: southern hemisphere cells.


OGU
Lat
Long
C. durbanensis Thandar, 1996
C. eximia Haacke, 1880
C. rigida Semper, 1868
C. stuhlmanni Lampert, 1896
C. violacea J. Müller, 1850
P. fusca (Quoy & Gaimard, 1833)
T. mira Cherbonnier, 1988
T. vivipara Cherbonnier, 1988
E. godeffroyi (Semper, 1868)
E. sinevirga (Cherbonnier, 1988)
L. mortenseni Heding, 1931
L. chela Mortensen, 1926
L. geyserensis Cherbonnier, 1988
L. knysnaensis (Cherbonnier, 1952)
L. naiga Thandar & Rowe, 1989
L. oblonga Cherbonnier, 1988
L. pustulosa Cherbonnier, 1970
L. tantula Cherbonnier, 1988
O. spatula Thandar & Rowe, 1989
O. glabra (Semper, 1868)
O. grisea (Semper, 1868)
O. kamaranensis A.M. Clark, 1951
O. mauritiae Heding 1928
O. serpentina (J. Muller, 1850)
O. spectabilis Fisher, 1907
P. crosslandi Heding, 1928
P. dumasi Cherbonnier, 1954
P. ooplax (von Marenzeller, 1881)
P. vaughani Cherbonnier, 1953
P. kefersteini (Selenka, 1867)
P. autopista (von Marenzeller, 1881)
P. magnihamula Heding, 1928
P. picardi Cherbonnier, 1988
P. pseudodigitata (Semper, 1868)
S. maculata (Chamisso & Eysenhardt, 1821)
S. mortenseni Heding, 1929
S. nigra (Semper, 1868)
S. reciprocans (Forskal, 1775)
S. recta (Semper, 1868)
S. vittata (Forskal, 1775)
A. bacilla Cherbonnier, 1988
A. bannwarthi Panning, 1944
A. crassa Panning, 1944
A. echinites (Jaeger, 1833)
A. lecanora (Jaeger, 1833)

| OGU | 6 6 6 6 6 5 6 6 6 6 7 7 7 7 7 8 8 8


OGU
Lat
Long
A. mauritiana (Quoy & Gaimard, 1833)
A. miliaris (Quoy & Gaimard, 1833)
A. obesa (Selenka, 1867)
A. serratidens Pearson, 1903
Actinopyga sp. 1
Actinopyga sp. 2
B. argus (Jaeger, 1833)
B. atra Massin et al, 1999
B. cf. paradoxa (Selenka, 1867)
B. cousteaui Cherbonnier, 1954
B. marmorata Jaeger, 1833
B. mitsioensis Cherbonnier, 1988
B. similis (Semper, 1868)
B. steinitzi Cherbonnier, 1963
B. subrubra (Quoy & Gaimard, 1833)
B. vitiensis (Semper, 1868)
H. (A.) pyxis Selenka, 1867
H. (C.) jousseaumei Cherbonnier, 1954
H. (C.) mammosa Cherbonnier, 1988
H. (C.) rigida (Selenka, 1867)
H. (C.) sucosa Erwe, 1919
H. (H.) atra Jaeger, 1833
H. (H.) edulis Lesson, 1830
H. (H.) mexicana Ludwig, 1875
H. (H.) pulla Selenka, 1867
H. (H.) fungosa Helfer, 1912
H. (H.) massaspicula Cherbonnier, 1954
H. (L.) duoturricula Cherbonnier, 1988
H. (L.) hawaiiensis Fisher, 1907
H. (L.) insignis Ludwig, 1875
H. (L.) lineata Ludwig, 1875
H. (L.) pardalis Selenka, 1867
H. (L.) verrucosa Selenka, 1867
H. (L.) albofusca Cherbonnier, 1988
H. (L.) aphanes Lampert, 1885
H. (L.) arenacava Samyn et al. 2001
H. (L.) fuscorubra Théel, 1886
H. (L.) hilla Lesson, 1830
H. (L.) leucospilota (Brandt, 1835)
H. (L.) papillifera Heding in Mortensen, 1938
H. (M.) albiventer Semper, 1868
H. (M.) brauni Helfer, 1911
H. (M.) fuligina Cherbonnier, 1988
H. (M.) horrida Massin, 1987
H. (M.) martensi Semper, 1868

OGU	6	6	6	6	6	5	6	6	6	6	7	7	7	7	7	7	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Lat	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
	4	4	4	5	5	5	6	6	7	7	8	9	0	0	1	1	2	2	2	2	3	3	3	3	3	4	4	4	4	4	4	4
Long	3	3	3	3	4	4	3	3	3	3	3	3	3	3	2	3	1	2	2	3	1	2	2	2	2	1	1	2	2	2	2	2
	3	5	6	3	4	7	2	3	2	3	2	1	0	1	9	0	8	8	9	0	8	5	6	7	8	8	9	0	1	2	3	4	5	6	7
A. mauritiana (Quoy & Gaimard, 1833)	0	1	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. miliaris (Quoy & Gaimard, 1833)	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. obesa (Selenka, 1867)	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. serratidens Pearson, 1903	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinopyga sp. 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Actinopyga sp. 2	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. argus (Jaeger, 1833)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. atra Massin et al, 1999	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. cf. paradoxa (Selenka, 1867)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. cousteaui Cherbonnier, 1954	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. marmorata Jaeger, 1833	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. mitsioensis Cherbonnier, 1988	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. similis (Semper, 1868)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. steinitzi Cherbonnier, 1963	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. subrubra (Quoy & Gaimard, 1833)	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B. vitiensis (Semper, 1868)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (A.) pyxis Selenka, 1867	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (C.) jousseaumei Cherbonnier, 1954	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (C.) mammosa Cherbonnier, 1988	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (C.) rigida (Selenka, 1867)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (C.) sucosa Erwe, 1919	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (H.) atra Jaeger, 1833	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (H.) edulis Lesson, 1830	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (H.) mexicana Ludwig, 1875	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
H. (H.) pulla Selenka, 1867	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (H.) fungosa Helfer, 1912	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (H.) massaspicula Cherbonnier, 1954	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) duoturricula Cherbonnier, 1988	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) hawaiiensis Fisher, 1907	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) insignis Ludwig, 1875	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) lineata Ludwig, 1875	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) pardalis Selenka, 1867	0	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) verrucosa Selenka, 1867	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) albofusca Cherbonnier, 1988	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) aphanes Lampert, 1885	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) arenacava Samyn et al. 2001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) fuscorubra Théel, 1886	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) hilla Lesson, 1830	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) leucospilota (Brandt, 1835)	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (L.) papillifera Heding in Mortensen, 1938	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (M.) albiventer Semper, 1868	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (M.) brauni Helfer, 1911	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (M.) fuligina Cherbonnier, 1988	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (M.) horrida Massin, 1987	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
H. (M.) martensi Semper, 1868	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

OGU	1 1 1 3 1 1 3 1 1 3 3 3 3 1 3 3 3 3 3 3 3 3 3 1 1 2 2 2 2 2 2 2 2 2 2 2 3 3 2 4 4 4 4	4 4 4 4 4 5 4 5 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 6 5 4 6 4 6 4 6 5 6 6 6 6 5 5 6 6 6
Lat	3 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2
	0 9 9 9 8 8 8 7 7 7 7 7 7 6 6 6 6 6 6 5 5 3 2 1 0 0 9 6 5 5 5 4 3 3 2 2 2 2 1 0 2 1 0	1 2 3 3 4 4 5 5 6 6 7 9 0 1 1 1 2 2 2 2 2 2 3 3 4 4 5 5 6 6 7 8 8 9 0 1 2 3 3
Long	3 3 3 5 3 3 5 3 3 4 5 5 5 3 5 5 5 5 5 5 5 5 6 3 3 4 4 4 3 4 4 4 4 4 4 4 4 5 4 4 4 4 4	4 4 3 4 3 5 3 5 3 5 3 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 3 4 3 5 5 3 3 4
	2 2 4 0 3 4 0 3 4 9 0 2 6 4 0 3 4 5 6 0 2 8 0 9 8 0 0 0 9 0 2 2 2 3 3 4 5 3 3 5 5 5 2	1 1 9 0 9 5 9 3 9 3 9 6 0 0 1 7 0 1 4 5 8 9 0 8 0 7 0 2 4 9 3 6 4 4 7 5 5 5 3
H. (M.) ocellata Jaeger, 1833	0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (M.) scabra Jaeger, 1833	0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0	1 0 1 1 1 1 1 1 0 1 0 0 0 1 1 0 0 1 1 0 0 1 0 1 0 1 1 1 0 1 0 0 1 0 1 0 1 1 0 1 1 1
H. (M.) scabra var. versicolor Conand, 1986	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (M.) timana Lesson, 1830	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (M.) tortonesei Cherbonnier, 1979	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (M.) fuscopunctata Jaeger, 1833	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (M.) nobilis (Selenka, 1867)	0 1 1 0 0 1 0 1 1 0 0 0 0 1 0 0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0	1 1 1 1 1 1 0 0 1 0 0 1 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 1 1 1 0 0 1
H. (P.) crosnieri Cherbonnier, 1988	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
H. (P.) difficilis Semper, 1868	0 1 1 0 1 1 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 1 0 0 0 1 0 0 0 0 1 1 1 0 1 0 0 0 0 1 0 0 1 0 0 0 1
H. (P.) excellens Ludwig, 1875	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (P.) insolita Cherbonnier, 1988	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
H. (P.) samoana Ludwig, 1875	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1
H. (R.) poli Delle Chiaje, 1823	0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (S.) bacilla Cherbonnier, 1988	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1
H. (S.) erinacea Semper, 1868	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1	0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 1 0 1 0 1 0 0 0 0 0 0 0 0 0 1
H. (S.) moebii Ludwig, 1883	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0
H. (S.) parva Krauss in Lampert, 1885	0 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 1 1 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1	1 0 0 0 0 0 1 0 1 0 0 1 0 0 0 0 1 0 1 0 0 1 1 1 1 0 1 0 0 0 0 0 0 0 0 0 1 1
H. (S.) spinea Cherbonnier, 1988	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (S.) vittalonga Cherbonnier, 1988	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
H. (S.) cinerascens (Brandt, 1835)	0 0 1 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 1 1 0 0 0 1	1 0 1 1 1 1 1 0 1 0 0 1 0 0 0 1 1 0 0 0 0 0 1 1 1 0 1 0 0 1 0 1 0 0 1 1 0 0 1
H. (S.) flavomaculata Semper, 1868	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
H. (S.) granosa Cherbonnier, 1988	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (S.) dofleini Augustin, 1908	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (S.) fuscocinerea Jaeger, 1833	0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0	1 0 1 1 1 1 0 0 1 0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 1 0 0 1 0 0 0 1 0 0 0 1
H. (S.) modesta Ludwig, 1875	0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (S.) olivacea Ludwig, 1888	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1
H. (S.) pervicax Selenka, 1867	0 0 1 0 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 1 0 0 0 0 1 1 0 0 1	0 0 1 1 1 1 0 0 1 0 1 0 1 1 1 1 0 1 1 0 1 0 0 0 1 1 1 0 1 0 0 0 0 0 0 1 0 0 1
H. (T.) hamata Pearson, 1913	0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (T.) klunzingeri Lampert, 1885	0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (T.) maculosa Pearson, 1913	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0 1 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
H. (T.) notabilis Ludwig, 1875	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0
H. (T.) spinifera Théel, 1886	0 0 0 1 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (T.) squamifera Semper, 1868	0 1 1 0 1 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (T.) turriscelsa Cherbonnier, 1980	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (T.) arenicola Semper, 1868	0 1 1 0 1 1 0 1 0 1 0 0 0 1 1 0 0 0 0 0 1 0 1 1 1 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0	1 0 0 1 1 1 0 0 1 0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 1 0 0 0 1
H. (T.) cf. arenicola Semper, 1868	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (T.) decorata von Marenzeller, 1882	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0
H. (T.) gracilis Semper, 1868	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (T.) impatiens (Forskal, 1775)	1 1 1 0 1 1 0 1 0 1 0 0 0 1 0 0 1 0 0 1 1 1 0 1 1 1 1 1 0 1 0 0 1 0 0 1 0 1 0 1 0 0 1	1 0 1 1 1 1 1 1 0 1 0 1 1 1 1 0 1 1 0 1 0 0 0 1 1 1 0 1 0 1 0 1 1 0 0 1 0 0 0 1
H. (T.) milloti Cherbonnier, 1988	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (T.) remollescens Lampert, 1885	0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
H. (T.) strigosa Selenka, 1867	0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0	0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1
L. pertinax (Ludwig, 1875)	0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	1 1 0 1 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
Labidodemas sp.	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
L. rugosum (Ludwig, 1875)	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1	0 0 0 0 0 1 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

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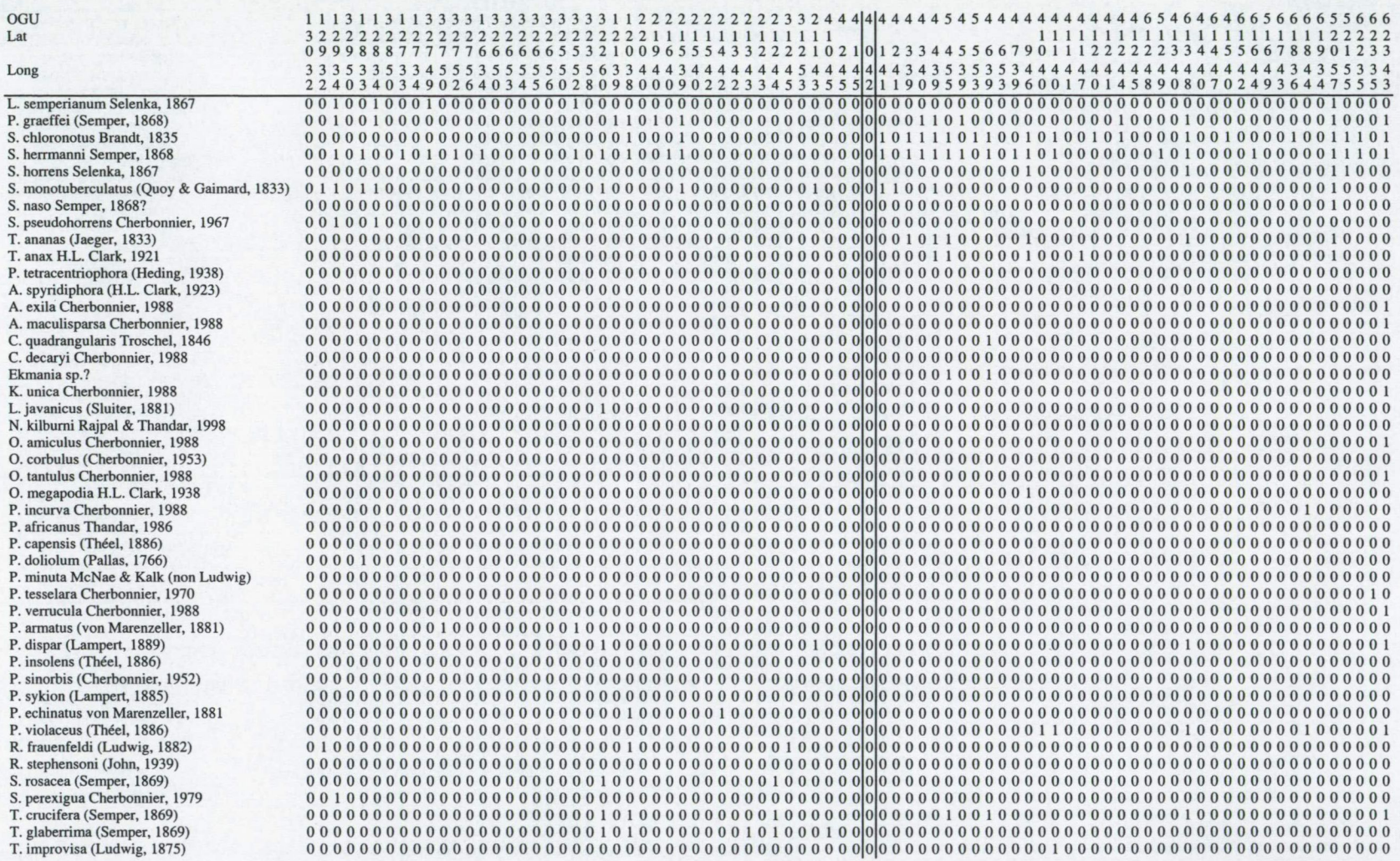
OGU
Lat
Long
L. semperianum Selenka, 1867
P. graeffei (Semper, 1868)
S. chloronotus Brandt, 1835
S. herrmanni Semper, 1868
S. horrens Selenka, 1867
S. monotuberculatus (Quoy & Gaimard, 1833)
S. naso Semper, 1868?
S. pseudohorrens Cherbonnier, 1967
T. ananas (Jaeger, 1833)
T. anax H.L. Clark, 1921
P. tetracentriophora (Heding, 1938)
A. spyridiphora (H.L. Clark, 1923)
A. exila Cherbonnier, 1988
A. maculisparsa Cherbonnier, 1988
C. quadrangularis Troschel, 1846
C. decaryi Cherbonnier, 1988
Ekmania sp.?
K. unica Cherbonnier, 1988
L. javanicus (Sluiter, 1881)
N. kilburni Rajpal & Thandar, 1998
O. amiculus Cherbonnier, 1988
O. corbulus (Cherbonnier, 1953)
O. tantulus Cherbonnier, 1988
O. megapodia H.L. Clark, 1938
P. incurva Cherbonnier, 1988
P. africanus Thandar, 1986
P. capensis (Théel, 1886)
P. doliolum (Pallas, 1766)
P. minuta McNae & Kalk (non Ludwig)
P. tesselara Cherbonnier, 1970
P. verrucula Cherbonnier, 1988
P. armatus (von Marenzeller, 1881)
P. dispar (Lampert, 1889)
P. insolens (Théel, 1886)
P. sinorbis (Cherbonnier, 1952)
P. sykion (Lampert, 1885)
P. echinatus von Marenzeller, 1881
P. violaceus (Théel, 1886)
R. frauenfeldi (Ludwig, 1882)
R. stephensoni (John, 1939)
S. rosacea (Semper, 1869)
S. perexigua Cherbonnier, 1979
T. crucifera (Semper, 1869)
T. glaberrima (Semper, 1869)
T. improvisa (Ludwig, 1875)

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Lat	3 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2
	0 9 9 9 8 8 8 7 7 7 7 7 7 6 6 6 6 6 6 5 5 3 2 1 0 0 9 6 5 5 5 4 3 3 2 2 2 2 1 0 2 1 0	1 2 3 3 4 4 5 5 6 6 7 9 0 1 1 1 2 2 2 2 2 2 3 3 4 4 5 5 6 6 7 8 8 9 0 1 2 3 3
Long	3 3 3 5 3 3 5 3 3 4 5 5 5 3 5 5 5 5 5 5 5 5 6 3 3 4 4 4 3 4 4 4 4 4 4 4 4 5 4 4 4 4 4	4 4 3 4 3 5 3 5 3 5 3 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 3 4 3 5 5 3 4
	2 2 4 0 3 4 0 3 4 9 0 2 6 4 0 3 4 5 6 0 2 8 0 9 8 0 0 0 9 0 2 2 2 3 3 4 5 3 3 5 5 5 2	1 1 9 0 9 5 9 3 9 3 9 6 0 0 1 7 0 1 4 5 8 9 0 8 0 7 0 2 4 9 3 6 4 4 7 5 5 5 3
H. cylindrica (Semper, 1868)	0 0 0

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OGU	1 1 1 3 1 1 3 1 1 3 3 3 3 1 3 3 3 3 3 3 3 3 3 1 1 2 2 2 2 2 2 2 2 2 2 2 2 2 2 3 3 2 4 4 4	4 4 4 4 4 4 5 4 5 4 4 4 4 4 4 4 4 4 4 4 4 4 6 5 4 6 4 6 4 6 6 5 6 6 6 6 5 5 6 6 6
Lat	3 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2
	0 9 9 9 8 8 8 7 7 7 7 7 6 6 6 6 6 6 5 5 3 2 1 0 0 9 6 5 5 5 4 3 3 2 2 2 2 1 0 2 1	0 1 2 3 3 4 4 5 5 5 6 6 7 9 0 1 1 1 2 2 2 2 2 2 3 3 4 4 5 5 5 6 6 7 8 8 9 0 1 2 3 3
Long	3 3 3 5 3 3 5 3 3 4 5 5 5 3 5 5 5 5 5 5 5 5 6 3 3 4 4 4 3 4 4 4 4 4 4 4 4 4 4 5 4 4 4 4	4 4 4 3 4 3 5 3 5 3 5 3 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 4 3 4 3 5 5 3 3 4
	2 2 4 0 3 4 0 3 4 9 0 2 6 4 0 3 4 5 6 0 2 8 0 9 8 0 0 0 9 0 2 2 2 3 3 4 5 3 3 5 5 5	2 1 1 9 0 9 5 9 5 9 3 9 3 9 6 0 0 1 7 0 1 4 5 8 9 0 8 0 7 0 2 4 9 3 6 4 4 7 5 5 5 3
P. ornatum (Ed. Perrier, 1893)	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0
R. gigantea Cherbonnier, 1970	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
R. minuta Cherbonnier, 1970	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
A. africana (Semper, 1868)	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1	1 0 1 1 0 1 1 0 1 0 0 1 0 1 1 0 0 0 0 0 1 0 1 0 0 0 0 0 0 1 0 0 1 0 0 0 1
C. aciculus (Semper, 1868)	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0
C. bifurcatus (Deichmann, 1944)	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
C. pichoni Cherbonnier, 1988	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
O. ehrenberghi (Selenka, 1868)	0 0 1 0 1 0 0 1 1 0 0 0 0 0 1 0 0 0 0 0 1 0 1 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 0	0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0 0 0 0 1 0 0 0 0 0 0 0 0 0 0 1
O. mauritiensis Heding & Panning, 1954	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 0 1
A. leucoprocta (H.L. Clark, 1938)	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 0 0 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

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Lat	2	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
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Long	3	3	3	3	4	4	3	3	3	3	3	3	3	3	2	3	1	2	2	3	1	2	2	2	2	1	1	2	2	2	2	2	2
	3	5	6	3	4	7	2	3	2	3	2	1	0	1	9	0	8	8	9	0	8	5	6	7	8	8	9	0	1	2	3	4	5	6	7
P. ornatum (Ed. Perrier, 1893)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
R. gigantea Cherbonnier, 1970	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
R. minuta Cherbonnier, 1970	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
A. africana (Semper, 1868)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. aciculus (Semper, 1868)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. bifurcatus (Deichmann, 1944)	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
C. pichoni Cherbonnier, 1988	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
O. ehrenberghi (Selenka, 1868)	0	0	0	0	0	1	1	0	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
O. mauritiensis Heding & Panning, 1954	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. leucoprocta (H.L. Clark, 1938)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Chapter Seven

35958

Taxonomists' requiem?

SAMYN, Y[1] and MASSIN, C.[2]

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The need to document and understand the world's natural history, with the sixth great mass extinction caused by *Homo sapiens* seemingly on the way *(1)*, is greater than ever, as J. McCarter and co-authors discuss in their Essay "Safeguarding the world's natural treasures" (Science's Compass, 7 Dec., p. 2099). And we agree that museums and other centers of excellence on biodiversity matters have a prime role to play in objectively assessing the history and future of biological diversity.

Scientists today have the will and the technological means to quickly catalog the world's fauna and flora *(2)*; however, young biologists are hardly encouraged to enter the narrow but rather competitive field of pure taxonomy because the possibilities to pursue an academic career are jeopardized by the current publication system. Indeed, description of new species and revisions at family or generic level are critical to provide a reliable estimate of biodiversity *(3)*, yet this research is seldom validated in terms of the widely (mis)-used impact factor system, this doom scenario applies especially to taxonomists working with certain invertebrate groups.

As an illustration, consider the papers published by the "big five" *(4)* holothurian taxonomists of the last century: 84% of their papers were published in journals with no impact factor at all, 15% was published in journals with an impact factor lower than one, while 1% only appeared in journals with an impact factor higher than one. On the other hand research relying on the work laid down by the taxonomists "easily" finds its way to the scientific journals with an impact factor comparable to that of *Science*.

Only if the publication system deters this malaise, and promotes taxonomic and faunistical works will more scientists be attracted to this highly proactive and satisfying branch of biology. Indeed, Robert May's bricks and cement *(5)* are necessary for constructing a solid building, but let's make sure we have enough brick-makers and bricklayers to build a solid and stable biodiversity house.

References and notes

1. W. Gibbs, *Sci Am.* **285,** 28 (2001).
2. The All Species Project [A. Lawler, *Science* **294,** 769 (2001)] is intended to provide the framework for such an inventory.
3. J. Veron [in *Corals of Australia and the Indo-Pacific* (Angus & Robertson, London, 1986)] listed nearly 400 nominal species in the genus *Acropora*, but after taxonomic revision [*Corals of the World* (Australian Institute of Marine Sciences, Townsville, 2000], only 170 species were retained under *Acropora*.
4. By "big five" we mean the five holothurian taxonomists that have had the highest impact on the current taxonomy of the Holothuroidea, from 1921 to date: E Deichmann, A. Panning, G. Cherbonnier, D. Pawson & F. Rowe.
5. R. M. May, *Nature* **347,** 130 (1990).

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Conservation of aspidochirotid holothurians in the littoral waters of Kenya.

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ABSTRACT

Aspidochirotid sea cucumbers (Echinodermata: Holothuroidea) are heavily fished in the littoral waters of Kenya, which results in plummeting stocks. In order to conserve and manage these natural resources appropriate conservation and management plans have to be developed. This can only be done if high quality research on different levels broadens our understanding of the stocks in question. This paper discusses five layers of understanding which should be achieved before holothurian conservation in East Africa can be effective.

Keywords

Echinodermata; Holothuroidea; Biodiversity; Conservation; East-Africa; Kenya.

Introduction

Along the Kenyan coast most aspidochirotid sea cucumbers are nowadays collected *en masse* and sold to foreign markets (sea cucumbers are not on the diet in Kenya). Ferdouse (1999) reports on the imports of beche-de-mer in Hong Kong and Singapore; the two main retailing centers in beche-de-mer. According to this source it appears that Kenya exports only towards Singapore, however with increasing levels (1.1 % of the total import in 1993; 2.9% in 1994; and 3.9 % in 1995). From the same dataset it is clear that the Kenyan export is rising while other East African countries like Madagascar and Tanzania decrease their export. The reasons for this decrease are basically unknown, probably because overfishing has decreased the stocks dramatically (Massin, pers. comm., pers. observ.) It appears that there is a shift from the collection sites from Madagascar and Tanzania towards mainly Kenya. However, in Kenya collecting is taking place in a rather unbridled way since; (a) no regulations whatsoever exist for collecting sea cucumbers outside the protected marine parks, and (b) the immediate financial benefits for the collector and trader are considerable.

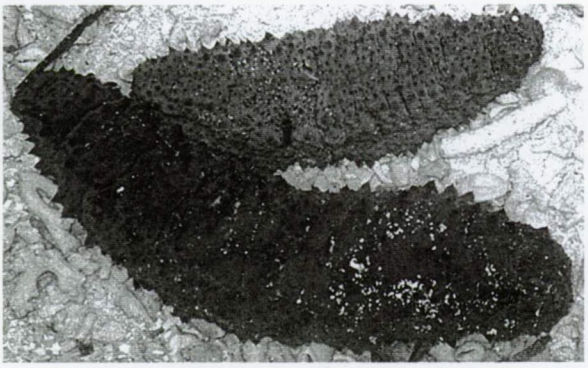
It is thus clear that, if a sustainable exploitation of the large sea cucumber market is desired, good conservation and management plans will have to be made. Only that way will it be possible to conserve and replenish Kenya's plummeting stocks (e.g. in Gazi Bay, some 60 km South of Mombasa all holothurians have disappeared since fishing started in 1995, pers. observ.).

This paper will discuss some of the different basic levels of scientific understanding that are essential in the fine tuning of conservation efforts for marine biota (and especially of sea cucumbers in the western Indian Ocean).

Level one: Nomenclature & Taxonomy

Conserving biodiversity involves in a first stage that we know what to conserve. For that we need to correctly name the players in a unequivocal and universally understood way. However, nomenclature and taxonomy are scientific disciplines that are often neglected by a large number of biologists, since these disciplines are often seen as a burden rather then a facility. The necessity for respecting the rules of nomenclature, which has as aim "to provide the maximum universality and continuity in the scientific names of animals compatible with the freedom of scientists to classify according to taxonomic judgements", can be illustrated with the following example of a commercially important species from the family Stichopodidae.

The large species, coloured bright-olive green with numerous conical light green papillae with dark green stripes and yellow to orange distal tips, bears the name *Stichopus variegatus* Semper, 1868 in a large part of the literature before 1995. *Stichopus variegatus* is however not a valid name since Rowe & Gates (1995) stated that *Stichopus horrens* Selenka, 1867 is the senior synonym of *Stichopus variegatus* Semper, 1868. The same authors elevated the variety *S. variegatus Herrmanni* Semper, 1868 to the species rank. When one should want to map holothurian biodiversity based on species accounts in literature, all records regarding *Stichopus variegatus* (and *Stichopus horrens*) must be regarded as doubtful and cannot be assigned to one or the other species unless one is able to examine the specimens *per se*.



Stichopus herrmanni Semper, 1868 as can be seen in the shallow reef lagoons in Kanamai, Kenya.

Level two: Systematics

Systematics is the discipline that describes and interprets the patterns that are produced by taxonomy. Systematics thus aims at understanding the relationships between lineages, the evolutionary trajectories, and the biogeographic distributions of organisms, knowledge which is crucial for understanding e.g. the ecological role of a species in an ecosystem.

The following two examples show that a profound knowledge of systematics and the existing literature is also necessary in naming, ordening and understanding biodiversity.

(1) The species *Stichopus variegatus* Semper, 1868 is known to be an invalid species (see above). The specimens collected as *S. variegatus* before 1995 are known to hold at least two different species (Massin, 1999; pers. comm.): *Stichopus herrmanni* Semper, 1868 and *Stichopus monotuberculatus* (Quoy & Gaimard, 1833). (2) The reef-dwelling species *Pearsonothuria graeffei* (Semper, 1868) was originally described as *Holothuria graeffei* Semper, 1868. Examination of the spicule morphology showed that this species is unrelated to the species in the genus *Holothuria*. Hence, it was transferred to the genus *Bohadschia* since the rosettes of the body wall bear some resemblance to the rosettes found in the genus *Bohadschia*. The taxonomic status of *Bohadschia graeffei* (Semper, 1868) was later critically examined by Levin, Kalinin & Stonik (1984), who found that the nature of the chemical characters of this species needed the erection of a new genus name: *Pearsonothuria* Levin, Kalinin & Stonik, 1984 was born. Indeed, by erecting the genus name *Pearsonothuria* the anomalous structure of the typical 'raquette-shaped' spicules, and the translucent and weakly developed calcareous ring, now get a more appropriate systematic position. However, the name *Bohadschia graeffei* still appears in numerous papers that deal with conservation of holothurians.

The consequence of such different classifications can easily be grasped if one considers the following hypothetical example. Suppose you were given a grant to study the inductive potential of diatoms on the metamorphosis of a sea cucumber that thrives in your study area: a species identified by specialists as *Bohadschia graeffei*. From literature you know that all the species studied thus far within your study area hold a sensitivity towards induction by diatoms. If you are unaware of the synonymous nature of *Bohadschia graeffei* and *Pearsonothuria graeffei* you could deduce the following two scenario's.

- Scenario one. You assume that each individual genus (and species) has a well-defined niche and that, as a consequence, larval metamorphosis will hardly be induced by the same diatom genera. You will start looking for different diatoms, but you'll end up puzzled, thousands of dollars poorer and frustrated that your project did not succeed.
- Scenario two. You assume that, since *Bohadschia* and *Pearsonothuria* belong to the same family, susceptibility to diatoms as a means of inducing metamorphosis is a monophylogenetic character at family level. You will be very happy with your deductive decision but you will possibly make erroneous conclusions about phylogeny.

It needs no further arguments, that incorrect taxonomy and systematics can bring erroneous conclusions at both the fundamental and the applied level. Unfortunately more grants go to the applied than to the fundamental level, so taxonomic and systematical errors are often perpetuated through time.

Level three: Faunistics

Assessing the holothurian biodiversity of a narrow political geographical entity like the Kenyan Coast is not a simple endeavor since only few recent studies have be devoted to this region (Levin, 1979; Humphreys; 1981; Rowe & Richmond, 1997). Our team, in collaboration with Kenya Wildlife Service and WWF Kenya, is currently re-evaluating the biodiversity of the Kenyan holothurian fauna. Our first results on the Kiunga Marine National Reserve (Samyn & Vanden Berghe, submitted), with its 250 km^2 the largest

marine reserve in Kenya, already show that the biodiversity of the aspidochirotid sea cucumbers in Kenya is currently underestimated (see fig. 1).

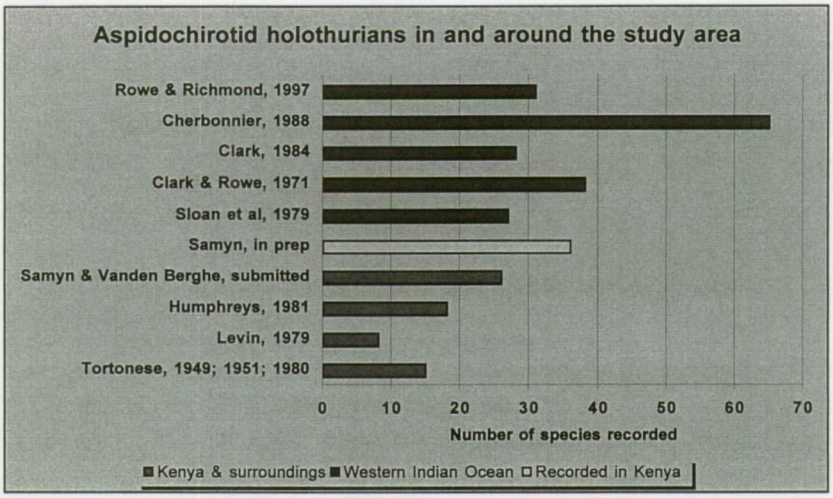


Figure 1 - Biodiversity of aspidochirotid sea cucumbers in and around Kenya as deduced from literature and sampling.

In the Kiunga Marine Reserve we observed 24 different aspidochirotid holothurians, and deduced from literature that two more species were to be expected within the boundaries of the Kiunga Marine Reserve. Our published (Massin et al., 1999) and unpublished data on the total Kenyan coastline adds at least seven more species to that list, and a search through literature indicates that three additional species can be added, bringing the total aspidochirotid fauna up to 37 species (see table 1).

Currrent Species name	Records our team	Rrecords by others	Known Geographical distribution
HOLOTHURIIDAE			
• *Actinopyga echinites* (Jaeger, 1833)	x	x	Indo-West Pacific
• *Actinopyga lecanora* (Jaeger, 1833)	xx	x	Indo-West Pacific
• *Actinopyga mauritiana* (Quoy & Gaimard, 1833)	x	x	Red Sea; Indo-West Pacific
• *Actinopyga miliaris* (Quoy & Gaimard, 1833)	x	x	Red Sea; Indo-West Pacific
• *Actinopyga plebeja* (Selenka, 1867)		x	Red Sea; Mombasa; Zanzibar; Querimba; Madagascar; Mauritius
• *Bohadschia atra* Massin et al., 1999	x		Western Indian Ocean
• *Bohadschia cousteaui* Cherbonnier, 1954	xx		Red Sea, Madagascar
• *Bohadschia marmorata* Jaeger, 1833	x	x	Red Sea; Indo-Pacific
• *Bohadschia similis* (Semper, 1868)	xx	x	Mauritius, Réunion, Philippines, New
• *Bohadschia subrubra* (Quoy & Gaimard, 1833)	x	x	Western Indian Ocean
• *Holothuria (Acanthotrapeza) pyxis* Selenka, 1867		x	Mombasa, Bay of Bengal; east Indies
• *Holothuria (Cystipus) rigida* (Selenka, 1867)	x		Red Sea; Indo-West Pacific
• *Holothuria (Halodeima) atra* Jaeger, 1833	x	x	Red Sea; Indo-Pacific
• *Holothuria (Halodeima) edulis* Lesson, 1830	x		Red Sea; Indo-Pacific
• *Holothuria (Lessonothuria) pardalis* Selenka, 1867	x	x	Red Sea; Indo-Pacific
• *Holothuria (Mertensiothuria) fuscocinerea* Jaeger,	x	x	Red Sea; Indo-West Pacific
• *Holothuria (Mertensiothuria) leucospilota* Brandt,	x	x	Red Sea; Indo-Pacific
• *Holothuria (Mertensiothuria) pervicax* Selenka,	xx	x	Red Sea; Indo-Pacific
• *Holothuria (Metriatyla) scabra* Jaeger, 1833	x	x	Red Sea; Indo-West Pacific
• *Holothuria (Microthele) fuscopunctata* Jaeger, 1833	xx		Indo-West Pacific
• *Holothuria (Microthele) nobilis* (Selenka, 1867)	x	x	Red Sea; Indo-Pacific
• *Holothuria (Platyperona) difficilis* Semper, 1868	x		Red Sea, Indo-Pacific
• *Holothuria (Selenkothuria) parva* Lampert, 1885		x	Red Sea, Indian Ocean
• *Holothuria (Semperothuria) cinerascens* (Brandt,	x	x	Red Sea; Indo-Pacific
• *Holothuria (Theelothuria) turriscelsa* Cherbonnier,	x		Indo-West Pacific
• *Holothuria (Thymiosycia) arenicola* Semper, 1868	x		Red Sea; Indo-West Pacific

Currrent Species name	Records our team	Rrecords by others	Known Geographical distribution
• *Holothuria (Thymiosycia) hilla* Lesson, 1830	x	x	Red Sea; Indo-West Pacific
• *Holothuria (Thymiosycia) impatiens* (Forskal,	x	x	Mediterranean Sea; Red Sea; Indo-
• *Labidodemas pertinax* (Ludwig, 1875)	x		Kenya, Glorioso Isl; Maldives; Java;
• *Labidodemas semperianum (Selenka, 1867)*		x	Red Sea; Indo-West Pacific
• *Pearsonothuria graeffei* (Semper, 1868)	xx		Red Sea; Indo-West Pacific
STICHOPODIDAE			
• *Stichopus chloronotus* Brandt, 1835	x		Indo-West Pacific
• *Stichopus herrmanni* Semper, 1868	x	x	Red Sea; Indo-West Pacific
• *Stichopus monotuberculatus* (Quoy & Gaimard,	x	x	Red Sea; Indo-West Pacific
• *Thelenota ananas* (Jaeger, 1833)	xx	x	Indo-West Pacific
• *Thelenota anax* H.L. Clark, 1921	xx		Indo-West Pacific

Table 1 - Aspidochirotid sea cucumbers from Kenya, as deduced from literature and sampling.
x indicates records from the Kiunga Marine National Reserve (Samyn & Vanden Berghe, submitted);
xx indicates unpublished records from Kenya.

When the holothurian fauna of the western Indian Ocean is examined, some 40 additional aspidochirotids have to be considered (see f.i. Cherbonnier, 1988). Whether these species also occur in the littoral waters of Kenya can only be known if further systematical sampling is done in the region.

Level four: Ecology

Protecting and managing the holothurian fauna of Kenya is not a simple endeavor, whereby conservation measures cannot be addressed onto the group of interest alone: the interconnectivity in ecosystems forces us to study not only in an autoecological but also in a synecological way. Indeed, both theoretical and experimental studies have shown that the stability of an ecosystem is influenced directly by the interactions between the various players. In coral reefs echinoderms are unmistakably important actors (reviewed by Birkeland, 1988), however the lack of knowledge on the level of the species (see the three levels above) and on the interactions between the other actors in the ecosystem, hinders in depth understanding of the ecological roles of sea cucumbers in coral reefs. As a consequence the impact of overfishing sea cucumbers in coral reefs are largely unknown.
Despite the large gaps in our knowledge on holothurians, we are not starting from nil; the biology and ecology of tropical holothurians was already reviewed by Bakus back in 1973. Since then, the ecology of several species is better known, however the need for further studies can be demonstrated with examples on the feeding biology of holothurians.
It is assumed that ecological distribution of sea cucumbers in coral reefs is largely dependent on microhabitat structure rather than on the type of food selected. Still, through literature one finds evidence that aspidochirotid sea cucumbers are selective for organic matter content in the sediment. The impact herewith on the environment appears to be temporarily and spatially variable and above all taxon-specific. For instance in Kenya we observed that *Pearsonothuria graeffei* is often found grazing on dead coral and sponges, and that *Actinopyga mauritiana* and *A. lecanora* are often found grazing on live as well as dead coral. However such observations are seldom made by reef ecologists since these researchers are hindered by the lack of correct species lists and descriptions for the holothurians that thrive in their study area.

Level five: Education

Conservation of holothurians depends on the participation of local communities, a fact that the Kenyan Government catched by creating the Community Wildlife Program (Western & Wright, 1994). This program allows the local communities to benefit from conservation effort, for instance through sustainable use of the natural resources (Muthiga, pers. comm.).
Over generations the coastal people of Kenya have developed traditional management strategies which enables them to conserve and protect their natural heritage and resources. The impetus for these local customs is however not conservation, but soothing of the spirits (McClanahan et al., 1997) In recent and future times these traditional conservation plans are or will not longer be sufficient for four main reasons. First, the coastal urban populations in Kenya are expanding rapidly, and are putting a larger demand on the environment. Second, in Kenya an islamization of the culture has occured, giving the traditional leaders less impact (McClanahan et al., 1997). As a consequence authority has shifted towards national organizations like Kenya Wildlife Services, organizations towards which the local communities show increasing resistance since it is thought that these instances will prohibit access to the resources (McClanahan et al. 1997). Third, the harvesting techniques nowadays employed by the sea cucumber fishermen can hardly be called traditional: with the advent of motorized boats and SCUBA-diving gear local fishermen can now reach areas which were formerly unreachable or inaccessible. In Gazi we witnessed local (depth gauge-less) SCUBA-divers at minus 45 m collecting holothurians. Fourth, not only

'locals' collect sea cucumbers on the fishing grounds; in Kenya SCUBA-divers are hired to go fishing on grounds which are hundreds of km away from their native fishing grounds. It needs little argument that these fishermen will not have the same incentive towards sustainable resource utilization. Education at all levels (from local resource users to local biology students to policy makers) can both trigger awareness of the problems and remediate the loss of traditional management strategies. Therefore our team makes it the highest priority to inform local people on the purposes and consequences of our research.



(a) Creating awareness through education of local sea cucumber fishermen in the Kiunga Marine Reserve, Kenya; (b) Education of postgraduate marine biologists during a postgraduate course in tropical marine biology.

Conclusion

Conservation and management plans will be optimal if five different levels are grasped. First, a correct naming according to the rules of zoological nomenclature allows communication between scientists in an unbiased way. Second, since scientific naming implies ordening of the living world, understanding of the observed biological patterns within biodiversity becomes possible. Third, complete faunistical lists must be constructed both for narrow political areas and for broader zoogeographical provinces, since these hold information that enables scientists to understand the faunal make-up of the landscapes and regions that need conservation. Fourth, since zoogeography is not only the consequence of history but also of ecological interactions, one must have a clear understanding of the current ecological interactions. Fifth, education at all levels, from scientists to policy maker to fisherman, will ensure that conservation efforts will be understood and valuated and that a sustainable management will replace untoughtfull environmental rape.
Enjoy your (Kenyan) Beche-de-mer!

Acknowledgements

My research on the holothurian fauna of Kenya is made possible through the Fund for Scientific Research Flanders (F.W.O.) and the Research Council of the Free University of Brussels (V.U.B.). Drs F. Bossuyt, Drs R. Tallon, Dr N. Koedam and especially Dr C. Massin provided insights and were always open to constructive discussion.

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Putting the *ALL-SPECIES* one-liner "Think big, act small, start now and don't deliberate it to death" to practice

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No serious biologist will deny that many, if not all, branches of biology rely considerably on sound taxonomic research (*1*). Despite this almost dogmatic reality, one is surprised to learn that taxonomy, and especially the descriptive or α-taxonomical part of it, has in recent decades been crippled by a lack of prestige and resources (*2*, *3*). Consequently, fewer and fewer young people are willing to thread the path of this research discipline (*4*, *5*) that not only culminates into sounder β-and γ-taxonomy (species formation and evolution in general), but also gives direction to more applied biological studies. However, if we want to respond to the biodiversity crisis with a clear and loud trumpet we'll have to counter this trend. This can be done by putting the ALL-SPECIES one-liner "Think big, act small, start now and don't deliberate it to death" (*6*) to practice. Our *modus operandi* to arrive at a trustworthy α-taxonomy in an amateur-unfriendly, non-glamorous, but nevertheless ecologically and socio-economically important group, aspidochirotid sea cucumbers (Holothurioidea: Aspidochirotida), will be detailed. At the same time, a critical re-evaluation of a recent example of β-to ω-taxonomy (*7*) shows how geographically biased α-taxonomy evokes possible jumpy conclusions.

We concur with the current belief that a complete, accurate, digitised and thus widely available species retrieval system will boost world-wide biodiversity description and understanding and ultimately will lead to larger public awareness and, in the longer term, even to sustainable conservation (*8*, *9*). To kick-start such a global research effort, it is of major importance to realise that we are not starting from scratch as the past 250 years of taxonomic research have yielded significant insights, which can and must be used to our advantage. However, before tackling the validity of past taxonomic judgements, it is of equal importance to inquire the causality of the historical creation of so many (apparently) invalid names. Such an analysis might seem trivial, but it is essentially prefatory to enable framing of an alternative *modus* that avoids further confusion, and leads to long-lasting falsifiable hypotheses on past and present biodiversity. It is demonstrated that the origin of past and present diseased taxonomic hypotheses have both biological and practical causes and that the curing medicine to these errors necessarily entails an electronically and programmatically networked teamwork. Once fully functional, this cooperative effort will reduce stochasticity in future biodiversity assessment and conservation efforts.

Ultimate causality of erroneous taxonomic decisions

The complexity of every biological unit - be it the gene, the species or the ecosystem - easily surpasses that of the inanimate world. Here we are concerned primarily with the level of the species which we want to distinguish from other species (α-taxonomy) and which we want to classify in a natural and heuristically sound system that allows prediction and information retrieval (β-taxonomy). Hereby, obviously, evolutionary relationships among species form the conceptual framework wherein this goal is to be attained. However, delimitation of what a species is has been a problem ever since man tried to describe the living world (his very own being included). This comes as no surprise, since the entity "species" is to a large extent masked by its ever-present intraspecific variation.

In holothuroid taxonomy identification and classification depends to a large extent on the shape, size and distribution of the ossicles in the different body parts. But, as intraspecific variation of these key-characters is seldom adequately known or made explicit, intensive splitting and/or polytypic species are the result. The need for such explicitness on character variation is however evident when one notices the modification of these components during their life span (*10-17*). Hence, representative series of individuals (population thinking), coming from the whole distribution area (geographical variation) and covering the different life stages of the species (ontogenic variation), must be examined (*18*). Other sources of ultimate erroneous taxonomic judgments originate from the ever-existing confusion between analogous and homologous characters, the interdependency and the weighting of characters. Without wanting to downgrade these

formidable difficulties, it is clear that they will largely resolve themselves once the genealogy is resolved and thus character evolution is known (*19*).

Proximate causality of erroneous taxonomic decisions

Consider the example where a biologist, working with the available identification keys and/or classifications, fails to identify specimens in his study area, and thus decides to establish one or several new species. To prove his hypothesis he is obliged to compare his specimens with specimens of closely related species, an enterprise that inclines that he has to decide where his specimens fit in the available (hierarchical) classification. Here several problems arise. If, by lack of experience or resources (literature, type material, appropriate reference collection, ...), he chooses the wrong part of the, supposed to be correct, classification, he will conclude that he has indeed found new species simply because he overlooked the sister-species. His new species will stand until competent taxonomists realise that their colleague has: (i) searched in the wrong clade or (ii) employed an artificial rather then a natural classification. In both cases the presumed new species will have been compared with non-related species, thus evoking erroneous taxonomic conclusions. To add to the difficulty of describing new species, it must be stressed that even if the above biologist employed a natural classification and has recognised the right clade in it, he still needs to compare his specimens with the existing species of the (natural) clade. In a first phase he thus will need to compare his descriptions with original descriptions of existing species. However, the latter often appeared in hard to trace, obscure journals or in expensive monographs that are available only in specialized libraries. Also in ancient publications it can seldom be taken for granted that descriptions are accurate and incorporate all the currently used characters (Fig. 1). Consequently he will necessarily need to examine voucher-specimens (type material and accurately identified specimens from the whole geographic range), which, as Murphy's Law predicts, will be located in a far-off, hardly accessible public collection. For researchers from developing countries, who often lack the financial and logistic means to get to the original publications and ancient collections of various European or American museums, comparative examination finds parallels with themes of *Mission Impossible*.

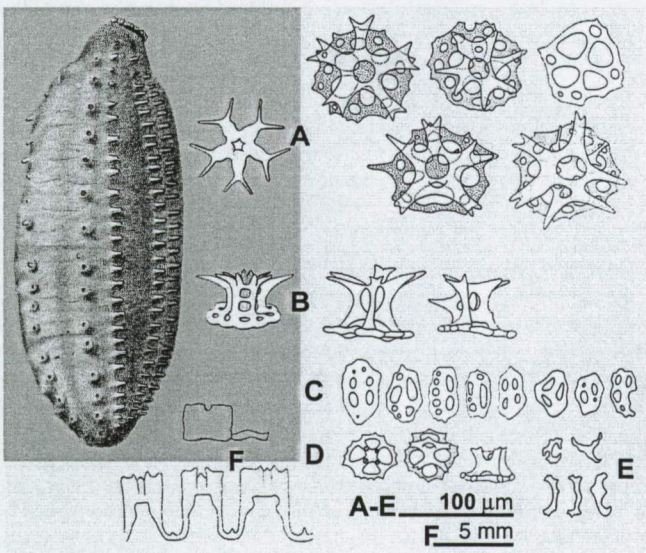

Figure 1. *L. semperianum* Selenka, 1867, the type species of the holothurian genus *Labidodemas* (Aspidochirotida: Holothuriidae). In accuracy, the original description (dark grey, *20*) largely differs from the revised description (light grey, *21*). (A, B) Table ossicles from the body wall; (C) button ossicles from dorsal body wall; (D) table ossicles from ventral tube feet; (E) rod ossicles from anal papillae; (F) calcareous ring.

But not all is negative; during the last decades the conceptuology of taxonomy and systematics has been profoundly rejuvenated with the advent of powerful technological (microscopy), computational (systematical software) and molecular tools that allow testing of classifications through phylogenetic reconstructions. But here again, one is often struck by the lack of attention, or at best, biased attention, that goes to α-taxonomy. A good example of this can be found in a recently discovered endemic radiation of >100 species of Old World tree frogs (Rhacophorinae) from Sri Lanka (*7*). Even though these authors, through molecular systematics, conclusively argue the validity of their spectacular finding, the geographically biased α-taxonomy they employed starts the sharpening of the scrutinizing axe of synonym-

designation. Indeed, whereas their maximum likelihood tree (Fig. 1 in *7*) clearly shows that an Indian species clusters within one of the presumed endemic (for Sri Lanka) clades of new species and whereas the character "direct development" possibly allows intermixing of Javan, Asian and Sri Lankan species in the reported phylogeny, they established the novelty of their radiated, endemic lineage by morphological comparison of their new species solely with Sri Lankan type material. As such they have overlooked the possibility that the reported radiation does not find its origin in Sri Lanka, but possibly even in Asia or Java. As they refrained from screening the available museum type material for these latter localities it remains to be investigated if their >100 new species are new to science or new to Sri Lanka.
Clearly, the above ultimate and proximate causes point to the need of an unambiguous identification and classification of ALL species. Such a list should, by intent, embrace ALL the historical collections as these represent the best global view of biodiversity we currently have.

Solutions to the impasses

As it is logistically and politically impossible to house a representative collection of the world's species under one roof, major museums are currently digitising their collections to make them more accessible for present and future biologists. Even though this courageous effort will *an sich* not resolve the already mentioned problems it will at least help to obtain a good estimate of where, what has been collected (voucher specimens and tissue for DNA studies). The question that remains is: how to deal with this overflow of information. For extant sea cucumbers, some of us have started to mould the foundations to a solution in an annotated catalogue (*22*). This unpublished manuscript contains diagnoses of the higher taxa and identifies synonymies (redundant names for the same species or taxon) of the majority of the known species. As such, it has become a mighty "secret weapon" in the hands of the few competent holothuroid taxonomists that have the know-how to employ it correctly. Unfortunately, a number of flaws in structure and content have made it a hard-to-use, and often misused, tool for the non-specialist end-user. Most daunting is that this annotated catalogue gives the false impression of taxonomic stability, evoking proximate erroneous conclusions. To resolve this, we have adapoted the ALL Species one-liner "Think Big, act small, start now and don't deliberate it to death" and have added constructive cooperation and online peer-review as unifying key-words (Fig. 2).

Think Big

Ultimately, we want to analyse and order the worldwide past and present species richness in a heuristic and natural classification, an enterprise that entails critical analysis of ALL published accounts and ALL voucher specimens. Even with ALL the holothuroid taxonomists currently active this sounds like another episode of *Mission Impossible*, especially since these specialists can be counted on two to three hands on which many digits reach the age of retirement. But is this really so? Not if we act small and start now.

Act small

A clear definition of all the available characters utilized in established classifications is undoubtly the first step in speeding the progress of identification and of testing the naturalness of the existing classifications. Even if such (rather boring) act is no sinecure for a notorious difficult group as holothuroids where detection and grouping of taxa depends to a large extent on microscopic ossicles that show a large degree of variation, it is critical in reducing character and character-state confusion. A well-defined character-matrix thus allows faster and more rigorous testing of the currently available diagnoses of the different taxonomic units.
Recently, we have started with the Order Aspidochirotida, which holds three or maybe four families (*23*) and some 400 presumed valid species. Hereby we typically proceed with a cyclic operation-flowchart (Fig. 2) that utilizes a bottom-up approach and incorporates the findings of the past 250 years. This works as follows. We start with a supraspecific taxon (subgenus or genus) taken from the last revision of a particular family (Fig. 2A). We trace back the original definition and all subsequent revisions and evaluate its current diagnosis by examining its type-species with the type series and representative specimens; a process that allows a clear typological description of the genus (preliminary definition of the evoked synapomorphies of the genus under study). Subsequently the species classified under the (now adequately diagnosed) genus are evaluated against the diagnosis, permitting the recognition of *nomina dubia* (names with unknown or doubtful application), *nomina nuda* (names that lack description or definition of the taxon it denotes), synonyms (redundant names) and possible new species. If it happens that all classified species correspond to the diagnosis, we analyse the neighbouring confamilial genera for other corresponding species (Fig. 2B); if such entities occur, they are moved systematically to the genus under study. Obviously, if the adding of

species reveals additional synapomorphies for the genus, its diagnosis is again altered. On the other hand if not all classified species correspond to the diagnosis (Fig. 2C) this might (again) just mean that the diagnosis is not accurate and needs emendment or it implies erroneous classification, in which case the wrongly classified species need to be moved to their correct systematical position. The latter becomes possible once all the genera of a family have been analysed in the same way. Evidently, the above grouping on the basis of similarity is largely subjective since convergent characters have not been discriminated from true synapomorphic ones and all characters have been given the same information content or weight. *A posterori* weighting in which those characters that are correlated with most natural groups, are given the highest weight, partly resolves the above shortcomings, but again does not yield a falsifiable natural classification. The next step thus necessarily involves the testing of the classification by putting forward the hypothetico-deductive hypothesis of common ancestry, whereby each taxon must be each other's closest relative (monophyly). Automatically, all the taxonomic characters are critically re-evaluated for their apomorph (derived) or plesiomorph (ancient) nature. We typically proceed by converting the putative classification (meta-taxonomy) into a cladogram from which the postulate of monophyly, allows to accept or reject the constructed classification (Fig. 2D). Such can easily be done with the character matrix from which we started in the first place.

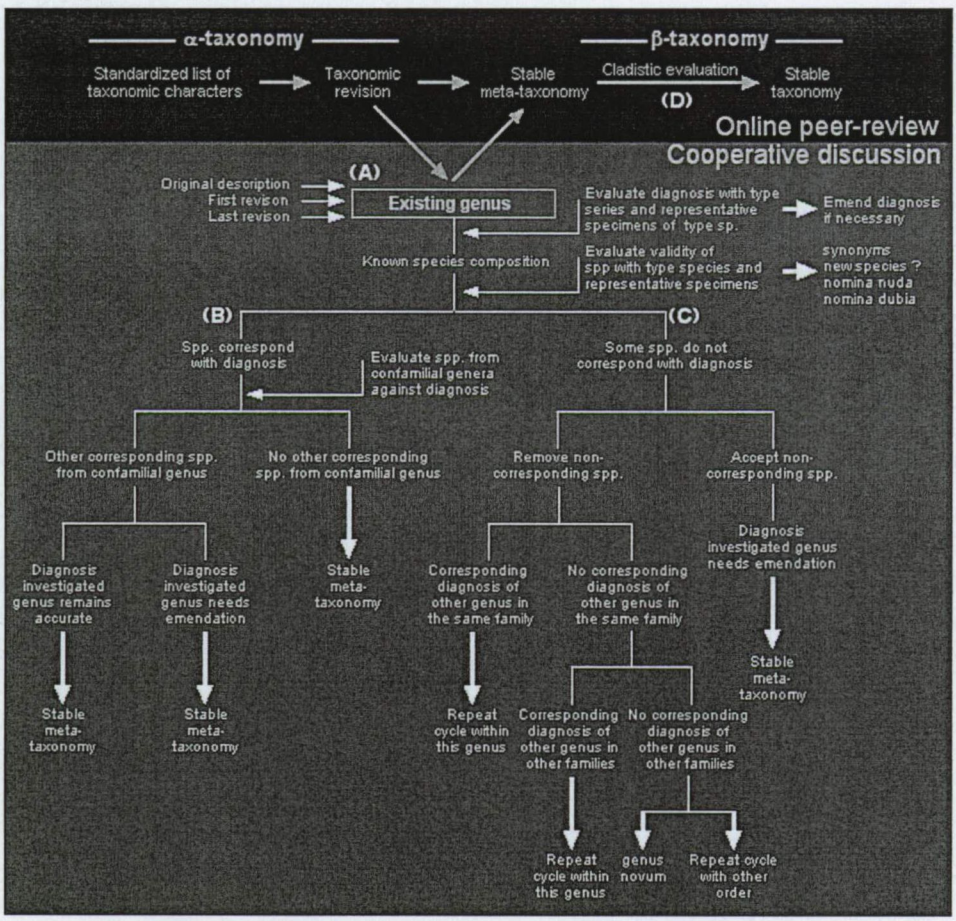

Figure 2. Usage of a bottom-up cyclic flowchart that incorporates the findings of the past 250 years of taxonomic research (A). This *modus* allows detection of ultimate and proximate erroneous taxonomic judgements and construction of a temporarily stable meta-taxonomy (B, C). The obtained meta-taxonomic classification is transformed into a stable taxonomy by testing its monophyletic signal (D).

Start now and don't deliberate it to death

By putting the character descriptions, the taxonomic revisions and the systematical testing of the obtained classification online we hope to attract the attention of fellow holothuroid taxonomists and as such provoke fast (and possibly also furious) peer-review. Also, we are convinced that such explicitness about methodology and preliminary results will boost the search for new (biochemical, behavioural, physiological, distributional...) taxonomic characters that will allow further testing of the obtained classifications.

Mayr (*24*), in a very interesting essay on the history of classification, quite correctly stressed that taxonomy and systematics are strictly a specialist's job. He's on record (*24*: p. 195) when he notes: "...but, as the history of systematics has proven again and again, satisfactory classifications – classifications based upon a critical evaluation of all the evidence – can be constructed only by those who do have a thorough knowledge of the group concerned". We concur with this non-taxonomist unfriendly statement, but nevertheless hope that our effort will add the desperately needed ferment to re-position α-taxonomy at the forefront of evolutionary and more applied biological research.
In addition by utilising the historical accounts of biodiversity (museum collections), framed within a natural classification, we are convinced that the stochasticity in biodiversity conservation will significantly reduce, because we will have obtained a clear picture of past and present taxonomic diversity.

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[18 Supporting online material]

Possible erroneous taxonomic judgement due to lack of knowledge of intraspecific variation

A notable work like that of the late Cherbonnier (*1*) on the holothuroids of Madagascar, contains descriptions of no less than 45 new species of a total of 122 species. However, blindly using these new species in biodiversity assessment (e.g. for α, β, γ - diversity measurements) or conservation action (e.g. endemism-based hotspot demarcation) is a dangerous enterprise, for a quick examination learns that 18 of these [*i.e. Holothuria (Selenkothuria) spinea, H. (S.) vittalonga, H. (Semperothuria) granosa, H. (Thymiosycia) milloti, H. (?Platyperona) insolita, H. (Platyperona) crosnieri, H. (Lessonothuria) duoturricula, H. (Cystipus) mammosa, Ocnus amiculus, Koehleria unica, Athyone maculisparsa, Thyone sineturra, Cucumella decaryi, Neothyonidium dissimilis, Thyonidiella exigua, Cladolabes pichoni, Leptosynapta geyserensis, Protankyra picardi*] were described from only a single specimen, and seven others [*i.e. Actinopyga bacilla, Bohadschia mitsionensis, Holothuria (Metriatyla) fuligina, Parathyone incurva, Phyllophorus (Phyllonovus) anomalia, P. (Phyllophorella) contractura, Opheodesoma sinevirga*] with only two specimens at hand (*2*). Therefore, it can be expected that several of these newly created species will turn out to be but synonyms of existing species. This observation is further strenghthened by the fact that: (i) many of these specimens are remarkably small, thus not excluding the possibility that they are but juveniles of already established species of which the intraspecific variation is inadequately known; (ii) some of them are obviously erroneously classified and thus have not been compared with their natural sister-species (e.g. *Opheodesoma sinevirga* obviously belongs to the genus *Euapta*).

In this regard it must also be noted that the opposite situation obviously also exists: single species that appear to be valid on traditional morphological characteristics later are found to comprise severeal species which can be distinguished only by examination of non-traditional characters (*e.g.* ossicle assemblage from the musculature). Moreover, the advent of molecular techniques allows identification of sibling or cryptic species, species that morphologically seem identical but that can be discerned wit molecular tools. How many such molecular species might exist is at this stage impossible to state.

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1. G. Cherbonnier, *Echinodermes: Holothurides* (Faune de Madagascar **70**, 292pp, 1988)
2. For the established species as described in the *Faune de Madagascar*; nine were described on just one and seven on just two specimens. Even though some of these species are certainly identified correct, the identifications of others is dubious and so is the validity of some species.

Summary

Summary

The study of the Holothuroidea, commonly known as sea cucumbers, started some 23 centuries ago when Aristotle defined them as a kind of motionless marine organisms. Only in the mid sixteenth century were holothuroids recognized as animals *per se*. Nowadays, Holothuroidea is firmly recognized as one of the five extant classes of echinoderms. Currently some 1600 species are described; these occur from the intertidal to the deep ocean trenches and from the polar to the tropical regions.

The ultimate aim of this dissertation is to understand the shallow-water holothuroid biodiversity of the western Indian Ocean, the area stretching from Suez to Cape Town and from the East African coast (Red Sea and Persian Gulf included) to 65 degrees East. To attain this goal, several expeditions to two contrasting regions of the western Indian Ocean (the tropical coast of Kenya together with Pemba Island in northern Tanzania and the subtropical coast of KwaZulu-Natal in the northeast of the Republic of South Africa) were undertaken. The purpose of these was to assemble a representative collection of species.

An extensive part of this dissertation is concerned with the construction of a reliable and up-to date faunistical list of the holothuroid fauna of these two case areas. The faunistics of the rest of the western Indian Ocean was filled in with the aid of important collections from the Seychelles and Inhaca (which were deposited as largely unidentified material in the collection of the Royal Africa Museum, Tervuren, Belgium), with detailed study of virtually all the available literature as well as with numerous loans of specimens from museums worldwide. In the course of the construction of this species inventory, my colleagues and I discovered several species and one genus new to science. We, however, did not blindly follow the standing biological classifications when describing our findings. *Au contraire*, while constructing the species lists we took great care to critically question the employed classifications. This attitude resulted in the taxonomic revision of the *Holothuria* subgenus *Mertensiothuria* and of the holothuriid genus *Labidodemas*. Interestingly, the type species of the latter genus revealed itself as a cryptic species. We were rewarded with the discovery of two additional new species.

Throughout this process, the historical opinions towards holothuroid taxonomy and systematics were never denied. This approach enabled us to revive methodically ignored characters such as the ossicles from the musculature. These characters proved not only diagnostic in the recognition of taxa, but also were informative in terms of recovery of phylogenies. By using our rejuvenated insights into such (and other) characters we were able to construct a large, morphology-based dataset, which allowed the recovery of the phylogeny of the Holothuriidae, the family best represented in this work. This cladistic analysis not only revealed that *Labidodemas* was indeed monophyletic (as suggested by our earlier systematic revision), but also allowed us to state that it has arisen from within the (now paraphyletic) genus *Holothuria*. As such, *Labidodemas* is evolutionary much younger than generally assumed. Our phylogenetic studies further suggest a close relationship between the genera *Actinopyga*, *Bohadschia* and *Pearsonothuria*, but unfortunately the recovered support proved low. Future studies (see also annex on CD Rom) will have to decide whether a new classification of the Holothuriidae is desired.

Taking all these caveats into account, we finally succeeded to construct the wanted faunistical list of the Holothuroidea from the western Indian Ocean. This list was then further used to analyze the patterns of biodiversity by means of cluster analysis on several β-diversity coefficients and parsimony analyses of endemicity. These analyses showed that the investigated holothuroid fauna of the western Indian Ocean is non-homogeneous and best split into several biogeographic units. These can be explained with (i) species' dispersion ability, (ii) the prevalent current patterns and (iii) the recent geological history.

Keywords

Echinodermata; Holothuroidea; Taxonomy; Systematics; Phylogeny; Faunistics; Zoogeography; Biodiversity; western Indian Ocean.

Samenvatting

Samenvatting

De studie van de Holothuroidea, beter gekend als zeekomkommers, startte zo'n 23 eeuwen geleden wanneer Aristotles hen als immobiele mariene organismen definieert. Het duurt evenwel tot midden de zestiende eeuw vooraleer zeekomkommers als dieren *per se* worden herkend. Vandaag worden zeekomkommers gezien als een van de vijf nog levende klasses echinodermem. Er zijn momenteel een slordige 1600 soorten beschreven; deze komen voor van de getijdenzones tot de diepzee en van de tropen tot de polen.

Het ultieme doel van deze dissertatie omhelst het begrijpen van de zeekomkommer biodiversiteit zoals die gevonden wordt in de ondiepe wateren van de West-Indische Oceaan, het gebied dat zich uitstrekt vanaf Suez tot Kaapstad en vanaf de kust van Oost-Afrika (inclusief de Rode Zee en de Persische Golf) tot 65 graden Oost. Ten einde dit doel te bereiken werden verschillende expedities naar twee contrasterende regio's van de West-Indische Oceaan (de tropische kust van Kenya, samen met de kust van Pemba in Noord-Tanzania en de subtropische kust van KwaZulu-Natal in het Noord-Oosten van de Republiek Zuid-Afrika) georganiseerd. Deze hadden tot doel een representatieve soortencollectie op te bouwen.

Een aanzienlijk deel van deze dissertatie betreft het opstellen van een betrouwbare en actuele faunistische lijst van de zeekomkommer fauna zoals aanwezig in deze twee sudiegebieden. De faunistiek van het overige deel van de West-Indische Oceaan werd ingevuld met behulp van belangrijke collecties afkomstig uit de Seychellen en Inhaca (deze waren als niet geïdentifieerd materiaal gedeponeerd in de collectie van het Koninklijk Africa Museum van Tervuren, België), met nauwlettende studie van vrijwel alle beschikbare literatuur en met een groot aantal specimens uitgeleend door musea van over de hele wereld. Tijdens de aanmaak van deze soorteninventaris, ontdekten mijn collegae en mezelf verschillende soorten en één geslacht die nieuw zijn voor de wetenschap. Tijdens de beschrijving van onze vondsten volgden we evenwel niet blindelings de beschikbare biologische classificaties. Integendeel, tijdens de constructie van de soortenlijsten, zagen we erop toe dat de biologische classificaties ten alle tijde kritisch werden benaderd. Deze attitude resulteerde uiteindelijk in de taxonomische revisie van het *Holothuria* subgenus *Mertensiothuria* en van het holothuriid genus *Labidodemas*. De type species van dit laatste genus bleek een cryptische soort te zijn. We werden beloond met nog eens twee nieuwe soorten.

Tijdens dit proces werd het historische gedachtengoed met betrekking tot de taxonomie en de systematiek van de Holothuroidea nooit ontkend. Deze aanpak stelde ons in staat om systematisch genegeerde karakters zoals de spicules van de spieren opnieuw op te waarderen. Dese karakters bleken niet allen diagnostisch in het herkennen van taxa, ze bleken daarenboven informatief bij het opstellen van fylogenieën. Onze vernieuwde inzichten in zulke (en andere) karakters stelden ons in staat om een omvangrijke, op morfologie gebaseerde, dataset op te stellen. Deze liet ons toe om de fylogenie van de Holothuriidae (de best vertegenwoordigde familie in dit werk) op te stellen. Deze cladistische analyse onthulde niet alleen dat *Labidodemas* inderdaad monofyletisch is (zoals aangeduid door taxonomische revisie), maar liet tevens toe te stellen dat dit genus afgeleid is uit het (nu parafyletische) genus *Holothuria*. Als dusdanig, is *Labidodemas* evolutief veel jonger dan algemeen werd aangenomen. Onze fylogenetische studies suggereren voorts een nauwe verwantschap tussen de genera *Actinopyga*, *Bohadschia* en *Pearsonothuria*. Helaas bleek de robustheid van deze tak laag. Verdere studies (zie tevens annex op CD Rom) zullen moeten uitmaken of een nieuwe classificatie van de Holothuriidae al dan niet gewenst is.

Onafgezien van deze valkuilen, slaagden we er uiteindelijk in om de fel bgeerde faunistische lijst van de Holothuroidea van de West-Indische Oceaan op te stellen. Deze lijst werd vervolgens gebruikt om de biodiversiteitspatronen te analyseren door middel van clusteranalyse van verschillende β-diversiteitscoëfficienten en parsimonie analyse van endemiciteit. Deze analyses toonden dat de bestudeerde zeekomkommer fauna van de West-Indische Oceaan niet homogeen is en best wordt opgesplitst in verschillende biogeografische units. Deze kunnen worden verklaard door (i) de dispersie capaciteit van de soorten, (ii) de oceaan stromingen en (iii) de recente geologische geschiedenis.

Trefwoorden

Echinodermata; Holothuroidea; Taxonomie; Systematiek; Fylogenie; Zoogeografie; Biodiversiteit; West-Indische Oceaan

Acknowledgments

Acknowledgments

This is perhaps the hardest part of a dissertation to write as one always will voluntary (or not) forget one or several people who one was keen to mention. In short, I will be short.

Many sincere thanks to all of you who allowed me to do this research my way, my pace. I sincerely hope that family, friends and colleagues, to whom I am in debt for support and constructive collaboration, will find their utmost satisfaction in the completion of this work.

Thanks again, and may our thoughts continue to be mutually illuminated.

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The study of the Holothuroidea, commonly known as sea cucumbers, started some 23 centuries ago when Aristotle defined them as a kind of motionless marine organisms. Their formal recognition as true animals, nevertheless, had to await the mid sixteenth century. Nowadays, Holothuroidea - with some 1600 described species - is firmly recognized as one of the five extant classes of echinoderms. As a highly successful group sea cucumbers have invaded the whole marine realm, from the intertidal to the deep ocean trenches and from the poles to the tropics.

The ultimate aim of this dissertation is to understand the shallow-water holothuroid biodiversity of the western Indian Ocean, the area stretching from Suez to Cape Town and from the East African coast (Red Sea and Persian Gulf included) to 65 degrees East. Framed within a solid review of the history of holothuroid classification, this dissertation offers a journey into recent taxonomic, systematic and phylogenetic findings. These culminate into an extensive species list of the shallow-water holothuroids of the region which, in turn, allows making important inferences on their causal zoogeography.

The here-accumulated knowledge will be of use for both students and scholars of holothuroid taxonomy and systematics as well as for conservationists who seek to fence their management plans in a biologically justified framework.

Keywords: Echinodermata - Holothuroidea - Taxonomy - Systematics - Phylogeny Faunistics - Zoogeography - Biodiversity - western Indian Ocean

Cover design: after Ruse (2001), Mystery of mysteries, Harvard University Press
Cover picture: from H. L. Clark (1921), The Echinoderm Fauna of Torres Strait, Pap. Dep. mar. Biol. Carnegie Instn Wash. 10: i-viii, 1-223, pls 1-38