UNIVERSITY OF SOUTHAMPTON

Systematics and Phylogeny of the Holothurian Family Synallactidae

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"I think the Almighty put synallactids on this earth
as some sort of punishment."
Dave Pawson

DECLARATION

This thesis is the result of work completed wholly while registered as a postgraduate in the School of Ocean and Earth Science, University of Southampton.

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ABSTRACT
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The sea cucumbers of the family Synallactidae (Echinodermata: Holothuroidea) are mostly restricted to the deep sea. They comprise of approximately 131 species, about one-third of all known deep-sea holothurian species. Many species are morphologically similar, making their identification and classification difficult. The aim of this study is to present the phylogeny of the family Synallactidae based on DNA sequences of the mitochondrial large subunit rRNA (16S), cytochrome oxidase I (COI) genes and morphological taxonomy characters. In order to examine type specimens, corroborate distributional data and collect muscles tissues for the DNA analyses, 7 institutions that hold holothurian specimens were visited. For each synallactid species, selected synonymy, primary diagnosis, location of type material, type locality, distributional data (geographical and bathymetrical) and extra biological information were extracted from the primary references.

17 species were screened for mitochondrial DNA in this thesis; 2 *Bathyplotes*, 5 *Mesothuria*, 3 *Pseudostichopus*, 1 *Pelopatides*, 2 *Paroriza*, 1 *Benthothuria*, 1 *Zygothuria* and the species *Isostichopus fuscus* (Ludwig), which was used as an outgroup for the phylogenetic analysis. The elasipodid species *Deima validum* was screened in order to evaluate the phylogenetic relation of the Elasipoda with the Synallactidae.

A new species of the genus *Pseudostichopus* is described based on molecular and morphology evidence. A new species of the genus *Mesothuria* is proposed based on geographical, morphological and molecular evidence, and a new species of the genus *Synallactes* is described based on morphological data.

The results of this study constitute the first phylogenetic test of the classification of Synallactidae. The family Synallactidae is a polyphyletic group. The family seems to be formed by 2 groups that can have different ancestors, a) a *Paroriza-Pseudostichopus-Pelopatides-Mesothuria-Zygothuria* group, b) a non-synallactid group with *Benthothuria funebris* and *Paroriza prouhoi*. There is morphological consistency in the Synallactidae, but it is not enough to validate the monophyly of the family. When combining elasipodid and synallactid mitochondrial DNA sequences in one analysis the "elasipodid clade", is separated into two branches. One branch is formed by *Deima validum*, *Paroriza prouhoi* and *Benthothuria funebris*. These three species have no morphological relation, but their mitochondrial DNA reveals their cryptic relationship. This study contributes to the understanding of the deep-sea synallactid holothurian taxonomy. Significant progress has been made in combining morphological and molecular approaches to taxonomy, demonstrating the need for more studies of this nature in the future.

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One **CD** with 247 images of the Synallactidae (JPG and BMP files) attached at the back of this thesis.

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Chapter One - General Introduction and aims

1.1. The phylum Holothuroidea (Echinodermata)

Holothurians are marine invertebrates that occur from the high intertidal zone to the greatest ocean depths. Most holothurians are epibenthic. Uniquely, among echinoderms, sea cucumbers can be holopelagic (Miller and Pawson, 1990) and even ectocommensal (Martin, 1969a, b; Gutt, 1990; Massin, 1992). They frequently dominate marine communities, particularly in tropical reef flats (Birkeland, 1989) and the deep sea (Pawson, 1966; Menzies *et al.*, 1973, Khripounoff and Sibuet, 1980; Billett, 1991; Tyler *et al.*, 1994a). In the deep sea they also form part of the benthic community in areas of manganese nodules (Pawson, 1988; Bluhm, 1994) and at hydrothermal-vents (Smirnov *et al.*, 2000). Holothurians dominate the deep-sea invertebrate megafauna, both numerically (Sibuet, 1985) and in terms of biomass (Zenkevitch, 1963; Rutgers van der Loeff and Lavaleye, 1986; Billett, 1991). Deep-sea holothurians can account for up to 90% of the ecosystem megafauna biomass, and because deep water covers over 70% of the surface of the earth, holothurians are among the dominant organisms on our planet (Hendler *et al.*, 1995).

Holothurians appear regularly in deep-sea photographs (Hansen, 1972; Lemche *et al.*, 1976; Pawson, 1988) and may be observed occurring singly or in large aggregations (Barham *et al.*, 1967; Billett and Hansen, 1982).

In contrast to the free-living asteroids, ophiuroids and crinoids, the holothurians lack arms. The ambulacral areas have been incorporated into the body so that the holothurians posses a bilaterally symmetrical body elongated along the oral/aboral axis. Symmetry is pentamerous modified by a dorsoventral plane of bilateral symmetry (Hyman, 1955). There are over 1400 described species divided into six orders: Dendrochirotida, Dactylochirotida, Aspidochirotida, Elasipodida, Apodida and Molpadiida (Pawson, 1976, 1982a; Smiley, 1994; Hendler, *et al.*, 1995; Solís-Marín and Laguarda-Figueras, 1998). Holothurians range in size from 1 mm (e.g. *Leptosynapata minuta*) to >5m (e.g. *Synaptula maculata*). The orders are taxonomically differentiated on the basis of the general shape of the body (Figure 1.1), tentacles, calcareous ring and ossicles (Figure 1.2), and the distribution and arrangement of the tubefeet (Pawson, 1982a).

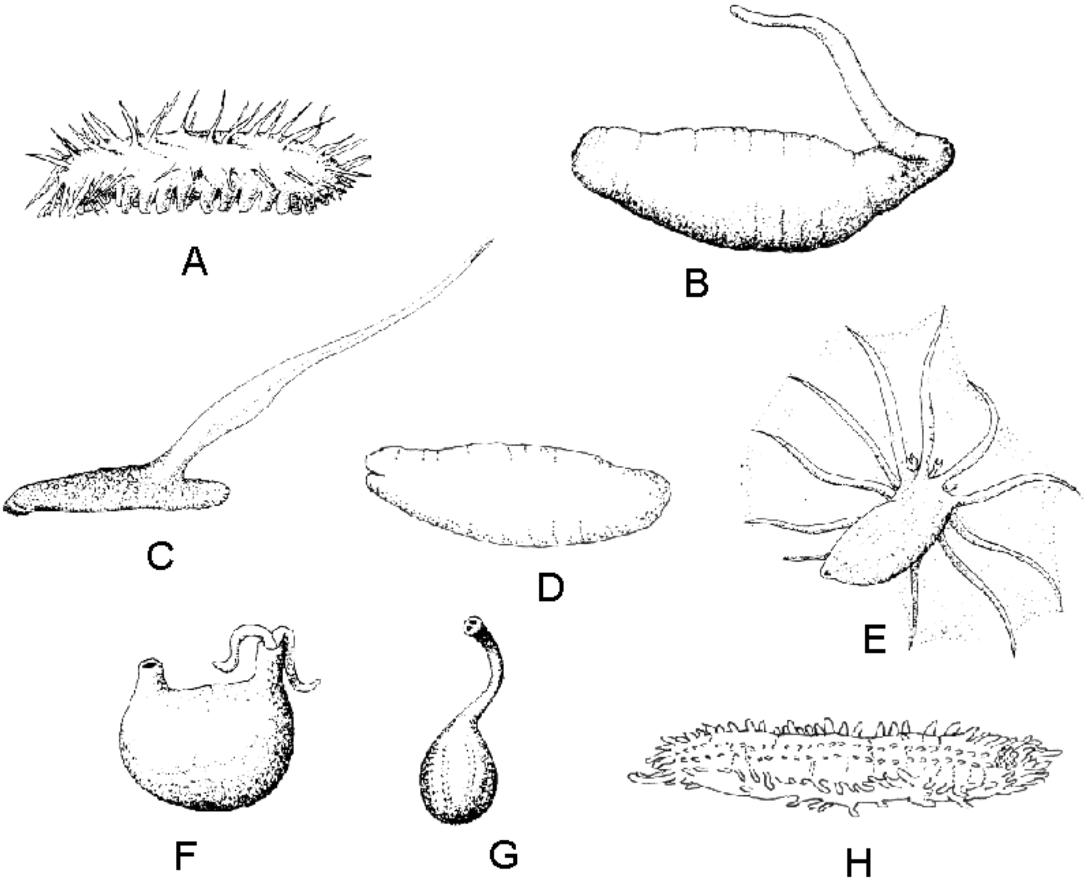

Figure 1.1. Representative holothurian body types. A. *Oneirophanta*, Deimatidae, Elasipoda; 100mm long (after Hansen, 1975). B. *Paracaudina*, Caudinidae, Molpadida; 200mm long (after Lambert, 1997). C. *Psychropotes*, Psychropotidae, Elasipodida; 150mm long (after Hansen, 1975). D. *Pseudostichopus*, Synallactidae, Aspidochirotida; 110mm long; E. *Pelagothuria*, Pelagothuriidae, Elasipodida; 80mm long. F. *Ypsilothuria*, Ypsilothuriidae, Dactylochirotida; 30mm long (after Kerr and Kim, 2001). G. *Rhopalodina*, Rhopalodinidae, Dactylochirotida; 50mm long (after Semper, 1868). H. *Amphigymnas*, Synallactidae, Aspidochirotida; 130mm long (ventral side) (after Deichmann, 1930).

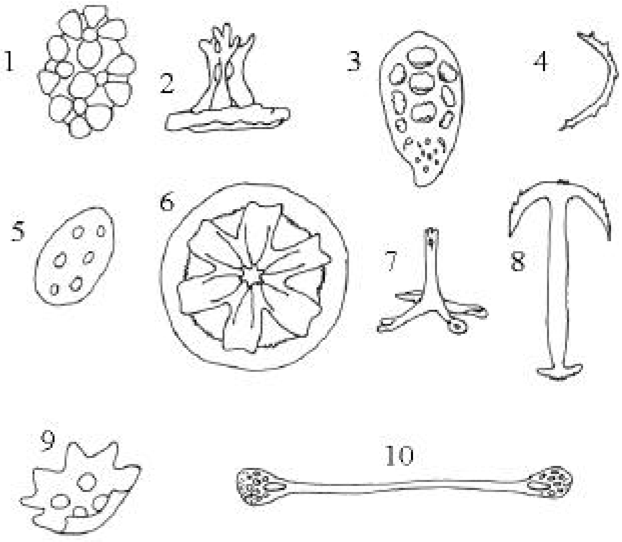

Figure 1.2. Some holothurian ossicles: 1. knobbed button; 2. table; 3. anchor plate; 4. rod; 5. smooth button; 6. wheel; 7. table with a singled spire; 8. anchor; 9. shallow cup; 10. slender, smooth rod. 1, 9. Dendrochirotida; 2, 7, 10. Aspidochirotida, Synallactidae; 4. Aspidochirotida, Holothuriidae; 6, Apodida, Chirodotidae; 3, 8. Apodida, Synaptidae.

The basic body plan is similar in all forms (Pawson, 1982a) (Figure 1.3). Around the mouth, the water vascular system supports eight to thirty, finger-like, branched or shield-shaped oral tentacles that are used for deposit or suspension feeding (Levin, 1999). Five radii run along the body from mouth to anus. Tubefeet are usually present, but are absent from the so-called "apodous" sea cucumbers. Their arrangement on the bodywall can vary considerably. They are often more numerous ventrally than dorsally and can be scattered in interradii as well as in the radii. Dorsal tubefeet may be modified to form papillae (Hyman, 1955). Holothurian tubefeet usually have a terminal skeletal disk, somewhat like echinoid tubefeet.

The interior of the bodywall is lined with circular muscles overlain by five radial longitudinal muscles. A calcareous ring, comprising 10 or more sizable pieces, encircles the oesophagus. The calcareous ring serves to support the oesophagus and is an attachment point for both the longitudinal muscles, which are used to contract the body, and, where present, the pharyngeal retractor muscles, which are used to withdraw the tentacles. The digestive system runs in a loop posteriorly, then anteriorly, then posteriorly again terminating at the posterior cloaca or rectum and anus (Figure 1.3).

Some holothurian taxa possess respiratory trees, into which water is pumped for dissolved gaseous exchange (Lawrence, 1987), but other groups of holothurians do not have any respiratory structures (e.g. elasipodids). Some species are known to eviscerate the posterior gut, including the respiratory trees, through the anus, on provocation. Others possess specific sticky or toxin-containing Cuverian Tubules, associated with the respiratory trees, for defence (Hyman, 1955). In most large and thick-bodied species branching respiratory trees occupy the posterior part of the coelomic cavity. They are composed of paired arborescent systems of tubes that are connected by means of a short duct to the terminal, enlarged part of the large intestine, the cloaca (Hyman, 1955).

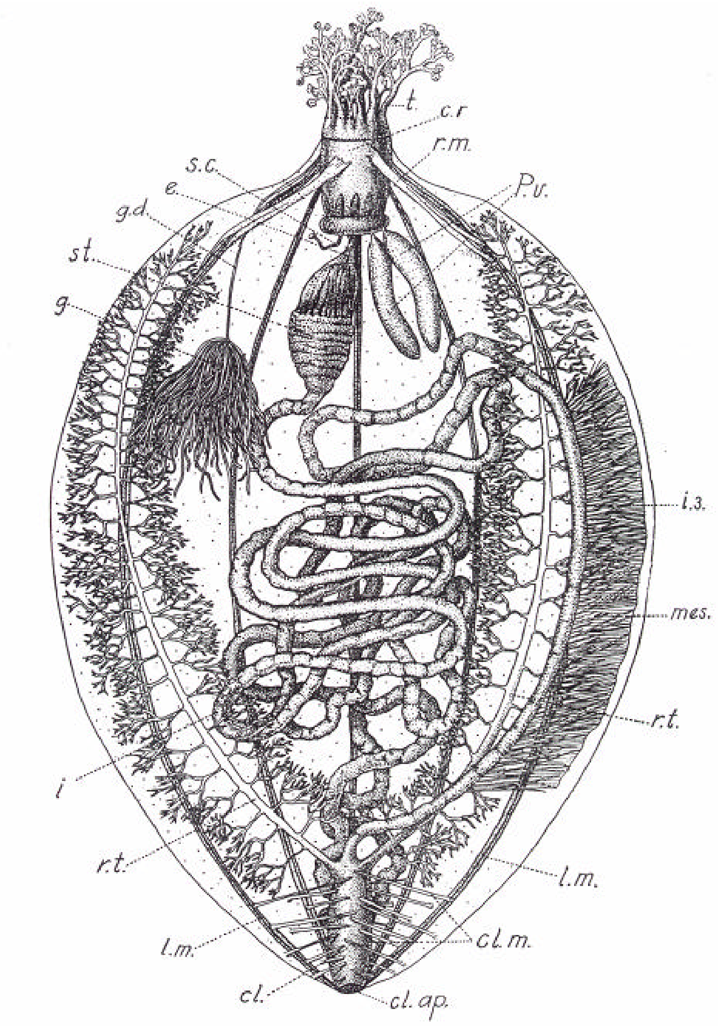

Figure 1.3. Internal anatomy of a dendrochirotid holothurian, dissected from the left side. *t*, tentacles; *cr*, calcareous ring; *sc*, stone canal; *rm*, retractor muscle; *pv*, polian vesicles; *g*, gonad; *gd*, gonad duct; *e*, oesophagus; *st*, stomach; *i*, intestine; *lm*, longitudinal muscle; *i?*, rete mirabile; *cl*, cloaca; *clm.*, cloacal suspension muscles; *cl p.*, cloacal aperture or anus; *mes*, mesenterium; *rt*, respiratory tree (after Forbes, 1841).

Holothurians have no visible madreporite on the bodywall. Instead, it lies free in the body cavity, with a stone canal leading to the water vascular ring that sits behind the posterior margin of the calcareous ring. One or more thin-walled, sac-like polian vesicles are also attached to the water vascular ring (Lawrence, 1987). The gonad comprises of one or two tufts attached to the dorsal bodywall. These tufts are usually composed of numerous branched or unbranched tubules. A single genital duct, running anteriorly in the dorsal mesentery, leads to an opening in the middorsal interradius, immediately posterior to the ring of tentacles (Sewell *et al.*, 1997).

An interesting feature of this group is the wide range of reproductive strategies that have been adopted. Although most species are gonochoric, three of the six holothurian orders have hermaphroditic representatives (Smiley *et al.*, 1991). Some species are capable of brooding their young (Ebert, 1996). In many species, development is indirect, proceeding via vitellaria, auricularia and doliolaria larval stages. Many of the elasipodids possess eggs of a “large” or “very large” size, and undergo direct development into juveniles omitting a larval stage (Hansen, 1975; Tyler and Billett, 1987; Billett, 1991; Gebruk *et al.*, 1997).

Holothurians either capture suspended or deposited food particles and transfer them to the pharynx by means of the circumoral tentacles (Hyman, 1955). During feeding, the tentacles are expanded into the substratum or into the water column. They then contract, and bend into the mouth releasing food into the pharynx (Féral and Massin, 1982; Massin, 1982; Roberts *et al.*, 2000). The tentacles are inserted rhythmically into the mouth as a result of the co-ordinated actions of the aquapharyngeal complex (Lawrence, 1987). The feeding strategies of deep-sea holothurians can be inferred by analysing their fatty acid composition, as shown by Ginger *et al.* (2000) or by pigment signatures (Billett *et al.*, 1988). Their feeding, faecal production and locomotory activities are of great importance in shaping benthic community structure and biogeochemical processes, such as the removal of phytodetritus (Ginger *et al.*, 2000; Roberts *et al.*, 2000; Witbaard *et al.*, 2001).

1.2. The family Synallactidae

1.2.1. General remarks

The family Synallactidae belongs to the order Aspidochirotida. This order is characterized by 1) 15-30 peltate, digitate or pelto-digitate tentacles, 2) respiratory trees, 3) the posterior loop of the intestine attached to the right ventral interradius, 4) gonads in one or two tufts, and 5) ossicles that are predominantly tables, crosses, or in some species, huge, perforated plates, with or without a trace of a spire. In certain species the ossicles are scarce and may be completely lacking in the mature or young individuals (Deichmann, 1930; Hyman, 1955; Pawson, 1982a).

The ossicles in the family Synallactidae are represented predominantly by tables or cross forms. Sometimes C-shaped ossicles can be observed, with huge perforated plates, with or without a trace of a spire. In certain species the ossicles are scarce and may be completely lacking in mature and/or young individuals. Most tables in the Synallactidae are typically four-pillared. They are common in the genus *Mesothuria*. The pillars rise over a single large central hole with a circle of relatively large peripheral holes (Figure 1.4). Characteristically, the margin is smooth and arched outwards around each hole. In synallactids, four-pillared tables are typically 80-100µm in diameter (Figure 1.4).

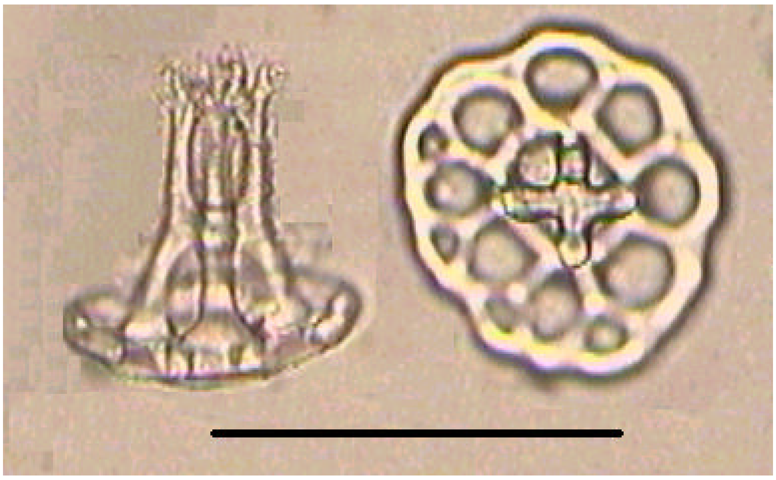

Figure 1.4. Synallactid ossicles. Tables from the bodywall of *Mesothuria intestinalis* (Ascanius, 1805). Left: lateral view of a four-pillar table, Right: upper view of the same kind of table. Scale bar= 110µm.

Ossicles from the tubefeet may be smaller, often with an irregular disc (i.e. with an odd number of small holes), than those from the bodywall. The diameter of the base plate is generally 120-200µm.

In general, the structure of the synallactid body is typical of holothurians. The family possesses some species that show a surprising similarity to the more advanced Elasipodida, while other forms resemble shallow-water Aspidochirotida, Dendrochirotida and even Molpadiida (Deichmann, 1930).

The order includes some of the largest species of holothurians, some reaching length of 1-2m (Ebert, 1978; Pawson, 1982a). Many of these are conspicuous tropical shallow-water forms (Bakus, 1968, 1973; Chao *et al*., 1995). The three aspidochirotid families (Holothuriidae, Stichopodiidae, Synallactidae) have approximately 400 species and are distinguished on the basis of structure of the gonad, and on the presence or absence of tentacle ampullae (Pawson and Fell, 1965; Pawson, 1982a). Aspidochirotids generally have thick bodywalls and few predators (Birkeland *et al*., 1982; Francour, 1997). They are usually found exposed in shallow-water tropical environments (Bakus, 1973). Synallactids, however, are mostly deep-water forms (Chao *et al*., 1995).

Some large forms are prized as food (bechê-de-mer, trèpang) in the Orient (Conand and Sloan, 1988). The protein-rich bodywalls of these species are dried and used in soups and other dishes.

The Synallactidae is one of the least-studied large taxa among the deep-sea sea cucumbers, and yet holothurians of this family are some of the most characteristic animals of the deep ocean. They appear repeatedly in photographic collections of abyssal megafauna (Pawson, 1976; Bluhm and Gebruk, 1999). The majority of the Synallactidae appear to spend their life upon the surface of the sediment, and not buried within it. Some synallactids are capable of active swimming (e.g. *Bathyplotes natans*) (Miller and Pawson, 1990). The epibenthic species traverse the seabed, feeding on the uppermost layer of sediment. Many photographs of the deep-sea floor show their characteristic tracks and faecal remains (Young *et al*., 1985; Bluhm and Gebruk, 1999), thus providing evidence of their important role in modifying the sediment landscape and in structuring the communities that live within it (Roberts *et al*., 2001).

The group appears to be primitive. Its first occurrence in the fossil record is represented by *Priscopedatus triassicus* from the Middle Triassic (Anisian) [250 million years] (Gilliland, 1993; Simms *et al.*, 1993).

1.3. Ecology

1.3.1. Feeding

Synallactids, like many other holothurians, use their peltate, digitate or pelto-digitate tentacles to collect particulate food. This high degree of adaptive radiation in synallactid tentacular structure, which facilitates habitat and feeding specialisation of different species, has been known for a long time (see Théel, 1882, 1886a). Most of synallactids are deposit feeders (Lawrence, 1987; Roberts *et al.*, 2000). They ingest sediments and extract organic material from them. Such animals are described as sedimentation interceptors relying on physical processes, such as sedimentation and water motion, to supply food particles (Taghon and Jumars, 1984).The diet of some synallactids was studied by Khripounoff and Sibuet (1980).

During feeding, tentacles are expanded into the water column or onto or into the substratum and, when loaded with particles, contract, bend into the mouth and release the food into the pharynx. Tentacles are inserted rhythmically into the mouth as a result of the co-ordinated actions of the aquapharingeal complex, which is essentially a similar structure in all holothurians (Hyman, 1955; Roberts *et al.*, 2000). In synallactids, feeding type may be inferred from tentacle structure (Table 1.1).

Table 1.1. Comparison of tentacles of synallactids (modified from Roberts *et al.*, 1991, 2000 and Moore, 1994). Feeding type is inferred from tentacle structure.

Species	Tentacle structure type	Feeding
Amphigymnas bahamesis	Pelto-digitate	Rake-feeder
Bathyplotes natans	Fine peltate	Sweeper
Paroriza pallens	Digitate	Rake-feeder
Paroriza prouhoi	Digitate	Rake-feeder
Pelopatides grisea	Digitate	Rake-feeder
Pseudostichopus villosus	Pelto-digitate	Rake-feeder
Synallactes chuni	Fine peltate	Sweeper
Mesothuria candelabri	Digitate	Rake-feeder
Zygothuria lactea	Digitate	Rake-feeder

The gut is long in almost all the synallactid species (Roberts *et al*., 2000). The intestine varies greatly among species in length and structure. One of the genera with a long intestine is *Mesothuria*. A strong muscled stomach is commonly found in the Synallactidae (e.g. *Amphigymnas*, *Benthothuria* and *Synallactes*).

Pelagic synallactids may also feed on suspended particles. The pelto-dendritic tentacles of *Scotothuria herringi* Hansen, 1978 indicate that this species may be able to capture particles in midwater (Hansen, 1978). However, analyses of pelagic aspidochirotid holothurian stomach contents show that only specimens caught close to the seabed have material in their guts and that this material comes from the sediment surface (Billett *et al*., 1985). In addition, observations made from submersibles and with cameras indicate that pelagic holothurians feed preferentially at the sediment surface (Pawson, 1982b; Billett, 1986).

The faeces of synallactids are often enclosed in a mucous casing. This casing may be produced to protect the gut lining as the often-irregular particles are moved through it by peristaltic action (Sibuet *et al*., 1982; Lawrence, 1987; Garcia-Arraras *et al*., 1998). The faeces of deep-sea holothurians have a higher organic content than the surrounding sediment, owing to initial selectivity by the sea cucumbers (Billett, 1991).

Unexpectedly, bacterial protein contributed only 3% of the total protein ingested by a deep-sea holothurian (Sibuet, 1984). Bacteria, however, are far from being irrelevant in the nutrition of holothurians. Digestion in deep-sea holothurians is aided by the presence of an enteric barophilic microbial population which is of a different taxonomic composition to that found in the sediment (Ralijaona and Bianchi, 1982; Bensoussan *et al*., 1984; Roberts *et al*., 2000). The bacteria are directly associated with the intestinal lining in the hindgut and are though to act as a commensal gut flora (Sibuet *et al*., 1982; Roberts *et al*., 2000). Bacteria release metabolites which will be taken up by the holothurian (Albéric *et al*., 1987).

Locomotory and feeding activities of synallactids have major impacts on the settlement and resuspension of both organic and inorganic particles in bottom sediments (Roberts *et al*., 2000). Suspension feeders tend to consolidate suspended particles and facilitate sedimentation (biodeposition or biosedimentation) (Thayer, 1983). By contrast, feeding and surface movements of deposit feeders holothurians result in the continued reworking and mixing of particles in the sediment mixed layer (bioturbation) (Thayer, 1983). This mixing affects sediment geochemistry and may lead to reduced or increased habitat heterogeneity, which in turn affects biodiversity (Roberts *et al.*, 2000). Some synallactid genera, like *Pseudostichopus*, form furrows about 1cm deep as they plough through the superficial sediment (Heezen and Hollister, 1971; Lemche *et al.*, 1976; Young *et al.*, 1985). Smooth plough marks made by *Pseudostichopus villosus* are one of the most common "Lebensspuren" (features on the sediment surface) in the Venezuela Basin (Young *et al.*, 1985) and similar features (simple furrows) are particularly common in an area of the Bay of Biscay, BIOGAS St. 2 (Mauviel and Sibuet, 1985), where species of *Pseudostichopus* and *Mesothuria* are found (Sibuet, 1977). In the North Atlantic, in some areas of the Porcupine Abyssal Plain and Porcupine Seabight, plough marks made by *Pseudostichopus villosus* and *Pelopatides grisea* are common (Billett, 1991).

1.3.2. Reproduction

Knowledge of reproductive processes in deep-sea holothurians, including the family Synallactidae, has been gained only in the last ten years, even though this process is of fundamental importance in understanding life histories.

Early taxonomic works described the gross morphology of the synallactid gonad (Théel, 1882). The only detailed studies of reproduction in the family Synallactidae have been on *Mesothuria intestinalis* (Smiley, 1988), *Paroriza pallens*, *Paroriza prouhoi* (Tyler *et al.*, 1992) and *Bathyplotes natans* (Tyler *et al.*, 1994b). The structure of ovaries has been described for *Hansenothuria benti* from bathyal depths in the Bahamas (Eckelbarger and Young, 1992).

Synallactids are mainly gonochoric with some hermaphroditic representatives such as *Mesothuria intestinalis*, *Paroriza pallens* and *P. prouhoi* (Tyler and Billett, 1987; Billett, 1991). Pairing behaviour was observed in the hermaphrodite genus *Paroriza* by Mauviel and Sibuet (1985) and Tyler *et al.* (1992). Pairing in these hermaphrodite synallactids appears to be an adaptative strategy which ensures successful fertilization in a low-density deep-sea population (Tyler *et al.*, 1992).

There is no evidence of seasonal reproduction in synallactids, as has been found in other deep-sea echinoderms (Tyler, 1986, 1988; Tyler *et al.*, 1982). The population structure of most of the bathyal holothurians, such as *Bathyplotes natans*, suggest a unimodal size structure with no evidence of any marked seasonal recruitment of juveniles

(Tyler *et al.*, 1994b). No obvious reproductive seasonality was evident in *B. natans* as well. Non-seasonality in breeding is a well-known characteristic of the deep-sea echinoderms (Gage and Tyler, 1991).

Very little information is available on larval development in synallactids. *Pseudostichopus* sp. 1, a species typical of the Porcupine Abyssal Plain (Billett *et al.*, 2001, referred as *Pseudostichopus* sp.), possess a variety of egg sizes that are present in any one ovary. The egg size is similar in samples taken at different times of the year. The maximum egg size is about 300µm (Billett, 1991). Continuous reproduction with development via an abbreviated lecithotrophic larval stage is likely (Billett, 1991).

As hardly any direct observations exist, conclusions regarding developmental types have to be inferred from the egg diameter attained (Hansen, 1975).

1.3.3. Swimming

The flexibility of the bodywall, and its potential for elaboration has permitted the evolution of swimming in some synallactids (Lawrence, 1987). Several synallactids possess conspicuous external features that appear to be morphological adaptations to swimming (Miller and Pawson, 1990). The most conspicuous of these are veils or brims that assist in swimming activities by flapping or undulating, providing some upward lift to the animal. Swimming movements usually involve contraction of the radial longitudinal muscles.

Most of the swimming synallactids are facultative swimmers (Miller and Pawson, 1990). *Bathyplotes natans* and *Hansenothuria benti* swim by powerful and quick sinous bends of the body in up-and-down directions (Miller and Pawson, 1989; Sars, 1868). *Pelopatides grisea* swims by undulation of the lateral brim (Billett *et al.*, 1985). *Scotothuria herringi* was sampled by pelagic nets in the mid-Atlantic (Hansen, 1978) several thousand of metres above the seabed. This species have a lateral brim of fused tubefeet and swims by undulation of the brim, as suggested by Hansen and Madsen (1956), in a manner similar to the swimming motion of the cuttlefish *Sepia* (Billett *et al.*, 1985; Billett, 1988).

Pelopatides gigantea is unlikely to gyrate more than a few metres from the sea floor. Other species of this genus, *P. retifer* and *P. confundes*, however, have been sampled 300 and 500-1000m above the seabed, respectively, indicating a more extensive pelagic life style than for *P. grisea* (Miller and Pawson, 1990). A large specimen (150mm long) of *Scothothuria herringi* was sampled swimming at an altitude of 3600m above the seabed (Hansen, 1978).

The efficient use of limited energy reserves may be an important consideration for deep-sea holothurians that subsist on nutrient-poor sediments. For some species, swimming or drifting as a means of dispersal may require expenditure of a minimal amount of energy. The ability of some synallactids to enter the pelagic realm, even temporarily, may provide an efficient means of long-distance dispersal.

1.3.4. Bathymetric distribution

The family Synallactidae occurs mainly at bathyal depths, rather than in shallow water. Several authors have noted a few broad zones in the deep sea, but there is some disagreement over the terminology of the zones and the bathymetric limits to which they should be assigned. Some authors have followed the terminology of Bruun (1950) and Hedgepeth (1957) dividing the deep sea from the shelf break into bathyal, abyssal and hadal zones (Hansen, 1975). Hansen (1975) from his work on elasipodid holothurians, recognized a hadal zone deeper than 6000m, an abyssal zone extending from between 1800 and 2600m to 6000m, and a bathyal zone from the shelf break (200 to 400m) down to 1800/2600m. The boundary between the abyssal and bathyal zones was not distinct and appeared to act more as an upper boundary for the abyssal species rather than a lower boundary for the bathyal species. In this thesis, the terms bathyal and abyssal are used to describe the depth distributions of the Synallactidae, as supported by Hansen (1975).

Hansen (1975) presented the bathymetric distribution of the genus *Synallactes*, showing its bathyal-abyssal distribution, together with the genera *Pelopatides*, *Benthothuria*, *Mesothuria* and *Pseudostichopus*. He also stated that the bathymetric distribution of the Synallactidae was restricted to the deep sea, mainly in the bathyal zone. In the same important monograph he concluded that the genera *Bathyplotes* and *Amphigymnas* are exclusively bathyal.

The bathymetric distribution of the family Synallactidae ranges from shallow-water (18m depth, *Mesothuria intestinalis* recorded in the Mediterranean Sea) to hadal depths (>7000m depth, *Pseudostichopus villosus* recorded in the Kermadec Trench at the Pacific Ocean). The Synallactidae are especially characteristic of the bathyal zone. The percentage of species inhabiting the different bathymetric zones is as follows: 56%

inhabit the bathyal zone, 18% the abyssal zone, 20% are bathyal-abyssal species, the 1% are hadal and 5% are eurybathyal species. The genera *Amphigymnas*, *Bathyplotes*, *Pelopatides*, *Synallactes* and *Benthothuria* are bathyal-abyssal. The monotypic genus *Hansenothuria* is bathyal. *Mesothuria* is a eurybathyal genus, but it is mainly composed by bathyal-abyssal species. The genus *Pseudostichopus* is bathymetrically distributed in the bathyal, abyssal and hadal zones, but it is mainly bathyal-abyssal. The genera *Paroriza* and *Zygothuria* are distributed in the bathyal, abyssal and hadal zones. No genera are confined to the abyssal zone.

The causes for the change in synallactid species composition with depth are complex and in any one area several factors will act together to produce the observed pattern. Many of the factors have gradients, each operating on its own scale (Billett, 1988). Many of these gradients are related to depth. Some are physiologically important, such as temperature and pressure (Somero *et al.*, 1983), while others are related to resources, for instance food availability and space. Most of them are too little known for an evaluation of a possible correlation between taxonomic affinity and depth range of their species. But such a correlation is evident in *Synallactes*. It comprises 25 species, which may be separated into an upper bathyal (728-1092m) and an abyssal (2098-4435m) group. The shallowest recorded species of the bathyal-abyssal group have been taken in the Arctic or Antarctic Oceans (e.g. *Bathyplotes moseleyi*, *B. rubicundus*). They may represent two of the few examples of deep-sea holothurians ascending to shallow depths in colder seas. It should be noted that the bathymetric distribution data could be strongly influenced by sampling artefacts because the different bathymetric zones have not been equally explored (see Hansen, 1975 for an example in the order Elasipodida).

1.3.5. Geographical distribution

The family Synallactidae has a cosmopolitan distribution, and some individual species are very widely distributed (e.g. *Bathyplotes natans*). Although the geographic distribution of some species is well known, the scarcity of collected specimens and problems surrounding their taxonomic identity, make records of distribution rather uncertain. Some species are difficult to distinguish and it is highly likely that distribution records have been confused. Species with an apparently wide geographic distribution may include two or more species that have been synonymised erroneously.

Many abyssal species are widely distributed, although only a few species have truly cosmopolitan distributions. Bathyal synallactids have more restricted distributions and none are known to occur throughout the World's oceans. Hansen (1975) concluded that in general the geographic ranges of holothurians were greater with increasing depth throughout the bathyal and abyssal zones.

The distributions of a few abyssal species are also possibly related to hydrographic features, but in general there appears to be little correlation with features of the physical environment (Hansen, 1975). Topographical barriers, however, do limit the distribution of some abyssal species. It is possible that holothurian geographical distributions are regulated to some degree by the total organic input to an area and the temporal variability of the food supply (Billett, 1988). Geographic distribution is not correlated with sediment type (Hansen, 1975; Billett, 1988).

Despite the few opportunities for isolation and speciation in the deep sea, Hansen (1975) considered that the deep-sea species have arisen mainly through speciation in the deep sea rather than through immigration from the sublitoral zone.

The geographical distribution of the Synallactidae is largely discussed in Chapter Six of this thesis.

1.4. History of exploration and taxonomic study of the deep-sea holothurians, with a particular reference on the family Synallactidae

Descriptions of deep-sea holothurians are almost exclusively found in the monographs from the various large deep-sea expeditions. A review of these expeditions and the work dealing with the collection of holothurians is therefore, at the same time, a history of exploration and the taxonomy of this family.

During its taxonomic history, the family Synallactidae have been placed in different taxa and within different groups. The study of the synallactids spans a short period of approximately 200 years. Before Ludwig's (1894) first attempt to unite the synallactids under a unified taxonomic name, the first paper to ever deal with a synallactid is that of Ascanius (1805), which includes an excellent description and detailed drawings, of the shallow-water synallactid *Holothuria intestinalis*, a former synonym of *Mesothuria intestinalis*.

The remoteness of the deep sea and the difficulties in studying this environment delayed the study of the group for more than 50 years. It was not until the last years of the nineteenth century, that the pioneering circumnavigation voyage of HMS *Challenger* laid the foundation for deep-sea biology and for the infant science of oceanography (Gage and Tyler, 1991). The specimens from this famous worldwide expedition were described by Théel (1882, 1886a, b). Théel (1886a) also examined a rich collection from the State Zoological Museum in Stockholm. No other holothurian monograph has ever covered such a wide geographic range as the Théel's *Challenger* report, describing more than 300 species. The collection of synallactids was not so rich in species, only 14 species, of which 4 were new to science. Although this work is one of the most important papers on the taxonomy of the Synallactidae, Théel did not confirm the status of the various genera belonging to this group. Instead he included them in the family "Aspidochirotae", establishing the genera *Pelopatides* and *Pseudostichopus*. Later, Théel (1886b), working on material collected by the United States *Blake* expeditions in 1880, recorded 6 species of synallactids including them in the genera *Holothuria* and *Stichopus*.

While the HMS *Challenger* brought home material from the three main oceans, some of the subsequent deep-sea expeditions explored restricted regions.

In 1874 the *Albatross* sampled around New Zealand, and collected some holothurians. Using this information, almost 100 years later, Pawson (1965) increased the previous known New Zealand holothurian fauna by 50%. The Norwegian North-Atlantic Expedition 1876-1878, with the research vessel *Vöringen*, explored the Norwegian Sea and the adjacent regions of the North Atlantic (Danielssen and Koren, 1882), providing information on the taxonomy and distribution of the holothurians in this region. In 1880 the *Blake* made an expedition to the Gulf of Mexico, Caribbean Sea and along the eastern coast of United States. In 1886 Théel published this information, providing new distribution records for 6 previously known synallactid species. In 1891 Walsh described the genus *Amphigymnas* from material collected by the *Investigator* (1887-1891) from Indian deep-sea waters. He also described the synallactid *Pannychia woodmasoni* a former synonym of *Synallactes reticulatus*. However, because he never stablished holotype specimens, it is very difficult to establish the true taxonomical identity of this species. Sladen (1891) describes a collection of Echinodermata from the Southwest coast of Ireland, dredged in 1888 by the Royal Irish Academy. He recorded 2 species of synallactids, under the families Holothuriidae and Stichopodidae.

In 1893 Marenzeller described 2 species of synallactids collected during the 1890-1892 expedition of *Albert I* to the North Atlantic and the Mediterranean Sea. He created the species *Pseudostichopus occultatus* (see Marenzeller [1893, 1895]). In the same year, Ludwig (1893), working on specimens collected by the *Albatross* in 1891 in the east Pacific and the Gulf of California, recorded 3 species of synallactids from that area. A year later, when working on the same *Albatross* material, Ludwig (1894) recorded 7 synallactid species, but this time included the synallactids as a formal taxonomic group within the subfamily Synallactinae. Subsequently, 5 new species and 3 new genera were erected. Here, he described the taxonomically difficult genera *Mesothuria*, *Synallactes* and *Meseres*.

Koehler (1895) worked on the *Caudan* dredge samples taken in the Bay of Biscay during 1890-1892. He described 5 new synallactid species placing them into the genera *Holothuria* and *Stichopus*. In 1895 and 1896, the Danish expeditions *Ingolf*, *Thor* and *Dana* explored the northernmost part of the North Atlantic and the south-west Norwegian Sea. The specimens collected there were analysed much later by Heding (1935, 1942a).

Two years after Ludwig's (1894) work was published, Östergren (1896) was the first holothurian taxonomist to specifically work with Synallactinae. He described 4 species of synallactids, and described the genus *Bathyplotes*, transferring *Stichopus natans* Sars, 1868 and *S. tizardi* Théel, 1882 to this new genus, and added a new species, *Bathyplotes fallax*.

Hérouard (1896), in his preliminary notes on Mediterranean Sea cruises of the *Princesse-Alice*, adopted Ludwig's classification scheme for the subfamily Synallactinae. He described a new species of synallactid as a "synaptinae" but he still used the *Stichopus* name for some synallactids. In 1899 Hérouard reported 11 species of synallactids (including 2 new species) collected by the *Travailleur* and *Talisman* cruises in the Atlantic Ocean.

Many authors support Ludwig's decision to erect the subfamily Synallactinae. Sluiter (1901b), reviewing the *Siboga* material from the Indonesian archipelagos, recorded 18 species of Synallactinae, naming 16 new species and a new genus;

Bathyherpustikes. Hérouard (1901) in his preliminary notes on the species collected in 1898 during the pioneering Belgium Antarctic Expedition described the species *Mesothuria bifucarta.*

In 1902 French naturalist Edmon Perrier, reviewing the *Travailleur* and *Talisman* holothurian specimens from the southeast Atlantic, decided to erect the family Synallactidae (previously known as a member of the family Holothuriidae, subfamily Synallactinae). 9 genera were included in this family: *Pelopatides*, *Pseudostichopus, Mesothuria*, *Meseres*, *Synallactes*, *Bathyplotes*, *Zygothuria*, and *Bathyherpystikes*. 13 species of synallactids were recorded, including 8 new species and 1 new variety. Perrier made one of the most important modifications for synallactid taxonomy, by synonymising the genus *Herpysidia* Perrier with *Bathyplotes* Östergren and stated differences between the genus *Mesothuria* and *Zygothuria*.

Subsequently, the number of genera included in the Synallactidae slowly began to grow. Hérouard (1902) added the genera *Allantis* and *Paroriza*, when analysing the *Princesse-Alice* (1892-1897) material collected at the Mediterranean Sea and North Atlantic (principally off Azores). 8 species of Synallactidae were recorded, including 3 new ones.

The most influencial synallactid taxonomic paper ever written is that of Koehler and Vaney (1905). It is an excellent monograph of the deep-sea holothurians collected by the *Investigator* in the Indian Ocean. Their work added 5 new genera, and 28 new species (including 1 variety) to the synallactid fauna. This is an important taxonomic paper for the Synallactidae, because the authors transferred, for the first time, synallactid species that were included in different families, such as *Stichopus moseleyi*, *Holothuria murrayi*, *Pannychia woodmasoni*, into the subfamily Synallactinae. For the first time the authors settled down on a good number of taxonomic characters to differentiate the group.

With the continuous exploration of the deep sea, new synallactid species were discovered and the once scarcely-represented genera became more robust. In 1906, in Hérouard's notes on the species collected during the Belgium Antarctic Expedition, he included a re-diagnosis for the genus *Mesothuria*. Such a re-diagnosis was increasingly necessary given the increasing number of species included in this genus.

Further new species of synallactids were added by Vaney (1906a, b) in his preliminary notes on the holothurians collected by the French Antarctic Expedition *Dr.*

Charcot. Fisher (1907) on the Hawaiian holothurians collected by the *Albatross* during the summer of 1902, and Augustin (1908) on some Japanese holothurians. Vaney (1908) described the holothurians collected on the National Scottish Antarctic Expedition (1903-1904) and Koehler and Vaney (1910) provided the revision of the records of the Indian Museum, with the description of new species of synallactid from the Arabian Sea. Hérouard (1912) described species from *Princesse-Alice* material from the Atlantic Ocean, Mitsukuri (1912) described holothurians from Japan seas (mainly from Sagami Sea) and Vaney (1914) examined material from the Second French Antarctic Expedition (1908-1910).

Clark, H. L. (1913) recorded one species of synallactid collected by the *Albatross* off Lower California, in the Mexican Pacific. This paper is very important because Clark was the first to recognise that the genus *Pseudostichopus* must contain a rather large group of forms, setting out the complexity of the genus.

Ohshima (1915) reviewed the holothurian material collected by the *Albatross* in 1906 from the Pacific around Japan. 96 holothurian species were reported, 46 of which were new to science, with 20 corresponding to the Synallactidae, including 10 new species. Unfortunately many of the holotypes named in this work were lost. In 1916-1919 Ohshima published a Chinese language version of his later work.

Not all taxonomists have always been in agreement over the systematics of the Synallactidae. When Clark (1920) described the *Albatross* material from several localities in the eastern tropical Pacific, seven species of synallactid were reported. Three new synallactid species were described, including the genus *Mesothuria* in the family Holothuriidae and the genus *Capheira* in the family Deimatidae. Although he might have made a mistake, he does not explain his taxonomic decisions. In 1911 H. L. Clark, made a subsequent review of the “old names” of *Holothuria* and *Stichopus*, and explained that the names were taken in a very wide sense, including forms now distributed in various families and orders. In his revision of the genus *Stichopus*, he proposed the inclusion of some “stichopus” forms into the subfamily Synallactinae. In this work, Clark listed 8 synallactid species that were previously erroneously included in the genus *Stichopus.*

In 1921 Grieg published a report containing very few comments on the echinoderm fauna collected during The *Michael Sars* North Atlantic expeditions. This paper listed 4 synallactid species. The true value of this work is that it provides bathymetric distributional records.

In 1923 Hérouard wrote his most important work on the Synallactidae. It describes the specimens collected by the *Princesse-Alice* in 1902 and *Hirondelle II*, both from expeditions in the North Atlantic. 13 species of Synallactidae were described, of which 7 were new to science. In this monograph, Hérouard added more information on the shared taxonomic characters in the subfamily Synallactidae. Another report of holothurian taxonomy containing information on Synallactidae, was that of Ekman (1925) on the Swedish Antarctic Expedition (1901-1903). In this study he argued the validity of different morphological characters in recognising different species into the family Synallactidae. In his compilation of the British Isles Echinoderms (North East Atlantic), Mortensen (1927) reported on 23 species of Synallactidae. He omitted the genus *Benthothuria* Perrier from the Synallactidae, which he considered to be a possible synonym of *Bathyplotes* Östergren. Grieg (1932) also reported 2 species of synallactids from his observations of the Northern Norway fiords in the spring of 1900.

A classic work on Atlantic sea cucumbers was published by E. Deichmann (1930). The review includes 104 shallow and deep-water species, including 24 species of synallactids, together with 2 new species. This monograph includes widespread species, mostly tropical and subtropical forms. Is based entirely upon museum material, and includes practically all the material available from the Atlantic cruises up until 1929. Like all Elisabeth Deichmann’s papers, it contains excellent taxonomic descriptions, but her drawings were seldom good enough to document or describe the shape and variability of the ossicles and even diagrams of the calcareous ring were omitted.

Heding’s works (1935, 1940, 1942a,b) have created more problems than solutions in the taxonomy of this group. In 1935, reviewing the material from the Danish *Ingolf*-Expedition, Heding erected the genus *Molpadodiademas* (a former synonym of *Pseudostichopus*) as a member of the Gephyrothuridae. In 1940 Heding wrote one of the most controversial papers on synallactid taxonomy. In this work, he described 10 new species and 1 new genus of Synallactidae, including the previously *incerta sedis* genus *Filithuria* Koehler and Vaney (1905) in the Gephyrothuridae. This paper contained 21 records of synallactids. In an attempt to simplify the taxonomy of the group, the genus *Pseudostichopus* was split into two subgenera, and the genus *Mesothuria* into four subgenera. Unfortunately, this taxonomic decision lacks strong supporting arguments and has been rejected by most specialists. The genera *Pseudostichopus*, *Paroriza* and *Benthothuria* were removed from the Synallactidae and included in the family Gephyrothuridae. This left the family Synallactidae with only 15 genera: *Mesothuria*, *Bathyherpystiches*, *Kareniella*, *Bathyplotes*, *Synallactes*, *Amphigymnas*, *Dendrothuria*, *Allopatides*, *Perizona*, *Bathyzona* and *Pelopatides*. At the same time, Heding erected the subgenus *Monothuria* and transferred the genera *Allantis* and *Zygothuria* to subgenera of the genus *Mesothuria*. New subfamilies for the family Gephyrothuriidae were also named; the subfamily Gephyrothuriinae, which includes the genus *Pseudostichopus* (split in two subgenera), *Filithuria*, *Plicatichopus*, *Paroriza*, *Molpadodiademas* and *Gephyrothuria*. These subgenera were erected without any diagnostic explanation. The Subfamily Benthostichopodinae included the genera *Platystichopus* and *Benthothuria* only. He described *Paradeima elongata* as new genus and species, including it as *incerta sedis*. This last species happens to be a member of the genus *Synallactes*. He also excluded a few synallactid genera from the synallactid family. However, most of the Heding's taxonomic decisions have been omitted in more recent papers by several authors (Deichmann, 1940, 1954; Cherbonnier and Féral, 1981; O'Loughlin, 1998).

Heding's classification, placing the genera *Benthothuria*, *Paroriza* and *Pseudostichopus* within the family Gephyrothuriidae, under the "order Aspidochirotacea", has now been rejected by most holothurian specialists (O'Loughlin, 1998). However, Heding's decisions may have lead to many mistakes in the subsequent literature. O'Loughlin (1998) excludes the genera *Gephyrothuria* and *Hadalothuria* from the Synallactidae, and reinstated the genera that Heding (1940) had excluded (*Pseudostichopus* Théel, 1886; *Meseres* Ludwig, 1894; *Benthothuria* Perrier, 1898; *Paroriza* Hérouard, 1902; *Filithuria* Koehler and Vaney, 1905; *Platystichopus* Heding, 1940 and *Peristichopus* Djakonov, 1952).

During the years 1947 and 1948, the Swedish Deep-Sea Expedition undertook cruises, trawling in the deep mid-Atlantic, with stations at hadal depths in the Puerto Rico Trench. Using specimens from these cruises Madsen (1953a,b) described 27 species of synallactids from the Pacific, Atlantic and Indian Oceans. During the Second World War, a preliminary list on the Allan Hancock Pacific holothurian material was compiled by Domantay (1953). This material included some of the famous *Velero III* cruises to the

Pacific Ocean (1932-1938). Unfortunately, the paper was rather hurriedly published by him without having any supposedly new species checked or compared with the type material. In his work he named three new synallactid species. These three species were *nomida nuda* after their formal taxonomic description by him years later (Domantay, 1961). In this thesis, his synallactid species are rejected once and for all.

The expedition of *Africana II* in 1959 to the Cape Peninsula, South Africa, collected 17 species of deep sea and shallow-water holothurians that were studied by Thandar (1999). Successive works by several authors produced more information about the taxonomy and geographical and bathymetric distribution of the synallactids from different oceans. This included the Pacific Ocean (Djakonov, 1949; Panning, 1952; Madsen, 1953a,b; Hansen, 1956; Baranova, 1957, Djakonov and Baranova, 1958; Pawson, 1963, 1965), the Atlantic Ocean (Deichmann, 1940, 1954) and the Mediterranean Sea (Tortonese, 1949, 1961, 1963, 1965). These works described new species (Cherbonnier, 1952; Djakonov, 1952; Domantay, 1953; Baranova, 1955) and a new genus for the family (Hansen and Madsen, 1956).

In the 1970s most of the research carried for the study of deep-sea holothurians was centred on obtaining ecological data (e.g. Carney, 1971). The introduction of the boxcore sampler, derived from devices used by geologists (Gage and Tyler, 1991), provided fortuitous discoveries of new synallactid species (e.g. Sibuet, 1978).

The French BIOGAS cruises (1972-1974) to the Bay of Biscay reported on the spatial and bathymetric distribution of 35 species of echinoderms from that area, including 13 synallactids (Sibuet, 1977, 1978). The 1975 *Meiring Naude* cruises collected holothurians from deep and shallow waters around the South African Coast. From that material Thandar (1992) described a new species of synallactid. The Spanish Iberian coast was sampled by the *Thalassa* (Cherbonnier, 1969, 1969-1970), Hespérides 76 (Montero, 1980) and BIOGAS (Laubier and Monniot, 1985). During the CAP-89 cruises in 1989, the Spanish Vessel *Garcia del Cid* collected 42 deep-sea echinoderm species from the Spanish Atlantic coast (De la Hoz and García, 1991). Expeditions in the Pacific Ocean have monitored the synallactid fauna in Indonesia (Massin, 1987a, b; Jangoux *et al.*, 1989), the Philippines (Cherbonnier and Féral, 1981), China (Liao, 1997) and the Japan seas (Imaoka *et al.*, 1990).

The British vessels RRS *Challenger* and RRS *Discovery* have collected deep-sea holothurians from the Northeast Atlantic. Numerous works, including information on synallactids, have been presented by Tyler and Gage (1983), Gage *et al*. (1983, 1985), Walker *et al*. (1987), Billett (1988, 1991), Harvey *et al*. (1988) and Tyler *et al*. (1985a,b; 1992; 1994b) and Gebruk *et al*. (1997). These papers provided information on the taxonomy, reproduction, distribution and other important ecological aspects of deep-sea holothurians.

The introduction of deep-diving submersibles has provided excellent information on the ecology and taxonomy of Caribbean synallactids. Pawson (1982b) and Miller and Pawson (1989, 1990) have used material collected from the research submersibles *Alvin* and the *Johnson Sea-Link I* and *II* to describe new synallactids (e.g. *Hansenothuria benti* Miller and Pawson, 1989) and to describe the swimming behaviour on some synallactid species (Miller and Pawson, 1990).

Gutt (1990a, b; 1991) presented information on the distribution and ecology of holothurians in the Weddell Sea. In 1984 German expeditions on board the *Polarstern* provided information on the distribution and ecology of three synallactid species. Massin (1992) described two species of synallactids from the Sub-Antarctic region at Marion and Prince Edwards Islands, presenting for the first time, an excellent description and drawings of the rare and taxonomically-controversial *Synallactes challengeri*. Later, Branch *et al*. (1993) presented taxonomic keys for the echinoderms of this region, recording 2 species of synallactids. The Scandinavian holothurians, including two species of Synallactidae, have been reviewed by Madsen and Hansen (1994). In the last seven years, the majority of papers on synallactids have been concerned with taxonomy. Rowe and Gates (1995) summarized some very important taxonomic decisions for the family Synallactidae. More recently, O'Loughlin (2002) working on material from the British, Australian and New Zealand Antarctic Research Expedition (BANZARE) 1929-1931 from Kerguelen Island and eastern Antarctica, is reviving the genus *Meseres*. O'Loughlin gives systematic and distribution notes on 14 synallactid species, including the description of 2 new synallactid species. More extensive explorations may, however, show that a somewhat richer synallactid fauna exists in the world oceans than has hitherto been supposed.

1.5. Basic problems with holothurian taxonomy

Taxonomists have been identifying holothurians since Greek times. The actual name "*holothuria*" came from the Greek "*olothurion*", a term assigned by Aristotle to the Holothuroidea (Forbes, 1841) meaning "worm-like". Holothurian morphological taxonomy has been built around variability in some external and internal characters (see Pawson, 1970, 1977 and 1982a) such as body form, tentacle shape, presence-absence of tubefeet, number of polian vesicles and madreporites. Lamentably, these morphological characters can vary owing to natural or artificial causes making taxonomic identification a complicated task. Deep-sea holothurians, such as the family Synallactidae, are even more complicated to identify because of the natural plasticity of their morphological characters and the collecting difficulties in the deep sea.

Explaining the complexity in the handling and interpretation of the taxonomic characters used in the holothurian and synallactid taxonomy can help in understanding the difficulty in identifying holothurians. The principal external characters in the classification of holothurians are: a) shape and number of the tentacles, b) shape and appearance of the whole body, c) position of the mouth and anus, d) presence and distribution of tubefeet and, e) presence and distribution of dermal accessories (e.g. papillae, anal teeth, fringes, etc).

When preserved, holothurians shrink, so all the external characters can easily be distorted. The shape and number of tentacles are morphological characters that can be affected easily by natural causes such as predation and age of the individual (Lawrence, 1987). The type of fixation method can dramatically affect the shape of the tentacles and dermal accessories. Formalin and even alcohol can shrink or burn the tips of the tentacles and papillae in few minutes and the specimens derived from these fixation techniques can be wrongly identified.

Although of great taxonomic value, the holothurian tentacle has received little attention (Roberts, 1982). Increasing consideration has been directed towards detailed structural studies of the aspidochirotid tentacle (Roberts, 1979, 1982; Bouland *et al.*, 1980) in order to explain the importance in the classification of the group. Taken together with ossicle studies, such as those of Rowe (1969) and Cutress (1996), a more thorough comprehension of the radiation of the group and a more natural classification should emerge.

The poor representation of juvenile stages of holothurians (owing to different collecting problems) in the scientific collections has led to their misidentification. The tubefeet increase in number with age and are a difficult taxonomic character to deal with (Deichmann, 1940). In very young individuals, there is a double row of pedicels along the midventral line and a single row down each side (e.g. *Pseudostichopus* spp.). Later these series widen, become densely crowded, and many even merge, so that the whole ventral surface is closely covered with pedicels. Meanwhile scattered pedicels occur on the dorsal surface and these increase in number with age, but never form definitive series.

The older literature is cluttered with worthless species, with identifications based on poorly preserved specimens or immature or aged individuals. Therefore the identification of specimens is naturally not a simple task and it is not unusual that with the passage of time a large number of specific names have been used in connection with the family Synallactidae.

Sometimes, even those specimens collected with care by submersibles and carried to the surface in seawater-filled containers have arrived aboard ship in very poor condition (Pawson, 1982a). During the journey from the seafloor to the surface, the epidermal and dermal tissues of the holothurians begin to slough off, and frequently the entire external bodywall is completely autotomized, leaving internal organs surrounded by the longitudinal and circular muscle layers. The bodywall contains such a high percentage of water that even the most carefully preserved specimens undergo a very great shrinkage, often amounting to >90% (Billett, 1991). If care is not taken in fixing and preserving, the animal not only shrinks but also becomes badly distorted, therefore most museum material gives little indication of their original form or size in life.

Among the principal internal characters in the classification of holothurians are: a) shape and distribution of ossicles, b) shape and consistence of the calcareous ring, c) presence-absence of respiratory trees, d) presence-absence of tentacle ampullae, e) presence-absence of *rete mirabile*, f) division of the longitudinal muscles, g) number of polian vesicles and, h) number, shape and distribution of gonad tufts.

Strong evidence has recently emerged that ossicles can change fundamentally over the life of an individual holothurian (Massin, 1994; Smiley, 1994; Cutress, 1996; Gebruk, 1998), resulting in new species being described based on juvenile characters. Externally, ossicles in synallactid can be found in the bodywall, tentacles, tubefeet and papillae. Internally they can be found in the gonads and respiratory trees. They are of paramount importance in classification, particularly at the level of the genus and species. The ossicles in juveniles usually are very different from those in adults of the same species (Cutress, 1996), and in some cases the juveniles have been described as separate species. Synallactid juveniles are not often collected, owing to their small size and cryptic existence. Occasional mention is made in the literature of a young specimen, but changes in the ossicles during growth have been carefully documented for very few species worldwide (Mitsukuri, 1897; Howaza, 1928; Thandar, 1987; Cutress, 1996).

Certain synallactid ossicles have convenient names, such as tables, rods, and baskets (Figure 1.2). Unfortunately, the ossicles are completely lacking in some synallactid genera (e.g. *Benthothuria* and *Paroriza*) and their taxonomic identification needs to be made on the basis of the external and internal morphology of the soft tissue elements. Resorbtion is also known to affect other patterns of ossicle change (Cutress, 1996). Ossicle variation in deep-sea holothurians is generally less well documented owing to the poor knowledge of juvenile stages (Gebruk, 1998). Unfortunately, formalin or other chemical acid agents can dissolve or alter the shape of ossicles, which make this highly valuable taxonomic character especially susceptible to external manipulation.

The number of polian vesicles in the family Synallactidae is not a safe guide to specific differences, for while the number is commonly 1-3 (e.g. *Synallactes ishikawai* Mitsukuri and *Synallactes triradiata* Mitsukuri) some species show great variation having from 9 to 13 vesicles (e.g. *Synallactes multivesiculatus* Ohshima, 1915). The presence of a tuft of gonads on each side of the dorsal mesentery has long been regarded as the chief distinguishing feature at genus level in the family Synallactidae (e.g. to differentiate between the genus *Mesothuria* [single tuft] and *Bathyplotes* [double tuft]). But there is need of further study on living, or fresh, material, to ascertain what the age or seasonal differences may be. The calcareous ring is of particular importance in holothurian taxonomy (Pawson and Fell, 1965). The ring may have a well-developed structure (e.g. *Mesothuria*), a moderately developed structure (e.g. *Pseudostichopus*) or be completely absent (e.g. *Benthothuria*). The ring itself is typically composed of 10 pieces (5 radial and 5 interradial). The shape of each piece (radial or interradial) can vary depending on its position in relation with the whole body (e.g. dorsal, ventral, midorsal, midventral, etc.).

In deep-sea holothurians, even when the specimens were carefully collected and fixed, there is still the chance to only obtain completely eviscerated bodies, which makes all the internal characters completely useless, forcing the taxonomist to rely strictly on the external characters and kind of ossicles. Even with all the problems mentioned above, attempts to reconstruct the holothurian phylogeny have been made using only morphological data (Kerr and Kim, 2001).

1.6. Molecular taxonomy

In the 1960's, the newest era in the history of biology, molecular biology, began making important contributions to one of the most established biological disciplines, systematics. Until then, the classification of life had been primarily based on morphological studies. Although there has been considerable cross-fertilization between morphological and molecular systematics, there has also been conflict of results and disagreement among practitioners of these two subfields (Hillis and Wiens, 2000). This has led to the perception of a battle of sorts between molecular and morphological systematics. Morphological and molecular approaches to systematics have different strengths, but also have many problems and difficulties of analysis in common (Hillis and Moritz, 1990). The coordinated effort between morphological and molecular systematics is necessary to make real progress in assessing the World's biodiversity. Significant inconsistencies between molecular and morphology-based phylogeny are rare. Most of the apparent conflicts do not stand up to statistical scrutiny (Littlewood *et al.*, 1997). Moreover, the two approaches to systematics are largely complementary, and each approach has advantages and disadvantages. Morphological and molecular studies can each address questions that cannot be addressed by the other (Littlewood *et al.*, 1997; Hillis and Wiens, 2000). And, where the two fields overlap, agreement of the results overwhelms any incongruity.

A similar combined morphological and molecular approach has been successfully applied to resolving relationships within individual echinoderm classes involving a large number of individual taxa: asteroids (Lafay *et al.*, 1995), echinoids (Littlewood and Smith, 1995), ophiuroids (Smith *et al.*, 1995) or as a whole group (Littlewood *et al.*, 1997).

Molecular techniques are particularly useful because the classification of the Synallactidae is often complicated by the morphological plasticity of the family. Thus plasticity has led to uncertainties in systematics at the generic and species level.

This is often because of 1) difficulties in preserving synallactid specimens, 2) great variability in shape, 3) predominance of cosmopolitan or widely distributed species, 4) highly specious genera and 5) lack of reliable and constant characters. This all makes the family Synallactidae a very good candidate to combine both molecular and morphological taxonomy to study its phylogeny.

1.6.1. Advantages of molecular data

The greatest advantage of molecular data in systematics appears to be the large number of characters available for analysis (Hillis, 1987). Theoretical and empirical studies have shown that a sufficient number of characters is crucial in estimating phylogeny (Hillis and Wiens, 2000). Typical molecular studies involve several hundreds or several thousand characters, and studies that include tens of thousands of characters even are becoming common (e.g. Bailey *et al*., 1992). This contrasts with morphological studies, in which a given analysis rarely includes more than a few hundred characters and averages about three characters per taxon (Sanderson and Donoghue, 1989). The potential number of morphological characters may not be much greater than the number actually used in studies, but the potential number of molecular characters is much greater.

Another advantage of molecular data is the wide range of substitution rates that exist across nucleotide sites (Hillis and Moritz, 1990). This permits phylogenetic analysis of everything from morphologically indistinguishable conspecifics to the most distantly related linages of life (Hillis and Wiens, 2000).

Molecular data also have the advantage that their genetics basis is usually known, whereas the genetic basis of most morphological characters is merely assumed. To date, few (if any) morphological phylogenetic findings have been discredited for being based on non-heritable variation (e.g. Haeckel, 1866). However, non-independence is likely to be a major problem in morphology, even though there are few good examples of non-independence in the literature (Emerson and Hastings, 1998). A lack of knowledge regarding the genetic basis of morphological characters makes the potential for non-independence in morphology-based phylogenies a largely intractable problem. Although molecular data sets could likewise have the flaw of non-independence, discovering the flaw and finding appropriate alternatives (e.g. Dixon and Hillis, 1993) are likely to be much easier than for morphological data sets.

Another advantage of the molecular approach is that characters can be selected and defined in a relatively objective manner. For example, a molecular systematist picks a gene and analyses all of its nucleotide sequences. Although alignment decisions and choice of the gene to be sequenced involve subjectivity (Hillis and Moritz, 1990), the criteria used to delimit characters typically are straightforward and objective (Hillis and Wiens, 2000). In morphological systematics, the characters must be discovered and delimited by the systematist, usually without any explicit criteria for character selection or coding. Thus, morphological data sets have the potential to be quite arbitrary (e.g. Gift and Stevens, 1997). For example, morphologists do not generally report their criteria for including or excluding characters, and when criteria are given, they vary considerably among studies (see Paul and Smith, 1988). There is little to prevent morphologists from excluding those characters that cause their preferred hypothesis to be rejected, and morphological studies typically include too few characters anyway. These concerns would be greatly alleviated if morphologists routinely provided well-defined criteria for selecting and delimiting characters.

1.6.2. Advantages of morphological data

The greatest advantage of morphological studies is that they allow for much more thorough taxonomic sampling than is possible with molecular analyses. Sampling a large number of taxa for molecular studies can be difficult because of the cost of sequencing, the need for relatively fresh material, the rarity of species, and the inaccessibility of the areas where certain taxa occur. In contrast, museum specimens can be used to cheaply and easily score many morphological characters for a vast array of taxa. Thorough taxon sampling is important for systematic revisions, studies of character evolution, and phylogenetic estimation. The greatest benefit of including additional taxa may be the potential to subdivide long branches in the estimated tree, which if insufficiently subdivided can result in inaccuracies in character reconstructions and in phylogenetic estimation. Long branches can mislead all phylogenetic methods and thus can lead to answers that are strongly supported, but wrong (Felsenstein, 1978; Huelsenbeck, 1995).

Another advantage of morphology-based phylogenetics is that each morphological character is probably encoded by a different gene or set of genes, whereas in molecular data sets, many or all nucleotide characters may be drawn from the same gene. If the evolution of a gene differs from that of a species, trees reconstructed from molecular data may give well-supported wrong answers to questions about species phylogeny (Doyle, 1992). Therefore, estimates of species phylogeny based on only one gene should be taken with caution. Morphological data sets are virtually immune to this problem and can be used as an important "reality check" to phylogenetic estimates that are based on the molecular characters of a single gene (Doyle, 1992).

Finally, in addition to phylogeny reconstruction, morphology continues to play a crucial role in alpha taxonomy. In almost all groups of organisms, species are described and identified on the basis of morphological data. Therefore, even molecular systematists depend largely on morphology to determine which species they have sampled.

1.6.3. Integrating molecular and morphological data

Given that molecular data and morphological data have distinct advantages, they can be integrated to find the best estimate of phylogeny (Hillis and Wiens, 2000). One way to integrate these two types of data is through combined analysis, analysing all the data simultaneously in a single matrix. The results of the combined analysis may then be compared with the results of each of the individual analyses, a process that is much like a standard statistical meta-analysis (Hillis, 1987). In many circumstances, the combined analysis yields a better estimate of phylogeny than any of the separately analysed data sets yield. In such cases, combined analysis should improve the estimate by increasing the number of characters applied to the problem, and it may also reveal groups not seen in the trees from the separate data sets (Barrett *et al*., 1991; Chippindale and Wiens, 1994).

1.6.4. The advances in using mitochondrial DNA as a phylogenetic tool

Mitochondrial DNA is a popular phylogenetic tool for marine invertebrate studies. Several recent reviews have listed cases where mitochondrial DNA analyses have played a critical role in the recognition of species boundaries in the sea (Knowlton, 1993; Thorpe and Solé-Cava, 1994; Creasey and Rogers, 1999; Knowlton, 2000).

Mitochondrial DNA has enormous potential for clarifying the nature of species boundaries in echinoderms (Rutherford, 1977; Arndt *et al.*, 1996; Edmans *et al.*, 1996; Littlewood *et al.*, 1997; Williams, 2000; Sooner *et al.*, 2001; Flowers and Foltz, 2001).

Mitochondrial DNA is preferred over nuclear DNA in phylogenetic studies (Jacobs *et al.*, 1988). Using nuclear DNA introduces a number of problems: these include the difficulty of distinguishing orthologous from paralogous genes in multigene families, uncertainty whether sequences have evolved at constant rates in different lineages (Jacobs *et al.*, 1988), and the unknown contribution of gene conversion and "promiscuous exchanges" to observed sequence differences (Jacobs *et al.*, 1988; Hillis and Moritz, 1990). All these indicate the unreliability of phylogenetic relationships deduced solely from these types of data.

The animal mitochondrial genome is a supercoiled, circular DNA of 15-20kb (Hillis and Moritz, 1990), which always (except in nematodes) encodes the same thirteen polypeptide subunits of the mitochondrial inner membrane respiratory complexes, as well as the rRNAs and tRNAs required for their synthesis inside mitochondria (Bibb *et al.*, 1981; Roe *et al.*, 1985; Clary and Wolstenholme, 1985; Jacobs *et al.*, 1988). Mitochondrial DNA replication, transcription and translation are semi-autonomous processes within the cell, which nevertheless require proteins (Wong and Clayton, 1986) encoded by nuclear genes. In animals, nuclear and mitochondrial genomes are physically and functionally separated, operating on principles as different as, if not more so, those between prokaryotes and eukaryotes (Jacobs *et al.*, 1988). The only genetic exchange between them, which has been demonstrated, is the rare incorporation of sequences of mitochondrial origin into nuclear DNA (Lewin, 1983; Gellissen *et al.*, 1983). In animals, mitochondrial DNA is inherited uniparentally through the maternal line (Lansman *et al.*, 1983). In each generation the mitochondrial DNA of an individual is believed to derive clonally from just a few mitochondria present in the developing oocyte (Hauswirth and Laipis, 1985). It seems reasonable, therefore, to discount the possibility that variant mitochondrial genomes might coexist in a linage over appreciable lengths of time and suffer periodic quantal changes (Jacobs *et al.*, 1988) as a result of gene conversion phenomena, such as occur in nuclear gene families. Mitochondrial DNA may, therefore, be regarded, as it has behaved over long evolutionary periods, as a set of true single-copy genes (Hillis and Moritz, 1990), even though it is physically present at hundreds of copies per cell. Moreover, mitochondrial DNA exhibits highly conserved amino acid sequences over much of its length, and the overall gene content and mode of organization appear to be universally conserved across the animal kingdom, with rearrangements in gene order occurring only extremely rarely (Edmans *et al.*, 1996). These conservative features permit useful phylogenetic inferences to be drawn from studies of the mitochondrial genome in different taxa (Dowling *et al.*, 1996).

1.7. Aims of the present work

Following the points stressed in section 1.3, this thesis has as its primary aim the production of a comprehensive understanding the phylogeny and systematics of the holothurian family Synallactidae. This study also intends to aid the future identification of synallactid species. The phylogenetic study is based on both morphological and molecular data. Partial DNA sequences of two mitochondrial genes, 870 nucleotides of Cytochrome Oxidase subunit 1 (COI) and 350 nucleotides of the large ribosomal RNA subunit (lrRNA) have been used in order to provide an accurate phylogenetic hypothesis regarding the phylogeny of the family Synallactidae.

Chapter Two - General Materials and Methods

2.1. Holothurian collection and fixation

Specimens were collected by trawling using a Semi-Balloon Otter Trawl (OTSB) and the IOS Epibenthic sledge (BN) from research ships RRS *Challenger* and RRS *Discovery*. Most of the species were collected from the Porcupine Abyssal Plain and Porcupine Seabight in the North East Atlantic (Figure 2.1), with the exception of *Isostichopus fuscus* (Ludwig), which was collected using SCUBA diving from a shallow-water site (15m depth) in the East Pacific, off the coast of Jalisco, Mexico (21ºN) in the year 2000. This latter species was used as an outgroup in the molecular studies described in this thesis. Details of sample stations are given in Tables 3.1, 3.2 in Chapter 3; Table 4.1 in Chapter 4. Descriptions of the sampling programmes are presented in Rice *et al.* (1991) and Billett and Rice (2001).

Specimens for morphological study were sorted on deck, cleaned in seawater and fixed in 4-8% formalin neutralized with borax (prepared with sea water). The specimens were transferred to 70% alcohol after a period of 24 to 72 hours. Ordinary non-buffered formalin dissolves the deposits and should never be used for specimens for taxonomic studies. Specimens first kept in formalin in some instances proved to have retained their natural shape better than specimens transferred directly to alcohol.

Holothurians for the reproduction studies were dissected onboard ship. To excise the gonads an incision was made in the dorsal surface, which exposed the oesophagus and intestine as well as the gonad. The gonad was removed whole by cutting the gonoduct. The gonads were fixed in 8% formalin for 48hrs, and then transferred to 70% alcohol for storage.

Total length (TL) and wet weight (WW) were determined after the coelomic fluid had been drained and the body had been wiped free of surface water. Dry weight (DW) was determined after drying the specimens in a freeze-dryer or under vacuum at 60ºC for up to 14hrs. Subsamples were then analysed for ash-free dry weight (AFDW) by heating in a muffle furnace at 500ºC for 4 hours.

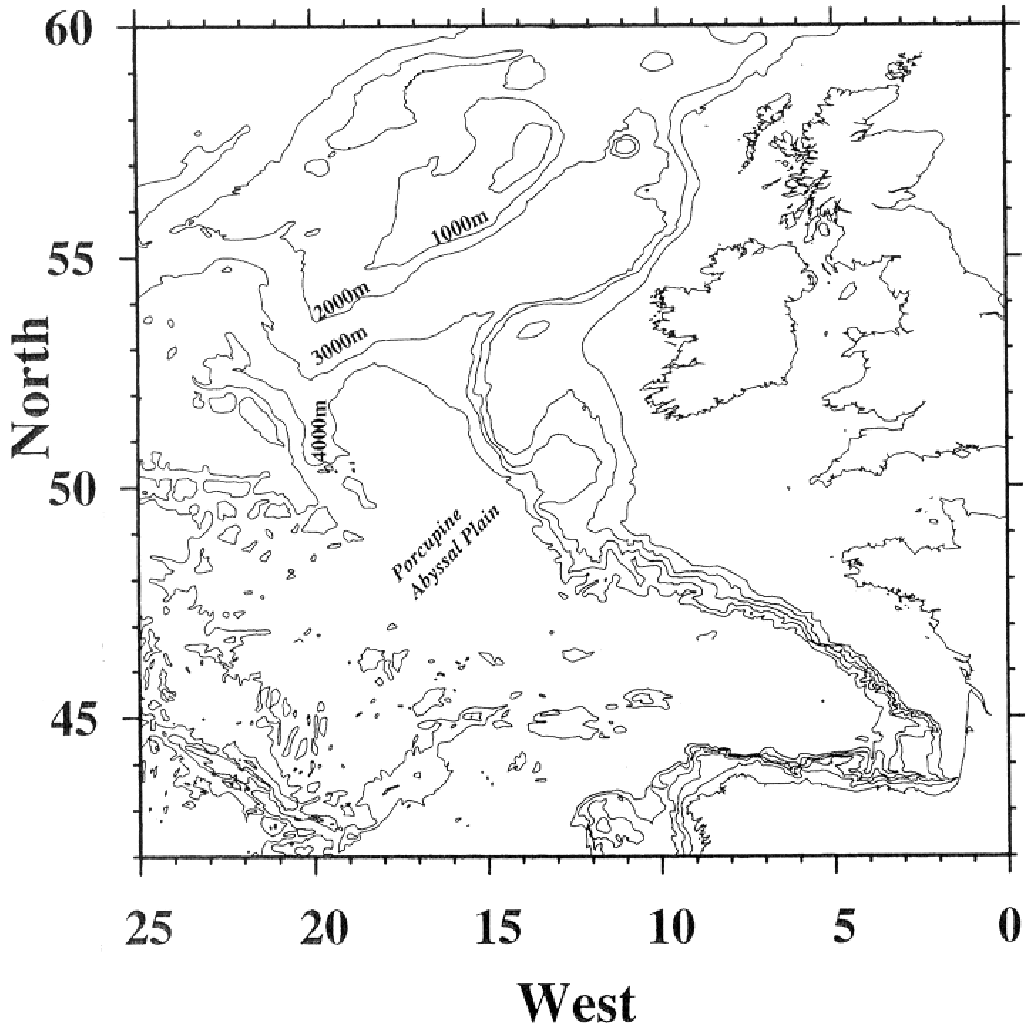

Figure 2.1. Bathymetric chart of the study area in the North Atlantic with 1000-4000m isobaths.

Molecular analyses require tissues to be sampled in a state in which the proteins and nucleic acids are maintained in the same structure as they occurred when they were physiologically active. Toward this goal, specimens collected for molecular analyses were immediately placed in chilled seawater on board ship and transferred to a temperature-controlled room (4°C). Individuals were dissected to obtain a sample of longitudinal muscle from the bodywall, which was immediately placed in 99% ethanol.

Supplementary material for DNA comparison was obtained from museum specimens (Appendix 1) that I personally dissected, and some other were sent by colleagues from different Institutions. Some of these specimens had been stored in 70% alcohol since they were collected.

2.2. Dissection of the specimens

Specimens for morphological study are best dissected by making a longitudinal incision along the left or right side of the body. Most organs are easily seen when the body cavity is opened in this way. In order to distinguish and record features of the internal anatomy for the identification and description of the species, whenever possible from fresh and/or museum material, one or several individuals of each species were dissected (Figure 2.2). External examinations were made with the naked eye or aided by use of a dissection microscope (Leica MZ-8) and a compound microscope (Olympus BH-2). Total length (TL) was measured from the tip of the anterior part of the body to the posterior end. Width (W) was measured from the widest part of the body at the mid ventral region. For each set of measurements, when possible, the maximum, minimum and median values were recorded. All measurements are in millimetres. These data are provided in Appendix 1.

Figure 2.2. "Fresh" specimen of *Benthothuria funebris* Perrier dissected on board RRS *Discovery* Cruise 250, Station 13914#1. Scale: 15cm.

2.3. Photographic records

Because of the shape and colour changes that the freshly sampled synallactid specimens suffer when they are transferred to formalin and alcohol, a series of digital photographs were taken on RRS *Discovery* Cruise 250 in order to record shape and colour of the fresh material (e.g. Figure 2.2). When visiting the scientific collections (Table 2.1) digital images from holotype-series and non-type specimens were taken and stored for future taxonomic reference. The images included general body shape (external characters), internal anatomy and ossicles from different body regions. Because the great number of photographs and the limited space in this thesis, I have attached a CD at the end of this thesis that contains 127 images. These are referenced in Chapter Five of this thesis.

Table 2.1. Museums and collections visited or mentioned in the present study.

ICML-UNAM: Coleccion Nacional de Equinodermos, Mexico City.*

IRSNB: Institut Royal des Sciences Naturelles de Belgique, Brussels.•

LACM: Los Angeles County Museum, Los Angeles, California, U.S.A.•

MCZ: Museum of Comparative Zoology, Cambridge, Masachusetts, U.S.A.•

MFPLH: Museo Felipe Poey, University of Cuba, La Habana, Cuba.*

MNHN: Museum National d'Histoire Naturelle, Paris.*

MOM: Musee Oceanographique, Monaco.•

NHM: Natural History Museum, London, England.*

RMNH: Rijksmuseum van Natuurlijke Historie, Leiden, Holland.•

RSM: Royal Scottish Museum, Edinburgh, Scotland.•

SAM: South African Museum, Cape Town, South Africa.•

SMBL: Seto Marine Biological Laboratory, Japan.•

SOC: Southampton Oceanography Centre, RRS *Discovery* Collection, Southampton, England.*

USNM: United States National Museum, Smithsonian Institution, Washington, D.C., U.S.A.*

ZIAS: Zoological Institute Academy of Sciences, Leningrad, St. Petersburg, Russia.•

ZMA: Zoological Museum, Amsterdam.•

ZMUC: Zoological Museum, University of Copenhagen.*

ZS: Zoologische Staatssammlung, Munich, Germany. •

(*)= visited; (•)= not visited.

2.4. Systematics

Most of the taxonomic information was obtained by surveying both the grey and primarily recent literature on the family Synallactidae. Original taxonomic descriptions of the material described in this thesis were written in English, German, French, Russian and Chinese. The majority of the information is contained in the taxonomic works of Marenzeller (1893a,b), Ludwig (1894), Sluiter (1901a,b), Hérouard (1902, 1923), Mitsukuri (1912), Deichmann (1930), Imaoka (1978) and Cherbonnier and Féral (1981).

2.4.1. Taxonomic identification

Identifications were made using original descriptions and taxonomic keys prior to any further analyses mentioned in this chapter (Walsh, 1891; Marenzeller, 1893a,b; Ludwig, 1894; Östergren, 1896; Sluiter, 1901; Hérouard, 1902, 1906, 1923; Mitsukuri, 1912; Mortensen, 1927; Deichmann, 1930, 1940; Heding, 1940; Djakonov, 1952; Djakonov *et al.*, 1958; Fisher, 1907; Hansen, 1978; Imaoka, 1978; Cherbonnier and Féral, 1981; Miller and Pawson, 1984, 1989; Imaoka, *et al.*, 1991; Massin, 1992).

2.4.2. Re-examined material from museums collections

In order to 1) examine type specimens, 2) corroborate distributional (geographic and bathymetric) data and 3) collect muscles tissues for the DNA analyses, a variety of institutions were visited (Table 2.1). A list of the specimens examined together with their deposition numbers and collection information is available in Appendix 1.

For each species, selected synonymy, primary diagnosis, location of type material, type locality, distributional data (geographical and bathymetrical) and extra biological information were extracted from the primary references. This information is summarised in Chapter Five. Geographical and bathymetrical information was also gained when studying the different museum collections.

2.4.3. Ossicle preparation

Ossicles are generally smaller than 1mm in diameter. Many are less than 50µm and must be examined with a compound microscope. Ossicles were isolated from the bodywall (anterior, central, posterior [dorsally and ventrally]), tentacles, respiratory trees and gonad tubules, by dissolution in fresh bleach (concentrated sodium hypochlorite) followed by water rinses before being mounted on glass slides (Pawson, 1977; Massin, 1999) and examined with a compound light microscope. Nomenclature used for the ossicle categories follows that of Pawson (1970).

Some of the illustrations of ossicles and calcareous rings, presented in the CD attached to this thesis are based on sketches made by different authors; the remaining ones I made from 1) my own slide preparations, 2) slides in museums, and 3) in few cases, the scientific literature. To illustrate some species I have used some hitherto unpublished photographs and few new photographs of preserved specimens.

At the Museum National d'Histoire Naturelle, Paris a slide collection containing more than 3000 slides, including type material from museums around the world, was analysed. This slide collection was made principally by Dr. Gustave Cherbonnier. The collection also contained original preparations made by Edward Hérouard in the 1900s (Appendix 1).

The specimens collected were deposited in the *Discovery* Collections, Southampton Oceanography Centre, Southampton, England. The type specimens of the proposed new species were deposited in the Natural History Museum, London (NHM); the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); the Zoological Museum, Copenhagen, Denmark (ZMC); Echinoderm National Collection, Universidad Nacional Autonoma de Mexico, Mexico City, (ICML-UNAM).

2.5. Reproduction

2.5.1. Histology

Water must be removed from gonad tissues before it was embedded in paraffin wax by immersing the tissue in 95% alcohol for 24hrs, then in absolute alcohol for 2hrs, with two subsequent changes of alcohols each after 2hrs. A wax solvent (histoclear or xylene) was used to replace the alcohol. Most solvents have the effect of raising the refractive index of tissue, which makes them appear clear. This stage is known as clearing. The tissues were blotted between each step and left in histoclear for at least 8 hours. The tissue was then impregnated with paraffin wax in an oven heated to 70ºC, after blotting lightly with tissue paper. The gonad was transferred from the clearing agent to molten paraffin wax where it was left to impregnate for around 8 hours. Fresh molten wax was poured into a plastic mould, the tissue added and the label placed in the cover, and then the block was allowed to set.

Prior to sectioning, the wax blocks were chilled in iced water to facilitate clean cutting. Fine (7µm) sections were floated in a water bath (40ºC) to remove the creases. A clean slide was half submersed partly in the water to remove the wax section. The mounted sections were left on a drying rack at 37ºC over night to dry before staining.

2.5.2. Staining

Slides were processed through a series of different stains, starting with removal of the wax in Histoclear^{TM} for 2mins. Hydration of the tissue with graded alcohol started in 100% alcohol for 1min followed by 70% alcohol for 1min. The slides were transferred to haematoxylin and left for 5 min. After draining of excess haematoxylin, they were transferred to a slide-washing tray and washed until sections were blue, usually after 15mins. The sections were transferred to 1% eosin for 2-4 min and rinsed in the slide-washing tray. The tissue was then rehydrated in 70% alcohol for 2mins, 100% alcohol for 2mins, and cleared in Histoclear^{TM} for 2mins. The slides were drained from the Histoclear^{TM} solution. One or two drops of DPX were placed on the section before the cover slip was placed on top.

2.5.3. Image analysis

Sections of gonad were examined under a dissection microscope (Leica MZ-8) and a compound microscope (Olympus BH-2). Using a JVC video camera (TK 1280E) and Matrox-Rainbow RunnerTH PC-VCR sofware, microscope images of the gonads were transferred to bitmap image files. In order to analyse pattern of oogenesis, the eggs within the ovary sections were measured using Jandel Scientific SigmaScanPro^{TM} 4 image analysis software. Only eggs that had been sectioned through the nucleus were measured ensuring that their maximum diameter was recorded and that each egg was only measured once. The feret diameter of each oocyte was measured. The measure of feret diameter gives the diameter of a fictious circular object with the same area as the object measured. Fifty oocytes from each specimen were measured and the data for each sample were combined.

2.6. DNA analyses

Before finding the most successful methodology for the achievement of the different tasks presented in this thesis, it was necessary to implement and to improve the already described holothurian genetic techniques. This phase of experimentation required almost 6 months.

Although fresh material was sampled whenever possible, it was necessary sometimes to use museum material as a result of the rarity and scarcity of some synallactid species. Genetic analyses on long-preserved holothurians specimens have inherent difficulties, owing to the slow degradation of DNA in the presence of a fixative. The DNA damage that occurs in preserved samples is primarily due to oxidation and hydrolysis (Lindahl, 1993). This type of damage hinders the polymerase chain reaction (PCR), as damaged DNA is rarely successfully amplified by PCR. Although the probability of getting DNA amplifications from museum specimens, using conventional DNA extraction protocol is low, a total of 198 samples were processed. 48 DNA extractions were successful, but only 28 had the right concentration that permitted successful sequencing. Even to veteran molecular biologists, PCR amplification often remains a “mystery” (Palumbi, 1996). Why does one set of cycles work while others do not? Why does one set of primers work while others do not?

The only published studies on holothurian DNA techniques are on shallow water species (Arndt *et al*., 1996). The primers used to amplify the shallow-water holothurian mitochondrial gene16S used by Arndt *et al*. (1996) were tested on the deep-sea synallactids. Only two sets of primers from the nine presented by Arndt *et al.* (1996) were successful, and in very few deep-sea holothurian specimens. Thermal cycle amplification step proposed by Arndt *et al*. (1996) was also optimised.

2.6.1. DNA extraction

17 species were screened in this thesis; 2 *Bathyplotes*, 5 *Mesothuria*, 3 *Pseudostichopus*, 1 *Pelopatides*, 2 *Paroriza*, 1 *Benthothuria*, 1 *Zygothuria* and the species *Isostichopus fuscus* (Ludwig), which was used as an outgroup for the phylogenetic analysis. The elasipodid species *Deima validum* was screened in order to evaluate the phylogenetic relation of the Elasipoda with the Synallactidae. All samples consisted of small slices of longitudinal muscles preserved in 99% ethanol. Some samples were

obtained from different museums and laboratories (Appendices 1, and 2). In the case of museum material, individuals were preserved between 2 and 10 years in 70% ethanol.

DNA was extracted through digestion of a small piece of muscle (approximately 200 mg) in 100mM Tris-HCL, pH 8.0, 1.25% SDS, and 390 ng/µl^{-1} proteinase K (approximately 0.012% units/µl^{-1} of Boeghringer Mannheim, Cat. No.1373-196). These 400µl preparations were incubated for 2h at 55°C in an incubator and then a standard phenol/chloroform-isoamyl alcohol extraction was carried out with precipitation of DNA by 2:1 ice-cold 100% ethanol plus 1:10 3 M sodium acetate. Polymerase chain reactions (PCR) were carried out in 20µl total volume using sterile water, and contained 160 µM each dNTP, 10 mM Tris-HCL, pH 8.3, 40mM KCL, 2 mM MgCl$_2$, 1 µM each primer, 1 unit *Taq*-polymerase, and 10 to 30ng template DNA. Amplification of specific mitochondrial DNA fragments was accomplished by using conserved primers (Kocher *et al.*, 1989) based on published sea urchin, starfish and sea cucumber sequence data (Jacobs *et al.*, 1988; Smith *et al.*, 1993; Arndt *et al.*, 1996). The primers used to amplify the 3’ end of the 16S gene and their position in the mitochondrial map of the sea urchin *Strongylocentrotus purpuratus* are shown in Table 2.2 (Jacobs *et al.*, 1988; Arndt *et al.*, 1996).

Table 2.2. Oligonucleotide primers sequences used in the present study.

Primer	**Sequence 5’ ? 3’**	**Mitochondrial map position** (*Strongylocentrotus purpuratus*)	**Direction**
COIef	ATAATGATAGGAGG[A/G]TTTGG	6000-6019	Forward
COIer	GCTCGTGT[A/G]TCTAC[A/G]TCCAT	6692-6673	Reverse
16Sb	GACGAGAAGACCCTGTGGAGC	5297-5317	Forward
16Sr	ACTTAGATAGAAACTGACCTG	5710-5687	Reverse

PCR was performed either using a Perkin-Elmer 480 or a Hybaid PCR-Express thermocycler. Products were visualized on a 1.5% agarose gel stained with ethidium bromide. PCR products were purified with Qiagen Qiaquick PCR purification columns (Cat. No. 28106), according to manufacturer’s guidelines. 10µl cycle-sequencing reactions were prepared using Perkin-Elmer BigDye Terminator Ready Reaction mixes (Cat. No. 4303152), using the manufacturers guidelines. The products of the cycle-sequencing reactions were purified using Qiagen DyeEx Spin kits (Cat. No. 63104) and sequences visualised using a Perkin-Elmer ABI 377 automated DNA sequencing machine.

2.6.2. Thermal cycle amplification

One hundred nanograms of template DNA and 25 pmol of each primer were placed in a *taq* DNA polymerase reaction mixture, overlaid with mineral oil, and held on low temperature (-4 ºC) until the thermal cycle had reached denaturation temperature. The amplification profile was as follows: An initial cycle of 94°C for 240 seconds (s); 50°C, 30 s; 72°C, 60 s; followed by 30 cycles of 94°C, 30 s; 50°C, 30 s; 72°C, 60 s; followed by a final cycle with a 10-min extension time. Oil overlay or hot lid worked equally well.

2.6.3. Product purification

Amplified products were separated from unincorporated primers by electrophoresis through 1% agarose gels in a 40 mM Tris-acetate, 2 mM EDTA buffer (1XTAE) containing 0.1 µg/ml ethidium bromide. Product bands, were visualized under U-V light using U-V DOC System (Bio-Rad). This was to verify that the correct size product had been amplified. PCR products were cleaned using Qiagen PCR clean-up Kit (Qiagen).

2.6.4. Sequencing

DNA sequencing was based on the chain termination method (Sanger *et al.*, 1977; Hattori and Sakaki, 1986). Cycle sequencing was performed on all samples. Samples were run on polyacrylamide gels. All samples were double checked by reverse sequencing.

A BLAST search (Altschul *et al.*, 1990, 1997) was carried out in all the samples in order to compare the sequences with similar ones already in existence within the international nucleic acid and protein databases. In all cases the amplified DNA was corroborated to be echinoderm-holothurian DNA.

2.7. Phylogenetic analysis inferred from molecular characters

2.7.1. Sequence alignments

All sequences were manually entered, aligned and visualized using the Chromas (Ver. 1.41). The lrDNA sequences were aligned using Clustal X (Ver. 1.81) program (Higgins *et al.*, 1992; Thompson *et al.*, 1997) with a gap penalty of 10 and subsequently visually inspected to improve alignment. A consensus sequence for each species was drawn from the initial set. The consensus sequences retain the variable sites, which were very small in number in this study. The reported sequence for *Pseudostichopus mollis* Théel (detailed in Arndt *et al.*, 1996) (GenBank Accession number U32221) was also included in the analysis.

2.7.2. Phylogenetic analysis

The molecular phylogenetic analysis, as well as basic statistics, were performed using PAUP* 4.0b 10 (Swofford, 2002) version. Three methods of tree building were used: maximum-likelihood, maximum-parsimony, and neighbour-joining. For all methods, tree topology was evaluated by bootstrapping of the original data set. For maximum-likelihood and maximum-parsimony a heuristic search was employed and starting trees were always obtained by random sequence addition. Tree visualization and drawing were carried out using TreeView version 1.5 (Page, 1996). Maximum-likelihood was performed under the General Time-Reversible (GTR) model of base substitution. The modeltest 3.0 (Posada and Crandall, 1998) algorithm was used to evaluate the choice of GTR model, which produced the most significant log-likelihood values, among various models tested. Site-specific substitution rates (SSR) and discrete approximation of the gamma (?) distribution were used in two separate substitution rates. On GTR+SSR analysis, substitution rates were calculated considering the structural analysis by Machado *et al.* (1993), which divided the 3'end of the 16S gene into two domains: domain A, with higher substitution rates, corresponded to sites 209-371 in my sequences. Base frequencies, substitution rates for the six different substitution types, and relative rates for the two domains considered, or the shape parameter for the ? distribution (a), were estimated from the data set through maximum-likelihood, considering the topology of an initial neighbour-joining tree.

The estimated values were used in searches with 1000 sequence addition replicates and in the subsequent bootstrappings, which consisted of 100 replicates with 100 sequence additions per replicate.

On maximum-parsimony analysis, gaps were considered as meaningful characters and multistate sites on the consensus sequences were considered polymorphic. The tree presented in Chapter Six (section 6.2.3) was found through a search with 1000 additions. Bootstrapping of the maximum-parsimony tree consisted of 1000 bootstrap replicates. Finally, a neighbour-joining tree was constructed from the distances calculated under the GTR+SSR model with the same parameters used in the maximum-likelihood analysis. The topology of the neighbour-joining tree was evaluated by 1000 bootstraps.

Different model tests were used for each phylogenetic analysis in chapters Three and Four of this thesis. Details are given in each chapter.

2.8. Phylogenetic analysis inferred from morphology

2.8.1. The ingroup

In order to delimit the group of organisms to be analysed, the family Synallactidae was defined by species sharing the following synapomorphies:

a) lack of free tentacle ampullae,
b) respiratory trees well developed, usually not connected with the alimentary canal through a *rete mirabile*,
c) head of the stone canal usually in connection with the bodywall, sometimes opening outwards through it,
d) Cuverian organs absent,
e) gonads in one or two tufts,
f) ossicles predominantly as tables or crosses; in some forms developed as huge, perforated plates, with or without a trace of a spire. In certain species the spicules are scarce and possibly may be lacking completely.

Upon re-examination of type material, grey literature and the application of the *sensu stricto* diagnosis for the family Synallactidae, after Ludwig (1894) (see Chapter Five) 14 synallactid genera were excluded and placed in temporal *incerta sedis* status. Two representatives from all 10 recognized valid genera were included in the phylogenetic analysis inferred from morphology (excepting the monotypic genus *Hansenothuria* Miller and Pawson). Type species were preferred over non-type species, because these species are supposed to possess the representative (diagnostic) characters of the groups concerned. However, in some cases, type species could not be used because I lacked access to the material or they were too poorly described. In these instances, a well-described species, certainly possessing the autapomorphies of the group concerned, was included.

2.8.2. The outgroup

In order to root the phylogenetic tree, at least one and preferably several outgroup(s) should be included in any analysis (Maddison *et al*, 1986). In the absence of a suitable outgroup, the data for the ingroup can be used to produce an unrooted tree, which provides valuable information, but it is usual to aim for a rooted tree (Hillis and Moritz, 1990). Ideally, the root would be the common ancestor from which all the ingroup synallactid have descended. This common ancestor (almost) always has the best combination of character states that places it in the unrooted ingroup tree so that it correctly roots the tree.

One way of rooting is by traits of fossils. Regrettably, holothurian fossil taxa often lack soft tissue preservation and hence consist mainly in skeleton relicts. It is, however, very hard to prove if the remnants, sorted out of a larger aggregation, belong to only one specimen. Fossils of groups closely related to the synallactids to use as outgroup are very poor. Only one imprint of a synallactid body-type is known (*Bathysynactites viai* Cherbonnier, 1976) and so far synallactid tables have been found only in *Priscopedatus triassicus* from the Middle Triassic (Anisian) [250 million years] (Simms *et al*., 1993). There are no data about the internal anatomy and further comparable taxonomic characters. The few available fossils assigned to the Synallactidae indicate that synallactids appear to have their origin in the Mesozoic Era. However, the few available fossils belonging to closely-related groups makes it impossible for rooting based exclusively on fossils.

Rather, one can reconstruct a hypothetical ancestor by combining characters from both , 1) fossil and 2) extant, closely related, groups (ancestor rooting). It is also possible to include one or more taxa that are assumed to be placed outside the ingroup. Choosing outgroups is an exercise in trying to get a set of ancestral states at the base of the outgroup taxa that most closely resemble those of the ingroup common ancestor. These character states, permitting a correct rooting, are the plesiomophies held in common at the base of the ingroup.

Based on morphology (Kerr and Kim, 2001) the Stichopodidae and the Holoturiidae appear to be sisters groups to the Synallactidae, and therefore lend themselves as good outgroups. It is recommended to include more than one outgroup taxa as a means of testing the assumption of ingroup monophyly (Swofford *et al*., 1996). Therefore, two species belonging to different holothuriid and stichopodid genera were used as outgroups. Furthermore, the combination of distantly related genera as outgroups possibly could give a better estimate of the character states at the base of the Holothuriidae, than would congeners. In this study, four aspidochirotid species, each one from two stichopodid genera and two species from one holothuriid genus, were chosen as outgroups.

2.8.3. Phylogenetic analysis

The data matrix was analysed using PAUP* 4.0b 10 (Swofford, 2002) version. The phylogeny was performed by the maximum-parsimony optimal criterion. The analysis was executed under the heuristic search mode, because the larger number of taxa computationally excluded branch-and-bound or exhaustive searching. In the heuristic mode the following options were retained: only best trees were kept; starting tree(s) were obtained via stepwise addition; where multiple starting trees existed, only the best trees were swapped; addition sequence of 1000 random replicates with random trees (not just addition sequence) were used as starting points, holding one tree at each step during stepwise addition; tree bisection-reconnection (TBR) was used as branch swapping algorithm; the steepest descent was not in effect; accelerated transformation optimisation (ACCTRAN) was used; collapse branches (creating polytomies) were used if maximum branch length is zero; topological constrains were not enforced; multiple trees were saved; when saving N best trees, only best trees were swapped; multistate characters were interpreted as polymorphism. In the analysis, all characters were run unordered. Differential character weighting was applied as it is presumed that not all characters had the same informativeness and predictive value. As such, successive weighting based on the rescaled consistency index (**rc**), with base weight 1, was executed in PAUP*. The **rc** represents the consistency index (**ci**) multiplied by the retention index (**ri**). The **ci** is commonly estimate the degree of homoplasy and is equal to the minimum possible length of tree/actual tree length. However, the **ri** is a better estimate of homoplasy, since **ci** dos not remove autopomorphies (which have an automatic **ci** of 1.0) as is highly correlated with the number of taxa in a data set (Darly and Tassy, 1993). Rooting the tree was done by the use of several outgroup taxa considered to be sister groups with the assumption of ingroup and outgroup monophyly.

Bootstrapping using 500 replicates, under a simple heuristic search, assessed data quality in phylogenetic studies using parsimony. Examination of data quality was also carried out by evaluation of the number of most-parsimonious trees. To distinguish phylogenetic signal from random noise, the skewness of tree-length distribution (g_1), generated from 10^6 trees randomly produced from the data was examined. This way, the hierarchical structure could be measured to test if they significantly differ from random variation among taxa. Among the most parsimonious trees, the best tree was extracted by either the 50% majority-rule consensus or the strict consensus rule.

Chapter Three – Molecular taxonomy, distribution and reproductive biology in the genera Mesothuria and Zygothuria (Holothuroidea: Synallactidae) from the North Atlantic Ocean

3.1. Introduction

At bathyal depths in the North Atlantic Ocean, one of the most speciose megabenthic taxa are the aspidochirotid sea cucumbers. Among these, members of the family Synallactidae Ludwig, 1894 have been one of the least-studied large taxa among the deep-sea cucumbers. In particular, no major revision of the genus *Mesothuria* Ludwig, 1894 has been undertaken since Deichmann (1930) and Heding (1942a).

It seems very likely that the genus *Mesothuria* in its modern understanding is a combination of at least two genera. Heding (1940) divided *Mesothuria* into six subgenera, but with little morphological support and differentiated only by a key. Much more tenable seems to be the position of Deichmann (1930, 1940, 1954), who, besides *Mesothuria*, supported also the genus *Zygothuria* Perrier, 1898. The latter genus, as suggested by Perrier (1902) and Deichmann (1930), includes *Z. connectens* Perrier, 1902, *Z. candelabri* (Hérouard, 1923), *Z. lactea* (Théel, 1886a,b), *Z. marginata* (Sluiter, 1901) and *Z. thomsoni* (Théel, 1886a). The two genera exhibit a major difference in the arrangement of ambulacral appendages (Perrier, 1902). *Mesothuria* has a cylindrical body, with the ventral side usually somewhat flattened, with papillae all over the body, uniformly covering the dorsal side and being small and equal size, or much smaller dorsally. In contrast, *Zygothuria* is flat or has a well-differentiated sole, with tubefeet arranged exclusively in a single or double row along ventrolateral ambulacra, placed on the margin of the sole, which often forms a fringe. Tubefeet are widely spread and may be quite big; dorsal papillae are minute, not numerous, irregularly distributed or arranged in two simple rows and sometimes totally absent. Further differences described in this chapter include the structure of the calcareous ring, which has radial segments of triangular shape in *Zygothuria* and rectangular radial segments in *Mesothuria*. However, the structure of the calcareous ring is unknown for most of the species in these genera and this character requires further study. There is a difference between *Mesothuria* and *Zygothuria* also in the shape of the bodywall ossicles. In the present chapter I shall use the name *Zygothuria* following Perrier and Deichmann emphasizing, however, that the definition of genus in synallactid is not fully resolved. Despite their ecological importance, many aspects of the biology of species of the genera *Mesothuria* and *Zygothuria* are poorly understood and there is still much debate about fundamental issues, such as systematics, population dynamics and reproduction. In the present chapter, the systematic relationships of the synallactid genera *Mesothuria* and *Zygothuria* are analysed through partial sequences of the 16S mitochondrial region. The status of *Mesothuria* sp.1, usually identified in the North East Atlantic records as *M. verrilli* (Théel, 1886a), is also investigated. Morphological variation within the ossicles of *M. verrilli* and *Mesthuria* sp.1 indicates that these Atlantic forms are different species. *M. bifurcata* Hérouard, 1901 was added to the molecular analysis in order to increase the number of ingroup species in the study on the monophyly of the *Mesothuria* species. The description of the life history biology of *Mesothuria* sp. 1 and *Z. lactea,* both deep-sea species from the North East Atlantic, is also given.

3.2. Materials and methods

Almost all specimens were obtained from the North Atlantic Ocean, in the Porcupine Seabight and on Porcupine Abyssal Plain to the southwest of Ireland, at depths ranging from 1140 to 1980m (Tables 3.1 and 3.2). The collecting was made between the years of 1978 and 1985, with either the IOS epibenthic sledge, semi-balloon otter trawl with a 14m footrope or Granton trawl. Rice *et al.* (1991), Rice (1992, 1996, 1997), Sibuet (1999), Billett (2000) and Billett and Rice (2001) provide descriptions of the study area.

The collection, sorting and fixation methods are referred in Chapter 2, section 2.1 of this thesis. In addition to North East Atlantic specimens, the stichopodid species *Isostichopus fuscus* Ludwig was collected by SCUBA diving from a shallow water locality (15m depth) in the East Pacific, off the coast of Jalisco, Mexico (21ºN) in the year 2000. The mitochondrial DNA sequence obtained from this species was used as the outgroup in the molecular analysis. *Mesothuria bifurcata* specimens were collected in two sites at the Antarctic (58° 44.35' S, 25° 10.48’ W and 65° 20.15’ S, 54° 14.35' W) at 752.7 and 1122m respectively, in March 2002.

Supplementary material for DNA comparison was obtained from museum specimens. 10 specimens of the species *Mesothuria multipora* Clark from the Pacific Ocean were obtained from the Museum National d’Histoire Naturelle, Paris (MNHN). Specimens had no catalogue number, but were collected by the R/V *Alis* MUSORSTOM 7, St. DW620, Pacific Ocean, 12º 34’S, 178º 11’W, 28 May 1992, 1280m depth. These specimens have been kept in 70% alcohol since they were collected (Nadia Ameziani, Museum National d’Histoire Naturelle, Paris. Pers. Comm.).

Additional material for this taxonomic study was obtained from Harbour Branch Oceanographic Institution (HBOI), the Museum of Comparative Zoology (MCZ), Harvard University and the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Other museum abbreviations are listed in section 2.3 (see Table 2.1).

Table 3.1. List of stations where *Zygothuria lactea* was collected by RRS *Discovery* and RRS *Challenger*. Gear abbreviations= BN: IOS Epibenthic Sledge; OTSB: Semi Balloon Otter Trawl, GT: Granton Trawl. (*): Samples used in biomass estimation.

Station	**Date**	**Lat. (N)**	**Long. (W)**	**Depth (m)**	**Gear**
9754#3	09-04-78	51º 08.9’	12º 01.6’	1484	BN 9779#1
24 -04-78	49º 21.5’	12º 49.3’	1140-1398	BN	
50509#1	03-06-79	51º 14.1’	13º 17.8’	1500	OTSB
50602#2	01-07-79	51º 01.1’	13º 07.0’	1955-1980	BN
50602#3	02-07-79	51º 06.8’	13º 20.6’	1815-1939	OTSB
10111#8	09-09-79	49º 32.6’	13º 06.5’	1630-1640	BN
50703#1	13-10-79	49º 33.0’	12º 34.0’	1625-1575	OTSB
50715#1	21-10-79	51º 19.5’	12º 57.0’	1635-1720	OTSB
50902#1	07-11-80	51º 17.4’	12º 47.0’	1325-1866	OTSB
51009#1	02-10-81	51º 34.2’	12º 54.2’	1474-1485	OTSB
51113#2	30-10-81	51º 15.2’	13º 12.3’	1530-1540	BN (*)
51307#1	19-02-82	51º 26.4’	13º 01.4’	1415-1490	OTSB
51308#1	20-02-82	51º 13.0’	13º 02.0’	1715-1770	OTSB
51403#1	26-03-81	51º 36.7’	12º 59.6’	1319-1333	BN (*)
51407#1	27-03-81	51º 19.5’	13º 05.0’	1489-1511	BN (*)
51409#1	28-03-81	51º 16.5’	13º 00.2’	1651-1717	OTSB
51419#1	01-04-81	51º 19.0’	13º 05.4’	1488-1529	OTSB
51708#2	13-04-83	51º 31.1’	12º 59.0’	1430-1470	BN (*)
51708#2	21-08-84	51º 36.0’	13º 00.0’	1600-1682	BN
52203#1	16-06-85	51º 25.6’	13º 00.5’	1521-1531	BN
52211#1	18-06-85	51º 10.2’	13º 15.0’	1693-1738	BN

Table 3.2. List of stations where *Mesothuria* sp. 1 was collected by RRS *Discovery* and RRS *Challenger*. Gear abbreviations= BN: IOS Epibenthic Sledge; OTSB: Semi Balloon Otter Trawl, GT: Granton Trawl.

Station	**Date**	**Lat. (N)**	**Long. (W)**	**Depth (m)**	**Gear**
9754#3	09-04-78	51° 08.9'	12° 01.6'	1484	BN
9774#1	21-04-78	51° 50.0'	12° 01.0'	1494-1572	OTSB
50519#1	08-06-79	49° 29.7'	12° 46.2'	1431-1465	OTSB
50611#1	08-07-79	51° 17.5'	13° 17.8'	1365-1415	OTSB
50703#1	13-10-79	49° 33.0'	12° 34.0'	1575-1625	OTSB
50713#1	20-10-79	51° 22.0'	13° 18.0'	1245-1275	GT
51009#1	02-05-81	51° 34.2'	12° 54.2'	1474-1485	OTSB
51023#1	09-05-81	49° 30.1'	12° 10.8'	1270-1275	OTSB
51307#1	19-02-82	51° 26.4'	13° 01.4'	1415-1490	OTSB
51314#1	22-02-82	49° 31.8'	12° 29.1'	1425-1455	OTSB
51419#1	01-03-81	51° 18.0'	13°06.0'	1488-1529	OTSB
51708#2	13-04-83	51° 31.1'	12°59.0'	1430-1470	BN
52017#1	21-08-84	51° 31.8'	12°58.0'	1457-1472	BN

3.2.1. Identification

Prior to the DNA analysis, taxonomic identification was carried out based on original descriptions and keys (Perrier, 1902; Hérouard, 1902, 1923; Deichmann, 1930) using external and internal anatomy. Ossicle preparations, and morphological methods are given in Chapter 2 of this thesis.

The specimens were deposited in the collections of the Natural History Museum, London (NHM); the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); the Zoological Museum, Copenhagen, Denmark (ZMC); Echinoderm National Collection, Universidad Nacional Autonoma de Mexico, Mexico City, (ICML-UNAM) and the *Discovery* Collections, Southampton Oceanography Centre, UK.

3.2.2. Molecular analysis

DNA extraction, polymerase chain reactions (PCR) (preparation and performance), PCR purification, cycle-sequencing reactions and DNA sequencing methods are referred in Chapter 2 of this thesis.

The oligonucleotide primers used for the molecular analysis are shown in Table 3.3.

Table 3.3. 16S Oligonucleotid primers sequences used in the present study*.

Primer	**Sequence 5’ ? 3’**	**Mitochondrial map position** (*Strongylocentrotus purpuratus*)	**Direction**
16Sb	GACGAGAAGACCCTGTGGAGC	5297-5317	Forward
16Sr	ACTTAGATAGAAACTGACCTG	5710-5687	Reverse

* Primers were designed by Arndt *et al.* (1996).

The genetic variation of the genera *Mesothuria* and *Zygothuria* was analysed using partial 16S sequence with all bases included. The analysis sample set comprised the 16S sequences for *M. multipora, Mesothuria* sp. 1, *Zygothuria lactea* and *Isotichopus fuscus* (Table 3.4).

These represent consensus sequences determined from the original sequence data set of 18 individuals in which all identical sequences were collapsed. The 16S amino acid sequence was used for the best possible alignment. All sequences were aligned using Clustal X (Thompson *et al.*, 1997).

Table 3.4. DNA sequences used in the molecular analysis.

Species	**No. Seqs.**	**GenBank Accession No.**
Mesothuria multipora Clark, 1920	4	AY153485, AY153486, AY153487, AY153488
Mesothuria bifurcata Hérouard, 1901	2	AY153492, AY153493
Mesothuria sp. 1.	5	AY151131-35
Zygothuria lactea Perrier, 1898	3	AY153489, AY153490, AY153491
Isostichopus fuscus Ludwig, 1875	6	AY153494, AY153495, AY153496, AY153497, AY153498, AY153499

Phylogenetic analysis was performed on the nucleotide sequence data. Non-parametric bootstrap analysis was performed using Maximum Parsimony (MP) and

Maximum Likelihood (ML) optimal criteria using PAUP* 4.0b 10 version (Swofford, 2002). Starting trees were obtained by neighbour joining for ML and via stepwise addition with random sequence addition for the MP analysis. In the Maximum Parsimony analysis, gaps were treated as missing, and of the 238 characters only 47 were parsimony-informative. For all optimal criteria a heuristic search was employed using the tree-bisection-reconnection (TBR) branch-swapping algorithm.

The best model of evolution for Maximum Likelihood analysis was determined by hierarchical likelihood ratio tests (hLRTs) using Modeltest v3.0 (Posada and Crandall, 1998). The General Time Reversible model with I (GTR + G) was chosen above others as the most suitable model of evolution for the data set. The estimations from the hLRTs were used to refine the optimal criteria settings as follows; the proportion of invariable sites (G) was set to 0.6776, gamma distribution (the distribution of rates at variable sites) was assumed equal, the substitution model was based on the rate matrix (Table 3.5) and, base frequencies were set to A = 0.2946, C = 0.1806, G = 0.2295 and, T = 0. 2953.

For all searches, starting branch lengths were obtained using Rogers-Swofford approximation method and a molecular clock was not enforced.

Table 3.5. Nucleotide substitution rate matrix.

	A	C	G	T
A	-	0.96	3.72	5.95
		-	0.01	8.70
			-	1
				-

The methods to study population structure and reproduction were described in Chapter 2. For species collected in abundance, *Zygothuria lactea* and *Mesothuria* sp. 1, oocyte size/frequency data were obtained.

3.3. Results

3.3.1. Systematics

Family Synallactidae Ludwig, 1894

Genus ***Mesothuria*** Ludwig, 1894

Mesothuria Ludwig, 1894: 31; Perrier, 1899: 244; 1900: 301; 1902: 301-304; Hérouard, 1906: 6-7; Fisher, 1907: 679; Mortensen, 1927: 379; Deichmann, 1930: 91; Heding, 1940: 331-334; Thandar, 1992: 161; Madsen & Hansen, 1994: 76; Rowe, 1995: 330.
Allantis Hérouard, 1902: ?
Mesites Ludwig, 1893a: 2; 1893b: 179.

Diagnosis (modified from Hérouard, 1906 and Deichmann, 1930). Body usually nearly cylindrical, slightly attenuating toward both ends, without marginal fringe. Ventral side usually somewhat flattened; dorsal side more or less uniformly covered with small pedicels, which are small and equal size, or much smaller dorsally, where they are sometimes hardly visible. Tube feet with sucking disc scattered over the entire body. Usually twenty tentacles, very occasionally varying between 18-22. No tentacle ampullae; stone canal attached to bodywall without penetrating it. Mouth terminal, anus ventral, or subventral, without special arrangement. Calcareous ring with rectangular radial segments. Gonads only on the left side of the dorsal mesentery, in a single tuft. Ossicles of the bodywall are quadriradiate tables with the central primary cross elevated from the disc.

Type species. *Mesothuria multipes* Ludwig, 1894, by monotypy.

Mesothuria verrilli (Théel, 1886a)

Figures 3.1; 122-123 in CD

Holothuria verrilli Théel, 1886a: 6 (*passim*).

Mesothuria verrilli (Théel, 1886a); Deichmann, 1930: 93-94, plate 6, figs. 1-8; 1940: 192-193; 1954: 385.

Non *Holothuria verrilli* Théel, 1886a; Marenzeller, 1893b: 7-9, Pl. 1, fig. 2, Pl. 2, fig. 2. (=*M. intestinalis*).

Non *Mesothuria verrilli* (Théel, 1886a); Östergren, 1896: 345; Perrier, 1902: 307-312, Pl. 16, figs. 22-31; Hérouard, 1923: 10-13; Mortensen, 1927: 381-382; Grieg, 1932: 4.

Non *Allantis intestinalis* var. *verrilli* (Théel, 1886); Hérouard, 1902: 18-21, Pl. 1, figs. 306.

Mesothuria gargantua Deichman, 1930: 95-96 (*passim*).

Diagnosis (after Théel, 1886a and Deichmann, 1930). Body cylindrical, with relatively thick skin, the outer layer often much wrinkled. Maximum known size in preserved specimens 300mm. Mouth almost terminal, slightly directed ventrally, anus terminal. Pedicels minute, in large specimens hard to observe, easier to observe near the ends, especially on the ventral side near the anus; they are uniformly distributed, being absent only on the anterior part of ventrum. Tentacles about 20, relatively small, usually retracted. **Ossicles** are quadri-radiated tables (Figures 3.1 D-E), similar on dorsal and ventral sides, except in the young specimens, <80 mm, having ventral ossicles slightly smaller than dorsal. The main form of ossicles in the type specimen have a rounded or almost square disk (Figure 3.1, A), 0.10-0.12mm in diameter, surrounded by a single crown of 10-12 marginal holes, rarely up to 14, or as little as 8; holes almost equal in size, however, some variations exist (Figures 3.1, A-C). Spire low, usually about a half of a disk diameter in height, but up to the size of the diameter, built up of four rods and 1, more rarely 2, transverse beams; it terminates with 4 distinct teeth, often spinous at the ends (Figures 3.1, D-E). In the tubefeet a small plate is usually present and a number of abortive small tables with disk resorbed and often a partly resorbed spire.

Remarks. Considerable variation exists in the form and size of ossicles between larger and smaller specimens (Table 3.6). Compared to the ossicles in the type specimen, the 70mm long specimen has ossicles with an obviously smaller disk diameter and the number of marginal holes is fewer. In addition, ossicles on the ventrum are smaller than on the dorsum in the 70mm specimen. This difference gradually disappears with size and is not observed in animals >90mm long. Dorsal ossicles are also known to exceed ventral ones in size as in *M. intestinalis* (Heding, 1942a). No major differences were found between the 90mm long specimen and the type specimen, whereas in the larger specimens (>250mm) 1) the ossicles diminished in size and, 2) the number of marginal holes decreased to 8. Thus, there seems to be a peak state in this species of both in ossicle size and shape in individuals ca. 100-200mm long. The size series available in this study was not enough to establish a precise animal size relationship at which the "peaking" of ossicles size occurs. In smaller specimens ossicles in general are of "mature" type, but smaller. In the largest specimens (250-300mm long), disks and spires are partly resorbed, teeth of the spire are short and smooth, relative size of holes diminishes and ossicles are more robust than in smaller individuals (Deichmann, 1930).

Table 3.6. Age variation of ossicles in *Mesothuria verrilli*.

Preserved specimen length (mm)	**Ossicle disk diameter (mm)**	**Number of marginal holes**	**Material source**
70	0.08-0.11 (dorsal)	8-10	Type series, MCZ cat. No. 450*
	0.08-0.09 (ventral)	8-10	Type series, MCZ cat. No. 450*
90	0.10-0.12	9-11	Type series, MCZ cat. No. 450*
230	**0.10-0.12**	**10-12**	**Holotype, MCZ cat. No. 448***
250-300	0.08-0.09	8	Deichmann, 1930

* Type series. Holotype in bold. (Gebruk, unpublished information).

Type material. Holotype, MCZ Cat. No. 448; Type series, MCZ Cat. No. 450, 2 specimens, (TL: 70 and 90mm).

Type locality. Off Ambergris Cay, Belize, former British Honduras, 1100m (after Gebruk, unpublished. information).

Other material examined USNM E16547, 1 specimen (TL: 180mm, w: 50mm), *Alvin* St. 697 North Atlantic Ocean, Bahamas, Great Bahama Bank, 23º 54'N, 77º 10'W, 1337-1355m, Jan 1977, Id. by Pawson; USNM E46781, 1 specimen (TL: 210mm, W: 40mm), *Oregon II* St. 11242 North Atlantic Ocean, Caribbean Sea, Colombia, North of Gulf of Morrosquillo, 10º 10'N, 76º 14'W, 1097m, 5 Nov 1970, Id. by Pequegnat, W. E. See also appendix 1, Table 40.

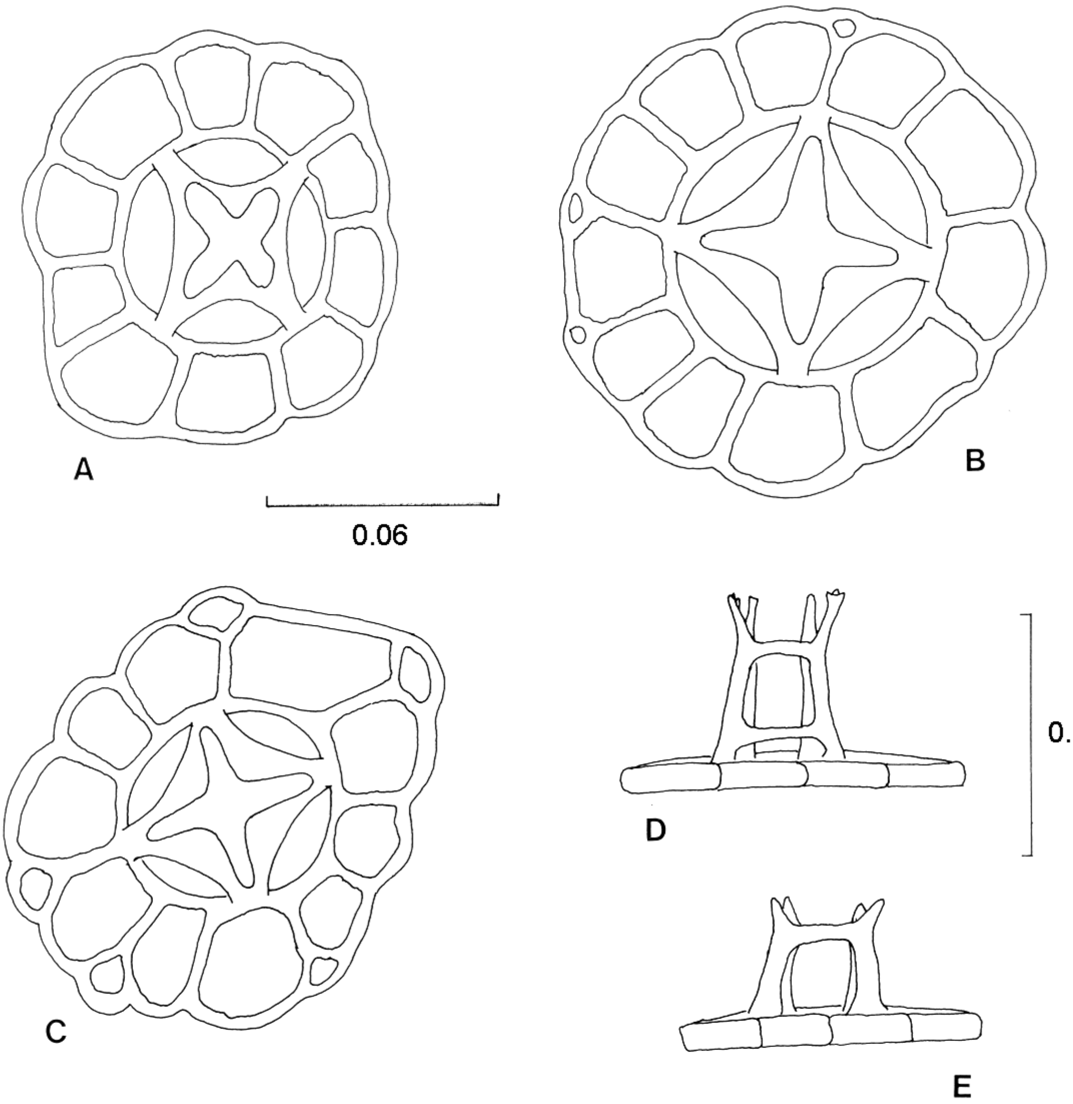

Figure 3.1. *Mesothuria verrilli* (Théel, 1886). Dorsal ossicles from type specimen (MCZ cat. No. 448). A-C tables disks; D-E, spires. Scale bar 0.06mm for A-C; 0.1mm for D-E. (Gebruk, unpublished drawing).

Remarks. As previously indicated (von Marenzeller, 1893b; Perrier, 1902; Deichmann, 1930) the original description of *M. verrilli* (Théel) includes under this name at least two to three species of *Mesothuria*, namely *gargantua* and possibly *intestinalis*. This has resulted in confusion with the name "*verrilli*". The original morphological description of *M. verrilli* was based on a 110mm long specimen "dredged at St. Vincent", corresponding apparently to *M. gargantuan* Deichmann, 1930. Ten other specimens from the type series were sampled from different localities in the Caribbean. A specimen from the west Caribbean, off Ambergris Cay, 230mm long, was later recognized as the type for *M. verrilli* (Deichmann, 1930). In the description of variation of ossicles by Théel, some characters correspond to *M. verrilli* (".. in two of the specimens from Dominica, the spire often, but not always, terminates in four smooth teeth"), and others to *M. intestinalis* ("..in others, for instance those from Barbados and Grenada, the top of the spire has a very irregular aspect, from numerous longer or shorter teeth, which are placed not only round the opening of the top itself, but also on a cross-like rod which covers the opening").

In addition to the poorly described characters of ossicles, the type description lacks illustrations of ossicles, and therefore the name "*verrilli*" was widely used later by von Marenzeller, Perrier and others for the specimens from the East Atlantic having a spire with four smooth teeth. The difference, however, between *M. verrilli* from the Caribbean and all the East Atlantic specimens attributed to this species is obvious and is discussed in detail under *Mesothuria* sp. 1.

A number of specimens from the Mediterranean and off the Azores described as *Allantis intestinalis* var. *verrilli* (Hérouard, 1896, 1902), and attributed later to *M. verrilli* (Perrier, 1902; Deichmann, 1930), most likely belong to *M. intestinalis*. This follows from the number of circles of holes on the disks, which may reach 3-4 according to Hérouard, and the size of disks reaching 0.137mm in diameter in juveniles, unknown for *M. verrilli*, even in the youngest specimens. The illustrations of ossicles given by Hérouard (1902) are quite confusing, presenting only one extreme type of ossicle from the range of variation typical for *M. intestinalis*, and this extreme type resembles *M. verrilli.*

In view of the confusion with the name *verrilli*, all other records of this species in the West Atlantic, not provided with morphological details, cannot be considered reliable. These records include samples off the Bahamas (Pawson, 1982), the Gulf of Mexico (Miller and Pawson, 1984) and records from the Caribbean (Suchanek, *et al.*, 1985). If the last record corresponds to true *M. verrilli*, this would increase the bathymetric limit of this species to 3720m.

Relationships. The species is most closely related to *Mesothuria* sp. 1. Details are given under *Mesothuria* sp. 1.

Geographic distribution Reliable records in the Caribbean (Figure 3.2). Type locality, as indicated by Deichmann, off Ambergris Cay (Belize, former British Honduras), depth 1100m. Distribution data in the eastern and western Atlantic for *M. verrilli* may definitely belong to *Mesothuria* sp. 1.

Bathymetric distribution Reliable bathymetric range from 700 to 1800m, but may be deeper.

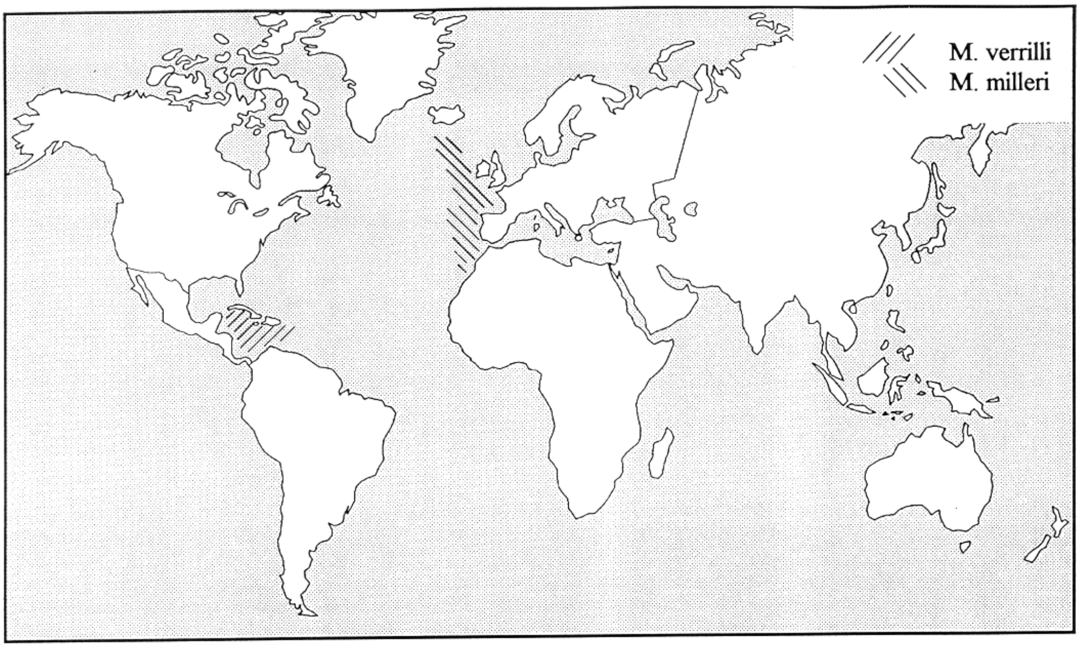

Figure 3.2. Distribution of *Mesothuria verrilli* and *Mesothuria* sp. 1. (Gebruk, unpublished information).

Mesothuria sp. 1.

Figure 3.3.

Holothuria verrilli Théel, 1886a; Marenzeller, 1893b: 7-9, Pl. 1, fig. 2, Pl. 2, fig. 2.
Mesothuria verrilli (Théel, 1886); Östergren, 1896: 345; Perrier, 1902: 307-312, Pl. 16, figs. 22-31; Hérouard, 1923: 10-13; Mortensen, 1927: 381-382, fig. 224: 4-5; ?Grieg, 1932: 4.
Non *Mesothuria intestinalis* (Ascanius, 1805), Koehler, 1896: 106; Ludwig, 1901: 138.

Diagnosis. Body elongated, cylindrical; skin thick but not wrinkled, except in some large specimens. Maximum known size 200mm (preserved). Mouth and anus terminal. Pedicels minute, all over the body, may be absent on the anterior part of the ventrum and always concentrated in the posterior ¼ section of ventrum. Tentacles 19-22, relatively small, often retracted. Ossicles are quadriradiate tables, almost similar on dorsal and ventral side. In holotype disks are rounded, 0.07-0.09mm in diameter, surrounded by a single crown of 8 marginal holes, rarely 9, equal in size (Figures 3.3 A-B). Disks with more narrow holes (Figure 3.3 C) are common on ventrum, but occasionally occur on dorsal side too. Spire tall, its height approximately equal to the diameter to the disk, built up of 4 rods and always 2 transverse beams; it terminates with 4 teeth, usually smooth (Figures 3.3 F-G). In the tubefeet small terminal plates and abortive tables are common. Radial segments of the calcareous ring have processes directed anterior-laterally, resembling "wings" (Figure 3.3 J). General outline of the radial pieces is nearly rectangular.

Remarks. Some variation exists in the size and form of the ossicles between larger and smaller specimens and these data are presented Table 3.7. The longest specimen from more than 200 examined was 180mm (preserved length). Disk diameter is slightly greater in the larger >100mm long specimens, compared to smaller 30-80mm long holothurians. The number of marginal holes increased slightly in larger specimens. There is no major difference between 110 and 180mm long specimens. Ossicles in the bigger specimens are usually more irregular and have lower spire and shorter teeth (Figures 3.3 D-E, H-I). No resorbtion of ossicles occurs in the bigger animals is observed unlike *M. verrilli* (Gebruk, unpublished information).

Material examined. See appendix 1, Table 31; appendix 2, Table 7.

Type Material. Holotype, NHM 2002.979 (80 mm long); Paratypes, NHM 2002.980-981, all measurements are in mm (2 specimens, TL_{max}=107, TL_{min}=83, W_{max}=23, W_{min}=19); USNM (2 specimens, TL_{max}=149, TL_{min}= 111, W_{max}= 25, W_{min}= 20); ZMUC (1 specimen, TL=124, W= 30); ICML-UNAM-5.131.0 (1 specimen, TL=153,W= 39).

Type locality. North East Atlantic Ocean, 51º 31.1'N, 12º 59.0'W, RRS *Discovery* St. 51708#2, 1470-1430m, 13 Apr 1983.

Table 3.7. Variation of ossicles according to specimen size in *Mesothuria* sp. 1.

Preserved specimen length (mm)	**Ossicle disk diameter (mm)**	**Number of marginal holes**	**Material source**
36	0.06-0.08	8	51708#2
50	0.07-0.09	8	50519#1
80	**0.07-0.09**	**8-9**	**51708#2**
110	0.08-0.10	8-10	51708#2
180	0.08-0.10	8-10	9754#3

(holotype in bold; several specimens (3-5) of each size class have been examined, except for a single 180mm long specimen) (Gebruk, unpublished information).

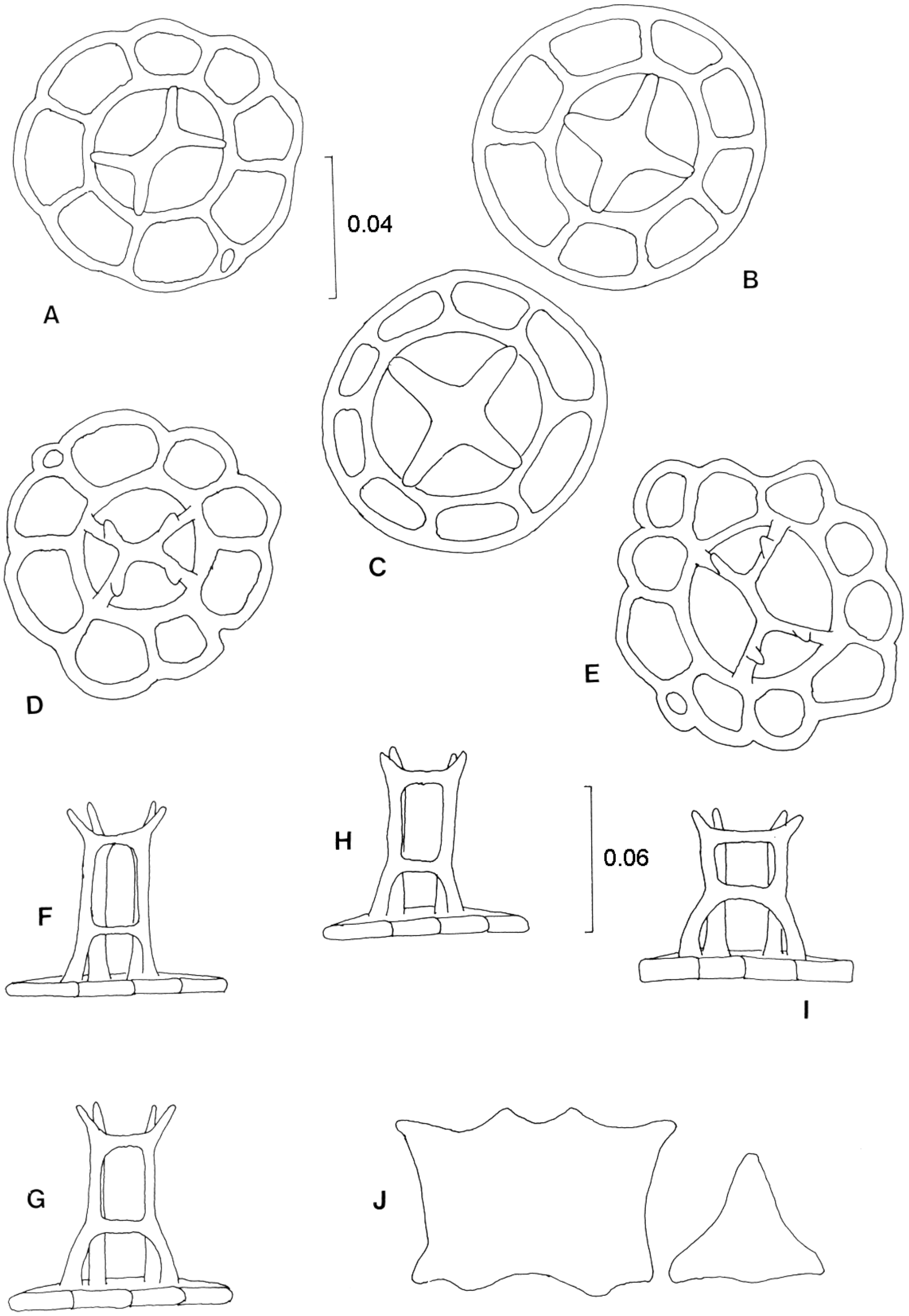

Figure 3.3. *Mesothuria* sp. 1. Ossicles (A-G) and segments of calcareous ring (J) from holotype specimen (RRS *Discovery* St. 51708 #2). A-E disks; F-G, spires. Scale bar 0.04mm for A-E; 0.06mm for F-G. (Gebruk, unpublished drawing).

Remarks. Owing to the poor original description of *Mesothuria verrilli*, a species common in the Caribbean, this name has been widely used for similar looking holothurians from the eastern Atlantic. Additional problems arise because of the similar type of ossicles found in the older specimens of two species. However, the difference in ossicles between younger specimens (<100mm in the preserved state) of the two species is obvious.

In specimens smaller than 100mm, *M. verrilli* ossicles have, 1) a disk diameter of 0.10-0.12mm, 2) 10-11 marginal holes, and 3) a low spire, often with only 1 transverse beam and with squarish outline. Specimens of *Mesothuria* sp. 1 of the same size 1) a disk about 0.08mm in diameter, 2) usually 8 marginal holes, 3) a more regular, circular outline of the disk, and 4) a relatively tall spire always with 2 transverse beams. Ossicles diminish in size in the larger specimens (>200mm) of *M. verrilli*. This trend is also known in *M. intestinalis* (Östergren 1896). However, the ossicles get slightly bigger in the larger specimens of *Mesothuria* sp. 1. In *M. verrilli* the number of marginal holes decreases from 10-12(14) in specimens about 110mm long to 8 in specimens >250mm, whereas in *Mesothuria* sp. 1 this number increases from 8 in 80mm-long specimens to 8-10 in 110mm specimens, and remains the same in specimens up to 180mm long. This is about the maximum size for this species in the preserved state. Finally, in *M. verrilli* ossicles reach their maximum size in ca. 200mm long specimens and then significantly diminish in the older animals, whereas in *Mesothuria* sp. 1 which is relatively smaller, no peak state and consequent regression could be distinguished. The tables are slightly larger in 100mm animals. These two different trends result, however, in very similar types and sizes of ossicles in both species in specimens >100mm long in *Mesothuria* sp. 1 and >200mm long in *M. verrilli* (both preserved state).

Different trends related to specimen size (age) in *M. verrilli* and *Mesothuria* sp. 1 help to recognize the latter in the descriptions of von Marenzeller, Perrier, Östergren, Hérouard and Mortensen. Thus, von Marenzeller indicate the disk diameter 0.07-0.09mm for 110mm long specimen (preserved). Disks having 0.08mm in diameter with 8 marginal holes are very clearly described as dominant and illustrated by Perrier, who pointed out the similarities between his specimens and those of Hérouard. The description provided by Mortensen (1927) is uncharacteristically poor, but the ossicles he illustrated, having a tall spire with smooth teeth, indicates *Mesothuria* sp. 1. As a result of the confusion of *M. verrilli* with *M. intestinalis*, as pointed out by Deichmann (1930), in some earlier publications, the latter name was often used for specimens with the characters of *M. verrilli* (Koehler, 1896; Ludwig, 1901). Owing to similar types of ossicles in the large specimens of two species, earlier identifications of these holothurians are not always reliable. This is especially true when the illustrations of ossicles and their details, e.g. size, are missing (Koehler, 1896; Ludwig, 1901; Grieg, 1932). Additionally, age variations of ossicles were not recognized earlier. Hence from the literature it is not always clear the size of the animal to which certain ossicles relate, also making doubtful some old descriptions. I cannot exclude the occurrence of either species both in the West and East Atlantic, although, there is no absolute evidence at present.

Relationships. On the basis of morphology, *Mesothuria* sp. 1 is most closely related to *M. verrilli*. The major differences between the two include 1) ossicles being bigger, given the same size of specimens, in *M. verrilli* (except in big animals), 2) disks with more marginal holes, 3) spire relatively smaller and 4) teeth often spinous.

Trends of ossicles variation with body length. In *M. verrilli* ossicles grow slightly throughout life, reaching a peak size ca. 200mm long animals and then diminishes significantly. In *Mesothuria* sp. 1 ossicles get slightly bigger in the specimens >100mm long.

Geographic and bathymetric distribution The distribution range is not known with certainty, partly as a result of confusion with the name "*verrilli*" and close similarity between large specimens of *M. verrilli* and *Mesothuria* sp. As discussed above, a strong case can be made that all previous records of *M. verrilli* in the East Atlantic correspond to *Mesothuria* sp. 1 (Figure 3.2). If true, then this species is widely distributed in the north northeast Atlantic: off northwest Africa, the Canary Islands (Perrier, 1902; Grieg, 1932) the Azores (Hérouard, 1902, 1923; Perrier, 1902), the Bay of Biscay (Koehler, 1896; Perrier, 1902) the Porcupine Seabight (Mortensen, 1927, plus present material), Goban Spur, Rockall Trough (Harvey *et al.*, 1988), off British Isles, the Azores, the Canaries Islands and Morocco (Perez *et al.*, 1984). The bathymetric range of this species based on the literature is from 550m off northwest Africa (Perrier, 1902) to 4255m off the Azores (Perrier, 1902). Perrier, however, was uncertain about two records deeper than 4000m, the lower limit then being 3018m off the Azores (Hérouard, 1923). In the Porcupine Seabight this species is found most commonly between 1430m and 1530m (82% of the specimens from the Porcupine Seabight material, detailed distribution displayed in Billett, 1988). Owing to confusion with the name "verrilli", as *M. verrilli* in the West Atlantic, the records in the East Atlantic not supported by morphological details (2100m in the Bay of Biscay, Sibuet, 1977) are not reliable.

Mesothuria bifurcata Hérouard, 1901

(Figures 54-58 in CD)

Mesothuria bifurcata Hérouard, 1901: 40; 1906: 4-6, Pl. 2, fig. 3; Jangoux & Massin, 1986: 84 (list); O'Loughlin *et al.*, 1994: 553-554; O'Loughlin, 2002: 313, 315.
Mesothuria (*Mesothuria*) *bifurcatata* Hérouard, 1901: 40; Heding, 1940: 333; 1942a: 8, textfig. 7, figs. 1-6.

Diagnosis: (after Hérouard, 1901 and O'Loughlin, 2002). Body subcylindrical, rounded anteriorly, slightly tapered posteriorly; flattened dorso-ventrally. Mouth ventral, anus posterior. Bodywall thick, firm, flexible; up to 20 peltate tentacles. Ambulacral tubes in two rows, in each radius, except in the medium-ventral radius where there are 2 small tubes. Latero-ventral radius with tubefeet. Very small tubefeet scattered dorsally, laterally, few ventrally, absent midventrally. Calcareous ring solid, lacking posterior prolongations, radial plates as high as wide with anterior V-shaped notch, interradial plates at least twice as wide as high. Gonad tubules with multiple branching. Respiratory trees well developed. **Ossicles**, tables, disk with six holes, column with three stems extremes divergent ending in simple forks.

Material examined. See appendix 1, Table 20; appendix 2, Table 3.

Type material. Holotype, IRSNB Cat. No. IG 10131.

Type locality. *Faubert II*, St. 2. Western Antarctica, Bellingshausen Sea, 71º 14'S, 89º 14' W, approximately 800m (depth estimated from given latitude and longitude by O'Loghlin [2002]), 12 May 1898. Specimen in poor condition. No ossicles were found by O'Loghlin (2002).

Geographic distribution Antarctic species. Heding (1942a) record one specimen of this species at the North West Atlantic (*Ingolf* St. 18, 61º 44'N, 30º 29'W, 2337m).

Bathymetric distribution 320-2337m (Heding, 1942a; O'Loughlin, 2002).

Genus ***Zygothuria*** Perrier, 1898

Zygothuria Perrier, 1898: 1665; 1899: 245-246, 1902: 321-322; Deichmann, 1930: 108.

Diagnosis (modified from Perrier, 1902). Body ovoid, flattened, but with a well-differentiated sole; integument often wrinkled. Tubefeet arranged exclusively in a single or double row along ventrolateral ambulacra, placed on the margin of the sole, which often forms a fringe. Tubefeet are widely spread and may be quite big; dorsal papillae minute, not numerous, irregularly distributed or arranged in two simple rows and sometimes totally absent. 20 tentacles, rarely 13-19; no tentacle ampullae; madreporite placed close to bodywall, without penetrating it. Mouth ventral or terminal, anus terminal, without special arrangement. Calcareous ring, with triangular radial segments. Ossicles of the integument tri-radiate tables.

Type species. *Zygothuria lactea* (Théel, 1886a) designated by Hérouard (1902).

Zygothuria lactea (Théel, 1886a)

Figures 3.4, 3.5.

Holothuria lactea Théel, 1886a: 6-7: 1886b: 183-184, Pl. 9, fig. 15.

Mesothuria lactea (Théel), Sluiter, 1901; 25; Hérouard, 1902: 21-23, Pl. 1, figs. 17-19; 1923: 13-15, Pl. 4, figs. 1-3; Mortensen, 1927: 382-383 (*partim*), fig. 227.

Mesothuria (*Zygothuria*) *lactea* (Théel), Heding, 1940: 340-341, fig. 7.

Mesothuria (*Zygothuria*) *lactea lactea* (Théel), Heding, 1942a: 9-10, fig. 9.

Mesothuria lactea (Théel), Perrier, 1902: 322-327 (*partim*), Pl. 17: 1-6; Deichmann, 1930: 108-111, Pl. 8, figs. 8-9; 1940: 190-191; 1954: 386.

Diagnosis (modified from Deichmann, 1954). Body oval, rather flat, marginal fringe present, ventral surface evidently flatter than dorsal; skin soft, usually wrinkled, colour whitish. Maximum known size 150mm (preserved). Mouth ventral, anus almost terminal. Tentacles small, about 20, usually retracted. Ventro-lateral tubefeet are large, arranged in two simple rows along each side, up to 15-20 in a row, placed at some distance from each other. The odd ambulacrum is naked. Dorsal papillae minute, easily lost, arranged in two simple rows along each ambulacra, placed about 10mm from each other. One ventral polian vesicle and a dorsal stone canal that reaches the dorsal side. **Ossicles** are fragile tables of triradiate type, similar in both the dorsal and ventral sides. Disks rounded or stellate with 6 angles, but often irregular in outline, with 6 large holes around a small central hole.

Type material. NHM, no catalogue number.

Type locality. HMS *Challenger* Station, off New Zealand.

Material examined. 2 juvenile specimens (prom. TL: 22mm, W: 8mm), USNM E16502, *Yaquina*, North Pacific Ocean, United States, 44°40’42”N, 133° 28’06”, 3717m, year 1970; 1 specimen in poor condition, USNM E16924, *Commando*, North Pacific Ocean, United States, Washington, 45° 49’N, 125° 10’W, 1646m, 6 Sep 1962, Id. by: Pawson as *Mesothuria* *lactea*; 2 specimens (prom. TL: 57mm, W: 12mm), USNM E18894, *Gilliss* St. 97, North Atlantic Ocean, United States, off the coast of Virginia, 37º 00’18”N, 74º 15’00”W, 1400-1460m, 23 Nov 1974, Id. by: Carney, R. S. as *Mesothuria lactea*; 1 specimen in poor condition, USNM E2572; 3 specimens (prom. TL: 72.6mm, W: 22.3mm), *Albatross* St. 2393, North Atlantic Ocean, Gulf of Mexico, United States, Louisiana, South East of the Mississippi Delta, 28º 43’00”N, 87º14’30”W, 945m (525fm), 13 Mar 1885; USNM E20328, *Gilliss* St. GI-93, North Atlantic Ocean, United States, off the coast of Virginia, 37º 37’06”N, 74º 25’00”W, 1795-1810m, 19 Sep 1975, Id. by: Carney, R. S. as *Mesothuria lactea*; 1 specimen (TL: 114mm, W: 45mm), USNM E41388, *Cape Hatteras* N1:05/06, North Atlantic Ocean, United States, Massachusetts, George Bank, Lydonia Slope, 40º 04’58”N, 67º 26’35”W, 1950-12305m, 6 Nov 1984; 1 specimen (TL: 230mm, W: 90mm), USNM E46761, *Oregon II* St. 10880, North Atlantic Ocean, Gulf of Mexico, Mexico, Tamaulipas, east of Boca de Sandoval, 24º 57’N, 96º 13’W, 1234m, 23 Jan 1970, Id. by: Pequegnat, W. E. as *Mesothuria lactea*; 13 specimens (prom. TL: 97.6mm, W: 39.6mm), USNM E9875, *Albatross* St. 4656, South Pacific Ocean, Peru, Lambayeque, West of Lobos de Afuera Island, 6º 55’00”S, 83º 34’00”W, 4046m, 13 Nov 1904; 1 specimen (TL: 52mm, W: 8mm); USNM E9914, *Albatross* St. 4658, South Pacific Ocean, Peru, Lambayeque, South West of Lobos de Afuera Island, 8º 30’00”S, 85º 36’00”W, 4334m, 14 Nov 1904. See appendix 1, Table 77; appendix 2, Table 14.

Remarks. Ossicle large holes usually 0.15-0.18mm in diameter, but may reach 0.20 or more (Figures 3.4 A-C). Hexagonal disks (Figures 3.4 D), 0.20-0.23mm in diameter, are more common on a ventral side. Spire high, usually with 3 long, slender, usually equal in length, smooth arms on top, 0.20-0.24mm high; one transverse beam between the base and top is present; occasional minute spines may occur on arms, more common, on ventral side (Figures 3.4 A-B). Occasionally 4 arms may develop. The spire is often single-pointed; the strong central single spine may be directed somewhat laterally (Figures 3.4 C-E) (Figures 3.5 A-E). No terminal plates occur in the tubefeet. The ossicles in tubefeet are smooth rods varying in shape and reduced tables. Radial pieces of the calcareous ring have a nearly triangular outline; the "wings", typical of *Mesothuria* sp. 1 for instance, are missing (Figure 3.4 E) (Gebruk, unpublished information).

Ossicles of similar size and type were found in small specimens 4mm long and large specimens greater than 100mm long. Single-pointed tables occur already in juveniles <10mm long. Some juveniles possess table disks that resemble in shape those from the genus *Mesothuria* (see *Mesothuria maroccana* Perrier, USNM E2333, *Albatross* St. 2117, North Atlantic Ocean, Caribbean Sea; Venezuela, Aves Island, 15º 24'40"N, 63º 31'30"W, 1229m (683fm), 27 Jan 1884).

In the introduction of this chapter it was indicated that considerable differences exist between the genera *Zygothuria* and *Mesothuria*. However, so far, only Perrier and Deichmann recognized the genus *Zygothuria*. The form and the size of ossicles in *Z. lactea* are very characteristic. Some confusion, however, has arisen owing to variation in the number of arms, which is normally three but sometimes just one. Single-pointed ossicles were not indicated by Théel (1886b) in the type material (one station off New Zealand and one in the East Atlantic). However, he added this feature later, based on the additional material from the north Atlantic (Théel, 1886a). A new variety (*oxysclera*), based on the specimens from East Atlantic with single-pointed tables exclusively was described by Perrier (1902). Deichmann (1930) suggested that single-pointed ossicles might become more numerous in the older animals, because many of Perrier's specimens were large. In the material reviewed for this thesis, single-spined ossicles were equally common in small (<50mm) and large (>100mm) specimens. Owing to this variation, common in *Z. lactea*, the variety *oxysclera* was not recognized either by Hérouard (1923) or Heding (1942a). The co-occurrence of single and three-armed tables was also stressed by Sluiter (1901) as an argument against a new variety. There are, however, clear differences between *Z. lactea* and *Z. oxysclera*. The latter species is described below as a valid species.

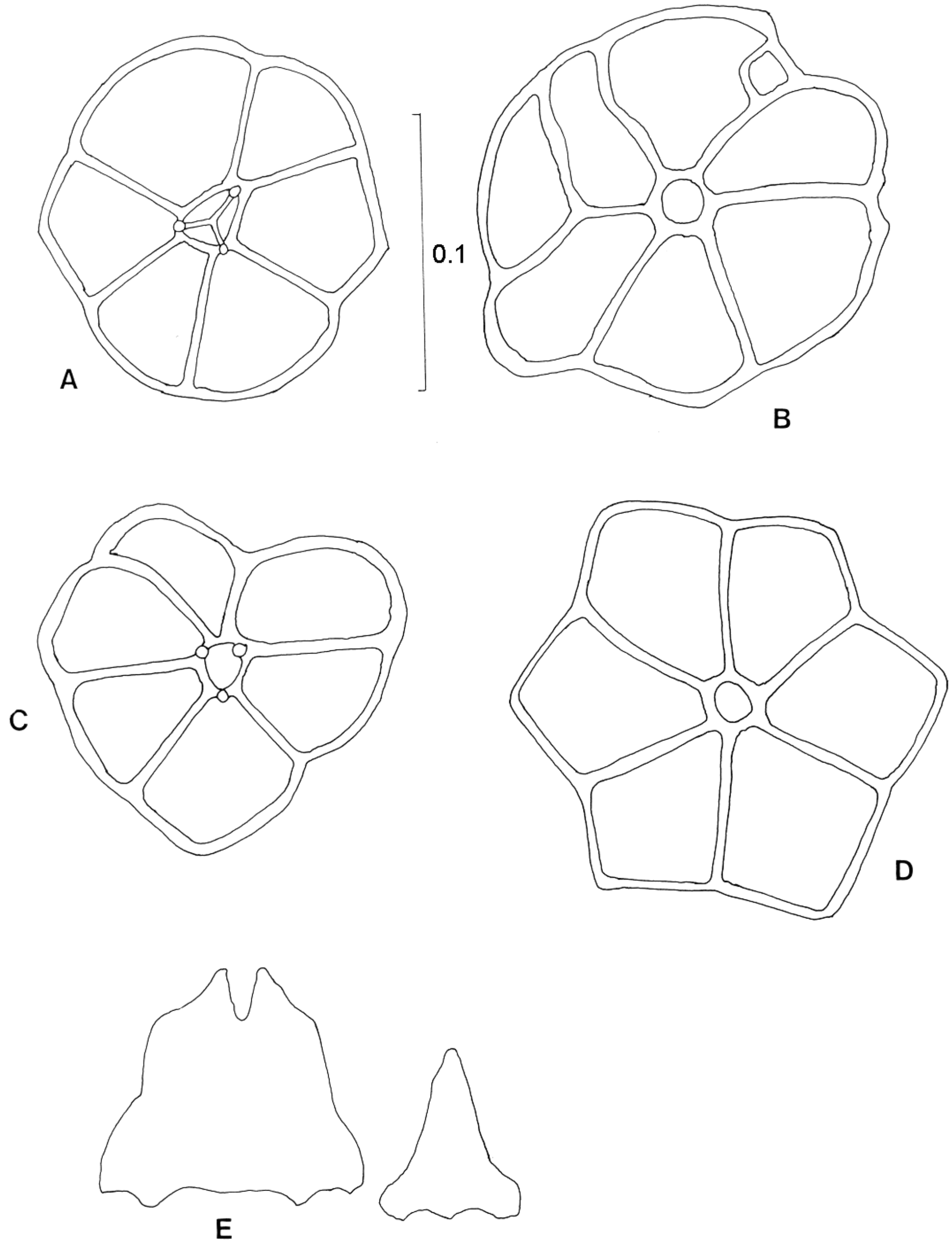

Figure 3.4. *Zygothuria lactea* (Théel, 1886). Disks (A-D) and segments of calcareous ring (E). RRS *Discovery* St. 51419 #1. Scale bar 0.1mm for A-D. (Gebruk, unpublished drawing).

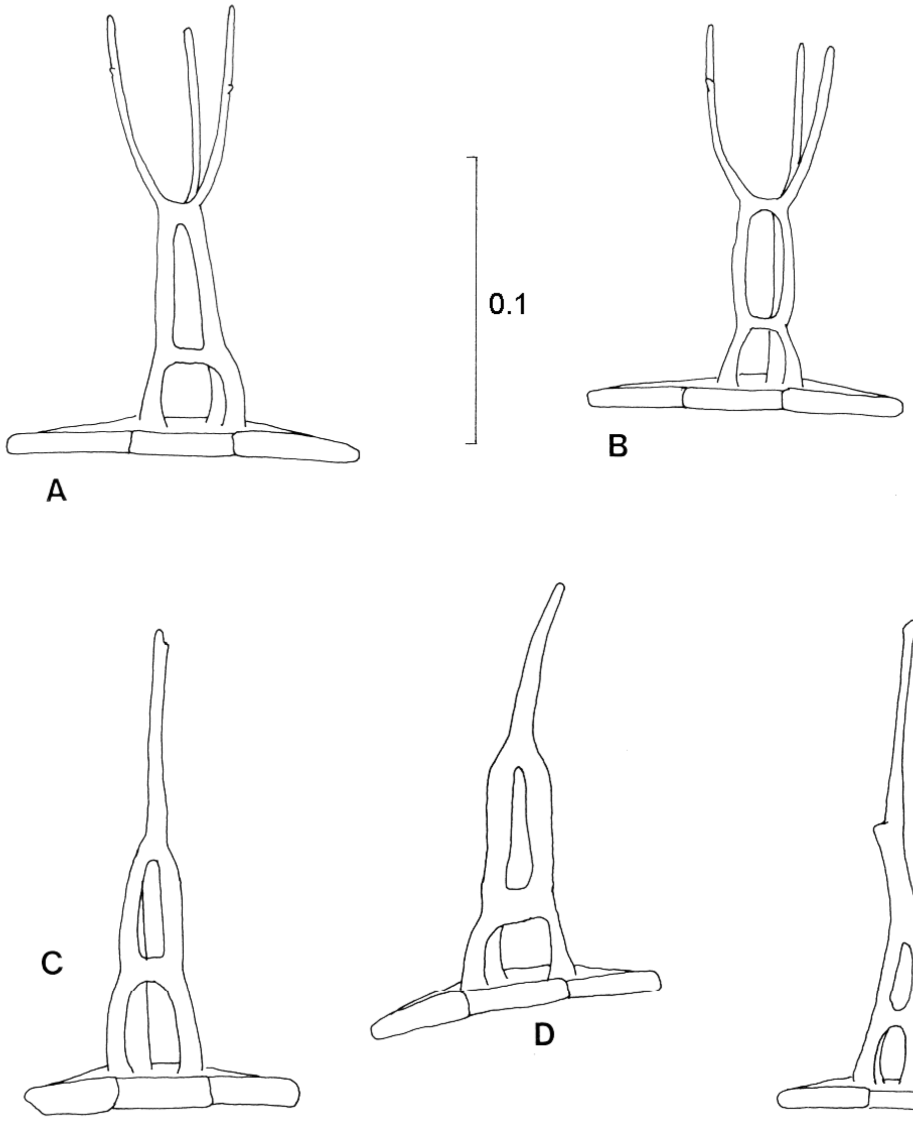

Figure 3.5. *Zygothuria lactea* (Théel, 1886). Table spires. RRS *Discovery* St. 51419.#1 Scale bar 0.1mm. (Gebruk, unpublished drawing).

Relationships. Most close to *Z. candelabri* Hérouard, 1923 and *Z. connectens* Perrier, 1902, all these forms having triradiate tables with three long arms.

Geographic distribution Cosmopolitan species (Figure 3.6). However, some old records may not be reliable because most authors did not recognize the variety *oxysclera* and these two species could have been confused. This is especially likely with the records from the Gulf of Mexico and the Caribbean (Deichmann, 1930) where *Z. oxysclera* occurs. Numerous records from east-northeast Atlantic, also known from the northwest Atlantic, off west Africa, southeast Atlantic, Indo-Malayan archipelago and New Zealand.

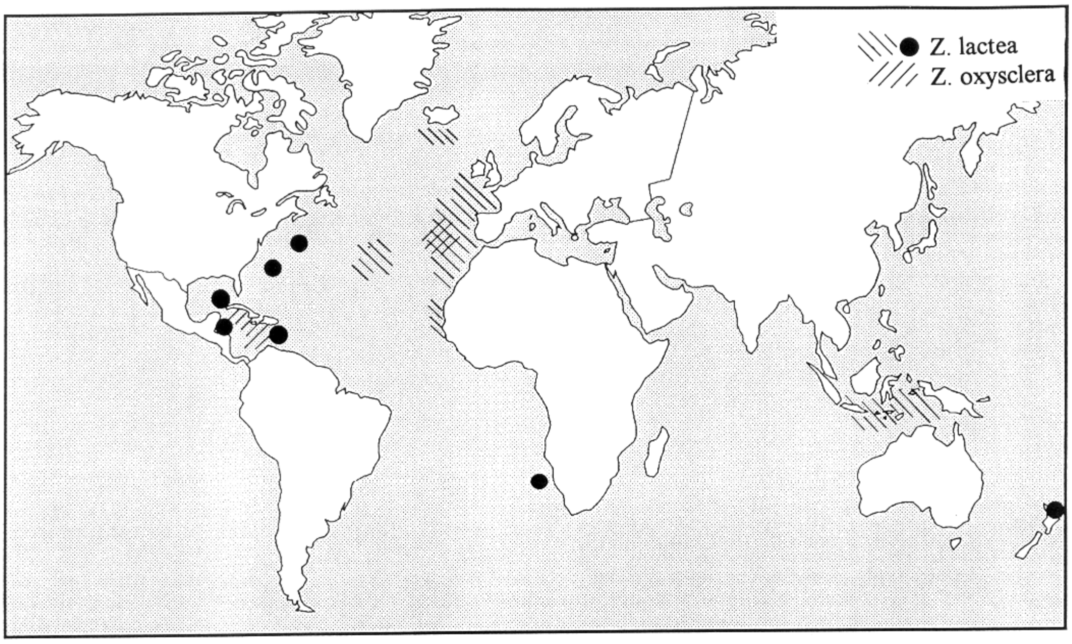

Figure 3.6. Distribution of *Zygothuria lactea* and *Z. oxysclera* (Gebruk, unpublished information).

Bathymetric distribution. Reliable bathymetric range from 694m (Sluiter, 1901) to 2102m (Hérouard, 1902). *M. lactea* var. *spinosa* (Heding, 1940), recorded from 5108m, differs significantly from *Z. lactea* both in the shape and the size of ossicles and should probably be assigned to *Z. candelabri* (Hérouard, 1923). Another deep record, from 4400m (Sibuet, 1977), was not supported by morphological details and hence is not reliable. In the Porcupine Seabight, most of the specimens (83%) occurred between 1430 and 1930m (detailed distribution displayed in Billett, 1988).

Zygothuria oxysclera (Perrier, 1902)

Figure 3.7, Figures 240-247 in CD

Zygothuria lactea var. *oxysclera* Perrier, 1902: 323-327, Pl. 17, figs. 7-10 (*parssim*).

Diagnosis (modified from Perrier, 1902). Body oval, ventral surface evidently flatter than dorsal; skin very thick, usually wrinkled; two layers of skin often seen. Maximum known size 370mm (live). Mouth ventral, anus almost terminal. Tentacles small, from 15 to 20 in number, usually retracted. Ventro-lateral tubefeet are large, arranged in two simple rows along each side, up to 15-20 in a row, placed at some distance from each other, often withdrawn. The odd ambulacrum is naked. Dorsal papillae small, scattered over dorsal side, partly arranged in two rows. Ossicles robust triradiate tables, single-spined. Disks of irregular shape, 0.15-0.20mm in diameter; central hole surrounded with a meshwork of holes of different size (Figures 3.7 A-B, D). Spire high, with only one central strong arm, often bearing minute spines (Figures 3.7 C, E).

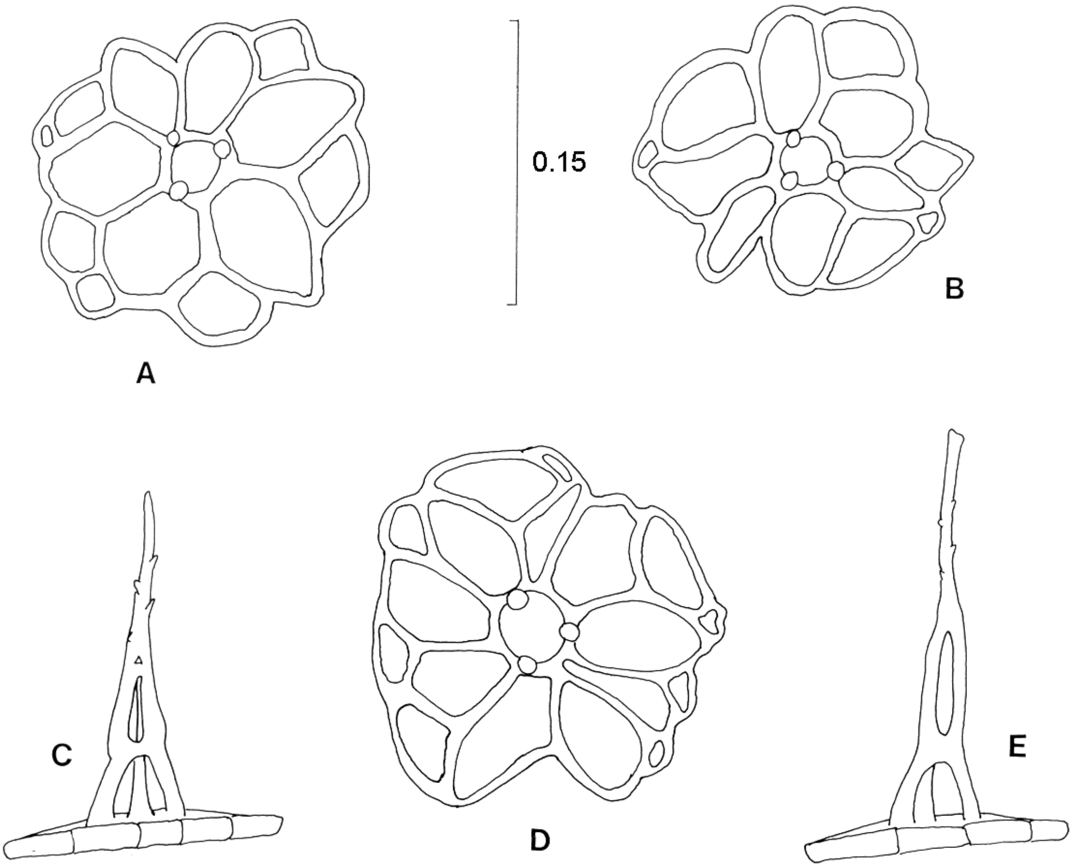

Figure 3.7. *Zygothuria oxysclera* (Perrier, 1902). Ossicles. *Johnson-Sea Link*, Dive 1735. A, B, D disks; C-E spires. Scale bar 0.15mm (Gebruk, unpublished drawing).

Holotype. MNHN, no catalogue number.

Type locality. *Talisman*, "Dredge 20", off Morocco, 33º 43'N, 11º 22'W, 1105m, 14 Jun 1883.

Material examined. 1 specimen, *Johnson-Sea-Link II*, Dive 1731 (760-840m), off Barbados; 2 specimens, *Johnson-Sea-Link II*, Dive 1735 (690-760m), 335 and 370mm long (live size). See appendix 1, Table 79.

Remarks. In young specimens (<50mm), besides tables with irregularly-shaped disks, there are tables with disks having 6 holes only, resembling those of *Z. lactea*. However they are always single-spined. In addition, disks of intermediate form, with 6 main holes and a series of small holes in the outer circle, are also common in small specimens.

The characteristic single-spined ossicles of *Z. oxysclera*, first noticed by Perrier, occur also in *Z. lactea* together with typical three-arms tables. This resulted in Perrier's variety *Z. lactea* var. *oxysclera* being rejected by many authors. Deichmann suggested that single-spined tables become more common in the old specimens of *Z. lactea*, because the description of Perrier was based mainly on large specimens, 150-230mm long. Apparently, she overlooked that Perrier has also examined a 50mm long specimen which had the single-spined tables only. Besides single-spined tables, there are some other characteristic features distinguishing *Z. oxysclera* from *Z. lactea*. The meshwork of holes on the disks is more complicated in the former and the tables are slightly bigger in general, although the whole size range of ossicles is quite similar in the two species. The skin seems to be much thicker in *Z. oxysclera* and double-layered. However, this is especially typical for the large specimens, exceeding 150-200mm, a size unknown for *Z. lactea*.

Relationships. The species is closest to *Z. marginata* (Sluiter, 1901), also having triradiate single-spined tables. *Z. marginata* is the only other *Zygothuria* species, besides *Z. lactea*, to have had the details of its calcareous ring described (Heding, 1940). Both species have the triangular shape in the radial segments of calcareous ring. Differences between *Z. oxysclera* and *Z. lactea* are discussed in remarks.

Geographical and bathymetric distribution East Atlantic (from 865 to 1319m), Caribbean (ca. 700-850m) (Figure 3.6). Some old records of *Z. lactea* from the Caribbean, the Gulf of Mexico and East Atlantic may also correspond to *Z. oxysclera.*

The list of *Mesothuria* and *Zygothuria* species known from the Atlantic, based on the revisions of Deichmann (1930, 1954) and Heding (1940) with the new species added, is as follows (all reliable species are marked in bold, comments given below):

1. ***M. intestinalis* (Ascanius, 1805)**
2. ***M. verrilli* (Théel, 1886a)**
3. ***M. murrayi* (Théel, 1886a)**
4. ?*M. expectans* Perrier, 1902
5. *M. maroccana* Perrier, 1902
6. ***M. bifurcata* Hérouard, 1901**
7. *M. rugosa* Hérouard, 1912
8. *M. grandipes* (Hérouard, 1923)
9. ***M. gargantua* Deichmann, 1930**
10. ***M. cathedralis* Heding, 1940**
11. ***Mesothuria* sp. 1.**

1. ***Z. lactea* (Théel, 1886a)**
2. ***Z. connectens* Perrier, 1898**
3. ***Z. oxysclera* (Perrier, 1902)**
4. *Z. candelabri* (Hérouard, 1923)
5. *Z. thomsoni* (Théel, 1886a)

M. intestinalis is a well defined species, although in the old publications it was often confused with *M. verrilli* and possibly with *M. gargantua*. The type specimen no longer exists. It was described in detail by Östergren (1896) and Heding (1942a). The age variation of ossicles is similar to *M. verrilli*, i. e. ossicles in young specimens are larger than in older specimens. It is a large form, growing up to 300mm in length. It is distributed all over the north Atlantic, including West Indian seas and Mediterranean (see also Madsen and Hansen, 1994). Recent records in Mediterranean include Zavodnik and Simunovic (1985). Bathymetric range believed to be 20-2000m. Shallower records tend to occur in more northerly waters. In the Porcupine Seabight is found between 460 and 1465m depth (Billett, 1988). *M. intestinalis* also can be easily separated from the other *Mesothuria* species by looking at the gonads. The sequential hermaphrodite gonads of *M. intestinalis* consists of many long tubules, arranged loosely inside the body cavity.

M. murrayi (var.?) and *M. murrayi* (Figure 3.8). The type material of *M murrayi* comes from the Pacific, off the Chilean coast, at a depth of ca. 2500m. Hérouard's *M. rugosa* from off the Cape Verde Islands is identical in detail to *M. murrayi*. This was first noticed by Deichmann, who surprisingly considered *M. murrayi* as a junior synonym of *M. rugosa*, although the priority of Théel's name is obvious. There is also a clear similarity between *M. murrayi* and Perrier's *M. maroccana* from off Morocco, also known from the Caribbean, the east Gulf of Mexico and the northeast Atlantic (Billett, 1988). The two species have absolutely identical ossicles, but there are some differences in the arrangement of the tubefeet, which may well be an age variation, because Théel's specimens were 240mm long whereas those of Perrier were only 50mm. Perrier has pointed out the similarities between his specimens and *M. murrayi* (var.?) known from Gibraltar. The similarity between *M. maroccana* and *M. murrayi* (var.?) was also noticed by Grieg (1932). Further confusion was created by Deichmann (1930, 1940, 1954), who gave the morphological details of *M. murrayi* (Théel) in her descriptions, but assigned her specimens, 40-60mm long, from the West Indian seas, to *M. maroccana* Perrier. This group of species evidently requires further study. That is also true for *M. murrayi* var. *grandipes*. Illustrations of the ossicles of this species are lacking, but the size given for the table disks, 0.15-0.18mm in the 80mm long specimen, significantly exceeds that of the main "murrayi group" (0.07-0.12mm). *M. murrayi* has also been reported from the Indonesian seas, from 400-522m (Sluiter, 1901) (Figure 3.8).

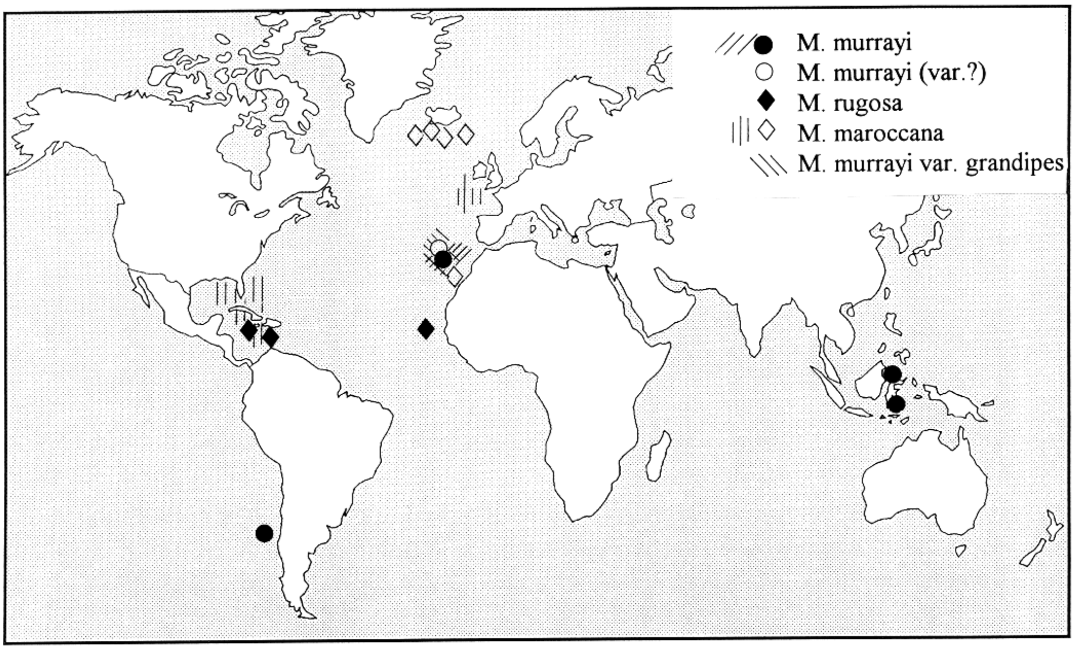

Figure 3.8. Distribution of a group of *Mesothuria* species (Gebruk, unpublished information).

?*M. expectans* as observed by Perrier and Deichmann, may well correspond to the genus *Paroriza*. The description was based on a single specimen, and ossicles were completely lacking.

M. bifurcata has very characteristic ossicles, which were carefully described by Heding (1942a). The type locality is in the Southern Ocean Pacific (Figure 3.9).

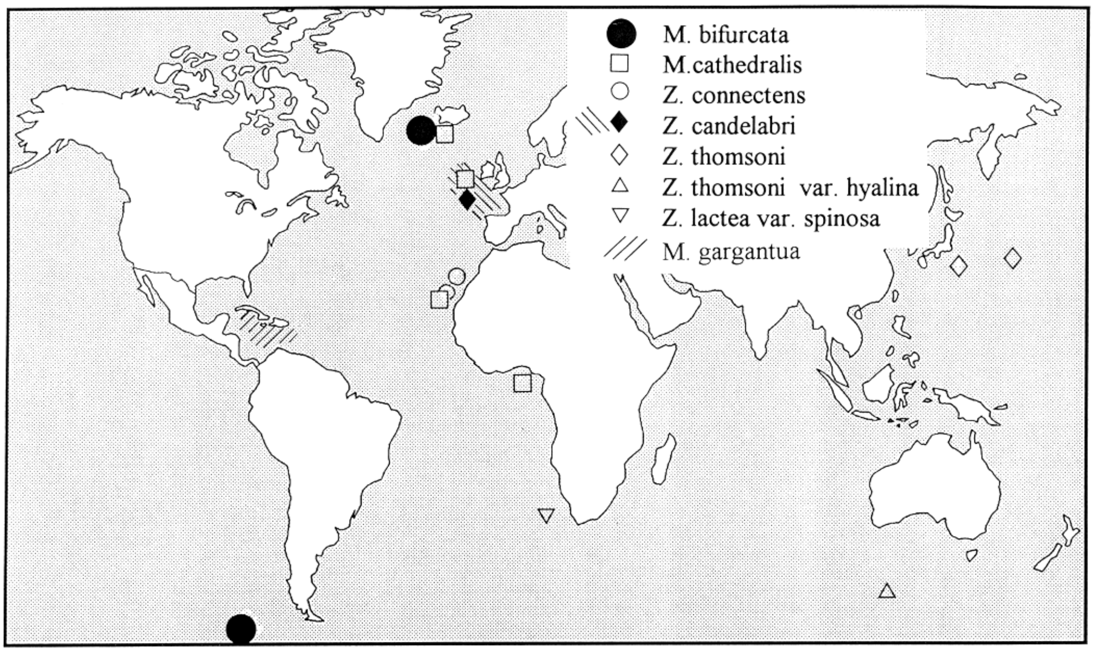

Figure 3.9. Distribution of a group of *Mesothuria* and *Zygothuria* species (Gebruk, unpublished information).

M. gargantua is characterized by very large and robust quadri-radiate (rarely 5-radiate) tables (disk diameter up to 0.25mm). It was described carefully by Deichmann, but a single illustration of ossicle she provided was insufficient. More clear illustrations, based on the preparations from the type material (MCZ, Cat. No. 449) are represented on Figure 3.10. A photo of *M. gargantua in situ* is given in Rice and Miller (1991).

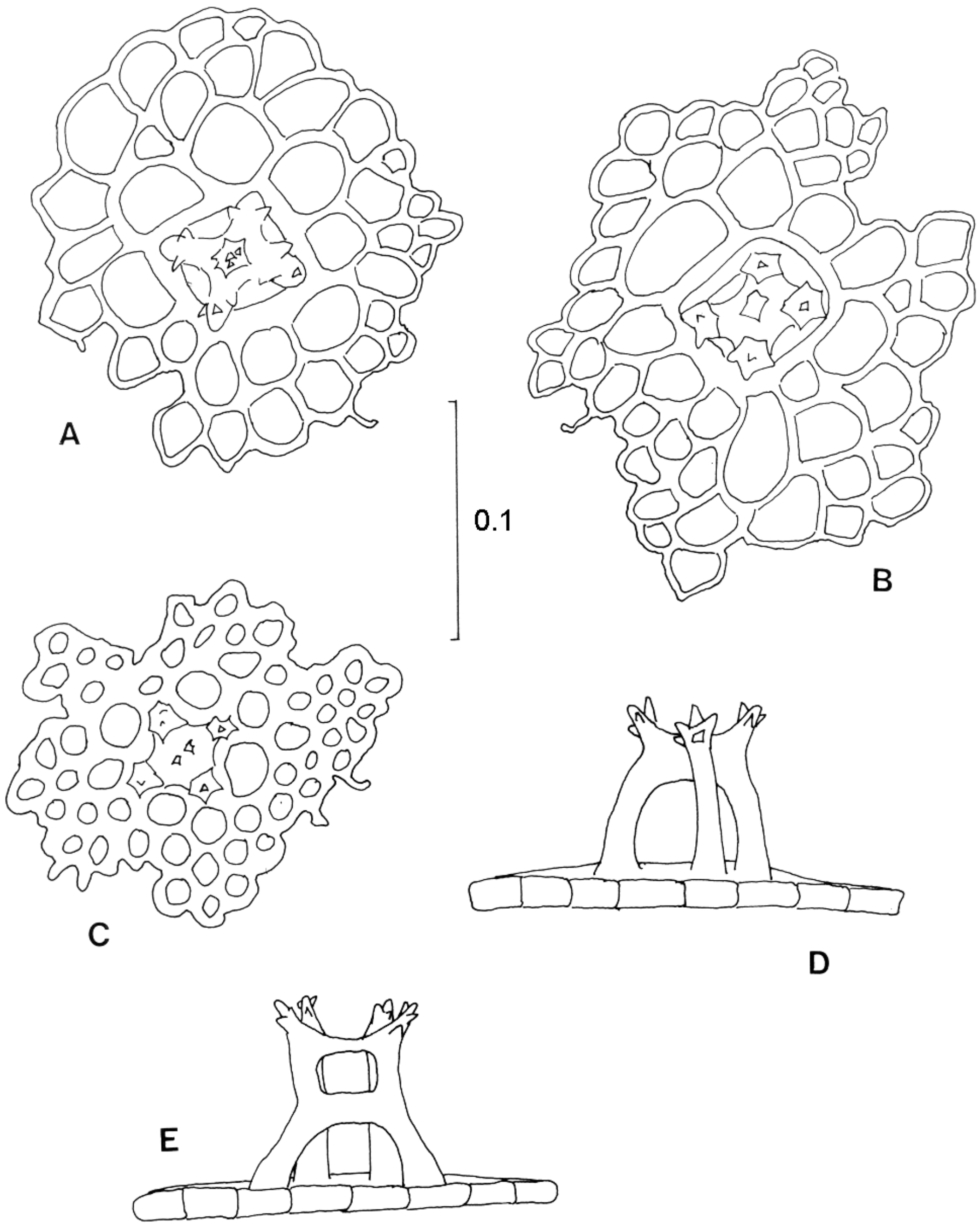

Figure 3.10. *Mesothuria gargantua* Deichmann, 1930. Ossicles from type specimen (MCZ cat. No. 449). (Gebruk, unpublished drawing).

M. cathedralis was well defined and carefully described by Heding. Characterized by quadriradiate tables with four short spinous arms on top the spire and disks with 1-2 crowns of 8 perforations in each. It is distributed throughout the East Atlantic (Figure 3.9).

The original description of *Z. candelabri* was based on fragments. It is a deep-living form recorded from 3757 to 4870m in the northeast Atlantic (Billett, 1991). The ossicles are identical to those of *Z. thomsoni* (Théel, 1886) (length 125mm) in both form and size. *Z. thomsoni* is known from the western Pacific from the depths 3430-5300m. This is also true for *Mesothuria* (*Zygothuria*) *lactea* var. *spinosa* (Heding, 1940), size unknown, recorded from 5108m in the Southeast Atlantic (Figure 3.9). All these forms are likely to be age variations of *Z. thomsoni*. There is also a similarity between these forms and *Z. connectens*, 60mm long, recorded off northwest Africa from 1975-2518m. A difference occurs, however, in that the arms of spire in the former are spinous, while they are smooth in the latter. Confusion is added by the variety *Z. thomsoni* var. *hyalina* (Théel, 1886), 68mm long, known from the Southern Ocean (off southern Australia) from ca. 3300m (Figure 3.9), which differs from the type in the arms of spire being less spinous. All these forms are closely related and they require further study. Records of *Z.* (*Mesothuria*) *candelabri* from the Kermadec Trench (South West Pacific) by Hansen (1975) need to be confirmed as well (Gebruk, unpublished information)

3.3.2. Molecular analysis

The overall length of the amplified mitochondrial DNA 16S products varied between 226 base pairs (*Zygothuria lactea*) and 235 base pairs (*Mesothuria bifurcata*) at the 3' end of the gene. The consensus DNA sequences of the amplified fragments have 238 base pairs (Figure 3.11). The sequences have been submitted to the GenBank data base (Table 3.4).

```
                                                        50
Zl1   TTTTGATTGGGGTAATCATAAAGCTAA---AATCTCTAGT-TAAATAGAA
Zl2   ...........................---..........-.........
Zl3   ...........................---..........-.........
Mm1   .....G.........C...GG..T.T.---.........AA.TT......
Mm2   .....G.........C...GG..T.T.---.........AA.TT......
Mm3   .....G.........C...GG..T.T.---.........AA.TT......
Mm4   .....G.........C...GG..T.T.---.........AA.TT......
Msp1  .....G.........C....G..T.G.---..........-.TT......
Msp2  .....G.........C....G..T.G.---..........-.TT......
Msp3  .....G.........C....G..T.G.---..........-.TT......
Msp4  .....G.........C....G..T.G.---..........-.TT......
Msp5  .....G.........C....G..T.G.---..........-.TT......
Mb1   C....G......C..C...GG......TTT.GC...C...TATT.A..CT
Mb2   C....G......C..C...GG......TTT.GC...C...TATT.A..CT
If1   C....G......C..C...GG..TA..AGC.GC...C...T.TTCAG.T.
If2   C....G......C..C...GG..TA..AGC.GC...C...T.TTCAG.T.
If3   C....G......C..C...GG..TA..AGC.GC...C...T.TTCAG.T.
If4   C....G......C..C...GG..TA..AGC.GC...C...T.TTCAG.T.
If5   C....G......C..C...GG..TA..AGC.GC...C...T.TTCAG.T.
If6   C....G......C..C...GG..TA..AGC.GC...C...T.TTCAG.T.
                                                       100
Zl1   GATTATAA-ATCTCTATATA---ATATTT--GAACCAGTT-ATTCTG-AA
Zl2   ........-...........---......--.........-......-..
Zl3   ........-...........---......--.........-......-..
Mm1   ..G.T.TC-C......A.A.---..C...TT.........AT.....-..
Mm2   ..G.T.TC-C......A.A.---..C...TT.........AT.....-..
Mm3   ..G.T.TC-C......A.A.---..C...TT.........AT.....-..
Mm4   ..G.T.TC-C......A.A.---..C...TT.........AT.....-..
Mmi1  ..G.T.T.-C......A.A.---.GT...AT.........-T.....-..
Msp2  ..G.T.T.-C......A.A.---.GT...AT.........-T.....-..
Msp3  ..G.T.T.-C......A.A.---.GT...AT.........-T.....-..
Msp4  ..G.T.T.-C......AAA.---.GT...AT.........-T.....-..
Msp5  ..G.T.T.-C......A.A.---.GT...AT.........-T.....-..
Mb1   ..A.T..GGC.....T..A.---.AT..CAT.........A......G..
Mb2   ..ACT..GGC.....T..A.---.AT..CA..........A......G..
If1   ..AA.CC.TTCTC...A...CAC.ACC.CAA......AAA-...T..G..
If2   ..AA.CC.TTCTC...A...CAC.ACC.CAA......AAA-...T..G..
If3   ..AA.CC.TTCTC...A...CAC.ACC.CAA......AAA-...T..G..
If4   ..AA.CC.TTCTC...A...CAC.ACC.CAA......AAA-...T..G..
If5   ..AA.CC.TTCTC...A...CAC.ACC.CAA......AAA-...T..G..
If6   ..AA.CC.TTCTC...A...CAC.ACC.CAA......AAA-...T..G..
                                                       150
Zl1   ATTAGAATAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTGAGAGTTC
Zl2   ..................................................
Zl3   ..................................................
Mm1   ..C.............................................C.
Mm2   ..C.............................................C.
Mm3   ..C.............................................C.
Mm4   ..C.............................................C.
Mmi1  ..C...............................................
Msp2  ..C...............................................
Msp3  ..C...............................................
Msp4  ..C...............................................
Msp5  ..C...............................................
Mb1   ..C....C................................C.A.....C.
Mb2   ..C....C................................C.A.....C.
If1   .ACG...A..............................T.C......CC.
If2   .ACG...A..............................T.C......CC.
If3   .ACG...A..............................T.C......CC.
If4   .ACG...A..............................T.C......CC.
```

```
If5   .ACG...A..............................T.C......CC.
If6   .ACG...A..............................T.C......CC.

                                                     200
Zl1   TTATTGACAAGAAGGATTGCGACCTCGATGTTGGATTGAGGCATCCTTAA
Zl2   ..................................................
Zl3   ..................................................
Mm1   ......................................G.A........G
Mm2   ......................................G.A........G
Mm3   ......................................G.A........G
Mm4   ......................................G.A........G
Mmi1  ......................................G..........G
Msp2  ......................................G..........G
Msp3  ......................................G..........G
Msp4  ......................................G..........G
Msp5  ......................................G..........G
Mb1   .A...............................................T
Mb2   .A......G.............................G..........T
If1   ........G.A...........................G..T.A..AG.G
If2   ........G.A...........................G..T.A..AG.G
If3   ........G.A...........................G..T.A..AG.G
If4   ........G.A...........................G..T.A..AG.G
If5   ........G.A...........................G..T.A..AG.G
If6   ........G.A...........................G..T.A..AG.G
                                         238
Zl1   GGTGTAGCAGCTTTAAAGGGTTGGGCTGTTCGCCCATT
Zl2   ......................................
Zl3   ......................................
Mm1   ....C.......C...........A.......T.....
Mm2   ....C.......C...........A.......T.....
Mm3   ....C.......C...........A.......T.....
Mm4   ....C.......C...........A.......G.....
Mmi1  ........................A.......T.....
Msp2  ........................A.......T.....
Msp3  ........................A.......T.....
Msp4  ........................A.......T.....
Msp5  ........................A.......T.....
Mb1   ....C.......A...........A.......T.....
Mb2   ....C.......A...........A.......T.....
If1   ....C.......C.CT.A......A.......T.....
If2   ....C.......C.CT.A......A.......T.....
If3   ....C.......C.CT.A......A.......T.....
If4   ....C.......C.CT.A......A.......T.....
If5   ....C.......C.CT.A......A.......T.....
If6   ....C.......C.CT.A......A.......T.....
```

Figure 3.11. Aligned nucleotide sequence of the 3’ segment of the mitochondrial 16S gene from 5 species of sea cucumbers. Dots indicate identical nucleotides. Hyphens indicate missing data. Abbreviations: Zl, *Zygothuria lactea*; Mm, *Mesothuria multipora*; Msp, *Mesothuria* sp. 1; Mb, *Mesothuria bifurcata*; If, *Isostichopus fuscus*.

The identity of the partial sequence of the 16S gene was confirmed by similarity of the peptide sequence to the 16S gene of the sea urchin *Strongylocentrotus purpuratus* (Jacobs *et al.*, 1988) and the 16S data from holothurians published by Arndt *et al.* (1996) (GenBank Acc. Nos. U31901, U32210-U32221, U32198 and U32199).

The average contributions of bases across the studied sequences were A= 27%, C= 16%, G= 23%, and T= 32%. No significant differences in base composition across the 4 taxa were detected (?^{2}= 20.33; *df*= 42; *P* > 0.998).

In the *Mesothuria* group, the GC content of the sea cucumber 16S gene fragments ranged from 38% in *Mesothuria* sp.1 to a high of 42% in *M. bifurcata* and *M. multipora* with an average of 39%. The *Zygothuria lactea* data set show a GC average content of 35%. As reported for numerous organisms, including a number of other echinoderms (Jacobs *et al.*, 1988; Cantatore *et al.*, 1989; Asakawa *et al.*, 1991; Arndt *et al.*, 1996), the proportion of guanine (G) in the third position was low (7-10%) with a corresponding increase in adenine (A) to an average of 42%.

There is no significant intraspecific divergence between regions of the 16S gene (0.06%). Table 3.8 represents the average pairwise GTR + SSR distances matrix for the studied 16S sequences. *Mesothuria.* sp.1 shows a degree of genetic divergence from *M. multipora*, comparable to the pairwise distances between *M. bifurcata* and *M. multipora*.

Table 3.8. Holothurian Pairwise Distances Matrix[1].

	Zl1	**Zl2**	**Zl3**	**Mm37**	**Mm38**	**Mm42**	**Mm43**	**Msp1**	**Msp2**	**Msp3**	**Msp4**	**Msp5**	**Mbi1**	**Mbi2**	**If(6)**
Zl1	-														
Zl2	0.00	-													
Zl3	0.00	0.00	-												
Mm37	0.11	0.11	0.11	-											
Mm38	0.11	0.11	0.11	0.00	-										
Mm42	0.11	0.11	0.11	0.00	0.00	-									
Mm43	0.11	0.11	0.11	0.00	0.00	0.00	-								
Msp1	0.09	0.09	0.09	0.04	0.04	0.04	0.05	-							
Msp2	0.09	0.09	0.09	0.04	0.04	0.04	0.05	0.00	-						
Msp3	0.09	0.09	0.09	0.04	0.04	0.04	0.05	0.00	0.00	-					
Msp4	0.09	0.09	0.09	0.04	0.04	0.04	0.05	0.00	0.00	0.00	-				
Msp5	0.09	0.09	0.09	0.04	0.04	0.04	0.05	0.00	0.00	0.00	0.00	-			
Mbi1	0.16	0.16	0.16	0.13	0.13	0.13	0.14	0.13	0.13	0.13	0.13	0.13	-		
Mbi2	0.16	0.16	0.16	0.13	0.13	0.13	0.14	0.13	0.13	0.13	0.13	0.13	0.00	-	
If(6)	0.25	0.25	0.25	0.21	0.21	0.21	0.22	0.22	0.22	0.22	0.22	0.22	0.20	0.20	-

[1] Average pairwise GTR + SSR distances.

Abbreviations: Zl, *Zygothuria lactea*; Mm, *Mesothuria multipora*; Msp, *Mesothuria* sp. 1; Mb, *Mesothuria bifurcata*; If, *Isostichopus fuscus*. In parentheses the number of specimens for *Isostichopus fuscus*.

Maximum Parsimony and Maximum Likelihood (heuristic search) analyses produced identical 50% majority-rule bootstrap consensus tree topologies, with varying bootstrap values. Of the 189139 trees evaluated in the heuristic search, a single tree was retained with the best score of –lnL 723.9049 (Figure 3.12). The six 16S sequences in *Isostichopus fuscus* are identical, and were collapsed in the outgroup branch.

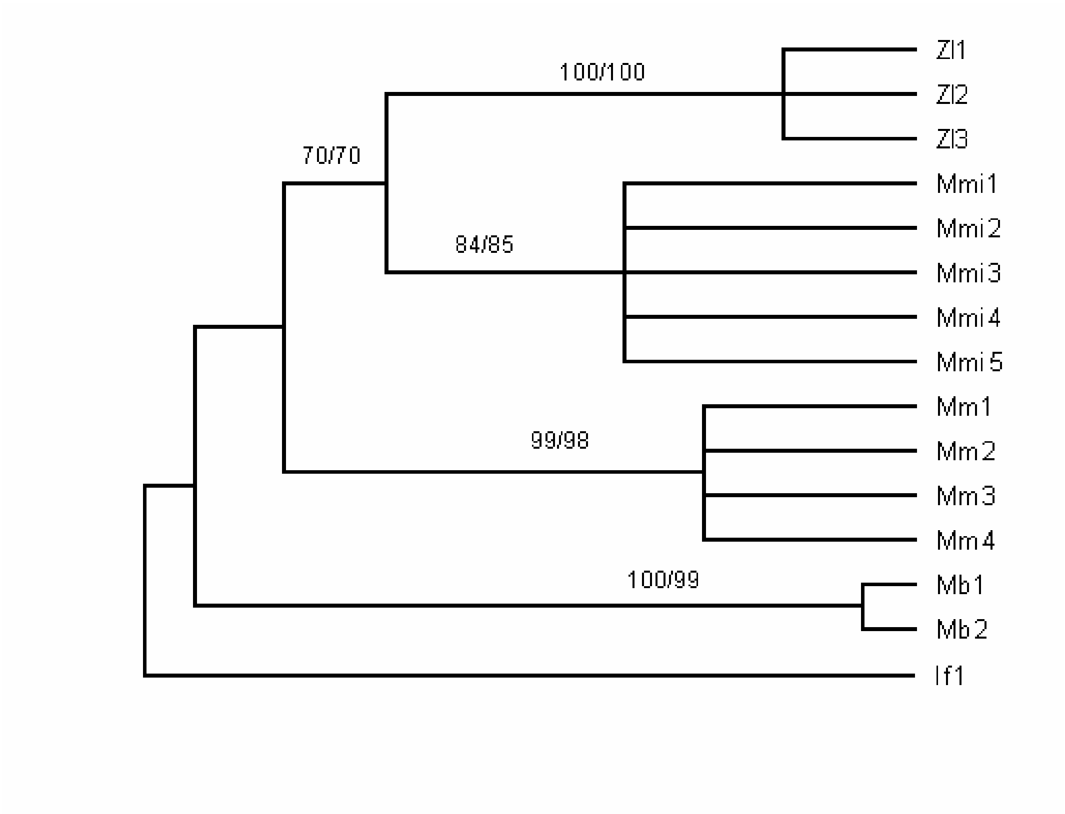

Figure 3.12. Maximum Parsimony (MP) and Maximum Likelihood (ML) 50% majority-rule bootstrap consensus tree topologies. Bootstrap values are given for MP and ML respectively. Abbreviations: Zl, *Zygothuria lactea*; Mm, *Mesothuria multipora*; Mmi, *Mesothuria* sp. 1; Mb, *Mesothuria bifurcata*; If, *Isostichopus fuscus*.

3.3.3. Population structure and biomass of *Mesothuria* and *Zygothuria* species in the North East Atlantic Ocean

Only *Zygothuria lactea* occurred in sufficient numbers to permit the construction of size/frequency histograms (Figure 3.13). Most of the samples are dominated by large (>70mm) specimens although two samples are composed mainly of small (<60mm) specimens. There is no relationship of depth or time of year with the population size distribution. However, the occurrence of small *Z. lactea* was concomitant with the appearance of small specimens of the elasipodid *Benthogone rosea* and over 2000 specimens of the minute holothurian *Elpidia*, which taken together may indicate patchy and periodic (but not necessarily seasonal) recruitment to the adult population.

The biomass of *Z. lactea*, in terms of wet and dry weight, ash-free dry weight and calorific content, are shown in Table 3.9. A maximum AFDW of 230g hectare^{-1} was found at 1500m, although nearby stations had values less than 53g hectare^{-1}, again emphasizing the patchy nature of the distribution of this species. These data correspond closely to those of Walker *et al.* (1987) that reported a caloric value for this species of 26.24J mg^{-1} giving a biomass of 6085 KJ/hectare^{-1}.

Table 3.9. The wet weight (WW), dry weight (DW), ash-free dry weight (AFDW) and calorific biomass of *Zygothuria lactea* expressed as g or KJ per hectare.

Station	**Depth**	**WW**	**DW**	**AFDW**	**Calorific Biomass**
51113#2	1535	1808	103	35	918
51403#4	1326	1787	141	25	625
51708#2	1450	-	180	53	1391
51407#1	1500	14471	596	230	6035

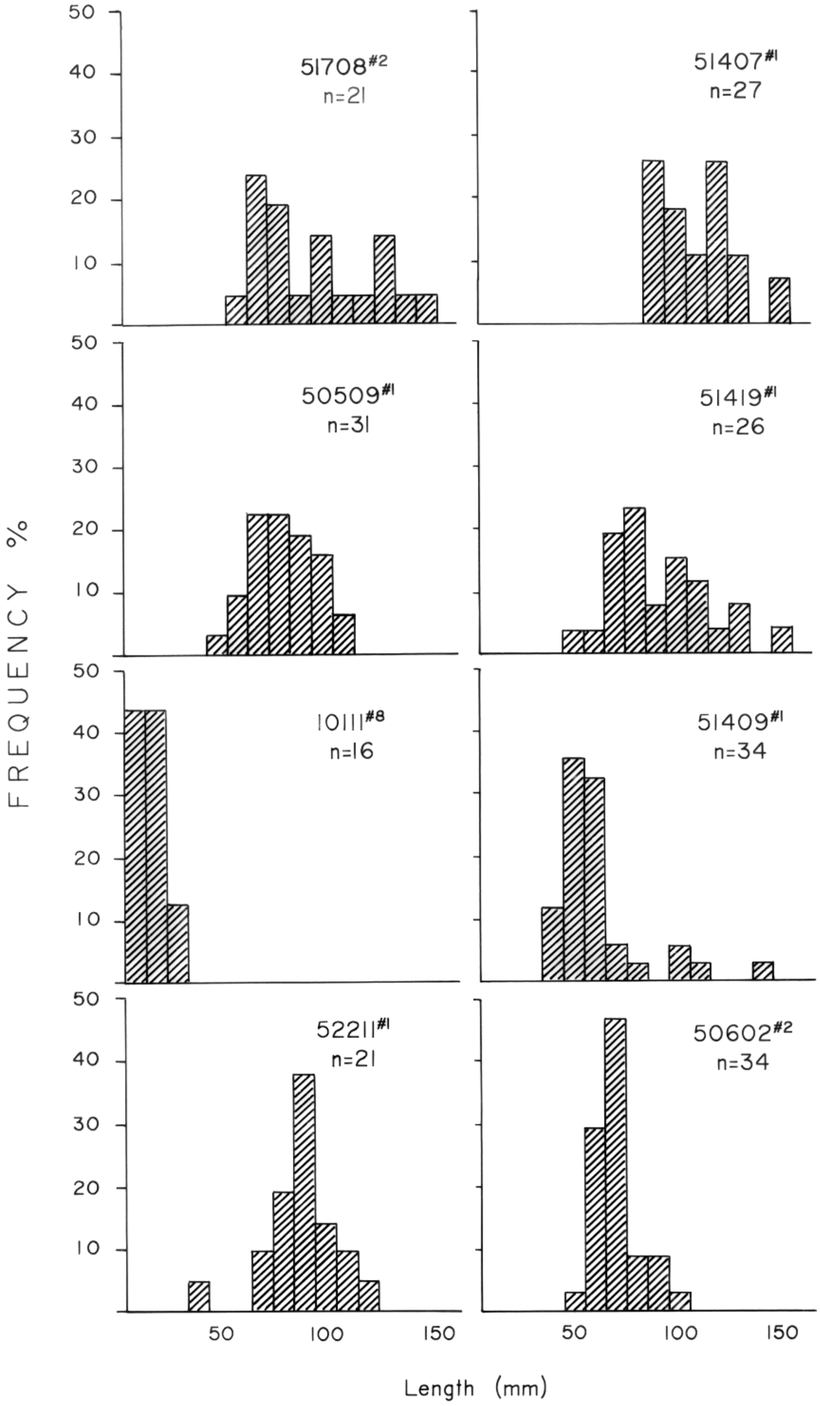

Figure 3.13. Population structure of *Zygothuria lactea* in Porcupine Abyssal Plain, during the RRS *Discovery* cruise 105 and RRS *Challenger* cruises 505, 514, 517, 522, during the years 1979-1985. Top right numbers are RRS *Discovery* or RRS *Challenger* station numbers.

3.3.4. Reproduction

3.3.4.1. Gonad morphology and gametogenesis

The ovary of specimens of *Mesothuria* and *Zygothuria* (except *M. intestinalis* which is a sequential hermaphrodite [Mortensen 1927]) consists of many short tubules, which are arranged tightly about the central branching system of ducts, which arise from the gonoduct (Figure 3.14a, b). On dissection of live material of *Z. lactea* was found to have large bright pink yolky oocytes. In all species examined the testes consisted of numerous uniformly shaped tubules of similar length and diameter.

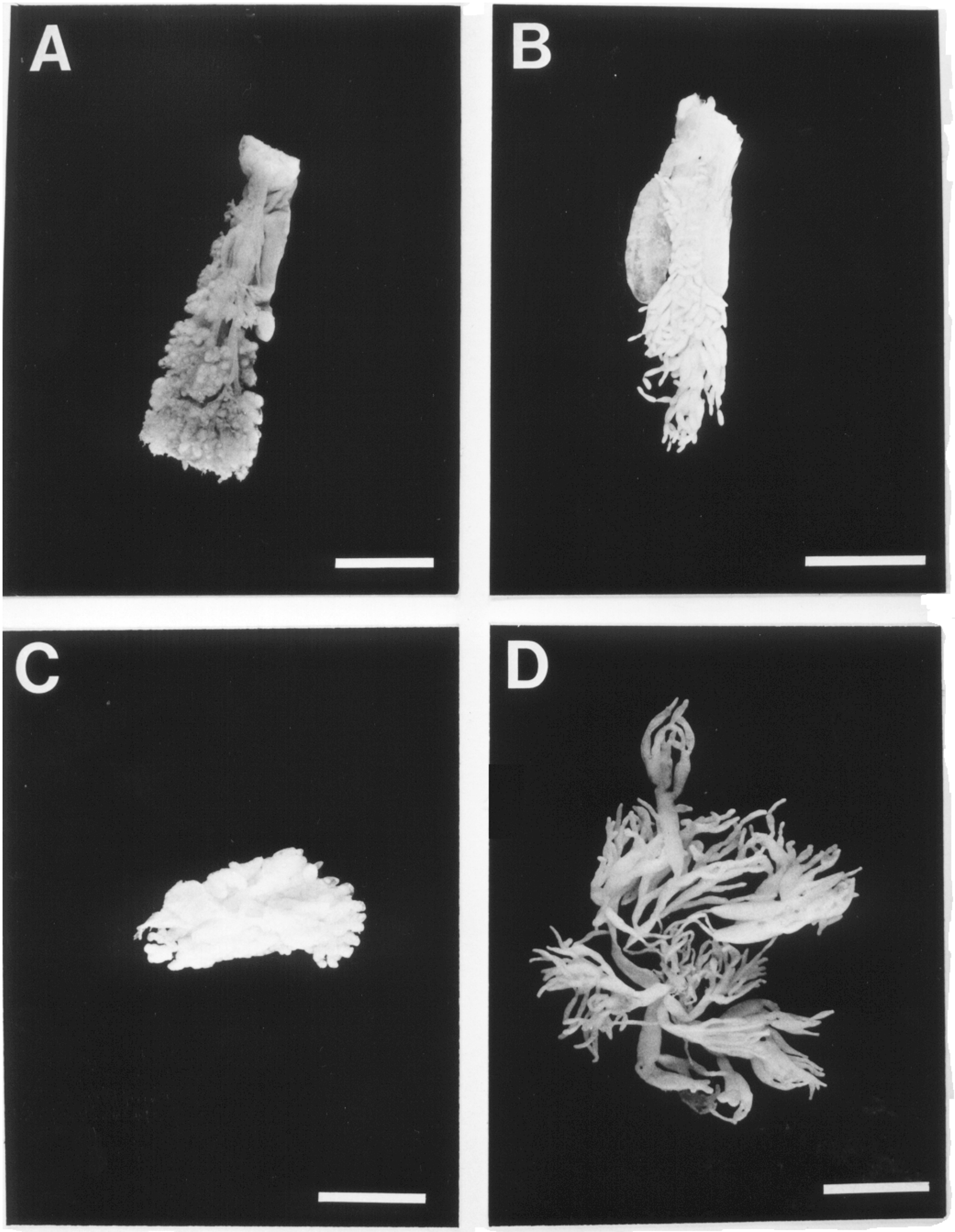

Figure 3.14. Gross morphology of the gonads in *Mesothuria* and *Zygothuria*. A. Morphology of the ovary of *Mesothuria* sp. 1; B. Morphology of the testis in *Mesothuria* sp. 1; C. Ovary of *Zygothuria lactea*; D. Testis of *Z. lactea*. Scale bar= 10mm.

3.3.4.2. Oogenesis in *Mesothuria* and *Zygothuria* species

In the newly developing tubules the wall is ca. 40µm thick and consists of three layers; an outer coelomic epithelium, a muscle layer and a connective tissue layer. The inner part of the wall is the germinal epithelium. As the oocytes develop the wall becomes progressively thinner with the muscle layer becoming unrecognisable and the connective tissue layer decreasing in thickness. Newly-developed previtellogenic oocytes occur peripherally on the internal surface of the ovarian tubule and are often covered with a layer of follicle cells contiguous with the germinal epithelium (Figure 3.15a). As with oogenesis in most echinoderms, these previtellogenic oocytes are basophilic and are surrounded by a strong ß-metachromatic band. Beyond this stage there appears to be subtle differences between species in the progress of oogenesis.

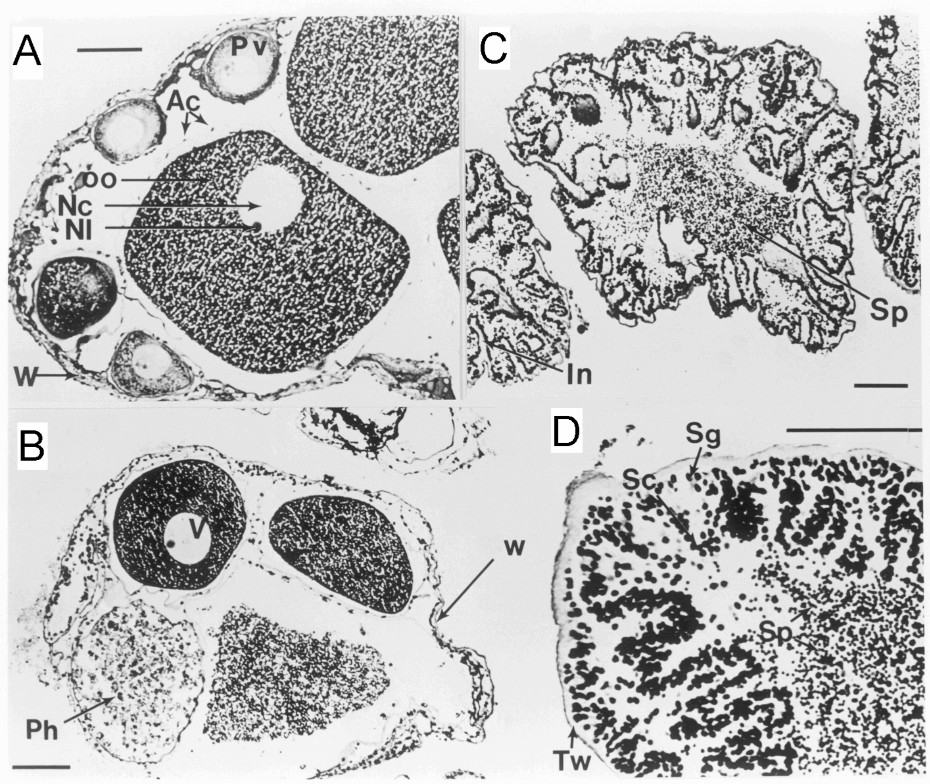

Figure 3.15. Gametogenesis. A. Oogenesis in *Z. lactea*. B. Oogenesis in *Mesothuria* sp. 1. C. Early spermatogenesis in *Z. lactea*. D. Advance spermatogenesis in *Mesothuria* sp. 1. Abbreviations: Ac= follicle cells; Pv= Previtellogenic oocytes; V= Vitellogenetic oocyte; W= Ovary wall; Oo= Ooplasma of vitellogenic oocyte; Nc= Nucleus and N1= Nucleolus of vitellogenic oocyte; Ph= Phagocytosed oocyte; Tw= Testis wall; Sp= Spermatozoa; Sc= Spermatocyte; Sg= Spermatogonia; In= Indentation of testis wall. Scale bar= 100µm. A is PAS and Haemalum; B,C, and D are Haemalum and Eosin.

In *Z. lactea* the previtellogenic oocytes continue to grow to ca. 200µm diameter at which size the basophilic material becomes peripheral in the ooplasm whilst the rest of the ooplasm becomes filled with PAS-positive material that increases until the oocyte size attains its maximum of 650µm diameter (Figure 3.15a). During this development, however, there are two periods of oocyte break down. The first occurs at a diameter of ca 150µm where some oocytes breakdown and become filled with globular breakdown products. There are no obvious phagocytes. This process is reminiscent of the “nurse cell” activity seen in *Bathybiaster vexillifer* (Tyler *et al.*, 1982). The second phase of oocyte breakdown is the more typical phagocytosis of unspawned oocytes, as seen in the other deep-sea echinoderm species (Tyler *et al.*, 1985a). In this case the large oocytes become filled with phagocytes followed by internal degeneration of the ooplasm (Figure 3.15b). Two hermaphrodites of *Z. lactea* were found. One showed different tubules of different sexes and the other showed intra-tubular hermaphroditism. This gives an incidence of hermaphroditism in this species of <2%.

Oogenesis in *Mesothuria* sp. 1 is very similar to that in *Z. lactea* except that there is no “nurse cell” development. Maximum oocyte size would appear to be similar to that of *Z. lactea*. In some specimens of *Mesothuria* sp. 1 the proportion of phagocytosed oocytes is very high. In some cases the entire tubule is filled with this material suggesting that the mature oocytes can only be maintained for a certain period before they have to be resorbed.

Examination of the oocytes size/frequency data for these two species (Figures 3.16, 3.17) shows that the most oocytes are less than 200µm diameter. About 10% appear to be undergoing development to the maximum oocyte size.

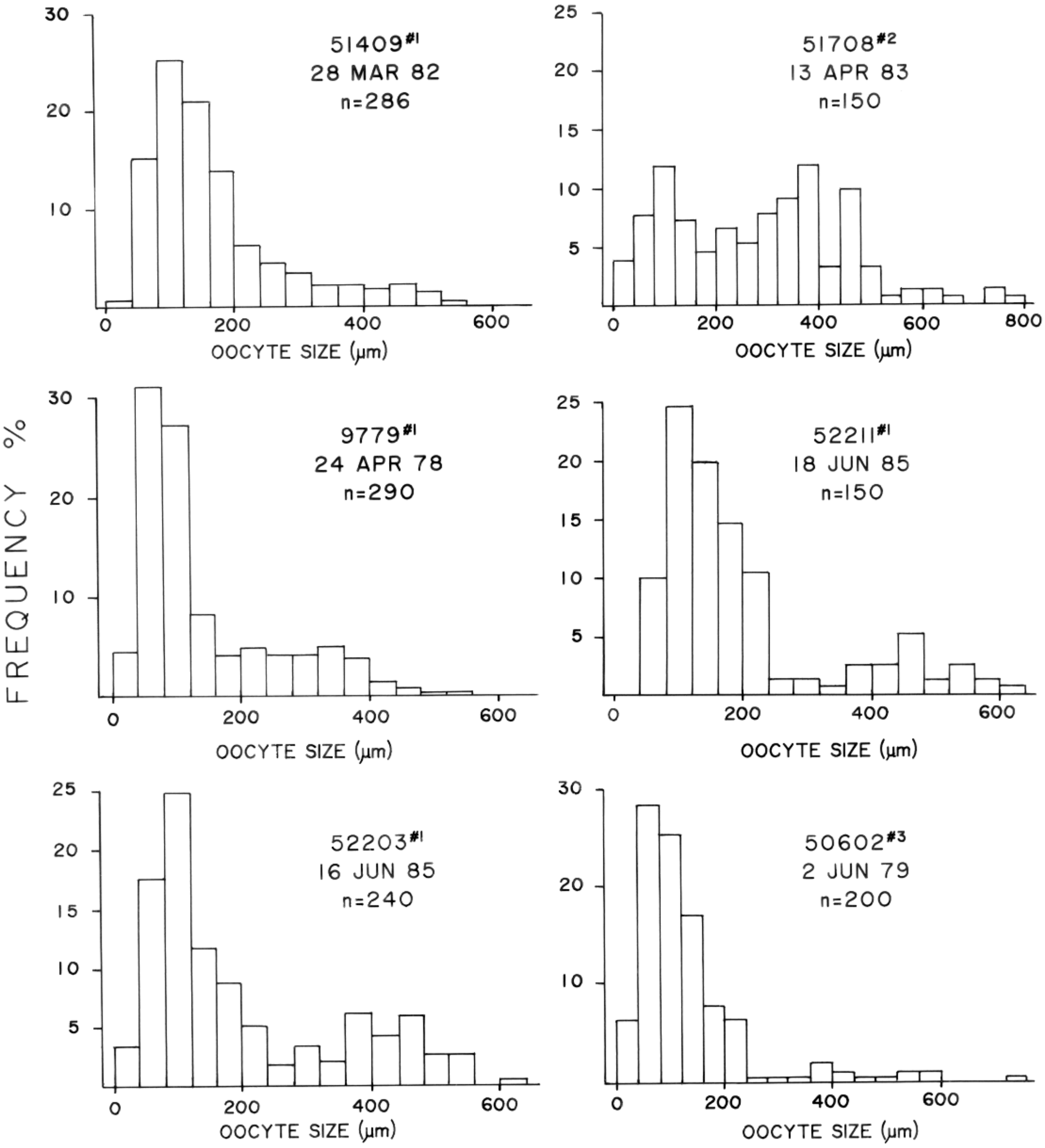

Figure 3.16. Oocyte size/frequency distributions for *Zygothuria lactea*.

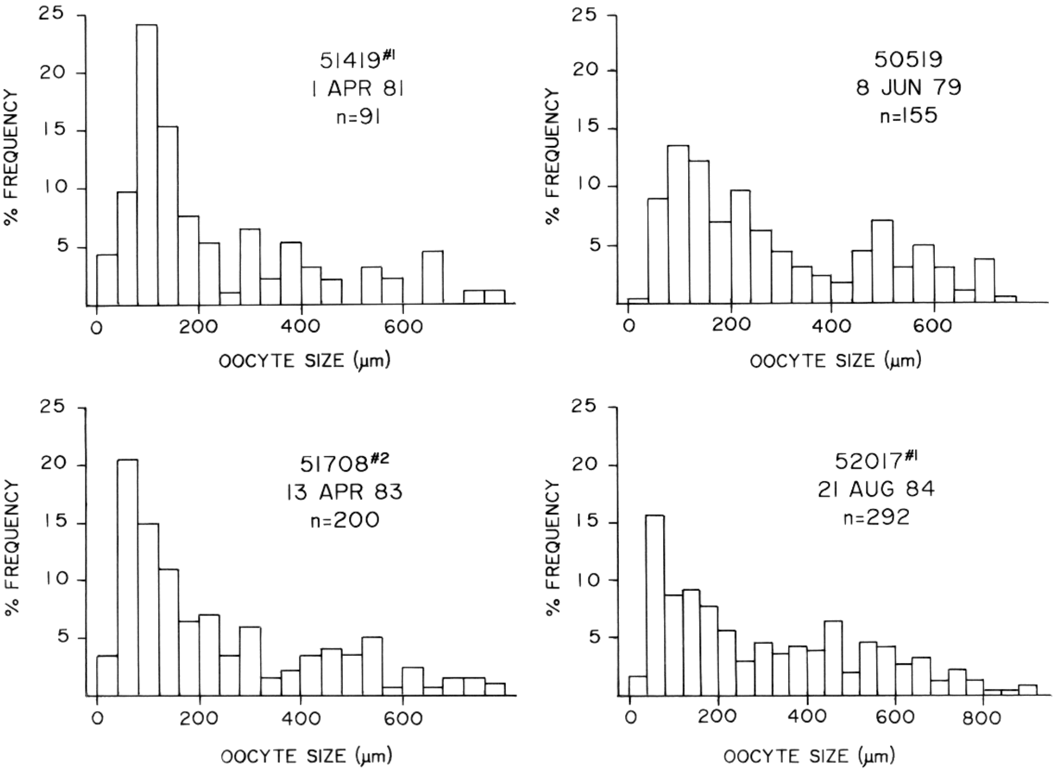

Figure 3.17. Oocyte size/frequency distributions for *Mesothuria* sp. 1.

There is no evidence of any reproductive seasonality in either species. *Mesothuria intestinalis* is a hermaphrodite, although “male and female products are not found ripe at the same time” (Mortensen, 1927). Examination of the limited number of specimens from the Porcupine Seabight support the observations of Mortensen. Male development occurs first. At a body length of ca. 80 to 110mm female development occurs and all specimens greater than 110mm, up to a maximum size observed of 155mm, are developing, developed or spent females. Only one specimen was observed to contain both eggs and sperm. These data suggest protandry. Oogenic development is very similar to that of *Z. lactea* (see above) including the two periods of oocyte breakdown. In the limited number of specimens of *M. maroccana* available, the smallest specimen is female, whilst larger specimens are either male or show both eggs and spermatogonia. The data for this species are too limited to speculate about its reproductive processes. In *M. candelabri* only three specimens were examined of which one was a female. This specimen was poorly preserved and thus we are unable to comment on the production of oocytes.

In all species of *Mesothuria* examined, spermatogenesis would appear to be similar. In early development the testis tubules have a highly convoluted inner surface (Figure 3.15c). As development proceeds a distinct band of spermatogonia and spermatocytes can be distinguished from mature spermatozoa. In well-developed testes the lumen is packed with spermatozoa (Figure 3.15d). The only obvious difference between the species is the thickness of the connective tissue layer of the testis wall during early development, which is thin in *Z. lactea*, *Mesothuria* sp. 1 and *M. candelabri* and thick in *M. intestinalis* and *M. maroccana*.

3.4. Discussion and conclusions

3.4.1. Alpha and molecular taxonomy

Morphologically, the genus *Zygothuria* differs from the genus *Mesothuria* in the general external body shape appearance. The two genera exhibit a major difference in the arrangement of ambulacral appendages. *Mesothuria* has a cylindrical body, with the ventral side usually somewhat flattened, with papillae all over the body, uniformly covering the dorsal side and being small and equal in size, or much smaller dorsally. *Zygothuria* is flat or has a well-differentiated sole, with tubefeet arranged exclusively in a single or double row along ventrolateral ambulacra, placed on the margin of the sole, which often forms a fringe. Tubefeet are widely spread and may be quite big. The dorsal papillae are minute, not numerous, irregularly distributed or arranged in two simple rows and sometimes totally absent. The radial pieces of the calcareous ring in *Zygothuria* are basically triangular in shape, whereas in *Mesothuria* they are rectangular. The bodywall ossicles in *Mesothuria* are quadriradiate tables with the central primary cross elevated from the disc. In the genus *Zygothuria* the ossicles of the integument are basically triradiate tables.

Although the morphologic differences are clear and good enough to distinguish and separate both genera, the DNA analysis shows a different perspective.

The sequences of the first (*Zygothuria lactea*) and second (*Mesothuria* sp. 1) clusters in Figure 3.12 and that of *Mesothuria multipora* formed a monophyletic group supported by a rather low bootstrap probability (70%). The sequence obtained from two individuals of *M. bifurcata* from the Antarctic appears as the common ancestor of *Zygothuria lactea*, *Mesothuria* sp. 1 and *M. multipora*.

The phylogenetic analysis, as it stands, confirms that *Mesothuria* sp. 1 and *M. multipora* are separate species, but it is also clear that *Zygothuria lactea* and *Mesothuria* sp. 1 share another *Mesothuria* as a common ancestor. This is maybe an artefact of having only one *Zygothuria* species sequences on the tree.

The current application of the genera name *Zygothuria* is not consistent with the phylogenetic inference. This kind of problem may occur because phenotypic discontinuities that define traditionally recognized taxa may not always correspond to genetic or reproductive boundaries. For instance, recent or incomplete speciation events can often lead to conflicting patterns of genetic and morphological variation. These conflicts may be due to hybridisation (Marko, 1998), incomplete lineage sorting (Palumbi, 1996) or limited morphological divergence between genetically distinct species (Knowlton, 2000). Alternatively, morphologically differentiated taxa may be genetically indistinguishable, a pattern that has been found frequently in genetic analysis of marine invertebrates.

One possible reason for the small degree of genetic differentiation between *Zygothuria* and *Mesothuria*, in what appear to be reproductive isolated taxa, is that rates of molecular evolution of these groups may be unusually slow, as shown by other marine invertebrates (Romano and Palumbi, 1997). Alternatively, the lack of genetic differentiation could reflect the effects of regular hybridisation. This perspective has been strongly argued by Veron (1995) for corals.

With slow rates of molecular evolution, a relatively recent origin may contribute to the difficulty in finding fixed genetic markers associated with barriers to gene exchange (Knowlton, 2000). The extent to which hybridisation blurs species boundaries of marine organisms remains a subject of debate in groups like the synallactids.

The lack of diagnostic molecular differences between the two taxa means that they are currently identifiable only by morphological criteria. Because morphologically defined taxa are still the basis for most ecological, physiological, and anatomical research, I propose to maintain *Zygothuria* and *Mesothuria* as separated genera in the family Synallactidae. Future molecular analyses should help to resolve many of these issues, particularly if coupled with other biological approaches such as reproduction and population studies.

3.4.2. Distribution

Both *Zygothuria* and *Mesothuria* have a cosmopolitan distribution (Figures 3.2, 3.6, 3.8 and 3.9). Some groups of species, however, demonstrate clear distributional patterns. The first group, including *M. gargantua* (Figure 3.9) and *M. verrilli* (Figure 3.2), are endemic to the Caribbean. The second group, including *M. intestinalis* and *Z. oxysclera* have amphi-atlantic distributions restricted, however, to the Caribbean in the west and known from low to high northern latitudes in the East Atlantic. The third group of species has a wider distribution, always occurring in low latitudes, but penetrating also temperate and high latitudes in both hemispheres (Gebruk, unpublished information). This group includes *Z. lactea* (Figure 3.6), *M. cathedralis* (Figure 3.9) and groups related to *M. murrayi* and *Z. candelabri*. Finally, *M. bifurcata* is known only from the Southern Ocean and high latitudes in the north Atlantic (Figure 3.9). While *Mesothuria* sp. 1 occurs only in the northeast Atlantic. (Figure 3.2).

The clear links at low latitudes point towards a Tethys origin of the fauna as in many other deep-sea groups. The important role of the Tethys basin as a centre of species origin and distribution has been discussed in particular by Ekman (1953), Madsen (1961), Menzies *et al.* (1973), Mironov (1985) and Gebruk (1994). The break up of the Tethys Sea was completed in the Miocene, resulted in the formation of four Tethys-derived areas: the isolated temperate Northern Gulf of Mexico, the isolated tropical Caribbean, the isolated Mediterranean and the isolated tropical Indo-Pacific. The modern distribution of the *Mesothuria* and *Zygothuria* species indicates links with three of these areas: Caribbean, Mediterranean and Tropical Indo-Pacific (Gebruk, unpublished information).

It has been suggested that the Tethys basin has played an important role in the history of the other major of deep-sea holothurians, the Order Elasipodida (Gebruk, 1994). The elasipodid fauna, believed to be widely distributed in the Tethys Sea, was split into at least three parts, following the break up of the Tethys Sea into the Indo-Malayan, the Mediterranean and the West-Pacific sections, the latter remaining in the Panama Gulf area after this region had been split in two by the Central American Isthmus. It has been also suggested that elasipodids invaded bathyal Antarctic waters moving along the South American continental slope, either from the Caribbean, or more likely from the Panama Gulf area, where the primitive forms are still present (Gebruk, unpublished information). This is different from the elasipodids, which are believed to have then expanded world-wide from the Antarctic within the abyssal zone. In contrast, the synallactids remained closely related to the Tethys-derived areas in low latitudes, similar to the distribution of primitive bathyal elasipodid holothurians (e.g. *Psychrelpidia*, *Penilpidia* and *Psychroplanes*) (Gebruk, 1994). Evolving mainly within low latitudes, synallactids, however, have penetrated high latitudes widely in the North Atlantic, presumably from the post-Tethys Mediterranean, as discussed for some other groups by Menzies *et al.* (1973). The synallactids have also penetrated moderate and high latitudes widely in the southern Hemisphere (but not the abyssal Antarctic). The distribution of the group of species related to *M. murrayi* support the southern pathway from the Panama Gulf area along the South American continental slope. Poor taxonomy of this group and little reliable data on the distribution of other synallactid genera however do not allow a more precise biogeographical analysis (Gebruk, unpublished information).

In the North East Atlantic populations, there are subtle differences in the distribution, zonation, and natural history of the main species. The shallowest living species is *M. intestinalis* which, although not abundant in the Porcupine Seabight is found associated with the *Pheronema* community. It also occurs in shallow water further north in the Atlantic, suggesting it is following an isotherm in its southerly distribution. *Z. lactea* and *Mesothuria* sp. 1 have very similar bathymetric distributions in the Porcupine Seabight (~1200-1900m). It is possible that the distribution of these two species is controlled by water of Mediterranean origin that bathes the continental slope in this area (Tsuchiya *et al.*, 1992; Price *et al.*, 1993; Soler, 2002), as has been described for *Ophiocten abyssicolum* (Paterson *et al.*, 1982). Towards the lower end of their vertical range these two species are replaced by *M. maroccana* that has a depth distribution, which corresponds to the North-East Atlantic Deep Water. At considerably greater depths, possibly at the limit of Antarctic Bottom Water (>3750m), *M. candelabri* is found. It is possible that the isolated occurrence of *M. candelabri* in the Kermadec Trench (SW Pacific) may reflect the impact of the Antarctic Bottom Water (AABW) has on this trench in this area. Although I do not maintain that these species distributions are determined by the salinity/temperature characteristics of the seawater masses, there may be some form of chemical or biological conditioning within these water masses that determines their distribution.

3.4.3. Reproduction

The natural history, especially the reproductive biology of *Mesothuria* and *Zygothuria*, is conservative. The two most similar species are *Z. lactea* and *Mesothuria* sp. 1, which are dioecious and have a similar large egg size indicative of lecithotrophic development. The only substantial difference is that *Z. lactea* has evidence of nurse cell activity not found in *M. verrilli*, possibly representing generic differences. Conversely *M. intestinalis* and possibly *M. maroccana* are hermaphrodites, the former being protandric. In the latter there are insufficient specimens to determine the type of hermaphroditism. In the female phase of gametogenesis *M. intestinalis* has a similar pattern to that of *Z. lactea* including the nurse cell activity. It is of interest that in the dioecious *Z. lactea* two individuals were found to be hermaphrodites. Unfortunately too few specimens of *M. candelabri* were available to determine the reproductive pattern. In none of the species examined is there any evidence of seasonality in reproduction. No seasonality in reproduction has been found in any deep-sea holothurian yet. In all females, however, there appears to be the breakdown of unspawned oocytes. This has been reported to be fairly common in deep-sea echinoderms that breed all year round (Tyler, 1986) and suggest that the mature eggs are held for only a limited time. If not released for fertilization they are resorbed for recycling within the adult in this energy-poor environment. It is possible that the limiting factor is the ability of the adult to supply oxygen to the eggs. Bookbinder and Schick (1985) have shown that in the shallow water echinoid *Strongylocentrotus droebrachiensis* anaerobiosis dominates respiration owing to the mass and lack of perfusion within the ovary. There will be a point when the mature oocyte can no longer be maintained and if not spawned will breakdown naturally whilst phagocytes clear up the debris.

Chapter Four -Mitochondrial DNA sequence evidence supporting the recognition of a new North Atlantic **Pseudostichopus** *species (Echinodermata: Holothuroidea)*

4.1. Introduction

The genus *Pseudostichopus* Théel, 1886 is one of the oldest established synallactid taxa (Imaoka, 1978). It contains more than 18 "highly controversial" nominated species and typifies many of the fundamental problems outlined in Chapter one, section 1.3 of this thesis. Despite the efforts of numerous workers over the past 200 years, the taxonomy of the genus still contains many areas of uncertainty. The group has a very tortuous synonymy, a summary of which is given in the Chapter 5 of this thesis.

Holothurians collected by RRS *Discovery* and RRS *Challenger* from the deep-sea floor of the Porcupine Abyssal Plain, North East Atlantic during the BENGAL programme (High-resolution temporal and spatial study of the benthic biology and geochemistry of a north-eastern Atlantic abyssal locality) from 1991 to 1999 (Billett and Rice, 2001) included numerous specimens of *P. villosus*, and many examples of a smaller *Pseudostichopus* morphotype. Previous records from the North East Atlantic have shown that seven species of *Pseudostichopus* are present in the area (Mortensen, 1927; Miller and Pawson, 1984; Gage *et al.*, 1985; Billett *et al.*, 2001). Whether this morphotype represented a separate species or was merely a life stage of one of the other Atlantic *Pseudostichopus* was uncertain. Previous descriptions of the external features and ossicle morphology of the previously known *Pseudostichopus* species reported for this area have been ambiguous (Marenzeller, 1893b; Hérouard, 1902, 1923; Mortensen, 1927; Deichmann, 1930, 1940). Differences in general body shape and internal anatomy between Atlantic *Pseudostichopus* specimens is often small and may simply represent intraspecific variation. Furthermore, descriptions of the ossicles of species such as *P. villosus*, *P. occultatus*, *P. marenzelleri* and *P. mollis*, are frequently contradictory (see Marenzeller, 1893b; Hérouard, 1923; Deichmann, 1940; Lambert, 1997).

Studies of DNA sequence variation have been used to resolve problems of taxonomic identity in many invertebrate groups (Foltz, 1997, 1998; Flowers, 1999; Creasey and Rogers, 1999; Knowlton, 2000; Williams, 2000; Flowers and Foltz, 2001) including holothurians (Arndt *et al.*, 1996). In the deep sea this has lead to the discovery that ecologically important species are complexes of previously unrecognised sibling or cryptic species [(e.g. *Eurythenes gryllus* France and Kocher (1996); *Cyclothone* spp. Miya and Nishida (1996, 1997)]; gastropods and bivalves (Etter *et al.*, 1997). Such discoveries indicate that preconceptions about the homogeneity of the deep sea and the global distribution of deep-sea species are incorrect.

In the present study molecular and morphological approaches are combined to provide strong evidence for the presence of a new species of *Pseudostichopus* on the Porcupine Abyssal Plain.

4.2. Materials and methods

4.2.1. Sampling

Three species were screened in the present study, 2 *Pseudostichopus* species and *Isostichopus fuscus*. The latter was used as the outgroup for the phylogenetic analysis.

Pseudostichopus specimens were collected from 14 sites on the North East Atlantic, at the Porcupine Abyssal Plain to the southwest of Ireland, ranging from 4764 to 4849m in depth (Table 4.1), between the years 1991 and 1999. Rice (1992, 1996, 1997). Sibuet (1999), Billett (2000) and Billett and Rice (2001) provide descriptions of the study area, and the sampling strategy and gear used to collect the material used in the present study.

In addition to North East Atlantic specimens, *I. fuscus* was collected using SCUBA diving from a shallow water site (15m depth) in the East Pacific, off the coast of Jalisco, Mexico (21ºN) in the year 2000.

The collection, dissection, fixation methods were mentioned in Chapter 2, sections 2.1-2.4 of this thesis.

Table 4.1. List of stations where *Pseudostichopus* sp 1 was collected. RRS *Discovery* cruises 222(2), 226, 237 and RRS *Challenger* cruises 79, 142 (Rice 1992, 1996, 1997; Sibuet 1999; Billett 2000).

Station	Date	Lat. (N)	Long. (W)	Lat. (N)	Long. (W)	Depth (m)	No. of specimens
		Position start		Position end			
52701#42	24 -05-91	48º 52.70’	16º 38.50’	48º 51.20’	16º 28.50’	4849-4843	85
12930#46	09-09-96	48º 47.21’	16º 43.31’	48º 49.49’	16º 32.62’	4837-4841	53
12930#78	16-09-96	48º 53.04’	16º 30.49’	48º 50.03’	16º 41.92’	4836-4840	82
13078#29	04-04-97	48º 56.20’	16º 22.77’	48º 47.35’	16º 33.23’	4844-4847	183
13627#10	30-09-98	48º 53.06’	16º 42.06’	49º 02.00’	16º 53.03’	4835-4837	68
54901#5	28-04-99	48º 44.87’	16º 40.53’	48º 48.16’	16º 36.24’	4835-4838	97
54901#7	29-04-99	48º 47.45’	16º 48.88’	48º 50.82’	16º 46.04’	4836-4838	2
54901#9	30-04-99	48º 46.89’	16º 41.59’	48º 50.58’	16º 36.36’	4837-4841	111
54903#1	03-05-99	49º 32.09’	15º 56.02’	49º 28.11’	15º 56.52’	4810-4817	545
54905#1	04-05-99	50º 32.65’	16º 57.77’	50º 28.66’	16º 59.43’	4764-4786	72
						Total:	1298

4.2.2. Identification

Taxonomic identification was carried out prior to the DNA analysis, based on original descriptions and keys (Sluiter, 1901; Hérouard, 1902, 1923; Mitsukuri, 1912; Mortensen, 1927; Deichmann, 1930; Heding, 1940; Imaoka, 1978; Thandar, 1992; Liao, 1997) using ossicles morphology and external-internal anatomy.

The ossicle preparation and nomenclature are given in Chapter 2, section 2.4.3. Total length (TL) as indicated in the holotype and paratypes examined was measured from the tip of the anterior part of the body to the posterior end. Width (W) was measured from the widest part of the body at the mid ventral region. For each set of measurements, the maximum, minimum and median values were recorded. All measurements are in millimetres. The specimens were deposited in the collections of the Natural History Museum, London (NHM); the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM); the Zoological Museum, Copenhagen, Denmark (ZMC); Echinoderm National Collection, Universidad Nacional Autonoma de Mexico, Mexico City, (ICML-UNAM) and the Discovery Collections, Southampton Oceanography Centre, UK.

DNA extraction, PCR and sequencing methods are given in Chapter 2, section 2.6.

Table 4.2. Oligonucleotid primers sequences used in the present study

Primer	Sequence 5' ? 3'	Mitochondrial map position (*Strongylocentrotus purpuratus*)	Direction
COIef	ATAATGATAGGAGG[A/G]TTTGG	6000-6019	Forward
COIer	GCTCGTGT[A/G]TCTAC[A/G]TCCAT	6692-6673	Reverse

4.2.3. Molecular Analysis

The potential interspecific variation of the putative species of *Pseudostichopus* was analysed using a 597 base pair partial Cytochrome Oxidase I (COI) sequence with all bases included (bp 1 – 597, GenBank acc. nos. AF486424-AF486436). The analysis sample set comprised of COI sequences for *P. mollis*, *P. villosus*, the *Pseudostichopus* morphotype and the outgroup *Isostichopus fuscus* (Table 4.3). These represent consensus sequences determined from the original sequence data set of 14 individuals in which all identical sequences were collapsed. The COI amino acid sequence was used for the best possible alignment. All sequences were aligned using Clustal X (Thompson *et al*. 1997).

Table 4.3. Sequences used in molecular analysis.

Species	No. Seqs.	GenBank Accession No.	Reference
Pseudostichopus mollis	1	U32221	Arndt *et al*. (1996)
Pseudostichopus villosus	3	AF486434, AF486435, AF486435.	This work
Pseudostichopus sp. 1	4	AF486430, AF486431, AF486432, AF486433	This work
Isostichopus fuscus	6	AF486424, AF486425, AF486426, AF486427, AF486428, AF486429.	This work

Phylogenetic analysis was performed on the nucleotide sequence data. Non-parametric bootstrap analysis was performed under Minimum Evolution (ME), Maximum Parsimony (MP) and Maximum Likelihood (ML) optimal criteria using PAUP* 4.0b 10 (Swofford, 2002) version. Starting trees were obtained by neighbour joining for ME and ML and via stepwise addition with random sequence addition for the MP analysis. In the Maximum Parsimony analysis, gaps were treated as missing and of the 597 characters 144 were parsimony-informative. For all optimal criteria a heuristic search was employed using the tree-bisection-reconnection (TBR) branch-swapping algorithm, in addition to an exhaustive Maximum Likelihood search.

The best model of evolution for Minimum Evolution and Maximum Likelihood analysis was determined by hierarchical likelihood ratio tests (hLRTs) using Modeltest v3.0 (Posada and Crandall, 1998). The General Time Reversible model with I (GTR + I) was chosen above others as the most suitable model of evolution for the data set. The estimations from the hLRTs were used to refine the optimal criteria settings as follows; the proportion of invariable sites (I) was set to 0.5618, gamma distribution (the distribution of rates at variable sites) was assumed equal, the substitution model was based on the rate matrix (Table 4) and, base frequencies were set to A = 0.2804, C = 0.2079, G = 0.1735 and, T = 0.3382.

For all searches, starting branch lengths were obtained using Rogers-Swofford approximation method and a molecular clock was not enforced.

Table 4.4. Nucleotide substitution rate matrix.

	A	C	G	T
A	-	7.0	19.5	47.9
		-	3.9	91.2
			-	1.0
				-

4.3. Results

4.3.1. Systematics

Genus *Pseudostichopus* Théel, 1886a

Pseudostichopus Théel, 1886a: 169; Sluiter, 1901: 52-53; Hérouard, 1902: 11; Perrier, 1902: 332; Fisher, 1907: 691; Mitsukuri, 1912: 3; Hérouard, 1923: 21-23; Mortensen, 1927: 386-388; Deichmann, 1930: 86; Heding, 1940: 356; Imaoka, 1978: 377-378; Thandar, 1992: 164; Liao, 1997: 79.
Meseres Ludwig, 1894: 34-37.
Molpadodiademas Heding, 1935: 77-78; 1940: 357; Deichmann, 1940: 209-211.
Platystichopus Heding, 1940: 144.
Trachostichopus Heding, 1940: 357, 361; Imaoka, 1978: 380; 1990: 152.
Plicastichopus Heding, 1940: 357.

Diagnosis (emended). Body cylindrical, subcylindrical or slightly flattened ventrally. Bodywall soft, fragile or leathery and wrinkled. Mouth subterminal directed downwards, anal opening in a vertical furrow; from sixteen to twenty peltate tentacles; no tentacle ampullae; stone canal connected with bodywall, sometimes perforating it, in some species apparently absent. Ambulacral appendages cylindrical, or conical, small and numerous especially around mouth and anus, and on the back and ventrolateral margins of the body, sometimes distributed in pairs, which gives the appearance of a serial arrangement. Tube feet very small and numerous, often apparently double or triple, often distributed and most conspicuous on the ventrolateral margins. The gonads form two tufts, one on each side of the dorsal mesentery. The retractor muscles are developed in the posterior end of the four-paired ambulacra, not on the mid-ventral. Ossicles in the skin rarely present, and then only sparsely, often entirely wanting. Ossicles sometimes present in tentacles, papillae and tubefeet, gonad and respiratory trees: branched and/or unbranched arched rods, sacciform rods sometimes knobbed and calcareous mesh bodies of different complexity.

Type species: *Pseudostichopus mollis* Théel, 1886a (by subsequent designation of Fisher, 1907: 691).

Remarks: the genus *Pseudostichopus* has a history of taxonomic uncertainty. It has contained different genera and has been placed in different families. Heding's (1940) classification, which placing the genera *Pseudostichopus*, *Benthothuria* and *Paroriza* within the family Gephyrothuriidae under the order Aspidochirotacea, has been rejected by most specialists (O'Loughlin, 1998).

***Pseudostichopus* sp 1.**

(Figures 4.1a-i)

Pseudostichopus sp. Billett, 1988: 196-197; 1991: 286, 301; Billett *et al.*, 2001: 325-348.

Diagnosis: a medium-sized species up to 146mm long. Conspicuous dorsal papillae, arranged in six parallel series. Two double rows along the dorsal ambulacra and two single rows on the dorso-lateral ambulacra. Papillae slightly longer and more abundant in the posterior part of the body. Twenty tentacles. Calcareous ring stout, and well developed. Radial pieces of different robustness and shape, depending on the position in the calcareous ring. Interradial pieces of similar aspect and size. One ventral polian vesicle. Unbranched gonads forming two tufts at both sides of the dorsal mesentery. Ossicles of the tentacles: sacciform rods with one or two knobs and flat or knobbed calcareous bodies of different complexity. Spicules in the gonads: branched and unbranched arched rods with pointed ends, with one, two or three spiny tips. Some rods with a single knobbed centre. No ossicles present in the bodywall, papillae and respiratory trees.

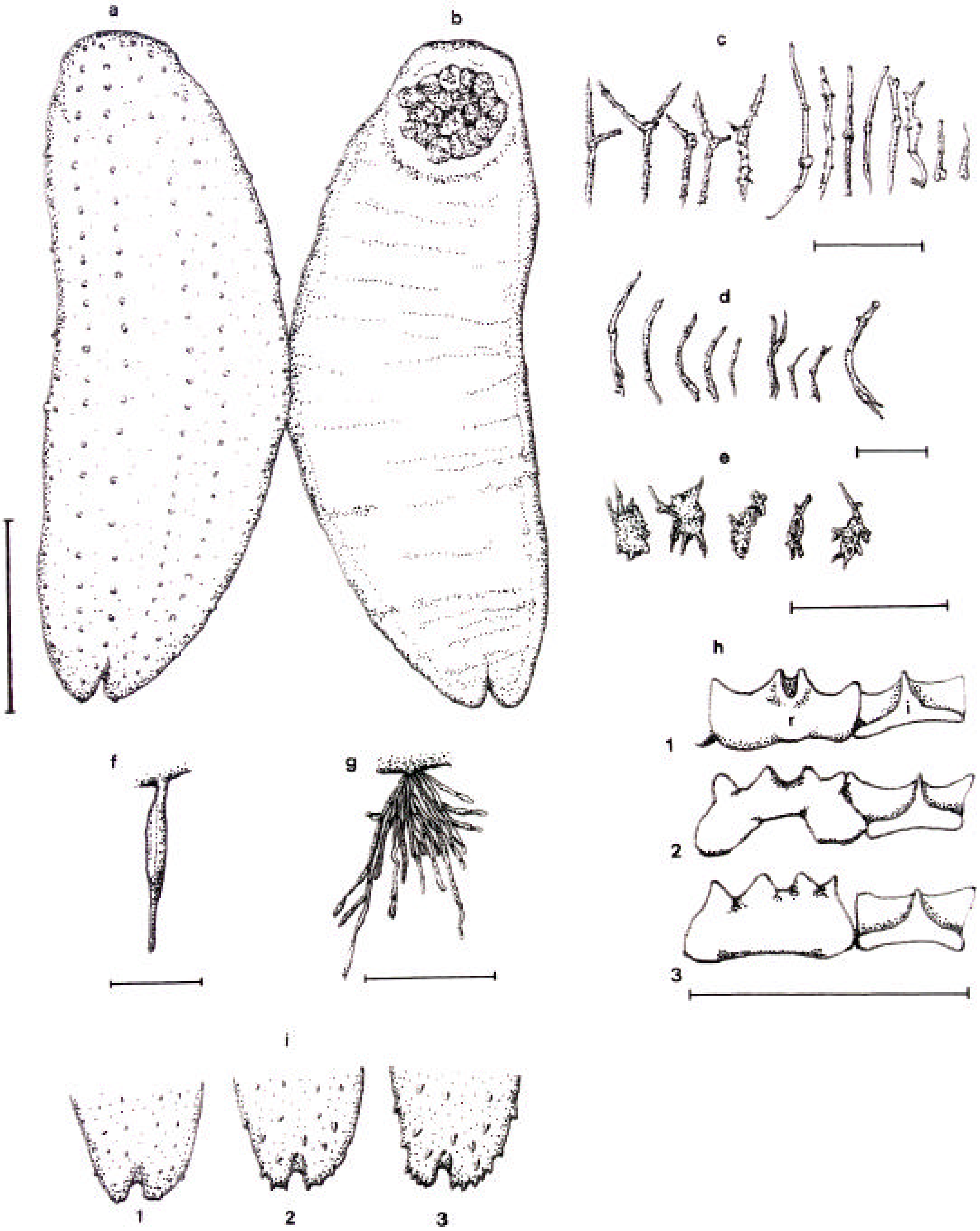

Figure 4.1. *Pseudostichopus* sp 1. (ICML-UNAM 5.125.0). a. Entire animal, dorsal side; b. Entire animal, ventral side; c. Tentacular ossicles; d. Gonad ossicles; e. Irregular calcareous bodies from tentacles; f. Polian vesicle; g. One half of left gonad; h_{1-3}. Calcareous ring, h_1. Ventral pieces, h_2. Lateral pieces, h_3. Dorsal pieces; i. Different morphologies of the posterior anal lobules. Scale bars: a, b= 20mm; c= 5µm; d= 7µm, e= 15µm, f, g= 5mm; h= 10mm.

Description: of the 1298 specimens examined (Table 4.5), the largest measures 146mm in total length (TL) and 22mm wide (W). The body is more or less fusiform, cylindrical as a whole (Figures 4.1a-b). However, the ventral and dorsal surfaces are somewhat flat, but the transverse section shows a somewhat arched dorsal surface. The body surface is sometimes encrusted with foraminiferan shells and sand. Some specimens (i.e. from St. 13078#29), either small (<20mm) or big (>100mm), are completely covered by foraminiferans. The tegument is pale yellowish white and opaque. It is about 2mm in thickness, and of moderate hardness.

The tentacles, 20 in number, are small, shield-shaped and coloured faint pale yellowish. The mouth is situated ventrally on the anterior part of the body. The anus is situated in the shallow vertical furrow on the posterior part of the body. The small podia are arranged in two double rows and two single ones along the dorsal and dorso-lateral ambulacra, respectively (Figure 4.1a). They vary in number between 10 and 23 along each row of the dorsal radii and between 6 and 13 in the dorso-lateral ones, depending on specimen size. They vary little in size, with an average diameter of 0.8mm and an average length of 0.5-1.5mm preserved. No podia along the ventral part of the body. Ventral side completely naked (Figure 4.1b). In some individuals longer than 100mm, the specimens appear to lack any dorsal papillae. The posterior anal lobules can exhibit different morphology depending on the size of the posterior dorsal podia that converge in that area of the body (Figures 4.1i_{1-3}).

The calcareous ring consists of five radial pieces and five interradials. The radial pieces are wide and stout, bearing different shapes depending on their position in the calcareous ring (Figures 4.1h_{1-3}). They have two central anterior processes and two single antero-lateral ones. The ventral radial pieces are slightly narrower on the posterior part than on the anterior part, being 6.5mm and 5mm, respectively. Their posterior parts are gently curved (Figure 4.1h_1). The lateral radial pieces are narrower on the anterior part than on the posterior one, 15mm and 10mm respectively, and with a strong posterior indentation (Figure 4.1h_2). The dorsal radial pieces are narrower on the anterior part than on the posterior part, 5mm and to 7.5mm, respectively (Figure 4.1h_3). The interradial pieces are wider on the anterior part than the posterior part, 5mm reducing to 3mm respectively. They have an antero-central process and a pair of antero-lateral “wings”, the antero-lateral edge of which is extended. The lateral side of the interradial pieces contacts with the lateral side of the radial pieces from the anterior to posterior ends. The posterior part is gently concave (Figures 4.1h$_{1-3}$).

The stone canal is attached to the bodywall and is difficult to detect. Two well-developed respiratory trees issue from a common base in the cloaca. The respiratory trees reach the anterior one-third of the body length. The gonad consist of two unbranched tufts, one on each side of the dorsal mesentery. They are slender and long, approximately 12mm in length (Figure 5.1g). The Polian vesicle is single. It is long and slender, from 2-3 mm in diameter and 13-15mm length (Figure 4.1f). Tentacular ampullae are absent.

Ossicles are exclusively rods, in the tentacles and gonads only. No ossicles are present in the bodywall or podia. The tentacular rods (Figures 4.1c, 2e) are very numerous and can be of two types: slender, spiny-bifurcated (from 3 to 11 µm), and smooth-slender with a central knob (from 3.1 to 17µm). Some rods are slightly bent. It is very common to find irregular flat or knobbed bodies, up to 8µm, of different complexity in the tentacles (Figure 4.1e). The rods in the gonads are smaller (from 6 to 15µm) and thinner, with short processes near the extremities (Figure 4.1d). A central knob is present in some of the smaller ones (10µm).

Table 4.5. List of material examined.

Station number	**No. of specimens**	**Total length (mm)**			**Width (mm)**		
		max	min	median	max	min	median
52701#42	85	115	30	72	19	9	18
12930#46	53	114	30	75	33	8	25
12930#78	82	116	34	74	20	11	20
13078#29	183	117	29	71	27	10	20
13627#10	68	109	40	72	27	10	17
54901#5	97	123	39	75	35	11	21
54901#7	2	95	89	-	23	20	-
54901#9	111	107	38	69	32	11	20
54903#1	545	100	20	58	43	5	17
54905#1	72	95	70	71	27	16	18

Note: see also appendix 2, Table 12.

Distribution: North East Atlantic, Porcupine Abyssal Plain (Billett *et al.*, 2001).

Bathymetric distribution: from 4350 to 4880m.

Holotype : NHM 2001.7066 (1 specimen, TL= 84mm, W= 25mm).

Paratypes: NHM 2001.7067-7069, all measurements are in mm (3 specimens, TL_{max}=103, TL_{min}= 60, median= 78, W_{max}= 21, W_{min}= 14, W_{median}= 18); USNM (3 specimens, TL_{max}=92, TL_{min}= 67, median= 76, W_{max}= 30, W_{min}= 16, W_{median}= 22); ZMC, HOL 00156 (3 specimens, TL_{max}=80, TL_{min}= 66, median= 74, W_{max}= 24, W_{min}= 22, W_{median}= 23); ICML-UNAM 5.125.0 (3 specimens, TL_{max}=97, TL_{min}= 67, median= 80, W_{max}= 24, W_{min}= 17, W_{median}= 20); Southampton Oceanography Centre, Discovery Collections (3 specimens, TL_{max}= 81, TL_{min}= 61, median= 73, W_{max}= 24, W_{min}= 17, W_{median}= 20).

Type locality: RRS *Discovery* St. 54901#5, 28th April 1999, OTSB 14, from 48º 44.87'N, 16º 40.53'W to 48º 48.16'N, 16º 36.24'W, from 4835 to 4838m depth.

Remarks: *Pseudostichopus* sp. 1 is a species typical of the Porcupine Abyssal Plain (Billett *et al.*, 2001, referred as *Pseudostichopus* sp.). A variety of egg sizes are present in any one ovary and the egg size is similar in samples taken at different times of the year. The maximum egg size is about 300µm (Billett, 1991). Continuous reproduction with development via an abbreviated lecithotrophic larval stage is likely (Billett, 1991). Two specimens in a sample of 545 individuals (St. 5490#1) showed scars created probably by a commensal actiniarian *Kadosactis commensalis* (Bronsdon, *et al.*, 1993, 1997). These scars were located near the anterior and posterior ends. The abundance of *Pseudostichopus* sp. 1 in the Porcupine Abyssal Plain, reported by Billett *et al.* (2001), ranged from 2 to 461 individuals per hectare (trawl samples). Along with *Amperima rosea*, *Ellipinion molle*, *Psychropotes longicauda* and *Peniagone diaphana*, *Pseudostichopus* sp. 1 has contributed to the radical, long-term faunal composition changes in the megabenthos of the Porcupine Abyssal Plain (Billett *et al.*, 2001) in recent years. Changes in megafauna abundance may be related to food supply rather than stochastic population variations (Billett *et al.*, 2001).

4.3.2. Molecular analysis

The overall length of the amplified mitochondrial DNA products varied between 610 base pairs (*Pseudostichopus villosus*) and 690 base pairs (*Pseudostichopus* sp. 1) at the 3' end of the gene. The consensus DNA sequences of the amplified fragments have 597 base pairs (Figure 4.2) the sequences have been submitted to the GenBank data base (acc. nos. AF486430 - AF486433).

```
                                                                  60
If2   ATGGCTTTCCCCCGAATGAACAACATGAGTTTTTGGTTAGTACCACCTTCTTTTATTTTA
If10  ............................................................
If15  ............................................................
If1   ............................................................
If4   ............................................................
If7   ............................................................
Pv6   .....C..T..T........T..T...........A...C.T..C.....C..C...C.T
Pv7   .....C..T..T........T..T...........A...C.T..C.....C..C...C.T
Pv1   .....C..T..T........T..T...........A...C.T..C.....C..C...C.T
Pa5   ........T..AG.T.....A..A.....C..C..A...C.C..T.....A.....A...
Pa8   ........T..AG.T.....A..A.....C..C..A..TC.C..T.....A.....A...
Pa2   ........T..AG.T.....A..A.....C..C..A..TC.C..T.....A.....A...
Pa1   ........T..AG.T.....A..A.....C..C..A..TC.C..T.....A.....A...
Pm    ...........A........A..A.....C..C..A..TC.T..T...........AC.T
                                                                 120
If2   CTTCTAGCCTCAGCTGGAGTTGAAAGAGGAGCCGGAACTGGATGAACCATTTACCCTCCA
If10  .....................................................T......
If15  .....................................................T......
If1   .....................................................T......
If4   .....................................................T......
If7   .....................................................T......
Pv6   ...T..........CA..A.A....A......T.....A..T.....AT.A..T.....T
Pv7   ...T..........CA..A.A....A......T.....A..T.....AT.A..T.....T
Pv1   ...T..........CA..A.A....A......T.....A..T.....AT.A..T.....T
Pa5   T.AT...TA..CT....TT.A...GC.....TA..T.....T.....A..C..T..A..T
Pa8   T.AT...TA..CT....TT.A...GC.....TA..T.....T.....A..C..T..A..T
Pa2   T.AT...TA..CT....TT.A...GC.....TA..T.....T.....A..C..T..A..T
Pa1   T.AT...TA..CT....TT.A...GC.....TA..T.....T.....A..C..T..A..T
Pm    ..A...ATT..TT.....A.A...GC.....TA..............A..A..T..A..T
                                                                 180
If2   CTATCTAGTAATATAGCTCACGCAGGAGGATCTGTAGATCTGGCCATTTTTTCACTTCAC
If10  ............................................................
If15  ............................................................
If1   ............................................................
If4   ............................................................
If7   ............................................................
Pv6   ..C...........T..A..TATT....C.........CT.A..A........C......
Pv7   ..C...........T..A..TATT....C.........CT.A..A........C..C...
Pv1   ..C...........T..A..TATT....C.........CT.A..A........C..C...
Pa5   .....C.....C..TT....TA..........C.....C..C..A..A...........T
```

```
Pa8   .....C.....C..TT....TA..........C.....C..C..A..A...........T
Pa2   .....C.....C..TT....TA..........C.....C..C..A..A...........T
Pa1   .....C.....C..TT....TA..........C.....C..C..A..A...........T
Pm    T.............TT....TA..........A........A..T..A........A..T
                                                               240
If2   TTAGCAGGTGCCTCTTCAATACTTGCTTCAATCAACTTTATTACAACTATAATAAAAATG
If10  ............................................................
If15  ............................................................
If1   ............................................................
If4   ............................................................
If7   ............................................................
Pv6   C....C..A..T..C.....TT.A...G....A.................T..T..T...
Pv7   C....C..A..T..C.....TT.A...G....A.................T..T..T...
Pv1   C....C..A..T..C.....TT.A...G....A.................T..T..T...
Pa5   C.............C.....T......G.T..A..........G...A..T.........
Pa8   C.............C.....T......G.T..A..A.......G...A..T.........
Pa2   C.............C.....T......G.T..A..A.......G...A..T.........
Pa1   C.............C.....T......G.T..A..A.......G...A..T.........
Pm    ........A..T..A..............C..A..A........T..A.CC.........

                                                               300
If2   CGAACCCCAGGAGTTACCTTCGATCGATTACCATTATTTGTCTGGTCAGTCTTTATAACT
If10  ............................................................
If15  ............................................................
If1   ............................................................
If4   ............................................................
If7   ............................................................
Pv6   ...G.A.....G.....T..T.....TC.............T.....CACT..G......
Pv7   ...G.A.....G.....T..T.....TC.............T.....CACT..G......
Pv1   ...G.A.....G.....T..T.....TC.............T.....CACT..A......
Pa5   ...G.......T..A..A..T..C..T......C.......T..A..C.C...C......
Pa8   ...G.......T..A..A..T..C..T......C.......T..A..C.C...C......
Pa2   ...G.......T..A..A..T..C..T......C.......T..A..C.C...C......
Pa1   ...G.......T..A..A..T..C..T......C.......T..A..C.C...C......
Pm    ...G.A.....T..AT.A..T......C....TC.......A..A....CT..C..T..A

                                                               360
If2   GCATTTCTTTTATTACTTAGACTACCGGTCCTTGCAGGAGCTATAACTATGCTTCTTACA
If10  ............................................................
If15  ............................................................
If1   ............................................................
If4   ............................................................
If7   .........................................C..................
Pv6   ..CA.C...C.TC.T.....T..C..A.....A..T.....A.....A......T.....
Pv7   ..CA.C...C.TC.T.....T..C..A.....A..T.....A.....A......T.....
Pv1   ..CA.C...C.TC.T.....T..C..A.....A........A.....A......T.....
Pa5   ..C......C..C.T..C.....T.....AT.A.....G..C.....A.....C..C...
Pa8   ..C......C..C.T..C.....T.....AT.A.....G..C.....A.....C..C...
Pa2   ..C......C..C.T..C.....T.....AT.A.....G..C.....A.....C..C...
Pa1   ..C......C..C.T..C.....T.....AT.A.....G..C.....A.....C..C...
Pm    .....C...C.TC.T......T....A..TT.A..T..T........A...T.A......

                                                               420
If2   GACCGAAAAATAAAAACAACCTTTTTTGACCCAGCTGGAGGAGGAGACCCTATTTTATTC
If10  ............................................................
If15  ............................................................
If1   ............................................................
If4   ............................................................
If7   ............................................................
Pv6   ..T.....CT.............C.....T....................A..A.....T
Pv7   ..T.....CT.T...........C.....T....................A..A.....T
Pv1   ..T.....CT.T...........C.....T....................A..A.....T
Pa5   ..T........T..T..T..A........T..T..A...........T......C....T
```

```
Pa8   ..T........T..T..T..A........T..T..A...........T......C....T
Pa2   ..T........T..T..T..A........T..T..A...........T......C....T
Pa1   ..T........T..T..T..A........T..T..A.....G.....T......C....T
Pm    ........T..T..T.....A...........T..A.................A.....T

                                                               480
If2   CAACACCTCTTTTGATTTTTTGGTCATCCGGAAGTTTATATTCTAATTCTTCCTGGGTTT
If10  ............................................................
If15  ............................................................
If1   ............................................................
If4   ............................................................
If7   ............................................................
Pv6   ........A..............C.....A.....A......T.G........A..A...
Pv7   ........A..............C.....A.....A......T.G........A..A...
Pv1   ........A..............C.....A.....A......T.G........A..A...
Pa5   .....T..A........C.....C..C..T...........C......T.A..A..T...
Pa8   .....T..A..C.....C.....C..C..T...........C......T.A..A..T...
Pa2   .....T..A..C.....C.....C..C..T...........C......T.A..A..T...
Pa1   .....T..A..C.....C........C..T...........C......T.A..A..T...
Pm    .....T..G..C.....C...........A.....A.....A......T.A..A..T...

                                                               540
If2   GGGATGATTTCTCACGTAATTGCCCATTATAGAGGTAAGCAAGAACCCTTTGGTTACCTA
If10  ....G.G.....................................................
If15  ............................................................
If1   ............................................................
If4   ............................................................
If7   ............................................................
Pv6   ..A...G.......T......A.A..C........A...A....G..T........TT..
Pv7   ..A...G.......T......A.A..C........A...A....G..T........TT..
Pv1   ..A...G.......T......A.A..C........A...A....G..T........TT..
Pa5   ..T.....A.....T.....A.....C........A...A.......T..C.....TT..
Pa8   ..T.....A.....T.....A.....C........A...A.......T..C.....TT..
Pa2   ..T.....A.....T.....A.....C........A...A.......T..C.....TT..
Pa1   ..T.....A.....T.....A.....C........A...A.......T..C.....TT..
Pm    ..T.....A......A....A..T...........A...A................TT..

                                                            597
If2   GGAATGGTTTATGCTATGGTAGCCATAGGAATCCTAGGATTCCTAGGTCTGAGCCCC
If10  .........................................................
If15  .........................................................
If1   .........................................................
If4   .........................................................
If7   .........................................................
Pv6   .........................................T..T..A........A
Pv7   .........................................T..T..A........A
Pv1   .........................................T..T..A........A
Pa5   ..................A.T.........G.GT.......TT...TA........A
Pa8   ..................A.T.........G.GT.......TT...TA........A
Pa2   ..................A.T.........G.GT.......TT...TA........A
Pa1   ..................A.T.........G.GT.......TT...TA........A
Pm    ........A.........A....T......G.TT............T.........A
```

Figure 4.2. Aligned nucleotide sequence of the 3’ segment of the mitochondrial COI gene from 4 species of sea cucumber. Dots indicate identical nucleotides. If, *Isostichopus fuscus*; Pv, *Pseudostichopus villosus*; Pa, *Pseudostichopus* sp. 1; Pm, *P. mollis*.

The identity of the partial sequence of the COI gene was confirmed by similarity of the peptide sequence to the COI gene of the sea urchin, *Strongylocentrotus purpuratus*

(Jacobs *et al.*, 1988) and the COI data from holothurians published by Arndt *et al.* (1996) (GenBank Acc. Nos. U31901, U32210-U32221, U32198 and U32199). The sequence containing the putative COI gene fragment was translated using the echinoderm codon table (Himeno *et al.*, 1987). The resultant amino acid sequences of the sea cucumber COI fragment are aligned in Figure 5.3. The COI gene is assigned ATG as the initiation codon. All specimens of the same species have identical amino acid sequences. The number of amino acid differences among the *Pseudostichopus* species ranges from 4 to 18. The maximum difference (18) occurs between *P. villosus* and *P. mollis*. There are only 7 amino acid differences between *Pseudostichopus* and *Isostichopus*.

```
                                                               60
Pm   MAFPRMNNMSFWFLPPSFILLLISSGIEAGVGTGWTIYPPLSSNISHTGGSVDLAIFSLH
Pv   ............L.........A.AS..N.A.....L........A.I.A..........
Pa   ....G.................V...L.................................
If   ............LV........A.A.V.S.A..............A.A............

                                                            120
Pm   LAGASSILASINFITTTINMRAPGVSFDRLPLFVWSAFITAFLLLLSLPVLAGAITMLLT
Pv   .........A......I........T..........TL...I..................
Pa   .........A....S.I........T..................................
If   ................I....T...T..........V.......................

                                                            180
Pm   DRNINTTFFDPAGGGDPILFQHLFWFFGHPEVYILILPGFGMISHIIAHYSGKNEPFGYL
Pv   ...F......................................V..V.T............
Pa   .............................................V..............
If   .............................................V.......Q......

                   199
Pm   GMVYAMIAIGVLGFLVLSP
Pv   ......V...I....G...
Pa   ...................
If   ......V...I....G...
```

Figure 4.3. Inferred amino acid sequences for the sea cucumber Cytochrome Oxidase 1 gene fragments. The echinoderm mitochondrial codon table (Himeno *et al.*, 1989) was used to translate the nucleotide sequences. Dots indicate identical amino acids. Abbreviations as in Figure 4.2.

The average contributions of bases across the studied sequences were A= 27%, C= 20%, G= 17%, and T= 34%. No significant differences in base composition across the 4 taxa were detected ($?^{2}$= 10.16; *df*= 39; *P* > 0.999).

In the *Pseudostichopus* group, the GC content of the sea cucumber COI gene fragments ranged from a low of 30% in *P. mollis* to a high of 37% in *Pseudostichopus* sp. 1 and *P. villosus*, with an average of 35%. As reported for numerous organisms, including a number of other echinoderms (Jacobs *et al.*, 1988; Cantatore *et al.*, 1989; Asakawa *et al.*, 1991; Arndt *et al.*, 1996), the proportion of guanine (G) in the third position was low (6-11%) with a corresponding increase in adenine (A) to an average of 45%.

There is no significant intraspecific divergence between regions of the COI gene (0.06%). For the COI gene, the observed directional mutation pressure results in a restricted substitution pattern where C? T transitions and transversions involving A predominate. Table 4.6 represents the average pairwise GTR + SSR distances matrix for the studied COI sequences. *Pseudostichopus* sp. 1 shows a degree of genetic divergence from *P. villosus*, comparable to the pairwise distances between *P. mollis* and *P. villosus*.

Table 4.6. Holothurian Pairwise Distances Matrix[1].

	If2	**If10**	**If15**	**If1**	**If4**	**If7**	**Pv6**	**Pv7**	**Pv1**	**Pa5**	**Pa8**	**Pa2**	**Pa1**	**Pm**
If2	-													
If10	0.20													
If15	0.12	0.16												
If1	0.16	0.12	0.12											
If4	0.08	0.20	0.12	0.16										
If7	0.23	0.12	0.20	0.16	0.23									
Pv6	0.36	0.23	0.31	0.28	0.36	0.20								
Pv7	0.36	0.23	0.31	0.28	0.36	0.20	0.08							
Pv1	0.31	0.20	0.28	0.23	0.31	0.16	0.12	0.12						
Pa5	0.40	0.28	0.36	0.31	0.40	0.23	0.28	0.28	0.23					
Pa8	0.44	0.31	0.40	0.36	0.44	0.28	0.31	0.31	0.28	0.12				
Pa2	0.44	0.31	0.40	0.36	0.44	0.28	0.31	0.31	0.28	0.12	0.08			
Pa1	0.36	0.23	0.31	0.28	0.36	0.20	0.23	0.23	0.20	0.12	0.16	0.16		
Pm*	0.31	0.20	0.28	0.23	0.31	0.16	0.20	0.20	0.16	0.16	0.20	0.20	0.12	-

[1] Average pairwise GTR + SSR distances.

*****Distances calculated between consensus sequences and COI GenBank Accession Nos. U31901, U32210-U32221, U32198 and U32199. Abbreviations: If, *Isostichopus fuscus*; Pv, *Pseudostichopus villosus*; Pa, *Pseudostichopus* sp. 1; Pm, *P. mollis*.

Minimum Evolution, Maximum Parsimony and Maximum Likelihood (heuristic search) analyses produced identical 50% majority-rule bootstrap consensus tree topologies, with varying bootstrap values (Figure 4.4a). The Maximum Likelihood exhaustive search produced a very similar phylogenetic tree differing only in the intraspecific relationships of *Pseudostichopus* sp. 1. Of the 135135 trees evaluated in the exhaustive search, a single tree was retained with the best score of –lnL 1834.16 (Figure 4.4b).

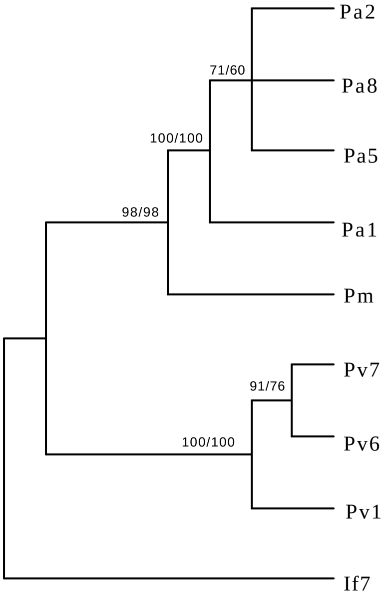

Figure 4.4a. Minimum Evolution (ME) and Maximum Parsimony (MP) 50% majority-rule bootstrap consensus tree topologies. Bootstrap values are given for ME and MP respectively. Abbreviations as In Figure 4.2. If, *Isostichopus fuscus*; Pv, *Pseudostichopus villosus*; Pa, *Pseudostichopus* sp. 1; Pm, *P. mollis*.

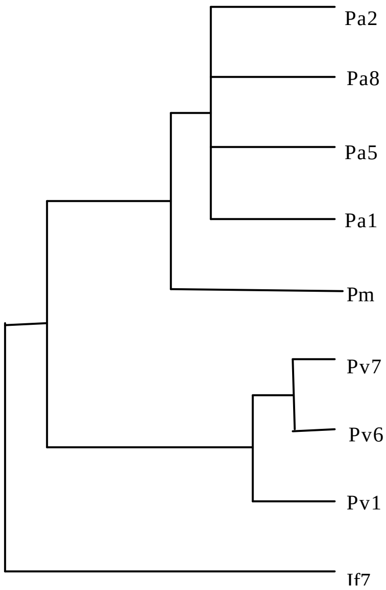

Figure 4.4b. Maximum Likelihood exhaustive search tree. Abbreviations as in Figure 4.4a.

4.4. Discussion and conclusions

Mortensen (1927) recorded seven species of *Pseudostichopus* from the North East Atlantic: *P. atlanticus* R. Perrier, from 42° 19'N, 23° 36'W, 4060-4068m; *P. depressus* Hérouard, 39° 54'N, 20° 17'W, 4360m ("*Princesse Alice*"; only one specimen known); *P. globigerinae* Hérouard, Bay of Biscay, 4380m ("*Princesse Alice*"); *P. lapidus* Hérouard, off Azores, 4020m ("*Princesse Alice*"; only one specimen known); *P. marenzelleri* Hérouard, 36° 54'N, 20° 46'W, 4400m ("*Princesse Alice*"); *P. occultatus* Marenzeller, off N.W. Spain, 500m ("*Hirondelle*"); also found in the Mediterranean, 415-1445m; *P. villosus* Théel, 37° 16'N, 20° 11'W, 4275m ("*Princesse Alice*"), otherwise of cosmopolitan distribution, 2600-5300m.

Perrier (1901), Deichmann (1930) and Billett (1988) had suggested the synonymy of *P. atlanticus* and *P. villosus*. The last author mentioned that there is a "gradation" in form from typical *P. atlanticus* to some specimens that are comparable to *P. villosus* sampled by the HMS *Challenger* Expedition in the Pacific (Théel, 1886). These specimens were analysed by Billett (1988) at the Natural History Museum, London, and only the smallest specimens (<30mm TL) can be said to be true "villosus" or hairy. I analysed the type series of *P. atlanticus* at the Paris Museum (Holotype MNHN EcHh 2772, Paratypes MNHN EcHh 2773). I also conclude that *P. atlanticus* is synonymous with *P. villosus* sharing exactly the same shape of body, tentacles, Polian vesicle, respiratory trees, gonad tubules, calcareous ring and tentacular ossicles.

Deichmann (1930) was the first author to suggest the synonymy of *P. globigerinae* and *P. villosus*. The holotype of *P. globigerinae* is a juvenile form that measures 30mm TL. Hérouard (1923) states that his specimen was a juvenile because of its size and because the gonads were not developed. An examination of Dr. Cherbonnier's slide collection (MNHN, Paris) shows that the tentacle ossicles of the holotype of *P. globigerinae* (Museum of Monaco, "*Princesse Alice*", St. 2964, 4380m, Year 1910) are exactly the same of those found in juveniles of *P. villosus* of approximately the same size. It is concluded that *P. globigerinae* is synonymous with *P. villosus* sharing exactly the same shape of tentacular ossicles and external body shape when comparing individuals of the same body size.

The list of *Pseudostichopus* species known from the North Atlantic, based on this revision with the new species added, is as follows (in alphabetic order):

Pseudostichopus sp. 1.
P. depressus Hérouard, 1902
P. lapidus Hérouard, 1923
P. marenzelleri Hérouard, 1923
P. occultatus Marenzeller, 1893a
P. villosus Théel, 1886a

Pseudostichopus sp 1 differs from *P. marenzelleri* in the lack of small thread-like appendages over whole body. Also, in *P. marenzelleri*, ventral papillae form irregular groups around the mouth and in the inferior third of the body. These were not apparent in *Pseudostichopus* sp. 1.

Pseudostichopus sp. 1 has ossicles in the gonad wall. This is unlike *P. occultatus*. In addition, the shapes of the tentacle ossicles in the two species are different. Moreover the calcareous ring is short and stout in *Pseudostichopus* sp. 1 and tall and thin in *P. occultatus*.

P. depressus and *P. lapidus* lack ossicles in any internal organ, unlike *Pseudostichopus* sp. 1. Moreover, the general body shape of *P. depressus* is completely different to *Pseudostichopus* sp. 1. In *P. depressus* the body is flat with a marginal rim while in *Pseudostichopus* sp. 1 it is more cylindrical, although it does have a flat ventral surface.

P. lapidus differs from *Pseudostichopus* sp. 1 in having a row of 25 ventral tubefeet along the lateral edge of the body. These are restricted to the middle part of the body. Moreover, *P. lapidus* possesses one row of papillae along each dorsal radius, with 4 papillae in each row.

Pseudostichopus sp. 1 differs from *P. villosus* in the general external body shape appearance. *Pseudostichopus* sp. 1 possesses a well defined flat ventral region, while *P. villosus* is much more rounded, and does not have a well-defined ventral region.

Pseudostichopus sp. 1 has well-developed dorsal papillae arranged in double rows, but these are absent in *P. villosus*.

The distinguishing diagnostic characters of *Pseudostichopus* sp. 1 are:

1) the presence of dorsal papillae arranged in 2 double rows along each radius,
2) the shape of the ossicles in the gonads - irregular bodies and rods with short processes near the ends,
3) the shape of the ossicles in the tentacles - slender, spiny-bifurcated and smooth-slender rods with a central knob.

The nucleotide distance between *Pseudostichopus* sp. 1, *P. villosus* and *P. mollis* is COI: d=39%, sufficient to support distinct species status. In sea cucumbers, a COI: d=15% is enough to identify a distinct species status, as argued by Lambert (1985) and Arndt *et al.* (1996). Therefore, based on partial sequences of the COI gene from sympatric specimens and ossicle morphology, we conclude that *P. villosus* and *Pseudostichopus* sp. 1 are not conspecific.

There are only 7 amino acid differences in the DNA sequences of the mitochondrial gene COI gene between the aspidochirotid families Synallactidae (*Pseudostichopus* spp.) and Stichopodidae (*Isostichopus fuscus*) (Figure. 5.2). Other pairwise amino acid comparisons between families and orders of sea cucumbers show differences ranging from 11 to 31 amino acids (Arndt *et al.*, 1996). The difference in the number of amino acids within the *Pseudostichopus* species ranged from 4 to 18. This is higher than that found by Arndt *et al.*, (1996) within the family Cucumariidae, were it ranged from 1 to 8.

The large variation in amino acids in the species of *Pseudostichopus* shows that the intergeneric relationships within Synallactidae are possibly confused. This is reflected in the trichotomy of the unrooted tree (Figure 4.4a). However, in relation to *P. villosus* and *Pseudostichopus* sp. 1 the phylogenetic analysis clearly supports separate species status of these sympatric morphotypes (Figure 4.4b), as indicated by the morphological analysis. *P. villosus* forms a distinct and separate clade to

Pseudostichopus sp. 1 and *P. mollis* in all tree topologies with bootstrap values of 100%. *Pseudostichopus* sp. 1 is also well supported as a monophyletic clade by 100% bootstrap values. *P. mollis* appears as the sister group to the *Pseudostichopus* sp. 1 clade with bootstrap values of 98% and 100% (Figure 4.4a). The trees are all rooted with *Isostichopus fuscus* as the outgroup. No further assumptions can be made on the intrageneric relationships of *P. villosus*, *P. mollis* and *Pseudostichopus* sp. 1. These preliminary findings suggest that molecular analysis on the inclusive species of the *Pseudostichopus* genus is required to clarify the current controversial taxonomic classification of the genus, and possibly as a result of these initial results, of the inclusive families of the Aspidochirotida.

The genus *Pseudostichopus* is a taxon where external morphology and ossicle shape simplicities have led to uncertainties in the taxonomy at the species level. The recognition of new species using morphological and molecular characters together will bring a better understanding on the systematics of this group.

Chapter Five – Systematics of the Synallactidae

Diagnosis, descriptions, taxonomic keys and figures of synallactids are scarce and are almost exclusively found in some monographs from the various large deep-sea expeditions. Because of the lack of such records, a major taxonomic revision of the family Synallactidae was needed. In this chapter I deal with the systematics of the Synallactidae. This is the first attempt ever made to review the whole family and unite it under a unified taxonomic name.

Class Holothuroidea
Subclass Aspidochirotacea
Order Aspidochirota Grube, 1840

Family Synallactidae Ludwig, 1894

Synallactidae Ludwig, 1894; 8, 26, 38; Perrier, 1898: 1665; 1902: 299; Koehler & Vaney, 1905: 9; Mortensen, 1927: 377; Deichmann, 1930: 85; Heding, 1940: 330-331; Cherbonnier, 1952: 473; Pawson, 1963: 89; 1982: 816; Thandar, 1992: 160; 1999: 376; Madsen and Hansen, 1994: 76; Rowe & Gates, 1995: 328; O'Loughlin, 1998: 497.

Diagnosis. Body usually flattened, with a ventral sole with ambulacral feet, dorsal surface with papillae. Head of the stone canal usually in connection with the bodywall, sometimes opening outwards through it. Respiratory trees well developed, usually not connected with the alimentary canal through a *rete mirabile*. Tentacular ampullae absent. No Cuverian organs. Gonad in one or two tufts. **Ossicles**. Tables, C-shaped ossicles, rarely buttons, sometimes completely absent from bodywall.

Remarks. A heterogeneous group of Aspidochirotida, characterized by their lack of free tentacle ampullae. Disk of tentacles little modified, often with a few marginal lobes. Formerly the family contained approximately 23 genera (10 are monotypic), and 144 species (around 10% of the worldwide known species of holothurian). The present thesis reduces the number of valid genera went down to 10, including 131 valid species. The group appears to be primitive, with some species having a surprising similarity to the more advance Elasipodida, while other forms resemble shallow water Aspidochirotida, Dendrochirotida or even Molpadiida.

First occurrence in the fossil record: *Priscopedatus triassicus*, from the Middle Triassic [250 million years] (Simms, *et al*., 1993; Gilliland, 1993).

Genus ***Amphigymnas*** Walsh, 1891

Amphigymnas Walsh, 1891: 199; Deichmann, 1930: 106; 1954: 387.

Diagnosis (modified from Walsh, 1891 and Deichmann, 1930). Body elongated. Skin thin, glass-like, filled with large deposits derived from tables. Tentacles 15-20. Dorsally large conical papillae, ventrally a lateral row of large conical pedicels, and a midventral row of smaller ones, packed with numerous supporting rods and a rudimentary end plate. **Ossicles**. Tables with spire three or four pillared with 1-2 cross beams and no teeth on top, often reduced or entirely absent, so the large plates resemble the plates found in the deimatids.

Type species: *Amphigymnas multipes* Walsh, 1891 (Walsh never specified the type species, Deichmann did it in her 1930 paper).

Remarks. This genus is represented by 2 species.

Amphigymnas bahamensis Deichmann, 1930

(Figures 1-6 in CD)

Amphigymnas bahamensis Deichmann, 1930: 107-108, Pl. 9, fig. 8, Pl. 10, figs. 1-6; 1940: 189-190, Pl. 32, figs. 1-10; 1954: 387.

Diagnosis (modified from Deichmann, 1930, 1940). Body elongated, with four rows of large dorsal papillae, a lateral row of still larger papillae and a midventral double row of small tubefeet. Tentacles 20, mouth ventrally placed, anteriorly overhung by the dorsal papillae; anus terminal. Skin thin, parchment like or more thick and gelatinous, according to the degree of contraction; rough to the touch. **Ossicles**. Large tables with well-developed disk, mostly with four large central holes and a varying number of smaller marginal holes. Spire mostly four-pillared and of varying height often partly reduced. Besides a number of smooth perforated plates are present with holes approximately uniform in size. Feet with or without an end plate and with numerous supporting rods, often with dentate edge, and smaller tables with 3-4 short pillars in the spire. In the dorsal papillae tables of varying size and curved supporting rods, but apparently no end plate.

Material examined. See appendix 1, Table 1.

Type material. Holotype, USNM 14718; Paratypes, 3 specimens, USNM E53253; 1 specimen, ZMUC.

Type locality. North Atlantic Ocean, Georgia, Cumberland Island, *Albatross* St. 2666 between Bahamas and Cape Fear, 30º 47’ 30” N, 79º 49’ 00” W, 493m, 5 May 1886.

Geographic distribution. Type locality, waters around Cuba, Florida and Colombia. In the Gulf of Mexico was taken at the south of the Mississippi Delta.

Bathymetric distribution. 408-802m.

Remarks. It is possible that the perforated plates mentioned by Deichmann (1940) represent a juvenile character that gradually disappears with increasing size. The type specimens may be immature animals. With increasing size larger tables gradually dominate. The ossicles of the few specimens that have been examined show great variation, but there seems no doubt that they all belong to the same species.

Amphigymnas multipes (Walsh, 1891)

(Figures 7-10 in CD)

Pannychia wood-masoni Walsh, 1891: 198-199.
Amphigymnas multipes Walsh, 1891: 199.
Synallactes reticulatus Sluiter, 1901a: 9-10; 1901b: 46-48, Pl. 3, figs. 1-2, Pl. 8, figs. 9a-c.
Synallactes woodmasoni, Koehler & Vaney, 1905: 14-16, Pl. 9, figs. 26-30.

Diagnosis. Body elongated, with four rows of large dorsal papillae, a lateral row of still larger papillae and midventral double row of very short tubefeet. Tentacles 20, mouth ventrally placed, anteriorly overhung by the dorsal papillae; anus terminal. Skin thin. Respiratory trees well developed. **Ossicles**. Table discs with four large central holes surrounded by a certain number of peripheral ones of smaller diameter. The other ossicles are flat, wide rods, sometimes with branched ends.

Material examined. See appendix 1, Table 2.

Type material. Walsh (1891) never named the type.

Type locality. Indian Ocean, Andaman Sea, 11º 31’ 40” N, 92º 46’ 40” E off Dyer Point and N. of Clinque Island.

Geographical distribution. Type locality; Bay of Bengal; Philipines; Indonesia; Malaysia; New Guinea (record from *Synallactes woodmasoni* Madsen, 1953).

Bathymetric distribution. 290-3295m.

Biological information. This species have been found on green mud.

Remarks. Walsh (1891) doesn't present any drawings of this species. He describes the species using only one specimen and with no figures at all. To the naked eye this species resembles a deimatid in its external appearance.

Genus ***Bathyplotes*** Östergren, 1896 [new comb.]

Bathyplotes Östergren, 1896: 351-352; Perrier, 1902: 345-350; Fisher, 1907: 687; Mortensen, 1927: 383; Deichmann, 1930: 99-100; 1940: 186; 1954: 386; Heding, 1940: 342-343; Pawson, 1963: 89; Gutt, 1990: 120; Madsen and Hansen, 1994: 79.
Herpysidia Perrier, 1898: 1665; 1899: 247; 1902: 352.
Bathyherpystikes Sluiter, 1901a: 5; 1902: 358-359.
Kareniella Heding, 1940: 349.

Diagnosis. Synallactidae with 15-20 tentacles; mouth ventral, anus dorsal, subdorsal or nearly terminal. Skin rather thick. Body with sole-like ventral side, usually with marginal appendages; midventral ambulacrum naked or provided with a few tubefeet; ventrolateral ambulacral with tubefeet in a single row or more. Dorsally, papillae more or less distinctly in rows. Tubefeet well developed ventrolaterally, but are often lacking midventrally. Dorsal side with double row of papillae along each radius. Musculature in most cases undivided; genital organs in two tufts, located on both sides of mesentery. Calcareous ring weakly developed, sometimes completely absent. **Ossicles**. Tables with cross shaped disc and a spire built up of 4 rods, usually with several cross beams; "C" shaped bodies maybe present. Ossicles in tentacles, simple or branched rods, sometimes smooth, sometimes spiny.

Type species: *Bathyplotes natans* (Sars, 1868) by original designation.

Remarks. This cosmopolitan genus is represented by 19 valid species. It is closely related with *Synallactes* but differs from it in having an ossicle stem formed by 3 or 4 pillars united by one or several beams. Known bathymetric range is from 60m (*B. rubicundus* Sluiter) to about 3000m (*B. profundens* Koehler and Vaney).

Deichmann (1940) was the first to suggest the synonymy of the genus *Bathyherpystikes* with *Bathyplotes*, based on a comparison of *Bathyplotes bigelowi* with *Bathyherpystikes punctatus* Sluiter. Later, Rowe (1989) and Rowe and Gates (1995) included the genus *Bathyherpystikes* Sluiter, 1901a and *Kareniella* Heding, 1940 as a synonym of *Bathyplotes*. There are some *Bathyplotes* species that are difficult to distinguish because they overlap in details of ossicle shape, such as *B. roseus*, *B. variabilis* and *B. crenulatus*.

Bathyplotes angustus (Cherbonnier & Féral, 1981) [new comb.]

Synallactes angustus Cherbonnier & Féral, 1981: 377, textfig. 12, figs. A-M.
Not *Synallactes angusta* Cherbonnier & Féral, 1981: 358 (list).

Diagnosis (after Cherbonnier and Féral, 1981). Cylindrical body, dorsal face slightly curved, ventral face flattened. Skin very thick. On the ventro-lateral radii the podia lay out in two longitudinal rows. On the edge of the ventral face, a row of large conical papillae. Mouth and anus ventral. 20 tentacles. Calcareous ring with broad radial pieces and very thin interradial pieces. One Polian vesicle. Gonads in two simply tufts. **Ossicles**. Those from the ventral tegument definitely different from those of the dorsal tegument. In the ventral tegument they are represented by plates with a very broad disc with four large central holes with perforated extremities, the central main perforation is surrounded by a circle of smaller holes, with a variable number of very small holes located at the periphery; many tables have incomplete disc; all these tables are provided with a stem formed by 4 pillars, top of the spire crown by a tuft of small spines. The tables of the dorsal tegument have a larger disc, surrounded by four hexagonal central holes with an external circle of smaller and irregular holes; their stem has four pillars, and is higher than that of the tables from the ventral tegument, but less spinous. The ventral tubefeet have simple supporting rods and a calcareous end plate. The rods of the tentacles are very large, simple, or with a central perforated apophysis, and can be transformed into pseudo-plates.

Material examined. See appendix 1, Table 3.

Type material. Holotype, MNHN 3022.

Type locality. *Musorstom* St. 50, North West Pacific Ocean, Philippines, 13° 49' 2"N, 120° 01' 08"E, 510-515m, 25 Feb 1976.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 510-515m.

Remarks. *Synallactes angusta* Cherbonnier and Féral, 1981 maybe a misspelling of the name of this species (see Cherbonnier and Féral, 1981: 358). The International Zoology Code (Article 19) states that multiple original spellings that become incorrect by the choice of a first reviser cease to be available names. I state that the name *Synallactes angustus* Cherbonnier and Féral, 1981 should be conserved.

Bathyplotes bigelowi Deichmann, 1940

Bathyplotes bigelowi Deichmann, 1940: 187-189, pl. 31, figs. 1-2; 1954: 387.

Diagnosis (after Deichmann, 1940). Strongly flattened body with a continuous lateral brim of papillae interrupted only at the posterior end. Mouth ventral with 20 tentacles surrounded by a strong sphincter; anus terminal or subventral. Ventral side with cylindrical tubefeet scattered without order, most numerous on the posterior part of the ventrum; a varying number of small "fungiform" papillae are present, forming two longitudinal rows. Dorsal side with two median rows of papillae often completely retracted, and besides a few smaller papillae irregularly distributed. One Polian vesicle, a delicate stone canal embedded in the dorsal mesentery. Respiratory trees well developed, with short lateral branches. The gonads form two clusters of dichotomously divided tubes, attached closely behind the calcareous ring and opening dorsally near the attachment for the stone canal. Skin rough to the touch on account of the large number of ossicles. **Ossicles**. A crowded layer of large tables with delicate lace-like disks with four large central holes and several smaller marginal holes; spire tall with four rods, several cross-beams and spine on the sides. Ventral tubefeet with small end plate and curved supporting rods. Dorsal papillae lacking end plate.

Material examined. None.

Type material. Holotype in MCZ (Deichmann, 1954).

Type locality. *Atlantis*, St. 2323, 22° 00’N, 81° 09’30”W, Near Bahía de Cochinos, Sta. Clara province, southern Cuba, 4 March 1939, 522-576m (Deichmann, 1954).

Geographic distribution. Caribbean Sea, Cuba (Deichmann, 1954). So far it has been reported only in the Gulf of Mexico, from the northwest coast of Cuba, but it will undoubtedly prove to belong to the fauna of the waters around Yucatan (Deichmann, 1954).

Bathymetric distribution. 396-576m.

Remarks. Its appearance, *B. bigelow* resembles *B. natans*, but has two bands of large fungiform papillae on the ventral side, and the ossicles are large delicate tables usually with a circular disk with large holes in the ends of the four arms. *B. bigelowi* differs from *B. natans* and *B. pourtalesi* in its terminal or subventral anus and its crowded layer of ossicles, which consists of tables with a complet disck.

Bathyplotes bongraini Vaney, 1914

Bathyplotes bongraini Vaney, 1914: 5-8, Pl. 1, fig. 4, Pl. 2, figs. 4, 7-9 and 11-12; O'Loughlin, 2002: 301-303.

Bathyplotes moseleyi, Ekman, 1925: 25-28, fig. 3.

Bathyplotes fuscivinculum Gutt, 1990a: 121-123, figs. 4-6, Pl. II; 1991b: 324.

Bathyplotes sp. MoV 2018, O'Loughlin *et al.*, 1994: 553-554.

Diagnosis (after Vaney, 1914). Body slightly flattened. Bodywall thin and pliable. The mouth is ventral and almost final. Anus subterminal. 19 tentacles. A ventral sole well delimited by a series of lateral papillae along over the entire length of the body and continuing, ahead above the circle of the tentacles. Ventrally, a series of 3 to 4 longitudinal rows of small pedicels. Dorsally, 12 appendices are spread out along each dorsal radius; they are more or less arranged according to a double alternate row. Most papillae are cylindrical. Respiratory trees well developed. 2 gonads, one Polian vesicle. **Ossicles**. Tables of characteristic form; the disks are cross- or star-like, with three arms radiating from a common centre, and with the ends of the arms enlarged and pierced with holes; sometimes the enlarged ends of some or all of the arms are connected with one another, thus constituting a perforated plate; the spire is composed of four stems, and a transverse beam connected at the top. Ventral tubefeet with small tables similar to the ones in the bodywall and supporting spiny rods with bifurcated ends.

Material examined. See appendix 1, Table 4.

Type material. Holotype, MNHN.

Type locality. Western side of Antarctic Peninsula, 68º 00' S, 70º 20' W, 250m, 21 Jan 1909 (after O'Loughlin, 2002).

Geographic distribution. Western Antarctica, Wedell Sea (Gutt, 1991, as *B. fuscivinculum*); western side of the Antarctic Peninsula. Eastern Antarctica, Prydz Bay.

Bathymetric distribution. 120-768m.

Bathyplotes cinctus Koehler & Vaney, 1910

(Figures 11-15 in CD)

Bathyplotes cinctus Koehler & Vaney, 1910: 91, Pl. 1, figs. 1-10; Heding, 1940: 343-345, textfig. 9, figs. 1-20.
Bathyplotes mammillatus Heding, 1940: 345-346, textfig. 10, figs. 1-22 [new synonymy].
Bathyplotes elegans Heding, 1940: 346-347, textfig. 11, figs. 1-16 [new synonymy].

Diagnosis. Body oval and flattened, mouth ventral, anus dorsal. Medium ventral region with 2 pedicels irregularly distributed in longitudinal rows. Lateral parts of the ventral sole with a series of ambulacral pedicels. On the edge of the ventral sole there are some big papillae with a big base, more or less contiguous, forming a lateral fringe. At the front they form a peri-bucal ring with about 20 lobes. On the dorsal face, big papillae. 1 Polian vesicle. **Ossicles**. Quadri-radiate bodies with broad, perforated distal extremities. Central spire of the ossicle formed by 4 convergent stems. Top of the spire with some spines. Stems joined by 3 or 4 beams. In the dorsal papillae this quadri-radiated ossicles are more elongated and the beams are closer to the top. "C" shaped bodies. Ventral pedicels with bent rods, some spines either at the top or along their edge. Dorsal papillae with similar rods, with more spines.

Material examined. See appendix 1, Table 5.

Type material. Location unknown.

Type locality. Indian Ocean, *Investigator,* St. 332, 10º 21'N, 92º 46'E, 502m.

Geographic distribution. Type locality and North Pacific Ocean, Philippines.

Bathymetric distribution. 450-768m.

Remarks. This species was described by Koehler and Vaney (1910) from a single small specimen (80mm L). Heding (1940) described *B. mammillatus* using only 2 pieces of skin from the dorsal and lateral bodywall. During a visit to the ZMUC collection, I reviewed the holotype material and found a complete specimen of this species (including internal organs) identified by Heding. It is strange that Heding (1940) never mentioned this specimen and on his diagnosis he could assert the position of the mouth and anus using only skin fragments. Following the examination of the type material and the whole specimen identified by Heding, I can state that *B. mammillatus* Heding is synonymy of *B. cinctus* Koehler and Vaney. They share the same shape of calcareous ring, and ossicles. Both species have the big papillae on the dorsal side and an anal slit. The ossicles illustrations presented by Heding (1940) for *B. mammillatus* happen to be just ossicle variation present in *B. cinctus*.

Reviewing the holotype of *B. elegans*, ZMUC (no catalogue number), shows that although Heding (1940) stated that he described this species from only one specimen, there are 2 specimens in the type jar belonging to the same species. In this last specimens I was able to see the calcareous ring and make a comparison with *B. mammillatus*. The two calcareous rings were similar. Externally this specimen resembles *B. mammillatus* and *B. cinctus*. The only difference that I noticed in *B. elegans* Heding was the presence of numerous big C-shaped ossicles, but this may be just a variation of ossicles that depends on where the bodywall sample was taken.

Bathyplotes crebrapapilla (Cherbonnier & Fèral, 1981) [new comb.]

Synallactes crebrapapilla Cherbonnier & Fèral, 1981: 375, textfig. 11, figs A-Q.

Diagnosis. Body cylindrical, slimming slightly towards the posterior end. Tegument very folded. Mouth ventral, encircled by a half-circle of small dorsal papillae. The anus is terminal. 20 tentacles. The ventral surface is crossed by a median furrow, arrangeg with two subcylindric podia, approximately 150 by row; these podia terminate in a broad suction cup supported by a calcareous disc of 580-600µ of diameter. Both interradius are occupied by a double row of papillae of 6-8mm length, fewer than the podia. On the edges of the dorsal face, two rows of 40 papillae reaching 20mm length. On the radii, the papillae are not longer than 8-10mm. The interradius is naked. One Polian vesicle. Gonads in two tufts of very large simple tubes. **Ossicles**. Tables of different sizes, generally formed by a short spire with four pillars. These tables reach a very big size in the dorsal bodywall, and cruciform bodies with irregular spires. The bodywall of the ventral podia is supported by widened rods perforated in the centre. Rods in tentacles can be thin and simply or broad and perforated.

Material examined. See appendix 1, Table 6.

Type material. Holotype, MNHN 3009.

Type locality. *Valdivia*, St. 50, Philippines, 13° 49’ 2”N, 120° 01’ 08”E, 415-410m, 25 March 1976.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 415-410m.

Bathyplotes crenulatus Koehler & Vaney, 1905

Bathyplotes crenulatus Koehler & Vaney, 1905: 23-25, Pl. 10, figs. 4-8.
Non *Bathyplotes crenulata* Koehler & Vaney, 1905: 2 (list).

Diagnosis (after Koehler & Vaney, 1905). Body strongly flattened. Mouth ventral, anus dorsal. 17 tentacles. The lateral edges of the ventral side are soft and gelatinous and are strongly inflate. The median ventral radius is naked. Along the whole length of the ventral radius there are retractile pedicels laid out irregularly in three or four rows; these rows continue to either side of the mouth where they form a single row. The dorsal face is more or less wrinkled and does not show the least trace of appendices. **Ossicles**. On the bodywall of three kinds: tables, “C” shaped bodies, and spiny rods. The base of the tables sometimes forms a cross with four branches and sometimes forms a wheel with four or five rays. The distal tip of the prolongations can be united by a contiguous circular, indented rim.

Material examined. None.

Type material. Location unknown.

Type locality. Indian Ocean, *Investigator*, St. 222, 13º 27'N, 93º 14' 30"E, 729m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 729m.

Remarks. *B crenulatus* is distinguished from all the *Bathyplotes* species described by the total absence of appendices on the dorsal surface.

Bathyplotes goldenhindi Mitsukuri, 1912

Bathyplotes golden-hindi, Mitsukuri, 1912: 26-31, Pl. 2, figs. 16-17; textfig. 6.

Diagnosis (after Mitsukuri, 1912). Body subcylindrical; dorsum convex and ventrum flat. Mouth ventral, 20 tentacles of uniform size. Anus dorsal. In active life there is probably some slight marginal border; a single series of large transparent papillae which surround the whole body extending anteriorly dorsal to the mouth and posteriorly ventral to the anus. There was a slight neck-like constriction separating the anterior head-like portion from the rest of the body (this contraction is lost in preserved specimens). Ventrally, the median ambulacrum is entirely naked, with a deep groove. There is a zone of pedicels formed by two irregular rows on each side, inside the marginal papillae. Anteriorly, they stop at the neck-like constriction, and do not extend into the head-like portion. Dorsally the marginal papillae are irregularly distributed in two irregular longitudinal zones, each corresponding to one of the dorsal ambulacral zones. Two genital tufts, branched. Calcareous ring weakly developed. One Polian vesicle, long and cylindrical. Respiratory trees well developed, extending to about the middle of the body. **Ossicles**. "C" shaped bodies and cross-shaped tables. In the posterior-most parts of the ventral surface cross-shaped bodies. Few "C" shaped bodies in the cloacal wall. Cross shaped tables somewhat scantily scattered in the perisoma. Both ventrally and posteriorly they are of about the same size and shape. The disk of the table consists of four arms, frequently five. Spire poorly developed, with four pillars and one or two cross beams, crown very irregular. Supporting rods are found in the pedicels and papillae. They are large in the ventral pedicels, they are roughened at the ends. In the dorsal papillae the rods are shorter and more slender. Well developed end-plates in the ventral pedicels.

Material examined. None.

Type material. Location unknown.

Type locality. Uraga Channel, north side, Takeyama in line with Amezaki (Mitsukuri, 1912).

Geographic distribution. Only known from its type locality.

Bathymetrical distribution: 594m.

Remarks. This species is very close to *Bathyplotes rubicundus* Sluiter, but there are some differences: 1) The most important difference lies in the presence of the large irregular calcareous bodies in the posterior-most parts of the body in the present species. Sluiter makes no mention of such bodies in *B. rubicundus*. 2) *B. goldenhindi* posses 20 tentacles, all alike in size, while in *B. rubicundus* there are only 12 short tentacles, of which the two ventral ones are much smaller than the others (Sluiter, 1901). 3) The colour of the body, been carmine in *B. goldenhindi* while *B. rubicundus* is brick red. 4) The longitudinal muscles are distinctly divided into two in *B. goldenhindi*, while it is said to be undivided in *B. rubicundus*. 5) Marginal papillae are much larger than dorsal papillae in *B.*

goldenhindi, while the contrary is stated to be true in *B. rubicundus*. This may possibly be due to the state of preservation in Sluiter's specimens.

Bathyplotes imperfectus Cherbonnier & Féral, 1981

Bathyplotes imperfectus Cherbonnier & Féral, 1981: 377-380, text-fig. 13, a-j.

Diagnosis (after Cherbonnier and Féral, 1981). Ventral side flat, dorsal side slightly convex. Mouth ventral, anus terminal. Tegument thick, soft and gelatinous. Ventral face of the body with a deep furrow occupied by 5 to 6 rows of many and very small retractile pedicels. Two rows of ventro lateral conical papillae; the ventral face is entirely naked. The margin of the body makes an edge formed by a group of short papillae with very widened bases. The medium line of the dorsal surface is occupied by a double row of papillae, going from the mouth to the anus; over the rest of this face, there are very dispersed, conical papillae. **Ossicles**. Four branched cruciform tables with broad, perforated, flattened ends; the ends may be united to form a circular table disk with four large central holes and four triangular smaller perforations. The top of the spire is rather high, with four spiny pillars. Ossicles of the papillae around the anal area, small rods.

Material examined. See appendix 1, Table 7.

Type material. Holotype, MNHN 3023.

Type locality. North Pacific Ocean, Philippines, *Valdivia,* Musorstom, St. 50, 13º 49.2'N, 120º 01.8'E, 415-510m, 25 March 1976

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 415-510m.

Remarks. Cherbonnier and Féral (1981) described this species using a poorly preserved organism, with out calcareous ring, tentacles and internal organs.

Externally *B. imperfectus* resembles *B. variabilis* (Koehler and Vaney, 1905) which presents a naked ventral surface, but the cruciform or circular ossicles are definitely different, as well as the rods of the papillae, and *B. variabilis* has "C" shaped bodies.

Bathyplotes moseleyi (Théel, 1886a)

(Figures 16-20 in CD)

Stichopus moseleyi Théel, 1886a: 165-167, Pl. 10, figs. 19-20; Ludwig, 1889-1892: 331.
Bathyplotes moseleyi Östergren, 1896: 355; Ludwig, 1898a: 8; Djakonov, 1949: 115, Pl. 18, fig. 104 a-e; Imaoka, 1990: 145, textfigs. 1a-b.
Synallactes(?) [*Stichopus*] *moseleyi* Perrier, 1902: 339, 349.
Synallactes moseleyi Perrier, 1902: 339, 349; 1905: 6-11, textfig. a.
Non *Bathyplotes moseleyi*, Mitsukuri, 1912: 31-35, textfig. 7; Ohshima, 1915: 224; Liao, 1997: 72-73, fig. 38.
Synallactes sp.?, Augustin, 1908: 20.
Synallactes(?) *gourdoni* Vaney, 1914: 4-5, Pl. 2, figs. 1-3, 5-6 [new synonymy].
Bathyplotes gourdoni, O'Loughlin, 2002: 303.
Non *Bathyplotes moseleyi*, Liao, 1997: 72-73, textfig. 38.
Bathyplotes sp. I, Gutt, 1988: 24, 32, 35, 73.
Bathyplotes rubipunctatus Gutt, 1990: 120-132, figs. 1-3, Table 1; 1991: 147 (list).

Diagnosis (after Théel, 1886a). Body elongated, almost cylindrical, slightly flattened on the ventral surface. Mouth bent toward the ventral surface; anus almost terminal. Ventral surface with three series of pedicels, the middle one forming a thin double row, the two rows forming a simple zigzag. Each of the two dorsal ambulacra with a narrow double row of small conical papillae. The two dorsal interambulacra carry a number of low whitish warts; the ventral surface also contains such warts though more sparingly. A crown of small papillae surrounds the mouth. Tentacles seventeen (?). One Polian vesicle. Respiratory trees well developed. Body-wall thin and pliable. Calcareous ring absent. **Ossicles**. Tables of characteristic form; the disks are cross- or star-like, with from four to eight arms radiating from a common centre, and with the ends of the arms enlarged, flattened, and pierced with holes; sometimes the enlarged ends of some or all of the arms are connected with one another, thus constituting a perforated plate; the spire is composed of fours rods, and one, seldom two, transverse beams; the spire is often devoid of transverse beams. The top of the spire is irregularly spinous, often with four larger teeth. Tubefeet with supporting rods. Tentacles with spiny rods.

Material examined. See appendix 1, Table 8.

Type material. Syntypes, NHM 1886.10.2.136 (2 specimens), NHM 1886.10.2.137 (fragments), NHM 1886.10.2.138 (2 specimens) and ZMA E2993 (1 specimen).

Type locality. South East Pacific Ocean, off Chile.

Geographic distribution. South Pacific Ocean, Antarctic; South Atlantic Ocean, Antarctic Peninsula, Scotia Sea; Sagami Sea, Sagami Bay, Tokyo Bay, Uraga Channel; Suruga Bay; off Cape Terpyeniya Sakhalin, Japan (Augustin, 1908, Mitsukuri, 1912; Imaoka, 1990). West coast of Patagonia (Théel, 1886a); between Navarin Island and Hoste Island (Perrier, 1905).

Bathymetric distribution. 50-1730m.

Bathyplotes natans (M. Sars, 1868)

(Figures 23-30 in CD)

Holothuria natans M. Sars, 1868: 20.

Stichopus natans, G. O. Sars, 1872: 30; M. Sars, 1877: 58, Pl. 7, figs. 18-41; Théel, 1886a: 193; Bell, 1892: 51.

Stichopus pourtalesii Théel, 1886a: 4.

Stichopus(?) *tizardi* Théel, 1892: 696; 1886: 193; Bell, 1892: 51; Koehler, 1895: 48-50, textfigs. 13-14.

Bathyplotes tizardi, Östergren, 1896: 354; Ludwig, 1901: 138, Pl. 12, figs. 3-4; Pl. 18, fig. 19; Perrier, 1902: 350; Mitsukuri, 1912: 35-39, textfig. 8; Grieg, 1932: 4.

Bathyplotes pourtalesii (Théel, 1886a), Mortensen, 1929; Deichmann, 1930: 102, pl. 9, figs. 3-7; 1940: 186, pl. 31, figs. 34; 1954: 386; Rowe and Gates, 1995: 328.

Bathyplotes fallax Östergren, 1896: 355, Pl. 18, fig. 44.

Herpysidia reptans Perrier, 1898: 247-248.

Bathyplotes reptans R. Perrier, 1902: 352-358, Pl. 12, figs. 3-4, Pl. 18, figs. 1-9; Mortensen, 1927: 384 [new synonymy].

Bathyplotes assimilis Koehler & Vaney, 1905: 25-26, Pl. 3, fig. 3, Pl. 10, figs. 1-3.

Bathyplotes papillosus Koehler & Vaney, 1905: 28-29, Pl. 10, figs. 21-24.

Not *Bathyplotes papillosa* Koehler & Vaney, 1905: 2 (list).

Bathyplotes patagiatus Fisher, 1907: 688-690, Pl. 72, figs 1, 1a-k.

Bathyplotes östergreni Ohshima, 1915: 225-226, Pl. 8, figs. 3a-d.

Bathyplotes heterostylides Heding, 1942a: 12-13, textfig. 12, figs. 3-5, textfig. 13, figs. 1-15 [new synonymy].

Bathyplotes natans, Östergren, 1896: 352-353, Pl. 18, figs. 27-35; 1902; 6; Ludwig, 1901: 137; Grieg, 1921: 7; Mortensen, 1927: 384-385, textfigs. 228: 2, 229; Deichmann, 1930: 100-102, Pl. 9, figs. 1,-2, 9; 1954: 386; Heding, 1942a: 10-12, textfigs. 10, 11, figs. 1-10, textfig. 12:1-2; Pawson, 1963: 90-94, Pl. 7, figs. 1-7; 1965: 16-18, fig. 4; Gage *et al.*, 1985: 194; Harvey *et al.*, 1988: 183; Miller & Pawson, 1990: 4; Madsen & Hansen, 1994: 79-82, figs. 48-50, map 20; Rowe & Gates, 1995: 328; Liao, 1997: 73-74, fig. 39.

Bathyplotes bipartitus Hérouard, 1912: ?, 1923: 34-36 [new synonymy].

Diagnosis: (modified from Théel 1886a). Body elongated, equally rounded at each extremity, flattened. Mouth ventral, anus subdorsal. Tentacles 20 in the adult, usually less than 20 in immature specimens. Dorsal surface with conical processes, few in number, of unequal size; those processes which attain a greater size are thinly placed on or in the neighbourhood of the two dorsal ambulacra, while the smaller are to be found partly in very limited numbers scattered among the larger, partly more crowded, forming a simple row along the sides of the body and round the anterior extremity of the body. The pedicels appear to form a double row along each latero-ventral ambulacrum, but, in contrast, the odd ambulacrum is marked out by a deep furrow. Calcareous ring very reduced, in the larger specimens absent. Two gonads tufts, one on each side of the dorsal mesentery. A single Polian vesicle. Bodywall thick. **Ossicles**. In the bodywall, tables. C-shaped ossicles may be found in the skin or in the inner organs. In some parts of the body the spines grow much larger and possess many more transverse beams; in others all the tables are very robust, with a greater number of holes in the highly dilated ends of the arms, and with the spire more irregularly developed and highly spinous.

Material examined. See appendix 1, Table 9; appendix 2, Table 1.

Type material. does not exist (Deichmann, 1930, 1954: 386; Rowe and Gates, 1995).

Type locality. Lofoten, northern Norway.

Geographic distribution. Essentially cosmopolitan. Reported to the Eastern and Northern Gulf of Mexico; the Rockall Trough, NE Atlantic (Gage *et al*., 1985); along the coast of northern Norway, Lofoten to south of Bergen, Faroe-Shetland Channel, west of Iceland; Faroe Channel (*Triton* specimens). Off the Irish West coast (*Flying Falcon* and *Helga* specimens). Also recorded from New Zealand. Wanganella Bank, Tasman Sea, East China Sea (Liao, 1997) and Japan (Ohta, 1983).

Bathymetric distribution. 193-2212m. It is known to have a wide distribution at bathyal depths throughout the World's oceans. This species was originally described (as *Stichopus natans* Sars, 1868) from the Lofoten Islands (Norway). By 1927 the known distribution of *Bathyplotes natans* was from Lofoten to Cape Verde on the east side of the Atlantic, from the West Indies and from Japan (Mortensen, 1927). The widespread distribution has been confirmed in more recent studies of samples from the northeast Atlantic (Gage *et al*., 1985; Billett, 1991), from the West Indies and Gulf of Mexico (Miller and Pawson, 1984) and from Japan (Ohta, 1983). Although *B. natans* has a wide geographical distribution the vertical distribution of this species varies with location. Mortensen (1927) records a total vertical range of 200 to 1600m depth. In the northeast Atlantic this species is taken between 600 and 1600m depth (Gage *et al*., 1985) although *B. natans* shows the greatest biomass between 1278 and 1333m depth (Billett, 1991). In the Gulf of Mexico, *B. natans* is taken from depths between 439 and 586m (Miller and Pawson, 1984). In Japan the species has a depth range of 300 to 572m, depths similar to its congeners *B. moseleyi* (Théel) and *B. goldenhindi* Mitsukuri.

Biological information. Facultative swimming holothurian (Ohta, 1983; Miller and Pawson, 1990). *B. natans* has long been known to be able to swim by undulating its body (Sars, 1868), hence the specific name. It swims by means of up and down movements. Wesenberg-Lund (1941) recorded a commensal polychaete, *Harmothoë bathydomus* Ditlevsen, 1917, on *B. natans*. Mortensen (1927) noted that the sexes are separated and the large, yolky eggs probably indicate direct development.

An observation from Japan (Mortensen, 1927) seems to indicate that it is brood-protecting, the male carrying the eggs attached its tentacles (Hyman, 1955). It has the peculiarity (common to various species of the genus) that the skin easily breaks up along the interradii. It lives on sandy to soft clay (muddy bottoms), feeding on detritus.

Remarks. In general, all the collections held specimens in poor condition. When specimens are alive, they are orange in colour and devoid of ossicles except in the papillae on which the identification is based (RRS *Discovery* Collections specimens).

Billett (1988) described ossicles from a juvenile of *B. natans* (1.7mm long). He states that at this size, *B. natans* could be confused with juvenile *Echinocucumis hispida* since both have primary cross ossicles with a spire. However, a detailed examination of the two species demonstrates that they are easily distinguished by external features.

Bathyplotes pellucidus (Koehler & Vaney, 1905) [new comb.]

Synallactes(?) *pellucidus* Koehler & Vaney, 1905: 21-22, Pl. 4, figs. 4-5, Pl. 9, figs. 22-25 [new synonymy].

Diagnosis (after Koehler and Vaney, 1905). Flattened and elongated body. Tubefeet on the midventral radius only shows at the posterior area of the body, and completely lacking in the rest of this radius; appendices of the four other radii are laid out in single rows. Long latero-ventral papillae run along lateral sides of the body. Dorsally, two rows of short papillae that runs longitudinally along the whole body. **Ossicles**. In the bodywall, short tables with a broad disk of crenulated rim. Spire formed by four stems united by a transvers beam that terminates at the top with few short spines.

Material examined. None.

Type material. Location unknown.

Type locality. *Investigator* St. 163, Indian Ocean, 13º 45’38” N, 80º 29’37”E, 378m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 378m.

Remarks. The only specimen analysed by Koehler and Vaney (1905) was incomplete and no internal anatomy was possible to described. The four-pillared tables and the presence of long papillae at the lateroventral side of the body, make this species a member of the genus *Bathyplotes*.

Bathyplotes phlegmaticus Sluiter, 1901a

Bathyplotes phlegmaticus Sluiter, 1901a: 4-5, 1901b: 36-37, Pl. 2, fig. 3, Pl. 8, figs. 14-15a-b.

Diagnosis (after Sluiter, 1902a). Body elongated, almost cylindrical, slightly flattened on the ventral surface. Skin soft and gelatinous. A delicate rim formed by free papillae at the front of the anterior part of the body (approximately 35) and along the sides of the anterior and posterior lateral edges (approximately 12 papillae at the edges). Ventral side with few papillae irregularly distributed, not limited to the radii. One Polian vesicle. **Ossicles**. Bodywall supported by tables of characteristic form; the disks are cross-like, with four arms weakly curved, radiating from a common centre, and with the ends of the arms enlarged, flattened, and pierced with holes; sometimes the enlarged ends of some or all of the arms are connected with one another, thus constituting a perforated plate; the spire is composed of four rods, with one, seldom two, or three transverse beams. The top of the spire is irregularly spinous, often with 3 to five larger teeth. Tubefeet with numerous curved, supporting rods, and a well developed endplate. Calcareous ring weakly developed. 2 branched gonads.

Material examined. None.

Type material. Holotype, ZMA E1178.

Type locality. North Pacific Ocean, Indonesia, *Siboga*, St. 139, 0° 11’S, 127° 25’E, 397m.

Geographic distribution. Only know from its type locality.

Bathymetric distribution. 397m.

Bathyplotes punctatus (Sluiter, 1901a)

(Figures 31-44 in CD)

Bathyherpystikes punctatus Sluiter, 1901a: 6; 1901b: 37-39, Pl. 8, figs. 12a-d,13.
Kareniella gracilis Heding, 1940: 349-351, textfig. 14, figs. 1-9; Cherbonnier & Féral, 1981: 381-383; Miller and Pawson, 1990: 5.
Bathyplotes punctatus, Rowe, 1989: 282.

Diagnosis (after Sluiter, 1901a). Flattened body, ventral side slightly curved. Skin moderately thick and rather soft. Mouth ventral, anus subdorsal. 18 tentacles. Middle ventral radius nearly naked, the two lateral radii with a row of tubefeet. Dorsal side with irregularly distributed papillae. One Polian vesicle. 2 branched gonads. Calcareous ring weakly developed. **Ossicles**. Tables with a circular, large disk, circular with 4, regularly 6, angular holes in the centre. Spire high, formed by 4 stems and 2 beams located almost at the top of the spire. The table's disk form perforated plates. Crown of the spire with few spines. No "C" shaped bodies.

Material examined. See appendix 1, Table 10.

Type material. Syntypes, ZMA E1005 (1 specimen); ZMA E1013 (1 specimen).

Type locality. Indo-Malayan Region.

Geographic distribution. North Pacific Ocean, Wanganella Bank, northern Tasman Sea; Philippines; Malay Archipelago. Indonesia, Nias Channel, off Puerto Rico (Miller and Pawson, 1990).

Bathymetric distribution. 310-614m.

Biological information. Facultative swimmer (Miller and Pawson, 1990).

Remarks. Rowe (1989) considered *Bathyplotes punctatus* a synonymy of *Bathyherpystikes punctatus* (Sluiter, 1901) and also, to be conspecific with *Kareniella gracilis* Heding, 1940. The synonymy of *B. punctatus* with *Bathyherpystikes punctatus* is followed here.

Bathyplotes roseus Koehler & Vaney, 1910

Bathyplotes roseus Koehler & Vaney, 1910: 92-94, Pl. I, figs. 11-17.

Diagnosis (after Koehler and Vaney, 1910). Ventral face flat, limited by a marginal fringe. Dorsal surface convex, with many papillae. Mouth ventral, anus dorsal. Along the middle ventral radius about 10 small appendices disposed in two rows more or less alternated. Dorsal face with papillae irregularly distributed. **Ossicles**. Bodywall mainly with quadri-radiate ossicles.

Material examined. None.

Geographic distribution. Indian Ocean, *Investigator* St. 279, 11º 35’ 15”N, 80º02’15” E, 540m; Indian Ocean, *Investigator* St. 280, 11º 29’ 45”N, 80º02’30” E, 802m.

Bathymetric distribution. 540-802m.

Remarks. The species was described by Koehler and Vaney (1910) using a single eviscerated specimen. The ossicles are exactly the same as *B. cinctus*. It is different from *B. phlegmaticus* and *B. natans* because the pedicels in the posterior region on the middle ventral radii are present but as in *B. natans* this pedicels can be present. *B. roseus* is different from *B. natans* because of the irregular disposition of the papillae and the shape of the ossicles, which also differ from those in *B. phlegmaticus*.

Bathyplotes rubicundus Sluiter, 1901a

(Figures 45-48 in CD)

Bathyplotes rubicundus Sluiter, 1901a: 2-3, 1901b: 34-35, Pl. 3, fig. 3, Pl. 8, figs. 16a-e.

Diagnosis (after Sluiter, 1901a). Flattened body, with a broad edge. Skin leather-like, moderately thick. Dorsal side curved, ventral side flat. A lateral brim formed by fused papillae, which seem to continue in front and above the mouth and posteriorly below the anus. Mouth ventral, anus dorsal. 12 tentacles, the 2 ventral ones smaller than the rest. The middle ventral radius naked. The two lateral ventral radii with numerous tubefeet in 3 to 4 double rows. Along the dorso-lateral radii, a simple line of conical papillae. A rather irregular line of short papillae occur in the middle part of the dorsal side. One Polian vesicle. Gonad in two tufts. Calcareous ring well developed. **Ossicles**. Bodywall supported by tables of characteristic form; the disks are cross-like, with four arms radiating from a common centre, and with the ends of the arms enlarged, flattened, and pierced with holes; sometimes the enlarged ends of some or all of the arms are connected with one another, thus constituting a perforated plate; the spire is composed of fours rods, and one or two transverse beams. The top of the spire is irregularly spinous, often with four larger teeth. Numerous "C" shaped bodies in the papillae. Tubefeet with supporting rods.

Material examined. See appendix 1, Table 11.

Type material. Syntypes, ZMA E1014 (1 specimen); ZMA E1016 (1 specimen).

Type locality. South East Pacific Ocean.

Geographic distribution. Only know from its type locality.

Bathymetric distribution. 56-450m. Label of the specimen ZMA E1016 reads "56m depth", but probably is wrong because the bathymetry of the area do not correspond with the latitude-longitud data.

Bathyplotes sulcatus Sluiter, 1901a

(Figure 49 in CD)

Bathyplotes sulcatus Sluiter, 1901a: 1-2, 1901b: 32-33; Heding, 1940: 347-348, textfig. 12, figs. 1-5.

Diagnosis (after Sluiter, 1901a). Ventral side flat, with a conspicuous furrow that runs along the whole side and stops behind the perisome. Skin smooth. Mouth ventral, anus terminal. 18 tentacles. Middle ventral radius completely naked. The lateral ventral radii with a simple line of moderate large tubefeet. In all the 5 interradii the tubefeet and papillae are irregularly distributed. Calcareous ring well developed. Two gonads weakly branched. One Polian vesicle. **Ossicles**. Bodywall supported by tables; the disks are cross-like, with four arms radiating from a common centre, and with the ends of the arms enlarged, flattened, and pierced with 4 to 6 holes; the spire is composed of four rods, and 3 to 5 transverse beams. Numerous "C" shaped bodies in bodywall, but particularly abundant in the anal area. Tubefeet with supporting rods weakly curved.

Material examined. None.

Type material. Location unknown.

Type locality. South West Pacific Ocean, *Siboga*, St. ?, 3º 37.7'S, 131º 26.4'E, 924m.

Geographic distribution. Only know from its type locality.

Bathymetric distribution. 450-924m.

Bathyplotes tizardi (Théel, 1882)

Stichopus tizardi Théel, 1882: 696; 1886a: 193; Ludwig: 1889-1892: 331; Bell, 1892: 51; Koehler, 1895a: 48; Koehler, 1896: 108, figs. 33-35; Clark, H. L., 1922: 47 (list).

Bathyplotes tizardi, Östergren, 1896: 354, Pl. 18, figs. 36-43; Ludwig, 1901: 138; Perrier, 1902: 350-352; Mitsukuri, 1912: 36-39, textfig. 8; Ohshima, 1915: 224-225; Rowe & Gates, 1995: 328.

Not *Bathyplotes tizardi*, Ludwig, 1901 (= *Bathyplotes natans*).

Herpysidia tizardi Perrier, 1898: 1665, *partim*= *Bathyplotes natans*.

Diagnosis (after Théel, 1886a: 193). Body elongated, equally rounded at each extremity, flattened. Mouth ventral. 20 tentacles. Anus subdorsal. Dorsal surface with conical processes, few in number, of equal size; those processes which attain greater size are thinly placed on or in the neighbourhood of the two dorsal ambulacra, while the smaller ones are to be found in very limited numbers, scattered among the larger, more crowded papillae, forming a simple row along the sides of the body and round its anterior extremity. The pedicels probably form a double row along each lateral ventral ambulacrum, but the odd ambulacrum is marked out by a deep furrow. The calcareous ring is very reduced and in the larger specimens absent. Two genital tufts, one on each side of the dorsal mesentery. A single Polian vesicle and madreporic canal. **Ossicles**. Bodywall thick, strengthened by C-shaped bodies and tables. In some parts of the body the spires grow much larger and possess many transverse beams. In others, all the tables are very robust and have a greater number of holes in the highly dilated parts of the arms. In these ossicles the spires are more irregularly developed and highly spinous. As a rule, the four rods that constitute the spire are almost parallel and are provided with spires. The dorsal processes carry numerous spinous and tables with very long spires.

Material examined. See appendix 1, Table 12.

Type material. Holotype, NHM 1900.4.1.162.

Type locality. *Knight Errant*, St. 6, Faroe Channel.

Geographic distribution. Faroe Channel (Théel, 1882); Bay of Biscay (Koehler, 1895); west coast of Morocco, Sahara, and Senegal (Perrier, 1902); Bergen (Östergren, 1896); Hardangerfjorden; Okinosé, Sagami Sea (Mitsukuri, 1912), South west of Shikoku; off Kii, Honshu; Pacific Ocean, *Albatross* St. 4959 and St. 4966 (Ohshima, 1915), Scandinavia.

Bathymetric distribution. 528-1297m.

Biological information. Ohshima (1915) found that in one male, the mouth was closed by a circular fold of skin, forming, a "mouth cavity". Many eggs were found attached to the tentacles, which were withdrawn into this cavity. The eggs diameter measured 0.9-1mm.

Remarks. Clark, H. L. (1922) was the first who stated that *Stichopus tizardi* was indeed a Synallactidae.

Bathyplotes triplax (Clark, 1920) [new comb.]

(Figures 50-51 in CD)

Synallactes triplax Clark, 1920: 145-146, Pl. 4, figs. 14-17 [new synonymy].

Diagnosis. Body flattened. Pedicels larger and more conspicuous on ventral surface; there are two well-marked series in each of the three ventral ambulacra. In each of the dorsal ambulacra is a double row of conical papillae. 20 tentacles. Calcareous ring well developed; interradial pieces wider than high with a conspicuous anterior point; radial pieces much larger with a strongly concave posterior margin and two conspicuous, truncate anterior projections. Respiratory tress well developed. **Ossicles**. Tables with simple spires of three rods united by three cross-bars, but with the points free, straight and parallel; disk tri-radiate, in the typical condition with three large oval perforations and a second series of three somewhat smaller holes alternating with them, usually a third, often a fourth and rarely a fifth series of perforations are present; height of spire equals disk-diameter or somewhat less. In many of the larger tables, the primary perforations are never closed in distally, so the disk remains a tri-radiate plate, with the outer end of each bar dichotomously branched and the final expansion perforated with 1-4 holes.

Material examined. See appendix 1, Table 13.

Type material. Syntype, USNM E10557.

Type locality. *Albatross*, St. 4642, Pacific Ocean, Galapagos Islands, Hood Island.

Geographic distribution. Pacific Ocean, Galapagos Islands.

Bathymetric distribution. 540-545m.

Biological information. On *Globiferina* ooze and broken shells substrates.

Remarks. This species described by Clark (1920) as *Synallactes*, is assigned to the genus *Bathyplotes* on the basis of the morphology of the ossicles. One of the diagnostic characters of *Bathyplotes* is that it possesses tables with spires united by cross beams. The genus *Synallactes* possesses a simple spire consisting of a single pillar, which may be divided or perforated, or both, at the upper end.

Bathyplotes variabilis Koehler & Vaney, 1905

Bathyplotes variabilis Koehler & Vaney, 1905: 26-28, Pl. 5, fig. 10, Pl. 10, fig. 9-18.

Diagnosis (after Koehler and Vaney, 1905). Body very flat, dorsal face slightly convex. Ventral face with a rather deep middle groove, along the entire length of the body. This ventral groove does not have any pedicels. On the ventral face, there are small pedicels on both sides of the groove in 2 to 3 rows. The dorsal face carries large papillae. These dorsal papillae seem to be arranged in 5 to 6 longitudinal rows. **Ossicles**. In the dorsal bodywall "C" shaped bodies and tables of characteristic form; the disks are cross-like, with from four arms radiating from a common centre, and with the ends of the arms enlarged, flattened, and pierced with holes; the enlarged ends of some or all of the arms are connected with one another, thus constituting a perforated plate; the final main branches generally have a large central perforation with one or two smaller ones that opens at their sides; the spire is composed of four rods, with three or four transverse beams. Dorsal papillae with "C" shaped bodies. Ventral pedicels with quadri-radiate ossicles. Tubefeet with supporting rods and calcareous end plate. Tentacles with spiny rods.

Material examined. None.

Type material. Location unknown.

Type locality. *Investigator* St. 282, Indian Ocean, 10º 08'N, 80º 49' 30" E, 896-1306m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 896-1306m.

Genus ***Benthothuria*** Perrier, 1898

Benthothuria Perrier, 1898: 1646; 1901: 365; 1902: 365; Mortensen, 1927: 378, also foot note; Deichmann, 1930: 91; Heding, 1942a: 6; Koehler & Vaney, 1905: 41-42.
Pseudothuria Koehler & Vaney, 1905: 47-48.
Dendrothuria Koehler & Vaney, 1905: 44-45.
Pelopatides Théel, 1886a:154, *partim.*

Diagnosis. Body elongate, little broader that high, marginal fringe inconspicuous. 20 tentacles; stone canal penetrating the bodywall; body with well defined sole, surrounded by a continuous series of conical papillae, which forms a very distinct border. On a ventral side, a double series of pedicels along the odd ambulacrum and on the posterior two thirds of the body. Besides these a double series of lateral pedicels placed on the posterior third part of the body in the ventral ambulacra. Dorsally irregularly distributed ambulacral and interambulacral papillae. Gonads disposed in two tufts. **Ossicles**. Absent from bodywall, tentacles and internal organs.

Type species: *Benthothuria funebris* Perrier, 1899.

Remarks. Heding (1940) proposed five species for the genus *Benthothuria* although he questioned the validity of *B. cristatus* and considered *B. funebris* to be synonymous with *B. valdiviae*. These latter two nominal species differed in two respects: the number of Polian vesicles and the presence or absence of large papillae along the dorsal ambulacra. The *Ingolf* specimen (Heding, 1942a) and the Rockall specimens (Gage *et al*., 1985) possess two Polian vesicles, which is at variance with the single Polian vesicle found in the type specimen of *B. funebris*. Two specimens of *Benthothuria* sampled off NW Africa (14º 50.8’N, 17º 50.6’W, 1430m) in an area not far from the type locality both possessed two Polian vesicles (Gage *et al*., 1985).

Koehler and Vaney (1905) erected the monotypic genus *Gephyrothuria* and the family Gephyrothuriidae for two *Investigator* specimens taken off Ceylon (3499 m). H. L. Clark (1907) described the monotypic genus *Himasthlephora* for four *Albatross* specimens in poor condition from off Georgia (1316m), although he considered that material might be congeneric with *Gephyrothuria*. Clark (1907) judged that the family Gephyrothuriidae was unnecessary and referred *Gephyrothuria* and *Himasthlephora* to the Molpadiidae. Hérouard (1923) synonymised *Gephyrothuria* with *Himasthlephora* describing a third *Gephyrothuria* species for a single specimen from off Spain (2320m), and included *Gephyrothuria* in the Synallactidae. Deichmann (1930) synonymised the Atlantic species *Gephyrothuria glauca* (Clark) and *G. europeensis* Hérouard, and referred the genus to the Molpadiidae. Heding (1935) maintained *Himasthlephora*, resurrected the family Gephyrothuriidae, erected an order Gephyrothurioidea, and described a third monotypic genus *Molpadiodemas* for two *Ingolf* specimens taken off Newfoundland and Greenland (3230m). Deichmann (1940) also resurrected the family Gephyrothuriidae, but restricted the family to *Gephyrothuria.* She also considered that *G. alcocki* Koehler and

Vaney and *G. glauca* (Clark) might be conspecific, excluded *G. europeensis* Hérouard as being probably a juvenile *Pseudostichopus*, and considered that *Molpadiodemas acaudum* Heding was probably conspecific with *Pseudostichopus atlanticus* Perrier.

Heding's (1940) classification placing the genera *Benthothuria*, *Paroriza* and *Pseudostichopus* within the family Gephyrothuriidae under the order Aspidochirotacea has been rejected by most specialists (O'Loughlin, 1998).

Deichmann's (1940) classification placing the Gephyrothuriidae, with the single genus *Gephyrothuria*, within the Molpadiida, and placing the genera *Benthothuria*, *Paroriza* and *Pseudostichopus* within the Synallactidae is generally adopted.

In the taxonomy of the genus *Benthothuria*, the number of Polian vesicles and the presence or absence of large papillae along the dorsal ambulacra are two characters that are useful to distinguish at species level in this genus.

The genus *Benthothuria* is related with *Pelopatides*. The ventral sole is clearly limited by an inconspicuous continuous row of conical papillae and the medium ventral radius have a double row of pedicels that only reach the posterior two-thirds of the body.

The genus *Benthothuria* is composed of 5 species.

Benthothuria cristatus Koehler & Vaney, 1905

Benthothuria cristatus Koehler & Vaney, 1905: 42-43, Pl. 1, fig. 4.

Diagnosis (after Koehler and Vaney, 1905). Body more or less curved, subcylindrical, the ventral region is more flattened than the dorsal one. Mouth ventral, nearly terminal. Anus terminal, largely opened. Ventral sole limited by a row of big papillae which extremity has tips all around the body, forming a peri-bucal ring and a subanal ring. On the posterior two-thirds of the mid ventral radius there are 2 rows of pedicels generally flattened laterally and also forming crests of quite irregular shapes and dimensions. In the anterior region these appendices are distinct, but on the back there are joined forming a longitudinal crest quite well developed. 20 tentacles(?). In the marginal fringe, between the big appendices, there are small papillae distributed in the latero-dorsal interradius and probably on the entire dorsal surface. Stone canal penetrating the bodywall. Respiratory trees well developed. 2 Polian vesicles. **Ossicles**. No ossicles are present in any part of the body, tentacles or internal organs.

Material examined. None.

Type material. Location unknown.

Type locality. *Investigator* St. 255, Indian Ocean, 9º 26’30”N, 91º 56’30”E, 1612-1643m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 1612-1643m.

Remarks. In *B. cristatus* the marginal papillae of the fringe are more developed than in *B. fusiformis* and they form real crests. The crests are always disposed in a single row, whereas in *B. fusiformis* they form a double row in the posterior region of the body. In *B. cristatus* the medium-ventral pedicels are very developed in a “crest” shape and they reach the radius much forward than in *B. fusiformis*.

Benthothuria distortus Koehler & Vaney, 1905

Benthothuria distortus Koehler & Vaney, 1905: 43-44, Pl. 3, fig. 5; Heding, 1940: 364-365.

Diagnosis (after Koehler and Vaney, 1905). Body slightly flattened, dorsal and ventral surfaces convex. Mouth ventral, bucal region slightly elevated, having the appearance of being terminal. Anus terminal. Ventral face limited by a row of short papillae, about 30 on each side. In the anterior region, about 20 papillae which form a peri-bucal ring. In the middle ventral region, thick plates (“escutcheon” in the original description) with irregular edge, most of them transversally elongated. These plates posses one or two pedicels disposed in 2 longitudinal rows. Lateral-dorsal interradius and dorsal interradius covered by small, numerous appendices that are also found from place to place on the ventral face. 18 tentacles (?), terminal disk with many tips. Dorsal tentacles with digitate extremities. 2 Polian vesicles. Stone canal fixed to the dorsal side of the bodywall. Respiratory trees well developed. **Ossicles**. No ossicles are found in any part of the bodywall, tentacles or internal organs.

Material examined. See appendix 1, Table 14.

Type material. Location unknown.

Type locality. *Investigator* St. 192, Indian Ocean, 15º 11'N, 72º 28'45"E, 1641-1675m.

Geographic distribution. Only know from its type locality.

Bathymetric distribution. 646-1675m.

Remarks. Closely related with *B. fusiformis* and *B. cristatus*, but differ in the presence of appendices in the odd radius, where they are supported by the thick plates ("escutcheon"). The marginal papillae and the peri-bucal ring are also different.

Benthothuria funebris Perrier, 1899

(Figure 52 in CD)

Benthothuria funebris Perrier, 1899: 248; 1902: 365-371; Mortensen, 1927: 378, also foot note; Deichmann, 1930: 91; Heding, 1940: 363-364; 1942a: 6; Gage *et al.*, 1985: 194-195; Harvey *et al.*, 1988: 183.

Diagnosis: Body elongated, semi-espheric. Flat ventral sole. Mouth ventral. Anus dorsal, terminal, but not situated at the posterior limit of the ventral surface. Ventral sole limited by a continuous row of papillae. 20 short, dendritic tentacles, disc divided in lobes, with small digitations, stem of the tentacle compressed. Two rows of big appendices in the odd ventral ambulacra. Ventral surface with numerous papillae. One Polian vesicle; 2 gonads, simple, unbranched. 2 respiratory trees well developed. No calcareous ring present. **Ossicles**. No ossicles are found in any part of the bodywall, tentacles or internal organs.

Material examined. See appendix 1, Table 15; appendix 2, Table 2.

Type material. Syntypes, MNHN 7801 (1 specimen), MNHN 7804 (1 specimen), MNHN 7805 (1 specimen).

Type locality. *Talisman*, Dredge. 62, 26º 20'N, 17º 13', North East Atlantic Ocean, coast of Sudan, 782m, 08 Jul 1883.

Geographic distribution. Off NW. Africa and SW. Greenland; Rockall Trough, North East Atlantic (Harvey *et al.*, 1988). Off Moroccan coast (specimens collected by the *Talisman*). Off Sudan, Senegal (Deichmann, 1930). North West Atlantic, *Ingolf* St. 36, 61º 50'N, 56º 21'W, 2700m (Heding, 1942a).

Bathymetric distribution. General range: 782-3757m. It appears that this species occurs deeper in more northerly latitudes in the North East Atlantic (2700-3757m) than off North West Africa (782-1230m) (Billett, 1991).

Biological information. This species appear to be neutrally buoyant. *B. funebris* may attain a considerable size and the dorsal surface appears to increase disproportionately in mass to the length of the animal during growth. Different authors have confirmed the patchy spatial distribution of this species (Billett, 1988; Gage *et al.*, 1985).

Remarks. The specimens are white dorsally and purple ventrally; although fairly robust when they first reach the deck the dorsal surface soon starts to break down into a gelatinous mass. The body cavity is less than one-third of the total body volume.

Benthothuria fusiformis (Sluiter, 1901a)

Pelopatides fusiformis Sluiter, 1901a: 7-8, 1901b: 42-43.
Benthothuria fusiformis, Koehler & Vaney, 1905: 41; Heding, 1940: 366.

Diagnosis. Ventral side flat, the dorsal side strongly arched, the whole animal is spindle-shaped, because the body is tapered at the front and at the back. Mouth ventral, anus dorsal. The two ventral radii on either side carry a single row of very large tubefeet that lie very closely next to each other. This resembles a narrow rim around the edge of the body. At the front this row continues as a more distinct edge with roughly 10 papillae. Below and behind the mouth no papillae or feet can be found. The central ventral radius carries a double row of quite widely spaced tubefeet. 20 tentacles. 2 Polian vesicles. Respiratory trees well developed. Gonads in two tufts and branched dichotomously. **Ossicles**. No ossicles are found in any part of the bodywall, tentacles or internal organs.

Material examined. See appendix 1, Table 16.

Type material. Syntypes, ZMA E1002 (1 specimen), ZMA E1009 (1 specimen), ZMA E1027 (4 syntypes).

Type locality. *Sibog*a, St. 88, North Pacific Ocean, Indonesia, 0º 34.6'N, 119º 8.5'E, 1301m.

Geographic distribution. North Pacific Ocean, Indonesia.

Bathymetric distribution. 470-2050m.

Benthothuria valdiviae Heding, 1940

(Figure 53 in CD)

Benthothuria valdiviae Heding, 1940: 365-366.

Diagnosis. Flattened, oval body. Ventral side weakly convex. Mouth ventral, anus dorsal. Large papillae along the dorsal ambulacra in addition to small papillae that are scattered over the dorsal surface, particularly in the lateral ambulacra. The large dorsal papillae are usually retracted and are exceedingly difficult to distinguish in poorly preserved specimens. Lateral papillae in a continuous line approximately around the whole body. Calcareous ring missing. 20 tentacles. 2 Polian vesicles. Respiratory trees well developed. Gonads in two tufts and branched dichotomously. **Ossicles**. No ossicles are found in any part of the bodywall, tentacles or internal organs.

Material examined. See appendix 1, Table 17.

Type material. Holotype, ZMUC.

Type locality. *Valdivia* St. 152, Indian Ocean, 63° 16.5’ N, 57° 51’E, 4636m, 17 Dec 1898.

Geographic distribution. Only know from its type locality.

Bathymetric distribution. 4636m.

Genus ***Hansenothuria*** Miller & Pawson, 1989

Diagnosis (after Miller and Pawson, 1989). Body fragile, translucent, semi-cylindrical, tapering gently interiorly and posteriorly, four to five times as long as broad. Ventral surface flat, body arched, middorsal interradial area depressed. Ventrolateral margin fringe with short to long papillae joined by continuous brim; brim broadest anteriorly, where component podia may reach 25 mm in length. Midventral radius; ventrolateral radii with numerous, miniscule hair-like feet in two or three rows. Each lateral dorsal radius with 10-31 short (15mm) sharply pointed papillae arranged in slightly zigzag row. **Ossicles**. With the exception of end plates in the ventral tubefeet, the ossicles are exclusively simple rods, occurring only in tentacles, papillae, and tubefeet. Gonad as two tufts of tubules, one to each side of dorsal mesentery.

Remarks. This genus differs from the similar *Bathyplotes* and *Pelopatides* and other synallactid genera in possessing very simple body ossicles. It further differs from *Bathyplotes* in having a dorsally positioned anus, and from *Pelopatides* in lacking feet along the midventral radius. The genus is monotypic.

Hansenothuria benti Miller & Pawson, 1989

Hansenothuria benti Miller & Pawson, 1989: 977-986, fig. 1, 3; 1990: 4, 5-8, figs. 1a, 2.

Diagnosis: after the genus.

Material examined. See appendix 1, Table 18.

Type material. Holotype, USNM E38201; Paratypes: USNM E38202 (1 specimen), USNM E38203 (1 specimen), USNM E38204 (1 specimen), USNM E38205 (1 specimen), USNM E38206 (1 specimen), USNM E38207 (1 specimen).

Type locality. *Johnson Sea-Link*, St. JSLII808, North Atlantic Ocean, Bahamas, Great Abaco Island, South of Cross Harbour Point, 25º 52’12”N, 77º 15’30”W, 699m, 09 Apr 1984.

Geographic distribution. West Atlantic Ocean, South of Great Abaco Island, Egg Island, Andros Island, Black Rock, New Province, Plana Cays, off Crooked Island, 22º 47.75’N, 74º 23.50’W, off San Salvador Island, Bahamas. St. Vincent in the Lesser Antilles.

Bathymetric distribution. 363-903m.

Biological information. This species is a "powerful active swimmer" that has been found to swim only in response to disturbance. Sequences of its active swimming movements have been described by Miller and Pawson (1989, 1990). *In situ* observations (Miller and Pawson, 1990) show that specimens were covered with a thick layer of fine sediment and *Halimeda* sp. flakes. *H. benti* can be relatively common at a given locality, but individuals are usually widely scattered and solitary.

Genus ***Mesothuria*** Ludwig, 1894

Mesothuria Ludwig, 1894: 31; Östergren, 1896: 351; Perrier, 1899: 244; 1901: 301; 1902: 301-304; Hérouard, 1906: 6; Fisher, 1907: 679; Mortensen, 1927: 379; Deichmann, 1930: 91; Heding, 1940: 331-332; Pawson, 1963: 94; 1965: 18; Thandar, 1992: 161; Madsen & Hansen, 1994: 76; Rowe, 1995: 330.
Allantis Hérouard, 1902: 21.
Mesites Ludwig, 1893a: 2; 1893b: 179.

Diagnosis (modified from Hérouard, 1906 and Deichmann, 1930). Body usually nearly cylindrical, slightly attenuating toward both ends, without marginal fringe. Ventral side usually somewhat flattened; dorsal side more or less uniformly covered with small pedicels, which are small and equal in size, or much smaller dorsally, where they are sometimes hardly visible. Tubefeet with sucking discs scattered over the entire body. Usually twenty tentacles, very occasionally varying between 18-22. No tentacle ampullae; stone canal attached to bodywall without penetrating it. Mouth terminal, anus ventral, or subventral, without special arrangement. Calcareous ring with rectangular radial segments. Gonads only on the left side of the dorsal mesentery, in a single tuft. **Ossicles**. In the bodywall are quadri-radiate tables with the central primary cross elevated from the disc.

Type species: *Mesothuria multipes* Ludwig, 1894 by monotypy.

Remarks. This genus is composed of 27 valid species.

Mesothuria abbreviata Koehler & Vaney, 1905

Mesothuria abbreviata Koehler & Vaney, 1905: 11, Pl. 12, figs. 19-20.
Mesothuria (*Mesothuria*) *abbreviata*, Heding, 1940: 333 (list).
Mesothuria media Ohshima, 1915: 226-227, Pl. 8, figs. 4a, b; Liao, 1997: 76-77, textfig. 41 [new synonymy].
Mesothuria (*Mesothuria*) *media*, Heding, 1940: 333 (list).

Diagnosis (after Koehler and Vaney, 1905). Mouth subventral, anus subdorsal. Body surface with small retractile tubefeet, irregulary distributed. Calcareous ring similar to that of *M. mulipes*. One Polian vesicle. One gonad tuft, long and branched. **Ossicles.** In the bodywall tables. Disk of the table circular, with a central hole, generally surrounded by six peripheral holes, alternating three big and three small ones. Spire formed by three or four pillars united by two transverse beams. Tip of the spire with few spines.

Material examined. See appendix 1, Table 19.

Type material. Location unknown.

Type locality. *Investigator* St. 197, Indian Ocean, 09º 34’57”N, 75º 36’ 30”E, 550m.

Geographic distribution. Pacific Ocean, Off Kii, Honshu, Japan; East China Sea.

Bathymetric distribution. 240-550m.

Remarks. *M. abbreviata* differs from *M. multipes* basically on the shape of bodywall ossicles. The tables in *M. abbreviata* have a shorter spire than in *M. multipes*. The top of the spire in *M. abbreviata* is short with few spines, and in *M. multipes* is long and without spines.

Mesothuria bifurcata Hérouard, 1901

Note: for all this information see Chapter 3, section 3.3.1 of this thesis.

Mesothuria carnosa Fisher, 1907

(Figures 59-64 in CD)

Mesothuria carnosa Fisher, 1907: 679-683, Pl. 70, figs. 4, 4a-f, Pl. 71, figs. 4, 4a.
Mesothuria (*Mesothuria*) *carnosa*, Heding, 1940: 333 (list).

Diagnosis (after Fisher, 1907). Cylindrical body, oblong, tapering at both ends. Mouth terminal, directed ventrally. Anus terminal. 18-20 tentacles. Small pedicels scattered over the ventral surface, the ventrolateral ones are larger than those in the midvenral region. One Polian vesicle. **Ossicles**. Tables of rather large size, very crowded, composed of a broad disk, irregular in outline with numerous perforations. Spire composed of four rods, one crossbeam (besides those of crown), and a crown of four upright often-divergent teeth, with one to several smaller denticles on sides. In pedicels the ossicles are comparatively very small tables with three or four uprights and reduced disks. There are also smooth, scattered, simple, very delicate and slender rods. Apparently no supporting rods in tubefeet. Tentacles with nearly straight to irregularly spiny rods.

Material examined. See appendix 1, Table 21.

Type material. Holotype, USNM 21215; Paratype, USNM 30413 (1 specimen).

Type locality. *Albatross* St. 4130, North Pacific Ocean, Unites States, Hawaii; Kauai Island, Hanamaulu Bay, 21º 58’15”N, 159º 20’55”W, 517-565m, 1 Jan 1902.

Geographic distribution. North East Pacific Ocean, Hawaii; South East Pacific Ocean, off Newcastle, Australia.

Bathymetric distribution. 195-1150m.

Mesothuria cathedralis Heding, 1940

(Figures 65-72 in CD)

Mesothuria (*Allantis*) *cathedralis* Heding, 1940: 336-338, textfig. 5, figs. 1-10.
Mesothuria (*Penichrothuria*) *cathedralis* Heding, 1942a: 8-9, textfig. 8, figs. 1-5.
Non *Mesothuria* (*Allantis*) *candelabri*, Heding, 1940: 334-335, textfig. 3, figs. 1-6.
Mesothuria cathedralis Heding, 1940: 336-338, textfig. 5, figs. 1-10; Gage *et al.*, 1985: 196.

Diagnosis (after Heding, 1940). Mouth ventral or subventral, anus terminal. 20 tentacles. Calcareous ring well developed. One Polian vesicle. **Ossicles**. Tables, mostly with seven to eight marginal holes; sometimes with 16 holes outside of the central hole. Margin of the table disk undulating; spire relatively high composed, normally by four long rods and ending in four diverging arms with few teeth. Feet with end plate and small tables of the same type as those in the skin, sometimes deformed.

Material examined. See appendix 1, Table 22; appendix 2, Table 4.

Type material. Holotype, ZMUC.

Type locality. *Valdivia* St. 56, South East Atlantic, 3º 10’N, 5º 28.5’ E, 2278m, 13 Sep 1898.

Geographic distribution. Previously know only from the Gulf of Guinea, from off Cape Bojador and in the Irminger Basin off southern Greenland.

Bathymetric distribution. 1292-4877.

Remarks. The juvenile specimen reported by Gage *et al.* (1985) (23 mm long) has tubefeet all over the body, small ventrally and larger laterally. The ossicles are tables generally with 8 holes in the base and with a tall spire ending in four points, which are almost smooth and not as thorny as figured by Heding (1940). Reduced tables are found in the tubefeet.

Mesothuria crebrapedes Cherbonnier & Féral, 1981

Mesothuria crebrapedes Cherbonnier & Féral, 1981: 371-373, textfig. 9, A-L.

Diagnosis (after Cherbonnier and Féral, 1981). Cylindrical body; anus slightly ventral; the mouth ventral. 21 tentacles. Tegument thin, rough. Entire body covered by long, cylindrical podia, whose suction cup is supported by a calcareous disc. The podia are apparently arranged without order on the radii and the interradius, dorsal podia a little shorter than the ventral ones. Calcareous ring well developed. One Polian vesicle. Respiratory trees well developed. One gonad made of simple tubes. **Ossicles**. Tables in the bodywall of identical shape ventrally and dorsally. There are three sizes: 1) small tables with narrow disc, with 6 to 8 periphery holes, with a massive stem; 2) tables with three pillars with a broad thorny crown on the top of the spire; 3) tables with larger disc, more holes, spire less massive but higher, with a very thorny crown. In the ventral tegument, ossicles with four flat branches, ending in a spatula, the spire of these ossicles have small spines over all their length and crowns. Pedicels with identical tables to those of the bodywall, but no rods are present. Straight or curved rods on the tentacles, more or less covered with spines or small warts.

Material examined. See appendix 1, Table 23.

Type material. Holotype, MNHN 3004.

Type locality. *Musorstom* St. 50, North West Pacific Ocean, Philippines, 13° 49’ 2”N, 120° 01’ 08”E, 415-510m, 25 Mar1976.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 415-510m.

Mesothuria deani Mitsukuri, 1912

(Figures 73-76 in CD)

Mesothuria deani Mitsukuri, 1912: 40-42, textfig. 9.

Mesothuria hokutenica Imaoka, 1990: 142-144, Fig. 1a-e [new synonymy].

Diagnosis (after Mitsuri, 1912). Body almost cylindrical. No marginal border. Ventral side rather flattened. Mouth distinctly ventral, anus terminal. Ambulacral appendages distributed uniformly over the whole body. Pedicels on lateral ambulacra larger than in other parts of the body, forming three or four irregular rows. The middle part of the ventral surface with smaller pedicels. Dorsal surface with small pedicels scattered all over the ambulacra as well as the interambulacra. The pedicels along the ventrolateral radii are arranged on the two incomplete rows, 40-50 along each row. They are larger than those on the dorsal surface. 20 tentacles. Calcareous ring well developed, consisting of five radial pieces and five interradial pieces. The radial pieces are of different robustness and shape, depending on their position in the calcareous ring. Interradial pieces of similar aspect and size. One or two Polian vesicles, different in size. One Polian vesicle is common in small individuals. One genital tuft on the left side of the dorsal mesentery. **Ossicles**. With the exception of end plates in pedicels, tables are the only kind of ossicle. Spire consists almost always of three pillars. It has generally only one crossbeam. The crown has several teeth on the top of each of the three pillars. Each point has from 3 to 6 teeth at the end. Many tables from the ventral side have no marginal holes. Tables on the pedicels not different in shape, but smaller in size. The disc has from 6 to 10 large holes fundamentally. A few marginal holes are often present. No supporting rods.

Material examined. See appendix 1, Table 24.

Type material. The type material was in the USNM, but it has been lost.

Type locality. Pacific Ocean, Japan, Okinose, outer edge, Iwado-line, Sagami Sea. 630m, 12 Apr 1897.

Geographical distribution. Pacific Ocean, Japan, Okinose, Uruga Channel, Oshima, Izu Island, Sagami Bay; Tosa Bay.

Bathymetric distribution. 160-5013m.

Biological information. The species inhabits hard bottoms substrates of compact shell sand. The animal covers itself with sand grains, small shells and shell fragments, which adhere by action of its numerous pedicels (Mitsukuri, 1912).

Remarks. The specimens have tables of the tri-radiate type and are very similar to those of *M. maroccana* Perrier. However, the tables in the latter species have disks with either six holes, or two or three additional holes in the primary circle, but never any outside that circle. *M. murrayi* (Théel) is also similar to *M. deani* Mitsukuri, but in *M. murrayi* large lateral pedicels are present in a single row on the outer edge of each lateral ambulacrum. The other pedicels are small. In addition, the shape of the spire of the tables is different: in *M. murrayi* the spire terminates in three long prolongations furnished with teeth, while in *M. deani* there are no such long prolongations.

Imaoka described *M. hokutenica* from 2 rather small specimens (TL: 49 and 52mm) collected in Tosa Bay, Japan. The number of holes in the table disc are fewer (fundamentally six) when *M. deani* is younger. It is strange that Imaoka (1990) doesn't mentioned the remarkable similarity of his species with Mitsukuri's *M. deani*. Ohshima (1915) synonymised *M. deani* under the species *M. parva* (=*M. murrayi*) based on Fisher's (1907) drawings, even though these represents *M. murrayi.* In this thesis I remove *M. deani* from the synonymy of *M. parva* (=*M. murrayi*), re-establishing the species as a valid one.

Mesothuria edwardensis Massin, 1992

(Figure 77 in CD)

Mesothuria edwardensis Massin, 1992: 311-313, figs. 1a-e; Branch *et al*., 1993: 55 (key).

Diagnosis (after Massin, 1992). Small holothurian (10-20mm); 18 tentacles; no midventral tubefeet; tubefeet of lateral rows longer than others. **Ossicles**. Bodywall and tubefeet with tables only, large tables in bodywall, small tables in tubefeet; disk of tables with one large central hole surrounded by 6-8 holes; spire of 3 pillars, each ending in a short smooth spine. The 3 spines diverge; spines of small tables often end in a few spinelets.

Material examined. None.

Type material. Holotype, SAM-A23728; Paratype, SAM-A23729 (1 specimen).

Type locality. South African Expedition, Edward Island, 46° 42’ 6”S, 37° 48.5’E, 250-260m, Sep 1984.

Geographic distribution. Indian Ocean, sub-Antarctic region, Crozet Island, Marion Island, Edward Island (Massin, 1992; Branch *et al*., 1993).

Bathymetric distribution. 92-260m.

Biological information. Lives on sandy bottom with volcanic rock (Massin, 1992).

Remarks. Massin (1992) compared *M. edwardensis* with other *Mesothuria* species such as *M. abbreviata*, *M. maroccana*, *M. abbreviata*, *M. hokutenica* (=*M. deani*), *M. bifurcata* and even with *Zygothuria lactea*. I found that *M. edwardensis* is very closely related with the Pacific species *M. murrayi* (Théel, 1886a). The bodywall tables of *M. edwardensis* are very similar with those of *M. murrayi*, the only distinction between them is their geographical distribution (see the ossicles illustrated by Jangoux *et al*., 1989).

Mesothuria gargantua Deichmann, 1930

(Figures 78-82 in CD)

Holothuria verrilli Théel, 1886b: 6, *partim*.
Mesothuria gargantua Deichmann, 1930: 95-96, Pl. 7, fig. 1; 1940: 191; 1954: 386.
Mesothuria (*Allantis*) *gargantua*, Heding, 1940: 333 (list).

Diagnosis (after Deichmann, 1954). Large robust form, with thick skin. Stout, cylindrical feet over entire surface, except the anterior part of the ventrum; dorsal feet slightly smaller. **Ossicles**. Tables with irregular disk with numerous holes and four-pillared spire with numerous spines on the top. Feet with vestige of end plate or none; tables almost the same size as those in the skin.

Material examined. See appendix 1, Table 25.

Type material. Holotype, MCZ 449.

Type locality. Caribbean Sea, off Barbados, 720m.

Geographic distribution. Off Lesser Antilles (*Blake's* specimens); north of Cuba (*Atlantis's* specimens). This species may possibly be common in deep water of coasts of Cuba and Yucatan (Deichmann, 1954).

Bathymetric distribution. 720- 936m.

Remarks. *M. gargantua* differs from *M. intestinalis* in the much larger and more solid tables; the reduction of end plates, the presence of numerous large feet on the posterior part of ventrum, the larger size.

Mesothuria grandipes (Hérouard, 1923)

Mesothria murrayi Théel var. *grandipes* Hérouard, 1923: 15-17, Pl. 4, figs. 7-9.
Mesothuria (*Mesothuria*) *grandipes*, Heding, 1940: 333 (list).

Diagnosis (after Hérouard, 1923). Mouth and anus ventral. Body cylindrical, but slightly flattened at the ventral side. Tubefeet present over the whole body, dorsally they are quite visible but ventrally they are smaller. One Polian vesicle. Branched gonads in one tuft. **Ossicles**. Very similar with those of *Mesothuria murrayi* Théel but tables with 3 stems, armed with 3 points at the top of the spire, table disk appreciably larger.

Material examined. None.

Type material. Location unknown.

Type locality. *Princesse-Alice*, St. 536, North Atlantic Ocean, 2178m, year 1895.

Geographic distribution. North Atlantic Ocean.

Bathymetric distribution. 1740-2178m.

Mesothuria holothurioides Sluiter, 1901a

(Figures 83-88 in CD)

Mesothuria holothurioides Sluiter, 1901a: 14-15, 1901b: 28-29, Pl. 9, fig. 3.
Mesothuria (*Mesothuria) holothurioides*, Heding, 1940: 333 (list).

Diagnosis (after Sluiter, 1901a). Cylindrical body, oblong, tapering at both ends. Mouth terminal, directed ventrally. Skin rather thin, soft leather-like. Anus terminal. 20 tentacles. Papillae rather large, the largest completely irregularly distributed on the two flanks of the body. The whole middle part of the ventral side without tubefeet. Calcareous ring well developed,. 2 Polian vesicles. One gonad, branched. **Ossicles**. Numerous tables of different sizes. Tables with a large hole in the centre and 8 or 9 smaller holes at the edge. The table is formed by 3 pillars and are united by a transverse beam almost half way up high the spire. At the top of the spire there are, at the distal ends of each stem, a group of little spines. Tubefeet with out supporting rods.

Material examined. See appendix 1, Table 26. Cherbonnier's slide collection at the Natural History Museum in Paris France. 1 slide with Holotype material (ZMA E1175, *Siboga*, St. 173).

Type material. Syntypes ZMA E1175 (10 specimens).

Type locality. *Siboga* St. 173, North West Pacific Ocean, 3° 27'S, 131° 0' 5"E, 567m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 567m.

Mesothuria incerta Koehler & Vaney, 1905

(Figure 89 in CD)

Mesothuria incerta Koehler & Vaney, 1905: 11-13, Pl. 1, fig. 6, Pl. 9, figs. 4-9.
Mesothuria (*Mesothuria*) *incerta* Koehler & Vaney, 1905; Heding, 1940: 333 (list).

Diagnosis (after Koehler and Vaney, 1905). Body flattened and oval. Ventral side flat. Dorsal side convex. The surface of the body is covered with tubefeet. The marginal edge is covered with numerous conical papillae, which are laid out in several rows and extend over the entire length of the lateral radii. Ventral tubefeet end in a suction disk. The ventral surface contains numerous small retractile. The big papillae are distributed without any order, throughout the ventral side in both the radial and interradial areas. The dorsal side possesses very developed papillae, particulary close to the latero-ventral radii. Calcareous ring well developed. One Polian vesicle. Gonad in only one tuft. **Ossicles**. The bodywall is rather thick and contains tables. Disc of the table with a central hole and six large peripheral ones, alternating sometimes with smaller marginal ones. Spire formed by three stems terminating in a few spines, and with two beams.

Material examined. See appendix 1, Table 27.

Type material. Location unknown.

Type locality. *Investigator* St. 229, Indian Ocean, 9° 29’ 34” N, 75° 38’ E, 648m.

Geographic distribution. Indian Ocean, Maldives.

Bathymetric distribution. 229-648m.

Mesothuria intestinalis (Ascanius, 1805)

(Figures 90-97 in CD)

Holothuria intestinalis Ascanius, 1805: 5, Pl. 45; Marenzeller, 1893a, 15; 1895: 21; Ludwig, 1883: 174; Théel, 1886: 209; 1902 1-38, Pls. 1-2, figs. 1-19, textfigs. 1-12; Bell, 1892: 48-49, Pl. 5, fig. 3; Hérouard, 1896: 163.
Fistularia mollis Sars, 1835: 40.
Holothuria mollis, Sars, 1835.
Thyonidium scabrum Sars, 1868 (according to G. O. Sars, 1871).
Holothuria verrilli, Marenzeller, 1893b: 7-9, Pl. 1, fig. 2, Pl. 2, fig. 2.
Allantis intestinalis var. *verrilli*, Hérouard, 1902: 18-21, Pl. 1, figs. 3-6, *partim*.
Allantis intestinalis, Heding, 1942a: 7, text fig. 6.
Not *Allantis intestinalis* var. *verrilli*, Hérouard, 1902 (= *Mesothuria verrilli*).
Mesothuria intestinalis, Östergren, 1896: 347-351, Pl. 18, figs. 1-26; 1902: 6-7; Perrier, 1902: 304-307, text figs. 1-2, Pl. 16, figs. 19-21; Ludwig, 1901: 139; Théel, 1902, 4-34, pl. 1-2, figs. 1-19 and 12 text figs.?; Hérouard, 1923: 10, Pl. 5, fig. 5-6; Mortensen, 1927: 381, text fig. 225, 228: 3; Koehler, 1927: 240, Pl. 15, fig. 3 *partim*; Deichmann, 1930: 94-95, Pl. 6, figs. 9-10; 1954: 385-386; Tortonese, 1949: 13 (list); 1965: 69-70, text fig. 26;

Sibuet, 1974: 795; Harvey *et al*., 1988: 184; Madsen & Hansen, 1994: 76-79, figs. 46-47, map 29; Massin, 1996: 43.

Mesothuria (*Allantis*) *intestinalis,* Heding, 1942a: 7, textfig. 6, figs. 1-7; Panning, 1952: 123-125, figs. 1-3.

Diagnosis (after Madsen and Hansen, 1994). Body nearly cylindrical, only slightly flattened ventrally and slightly attenuated towards both ends. Bodywall thin, soft, often becoming strongly wrinkled in preserved specimens. Mouth subventral, anus terminal. Tentacles 20 in adult, fewer in younger specimens, with slightly incised discs, completely retractile with a rim of the bodywall closed over them. Tubefeet small, most strongly developed in the ventro-lateral ambulacra (2 to 4 bands), but no distinct longitudinal series of large tubefeet; on the dorsal side the tubefeet are fewer and smaller, especially scarce along the mid-ventral radius, which appears almost naked; dorsal tubefeet very sparse. All tubefeet, including the smallest ones, usually have a sucking disc. 1 or 2 Polian vesicles. **Ossicles**. Tables of quadri-radiate type, with a spire built of the 4 rods, ending in a crown of several thorns; disk often with typically 8, regularly shaped small holes outside one circular central hole, usually also some smaller peripheral ones; but many deviations may occur. In small specimens the spire may be composed of only 3 rods. Tables of the tubefeet well developed, with a spire similar to the tables of the bodywall, but slightly smaller, and with a terminal plate. Ventral tables sometimes slightly smaller and more robust than dorsal ones. Spire of table consisting of 4 (very rarely 3 or 5) vertical pillars rising from a highly elevated primary cross and united by crossbeams distally where spire ends in a low, spinous crown. Tentacles with supporting rods.

Material examined. See appendix 1, Table 28; appendix 2, Table 5.

Type material. Does not exist.

Type locality. Coast of Norway (Deichmann, 1954). Western Norway (Bergen?).

Geographic distribution. Widely distributed in the North East Atlantic (Harvey *et al*., 1988) from off North West Africa (Hérouard, 1923) to the coast of Norway, although nowhere in the deep sea does it appear to be particularly common. A few specimens are known from the Mediterranean (see Perrier, 1902; Koehler, 1927; Sibuet, 1974) and the western Atlantic (Deichmann, 1930).

As far as the present records go, the species is not common in American waters, but it may very likely occur in numbers on the extensive areas of muddy bottom in the Gulf of Mexico (Deichmann, 1954).

Bathymetric distribution. From 18 to 4255m (Tortonese, 1949). The species has a wide bathymetric range, but reports of this species occurring as deep as 2000m, appear to be result of confusion with *M. milleri* sp. nov. (in the North East Atlantic) and *M. verrilli* (in the western Atlantic). The shallowest records come only from cold waters off Norway.

Biological information. The species is hermaphrodite (Théel, 1886a; Östergren, 1896; Hérouard, 1923), but male and female products are found ripe at the same time. Eggs large and yolky (>0.6 mm in diameter); the development, therefore, probably direct, without pelagic larval stage. It lives on muddy bottom and usually covers itself with shell fragments and other bottom material. It is rather difficult to preserve, as it usually eviscerates during capture. Lives on a variety of bottoms, from sand with pebbles to soft clay. Théel (1886a) was the first to suggest continuous reproduction in this species.

Remarks. Rathke has often been cited as a co-author of *H. intestinalis*, but he merely edited the volume after the death of Ascanius in 1803. Koehler (1896) regarded *Mesothuria verrilli* (Théel, 1886b) from the West Indies a synonym of *M. intestinalis*. Östergren (1896) found, that they were distinct species, while Hérouard (1902) regarded *M. verrilli* as a deep-water form. *M. verrilli,* differing from *M. intestinalis* by 1) having more slender and very crowded tubefeet, 2) the spire of the tables ending in four simple prolongations, and 3) reduced tables in the tubefeet. Madsen and Hansen (1994) pointed out that the tables of *M. intestinalis* resemble those of the dendrochirotid *Ekmania barthi*, but are rather heavier, shorter and thicker than those of *M. intestinalis*.

No ossicles age variation was observed by Madsen and Hansen (1994) in specimens 8-150mm long, nor was there any geographic variation. The whole variation evident in the form of the ossicles occurred at a single locality.

Hérouard (1923) reported that some specimens found in the Mediterranean Sea by the *Hirondelle II* had 22 tentacles. The 2 extra tentacles were smaller than the rest and were placed ventrally.

Mesothuria magellani (Ludwig, 1883)

Holothuria magellani Ludwig, 1883: 175-176; Théel, 1886a: 209.
Mesothuria magellani, Östergren, 1896: 351; Ludwig, 1898b: 8; Panning, 1929: 107 (synonymy list).

Diagnosis (after Ludwig, 1883). Cylindrical body, ventral side flattened. 20 tentacles. The odd ambulacrum is almost devoid of pedicels, and the dorsal surface carries thinly scattered small papillae. Lateral ventral ambulacra have a double row of well-developed pedicels. One Polian vesicle. Calcareous ring well developed. **Ossicles**. Tables with four pillars and four spines.

Material examined. None.

Type material. Location unknown.

Type locality. Antarctic Ocean, Strait of Magellan.

Geographical distribution. Only known from its type locality.

Bathymetric distribution. ?

Remarks. This species is doubtless closely related to *M. intestinalis*, and it seems almost impossible to point out any distinguishing character of importance. According to Ludwig

(1883) the odd ambulacrum is almost devoid of pedicels, and the dorsal surface carries thinly scattered small "papillae" while the lateral ventral ambulacra have a double row of well-developed pedicels. The Smithsonian Institution has a record of this species [USNM E4575, (TL: 6mm, W: 3mm)]. I examined the specimen and determined it to be a juvenile holothuriid from the Caribbean, probably from shallow waters. This is not a valid record.

Mesothuria maroccana Perrier, 1899

(Figures 98-104 in CD)

Mesothuria maroccana Perrier, 1899; 245; 1902: 312-317, Pl. 16, figs. 32-35; Hérouard, 1923: 17; Deichmann, 1930: 97, Pl. 7, figs. 2-7; 1940: 191; 1954: 385; Grieg, 1932: 4; Hansen, 1956: 46, fig. 14 a.
Holothuria intestinalis var. *verrilli*, Hérouard, 1896: 163.
Mesothuria murrayi var. *grandipes*, Hérouard, 1923: 15, Pl. 4, figs. 7-9.
Not *Mesothuria murrayi*, Théel, 1886a: 6; Hérouard, 1902: 23.
Mesothuria verrilli, Théel, 1886b: 6 *partim*.
Mesothuria (*Mesothuria*) *maroccana*, Heding, 1940: 333; 1942a: 8.

Diagnosis (after Deichmann, 1954: 385). Mouth ventral, anus terminal. 20 tentacles, tubefeet of unequal size, largest along the sides of the body, where a zig-zag or double row seems to be present; they are small but well-developed on the dorsum and totally lacking on the ventrum. **Ossicles**. Regular tables, mostly with six marginal holes and quite large central hole; margin smooth or undulating; spire relatively low composed of three short rods and ending in three diverging arms with few teeth. Feet with end plate and small tables of the same type as those in the skin, sometimes deformed.

Material examined. See appendix 1, Table 29; appendix 2, Table 6.

Type material. Syntype, MNHN 7155.

Type locality. *Talisman* St. ?, Off Morocco, 2105m, year 1883.

Geographic distribution. From off the Moroccan coast and between Spain and Azores. Spain (de la Hoz and García, 1991). Atlantic Ocean, from 38º N to 20º N (Madsen, 1953a). Southwest Jamaica, 990m (Deichmann, 1930). Eastern Atlantic; also wide spread in the West Indies; Eastern Gulf of Mexico; San Nicolas, northern Cuba, Caribbean.

Bathymetric distribution. 700-3120m.

Remarks. The species was first described from off Gibraltar by Théel (1886) as *H. murrayi*?; Perrier (1899) later gave a very careful description of it. Hérouard's (1923) *M. murrayi* var. *grandipes* is identical with Perrier's species. Hérouard (1923) pointed out (p. 17) several differences, 1) the arrangement of the lateral pedicels is in two rows rather than one, a very doubtful character when the variation caused by contraction or age is considered; 2) the serial arrangement of the dorsal appendages, also a very doubtful matter; and 3) larger deposits than those described by Théel and Perrier, the disk having a diameter of 0.15-0.18 by 0.10-0.12mm. With our present imperfect knowledge of the variation within species, this character is not of supreme importance. It may be that *M. murrayi* var. *grandipes* is a specimen that has retained some of its larger, juveniles tables, as shown by Deichmann (1930). Hérouard does not mention what the deposits are in the tubefeet. He gives no figures of the ossicles at all.

Mesothuria megapoda Clark, 1920
(Figures 105-109 in CD)

Mesothuria megapoda Clark, 1920: 143, Pl. 4, figs. 9, 10.
Mesothuria (*Mesothuria*) *megapoda* Clark, 1920: Heding, 1940: 333 (list).

Diagnosis (after Clark, 1920). Body rather uniformly covered with large pedicels, not arranged in series or bands. None of the pedicels are conspicuously larger than the others. **Ossicles**. Numerous tables with spires 100-135µ high; the three rods making up the spire are enlarged, curved outward and rough at the tip. The disks are 150-200µm across and are perforated with seven nearly equal holes, one at the centre and six around it; while they are not all exactly alike, there is little diversity. There are no supporting rods in the pedicels but there are well-developed terminal plates.

Material examined. See appendix 1, Table 30.

Type material. Holotype, USNM E9847.

Type locality. *Albatross* St. 4742, North East Pacific Ocean, 0º 3’ 24” N, 117º 15 48” W, 4243m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 4243m.

Remarks. Clark described this species using an eviscerated specimen in poor condition. It can be distinguished from *M. multipes* by the larger pedicels, the presence of a well-developed terminal plate and the larger, lower tables.

M. megapoda may be distinguished from *M. murrayi* by the uniform and large size of the pedicels and by the differences in the tables. In *M. murrayi* the disks are only 70-120µm across, and have more perforations.

***Mesothuria* sp. 1.**

Note: for all this information see Chapter 3, section 3.3.1 of this thesis.

Mesothuria multipes Ludwig, 1893

(Figures 110-115 in CD)

Mesothuria multipes Ludwig 1894: 31-34, Pl. 9, figs. 20-27; Sluiter, 1901b: 24-25; Koehler & Vaney, 1905: 10-11; 1910: 100; Clark, 1920; 143-144.
Mesites multipes Ludwig, 1893: 3.
Non *Mesites multiples* Ludwig, 1894: 31-34, Pl. 9, figs. 20-27 (see the fig. caption).
Mesothuria (*Mesothuria*) *multipes*, Heding, 1940: 333 (list).

Diagnosis (after Ludwig, 1894). Mouth subventral, anus ventral to subventral. Usually 20, sometimes 18-19 medium sized tentacles; whole body covered evenly with small, thin, cylindrical feet. Calcareous ring well developed. One Polian vesicle. One branched gonad on the left side of the mesentery. Respiratory trees well developed. **Ossicles**. Numerous ossicles in skin, fragile, tri-radiate tables. Disk of tables wheel-shaped mesh plate. In the simplest case the mesh is organised so that 6 peripheral holes surround a central round mesh. Of these 6, a small one alternates with a larger one. Ossicles of tubefeet supporting rods.

Material examined. See appendix 1, Table 32.

Type material. Holotype, USNM E9942; Syntypes, USNM 18279 (6 specimens); USNM E18280 (2 syntypes); Paratype, ZMUC (1 specimen).

Type locality. *Albatross* St. 3687, South Pacific Ocean, Society Islands, Tahiti, Point Venus, 17° 30'S, 149° 30'W, 1326m, 05 Oct 1899.

Geographic distribution. Indian Ocean, Near the Lacca dives and Ceylon; East Indies; off Panama to Peru (Madsen, 1953a). Cape Mala Point Aguja; Indo-West Pacific.

Bathymetric distribution. 724-4064m.

Biological information. On mud, ooze, sand, manganese and *Rhabdammina* substrates.

Remarks. This is the type species of the genus *Mesothuria*. Ossicles of Indian Ocean specimens reported by Koehler and Vaney (1905) possess taller table spires and a greater number of spines on its cusp than those from the Indo-West Pacific. The base of the spire has a greater number of peripheral holes.

Mesothuria multipora Clark, 1920

(Figures 116-121 in CD)

Mesothuria multipora Clark, 1920: 144, Pl. 4, figs. 11-13.

Mesothuria (*Allantis*) *multipora*, Heding, 1940: 333 (list) [new synonymy].

Diagnosis. Pedicels scattered all over the body, most sparse dorsally. Dorsal pedicels are present. The pedicels are much more numerous and twice as large at the posterior ventral end and in the area surrounding the mouth. Big cloaca, 20 tentacles disposed in two concentric circles. One Polian vesicle. One branched gonad with a conspicuous broad connection with the mesentery near the calcareous ring. **Ossicles**. Tables in the bodywall. There are all of the same type, but showing diversity chiefly in the number of perforations in the disk; spire with one cross-beam, the top bears about sixteen teeth; disk squarish, with a somewhat square central hole and thirty to fifty more or less circular perforations of small size.

Material examined. See appendix 1, Table 33.

Type material. Holotype, USNM E9942.

Type locality. In the original description (Clark, 1920: 144): *Albatross* St. 74. Tahiti: 4.8 miles N., 82ºW from Point Venus, 772(?) fm. In the Holotype label: *Albatross*, St. 3687, South Pacific Ocean, Society Islands, Tahiti, Point Venus, 17º 30’S, 149º 30’ W, 5 Oct 1899,1326m.

Geographical distribution. North East Pacific Ocean, Tahiti, Polynesia, South of Cook Islands.

Bathymetrical distribution: 600-1326m (?).

Remarks. Clark (1920) was unable to describe any internal character since the holotype consists only of bodywall. During my visit to the ZMUC (Apr 2002), I saw one specimen of this species named by Heding (labelled on the year 1943) as a "*M. danae* n. sp.", on a label, although he never formally described this species.

Mesothuria murrayi (Théel, 1886a)

Holothuria murrayi Théel, 1886a: 185-186, Pl. 10, figs. 16-18.

Mesothuria murrayi, Sluiter, 1901b: 24; Hérouard, 1902: 23-24; Fisher, 1907: 683-685, Pl. 71, figs. 1, 1a-h; Fisher, 1907: 683-685, Pl. 71, figs. 1, 1a-h; Hérouard, 1912: 23-24; Ohshima, 1915: 226; Hansen, 1956: 45-46, fig. 14b, d, e; Jangoux *et al*. 1989: 163 (list), 165-166, textfig. 3, figs. A-d.

Mesothuria murrayi var. *parva* Théel, 1886a: 186-187, Pl. 9, fig. 2; Pl. 16, figs. 4-5; Perrier, 1902; Augustin, 1908: 18-20, textfig. 14.

Mesothuria murrayi (var.?) Théel, 1886a: 187, Pl. 9, fig. 3.

Mesothuria murrayi var. *grandipes*, Hérouard, 1923 =*M.*(*Mesothuria*) *maroccana*.

Mesothuria parva, Ludwig, 1894; Fisher, 1907: 686-687, Pl. 71, figs. 2, 2a-c;

Ohshima, 1915: 226; Thandar, 1984: 341-343, textfig. 63; Thandar, 1992: 161-163, figs. 1a-h.

Mesothuria (*Mesothuria*) *murrayi* Théel, 1886a; Heding, 1940: 333 (list).

Mesothuria (*Mesothuria*) *parva* Ludwig, 1894; Heding, 1940: 333 (list).

Diagnosis (after Théel, 1886a). Body elongated, more or less distinctly cylindrical, with mouth and anus almost terminal. 20 tentacles. Each lateral ventral ambulacrum with numerous pedicels, the larger of which seem to form a continuous row along each side of the body; the remaining pedicels are of unequal size, and sparsely distributed over the adjacent interambulacra. The odd ambulacrum with numerous, very minute, almost imperceptible pedicels. Dorsal surface with few, small, and scattered papilla-like pedicels. The dorsal as well as the ventral interambulacra have only a few minute ambulacral appendages in their middle line. Perisome thin, flexible. Calcareous ring well developed. One Polian vesicle. Respiratory trees well developed. **Ossicles**. Tables, consisting of a more or less irregular, perforated disk, typically with six large holes round a central hole, and a spire built up of three rods and one transvers beam. The spire terminates in three rather long teeth, the free ends are spinous or branched.

Material examined. See appendix 1, Table 34.

Type material. Holotype, NHM 86.10.2.178; paratypes, NHM 86.10.2.176 (1 specimen), NHM 86.10.2.179 (2 specimens), NHM 86.10.2.177 (1 specimen).

Type locality. HMS *Challenger* St. 300, South East Pacific, 33° 42' S, 78° 18' W, 2502m, 17 Oct 1875.

Geographic distribution. Juan Fernandez, Hawaiian Islands; Japan; Indonesia; Philippines. West of Chile; of the Strait of Gibraltar; southeast of Flores, and Azores; Flores and Sulu Sea; Banda Trench (5° 18' S, 131° 18' E). Off Sta. Lucia Bay, Natal, South Africa.

Bathymetric distribution. 245-6550m.

Biological information. Habitat on fine sand, coral sand, lava specks, shells, *Globigerina* ooze, grey mud (Fisher, 1907).

Remarks. *Mesothuria murrayi* is closely related to two species: *M. rugosa* Hérouard and *M. maroccana* Perrier. *M. rugosa* and *M. maroccana* occur in the Atlantic with a depth-range of 1416-3890m and 909-3120m, respectively. The taxonomy of this species is rather intricate. *M. murrayi* was recorded also from the Atlantic, but according to Deichmann (1930) these records should be referred to *M. maroccana* and *M. rugosa*, all the safe records of *M. murrayi* are from the Pacific. The three species are distinguished by the ossicles and the distribution of the tubefeet, but both are very variable characters.

Mesothuria oktaknemus Sluiter, 1901a

Mesothuria oktaknemus Sluiter, 1901a: 14, 1901b: 27-28, Pl. 8, figs 5a-d; Cherbonnier & Féral, 1981: 373, textfigs 10a-l.
Mesothuria (*Allantis*) *oktaknemus*, Heding, 1940: 333 (list).

Diagnosis (after Sluiter, 1901a). Subcylindrical body, ventral side flattened, dorsal side curved. Skin rather soft and thick. Mouth ventral, anus terminal. 18 tentacles. Tubefeet distributed all over the body, only on the lateral ventral radii are numerous, thin and long, irregularly distributed. Calcareous ring weakly developed. One Polian vesicle. **Ossicles**. Exclusively tables of two different forms. Most table disks are 0.06mm in diameter, a large hole in the circle, and 8 smaller ones at the edge. Edge smooth, without thorns. Spire formed by 4 stems connected by a transverse beam. At the top of the spire, the 4 stems continue into long spiny extensions. No supporting rods in the tubefeet, only a small calcareous end plate is present.

Material examined. See appendix 1, Table 35.

Type material. Syntypes, ZMA E10042, (2 specimens).

Type locality. *Siboga* St. 211, 5º 40.7’S, 120º 45.5’E, 1158m.

Geographical distribution. Central Pacific.

Bathymetric distribution. 975-1158m.

Mesothuria oktaknemoides Heding, 1940

Mesothuria oktaknemoides Heding, 1940: 338-340, textfig. 6, figs. 1-15.

Diagnosis (after Heding, 1940). Mouth ventral, anus terminal. Tubefeet over the whole body, along the sides very long. 20 tentacles. Calcareous ring well developed. One Polian vesicle. **Ossicles**. Only small tables formed by three or four stems, table disk with usually only one circle of holes. No supporting rods are present in the tubefeet, but a calcareous end plate is present.

Material examined. See appendix 1, Table 36.

Type material. Holotype, ZMUC.

Type locality. *Valdivia* St. 219, Indian Ocean, 0° 2.3'S, 73° 24' E, 2253m, 20 Feb 1899.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 2253m.

Remarks. Heding specified on his paper that he review only one fragment but the holotype is an entire animal.

Mesothuria regularia Heding, 1940

Mesothuria (*Allantis*) *regularia* Heding, 1940: 121-122, textfig. 4.
Mesothuria regularia, Liao, 1997: 77-78, textfig. 42.

Diagnosis (after Heding, 1940). Mouth ventral to subventral, anus terminal. 20 tentacles. Papillae almost entirely over the whole body, absent only along the sides. Calcareous ring well developed. One Polian vesicle. **Ossicles**. Three or four pillared tables, with high spire. Tubefeet with no supporting rods, but with a calcareous end plate.

Material examined. See appendix 1, Table 37.

Type material. Holotype, ZMUC.

Type locality. *Valdivia* St. 203, Indian Ocean, off Sumatra, 1° 47.1'N, 96° 88.7' E, 660m, 4 Feb 1899.

Geographic distribution. Indian Ocean and off Zanzibar, Africa.

Bathymetric distribution. 448-1463m.

Mesothuria rugosa Hérouard, 1912

Mesothuria rugosa Hérouard, 1912: 1-3, textfig. 1; 1923: 19-21, Pl. 1, figs. 11-21, Pl. 2, figs. 1-2; Hansen, 1956: 46, fig. 14c; Deichmann, 1930: 98-99.
Holothuria murrayi, Théel, 1886a: 6, *partim*.
Mesothuria murrayi, Hérouard, 1902: 23.
Mesothuria (*Mesothuria*) *rugosa*, Heding, 1940: 333 (list).

Diagnosis (after Herouard, 1912). Oval body, flattened, presence of a ventral sole. Anus ventral, situated in a small depression. Body almost uniformly covered with very thin pedicels arranged in broad bands; these are absent in the mid-ventral ambulacrum. Gonads in one tuft situated at the right side of the dorsal mesentery. **Ossicles**. Tables with large disks, with numerous triangular or rectangular holes; spire high, ending in 3 arms, often of equal size, parallel with the axis of the spire and with some small teeth on the ends; in the tubefeet, typical small end plates and plates as in the bodywall, no supporting rods present in the tubefeet. Rim of the table disk strongly undulated and imperfectly developed.

Material examined. None.

Type material. Holotype, MOM.

Type locality. *Princesse-Alice* St. 1150, Near Cape Verde Islands, 3890m.

Geographic distribution. In the West Indies, off Guadeloupe and St. Vincent Islands.

Bathymetric distribution. 1600-3890m.

Mesothuria squamosa Koehler & Vaney, 1905

Mesothuria squamosa Koehler & Vaney, 1905: 13-14, Pl. 6, fig. 10, Pl. 9, figs. 10, 11.

Diagnosis (after Koehler and Vaney, 1905). The body is round and spindle-shaped; it is covered by many irregular protuberances that have a more or less flattened central area. Skin thick, flexible and spongy in appearance. Mouth subventral, anus sub-dorsal. Lateral parts of the body with appendices that extend along the lateral radii and the middle interradius. The ventral radius and the dorsal interradius are completely naked. Calcareous ring well developed. One Polian vesicle. One branched gonad placed at the left of the mesentery. **Ossicles**. Tables in the bodywall, three or four pillared. Disk table with a central opening and six to eight peripheral holes. Top of the spire formed by three short projections, each of them with one to three small spines. Papillae with the same kind of tables but smaller. Tubefeet with calcareous end plate.

Material examined. None.

Type material. Location unknown.

Type locality. *Investigator*, St. 280, Indian Ocean, 11° 29’ 45”N, 80° 02’ 36”E, 802m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 802m.

Mesothuria sufflava Cherbonnier & Féral, 1984

(Figures 122-123 in CD)

Mesothuria sufflava Cherbonnier & Féral, 1984: 661, figs. 1, a-h.
Mesothuria (*Penichrothuria*) *norfolkensis* Rowe, 1989: 260-261, figs. 1E-H; Rowe and Gates, 1995: 330 [new synonymy].

Diagnosis (emended). Thin and rough bodywall. The tubefeet are scattered over the body, but are most prominent along the ventro-lateral ambulacra. Ventral long, cylindrical tubefeet with big terminal plates (410-430µm diameter), arranged in 4 to 5 rows along the lateral radii, scarce in the interradial areas. Small tubefeet spread in the dorsal surface, with small terminal plates (220-310µm diameter). 16-17 tentacles, very stout, grey colour. Calcareous ring well developed, stout, with narrow interradial plates; radials plates with undulated posterior edge. Dorsal-lateral radial plates deeply notched posteriorly. One Polian vesicle, elongated, cylindrical. The madreporite lies to the right hand side of the dorsal mesentery. The gonad branched, with a single tuft on the left hand side of the dorsal mesentery. **Ossicles**. Bodywall with tables only. Supporting rods and perforated disc plates are additionally present in the tubefeet. Rarely in the tubefeet there are small, reduced tables. The tables of the dorsal bodywall have a disc diameter of 65-130µm, disc base with undulated edge. There is either a single peripheral ring of 8-10 holes or a inner ring of 8 larger holes alternating with a partial or complete outer ring hole of 4-10 holes. The spires are 52-75µm high and crowded with a ring of numerous small spines. The tables of the ventral bodywall are slightly smaller, with disc diameter up to about 112µm. The tables of the dorsal tubefeet are smaller with disc diameters ranging from 50-90µm and spires up to 52µm high. Otherwise, the tables have a similar appearance to those of the bodywall. The supporting rods are curved, perforated terminally and either side centrally. They are up to 187µm long. The end plates are up to 300µm in diameter. Small, irregular, reduced tables are present, but very few in number. Ossicles of the ventral and vetro-lateral tubefeet are similar, in all respects, to those of the dorsal tubefeet, except that the end plate of the ventro-lateral tubefeet have a diameter up to 550µm. Ossicles from the tentacles comprise more or less straight, or slightly curved, spiny rods. The largest on the stem, range in length and width up to about 400µm x 75µm, respectively. The smallest rods occur in the branches of the tentacles and range between about 60-120µm in length.

Examined specimens: see appendix 1, Table 38.

Type material. Holotype, MNHN EcHh 3043.

Type locality. South West Pacific Ocean, New Caledonia, 22º 45' S, 167º 14' 5''E, 395-400m.

Bathymetric distribution. 392-423m.

Geographic distribution. South West Pacific Ocean, New Caledonia, 22º 45' S, 167º 14' 5''E; Off Norfolk Island, Tasman Sea, 28º 57' 9" S, 167º 45' 5". This last record based of *M. norfolkensis* Rowe.

Biology notes: benthic, continental slope, detritus feeder, deposit feeder (Rowe and Gates, 1995).

Remarks. I reviewed the Holotype of *M. norfolkensis* and found no differences between this and *M. sufflava.* Both species came from same area and have a similar bathymetric distribution. *M. norfolkensis* has long flat rods as in *M. sufflava.*

Mesothuria triradiata Heding, 1942b

Mesothuria triradiata Heding, 1942b: 217-218, textfig. 1, figs. 1-6.

Diagnosis. Mouth ventral, anus terminal. Tubefeet spread all over the body. The ventro-lateral ones longer than the rest. Calcareous ring of the type typical of the genus and well developed. 20(?) tentacles of the same size. One large Polian Vesicle. Stone canal large, madreporite free in the cavity, round as a ball. **Ossicles**. Tables with 3 stems, short base. Terminal plate of the tubefeet irregular in shape, large and well developed.

Material examined. See appendix 1, Table 39.

Type material. Holotype, ZMUC.

Type locality. *Valdivia* St. 33, off Morocco, 24° 35' N, 17° 04'W, 2480m.

Geographic distribution. North East Atlantic Ocean, Off Morocco and off Africa.

Bathymetric distribution. 260-2480m.

Remarks. Heding (1942b) states that in general, this species resembles *Mesothuria maroccana*, but the ossicles are different. I would say thatit is more closely related to *M. intestinalis* because of body shape, tubefeet distribution and kind of body ossicles. One fragment was used by Heding to describe this species. However, I examined the holotype specimen and it is complete, with calcareous ring and some internal organs.

Mesothuria verrilli (Théel, 1886a)

(Figures 124-127 in CD)

Note: for all this information see Chapter 3, section 3.3.1 of this thesis.

Genus ***Paroriza*** Hérouard, 1902

Paroriza Hérouard, 1902: 25; Mortensen, 1927: 386; Deichmann, 1930: 112-113.

Diagnosis (after Hérouard, 1902). Body more or less cylindrical, slightly flattened on ventral side, with no marginal fringe, and no sole evident. 20 tentacles. Mouth ventral, anus ventral or subventral, sometimes, in a more or less distinct longitudinal furrow. No ambulacral tubefeet in the medium interradius. Tubefeet well developed, numerous, small, irregularly arranged over the whole body, ventral side with no tubefeet, but with irregularly distributed papillae. Dorsal papillae slender, scattered, straight curved or conical. Gonads on both sides of dorsal mesentery. Two respiratory trees. **Ossicles**. Lacking from bodywall, tentacles and any internal organs.

Type species: *Paroriza prouhoi* Hérouard, 1902 by monotypy.

Remarks. The genus is represented by 4 valid species.

Paroriza grevei Hansen, 1956

Paroriza grevei Hansen, 1956: 46-47, textfig. 15-17.

Diagnosis (after Hansen, 1956). *Paroriza* with the tentacles provided with cup-shaped discs, the edges of which are drawn out in four processes. The body in the larger specimens upwardly curved. The mouth is terminal, the anus subventral. In the larger specimens the body is characteristically upwardly curved. The tubefeet are conical and up to 5mm long. They usually form a more or less distinct double row along each ventro-lateral radius, but outside this double row they are scattered without any serial arrangement. The papillae are filiform and up to 10mm long. Along each dorsal radius a double row may be distinguished, but otherwise they are irregularly scattered. The ventral radius is naked in the larger specimens. Even up to a length of 160mm there are still some ventral tube feet present. The small specimens have a greater number of tube feet and papillae than the large specimens, not only in relation to the body-size, but total number too. In the large specimens the bases of the tube feet and papillae in the hindmost part of the body are very enlarged. Twenty Tentacles, all of the same size. The calcareous ring is well developed and consists of 10 pieces. The radial plates carry one median and two lateral ridges. The posterior edge of the radials is markedly curved inwards. The interradials pieces are more regular quadratic and have a undivided ridge in the middle of the plate.

Material examined. See appendix 1, Table 41.

Type material. Holotype, ZMUC; Paratypes, ZMUC (15 specimens).

Type locality. *Galathea* St. 495, South West Pacific Ocean, Banda Trench, 5° 26’ S, 130° 58’ E, 7250-7290m.

Geographic distribution. Only known from its type lolcality. Even when was also collected on *Galathea* St. 497, this station it is almost exactly the same as *Galathea* St. 495.

Bathymetric distribution. 6490-7290m.

Remarks. *P. grevei* differs from *P. prouhoi* Hérouard and *P. pallens* Koehler. They differ in size and distribution of the tube feet. In *P. pallens* they are all of the same size and evenly distributed over the whole of the body. *P. prouhoi* has small and large papillae scattered among each other, and the ventral radius is completely naked. In the general appearance the larger specimens of *P. grevei* are similar to *P. prouhoi.* Only two large specimens of *P. grevei* are known, both 230mm long. *P. prouhoi*, however, lacks the upward curvature of the body which is found in the larger specimens of *P. grevei*. This feature can be due to preservation method. Moreover, *P. grevei* is characterized by the peculiar shape of the tentacles. The tentacles differ from the usual aspidochirotid type in that the discs are more or less quadrangular, cup-shaped, with the edges drawn out in four processes.

Paroriza pallens (Koehler, 1895)

(Figure 128 in CD)

Stichopus pallens Koehler, 1895: 50-52, textfig. 15.
Paroriza pallens, Clark, H. L, 1922: 46 (list).

Diagnosis. Body fusiform, round, it is difficult to distinguish externally the dorsal from the ventral side. 20 tentacles. Mid-ventral radius with some scattered tubefeet. Body covered with ambulacral appendices having all the same form and the same size. These appendices are represented by short papillae, of which the largest are between 4 and 5mm long. They have, a widened base with a round end. There is no suction disk. One Polian vesicle. Two branched gonads. Respiratory trees well developed. The calcareous ring is constituted by 10 pieces. **Ossicles**. The ossicles are completely lacking, in the bodywall as in the ambulacral appendices and tentacles.

Material examined. See appendix 1, Table 42; appendix 2, Table 8.

Type material. Location unknown.

Type locality. *Caudan* St. 15, North Atlantic Ocean, 5º 22'N, 44º 2'W, 1300m.

Geographic distribution. North East Atlantic, from northern Spain, northwards to the Porcupine Seabight.

Bathymetric distribution. 1300-2900m.

Biological information. Pairing behaviour of this hermaphroditic species was observed by Tyler *et al.* (1992) at bathyal depths in the Bahamas and Porcupine Seabight and was considered to be related to reproduction. Khripounoff and Sibuet (1980) studied the feeding biology of *P. pallens* in the Gulf of Gascogne, France.

Paroriza prouhoi Hérouard, 1902

(Figure 129 in CD)

Paroriza prouhoi Hérouard, 1902: 24-25, Pl. 7, figs. 1-2, Pl. 8, fig. 30; 1923: 29-30, Pl. 2, figs. 3-4; Perrier, 1901: 323; Mortensen, 1927: 386; Deichmann, 1930: 112-113.
Mesothuria expectans Perrier, 1899: 245; 1902: 317-320; Deichmann, 1930: 92; Tortonese, E., 1949: 11 (list); Madsen, 1953a 168 (list).

Diagnosis (after Hérouard, 1902). Body subcylindrical, rounded at the posterior end, attenuated at the front. Skin thin. Mouth subterminal, ventrally directed. Anus ventral, subterminal. 20 tentacles, each one with 8-10 finger-like projections around the tip of each tentacles. The surface of the body is covered with pedicels, distributed in the ambulacral and interambulacral regions. Ventral face with small pedicels, uniformly distributed. On the sides of the ventral sole, papillae longer than the ventral ones. Dorso-lateral regions with two kinds of ambulacral appendices. Dorsal surface of the body covered with straight, curved, conical slender papillae. Papillae regularly spaced, more separated along the radial line. Midventral radius naked. Calcareous ring with a very marked apophysis. 1 Polian vesicle, 2 gonads. Respiratory trees small, well developed. **Ossicles**. No ossicles present in the bodywall or tentacles.

Material examined. See appendix 1, Table 43; appendix 2, Table 9.

Type material. Location unknown.

Type locality. *Princesse Alice*, St. 753, between Azores and Portugal, 4360m, year 1896.

Geographic distribution. North East Atlantic, from the Bay of Biscay and off the Azores, northwards to the Porcupine Seabight and the Mediterranean Sea.

Bathymetric distribution. 4080-4880m.

Biological information. The anemone *Kadosactis commensalis* have been reported to live on *P. prouhoi* (Bronsdon *et al.*, 1997).

Remarks. *Paroriza prouhoi* was described by Hérouard in 1902, but before that, Perrier described *Mesothuria expectans* in 1899. We know that *M. expectans* is a synonym of *P. prouhoi*. The priority rule indicates that the "real name" of *Paroriza prouhoi* should be *Paroriza expectans* (Perrier, 1899), but I consider that it is the best to keep the name as it is for the present.

Paroriza verrucosa Massin, 1987

(Figures 130-131 in CD)

Paroriza verrucosa Massin, 1987: 116-118, Text figs. 15-16.

Diagnosis (after Massin, 1987). Body fusiform. All the dorsal surface and the edges of ventral surface are covered with small warts. Ventral face smooth. The skin is thin. Mouth ventral, anus terminal. 16 tentacles, each one with 8 digitations. One Polian vesicle. Respiratory trees well developed. Massive calcareous ring. **Ossicles**. The ossicles are completely lacking in the skin and the tentacles.

Material examined. None.

Type material. Holotype, RMNH.

Type locality. *Snellius-II* St. 4276, North of Sumbawa, Sangar Bay, Indonesia, 8º 12'S, 118º 12'E, 750m (Massin, 1987).

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 750m.

Remarks. *P. verrucosa* differs from the rest of the species of the genus *Paroriza* in having only 16 tentacles. The other species possess 20 tentacles. If the number of tentacles (20) is a diagnostic character for the genus *Paroriza* Hérouard, 1902 it is necessary to modify the diagnosis of the genus to read "16-20 tentacles" (Massin, 1987) rather than "20 tentacles". Because the number of tentacles is variable during the ontogeny of this group, it is very likely that the two small specimens (the holotype 136mm) examined by Massin (1987) to erect this species were juveniles of *P. grevei*. They also share the same geographic distribution.

Genus ***Pelopatides*** Théel, 1886a [new comb.]

Pœlopatides Théel, 1886a: 154; Ludwig, 1889-1892: 332; Fisher, 1907: 693; Mortensen, 1927: 388; Deichmann, 1930: 104.
Perizona Koehler & Vaney, 1905: 51.
Bathyzona Koehler & Vaney, 1905: 53 [new synonymy].
Pelopatides, Perrier, 1902: 359-361; Koehler and Vaney, 1905: 29-30.

Diagnosis. Body more or less distinctly depressed, with a rather considerable brim surrounding it not only on the sides, but also round the extremities. Tentacles 15-20, peltate, or subdigitate on margin of the crown. Mouth ventral. Anus dorsal or subdorsal. The tubefeet form a double row along the odd ambulacrum, except on the anteriorly part where they are absent. The papillae form a simple row around the margin of the brim, and are, scattered along each of the two dorsal ambuacra as well. Interambulacra naked. Gonads on both sides of the dorsal mesentery. A *rete mirabile* is sometimes present. One or two Polian vesicles. Stone canals apparently lacking. No calcareous ring. **Ossicles**. Simple tri-radiate or quadri-radiate rods either smooth or spinous; with slightly branched tips; exceptionally deposits often entirely wanting.

Type species: *Pelopatides confundens* Théel, 1886a by monotypy.

Remarks. Perrier (1902) noted that Théel (1886a) spelt the genus name as *Pælopatides*; subsequent authors have hesitate using *Pælopatides* or *Pelopatides* (see Deichmann, 1930: 104). If we follow the ethymology (p????= loam or mud, pat??= to press) "*Pelopatides*" is the proper spelling (see Koehler and Vaney, 1905, 1910).

The species of this genus are sometimes difficult to distinguish owing to 1) the damage that the gelatinous body sustains during sampling and preservation, 2) the absence of both ossicles and a calcareous ring, and 3) the difficulty of preserving specimens in anything like their original shape.

Species of the genus *Pelopatides* are almost neutrally buoyant and have been observed from submersibles to swim by undulating their bodies (Pawson, 1976). A bottom photograph, taken using a combined trawl and forward-looking deep-sea camera system, clearly shows a large *Pelopatides* >40 cm long from 1942-1949m depth off the NW African coast (Rice *et al.*, 1979). It is interesting that the authors note that this specimen was not recovered in the trawl catch. These holothurians also appear to have a rather patchy distribution (Sibuet, 1977; Pawson, 1982; Gage *et al.*, 1985). This genus is composed of 19 valid species.

Pelopatides appendiculata Théel, 1886a

(Figures 132-133 in CD)

Pælopatides appendiculata Théel, 1886a: 158-159; Mitsukuri, 1912: 9-11; Ohshima, 1915: 232.
Pælopatides purpureo-punctatus Sluiter, 1901a: 8-9; 1901b: 43-44.

Diagnosis. Body fusiform, anterior and posterior ends rounded. The mouth is ventral and the anus is dorsal. 20 tentacles. On the ventral median ambulacrum, there are pairs of large pedicels. These are present nearly throughout the length of the body. There are about 17 pairs, but they are absent on the anterior part. On the outside of the median row, and about midway between it and the lateral edge, there is on each side two rows of large pedicels, one on each side of the mid-ventral radius, which extends over the posterior half of the body. Laterally there is a single row of large papillae arround the body; at the anterior end, this row of papillae is continuous passing dorsally to the mouth (19-20 papillae in this part), and, at the posterior end, ventrally to the anus. On the dorsal surface, the papillae are slender and are scattered. One or two Polian vesicles. Gonad tubes very long. Two respiratory trees well developed and almost reach the front of the coelomic cavity. No calcareous ring. **Ossicles**. No ossicles in the skin.

Material examined. See appendix 1, Table 44.

Type material. Syntypes, NHM 86.10.2.126.

Type locality. HMS *Challenger* St. 235, North West Pacific Ocean, off Japan, 34º 7'N, 138º 0'E, 1017m, 4 Jun 1875.

Geographic distribution. Honshu Island, Omae Zaki, Suruga Bay, off Kii, Honshu, Japan (Mitsukuri, 1912, Ohshima, 1915) and Bering Sea, Alaska.

Bathymetric distribution. 694-5349m.

Remarks. Théel (1886a) described this species based on three very macerated specimens. Additional specimens are housed in the collection of the Rijksmuseum van Natuurlijke Historie at Leiden, Netherlands (syntype of *Pelopatides purpureo-punctatus* Sluiter, 1901a), the collection of the Instituut voor Taxonomische Zoologie (University of Amsterdam) and in the collection of the Musée Océanographique de Monaco.

This is one of the most difficult species of *Pelopatides* to identify, owing to: 1) the total absence of both bodywall ossicles and a calcareous ring, and 2) the difficulty of preserving the specimens in anything like the original shape. The skin comes off almost entirely in shreds, exposing the white connective tissue and leaving the purple epidermis only as spots here and there on the surface. These purple points on the white surface form the striking feature of the specimens preserved in alcohol (Mitsukuri, 1912: 10). This last character is also presented by *Benthothuria funebris* when is preserved in alcohol. Mitsukuri (1912: 10) states that when alive, specimens can reach about 250mm length and 120mm broad, and when in alcohol, they reduced about 50% of their natural size.

Pelopatides atlantica Hérouard, 1902

Pelopatides atlantica Hérouard, 1902: 16, Pl. 1, fig. 15; 1923: 16; Mortensen, 1927: 388 (key); Deichmann, 1930: 106.

Diagnosis (after Hérouard, 1902). Body shape flattened dorso-ventrally. Dorso-lateral interradius with blunt papillae. 16(?) tentacles. Ambulacral tubefeet all over the dorsal radius, but are scarce. No regular pattern. Ventral side with no ambulacral tubefeet. 3 symmetrical pairs of tubefeet in the middle region of the medium radius, and 5 pairs in the inferior part of the ventro-lateral radius. A median furrow along the dorsal side. Dorsal papillae not arranged regularly. Ventral appendages are partly situated on the odd ambulacrum, partly on the lateral ambulacra. Calcareous ring well developed. 1 Polian vesicle. Respiratory trees well developed. 2 gonads, symmetrical on each side of the dorsal mesentery. **Ossicles**. No ossicles present.

Material examined. None.

Type material. Location unknown.

Type locality. *Princesse-Alice* St. 527, 38º N, 25º 5'W, East of São Miguel, Azores Islands, 4020m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 4020m.

Remarks. The species has never been collected again, and one suspects that the 140mm long holotype, from off the Azores, 4020m is a defective individual of *P. gigantea* also taken in these waters, and identified as *P. grisea*. The posterior midventral tubefeet have been lost and those indicated to be present laterally to the midline, may represent contractions which mimic feet. Also the low number of tentacles may be wrong, because they are often difficult to count. The deep violet colour of the body cavity may also be of little importance, as well as the supposed total lack of spicules.

Pelopatides confundens Théel, 1886a

(Figures 134-137 in CD)

Pelopatides confundens Théel, 1886a: 154-157, Pl. 9, fig. 7, Pl. 10, figs. 1, 7; Ludwig, 1894: 14-20, Pl. 1, figs. 9-24; Sluiter, 1901b: 39-40; Gage *et al.*, 1985; Miller and Pawson, 1990: 5.
Pelopatides agassizi Théel, 1886b: ?

Diagnosis. Body flattened and depressed, elongated, almost equally broad or slightly narrower posteriorly, with the anterior and posterior extremities obtuse and rounded. Mouth ventral. Anus dorsal. 19-20 tentacles. Brim surrounding the body with rounded low protuberances. The odd ambulacrum with a double row of fully retractile pedicels, excepting in its anterior third, which is naked. Each of the dorsal ambulacra with a simple row of short conical papillae. Calcareous ring absent?. 2 Polian vesicles. Respiratory trees well developed. Longitudinal muscles composed of two bands. **Ossicles**. Irregular three or four armed ossicles, with the ends of the arms slightly branched or pierced by a whole. The centre of each ossicle carries a strong vertical column, the flattened and dilated end of which is provided with long spines or processes.

Material examined. See appendix 1, Table 45.

Type material. Lectotype, NHM 1986.10.2.121 (1 specimen); Syntypes, NHM 1956.10.3.11 (1 specimen), NHM 1986.10.2.122 (2 specimens), NHM 1986.10.2.123 (1 specimen), NHM 86.10.2.124 (4 specimens).

Type locality. HMS *Challenger* St. 298, South East Pacific Ocean, off Chile, 34º 7’ S, 73º 56’ W, 4049m, 17 Nov 1875.

Geographic distribution. Pacific Ocean, from Monterey Bay, California to off Chile.

Bathymetric distribution. 450-4070m.

Biological information. On ooze-*Globigerina*, green and blue mud. Facultative swimmer (Miller and Pawson, 1990).

Remarks. In Hérouard's opinion this species is identical with *P. grisea* Perrier. According to Deichmann (in Mortensen, 1927: 388) it is probably identical with the West Indian *P. agassizi* Théel (which Ludwig erroneously identified with *P. confundens*). Ludwig (1893) suggested the synonymy of *P. agassizi* with *P. confundens*.

Pelopatides dissidens Koehler & Vaney, 1910

Pelopatides dissidens Koehler & Vaney, 1910: 94-95, Pl. 3, fig. 10.

Diagnosis (after Koehler and Vaney, 1910). Body flattened, ventral and dorsal faces slightly convex. Fringe very well developed. The anterior region is round and the posterior region is pointed. Anus dorsal, not terminal, mouth ventral, surrounded by 20(?) tentacles with terminal disks with 3 or 4 digitate tips. Pedicels in the mid-ventral radius. Respiratory trees well developed. **Ossicles**. No ossicles present.

Material examined. None.

Type material. Location unknown.

Type locality. *Investigator* St. 315, Indian Ocean, 10º 6'N, 92º 29'E, 1269m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 1269m.

Remarks. This species was described using a very small specimen, eviscerate (10mm long). It differs from *P. confundens* because the body shape and fringe are different, and because the absence of dorsal papillae and the very big ventral pedicels.

Pelopatides gelatinosa (Walsh, 1891)

(Figures 138-139 in CD)

Benthodytes gelatinosa Walsh, 1891: 200-202.
Pelopatides gelatinosa, Ludwig, 1893: 2.
Non "*Pelopatides gelatinosus*", Koehler and Vaney, 1905: 30-33, Pl. 5, fig. 5; Pl. 10, figs. 27-30.

Diagnosis (after Koehler and Vaney, 1905). Body shape flattened, dorsal face more convex than the ventral face. Mouth ventral. Anus dorsal. 20 tentacles, with 3 pairs of terminal tips, and few smaller internal tips. Around the body a fringe of marginal papillae join together at the basal part. In the anterior region this fringe forms a little ring around the mouth. About 20 papillae with a very large base and their extremities sometimes bifurcated. At the posterior end, the papillae of the fringe are very flattened and are joined together for much of their length. Median ventral radius with 2 sets of pedicels about 40 in number (sometimes 30-40). Dorsal radius papillae in rows, generally simple, approx. 20 papillae in each row. 2 Polian vesicles. Gonads in two tufts, formed by thin tubules, simple and unbranched. Respiratory trees well developed, present along the whole body length. **Ossicles**. In the tegument, rods, with branched extremities, tri-radiate ossicles with dichotomous ends. Some cross-like ossicles. Single spire with tips, large and perforated.

Material examined. See appendix 1, Table 46.

Type material. Holotype, NHM 1893.9.26.1. This specimen was donated by the Indian Museum of Calcutta to the British Museum.

Type locality. Indian Ocean, Andaman Sea off Port Blair, 2 Jan 1888, 487m.

Geographical distribution. Only known from the Indian Ocean.

Bathymetric distribution. 338-729m.

Remarks. Koehler and Vaney (1905) changed the name of *P. gelatinosa* to "*P. gelatinosus*" without any explanation. The priority rule in the Zoological Code states that you can transfer one taxa into another, but you have to use the species name. Because of this, the valid name of this species is *Pelopatides gelatinosa* (Walsh, 1891).

Ludwig (1893) was the first to suggest the inclusion of *Bathyplotes gelatinosa* into the genus *Pelopatides*. He criticized the classification of this species with the Elasipodida because of the presence of respiratory trees. He included the species in the genus *Pelopatides* because of the kind of ossicles and the presence of 15 tentacles. However, Koehler and Vaney (1905) found 20 tentacles in all the specimens they examined, including Walsh's type material.

P. gelatinosa differs from *P. confundens* in the presence of a marginal fringe formed by free papillae around the body. *P. confundes* has a continuous fringe.

Pelopatides gigantea (Verrill, 1884)

(Figures 140-141 in CD)

Benthodytes gigantea Verrill, 1884: 216; 1885: 538, Pl. 11, figs. 31 a-b; Grieg, 1921: 9, textfigs. 5-6.
Pelopatides agassizi Théel, 1886a: 3.
Pealopatides grisea Perrier, 1902: 381; Mortensen, 1927: 388.
Paelopatides gigantea, Deichmann, 1930: 104-106; Miller & Pawson, 1990: 5.

Diagnosis (after Verrill, 1884). Body flattened, broadly oval, with very broad lateral brim. Mouth ventral, tentacles very small, retracted into small pockets. Anus dorsal. Ventral midline for two-thirds of its length provided with small appendages; dorsal side likewise, with a few small, inconspicuous appendages along the ambulacra. Integument thick, gelatinous; the ossicles very rarely are abundant enough to give any roughness to the surface. Body cavity small and narrow, that does not extend into the lateral brim. No calcareous ring; one ventral Polian vesicle; one small dorsally attached stone canal. Respiratory trees well developed. **Ossicles**. Few present, only as large three-armed bodies with solid outer spire ending in a few teeth which are usually broken off; the arms are straight, but slightly inwardly bent and are provided with a few holes in their free end. No ossicles in the appendages; in tentacles there are several simple, pointed rods, smooth or with a few nodules.

Material examined. See appendix 1, Table 47; appendix 2, Table 10.

Type material. Location unknown.

Type locality. North Atlantic Ocean ?

Geographic distribution. North Atlantic Ocean, United States, Massachusetts, Nantucket Shoals; Azores and Canaries Islands (Deichmann, 1930; Pérez *et al*., 1984).

Bathymetric distribution. 2454-2653m.

Remarks. The species was originally described from off the coast of the United States, by Verrill, as *Benthothuria gigantea* close to the localities where Théel's *Pelopatides agassizi* was collected. The first of Verrill's three records must be misprinted, probably it was 70º 30'W instead of 10º 30'W. Deichmann (1930) studied Verrill's types and found that they have well-developed respiratory trees, and that the species was identical with Theel's *P. agassizi*. She also placed Perrier's *P. grisea* under Verrill's old name, *P. gigantea*. Ludwig, 1894 had the erroneous idea that Théel's *P. confundens*, was identical with *P. agassizi* while Perrier, made an effort to tabulate the differences between these two species.

Pelopatides grisea Perrier, 1899

(Figure 142 in CD)

Pelopatides grisea Perrier, 1899: 248; 1902: 361-365; Mortensen, 1927: 388; Heding, 1940: 351; Billett *et al.*, 1985: 407; Gage *et al.*, 1985: 195-196; Harvey *et al.*, 1988: 183; Miller & Pawson, 1990: 5.

Pelopatides gigantea, Deichmann, 1930 *partim*; Sibuet, 1977: ?; Miller and Pawson, 1990: 35.

Pelopatides sp., Pawson, 1976: 288, Pl. 1, fig. G.

Diagnosis (after Perrier, 1899). Body flattened, lateral fringes with very clear tubercle-like papillae. Fringe around the body, thick, broad continuous at the anterior and posterior ends. Tubercles very well developed on the fringe. Dorsal ambulacra with 16 papillae irregularly distributed in pairs. Mouth ventral, 20 digitate tentacles. Anus dorsal. 2 Polian vesicles. 2 gonads, very branched. **Ossicles**. Only three-armed ossicles in the bodywall, with bent arms. Stem shorter than the arms, one third of the arms length. Tip of the arms with irregular projections, or with an irregular mesh. 4 or 5 points at the end of the stem. Ambulacral appendages also have tri-radiate ossicles, smaller and simpler than in the bodywall. Some without central stem. No terminal disk on ambulacra. Rods in tentacles, slightly bent at both ends. Most of them straight and smooth.

Material examined. See appendix 1, Table 48; appendix 2, Table 11.

Type material. Holotype, MNHN 7144.

Type locality. *Talisman* St. ?, North East Atlantic, 1975m, year 1883.

Geographic distribution. From off the Canaries and between the Azores and Portugal. North East Atlantic, Rockall Trough and Porcupine Seabight (Gage *et al.*, 1985; Harvey *et al.*, 1988). Off Bahama Islands, Caribbean (Pawson, 1976).

Bathymetric distribution. 1695-4060m.

Biological information. Facultative swimmer. Grassle *et al* (1975) observed the species to be neutrally buoyant and swimming "with a 'flip-flop' motion over the bottom…". Seafloor photographs show the species swimming by sinusoidal undulations of the lateral brim (Miller and Pawson, 1990). Eggs grow to a size in excess of 1200µm (Gage *et al.*, 1985; Billett, 1991).

Remarks. Although Deichmann (1930), Billett *et al.* (1985) and Gage *et al.* (1985) considered *P. grisea* to be synonymous with the North West Atlantic species *P. gigantea* (Verrill, 1884), Heding (1940) believed that the two could be separated depending on the number of giant Polian vesicles. Like the holotype of *P. grisea*, the specimens reported by Gage *et al*. (1985) possessed two giant Polian vesicles, one of which is large while the other is of variable size, but generally small. As the number of Polian vesicles is the only known difference between *P. grisea* and *P. gigantea* and is a character of doubtful taxonomic significance, the NE and NW Atlantic forms of the holothurian may prove not to be specifically distinct when a thorough comparison can be made.

In the opinion of Hérouard this species is identical with *P. confundes* Théel. According to Deichmann (in Mortensen, 1927: 388) it is probably identical with the West Indian *P. agassizi* Théel (which Ludwig erroneously identified with *P. confundens*).

Pelopatides illicitus Sluiter, 1901a

(Figures 143-149 in CD)

Pelopatides illicitus Sluiter, 1901a: 9, 1901b: 45, Pl. 9, figs. 2a-c; 1901b: 45-46.

Diagnosis (after Sluiter, 1901a). Mouth ventral, anus terminal. Ventral side slightly flattened. Skin rather thin, leather-like. The middle ventral radius on the rear third with approximately 6 or 7 tubefeet. Calcareous ring missing. A very strong muscular pharynx. 2 Polian vesicles. Respiratory trees well developed. Gonads arranged in 2 unbranched tufts. **Ossicles**. On the ventral bodywall, curved spiny rods with dichotomised ends. Cross-shaped spiny ossicles.

Material examined. Cherbonnier's slide collection at the Natural History Museum in Paris France. 3 slides with Holotype material (ZMA E1034, *Siboga*, St. 18).

Type material. Holotype ZMA E1034.

Type locality. *Siboga* St. 18, South West Pacific Ocean, Indonesia, 7º 28.2'S, 115º 24.6'E, 1018m (see Jangoux, 1991).

Geographic distribution. Only known from its type locality.

Bathymetrical distribution: 1018m.

Remarks. The kinds of ossicles that this species possesses are completely different from any other synallactid. Related species are *P. megalopharinyx* and species of the controversial genus *Dendrothuria*. It is important to state that Sluiter described this species using a very small specimen, 110mm long, 22mm broad. Even though he found gonads on his specimen, he described it as an immature individual.

P. illicitus, *P. megalopharinyx* and the species of the genus *Dendrothuria* were described using very small individuals (approx. <200mm) and all they posses similar kinds of ossicles (spiny curved rods).

Pelopatides insignis Koehler & Vaney, 1905

Pelopatides insignis Koehler & Vaney, 1905: 38-39, Pl. 2, fig. 1, Pl. 11, figs. 22-23.

Diagnosis (after Koehler and Vaney, 1905). Body oval, flattened. Mouth ventral, prominent. Anus dorsal. Edge of the ventral sole limited by a continuous border of an undulating fringe. Elongated ventral papillae at the anterior and posterior part of the body. The medium ventral radius only have tubefeet in the posterior third, these tubefeet are arranged in 4 pairs. Dorsal radius with a double row of papillae. Each row with 11 short papillae along the whole length of the body. Tentacles (number?) with a disk with many tips. 2 Polian vesicles. **Ossicles**. In the marginal fringe simple rods, and some very spiny. Other with branched extremities.

Material examined. None.

Type material. Location unknown.

Type locality. *Investigator* St. 133, Bay of Bengal, Indian Ocean, 15º 43'30"N, 81º 19'30"E, 1220m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 1220m.

Remarks. Species closely related with *P. modestus*. They share the characters: oval body shape and presence of a marginal fringe, more or less undulated. Their ossicles are identical, but *P. insignis* have a rigid tegument and a lot of dorsal papillae, and *P. modestus* have a jelly tegument, and no indication of dorsal papillae. It is important to state that the presence/absence of the jelly tegument could be a preservation artefact.

Pelopatides mammillatus Koehler & Vaney, 1905

Pelopatides mammillatus Koehler & Vaney, 1905: 39-40, Pl. 1, fig. 7.

Diagnosis (after Koehler and Vaney, 1905). Dorsal and ventral face slightly convex. Fringe quite thick and large. Mouth ventral, anus dorsal. 12 tentacles (?). Tegument thick. Marginal fringe with a series of small conical papillae; in the anal region the papillae are less distinct. Anal ring with lobes. Middle ventral radius with 3 or 4 pairs of pedicels only in the posterior third part of the body. Respiratory trees well developed. 2 Polian vesicles. Dorsal papillae in 4 rows. **Ossicles**. No ossicles present.

Material examined. None.

Type material. Location unknown.

Type locality. *Investigator* St. 287, Arabian Sea, Indian Ocean, 21º 8’30”N, 65º 47’E, 2710m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 2710m.

Pelopatides megalopharynx Sluiter, 1901a

(Figures 150-154 in CD)

Pelopatides megalopharynx Sluiter, 1901a: 7; 1901b: 40-42.
Dendrothuria megalopharynx, Koehler & Vaney, 1905: 45.

Diagnosis (after Sluiter, 1901a). Ventral side flattened, dorsal side arched. Bodywall quite thin, but moderately firm. A fringe of fused papillae with a broad base surrounds the whole body. No tubefeet or papillae, neither dorsally nor ventrally. Mouth surrounded by a broad perisome. 20 tentacles of dendritic appearance. A big well developed gut, occupying most of the body. Two Polian vesicles. The stone canal runs to the front of the dorsal mesentery, and the madreporite is fixed inside the bodywall. Two gonad tufts slightly branched, one on each side of the dorsal mesentery. Respiratory trees well developed. No calcareous ring. **Ossicles**. Present only in the tentacles as rods; rods found in the ventral tentacles are more than twice as long as those of the dorsal tentacles.

Material examined. Cherbonnier’s slide collection at the Natural History Museum in Paris France. 3 slides with syntype material (ZMA E1039, *Siboga* St. 38).

Type material. Syntypes, ZMA E1039 (2 specimens)

Type locality. *Siboga* St. 38, 7º 35.4’S, 117º 28.6’E, 521m (see Jangoux, 1991).

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 521m.

Remarks. Sluiter (1901a) described this species using 2 small specimens of 133 and 143mm long and about 32mm wide. He stated that his specimens lacked tubefeet on the mid-ventral radius.

Pelopatides modestus Koehler & Vaney, 1905

Pelopatides modestus Koehler & Vaney, 1905: 37-38, Pl. 2, fig. 2, Pl. 11, figs. 24-26.

Diagnosis (after Koehler and Vaney, 1905). Very flattened body. Fringe around the body formed by papillae more or less separated and slightly joined at their base. Ventral sole. Along the odd radius there is a row of pedicles on the posterior third. Pedicels with terminal disks. Pedicels are scattered but as they get closer to the posterior extremity they become more numerous. Mouth ventral, quite distant from the anterior edge. 16 tentacles, with 3 pairs of digitations in the tips. Anus dorsal, situated in the posterior region. **Ossicles**. In papillae on the margin are of two kinds: Spiny-thin branched rods and smooth-thick branched rods. Tri-radiate ossicles with projections at the distal ends. Pedicels in the mid-ventral radius only present in the posterior half.

Material examined. None.

Type material. Location unknown.

Type locality. *Investigator* St. 224, Indian Ocean, 13º 50’30”N, 93º 26’E, 896m.

Geographic distribution. Arabian Sea, Indian Ocean.

Bathymetric distribution. 896m.

Remarks. This species is related with *P. aspera* because the flattened appearance, but differing because the fringe is formed by an undulating fringe. *P. modestus* has 20 tentacles, and *P. aspera* has 16.

Pelopatides mollis Koehler & Vaney, 1905

Pelopatides mollis Koehler & Vaney, 1905: 34-35.

Diagnosis (after Koehler and Vaney, 1905). Body slightly flattened. Tegument soft and quite thick. Mouth ventral, anus dorsal, largely opened. 20 tentacles, tentacle disk with 6 terminal tips. Ventral sole slightly convex with a distinct edge. A row of small appendices very clear, about 30 marginal papillae on each side. In the anterior region the peribucal ring is very well developed and has about 20 small papillae. In the posterior region, the marginal papillae form a sub-anal fringe. Mid-ventral radius with 40 pedicels in two rows in the posterior two thirds of the body. Each dorsal radius with 20 small papillae arranged in one row. Respiratory trees well developed, extending anteriorly with numerous ramifications. 2 Polian vesicles. **Ossicles**. No ossicles in any part of the body.

Material examined. None.

Type material. Location unknown.

Type locality. *Investigator* St. 116, Indian Ocean, Bengala Bay, 11º 25’5”N, 92º 47’6”E, 477m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 477m.

Remarks. This species is closely related with *P. gelatinosa* but they differ in the presence of a marginal fringe formed by many papillae and the complete absence of ossicles in the bodywall.

Pelopatides ovalis (Walsh, 1891)

Benthodytes ovalis Walsh, 1891: 200; Koehler & Vaney, 1905: 35-36, Pl. 3, figs. 6-7, Pl. 11, figs. 1-4; O'Hara, 1998: 206 (note on key).

Diagnosis (modified from Walsh, 1891 and after Koehler and Vaney, 1905). Body oval, flattened, about twice as long as broad. Dorsal surface slightly convex. A well-developed continuous fringe all around the body. On the periphery of the body there are some small papillae that are visible from the ventral side, especially in the anterior region and in some part of the lateral regions. Mouth slightly prominent, ventral. Anus dorsal. A double row of tubefeet on the middle ambulacrum of the trivium. Dorsally one pair of big dorsal papillae near the medium line. Lateral ambulacra with a single row of feet. Respiratory trees well developed, occupying the anterior extremity of the body. 2 Polian vesicles. One gonad tuft. **Ossicles**. Small tri-radiate ossicles with the end of each arm clubbed and perforated. Dorsal papillae with tri-radiate ossicles, and straight rods, slightly arched with bifurcated ends, sometimes with lateral projections.

Material examined. None.

Type material. Location unknown.

Type locality. Indian Ocean, Bay of Bengal, Andaman Sea, 7.5 miles East of North Cinque Islands, 882m, 12 Apr 1888.

Geographic distribution. Indian Ocean, Bay of Bengal, Andaman Islands; South West Pacific Ocean, Australia, east of Cape York, in the Coral Sea (O'Hara, 1998). O'Hara

(1988) states that this species were collected near Macquarie Island (54º 46.2’ S, 158º 42’ E), 930-815m, 17 Jan 1995, Id: O’Loughlin. Specimen NMV F80184.

Bathymetric distribution. 815-930m.

Pelopatides quadridens Heding, 1940

Pelopatides quadridens Heding, 1940: 351-353, textfig. 15, figs. 1-5.

Diagnosis. Body flattened, with convex dorsal side. Mouth ventral, anus dorsal. Tubefeet difficult to recognise (while in contracted specimens they are easily seen). Mid-ventral tubefeet alternating in two rows. Dorsal papillae in two rows, distributed along the dorsal ambulacra. Anal area with four large, lateral, soft anal teeth. Calcareous ring missing. Two Polian vesicles. The respiratory trees are well developed and very branched. **Ossicles**. In bodywall, small tri-radiate bodies united by a stem that has 3-4 small spines on its top.

Material examined. See appendix 1, Table 49.

Type material. Holotype, ZMUC.

Type locality. *Valdivia* St. 203, Indian Ocean, Indonesia, Nias Channell, 1º 47.1’ N, 96º 58.7’E, 660m, 4 Feb 1899.

Geographical distribution. Indian Ocean, Indonesia, Nias Channell; West Sumatra.

Bathymetric distribution. 660-3035m.

Pelopatides retifer Fisher, 1907

Pelopatides retifer Fisher, 1907: 693-694; Miller and Pawson, 1990: 5, 8-10, figs. 1b, 3.

Diagnosis (after Fisher, 1907). Body short and stout. Ventral surface more or less flattened, the dorsal surface markedly convex. Bodywall thick and jelly-like in life. Mouth ventral, anus dorsal. Mid-ventral radius with a double row of spaced pedicels (about 28), which extend about two-thirds length of animal, from the posterior end. Along each ventro-lateral radius there is a series of about ten rather large pedicels, which extend from posterior end to about middle of body. Above these on the edge of body is a single continuous series of papillae, which form a conspicuous brim only at anterior and posterior extremities, above mouth and below anus, respectively. Along each dorsal ambulacrum is a fairly regular series of widely spaced, slender papillae usually difficult to discern. Tentacles 19 to 20, rather large; crown sub circular, fleshy; four or five times divided, peltate. An extensive *rete mirabile* present. **Ossicles**. No calcareous deposits.

Material examined. See appendix 1, Table 50.

Type material. Holotype, USNM E21218. Paratype, USNM E30407 (1 specimen).

Type locality. *Albatross* St. 4151, North Pacific Ocean, Nihoa Island, Hawaii, 23º 05'N, 161º 52'W, 572-1463m, 05 Aug 1902.

Geographic distribution. Off Molokai, Bird (Mokumanu), Kauai, Hawaii, Niihau, off Oahu, off Kailua-Kona, Hawaiian Islands (Fisher, 1907; Miller and Pawson, 1990).

Bathymetric distribution. 405-1900m (Miller and Pawson, 1990).

Biological information. This species is facultative swimmer. Miller and Pawson, (1990) made a complete description of its swimming behaviour. It lives on fine coral and foraminiferan sand.

Remarks. Stasek (1966) states that the CAS 021364 specimen correspond to *Albatross* St. 4110. And *Albatross* station 4110 is: Kaiwi Channel, between Molokai and Oahu islands, 449 to 460 fathoms, gray sand. This specimen is not a Paratype or a Cotype.

Pelopatides solea Baranova, 1955

Pelopatides solea Baranova, 1955: 342, fig. 6; 1957: 238-239, textfig. 19; Baranova & Kuntsevitch, 1977: 116.

Diagnosis (after Baranova, 1955). Body shape oval. Ventrally flattened, dorsal side curved. Anterior and posterior body ends rounded. Mouth ventral, anus dorsal. 20 tentacles. A lateral fringe surrounds the body, more visible at the front and the back of the body. Papillae on the mid-ventral ambulacrum. In the dorsal side a well-defined furrow, starting behind the back of the mouth and extending to the fringe at the posterior end. No calcareous ring. Two Polian vesicles. Respiratory trees well developed. **Ossicles**. Three-armed bodies with a thin and long central stem. At the end of the ossicle arms and in the central stem, there are few branches with one or three holes.

Material examined. None.

Type material. Holotype, ZIAS 1/13938; Paratypes, ZIAS 2/13939; ZIAS 3/13940 (after Baranova and Kuntsevitch, 1977).

Type locality. Pacific Ocean, Cape Navarin, Commander Islands, Russia, Bering Sea.

Geographic distribution. Only know from its type locality.

Bathymetric distribution. 2220-2416m.

Pelopatides suspecta Ludwig, 1894

Pelopatides suspecta Ludwig, 1894: 20-21.

Diagnosis (after Ludwig, 1894). Mouth ventral, anus dorsal. 15 tentacles. A continuous fringe with long papillae. Dorsal papillae only on the two dorsal radii. Tubefeet on the mid-ventral radius. Two Polian vesicles. Gonads in two tufts. No calcareous ring present. **Ossicles**. No ossicles in the bodywall. A few three armed ossicles in tubefeet, tentacles and papillae.

Material examined. See appendix 1, Table 51.

Type material. Holotype, USNM E18174.

Type locality. *Albatross* St. 3392, North Pacific Ocean, Azuero Peninsula, Gulf of Panama, 07º 05' 30"N, 79º 40'W, 2311m (holotype label reads "2322m").

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 2311m.

Biological information. This species inhabits *Rhabdaminna* substrates.

Pelopatides verrucosus Koehler & Vaney, 1905

Pelopatides verrucosus Koehler & Vaney, 1905: 33-34, Pl. 10, figs. 25-26; 1910: 100.

Diagnosis: (after Koehler and Vaney, 1905). Body sub-cylindrical, ventral face convex. Mouth ventral, sub-terminal. Anus dorsal. Big conical papillae restricted to the fringe, terminating in a long tip. Mid-ventral radius with big pedicels arranged in 2 longitudinal rows. They extended over little more than the posterior one third of the body. Towards the posterior region, between the middle rows and the marginal rows there are 2 or 3 pairs of interradial pedicels. Each dorsal radius with a row of big conical papillae, about 15 on each radius. 15 tentacles with tentacular discs with 4 tips. Respiratory trees well developed. 2 Polian vesicles. **Ossicles**. In tentacles like those from *Pelopatides confundens*. Rods in the mid-ventral pedicels, with bifurcated extremities, in the middle part 1 or 2 short projections. There are also tri-radiate ossicles with extremities more or less branched.

Material examined. None.

Type material. Location unknown.

Type locality. *Investigator* St. 202, Indian Ocean, 7º 4’40”N, 82º 2’45”E.

Geographic distribution. Only known from the Indian Ocean.

Bathymetric distribution. 896-1251m.

Genus ***Pseudostichopus*** Théel, 1886a [new comb.]

Pseudostichopus Théel, 1886a: 169; Ludwig, 1893: 2; 1889-1892: 331; Perrier, 1902: 332-333; Fisher, 1907: 691; Mitsukuri, 1912: 3; Hérouard, 1923: 23; Deichmann, 1930: 86; Heding, 1940: 356, 358-360; Imaoka, 1978: 377-378; Thandar, 1992: 163.
Meseres Ludwig, 1893: 3; 1894: 34, 36, 38; O'Loughlin, 2002: 303-305.
Molpadiodemas Heding 1935: 77-78; Heding, 1940: 357; Deichmann, 1940: 209-211.
Trachostichopus Heding, 1940: 357, 361; Imaoka, 1978: 380; 1990: 152 [new synonymy].
Plicastichopus Heding, 1940: 357; 1942a: 5-6 [new synonymy].
Platystichopus Heding, 1940: 358 [new synonymy].
Peristichopus Djakonov, 1952: 125 [new synonymy].

Diagnosis. Body cylindrical or slightly flattened on the ventral side, which does not form a ventral sole and is usually not separated from the dorsal side by a marginal brim. Mouth subterminal, anus hidden in a distinct vertical furrow. 19 or 20 tentacles. Ambulacral appendages cylindrical, or conical, small and numerous especially on the back and sides of body, often distributed in pairs which gives the aspect of a serial arrangement. Stone canal connected with bodywall, sometimes perforating it; in other species apparently absent. Genital openings placed on the boundary between the first and second third of body; genital organs forming two symmetrical tufts, one on each side if dorsal mesentery. Calcareous ring often well developed. Anal retractors originating from paired ambulacra one, permitting the longitudinal muscle of the odd ambulacrum to contract the anal region into a deep furrow. **Ossicles**. Rarely found or completely lacking.

Type species: *Pseudostichopus mollis* Théel, 1886.

Remarks. Several authors have stated the great difficulty in the taxonomy of this genus (Deichmann, 1940, O'Loughlin, 2002) and its complexity demands very detailed work. No study has been conducted on the whole genus since its creation in 1886. This is the first attempt to review the genus *Pseudostichopus* as a whole, including all its morphologically similar taxa such as *Meseres*, *Molpadodiademas*, etc. After reviewing the diagnosis of the subgenera *Peristichopus* Djakonov, *Plicastichopus* Heding, *Platystichopus* Heding, *Trachostichopus* Heding, in comparison with the genus *Pseudostichopus* Théel, I can state that these taxa share exactly the same body shape, the presence of a vertical furrow, form of calcareous ring, shape of tentacles and kinds of ossicles. On basis of the similarities, I have synonymised the subgenera *Peristichopus* Djakonov, *Plicastichopus* Heding, *Platystichopus* Heding, *Trachostichopus* Heding with the genus *Pseudostichopus* Théel.

After reviewing the type species of the genus *Molpadiodemas* Heding, 1935, (*M. acaudum* Heding, 1935, ZMUC, *Ingolf*, St. 37, 60º 17'N, 54º 05'W, 3230), I can state that it is synonymous with *Pseudostichopus trachus* Sluiter, 1901a, because of 1) they share the same kind of body shape, 2) the distribution of pedicels on the body, 3) the same kind and shape of ossicles in the tentacles, and 4) identical calcareous ring shapes. The genus *Meseres* was erected by Ludwig in 1893 to include in the type species *M. macdonaldi.* On his diagnosis of the type species, Ludwig (1893) left diagnostic characters incompletely known, because of this, the genus *Meseres* has been a taxonomic problem for the past one hundred years. It has been synonymised under *Pseudostichopus* by different authors and recently O'Loughlin (2002) included it as a valid and separated genus.

The taxonomic differentiation between *Meseres* and *Pseudostichopus* proposed by O'Loughlin (2002) is very difficult and ambiguous. The taxonomic characters proposed by O'Loughlin, such as the softness of the bodywall and "distinct lateroventral margin" are too variable and often dependent on the preservation method. However, *P. aemulatus* sp. nov. is "softer" than *P. villosus*. Using the O'Loughlin criterion *P. aemulatus* might be more appropriately attributed to *Meseres*, but the molecular analysis does not bear this out. Unless there is good alpha and molecular taxonomic evidence to the contrary, there is no sufficient evidence to support *Meseres* and *Pseudostichopus* as separated genera.

Pseudostichopus **sp. 1.**

Note: for all this information see Chapter 4, section 4.3.1 of this thesis.

Pseudostichopus aleutianus Ohshima, 1915

Pseudostichopus aleutianus Ohshima, 1915: 228, Pl. 8, figs. 5a-c; Baranova, 1957: 239.
Pseudostichopus (*Trachostichopus*) *aleutianus* Heding, 1940: 357 (list).
Not *Pseudostichopus unguiculatus*, Liao, 1997: 81.

Diagnosis (after Ohshima, 1915). Body flat and elongated, rounded at both extremities. Mouth ventral, anus lodged in a vertical furrow. 20 tentacles. Pedicels of ventrolateral ambulacra largest, forming a double row. Scattered smaller papillae(?) forming a double row along each dorsal radius. Minute pedicels scattered on the mid-ventral ambulacrum, as well as on all interambulacra. Polian vesicle single. Gonads unbranched. Respiratory trees well developed. **Ossicles**. No deposits are found in general perisome or in respiratory trees. Cross shaped ossicles present in the walls of the gonads. Around the anus irregular, cross shaped ossicles and irregularly shaped rods are thinly scattered. Larger pedicels have end plates. Supporting rods of tentacles slender and bent, with low processes and often-slitlike perforations.

Material examined. None.

Type material. Holotype, USNM E34147 (lost?).

Type locality. North East Pacific Ocean, Aleutian Islands.

Geographic distribution. North East Pacific Ocean, Bering Sea, Aleutian Islands.

Bathymetric distribution. 557-1400m (Ohshima, 1915; Baranova, 1957).

Remarks. *P. aleutianus* resembles *P. occultatus* in the presence of the cross-shaped ossicles in the gonads, but differs in the absence of ossicles from respiratory trees and in the character of the ossicles in the perianal region.

Pseudostichopus arenosus Ohshima, 1915

Pseudostichopus arenosus Ohshima, 1915: 229, Pl. 8, figs. 5a-c.
Pseudostichopus (*Trachostichopus*) *arenosus* Heding, 1940: 357 (list).

Diagnosis (after Ohshima, 1915). Body more or less fusiform. Mouth terminal but directed ventrally, anus situated in a vertical furrow. 20 tentacles. Conspicuous rows of ambulacral appendages along dorso-lateral and lateral ambulacra. Along the odd ambulacrum no distinct row of pedicels can be found. Calcareous ring well developed, radials being very thick. Polian vesicle single. Undivided gonads arranged in two tufts. Respiratory trees well developed. **Ossicles**. Irregular spinous bodies similar to those in *P. molpadioides,* found scattered in the perianal region. Pedicels with end-plates. Supporting rods in tentacles bear numerous knobs. No other ossicles.

Material examined. None.

Type material. Holotype, USNM E34149 (lost).

Type locality. *Albatross* St. 4915, Off Koshiki Islands, west of Kyushu, Japan, 31º 31’N, 129º 25’30”E, 427m, 12 Aug 1906.

Geographic distribution. Only known from the type locality.

Bathymetric distribution. 427m.

Remarks. *P. arenosus* Ohshima resembles *P. molpadioides*, differing only in the absence of supporting rods in pedicels and in details of rods in tentacles.

Pseudostichopus depressus Hérouard, 1902

Pseudostichopus depressus Hérouard, 1902: 15-16, Pl. 2, fig. 15-18; Perrier, 1901: 337; Mortensen, 1927: 387; Deichmann, 1930: 88.
Pseudostichopus (*Pseudostichopus*) *depressus* Hérouard, 1902; Heding, 1940: 359 (key) [new synonymy].

Diagnosis (after Hérouard, 1902). Body flat. A broad, thick marginal brim in the anterior half of body (integument cartilaginous, specially in the small specimens). Mouth ventrally directed, anus in a very distinct vertical furrow. Madreporite large, externally visible as an oval impression on the dorsal side; the attachment of the stone canal is visible on the outer side. Appendages very visible in a broad band along mid-ventral ambulacrum, where they are quite distinct; if appendages are present on other parts of the integument they are extremely small. **Ossicles**. No calcareous deposits have been detected in any part of the body.

Material examined. None.

Type material. Location unknown.

Type locality. *Princesse-Alice* St. 753, North East Atlantic, between Portugal and Azores, 4360m.

Geographic distribution. This is a remarkable rare species hardly ever found. North East Atlantic Ocean, between Portugal and Azores and from the coast of South America, *Albatross* St. 2127, 39º 54’N, 20º 17’W (Deichmann, 1930). North East Atlantic, 40º N, 20º 5’W; 20º N, 75º W (Madsen, 1953).

Bathymetric distribution. 2995-4360m.

Pseudostichopus dilatorbis Imaoka, 1978

Pseudostichopus (*Pseudostichopus*) *dilatorbis* Imaoka, 1978: 378-380, Figs. 1a-e.

Diagnosis (after Imaoka, 1978). Dorsal side of the body arched, ventral side flat. Mouth ventral, near the anterior end of the body. The anus is situated on the ventral side at the bottom of the vertical furrow. Plain anal margin. 20 tentacles. Minute ambulacral appendages in double rows along the mid-ventral and the dorsal ambulacra, while irregularly in a single row along the ventro-lateral ambulacrum. Appendages near the posterior end become larger with the increasing body size. One Polian vesicle. Branched gonads in two tufts, Respiratory trees well developed. Longitudinal muscles in single bands. Calcareous ring with large radial pieces, with antero-lateral “wings”. Interradials narrow. **Ossicles**. Curved and bifurcated rods only find in the larger appendages near the posterior ventral end of the body. No ossicles are present in the rest of the external or internal parts of the body.

Material examined. None.

Type material. Holotype, SMBL Type-309; Paratypes, SMBL Type-310 (2 specimens).

Type locality. Shimo-Koshiki Island off the west coast of Kyushu Island, Japan, 400-450m, 27 Oct 1976.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 400-450m.

Biological information. This species has been found covered by sand, foraminiferan shells and ossicles of glass sponges. In a large specimen (119mm) some bryozoans, brachiopods, gastropods, bivalves and even an ascidian were found attached to the body surface (Imaoka, 1978). Eggs are 226-444µm in diameter, 359µm on an average (Imaoka, 1978).

Remarks. *P. dilaturbis* is related with *P. nudus* Ohshima in the presence of rods in the ventral tubefeet. *P. dilatubis* lacks ossicle in the tentacles and *P. nudus* posseses big and small spiny rods in the tentacles.

Pseudostichopus echinatus Thandar, 1984

Pseudostichopus (*Pseudostichopus*) *echinatus* Thandar, 1984: 345-349, textfig. 64; 1992: 164-167, textfig. 2; 1992: 164-167, Figs. 2a-c.

Pseudostichopus (*Pseudostichopus)* sp. Heding, 1940: 360, textfig. 16.

Non *Pseudostichopus* (*Trachostichopus*) *trachus*, Heding, 1940: 361, textfig. 17 (=*P. echinatus*).

Diagnosis (after Thandar, 1992). A medium sized species up to 65mm long. Bodywall incrusted with shells, foraminiferans, sand grains, etc. Tentacles 17 (?). Podia scattered, only slightly longer in ventro-lateral radii. Stone canal rudimentary or absent. **Ossicles**. Ossicles restricted to tentacles, in the form of large (up to 0.3mm), irregularly knobbed rods. Bodywall, podia, respiratory trees and gonad with no ossicles.

Material examined. See appendix 1, Table 52.

Type material. Holotype, SAM-A23435.

Type locality. SAM, R.V. *Meiring Naude*, SM 38, Indian Ocean, off Natal Coast, 28º 21’ 9” S, 32º 34’6” E, 28 May 1975, 775-825m, beam trawl.

Geographical distribution. Indian Ocean, off Natal Coast; Tanzania; Zanzibar Island.

Bathymetric distribution. 640-825m.

Remarks. This species is closely related with *P. trachus*.

Pseudostichopus hyalagerus (Sluiter, 1901a)

(Figures 155-157 in CD)

Meseres hyalagerus Sluiter, 1901a: 12, 1901b: 50-51, Pl. 5, fig. 2-4; Jangoux & De Ridder, 1987: 85 (list); O'Loughlin, 2002: 305-306.

Diagnosis (after Sluiter, 1901a). Ventral surface flattened, dorsal surface curved. Tubefeet very soft, thin and long, irregularly distributed all over the body, only in the flanks more numerous. Mouth and anus ventral. 15 tentacles. Calcareous ring well developed, approximately as in *P. involutus*. One Polian vesicle. Two gonads. **Ossicles**. Present in the tubefeet and tentacles as supporting rods. Lack of ossicles in the rest of the body.

Material examined. Cherbonnier's slide collection at the Natural History Museum in Paris France. 3 slides with ZMA material.

Type material. Holotype, RMNH ref. number 1928, Syntypes: ZMA E2177/1 (7 specimens), ZMA E2177/2 (1 specimen); ZMA E2492 (1 specimen).

Type locality. *Siboga* St. 251, South West Pacific Ocean, Indonesia, 5º 28.4' S, 132º 0.2' W, 204m (see Jangoux and De Ridder, 1987).

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 20-204m.

Remarks. Additional type specimens are housed in the collection of the Instituut voor Taxonomische Zoologie (University of Amsterdam) (Jangoux and De Ridder, 1987). The first name "*Meseres hyalegerus*" was probably a misspelling because later on Sluiter (1901b) used the name *M. hyalagerus*.

Pseudostichopus involutus (Sluiter, 1901a) [new comb.]

Meseres involutus Sluiter, 1901a: 11-12; 1901b: 49-50, Pl. 8, fig. 6; O'Loughlin, 2002: 306-307, fig. 2e [new synonymy].

Diagnosis (after Sluiter, 1901a). Ventral surface flattened, dorsal surface curved. Skin thin. Ventral surface with thin tubular tubefeet irregularly distributed, most conspicuous laterally. Mouth and anus ventral. 15 tentacles. Calcareous ring well developed. One Polian vesicle. 2 gonads. **Ossicles**. Elaborated perforated oblong plates and rods in the tentacles. Tubefeet with supporting rods.

Material examined. None.

Type material. Syntypes ZMA.

Type locality. *Siboga* St. 173, Indonesia, Seram Sea, 3º 27'S, 131º 01'E, 567m.

Geographic distribution. Indonesia and eastern Australia, Tasman Sea (O'Loughlin, 2002).

Bathymetric distribution. 567-3058m.

Remarks. *P. involutus* is closely related to *P. peripatus*. *P. involutus* is distinguished from *P. peripatus* by the form of the tentacle ossicles (include elongate, curved, distally tapered rods with mesh-like perforations); by branched gonad tubules and the absence of ossicles in the gonads.

Pseudostichopus japonensis Imaoka, 1978

Pseudostichopus (*Trachostichopus*) *japonensis* Imaoka, 1978: 382-384, figs. 3a-d.

Diagnosis (after Imaoka, 197). Mouth ventral. Anus open at the bottom of the vertical furrow. 20 tentacles. Ambulacral appendages very minute and wholly indiscernible along the mid-ventral ambulacrum. The appendages are arranged in double rows along the dorsal ambulacra and the ventro-lateral ones. Between 21 and 23 dorsal ambulacra along the inner and the outer rows of right, similarly 22 and 25 in left dorsal ambulacrum respectively. Ventro-lateral appendages larger than the dorsal ones. The interambulacral appendages exist only as in the surrounding of the ventro-lateral ambulacra; they are nearly as large as the ventro-lateral ambulacral appendages. One Polian vesicle. Respiratory trees well developed. Two unbranched gonad tufts. Calcareous ring well developed. Anterior margin of the radial pieces with a pair of median stouter dents and two lateral weaker ones, slightly concave around the middle of the posterior margin. **Ossicles**. Present only in the tentacles, appendages, ventral tegument and around the anus. The ossicles of the tentacles are simple and bifurcated rods, some can possess spiny ends. Rods from the dorsal appendages thin and bent. Rods found in the ventral tegument and around the anus are shorter and stouter than those from the dorsal appendages.

Material examined. None.

Type material. Holotype, SMBL Type-313; Paratypes SMBL Type-314 (4 specimens).

Type locality. Japan Sea, off the coast of Akita Prefecture, 200-300m, year 1972-1973.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 200-300m.

Remarks. *P. japonensis* resembles *P. nudus* Ohshima, *P. unuguiculatus* Ohshima, *P. molpadioides* Ohshima and *P. dilatorbis* Imaoka. However, it differs from *P. nudus, P. unguiculatus* and *P. molpadioides* in the shape of the calcareous ring and the presence of rods in the appendages and tentacles, and from *P. dilatorbis* in the appearance of the gonads, the distribution of the appendages and the absence of the ossicles in *P. japonensis*.

Pseudostichopus lapidus Hérouard, 1923

(Figures 158-161 in CD)

Pseudostichopus lapidus Hérouard, 1923: 26-28, Pl. 4, fig. 5; Heding, 1940; Mortensen, 1927: 387; Deichmann, 1930: 90;
Non *Pseudostichopus occultatus*, Hérouard, 1902; 14-15, Pl. 2, fig. 4-14 *partim*.

Diagnosis (from Hérouard 1923). Small species, ovoid body shape. Anus on ventral side in vertical furrow. Ventro lateral edge with 25 tubefeet in a row; two dorsal radiis with 4 papillae; a group of big papillae around the anus, some with three projections. On the dorsal inter-radii 14 to15 papillae. Ventral tubefeet not numerous with sucking disc present in the first two thirds of the body. Latero-dorsal warts, 14 on each side. 14 to15 appendages along dorsal and about 25 along ventro-lateral ambulacra. Unbranched gonads. **Ossicles**. No ossicles in the bodywall, gonads or any internal organ. Rods present in the tentacles.

Material examined. See appendix 1, Table 53. Cherbonnier's slide collection at the Natural History Museum in Paris France. 3 slides with Hérouard original preparations.

Type material. Holotype, MOM.

Type locality. *Princesse Alice* St. 527, North East Atlantic Ocean, off Azores, between 38º 09' N, 25º 30' W and 38º 08' N, 25º 39' W, 4020m, 25 Jun 1895.

Geographic distribution. From its type locality and Indian Ocean, Mozambique Channel.

Bathymetric distribution. 3485-4020m. Deichmann (1930) mentioned that this species is distributed at 3676m in the type locality, but type locality depth is 4020m.

Pseudostichopus macdonaldi (Ludwig, 1894) [new comb.]

Meseres macdonaldi Ludwig, 1894: 34-37; O'Loughlin, 2002: 306-307 [new synonymy].

Diagnosis (after Ludwig, 1894). Body flattened, rounded at the anterior and posterior ends, the sides of the body have a single row of very fine tubefeet. This looks like a fringe that runs around the whole body, passing dorsally to the mouth and anus. 15 shield-shaped tentacles. Mouth and anus are ventral, close to the anterior/posterior ends of the fringe mentioned above. A tiny, globular Polian vesicle. Two branched gonads. Two respiratory trees. **Ossicles**. No ossicles are found in the skin, the feet or the tentacles.

Material examined. None.

Type material. Syntypes, USNM E18190 (5 specimens); USNM E30501 (1 specimen).

Type locality. *Albatross*, St. 3362, North East Pacific Ocean, 5° 56'N, 85° 10' 30"W, 2125m, 26 Feb 1891.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 2125m.

Biological information. On rock, sand and green-mud sediments.

Pseudostichopus marenzelleri Hérouard, 1923

(Figures 162-164 in CD)

Pseudostichopus marenzelleri Hérouard, 1923: 25; Mortensen, 1927: 387-388; Deichmann, 1930: 90.
Non *Pseudostichopus occultatus*, Hérouard, 1902: 14-15, Pl. 2, fig. 4-14 *partim*.

Diagnosis (emended). Slight neck-like processes behind the anterior end of the body. Numerous small tubefeet on the dorsal side, with no apparent disposition, on the ventral side scarce. Big dorsal papillae, forming parallel series across the antero-posterior body length, this disposition is not apparent at both ends of the body, were the parallel series converge. On the ventral surface these papillae are present only occasionally and form irregular groups around the mouth and the posterior one third of the body. Mid-ventral radius completely naked. One Polian vesicle. Gonads in two tufts at both sides of the dorsal mesentery, situated in middle part of the body. **Ossicles**. No ossicles in the bodywall. Ossicles in the gonads: branched and unbranched arched rods with pointed ends, with one, two or three spiny tips. Some rods with a single knobbed centre. Tentacles with rods, sometimes smooth or with few spines, with a single knobbed centre.

Material examined. See appendix 1, Table 54. Ossicles from the Holotype, MOM.Cherbonnier's slide collection at the Natural History Museum in Paris France.

Type material. Holotype, MOM.

Type locality. *Princesse-Alice*, St. 650, from 36º 54'N, 20º 46'15" N and 36º 54'N, 20º 5'45" W, North East Atlantic Ocean, Between Portugal and the Azores, 22 Jun 1896, 4400m.

Geographic distribution. North East Atlantic Ocean, Between Portugal and the Azores, and the Mediterranean, off N. W. Spain. This last record based of *P. occultatus Hirondelle's* specimens.

Bathymetric distribution. 415-4400m.

Biological information. On *Globigerina* beds.

Remarks. Hérouard (1923) reviewed specimens from about 110mm of total longitude and 30mm wide. He doesn't describe the tentacular ossicles, but the slide preparation made by Cherbonnier on type material showed few rods with scattered spines and a single central knob.

Pseudostichopus mollis Théel, 1886a

(Figures 165-168 in CD)

Pseudostichopus mollis Théel, 1886a: 169-170, Pl. 10, figs. 5-6; Ludwig, 1894: 8-14, Pl. 9, figs. 5-9; Clark, H. L. 1913: 233; 1920: 146-147; 1923: 162; Ekman, 1925: 28-31, fig. 4-5, Branch *et al*., 1993: 55 (key).
Pseudostichopus (*Pseudostichopus*) *mollis*, Heding, 1940: 360 (key).

Diagnosis (after Théel, 1886a). Body more or less elongated, oval, equally rounded anteriorly and posteriorly. Mouth ventral. Anus vertical, hidden in a vertical furrow. 20 tentacles. Pedicels very minute, present only on the paired ambulacra; the odd ventral ambulacrum naked, sometimes some pedicels are present, but they are very rudimentary. Pedicels of the dorsal surface arranged in a narrow double row along each ambulacrum, those of the ventro-lateral ambulacra being more crowded and, as it seems, placed in two to five(?) rows. **Ossicles**. Absence of ossicles in the skin.

Material examined. See appendix 1, Table 55.

Type material. Syntypes, NHM 86.10.2.142 (3 specimens), NHM 86.10.2.143 (4 specimens), NHM 1956.10.3.6 (2 specimens), NHM 86.10.2.144 (2 specimens), ZMA E2999 (1 specimen).

Type locality. HMS *Challenger* St. 309A, South East Pacific Ocean, off Chile, 50º 56'S, 74º 14'W, 112m, 08 Jan 1876,

Geographical distribution. Cosmopolitan species. It has been reported in the Indian Ocean, Marion Island, Sub Antarctic Region (Branch *et al.*, 1993); Pacific Ocean, off California to Peru (Madsen, 1953); Southern Gulf of Mexico and Caribbean (Miller and Pawson, 1984 as *Pseudostichopus occultatus* von Marenzeller, 1893). Reported for the North-eastern Pacific, from the Gulf of Alaska to Oregon, also British Columbia, Queen Charlotte Sound (Lambert, 1997). Off Galapagos Islands, Hood Islands (Ludwig, 1894). Off Hermosillo, Sonora, Mexico (28º 30.0'N, 112º 22.0'W (Luke, 1982).

Bathymetric distribution. 100-5205 (Madsen, 1953).

Biological information. This species is common in deep water. It lives on rock and sand, on green mud, fine ooze-*Globiferina*, grey, sand and manganese substrates.

Pseudostichopus molpadioides Ohshima, 1915

Pseudostichopus molpadioides Ohshima, 1915: 228-229, Pl. 8, figs. 6a-c.
Pseudostichopus (*Trachostichopus*) *molpadioides*, Heding, 1940: 357.

Diagnosis (after Ohshima, 1915). Body cylindrical, not flattened, rapidly tapering at both extremities. Mouth terminal but directed ventrally. Anus lodged in a furrow. 20 tentacles. Small pedicels also present in interambulacra thinly scattered, those belonging to the midventral ambulacrum being almost indistinguishable from them. Larger pedicels forming a double row on each ventrolateral ambulacrum. In the dorsal ambulacra smaller papillae(?) are arranged in double rows. Calcareous ring well developed, radial segments having a pair of accessory processes near the outer edge of the anterior end. Polian vesicle single. Gonads unbranched and distributed in two tufts. Respiratory trees well developed. **Ossicles**. No ossicles are present in body wall or gonads. In the larger pedicels there is an end plate and a few supporting rods, always with a slight knob in the middle. Similar rods are found in tentacles, but these are much larger and are armed with short processes near the extremities. In the perianal region there are some scattered irregularly spiny bodies of varying complexity. The simplest ones are cross-shaped.

Material examined. None.

Type material. Holotype, USNM E34148 (lost).

Type locality. *Albatross* St. 4982, Off Shiribeshi, Hokkaido, Japan, 43ºN, 140º 10’30”E, 390m, 19 Sep 1906.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 390m.

Remarks. *P. molpadioides* agrees in many respects with *P. pustulosus* Sluiter, but differs from it above all in lacking the series of large stout warts along each side of the ventrum.

Pseudostichopus nudus Ohshima, 1915

(Figures 169-171 in CD)

Pseudostichopus nudus Ohshima, 1915: 230; Baranova, 1957: 240.
Pseudostichopus (*Trachostichopus*) *nudus* Heding, 1940: 357 (list), 359 (key).

Diagnosis (after Ohshima, 1915). Body subcylindrical. Mouth ventral, anus in a conspicuous vertical furrow. Tentacles 20. Numerous pedicels form a broad zone along the mid-ventral ambulacrum, there being about 8 pedicels in a transverse line. Toward the posterior part of the body, a groove along the median line. Pedicels very peculiar in shape, each consisting of a number of oval, knob-like parts. Along lateral margin of the ventrum are very small processes, often invisible, probably in alternate rows. Dorsal papillae forming a double row along each ambulacrum, very sparse, separated at intervals.

Calcareous ring well developed. Each segment often with a pair of minute teeth on the posterior margin. Polian vesicle single. Respiratory trees well developed. Gonads undivided, arranged in a row along each side of dorsal mesentery. **Ossicles**. Supporting rods of tentacles are curved, slightly spinous, often with irregular branches. Near tip of papillae are found slender rods usually with a knob-like thickening in the middle, but often irregularly branched. No other deposits.

Material examined. See appendix 1, Table 56.

Type material. Holotype USNM E34150 (lost). Syntypes,USNM E10787 (5 specimens).

Type locality. *Albatross* St. ?, North Pacific Ocean, Aleutian Islands or Japan, year 1906.

Geographic distribution. North East Pacific Ocean, Aleutian Islands; Alaska, Bowers Bank; off Kii, Honshu, Japan.

Bathymetric distribution. 244-1398m.

Remarks. Some strongly contracted specimens can show a low thickened ridge, "bourrelet epais" along each side of body as in *P. depressus* Hérouard and indicated by Ohshima (1915). *P. pustulosus* Sluiter differ from *P. nudus* in the shape and arrangement of ambulacral appendages.

Pseudostichopus occultatus Marenzeller, 1893a [new comb.]

Pseudostichopus occultatus Marenzeller, 1893a: 15-17, Pl. 4, figs. 9a-f; 1893b: 10, Pl. 2, fig. 3; 1895: 21-22 (list); Koehler, 1927:244, Pl. 11, fig. 18; Deichmann, 1930: 89-90; 1940: 190; 1954: 385; Tortonese, 1949: 13 (list); 1965: 71-72, textfig. 27.

Not *Pseudostichopus occultatus* Hérouard, 1902: 14, pl. 2, fig. 4-14 (*P. marenzelleri* Hérouard, 1923: 25).

Pseudostichopus occultatus v. *plicatus* Koehler & Vaney, 1905: 9-10, Pl. 3, fig. 8, Pl. 9, figs. 1-3.

Meseres occultatus von Marenzeller, 1893; O'Loughlin, 1998: 497; 2002: 307.

Plicastichopus ingolfi Heding, 1940: 357; 1942a: 5-6, textfig. 4, 5, figs. 1-6 [new synonymy].

Diagnosis (after Marenzeller, 1893a). Mouth ventral, anus terminal located in a slit. 20 tentacles. Skin thin. A double row of papillae along the dorsal sides that belongs to the inter-radii. Above anus, rows are close together and below they are more separated. Tubefeet over the whole body varying in size and shape. Larger tubefeet along sides of the body, smaller in the interambulacra. Dorsal tubefeet distributed in the radii. Dorsal feet bigger than the ventral ones. Tubefeet in the mid-ventral radius, similar to all the others on the ventral side. Tubefeet very dense above the mouth at the anterior end of the body, but very sparse below the mouth. One Polian vesicle. Respiratory trees well developed. Gonads in two tufts, unbranched. **Ossicles**. On the periphery of the anus irregularly elongated or round perforated plates and sometimes very compact bodies with irregular surface. The perforated plates are present in the ventral side of the anus, and the compact irregular bodies in the dorsal side of the anus, into the vertical furrow, around the anus. Tubefeet only with end plates, lacking supporting rods. Ossicles in tentacles straight or bended rods, sometimes with a central knob, with simple or bifurcated end. Ossicles present in the respiratory trees, short, and thick in the middle, bifurcated at both ends of which the one of the other bifurcated, again.

Material examined. See appendix 1, Table 57.

Type material. Holotype ?, MNHN 551, with no data. Deichmann (1940) says that the Holotype is possibly in Vienna. Tortonese (1965) stated that the Holotype is at the Museum of Monaco.

Type locality. West of Cape Finesterre, Spain, 363-510m.

Geographic distribution. Common in the Mediterranean Sea (Tortonese, 1949), also reported from the eastern coast of Spain (*Hirondelle* specimens). Indian Ocean, 12º 50’N, 90º 52’ E (Koehler and Vaney, 1905). In the western part of the Atlantic reported from waters off Havana, Cuba. Deichmann (1940) reported one specimen taken by the *Atlantis*, St. 3344, Off Southern Cuba, 21º 08’ N, 79º 56’ 30”W.

Bathymetric distribution. 232-4400m.

Remarks. Deichmann (1940: 190) reported this species as *Pseudostichopus occultatus* Marenzeller, and considered that the seven *Pseudostichopus* species already reported from the Atlantic could be united under one name. Although the validity of the taxonomic zoological concept “variety” is no longer in use (International Code of Zoological Nomenclature, article 45.6.3-4), it is important to state that *Pseudostichopus occultatus* var. *plicatus* Koehler and Vaney, 1905 is indeed a synonymy of *P. occultatus* Marenzeller. The latter authors erected this variety based on characters such as 1) size (>135mm), 2) presence of folds in the dorsal posterior part of the bodywall and 3) number of ossicles present in the tubefeet (numerous in *P. occultatus* var. *plicatus* and scarce in *P. occultatus*). All these character variations were found in specimens collected in the same area (e. g. MNHN 2429).

During the development of this study, I never found any thick perforated plates near the anus reported by Koehler and Vaney (1905) Deichmann (1930), etc. It is likely that these structures are indeed contaminants on slides derived from broken shells of foraminiferans (see Sluiter drawings, Koehler and Vaney, 1905: Pl. 9, figs. 1a. and 1b), as found in this study.

Pseudostichopus papillatus (Djakonov, 1952) [new comb.]

Peristichopus papillatus Djakonov, 1952 : 125-127, textfigs. 11-14; Baranova & Kuntsevitch, 1977: 117 [new synonymy]

Diagnosis (after Djakonov, 1952). Body more or less elongated, oval, equally rounded anteriorly and posteriorly. Skin thin and transparent. Mouth sub-ventral. Anus sub-ventral, hidden in a vertical furrow. 20 tentacles. Ventral side with very small tubefeet, very scarce, hardly visible. Papillae located only in the dorsal side and in the ventro-lateral radii, in two rows, irregularly distributed and often discontinuous. No tubefeet in the mid-ventral radius. One Polian vesicle. No stone canal. Calcareous ring well developed. Gonads in two tufts, not branched. Respiratory trees well developed. **Ossicles**. Rods present in papillae (80-800µm), tentacles (90-200µm) and in the perianal region (up to 300µm). The rods have a small central knob and those from the perianal region are thin and spiky. No ossicles are present in the gonads and respiratory trees.

Material examined. None.

Type material. In Russia?

Type locality. Pacific Ocean, Bering Sea, 4100-4200m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 4100-4200m.

Pseudostichopus peripatus (Sluiter, 1901a) [new comb.]

Meseres peripatus Sluiter, 1901a: 10-11, 1901b: 48-49, Pl. 5, fig. 5, Pl. 8, figs. 7a-b; O'Loughlin, 2002: 307-308 [new synonymy].

Diagnosis (after Sluiter, 1901a). Body flattened. 15-17? tentacles. Skin very thin. Dorsal side with long papillae, distributed in a simple row along the body length. Mouth and anus ventral. Calcareous ring well developed. A small Polian vesicle. Two gonads. **Ossicles**. Supporting rods, spiny and bent in the tubefeet, missing in the rest of the bodywall and any internal organ.

Material examined. None.

Type material. Syntypes: ZMA E1048 (3 specimens), ZMA E1049 (1 specimen), ZMA E1050 (7 specimens) (after Jangoux, 1991).

Type locality. *Siboga* St. 45, 7º 24'S, 118º 15.2'E, 794m.

Geographic distribution. South East Asia, Sunda Islands, Indonesia; North Atlantic, Indo-Pacific (O'Loughlin, 2002).

Bathymetric distribution. 794-1200m.

Pseudostichopus profundi Djakonov, 1952

(Figures 172-174 in CD)

Pseudostichopus profundi Djakonov, 1952: 127-129, figs. 15-18; Baranova & Kuntsevitch, 1977: 117.

Diagnosis (after Djakonov, 1952). Anus on a ventral side at bottom of a vertical furrow. 20 tentacles. Appendages more crowded and larger at each end of ventro-lateral ambulacra; very few along dorsal and mid-ventral lateral regions. Gonads unbranched. **Ossicles**. Perforated "pseudo-rods" in tentacles. Gonads rarely include small, short and flat rods. Rods present around the anal area.

Material examined. See appendix 1, Table 58.

Type material. Holotype, ZIAS 1/12303 (after Baranova and Kuntsevitch, 1977).

Type locality. North West Pacific Ocean, Southeast of Kamchatka Peninsula, Russia, 4100-4200m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 1445-4200m.

Pseudostichopus propinquus Fisher, 1907

Pseudostichopus propinquus Fisher, 1907: 691-693, Pl. 71, figs. 3, 3a-b, Pl. 72, figs. 2, 2a, Pl. 73, fig. 3, Pl. 74, fig. 1, Pl. 76, figs. 3, 3a-b.
Meseres propinquus (Fisher, 1907); O'Loughlin, 2002: 309 [new synonymy].

Diagnosis (after Fisher, 1907). Mouth terminal, ventral. Anus ventral, situated in a prominent vertical furrow. 18-20 tentacles. Ambulacral appendages very inconspicuous and small, in the form of minute pedicels and papillae scattered along ambulacra, those of ventro-lateral ambulacrum most prominent. Papillae on the dorsal ambulacra very slender, long, and thread-like, apparently not arranged regularly. **Ossicles**. Perisome devoid of any ossicles; no supporting rods or terminal plates in ambulacral appendages. Walls of gonad and respiratory trees contain branched rods.

Material examined. See appendix 1, Table 59.

Type material. Holotype, USNM E21217.

Type locality. *Albatross* St. 3866, northeast approach to Pailolo Channel, between Maui and Molokai Islands, Hawaii, 509-519m.

Geographic distribution. *Albatross* St. 3866, northeast approach to Pailolo Channel, between Maui and Molokai Islands, Hawaii.

Bathymetric distribution. 509-519m.

Pseudostichopus pustulosus Sluiter, 1901a

Pseudostichopus pustulosus Sluiter, 1901a: 16-17, 1901b: 53-55, Pl. 4, figs. 6a-b, Pl. 9, fig. 1.
Pseudostichopus (*Pseudostichopus*) *pustulosus*, Heding, 1940: 333 (list).

Diagnosis (after Sluiter, 1901a). Subcylindrical body. Skin thin. Ventral side flattened. 20 tentacles. Irregular blunt warts in an irregular row along mid-ventral ambulacrum and 20 along ventro-lateral radii. Ventral side completely naked. Mouth and anus ventral. 2 branched gonads. Respiratory trees well developed. Calcareous ring well developed. One Polian vesicle. **Ossicles**. Present in the tubefeet in the shape of little oblong, perforated plates. Bodywall and internal organs completely lacking ossicles.

Material examined. None.

Type material. Syntypes, ZMA E1011 (1 specimen), ZMA E1012 (1 specimen), ZMA E1006 (1 specimen), ZMA E1303 (1 specimen) (after Jangoux, 1991).

Type locality. *Siboga* St. 145, South West Pacific Ocean, Indonesia, 0º 45'S, 128º 39.9'E, 827m.

Geographic distribution. South West Pacific Ocean, Indonesia.

Bathymetric distribution. 827-924m.

Pseudostichopus spiculiferus (O'Loughlin, 2002) [new comb.]

Meseres spiculiferus O'Loughlin, 2002: 309, 312, figs. 1.a-f, 2. a-d [new synonymy].

Diagnosis (after O'Loughlin, 2002). Body flat ventrally, domed dorsally, rounded anteriorly and posteriorly. Posterior vertical furrow. Skin soft. Mouth and anus ventral. Ventro-lateral margin semi-acute, rounded, some reticulate ridges with very small digitate projections, lacking prominent ventro-lateral projections; up to 20 tentacles. Very small thread-like appendages variably present over whole body, typically 0.2mm diameter, prominent around mouth and furrow, frequently entangled; small radial tubefeet, up to 1mm diameter, largest along latero-ventral margin in bands up to 5 very irregular rows continuous around the anterior end of the body, irregular double rows dorso-laterally, sparse to absent mid-ventrally. One Polian vesicle. Calcareous ring plates solid, more wide than high, lacking posterior prolongations, radials frequently with four posterior teeth on edge of indentation. **Ossicles**. In tentacles, tubefeet, gonads, absent from bodywall, respiratory trees; tentacle ossicles, curved to straight rods up to 0.28mm long, frequently with central, seldom distal, swellings, very rarely branched, in a few cases bluntly spinous; tubefeet distally with support rods, up to 0.20mm long, same form as in the tentacles; "endplates" up to 0.13mm wide, open mesh of irregular thin knobbed branched rods; gonad tubules with abundant very irregular ossicles, frequently with large central swellings, rods to cross to Y-shaped and even complex branching, branches sometimes joined to create large perforations, up to 0.30mm long.

Material examined. None.

Type material. Holotype, NMV F81857; Paratypes, NMV F68054 (1 specimen), NMV F68156 (1 specimen), NMV F72542 (1 specimen), NMV F81805 (4 specimens), NMV F81806 (1 specimen).

Type locality. Prydz Bay, 67º 10'S, 74º 28'E, 428m.

Geographic distribution. Eastern Antarctica, off Wilkes, MacRobertson, Enderby Lands.

Bathymetric distribution. 177-695m.

Pseudostichopus tachimaruae Imaoka, 1978

Pseudostichopus (*Trachostichopus*) *tachimaruae* Imaoka, 1978: 380-382, figs. 2a-e.

Diagnosis (after Imaoka, 1978). Dorsal side arched, ventral side flattened. Mouth ventral, the anus is open on the ventral side at the bottom of the vertical furrow. 19(?) tentacles. Ambulacral appendages very minute and wholly indiscernible along the mid-ventral ambulacrum crowded more densely near the posterior end. The appendages are arranged in double rows along the dorsal ambulacra, while they occur in a single row along the ventro-lateral ambulacra. One Polian vesicle. Respiratory trees well developed. 2 unbranched gonad tufts. Calcareous ring narrow. Radial pieces with a central pair of anterior projections. Interradial pieces narrower than the radials. **Ossicles**. Present only around the anus and in the tentacles. Perforated delicate plates are found in the integument around the anus. Simple or knobbed rods are present in the tentacles.

Material examined. None.

Type material. Holotype, SMBL Type-311; Paratypes:, SMBL Type-312 (2 specimens).

Type locality. Shimo-Koshiki Island off the west coast of Kyushu Island, Japan, 27 Oct 1976, 400-450m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 400-450m (Imaoka, 1978).

Remarks. This is the only *Pseudostichopus* species that probably has “real” ossicles in the anal region, because the ossicles described for the anal region in other species of the same group are likely to be foraminiferan shells or their fragments. It is imperative to review the type material in order to probe the validity of this character.

Pseudostichopus trachus Sluiter, 1901a

(Figure 175 in CD)

Pseudostichopus trachus Sluiter, 1901a: 15-16; 1901b: 52-53, Pl. 5, fig. 1, Pl. 8, figs. 8a-b; Perrier, 1902: 337-8; Fisher, 1907: 693; Mitsikuri, 1912: 3-9, Pl. 1, figs. 1-5, textfig. 1; Oshima, 1915: 227-228; Heding, 1940: 361; Savel'eva, 1941: 74; Baranova, 1957: 239; Djakonov *et al*., 1958: 366; Cherbonnier & Féral, 1981: 383-385, textfigs. 16a-d; Liao, 1997: 79-80, textfig. 44.

Molpadiodemas acaudum Heding, 1935: 78-80, Pl. 6, figs. 1-2, Pl. 8, figs. 1-12, 1942a: 4-5, textfig. 3, figs. 1-3.

Non *Pseudostichopus* (*Trachostichopus*) *trachus*, Heding, 1940: 361-362.

Pseudostichopus alatus Imaoka, 1990: 147-148, textfig. 1a-e [new synonymy].

Pseudostichopus tuberculatus Imaoka, 1990: 150-152, textfig. 1a-g [new synonymy].

Meseres trachus, O'Loughlin, 2002: 312.

Diagnosis: (after Sluiter, 1901a: 15-16). Ventral side flat, dorsal side high arched, sharply divided from each other. On the dorsal side there are small flat skin warts, on which very small tubefeet stand in alternating double rows. On the mid-ventral radius the tubefeet are very small. On the dorsal side there are a few small tubefeet irregularly distributed. Anus situated in a conspicuous vertical furrow. Mouth ventral, 17 tentacles (but maybe 20 occur). One Polian vesicle. Gonads in two tufts of long, thin only seldom divided at the ends. The respiratory trees well developed. Calcareous ring with 10 strong, firmly conjoined pieces, the radial pieces with peculiar teeth on the posterior ondulation. **Ossicles**. Absent from the skin, present only in the disk of the tentacles as a few support rods, 0.13mm long, faintly spiny at the ends. The respiratory trees with no ossicles.

Material examined. See appendix 1, Table 60. Ossicles from a Syntype, ZMA E2496/1, *Siboga* St. 286, South West Pacific Ocean, Indonesia, 8º 50.2'S, 127º 2.2'E, 883m Cherbonnier's slide collection at the Natural History Museum in Paris France (ossicles from the tentacles, enhancement 10X).

Type material. Syntypes, ZMA E2496/1 (1 specimen), ZMA E2496/2 (1 specimen).

Type locality. *Siboga* St. 286, South West Pacific Ocean, Indonesia, 8º 50.2'S, 127º 2.2'E, 883m.

Geographic distribution. It is known from the Japan Sea, from coast of Japan, about Timor and Molucca islands. The Bering Sea, near Copper Island (Medny Island). Area near of Commandor Islands, Japanese Sea, near Pacific coast of Japan, Sagami, Suruga Bay (Baranova, 1957). Gulf of Peter Great (Saveljeva, 1941). Austral Kuril Islands, Tatar Strait near Antonovo, Laperuza Strait (Djakonov *et al*., 1958).

Bathymetric distribution. 110-5730m.

Remarks. Imaoka (1990) erected the species *Pseudostichopus alatus* based on the shape of the inter-radial and radial pieces of the calcareous ring (see Imaoka, 1990, fig. 1a). These characters are common in *P. trachus* as illustrated by Heding (1940) and Cherbonnier and Féral (1981). The rods on the tentacles are similar between *P. trachus* and *P. alatus*. Moreover their geographic and bathymetric distributions overlap. The synonymy of the spcecies is proposed.

Imaoka (1990) also erected the species *Pseudostichopus tuberculatus* based on the very characteristic ossicles found around the anus (see Imaoka, 1990, fig. 1d-f, page 151) and shape of the calcareous ring. Unfortunately, the "ossicles" illustrated by Imaoka (1990) that are supposed to be present around the anus are indeed complete foraminiferan shells or fragments of them, making the same mistake as Perrier (1902, see Pl. 7, fig. 20) and Heding (1940, see textfig. 17). The form of the tentacle ossicles, and the shape of calcareous ring, is similar to *P. trachus*, as illustrated by Heding (1940) and Cherbonnier and Féral (1981). Moreover the geographic and bathymetric distributions of the species overlap. The "conical knobs" mentioned by Imaoka (1990) present in the upper side of the ventro-lateral radii of *P. tuberculatus* are also present in *P. trachus*. The synonymy of the two species is proposed. Mitsukuri (1912) concluded that usually a calcareous body could be found on each side of the cloacal opening. He also doubted about the validity of many *Pseudostichopus* species (in 1912 he considered only the validity of 7).

Pseudostichopus unguiculatus Ohshima, 1915

(Figures 176-179 in CD)

Pseudostichopus unguiculatus Ohshima, 1915: 230, Pl. 8, figs. 7a-c; 1916: 212, textfig. 17, Pl.2, fig. 18; Liao, 1997: 80-81, textfig. 45.
Pseudostichopus (*Pseudostichopus*) *unguiculatus* Ohshima, 1915; Heding, 1940: 360.

Diagnosis (after Ohshima, 1915). Ventral side flat, dorsal side strongly vaulted. Mouth ventral, anus situated in a deep furrow. 20 tentacles. 18-20 conical warts arranged along the sides of the ventrum, with four or five curved papillae at the tip. In each dorsal ambulacra ther are two rows of short, slender papillae, about 25 in number. Near the lateral margin of ventrum small pedicels infrequently occur a rows. Scattered irregularly along the odd ambulacrum are found very minute pedicels. Calcareous ring well developed. One Polian vesicle. Respiratory trees well developed. Gonads unbranched, arranged in a row along each side of dorsal mesentery. **Ossicles**. Dorsal and lateral papillae contain only a very small number of smooth supporting rods. Pedicels of ventro-lateral ambulacra have imperfect end plates, but no supporting rods. Rods in tentacles are richly armed with spines. In gonads, scattered branching ossicles, normally cross-shaped, with a knob in the middle.

Material examined. See appendix 1, Table 61.

Type material. Holotype, USNM E34151 (lost).

Type locality. North West Pacific Ocean, Southwest of Shikoku; south of Totomi, Honshu, Japan, 578-918m.

Geographic distribution. Only known from its type material.

Bathymetric distribution. 578-1141m.

Remarks. *P. unguiculatus* is perhaps identical with *Pseudostichopus peripatus* (Sluiter), which has rows of warts with 4-5 claw-like papillae.

Pseudostichopus villosus Théel, 1886a [new comb.]

(Figures 180-190 in CD)

Pseudostichopus villosus Théel, 1886a: 170-171; Hérouard, 1896: 164 (distribution list); 1902: 11-13, Pl. 2, fig. 1-3, Pl. 7, fig. 3; 1923: 23; Vaney, 1908: 407-408; Grieg, 1921: 4; Hérouard, 1923: 23; Mortensen, 1927: 387, 388; Deichmann, 1930: 89; Heding, 1940: 353-360; Hansen, 1956: 47-48.

Pseudostichopus villosus var. *violaceus* Théel, 1886a: 172, Pl. 10, fig. 6b [new synonymy].

Pseudostichopus atlanticus R. Perrier, 1899: 246-247; 1902: 333-337, Pl. 17, figs. 15-20; Mortensen, 1927: 387 (*passim*); Deichmann, 1930: 87-88; O'Loughlin, 2002: 315.

Pseudostichopus globigerinae Hérouard, 1923: 23-25, Pl. 4, fig. 6; Mortensen, 1927: 386, 388; Deichmann, 1930: 90 [new synonymy].

Meseres villosus Théel, 1886; O'Loughlin, 1998: 497; 2002: 313, figs. 3a-b.

Molpadodiademas atlanticus Heding, 1940: 357.

Meseres acaudum (Heding, 1935); O'Loughlin, 1998: 497.

Meseres atlanticus (R. Perrier, 1902), O'Loughlin, 1998: 493, 497; Thandar, 1999: 376-379, textfig. 4.

Meseres globigerinae, O'Loughlin, 2002: 305.

Diagnosis. Large, sac-like, often flattened body. 15-20 tentacles. Mouth ventral, anus in a deep vertical furrow. Integument opaque, around the oral end there is an indication of a marginal thickening. Bodywall appendages small, but mostly arranged along the ventro-lateral ambulacra and below anus. Tubefeet very scarce or absent on the mid-ventral radius, of nearly equal size. No lateral series of larger tubefeet. Lateral tubefeet placed in bundles on distinct conical warts; ventrally the feet are uniformly distributed and dorsally they seem to be scarce and smaller. A well-developed calcareous ring deeply excavated and undulated. One Polian vesicle. Well-developed respiratory trees. In young specimens (20-30mm) there are lateral conical warts. Ventrally the tubefeet are uniformly distributed and dorsally they seem to be scarce and smaller. The tentacles are large and not much directed ventrally, anal furrow not very deep. **Ossicles**. Branched rods and reticulated plates in skin around mouth. Tentacle ossicles prominent, including curved rods, often thickened in middle.

Material examined. See appendix 1, Table 62; appendix 2, Table 13.

Type material. Syntype, NHM 86.10.2.146.

Type locality. HMS *Challenger* St. 156, 62^o 26’ S, 95^o 44’ E, 3594m, 26 Feb 1874.

Geographic distribution. Bay of Biscay, Mediterranean Sea (Tortonese, 1949). South Atlantic, African Coast, Southwest of Cape Point, Africa (Thandar, 1999). Off Rabat, Morocco. Between Azores and France (Deichmann, 1930, referred as *P. atlanticus*). Caribbean Sea, Off Bequia Island and Guadeloupe Island. (Deichmann, 1930, referred as *P. atlanticus*). The Pacific Ocean records need validation.

Bathymetric distribution. 351-7000m.

Biological information. Deep-sea photographs of *P. villosus* can be found in Lemche *et al.* (1976). Large populations of bacteria have been found in the gut of *P. villosus* (Bianchi *et al*., 1979) suggesting a symbiotic association.

Remarks. Perrier (1901), Deichmann (1930) and Billett (1988) had suggested the synonymy of *P. atlanticus* and *P. villosus*. The final author mentioned that there is a “gradation” in form from typical *P. atlanticus* to some specimens that are comparable to *P. villosus* sampled by the HMS *Challenger* Expedition in the Pacific (Théel, 1886a). These specimens were analysed by Billett (1988) at the Natural History Museum, London, and only the smallest specimens (<30mm TL) can be said to be true “villosus” or hairy. I analysed the type series of *P. atlanticus* at the Paris Museum (Holotype MNHN 2772, Paratypes MNHN 2773) and concluded that *P. atlanticus* is synonymous with *P.*

villosus, sharing exactly the same shape of body, tentacles, Polian vesicle, respiratory trees, calcareous ring and tentacular ossicles.

Deichmann (1930) was the first author to suggest the synonymy of *P. globigerinae* and *P. villosus*. The holotype of *P. globigerinae* is a juvenile form that measures 30mm TL. Hérouard (1923) states that his specimen was a juvenile because of its size and because the gonads were not developed. An examination of Dr. Cherbonnier's slide collection (MNHN, Paris) shows that the tentacle ossicles of the holotype of *P. globigerinae* (Museum of Monaco, *Princesse-Alice*, St. 2964, 4380m, Year 1910) are exactly the same of those found in juveniles of *P. villosus* of approximately the same size. It is concluded that *P. globigerinae* is synonymous with *P. villosus* sharing exactly the same shape of tentacular ossicles and external body shape. The variety "*violaceus*" named by Théel (1886a) was named for a dark violet specimens of *P. villosus*. Théel was unable to find enough characters to differentiate the variety, except for the colour of one specimen. For more information see Chapter 4, section 4.4 of this thesis.

Genus ***Synallactes*** Ludwig, 1893 [new comb.]

Synallactes Ludwig, 1893: 2; 1894: 24-26; Perrier, 1902: 338-339; Mitsukuri, 1912: 11-12; Mortensen, 1927: 378; Deichmann, 1930: 106; 1940: 186; Cherbonnier, 1952: 473.
Paradeima Heding, 1940: 371-372 [new synonymy].

Diagnosis. Body cylindrical or sub-cylindrical. 18-20 tentacles. Stone canal attached to the bodywall. Ventral surface flattened, but without any marginal border. Ventral pedicels and dorsal papillae in longitudinal series and confined to the ambulacra. On the ventral face, three zones of pedicels. Ventral tubefeet and dorsal papillae regularly arranged regularly along the ambulacra. Peculiar fungiform tubefeet occur in this genus. Gonads in two tufts (one right and one left). Anus not lodged in a vertical furrow. **Ossicles**. Present in the bodywall. The ossicles consists of three or four armed tables, the distal ends of which have a larger or smaller number of perforations, and often laterally send out processes that may unite with similar processes of other arms and produce an open circular latticework. The spire consists of a single pillar, which may be divided or perforated, or both, at the upper end. There are supporting rods in the ambulacral appendages.

Type species: *Synallactes alexandri* Ludwig, 1893.

Remarks. The origin of the name *Synallactes* came from the greek, **? s??a??a?t??** means a mediator (e.g. in arguments between two parties). Ludwig (1894) argues that, because of its characteristics, *Synallactes* lies between Holothuridae and the Elpidiidae (Elasipodida). New combinations and synonymies are presented in this thesis (see Table 1 and 2, Appenix 3). The genus *Synallactes* is composed of 22 valid species.

Synallactes aenigma Ludwig, 1893

(Figures 191-193 in CD)

Synallactes aenigma Ludwig, 1893: 106; 1894: 26-31, Pl. 12, figs. 9-15; Clark, 1920: 144-145, Pl. 3, fig. 4.

Diagnosis (after Ludwig, 1894). Ventral side and middle dorsal interabulacrum flattened; dorsal and peripheral papillae strongly developed and organised in long rows. Rim with flattened, conical papillae, separating the ventral and dorsal sides. The papillae of the rim arising from the ventro-lateral radii. Similar papillae on each of the two dorsal radii, organised in two separate long rows. Dorsal papillae are not flattened like the papillae on the rim, and are smaller. Cylindrical, flexible ambulacral appendices protrude from the tip of the papillae. Small, cylindrical tubefeet on the ventral side (only on the radii). On the mid-ventral radius, there are a few tubefeet organised in two long rows. Small warts between the peripheral rows of tubefeet and the papillae on the rim. Mouth ventral, surrounded by 20 small tentacles. Anus dorsal. Two well-developed respiratory trees. A well-developed calcareous ring. One Polian vesicle. Stone canal is connected with the dorsal mesentery. Two gonads, branched. **Ossicles**. Many ossicles in the bodywall. Ossicles on dorsal and ventral sides have the shape of a four-armed crosses. Arms are slightly broader at tip with several small perforations (1 to 5) and a simple stem that is separated into several elongated tips at the end (2 to10). Sometimes the stem has a small spike on the side. The arms of the ossicles never seem to be connected. Ossicles in tubefeet have spikes on the side and tip of the stem. They are more robust than in the bodywall and their bases are slightly flatter. In distal end of the tubefeet, there are supporting rods, spiny and bent. Well-developed mesh-like disc at the end of tubefeet. In papillae of rim and dorsal side the ossicles are similar to those of the bodywall, but thinner and the stem may have more spikes. Supporting rods in tentacles similar to those in tubefeet, but of a different size.

Material examined. See appendix 1, Table 63.

Type material. Syntypes, USNM E18207 (1 specimen), USNM E18206 (1 specimen).

Type locality. *Albatross* St. 4649, South Pacific Ocean, Galapagos Islands, between Galapagos and Peru, 05º 17’ 00” S, 85º 20’ 00” W, 4088m, 10 Nov 1904.

Geographic distribution. South East Pacific Ocean. This seems to be one of the characteristic species of the Easter Tropical Pacific. Pacific Ocean, off Acapulco, Mexico; Gulf of Panama; Colombia; Sechura Bay, North of Peru.

Bathymetric distribution. 2404-4520.

Biological information. On green mud, sand, ooze-*Globiferina* and manganese substrates.

Synallactes alexandri Ludwig, 1893 [new comb.]

(Figures 194-200 in CD)

Synallactes alexandri Ludwig, 1893: 2; 1894: 21-24, Pl. 9, figs. 10-19.
Bathyplotes hancocki Domantay, 1953: 136; 1961: 334-335 [new synonymy].
Bathyplotes maccullochae Domantay, 1953: 136; 1961: 335-336 [new synonymy].

Diagnosis. Subcylindrical body, slightly flattened. Six rows of papillae on dorsal side, a similar distance from each other. Four rows of papillae in dorsal radii. The ventro-lateral radii with tubefeet and papillae that protrude in the mouth area and (more pronounced) around the anus. 18-20 tentacles. No tentacular ampullae. Calcareous ring with interradial pieces loosely connected. Two gonads, consisting of 3-5 very long gonadal tubes. Each gonadal tube branches dichotomously 2-3 times. 2 respiratory trees well developed. From 1 to 4 Polian vesicles. **Ossicles**. Few ossicles in the thick bodywall. Bodywall tables more complex dorsally than ventrally. In dorsal bodywall four arms tables, of which one sometimes is missing; arms thick and short (stubby), one or several perforations at their distal end. Distal end of two or three, more rarely all four arms connected. Stem solid that extends from the middle of cross, spliting into three or more fine, connected projections, which are rounded off at their distal ends. In ventral bodywall, the ossicle disk and stem is less complex and simpler. Tubefeet and papillae ossicles similar to those in bodywall. Those in tubefeet smaller and more fragile than those in papillae. In tubefeet and papillae with numerous rounded connections. The connections have spines around the rim. Ossicles in tubefeet with a strong calcareous end plate. When adult, tables show smaller base discs and slender pillars.

Material examined. See appendix 1, Table 64.

Type material. Syntypes, USNM E18212 (2 specimens); USNM E18185 (1 specimen).

Type locality. *Albatross* St. 3354, North Pacific Ocean, Azuero Peninsula, Gulf of Panama, 07º 09’ 45”N, 80º 50’W, 588m, 23 Feb 1891.

Geographic distribution. Pacific Ocean, From California to Gulf of Panama and Galapagos Islands.

Bathymetric distribution. 273-1018m.

Biological information. On green mud and rock substrates.

Remarks. I review Domantay’s species type material of *Bathyplotes hancocki* Domantay, 1953 and *Bathyplotes maccullochae* Domantay, 1953, and they show exactly the same body and ossicle pattern as *Synallactes alexandri*.

Synallactes challengeri (Théel, 1886a)

(Figures 201-202 in CD)

Stichopus challengeri Théel, 1886a: 163-164, Pl. 10, fig. 21; Ludwig, 1889: 331; Edwards, 1907: 65-66, text fig. 12.

? *Stichopus challengeri*, Ludwig, 1894: 25.

Synallactes(?) [*Stichopus*] *challengeri*, Perrier, 1902: 339.

Synallactes challengeri, Östergren, 1896; Clark, 1922: 46 (list); Massin, 1992: 313-316, textfigs. 2-3; Branch *et al.*, 1993: 55 (key).

Diagnosis. Body cylindrical and elongated. Flaccid animal with thin transparent skin, mouth ventral, anus terminal. 20 peltate tentacles. Ventral tubefeet long, in 3 rows. Mid-ventral radius with 4 small tubefeet; both ventro-lateral ambulacra with 2 rows of long tubefeet. Tubefeet densely pack near the anus. Dorsal surface with 6 rows of papillae. Ventro-lateral radii with long papillae. Longitudinal muscles not divided. Calcareous ring made of small inter-radial pieces with one central anterior tooth and massive radial pieces with a posterior notch. From 2 to 5 Polian vesicles. Respiratory trees well-developed and independent from the digestive and hemal system. Gonads unbranched. **Ossicles**. In the bodywall, cruciform bodies with 3-4 arms. The end of each arm is bifurcated several times or perforated. Spire ending in a single point or in 2-4 spines. Each spine may end in several spinelets. The tubefeet contain rods, cruciform ossicles and end plates. The rods, which are straight or curved and sometimes forked, have perforated ends. Dorsal papillae contain rods and cruciform ossicles. Tentacles contain only rods, straight, curved, forked, and sometimes branched.

Material examined. See appendix 1, Table 65.

Type material. Holotype, MNHNP.

Type locality. HMS *Challenger* St. 148a, Indian Ocean, 46º 53’S, 51º 52’E, 990m, 3 Jan 1874.

Geographic distribution. This species occurs off Crozet, Marion and Prince Edward Islands (237-600) (Massin, 1992) and off southern Australia (O'Hara, 1998). In the north Pacific known from Uyak Bay, Kodiak Island, Alaska (Edwards, 1907) to northern Vancouver Island. These last localities need validation.

Bathymetric distribution. 20-1115m.

Biological information. This species feeds on bottom sediments with its peltate tentacles, like the members of the genus *Parastichopus* (Lambert, 1997). Found on rock and sandy substrates (Maluf, 1988), but occurs mainly on rocky bottoms.

Remarks. This species can be mistaken for a juvenile of a *Parastichopus*. The body colour, and size and shape of the papillae are fairly distinctive. Internally *S. challengeri* has no tentacle ampullae, and the ossicles are quite different. Östergren (1896) placed this species into the genus *Synallactes*. Clark (1922) also suggested that this species was not a *Stichopus*, but that it possessed the characters of the family Synallactidae. Massin (1992) mentioned that the species shows a great variation in the shape of ossicles, in proportion between the cruciform ossicles with perforated ends and the bifurcated ones. The perforated ends show a great variability.

Synallactes chuni Augustin, 1908

(Figures 203-206 in CD)

Synallactes chuni Augustin, 1908: 14-16, Textfig. 11, Pl. 1 fig. 5; Djakonov, 1949: 116, Pl. 18, fig. 106 a-b.

Diagnosis. Body elongated with tapering ends. Mouth broad. Anus terminal. 20 tentacles. Inter-radii naked; mid-ventral radius with two alternating rows of tubefeet. Dorsal side with large papillae, approximately 25 in number. Two gonads. Two Polian vesicles. Calcareous ring well-developed. **Ossicles**. Three-armed cross, the distal ends of which have a larger or smaller number of perforations. The spire consists of a single pillar, divided in three at its distal end. There are supporting rods in the ambulacral appendages and calcareous end plates.

Material examined. See appendix 1, Table 66.

Type material. Location unknown.

Type locality. Jagoshima, Japan, 600m.

Geographic distribution. North Pacific Ocean, Bering Sea, Russia, Commander Islands, east of Copper Island and Jagoshima, Japan.

Bathymetric distribution. 242-600m.

Synallactes crucifera Perrier, 1898

(Figure 207 in CD)

Synallactes crucifera Perrier, 1898: 1665; 1899: 247; 1902 : 339-345, Pl. 12, figs. 5-6, Pl. 17, figs. 21-35; Mortensen, 1927: 378 (key), textfig. 224, fig. 9; Deichmann, 1930: 106 (*passim*); 1940: 186, Pl. 31, figs. 5-6.

Diagnosis (after Deichmann, 1940). Mouth ventrally placed, anus subdorsal. Ventral side with cylindrical tubefeet in two lateral bands and in a scattered band along the mid-ventral ambulacrum. Dorsal side with conical papillae in several longitudinal rows, those nearest the midline usually with whip-like tips. **Ossicles**. Cross-shaped bodies with external spines, occasionally with a terminal slit-like perforation, but otherwise solid; arms of the cross with one or two perforations in the ends. Tubefeet with large end plates and branching or perforated rods.

Material examined. See appendix 1, Table 67.

Type material. Holotype, MNHN 7162.

Type locality. *Talisman*, coast of Morocco, 30° 3' N, 14° 2' W, 2212m, 24 Jun 1883.

Geographic distribution. North East Atlantic Ocean, coast of Morocco. Caribbean Sea, off Cuba, data from *Atlantis* specimen (one fragment, 60mm long), St. 2973, 21 09'N, 85 04'W, 2304m (Deichmann, 1940).

Bathymetric distribution. 2160-4097m.

Synallactes discoidalis Mitsukuri, 1912

Synallactes discoidalis Mitsukuri, 1912: 18-21, textfig. 3; Ohshima, 1915: 221; Liao, 1997: 78-79, textfig. 43.

Diagnosis (after Mitsukuri, 1912). Tentacles 20. Dorsal papillae in six rows. Ventral pedicels in three zones. One Polian vesicle. Genital tubes in two tufts. Calcareous ring well developed. **Ossicles**. Tables of the bodywall built to the same plan in all parts of the body, although there are differences in size and elaboration. Tri-radiated scarce except at the base of ventral pedicels. Single pillared spire. Supporting rods scattered among large basal disks of dorsal papillae. The rods are very long with many perforations in their ends. These rods are irregularly scattered, and occur even toward the tip of the papilla. Supporting rods in pedicels arranged parallel to the calcareous end plate.

Material examined. None.

Type material. Location unknown.

Type locality. Sagami Bay, Japan.

Geographic distribution. Sagami Bay and Sagami Sea, Japan (Mitsukuri, 1912); south of Joga Shima (Ohshima, 1915). East China Sea (Liao, 1997).

Bathymetric distribution. 358-728m.

Remarks. Mitsukuri (1912) named this species *"discoidalis"* in reference of the discoidal shape of the base of the tables. Mitsukuri analysed 5 specimens when described this species, ranging from 62-140mm length.

Synallactes elongata (Heding, 1940) [new comb.]

Paradeima elongata Heding, 1940: 372-373, textfig. 20, figs. 1-7 [new synonymy].

Diagnosis (after Heding, 1940). Ventral side weakly flattened. 20 tentacles. Mouth terminal. In front of the mouth there is a velum formed by approximately 14 large papillae. The form of this velum is not completely clear, because the right side is missing or only weakly developed. The left side is however formed by 7 large papillae. Tubefeet are found only along the ventro-lateral ambulacra and they are so small that they only can be seen if the circular muscle layer is lifted. Then the small tubefeet can be seen clearly between the larger papillae. The papillae are arranged in two lines along the body in the ventro-lateral and dorsal ambulacra. Only the mid-ventral ambulacrum is completely naked. The anus is terminal and its surrounded by large triangular papillae. One Polian vesicle. **Ossicles**. Spiny rods in tentacles, curved or straight. Ventral side of the body with cross-shaped tables, the disks consist of four arms, the distal ends of which have a larger or smaller number of perforations. The spire consists of a single pillar, which may be divided or perforated, or both, at the upper end. There are supporting rods and terminal disks in the ambulacral appendages. Long spiny rods are present in the ventral side of the bodywall. Ossicles of the papillae like those in the dorsal bodywall.

Material examined. None.

Type material. Location unknown.

Type locality. *Valdivia* St. 194, Indian Ocean, Nias Chanel, 0° 15.2’N, 98° 8.8’E, 614m, 01 Feb 1899.

Geographic distribution. Only knows from its type locality.

Bathymetric distribution. 614m.

Remarks. The only apparent reason given by Heding (1940) to include this specimen in a *incerta sedis* group was the presence of a “velum” in a partially destroyed specimen. It is important to state that no illustrations were made of this specimen, and that the type material probably doesn’t exist anymore. The presence of tri-radiate ossicles with a single stem terminating in a bifid point, and the distribution of the pedicels in the bodywall, indicated that this species belonged to the genus *Synallactes*.

Synallactes gilberti Ohshima, 1915

(Figures 208-209 in CD)

Synallactes gilberti Ohshima, 1915: 223-224, Pl. 8, figs. 2a, b.

Diagnosis: (after Ohshima, 1915). Mouth sub-ventral, anus terminal or turned dorsally. Skin smooth to the touch, with thick gelatinous subcutaneous tissue. Tentacles 20. Pedicels of the odd ventral ambulacrum rather scattered, not exceeding 25 in number, arranged in a zigzag or double row. Each ventro-lateral ambulacrum has numerous pedicels that form a zigzag row along the margin of sole. There are 4 rows of papillae on the dorsal surface Each papilla is situated on a conical wart. Papillae of the outer rows are larger than those of the inner. Each of these rows consists of 12-15 papillae. Much smaller papillae of the ventro-lateral ambulacra form a marginal row along each side. Calcareous ring weakly developed. One Polian vesicle. **Ossicles**. Cruciform table-like deposits are distributed uniformly in the bodywall. Each arm is perforated with a small hole at end.

Spire solid and high; the end is divided into 3 long processes, which unite again at some distance from the apex and thus give rise to a slit-like hole. End plate is well developed in pedicels. Supporting rods of tentacles are spinous and bent, often armed with some irregular branches.

Material examined. See appendix 1, Table 68.

Type material. Holotype, USNM 34144.

Type locality. *Albatross* St. 4979 or St. 5084(?), Pacific Ocean.

Geographic distribution. South of Totomi, Honshu, Japan.

Bathymetric distribution. 918-3021m.

Remarks. This species differs from *S. aenigma* Ludwig only in having a visible calcareous ring. *S. crucifera* Perrier, *S. horridus* Koehler and Vaney, and *Synallactes monoculus* Sluiter are allied to *S. gilberti*, but in none of them have the fungiform papillae been described, nor is the arrangement of the pedicels of the odd ventral ambulacra similar to that in this species.

Synallactes heteroculus (Heding, 1940) [new comb.]

Bathyplotes heteroculus Heding, 1940: 348-349, textfig. 13, figs. 1-4 [new synonymy].

Diagnosis. Dorsal side covered with papillae irregularly distributed, each with a thin terminal tip. **Ossicles**. Exclusively four armed tables. Each arm with an irregularly perforated end plate. Singular stem with several spines on the top, one or two small holes in the stem.

Material examined. See appendix 1, Table 69.

Type material. Holotype, ZMUC; Paratypes, ZMUC (4 specimens).

Type locality. Th. Mortensen's Pacific Expedition 1913-1916, St. 192, North Ocean Pacific, Philippines, 15 miles W. ½ S. of Jolo, 450m, 27 March 1914.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 450m.

Remarks. Heding (1940) described this species using a fragment of the bodywall and mentioned its affinity to *Bathyplotes monoculus* (=*Synallactes monoculus*). This fragment probably came from a juvenile specimen of *Bathyplotes monoculus* Sluiter, 1901. Heding (1940) did not explain the differences of this species and *B. monoculus*. He just said that both species could be placed in a new sub-genus because of the presence of the singled pillar spire. Moreover, the external appearance of both species is very similar.

Synallactes horridus Koehler & Vaney, 1905

(Figures 210-215 in CD)

Synallactes horridus Koehler & Vaney, 1905: 16-17, Pl. 12, figs. 15-18; Madsen, 1953: 169 (list).

Diagnosis. Subcylindrical body. Mouth ventral, anus dorsal, surrounded by numerous papillae. All the radii have, with the exception of the mid-ventral ambulacrum, large conical papillae. There are 14-15 of these papillae on the ventro-lateral radii. One Polian vesicle. **Ossicles**. The bodywall is rather thin and contains ossicles of two kinds: many cruciform bodies and rods. The cruciform bodies are generally four armed and the distal ends are perforated, the spire is solid and high; one or two small spines form the top of the spire. The cruciform bodies in the papillae have a longer and fragile stem than that from the bodywall. Supporting rods of tentacles are spinous and bent, often armed with some irregular branches.

Material examined. See appendix 1, Table 70.

Type material. Location unknown.

Type locality. *Investigator* St. 117, Indian Ocean, 11º 58'N, 88º 52' 17" E, 3146m.

Geographic distribution. Indian Ocean.

Bathymetric distribution. 975-3195m (Madsen, 1953).

Synallactes sp. 1.

(Figures 216-222 in CD)

Diagnosis. Subcylindrical body, slightly flattened ventrally. Smooth bodywall. Ventral tubefeet short, cylindrical, with a suck tip termination, each disc posseses a big perforated end plate. Distribution of tubefeet: 4 longitudinal series along the dorsal radii. Dorsal surface with short, conical papillae, arranged in 6 longitudinal rows at regular intervals. At the anterior end, these papillae are longer than the others. Mouth ventral, anus subdorsal. 20 tentacles. Calcareous ring low and weak developed. Radial pieces of different robustness and shape, depending on their position in the calcareous ring. Interradial pieces of similar aspect and size. 1 Polian vesicle. A small stone canal. Gonads branched in two tufts. Small cloaca. **Ossicles**. Spiny rods in tentacles, curved or straight. Ventral side of the body with cross-shaped tables, the disk consists of four arms, the distal ends of which have a larger or smaller number of perforations, and often send out processes laterally. This may unite with similar processes of the other arms and produce an open circular latticework. The spire consists of a single pillar, which may be divided or perforated, or both, at the upper end. There are supporting rods and terminal disks in the ambulacral appendages. Long spiny rods are present in the ventral side of the bodywall. Bodywall with smaller and robust four-armed tables. Dorsal bodywall with four-armed tables with the distal ends joined to produce an open circular latticework. Spire of the dorsal tables single, high and often with a bifid and perforated upper end. One or two pairs of small, short and robust spines on the lateral sides of the upper end of the spire. Ossicles in the papillae like those in the dorsal bodywall.

Material examined. See appendix 1, Table 71.

Type material. Holotype, ZMUC.

Type locality. Dr. Th. Mortensen's Expedition 1929-1930, *Pickle* Stn. 25, South Atlantic Ocean, South Africa, Off Durham, 29º 56' S, 31º 19' 30" E, 409m.

Geographic distribution. On its type locality and *Galathea* St. 196, South Africa.

Bathymetric distribution. 409-460m.

Remarks. The specimens identified here as belonging to *Synallactes* sp. 1 were identified erroneously as *Bathyplotes heteroculus* Heding, 1940, by Heding at the ZMUC, Denmark. The presence of single pillared tables and the arrangement of the pedicels in *Bathyplotes heteroculus* Heding, 1940 makes this species a member of the genus *Synallactes*. A similar case is presented by *Paradeima elongata* Heding, 1940, were the presence of single-pillared tables and the arrangement of podia and pedicles reveal that this species belongs to the genus *Synallactes*.

Externally, *Synallactes* sp. is similar to *S. profundus* Koehler and Vaney, 1905, but the arrangement of mid-ventral tubefeet distinguish it. *Synallactes* sp. 1 posseses a well developed mid-ventral row of tubefeet and *S. profundus* lacks pedicels in the anterior part of the mid-ventral ambulcrum. *Synallactes* sp. 1 has single-pillared tables with a pointed top as in *S. aenigma*, *S. horridus*, *S. robertsoni* and *S. profundus*. However, no other *Synallactes* species exhibits the well-elaborated open circular latticework of the table bases. *Synallactes alexandri*, *S. discoidalis*, *S. challengeri*, *S. horridus*, *S. monoculus*, *S. multivesiculatus*, *S. nozawai*, *S. rigidus*, *S. sagamiensis*, *S. triradiata* and *S. viridilimus* possess closed or opened circular table disks. Some of these species even developed a latticework-like table disk structure as in *S. discoidalis*, but this is very different from that in *Synallactes* sp. 1, which is irregularly elaborated.

Synallactes sp.1 is distributed in the South Atlantic Ocean, South Africa, off Durham. As far as I know, there is only one species of the genus that shares this distribution: *S. challengeri*.

Synallactes longipapillata Sibuet, 1978

Synallactes longipapillata Sibuet, 1978: 311-318, Plates 1-3.

Diagnosis (after Sibuet, 1978). Body elongated, almost cylindrical attenuated at both ends. Ventral face nearly flat, dorsal face convex. The ventral part is covered with many pedicels quite thick and rough. Mouth and anus ventral, around them, dorsally there are long papillae. 18 tentacles arranged in two distinct rings. Tentacles discs with 3 or 4 lobes dividing into two secondary lobules. Ambulacral appendages are arranged in regular series along the radii. The papillae are conical on the dorsal surface. Calcareous ring well developed. 1 Polian vesicle. Gonads in two tufts, branched, long. Respiratory trees well developed. **Ossicles**. In the papillae tri-radiate ossicles. They are made up of 3 branches, their distal ends form a lattice work. Ossicles very numerous in the dorsal papillae, the 3 branches each with perforated distal ends. Central spire unique, terminating in a simple delicate tip. Podia with tri-radiate ossicles, same structure as those found at the papillae, but smaller and arched, with dichotomous extremities. Pedicels with perforated plates. Tentacles with numerous rods more or less covered with spines.

Material examined. None.

Type material. Holotype, MNHN.

Type locality. BIOGAS, St. 2, DS 40, North East Atlantic, Bay of Biscay, France, 47° 36’ 4” N, 9° 04’ 2” W, 3345m.

Geographic distribution. North East Atlantic, Bay of Biscay.

Bathymetric distribution. 3345m.

Remarks. This species differs from all the rest in the arrangement of the papillae and the podia. It is closely related to *S. crucifera*.

Synallactes mollis Cherbonnier, 1952

Synallactes mollis Cherbonnier, 1952: 475-476, Pl. 36, figs. 1-15, 18, 19; Thandar, 1984: 350.

Diagnosis (after Cherbonnier, 1952). Body ventrally flattened. Bodywall very thin. Mouth subventral, anus terminal. 18 tentacles. Ventral tubefeet, long, cylindrical, with terminal disc, distributed in two longitudinal rows vetro-laterally and in 4 to 6 rows along the mid-ventral radius. Dorsal papillae long, conical, forming six longitudinal rows uniformly distributed on the radius. Calcareous ring well developed, massive, irregular, there is no distinction between radial and inter-radial pieces. 2 Polian vesicles. One stone canal. Respiratory trees in 2 high-branched tufts. **Ossicles**. Curved rods on ventral tubefeet. Can be spiny and with perforated ends. Rods of the dorsal papillae similar to those of the ventral side. Ventral bodywall with two different kinds of tables: the smallest ones with a base formed by 3 to 4 arms with perforated ends. Upper end of the cruciform bodies perforated or not perforated. Dorsal side with the same kind of ossicles, but bigger. The arms of the table never fused to form a discoidal body as in *S. viridilimus*. In the anal region, the ends of the arms of the tables are more reticulated. The rods of the tentacles can be of two different kinds: 1) big, spiny and slightly curved with one perforated end, and 2) small, curved, spiny and perforated in both ends.

Material examined. None.

Type material. Holotype, SAM.

Type locality. *Africana* St. 723, Atlantic Ocean, Off Morocco, 31º 30’ S, 17º E, 364m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 364m.

Remarks. Only one specimen is known of this species (TL: 145, W: 35). *S. mollis* differs from *S. viridilimus* in the number of tentacles, and in the arrangement of the ventral and dorsal papillae. It is closely related to *S. crucifera,* having similar tables but different upper ends of the spire.

Synallactes monoculus (Sluiter, 1901a) [new comb.]

Bathyplotes monoculus Sluiter, 1901a: 3-4, 1901b: 35-36, Pl. 8, figs. 11a-e [new synonymy].

Diagnosis (after Sluiter, 1901a). Ventral side flat, dorsal side weakly curved. Mouth ventral, with 18 moderately-large tentacles. Anus dorsal. Mid-ventral radius naked. One Polian vesicle. Gonad branched in 2 tufts. Respiratory trees well developed. **Ossicles**. Four-armed cross-shaped bodies. The spire is formed by one stem that widens itself in the centre and carries an oblong oval hole. Top of the spire formed by 2 points. In the tubefeet thorny, curved supporting rods.

Material examined. Syntypes.

Type material. Syntypes, ZMA E1176/1 (1 specimen); ZMA E1176/2 (1 specimen).

Type locality. *Siboga* St. 212 Philippines, 5º 54.5’S, 120º 19.2’E, 462m.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 310-462m.

Synallactes multivesiculatus Ohshima, 1915

(Figures 223-226 in CD)

Synallactes multivesiculatus Ohshima, 1915: 222-223, Pl. 8, figs. 1a-c.

Diagnosis (after Ohshima, 1915). Body slightly flattened, more tapering posteriorly than anteriorly. Mouth subventral, anus terminal. 20 tentacles. Scattered pedicels, but large. The mid-ventral radius has two zigzag rows of about 48 pedicels each; ventro-lateral ambulacra each with a zigzag row of 38 pedicels. Small papillae with no wart-like base, forming six rows in on the dorsal surface, each row consisting of about 45 papillae. Calcareous ring well developed, radial segments with bifurcated, prolonged anterior process. From 9 to 13 Polian vesicles. Stone canal situated in dorsal mesentery. Gonads in two tufts branched. Respiratory trees well developed. **Ossicles**. Table-like deposits scattered in the bodywall, almost exclusively tri-radiate. Scattered small tables and few delicate supporting rods in papillae, end-plate represented by a number of irregularly branched rods. Supporting rods of tentacles similar to those of papillae.

Material examined. See appendix 1, Table 72.

Type material. Holotype, USNM E34143; Syntypes, USNM 16254 (1 specimen).

Type locality. Japan, South of Hokkaido; off Ojika Peninsula, Honshu.

Bathymetric distribution. 194-844m.

Remarks. The presence of as many as 10 or more Polian vesicles is a character, which distinguishes *P. multivesiculatus* from all the other *Synallactes* species.

Synallactes nozawai Mitsukuri, 1912

(Figure 227 in CD)

Synallactes nozawai Mitsukuri, 1912: 23-25, textfig. 5; Ohshima, 1915: 221-222; Savel'eva, 1941: 74-76, textfigs. 1-2; Djakonov, 1949: 115, Pl. 18, fig. 105 a-b; Baranova, 1957: 237.

Diagnosis (after Mitsukuri, 1915). Pedicels of ventro-lateral ambulacra about 70 in each, forming a zigzag row; those of the ventral ambulacrum in two zigzag rows, each consisting of about 60 pedicels. Papillae of dorsum arranged in six rows, of which the median two consists of 30 papillae each, and the remaining four of 25 each. Two genital tufts. One Polian vesicle. Posterior notch of the radial pieces in the calcareous ring very deep. **Ossicles**. Quadri-radiate table-like ossicles are largest at base of papillae and pedicels, attaining the diameter of 430µm, while those scattered in ventrum and pedicels are smaller, with a diameter as small as 50µm. Tentacles are strengthened by bent, cylindrical rods with several short knobs usually in pairs, and perforated with very minute holes at each end.

Material examined. See appendix 1, Table 73.

Type material. Location unknown.

Type locality. Hokkaido, Japan.

Geographic distribution. Hokkaido (Mitsukuri, 1912); Bering Sea; north of Sado Island, west of Hokkaido; off Cape Terpyeniya, Sakhalin.

Bathymetric distribution. 108-787m.

Remarks. The principal points which distinguish this species from *S. triradiata* are, 1) the ventral median zone has fewer pedicels; 2) ossicles are nearly all four-armed, and very rarely three-armed; 3) large and peculiar supporting rods, present in the wart-like conical basal parts of dorsal papillae together with the cruciform bodies, form a very prominent feature. This also distinguishes it from *S. challengeri* and *S. alexandri*.

Synallactes profundus (Koehler & Vaney, 1905) [new comb.]

Bathyplotes profundus Koehler & Vaney, 1905: 22-23, Pl. 4, figs. 1-2, Pl. 10, figs. 19-20 [new synonymy].
Not *Bathyplotes profunda* (Walsh), Koehler & Vaney, 1905: 2 (list).
Not *Bathyplotes profundens*, Madsen, 1953: 168 (list).

Diagnosis (after Koehler and Vaney, 1905). Body flattened; the ventral face is plane and the dorsal surface is slightly convex. The mouth is ventral; the anus is terminal and surrounded by papillae. 17 tentacles. The ventral surface is surrounded by a continuous brim about 3mm wide The mid-ventral radius is not completely naked, there are few tubefeet near the anterior and posterior ends, but the centre area is naked. The dorsal surface possesses two rows of. 2 gonad tufts. **Ossicles**. Cruciform ossicles with a single long spire, arms of the cruciform ossicles four- or five-armed, with perforated, flattened ends. The top of the spire is more or less conical and often carries small spines. Sometimes it is completely smooth.

Material examined. See appendix 1, Table 74.

Type material. Location unknown.

Type locality. *Investigator* St. 111, Indian Ocean, 12º 50'N, 90º 52'E, 2959m.

Geographic distribution. Cosmopolitan species. North Pacific Ocean; South Atlantic Ocean, Scotia Sea, South west of South Georgia Island; Indian Ocean.

Bathymetric distribution. 2959-4925m.

Remarks. S. *profundus* fits into the diagnosis of the majority of the *Bathyplotes* species because the presence of appendices on the mid-ventral radius. But the presence of single pillared ossicles fits with the diagnosis of *Synallactes*.

Synallactes rigidus Koehler & Vaney, 1905

Synallactes rigidus Koehler & Vaney, 1905: 17-19, Pl. 5, fig. 1, Pl. 9, figs. 12-16.
Not *Laetmogone spongiosa*, Walsh, 1891: 200.
Synallactes anceps Koehler & Vaney, 1910: 90-91, Pl. 2, figs. 6-10 [new synonymy].

Diagnosis (after Koehler and Vaney, 1905). The ventral face is flattened and the dorsal face is strongly curved. Mouth ventral, anus sub-dorsal. 15-16 tentacles. The tegument is rigid and rough. The ventral face is limited laterally by a rim of rather long conical papillae. These marginal papillae surround the body, except the posterior area. The dorsal face is strongly folded and has a number of lateral papillae arranged in six longitudinal rows; there are 10 papillae in each row. 2 gonadal tufts. One Polian vesicle. **Ossicles**. The bodywall is rigid and rough with many cruciform bodies and rods. The arms of the cruciform ossicles are generally four-armed and they are spread out at their distal ends. The ends have perforations of variable dimensions. Spire formed by a conical stem, ending in two to three small points. Some ossicles have a greater number of arms; their final discs are greatly perforated uniting to form a latticework. Rods with bifid spiny ends are present in the tentacles.

Material examined. None.

Type material. Location unknown.

Type locality. Indian Ocean, Bay of Bengal, 10º N, 91º 7’E, 3463m.

Geographic distribution. Indian Ocean.

Bathymetric distribution. 2100-3520m.

Remarks. *S. anceps* and *S. rigidus* share the same bathymetrical distribution, depth, and kind of ossicles. Its is strange that as the two species are so closely related that Koehler and Vaney did not discuss the species in their 1910 paper. *S. anceps* was erected using a small specimen, only 55mm long (a juvenile?).

Synallactes robertsoni Vaney, 1908

Synallactes robertsoni Vaney, 1908: 408-409, Pl. 3, figs. 34-36.

Diagnosis (after Vaney, 1908). Body flattened. Posterior end slightly attenuated and rounded. Mouth and anus terminal. 16 tentacles. Ventral face slightly convex. Ventro-lateral radii with a single row of 30-40 pedicels, very close to each other towards the anal region. Along the med-ventral radius, on the posterior quarter, there are about 10 pedicels irregularly distributed in two rows. The middle part of the body, about half of the body length, does not have pedicels, but the anterior quarter has 10 appendices distributed in two rows. Papillae on dorsal face with a broad base distributed uniformly. Calcareous ring well developed. One Polian vesicle. 2 gonads not branched. Respiratory trees well developed. **Ossicles**. In the bodywall cross shaped bodies, four armed, each arm, at the distal end its flattened and, perforated with a big central whole and 1-2 smaller perforations. A single spire terminating in a tip with several projections. Ossicles in pedicels rods, with branched tips.

Material examined. None.

Type material. RSM 1921.143.1163.

Type locality. *Scotia* St. 295, 66º 40’ S, 40º 35’W, 4413.5m, 10 Mar1903.

Geographic distribution. Only known from its type locality.

Bathymetric distribution. 4413m.

Synallactes sagamiensis (Augustin, 1908)

(Figures 228-229 in CD)

Stichopus sagamiensis Augustin, 1908: 8-10, textfig. 6; Clark, H. L, 1922: 47.

Stichopus sagamiensis var. *alba* Augustin, 1908: 10, Pl. 1, fig. 3, textfig 7; Clark, H. L, 1922: 47; Jangoux *et al.*, 1987: 298 (list).

Synallactes ishikawai Mitsukuri, 1912: 21-23, textfig. 4; Ohshima, 1915: 221. [new synonymy].

Diagnosis. Subcylindrical body. Mouth ventral. 20 tentacles. Anus terminal. Tubefeet on the ventral surface in 3 rows in each radius. Inter-radii with tubefeet irregularly arranged. Dorsal inter-radii with no papillae. Papillae present only in the radial areas, arranged in alternating double rows. Papillae very small, no warts in the base of the papillae. Papillae slightly conical, approximately 10mm apart. 3 Polian vesicles. Two tufts of unbranched gonads, one in each side of the mesentery. Respiratory trees well developed. **Ossicles**. In the dorsal bodywall very much like those of other *Synallactes* species. The bases of the dorsal papillae are especially large. In the basal part there are also curved supporting rods with both ends perforated. There are some very weakly developed terminal plates. The ventral bodywall has very characteristic ossicles. There is a lower, very thickly crowded layer of rods and scattered over these are discoidal tri-radiate tables. Ventral pedicels have rods and tables of the same general character as those of the ventral bodywall. At the base there are no especially large tables. There is numerically a greater proportion of the tri-radiate ossicles in comparison to the circular ones. End-plates well developed.

Material examined. See appendix 1, Table 75.

Type material. Holotype, ZS 118/1.

Type locality. Misaki, Sagami Bay, Japan, 180m. Coll. Doflein (see Jangoux *et al*., 1987).

Geographic distribution. Gulf of Tehuantepec, Mexican Pacific; Misaki, Sagami Bay, Japan (Augustin, 1908; Mitsukuri, 1912); off Ojika Peninsula; south of Joga Shima, Sagami Bay. Various *Albatross* stations from the year 1906 in the Central Pacific (Sts. 5046, 5048, 5091, 5092, 5094) (Ohshima, 1915).

Bathymetric distribution. 128-4297m.

Synallactes triradiata Mitsukuri, 1912

Synallactes triradiata Mitsukuri, 1912: 12- 18, textfig. 2.

Diagnosis (emended from Mitsukuri, 1912: 13). Tentacles 20, may be reduced to 19 or 16. Body cylindrical or subcylindrical, without any marginal border between the ventrum and the dorsum. Mouth ventral, anus terminal. Dorsal papillae are in six longitudinal rows. Each papillae has a large wart-like conical base, from the top of which a much more slender papilla arises. The papillae on the dorsal side of the mouth have small bases, but are longer. Ventral pedicels are numerous, arranged in three rows along the mid-ventral and ventro-lateral radii. In each ventro-lateral zone the pedicels stand alternately in two rows. The mid-ventral zone has also numerous pedicels in three to four zigzag rows. The pedicels of ventro-lateral zones protrude, while those of the mid-ventral radius are strongly contracted. Gonads in two tufts. Stone canal single, running directly in front of, and along side, the genital duct attached to the dorsal bodywall. Polian vesicles from 1 to 3, tube-like or vesicle-like, attached to the ventral interradius. Two respiratory trees, branched, not long. **Ossciles**. With the exception of the supporting rods, the calcareous deposits are tri-radiate tables, the arms of which stand 120° apart. The distal ends of the arms are more or less enlarged and perforated. On the ambulacral appendages, the ossicles are rarely four armed ossicles. The spire terminates into several points. Tables of the bodywall of different sizes in different parts of the body. On the dorsal surface the ossicles between the basal conical warts of the papillae are much more sparse than within the warts. In the latter case the ossicles are generally smaller. The ossicles in the ventral bodywall are on the whole much smaller than those dorsally and also much less common. Quadri-radiate ossicles are found in the dorsal papillae above the basal conical warts, but never in any great number. In ventral pedicels the tri-radiate ossicles are sparse and a terminal disk is distinct. The supporting rods have both ends pointed. In dorsal papillae the ends of the rods are enlarged and perforated, not pointed. Ossicles in the tentacles are somewhat like those in the dorsal papillae but smaller.

Material examined. See appendix 1, Table 76.

Type material. Location unknown.

Type locality. Maye-no-Yodomi, Ike line, Sagami Bay, Japan, 1080m, 17 Jan 1896.

Geographic distribution. Sagami Bay and Sagami Sea (Mitsukuri, 1912). North East Pacific Ocean, Bering Sea, Alaska, Aleutian Islands, Fox Islands, Unalaska Bay.

Bathymetric distribution. 640-1092m.

Remarks. Mitsukuri (1912) analysed 19 specimens, ranging from 45-110mm in body length. He stated that this species resembles *S. challengeri* and *S. alexandri* in some aspects, but they differ basically in the ossicles shape, being quadri-radiate in *S. challengeri* and tri-radiate in *S. triradiata.*

Synallactes viridilimus Cherbonnier, 1952

Synallactes viridilimus Cherbonnier, 1952: 473-475, Pl. 35, figs. 1-17; Pl. 36, 16-17; Thandar, 1984: 351.

Diagnosis (after Cherbonnier, 1952). Body subcylindrical, slightly flat ventrally. Bodywall smooth, very thick. Mouth and anus ventral. 20 tentacles. The ventral tubefeet are long, cylindrical, with a broad suction cup containing an enormous reticulated calcareous disc. The tubefeet are very numerous and are laid out on two rows along the ventro-lateral radii, and in four rows along the mid-ventral radius. The dorsal side with long, conical papillae spaced apparently in 5-6 rows. The calcareous ring is weakly calcified, Two Polian vesicles. 2 gonads richly branched. **Ossicles**. Ventral feet with long rods with perforated ends. Same kind of rods in the dorsal papillae. Ventral bodywall with cross-shaped ossicles, spire ending in three points. Small tables with no basal disc. Dorsal bodywall with the same kind of ossicles as the ventral side (with exception of the small tables with out basal disc). Rods in tentacles, curved or straight.

Material examined. None.

Type material. Holotype, SAM 700 C.

Type locality. *Africana* St. 700, Atlantic Ocean, Off Morocco, 32º 33’ S, 16º 31’ E, 522m, 19 May 47 (Cherbonnier, 1952).

Geographic distribution. Only known from its type material.

Bathymetric distribution. 522m.

Genus *Zygothuria* Perrier, 1898

Zygothuria Perrier, 1898: 1665; 1899: 245-246, 1902: 321-322; Deichmann, 1930: 108.

Diagnosis (modified from Perrier, 1902). Body ovoid, flattened, but with a well-differentiated sole; integument often wrinkled. Tubefeet arranged exclusively in a single or double row along ventrolateral ambulacra, placed on the margin of the sole, which often forms a fringe. Tubefeet are widely spread and may be quite big; dorsal papillae minute, not numerous, irregularly distributed or arranged in two simple rows and sometimes totally absent. 20 tentacles, rarely 13-19; madreporite placed close to bodywall, without penetrating it. Mouth ventral or terminal, anus terminal, without special arrangement. Calcareous ring, sometimes with triangular radial segments. **Ossicles**. Integument with tri-radiate tables.

Type species: *Zygothuria lactea* (Théel, 1886a) designated by Hérouard (1902).

Remarks. This genus was rejected by Sluiter and Hérouard, but it seems to me reasonable to have a separate genus for this form that hardly has any tubefeet. In addition, the shape of the tables seems to be characteristic. Perrier mentions supporting rods in the feet of *Zygothuria*; they are few and often difficult to find, when the appendages are completely contracted, but I think their presence will prove to be a general character of the genus.

Zygothuria candelabri (Hérouard, 1923)

Mesothuria candelabri Hérouard, 1923: 17-19, Pl. 1, figs. 1-10; Madsen, 1953: 153.
Non *Mesothuria* (*Allantis*) *candelabri*, Heding, 1940: 334-335, textfig. 3 [= *Mesothuria* (*Penichrothuria*) *cathedralis*].
Zygothuria candelabri, Deichmann, 1930: 111.

Diagnosis. Body ovoid, flattened, but with a well-differentiated sole; integument often wrinkled. Tubefeet arranged exclusively in a single or double row along ventrolateral ambulacra, placed on the margin of the sole, which often forms a fringe. 20 tentacles. Calcareous ring well developed, with squarish radial pieces. **Ossicles**. Tables with stems formed by 3 columns, the three columns join to form a single stem at the top of the spire. The base of the table is formed by a circle of 7-8 rods. Consequently the discs the 8-9 main holes are surrounded by a number of smaller ones.

Material examined. None.

Type material. Syntype, MOM.

Type locality. *Princesse-Alice* St. 2986, Bay of Biscay, 4870m, year 1910.

Geographic distribution. North East Atlantic Ocean, Bay of Biscay; off Morocco.

Bathymetric distribution. 3890- 4870m.

Remarks. This species was described from some fragments. The type fragments came from the Gulf of Biscay, 4870m. The tables of the skin are indicated to have relatively few holes and excessively long diverging spines on top of spire, with a few small teeth scattered along the sides of the spines. Most likely identical with *Z. lactea*. Some authors have confused the spelling "c*andelabri*" with "*candelabra*".

Zygothuria connectens Perrier, 1898

Zygothuria connectens Perrier, 1898: 1665; 1899: 246; 1902: 327-332; Deichmann, 1930: 111.
Mesothuria connectens (Perrier, 1898); Mortensen, 1927: 380, textfig 224.

Diagnosis (after Perrier, 1902). No apparent papillae in the dorsal surface. Latero-ventral surface with big pedicels forming a row. Mouth ventral, subterminal. One gonad, slender tubes, branched. 1 Polian vesicle. Respiratory trees well developed. **Ossicles**. Tables, terminal tips of the spires, simple with no teeth. The spire is longer than in *Z. lactea*. Three pillared stem. Disk with a hole in the centre and 6 to 8 perimarginal holes. The ossicles are typically larger than those of *Z. lactea*. The disk is very irregular, the spire is high and ends usually in four long smooth arms, curving upwards.

Material examined. None.

Type material. Syntypes, MNHN 7135 (? Specimens), MNHN 7146 (? Specimens).

Type locality. *Talisman*, South East Atlantic Ocean, off Sahara, 1975-2518m.

Geographic distribution. South East Atlantic Ocean, off Sahara; off the Canaries Islands (Perrier, 1902; Pérez *et al*., 1984).

Bathymetric distribution. 1975-2518 m.

Remarks. The description of the species was based on three individuals in poor condition, from off the Canaries at 1975m, and off coast of Sahara, 2325-2518m. The tables were indicated to have numerous holes in disk, and a few were stated to be four or even five-rayed. The spines on top of spire were long, smooth and diverging.

Zygothuria lactea (Théel, 1886a)

Note: for all this information see Chapter 3, section 3.3.1 of this thesis.

Zygothuria marginata (Sluiter, 1901a) [new comb.]

(Figures 230-239 in CD)

Mesothuria marginata Sluiter, 1901a: 13, 1901b: 26-27, Pl. 8, figs. 4a-c; Liao, 1997: 75-76, textfig. 40 [new synonymy].
Mesothuria (*Monothuria*) *marginata*, Heding, 1940: 341-342, textfig. 8, figs. 1-5.
Zygothuria marginata, Perrier, 1902: 331.

Diagnosis. Cylindrical body. Skin thick, particularly at the sides of the body. A broad brim surrounds the body. The brim does not continue along the front or the back of the body. Mouth and anus terminal. 15 tentacles, each with 12 digits. Calcareous ring well developed. One Polian vesicle. One gonad on the left side of the dorsal mesentery. Respiratory trees well developed. **Ossicles**. Three pillared tables. The tree pillars are united at the centre of its length by a short stem. The top of the spire is formed by a single pillar, normally ornamented with few lateral spines. The base of the table is circular, with a central hole surrounded by 6 marginal holes connected to a bigger central hole, and with 10 to 12 small holes around the periphery of the disk. Rods present in the tubefeet as supporting rods. Tubefeet with calcareous end plates.

Material examined. See appendix 1, Table 78.

Type material. Syntypes, ZMA E1028 (1 specimen); ZMA E1029 (1 specimen).

Type locality. *Siboga* St. 87, Indonesia, 0º 32’S, 119º 39.8’E, 655m.

Geographic distribution. Southeast Asia, Indonesia, off Palu; East Asia, Japan; East China Sea; Oceania; Indonesia, Philippines.

Bathymetric distribution. 365-7860m.

Zygothuria oxysclera (Perrier, 1902)

Note: for all this information see Chapter 3, section 3.3.1 of this thesis.

Zygothuria thomsoni (Théel, 1886a) [new comb.]

Holothuria thomsoni Théel, 1886a: 184-185, Pl. 10, figs. 8, 11.
Holothuria thomsoni var. *hyalina* Théel, 1886a: 185.
Mesothuria thomsoni, Östergren, 1896: ? [new synonymy].

Diagnosis. Body oval. Mouth ventral. Anus terminal. 12 tentacles. A simple alternating row of pedicels along each side of the ventral surface, and some small papillae scattered on the ventral surface in the neighbourhood of these rows. No other ambulacral appendages are visible. Calcareous ring narrow, fragile, without posterior processes. Three Polian vesicles. **Ossicles**. Bodywall unusually rough, caused by an abundance of crowded tables consisting of large, irregularly perforated disks with the central hole usually smaller than the peripheral ones; the spire is composed of three rods and one transverse beam, and terminates in three very long, slender, and spinous teeth.

Material examined. None.

Type material. Location unknown.

Type locality. HMS *Challenger* St. 237, North Pacific Ocean, 34° 37’N, 140° 32’E, 3375m, 17 Jun 1875.

Geographic distribution. Only known from its type locality.

Bathymetrical distribution: 3375m.

Incertae sedis

Genus ***Allopatides*** Koehler & Vaney, 1905

Remarks. The genus *Allopatides* contains 2 species: *Allopatides dendroides* Koehler and Vaney, 1905 and *Allopatides corrugatus* Massin, 1987.

I have placed this genus as an *incertae sedis* genus because the presence of taxonomic characters that cannot be of fitted into the Synallactidae, such as the presence of dendritic bodies that are not present in the rest of the family. When naming the genus, Koehler and Vaney (1905) never mentioned the presence or absence of tentacle ampullae. The position of this genus in the Synallactidae is dubious. The specimen used by Koehler and Vaney (1905) to described both genus and type species (*A. dendroides*) was eviscerated so it was impossible for them to describe in detail the internal anatomy.

When Massin (1987) described *Allopatides corrugatus* he clearly used only the external appearance to classify his specimen. He states that because its external appearance *A. corrugatus* is a synallactid. The only specimen examined by him was completely eviscerated, and was in very poor condition with only part of a respiratory three, gonad and esophagus remaining internally, "*le animal est eviscere et seuls subsistent l'organe arborescent droit, una partie de la gonade et le oesophage*". Such characters are insufficient to place this genus and its species into the Synallactidae.

Genus ***Bathyzona*** Koehler & Vaney, 1905

Remarks. The genus *Bathyzona* Koehler and Vaney, 1905 was erected using a single, small (75mm long), eviscerated specimen.

Even though its external appearance and form of ossicles resembles the genus *Pelopatides*, the authors decided to create a new genus. The genus contains only the type species, *Bathyzona incerta.* No respiratory trees were found. Its position and validity as a genus into the Synallactidae needs further analysis.

Genus ***Capheira*** Ludwig, 1893

Remarks. This controversial genus contains 2 species: *Capheira sulcata* Ludwig, 1893 and *Capheria mollis* Ohshima, 1915. When Ludwig (1893) erected this genus, he placed it into the Elpidiidae. Clark, H. L. (1920) included this genus into the family Deimatidae. Baranova (1957) considered that *Capheria* was closer to the synallactids. He included the genus in the family Gephyrothuriidae. His idea survived for a long time. O'Loughlin (1998) clarified the position of various genera in the Gephyrothuriidae, but he forgot Baranova's ideas about including *Capheira*.

In this thesis I remove the genus *Capheira* from the Synallactidae, into the *incertae sedis* taxonomic position because of its aberrant characters that cannot be inclused with the synallactids. Such characters are 1) the presence of 30 tentacles, 2) numerous madreporic channels, and 3) the calcareous ring has 15 pieces (5 true radial pieces and 10 inter-radial).

Genus ***Dendrothuria*** Koehler & Vaney, 1905

Remarks. Koehler and Vaney (1905) created this genus to include some synallactid-like specimens that resembled the genus *Pelopatides*. The diagnostic characters that they used were 1) the presence of 20 dendritic tentacles, 2) a very well developed pharynx occupying more than the 50% of body the length, 3) a subcylindrical body, 4) big marginal papillae, 5) tubefeet in the mid-ventral radius and 6) branched, slender ossicles bearing small spines. When Koehler and Vaney (1905) erected the species *Dendrothuria similis*, they used one small specimen (110mm long, 20-30mm wide). They found pedicels in the mid-ventral radius. In analysing *Pelopatides megalopharinyx* Sluiter type specimens, they also found such appendages, and because of this, and the presence of a big pharynx, they decided to include Sluiter's species into their new genus, arguing that Sluiter overlooked these pedicels. I placed this genus into the *incertae sedis* group because the lack of characters consistent with the Synallactidae. The authors of this species don't describe the gonads. So, it is possible that they used immature specimens. I have seen a big pharynx in different juvenile deep-sea holothurians such as synallactids and elpidiids.

Genus ***Filithuria*** Koehler & Vaney, 1905

Remarks. *Filithuria* was erected by Koehler and Vaney (1905) as an *incertae sedis* genus to hold the species *Filithuria elegans* Koehler & Vaney, 1905.

This genus is known only from one poorly-preserved specimen of the type species. This lacked respiratory trees, which would indicate that *Filithuria* is an elasipodid. Therefore it would have to be placed in a special family, the Filithuriidae(?). However, Koehler and Vaney (1905) were uncertain whether the respiratory trees might have been present originally, as the internal organs were not well preserved. They preferred therefore to leave the genus as *incertae sedis*. The dermal filaments serve to distinguish the genus from every other know holothurian. Heding (1940) referred the genus *Filithuria* to the family Gephyrothuriidae This idea was followed by Djakonov (1952) and Hansen (1952). Finally O'Loughlin (1998) included the genus *Filithuria* in the Synallactidae, but I believe that there is not enough taxonomic evidence for this. I return this genus to its original *incertae sedis* position following Koehler and Vaney (1905).

Genus ***Galatheathuria*** Hansen & Madsen, 1952

Remarks. This genus contains only one species, *Galatheathuria aspera* (Théel, 1886). Hansen and Madsen (1952) created this genus to embrace specimens with a distinct head-like anterior end and cross-shaped ossicles with a high central spire. This features are typical of the Psycropotidae within the Elasipodida. Some species of *Pelopatides* posses a head-like fore-end (e. g. *Pelopatides confundens*). However, the presence of calcareous bodies as crosses with a high central spire relate this species with *Pelopatides aspera* Théel. Later on this species was transferred to the genus *Galatheathuria* by Hansen and Madsen (1956). The ossicles also show great similarity to *Scotothuria herringi* Hansen.

It is likely that *Galatheathuria* and *Scotothuria* are synonymous. *Scotothuria* may be the juveniles *Galatheathuria aspera*. They share same kind of tentacles and dermal ossicles, and moreover, 1) the position of the anus and 2) presence of a lateral brim, are similar in both genera. The dermal ossicles in *S. herringi* have a characteristic pointed tip that is very fragile and is often missing in *G. aspera* (including *Pelopatides aspera* Holotype specimen). Whether or not *Galatheathuria* is a valid genus, the kind of ossicles and very particular external anatomy makes me include it in a *incertae sedis* position until we have more taxonomic information.

Genus ***Perizona*** Koehler & Vaney, 1905

Remarks. The genus contains only one species, *Perizona magna* Koehler and Vaney, 1905. Koehler and Vaney (1905), using a single specimen, differentiated *Perizona* from *Pelopatides* in the development of the lateral fringe and the presence, on the ventral face of the body, of a row of pedicels along the whole length of the ventro-lateral radii. The validity of such variable diagnostic characters has been question by different authors (Deichmann, 1930; Hansen, 1975) and it's very easy to believe that *Perizona* and *Pelopatides* are indeed synonymous. Even when there is not enough taxonomic evidence to keep *Perizona* as a valid genus, I propose to keep the validity of this genus but as an *incertae sedis* group. It is imperative to collect more specimens in order to clear this problem.

Genus ***Pseudothuria*** Koehler & Vaney, 1905

Remarks. Koehler and Vaney (1905) created this genus to include and species closely related with *Pelopatides*, *Dendrothuria* and *Benthothuria*. They included *Pelopatides megalopharynx* (Sluiter) under this genus. The genus include the species *Pseudothuria duplex* Koehler and Vaney, 1905. The diagnostic characters used by the authors are not enough to place this genus into the Synallactidae, but at the moment there is no holothurian with such taxonomic characters. The presence/absence of a well-developed muscular pharynx is probably not a good diagnostic character when using very small specimens (<20mm). As in *Perizona*, I propose to keep the validity of this taxa, but as an *incertae sedis* group. It is imperative collect more specimens in order to establish or remove this genus.

Genus ***Scotothuria*** Hansen, 1978

Remarks. This genus was created to embrace one species, *Scotothuria herringi* Hansen, 1978. Even though *Scotothuria* is similar to *Galatheathuria* Hansen (1978) created a new genus to include this pelagic species. The family Synallactidae in its *sensu stricto* diagnosis needs to be emended to add taxonomic characters such as, 1) presence of dendritic tentacles and 2) presence of cross shaped ossicles with arms ending in a cluster of spines and with a central apophysis ending in a hood of downward bent hooks. The calcareous deposits of *Galatheathuria* and *Scotothuria* differ from those other Synallactidae in lacking dichotomous ramifications of the arms. This is a similarity to the deposits of the two elasipodid families Psychropotidae and Elpidiidae (Hansen, 1975: 185). The absence of ramifications is probably a secondary feature attained independently in the Aspidochirotida and Elasipodida. The terminal, spinous enlargement of the arms in *Scotothuria* and *Galatheathuria* indicates that the reduction of the ramifications is not quite complete in the Aspidochirotida.

Bathyherpystikes baculosus Massin, 1987

Remarks. The kind of ossicles and the internal anatomy made Massin (1987) decide to place this specimen in the genus *Bathyherpystikes*. He states that *B. baculosus* is almost identical to *B. punctatus*, the only difference between them is the presence of rods and calcified branched nodules in *B. baculosus*. In this case, the diagnosis for the genus created by Sluiter (1901) needs to be emended. Instead of “absence of rods” it should read “absence of rods in the bodywall”. It is very possible that this species is a synonymy of *Mesothuria abbreviata* Koehler and Vaney. The bodywall tables, and the number of tentacles are very similar to *M. abbreviata.* However, it is not possible to make a taxonomic decision without comparing the type material. Even if the genus *Bathyherpystikes* Sluiter, 1901a is a synonym of *Bathyplotes*, I consider that this species needs to be place in the *incertae sedis* group because its difficult to fit the species even into the genus *Bathyplotes*.

Species that have been erroneously identified and/or placed as synallactids

Bathyplotes veleronis Domantay, 1953

Remarks. This species was erected as *nomen nudum* in 1953, until its taxonomic description later in the same year by its author [type material LACM No. Cat. 1724-49 (ex AHF 1724-49)] It is very unlikely that the genus *Bathyplotes* occurs at the depth where this specimen was captured, 18m. Dr. E. Deichmann examined the specimen and she left a label saying “3cm young of *Holothuria paraprinceps* Deichmann” inside the jar. The ossicles observed confirm Deichmann’s statement. A Deichmann comment can be seeing in her *Velero* monographs of 1958 (see pag. 254).

Gephyrothuria europeensis Hérouard, 1923

Remarks. This species was described by Hérouard as a synallactid, but was then synonymised with *Gephyrothuria alcocki* Koehler and Vaney, 1905 and transferred to the family Gephirothuriidae Koehler and Vaney, 1905 by O’Loughlin (1998).

Stichopus richardi Hérouard, 1896

Remarks. Clark (1922) states that “probably” this is a Synallactidae. Hérouard (1896) states that “*les culs-de-sacs tentaculaires son bien developpes*”, so it cannot be a synallactid because it posseses tentacular ampullae.

Stichopus torvus Théel, 1886

Remarks. Clark (1922) states that is a synallactid. Recently O'Loughlin (2002) placed this species into the Synallactidae as *Meseres torvus*. However, the data presented by Théel (1886) are insufficient to confirm any synonymy.

Synallactes(?) dubius Koehler & Vaney, 1905

Remarks. This species was described with two specimens in very poor condition. It was impossible for Koehler and Vaney (1905) to indicate the exact distribution of any external structure. The ossicles illustrated in their work are not synallactid ossicles. Moreover, one of the specimens shows one gonad attached to the dorsal mesentery, making this species closer to *Mesothuria* than any other synallactid genus. The data are insufficient to confirm any synonymy.

Synallactes carthagei Vaney, 1906a

Remarks. The ossicles illustrated in Vaney (1906a) confirm that this species is not a synallactid and that it is closely related with the psolid genus *Staurocucumis*. Moreover, the presence of taxonomic characters such as the presence of 10 dendritic tentacles, anus ventral and the presence of a well-developed ventral sole confirms this point of view.

Chapter Six - Phylogeny of the Synallactidae

6. 1. Phylogeny of the Synallactidae inferred from morphology

6.1.1. Introduction

In this chapter the first morphological cladistic analysis aimed at elucidating high-level relationships within the Synallactidae is presented. The monophyly of the family is tested with representatives from each currently recognized extant genus.

Recently, Kerr and Kim (2001) used cladistic analysis to reconstruct the phylogeny of the Holothuroidea. This analysis supported the monophyly of the Aspidochirotida, the order to which Synallactidae belong. Within the aspidochirotids, Kerr and Kim (2001) found 60% bootstrap support for the clade [(Synallactidae (Stichopodidae, Holothuriidae)].

The family Synallactidae is a very important element of the deep-sea megabenthos worldwide. Despite their ecological importance, many aspects of the biology of the Synallactidae are poorly understood and there is still much debate about fundamental issues, such as systematics and population dynamics. The systematics of the group, in particular, has not yet been fully resolved, even for the abundant and commonly captured species. At the family level, taxonomic distinctions are dependent on a finer level of characters, such as 1) the morphology of dermal and internal organ ossicles, 2) the form of the calcareous ring, and 3) the distribution and morphology of the tubefeet. At the species level, the differences in morphological characters can be quite subtle, obscuring taxonomic distinctions.

Towards this goal, I have obtained partial sequences of the 16S mitochondrial region from 17 species of sea cucumbers, 15 synallactids, 1 elasipodids and 1 stichopodid from different areas of the World (see Table 6.4; Tables 3.1, 3.2 in Chapter 3; Table 4.1 in Chapter 4; Appendices 1 and 2). My molecular analysis focuses on recent evolution within the Synallactidae and has enabled me to re-examine a number of specific taxonomic and phylogenetic questions concerning these deep-sea holothurians.

6. 2. Methods

6.2.1. Ingroup taxa

In this chapter, two representatives from all ten currently recognized genera in the Synallactidae were included, except in the case of the monotypic genus *Hansenothuria*. The use of type species was preferred over non-type species, because these species are supposed to possess the representative (diagnostic) characters of the genera concerned. However, in some cases, type species could not be used because the type material was inaccessible or was poorly described. In these instances, a well-described species, possessing the autapomorphies of the group concerned, was included.

6.2.2. Outgroup selection and rooting

Rooting a tree is the most difficult step in any phylogenetic analysis (Swofford *et al.*, 1996). Ideally, the root should be the common ancestor from which all the ingroup synallactids have descended. This common ancestor (almost) always has the best combination of character states that places it in the unrooted ingroup tree so that it correctly roots the tree.

One way of rooting is by using traits of fossils. Unfortunately, synallactid fossil taxa often lack soft tissue preservation and hence consist mainly of skeletal relicts. It is very hard to prove if these remnants, sorted out from many pieces, belong to one specimen, one species, or to a variety of specimens and species. As a consequence, fossil taxonomy is primarily based on single ossicles. Our knowledge of fossils that are closely related to the synallactids and which might be used as outgroups is very poor. Only a few imprints of the body are available (Cherbonnier, 1976) and only synallactid table ossicles have been found (Gilliland, 1993). The small number of fossils belonging to closely related groups makes it impossible for rooting the synallactid phylogeny based exclusively on fossils. Despite this, one can reconstruct a hypothetical ancestor by combining the traits that both fossil and closely related, extant groups possess (ancestor rooting). It is also possible to include one or more taxa that are assumed to lie outside the ingroup.

Choosing outgroups is an exercise in trying to get a set of ancestral states at the base of the outgroup taxa that most closely resembles those of the ingroup common ancestor.

These character states, permitting a correct rooting, are the plesiomorphies held in common at the base of the ingroup and outgroup. Based on morphological evidence the Stichopodidae is a sister group to the Synallactidae and therefore is a good outgroup (Kerr and Kim, 2001). However, it is recommended to include more than one outgroup taxon as a means of testing the assumption of ingroup monophyly (Swofford *et al.*, 1996). Therefore, two different stichopodid genera were used as outgroups (*Stichopus* and *Isostichopus*). Furthermore, the use of more distantly related genera as outgroups might give a better view of the fundamental characters of the Synallactidae than would congeners.

Therefore, members of the family Holothuriidae were included as an additional outgroup because the family may have retained some synallactid plesiomorphies that were lost by the Stichopodidae. In this chapter, four aspidochirotids (two stichopodids and two holothuriids) were chosen as outgroups (Table 6.1).

There is, however, some reason to suspect that the Synallactidae are an unnatural assemblage (Kerr and Kim, 2001), and might be paraphyletic.

Table 6.1. Holothurian taxa used in the phylogenetic analysis inferred from morphology.

Family	
Holothuriidae Ludwig, 1894	
Genus	**Species used**
Holothuria Linnaeus, 1767	*Holothuria tubulosa* Gmelin, 1790 *Holothuria* (*Halodeima*) *atra* Jaeger, 1833
Family	
Stichopodidae Haeckel, 1896	
Genus	**Species used**
Stichopus Brandt, 1835	*Stichopus herrmanni* Semper, 1868
Isostichopus Deichmann, 1958	*Isostichopus fuscus* (Ludwig, 1875)
Family	
Synallactidae	
Genus	**Species used**
Amphigymnas Walsh, 1891	*Amphigymnas multipes* Walsh, 1891 *Amphigymnas bahamensis* Deichmann, 1930
Bathyplotes Östergren, 1896	*Bathyplotes natans* (Sars, 1868) *Bathyplotes crenulatus* Koehler & Vaney, 1905
Benthothuria Perrier, 1898	*Benthothuria funebris* Perrier, 1901 *Benthothuria cristatus* Koehler & Vaney, 1905
Hansenothuria Miller & Pawson, 1989	*Hansenothuria benti* Miller & Pawson, 1989
Mesothuria Ludwig, 1894	*Mesothuria multipes* Ludwig, 1894 *Mesothuria intestinalis* (Ascanius, 1805)
Paroriza Hérouard, 1902	*Paroriza prouhoi* Hérouard, 1902 *Paroriza pallens* (Koehler, 1895)
Pelopatides Théel, 1886	*Pelopatides confundens* Théel, 1886a *Pelopatides grisea* Perrier, 1899
Pseudostichopus Théel, 1886a	*Pseudostichopus mollis* Théel, 1886 *Pseudostichopus villosus* Théel, 1886a
Synallactes Ludwig, 1893	*Synallactes alexandri* Ludwig, 1893 *Synallactes aenigma* Ludwig, 1893
Zygothuria Perrier, 1898	*Zygothuria lactea* Perrier, 1898 *Zygothuria oxysclera* Perrier, 1902

6.2.3. Phylogenetic analyses

The methodology used in the morphological phylogenetic analyses is described in Chapter 2, Section 2.8 of this thesis.

6.2.4. Character selection

A total of 39 discrete post-larval characters (14 external characters, 20 skeletal, 3 soft-tissue and 2 behavioural) were scored, including 29 binary and 10 unordered, multistate characters (Table 6.2).

Characters were taken primarily from examined and dissected museum and field-collected specimens of all the representative genera in the Family Synallactidae. In addition, and because the rarity of some genera, characters were taken from taxonomic monographs (e.g. Théel, 1886a,b; Ludwig, 1894; Sluiter, 1901a,b; Hérouard, 1902, 1923; Deichmann, 1930; Féral and Cherbonnier, 1981) and other published references (e. g. Hansen, 1978; Sibuet, 1978; Miller and Pawson, 1989). It was not possible to dissect any specimen of *Benthothuria cristatus* Koehler and Vaney, 1905 because apparently, none specimen exist, apart from authors mention. Hence, published accounts were relied upon exclusively to determine the morphology of this species. In several poorly known genera, characters were scored on the basis of several species.

Table 6.2. Character matrix. Missing codings are indicated by "?", polymorphic states (0 and 1) are indicated by "a"; and "-" indicates not applicable. The taxonomic clades are represented by individual species.

	Characters							
Species	**1**	**6**	**11**	**16**	**21**	**26**	**31**	**36**
Holothuria tubulosa Gmelin, 1790	12001	10001	01101	12200	000-0	12001	10000	0100
Holothuria (*Halodeima*) *atra* Jaeger, 1833	12001	00000	00001	12211	00000	12000	00001	0100
Stichopus herrmanni Semper, 1868	20101	00001	01001	1211a	00000	12001	00000	1100
Isostichopus fuscus (Ludwig, 1875)	00211	10110	00001	10122	10000	02000	00000	1100
Amphigymnas multipes Walsh, 1891	00001	00101	00111	10102	00000	12001	1000?	11a0
Amphigymnas bahamensis Deichmann, 1930	00001	00101	00111	10102	00000	12011	11000	1110
Bathyplotes natans (Sars, 1868)	22101	10100	00001	02020	11010	12000	10000	11a1
Bathyplotes crenulatus Koehler & Vaney, 1905	22101	20101	00000	--222	11010	12000	0000?	1110
Benthothuria funebris Perrier, 1901	01211	20101	00000	--0--	-----	00000	00000	1110
Benthothuria cristatus Koehler & Vaney, 1905	20101	00110	00000	-----	-----	-----	----0	1120
Hansenothuria benti Miller & Pawson, 1989	01000	20111	1100-	--020	00000	11000	00000	1111
Mesothuria multipes Ludwig, 1894	00001	00110	00001	10022	00100	12000	10000	01a0
Mesothuria intestinalis (Ascanius, 1805)	00000	00110	00001	10112	00000	12000	10000	0010
Paroriza prouhoi Hérouard, 1902	00100	00000	00001	000--	-----	-----	----0	1120
Paroriza pallens (Koehler, 1895)	00100	00000	00001	00---	-----	-----	--000	11a0
Pelopatides confundens Théel, 1886a	20101	20101	00000	--0--	011-0	01000	00000	11a1
Pelopatides grisea Perrier, 1899	20101	20101	10000	--0--	001-0	11000	00000	1121
Pseudostichopus mollis Théel, 1886	00101	10100	00001	11---	-----	12000	00100	11a0
Pseudostichopus villosus Théel, 1886a	00101	10100	00001	11---	-----	00000	00000	11a0
Synallactes alexandri Ludwig, 1893	00001	20101	00001	020--	011-0	12110	00001	11a0
Synallactes aenigma Ludwig, 1893	20001	20101	00101	120--	011-0	12000	00000	1120
Zygothuria lactea Perrier, 1898	00101	00100	00001	100--	00120	12000	10000	11a0
Zygothuria oxysclera Perrier, 1902	00101	10010	00001	100--	00120	12000	10000	1110

6.2.5. Character selection and coding

In morphological phylogeny, explicitness about character selection is important to increase the rigor of morphological systematics (Poe and Wiens, 2000). One must be explicit on the basis of inclusion and/or exclusion of characters, because that will give an overall idea about the concordance between the data matrix and the nature of the organisms under investigation. Intraspecific variation, ontogeny, interdependency and continuity of measures are common problems encountered during coding of characters. Prior to the construction of the data matrix, a careful reflection on the selection of the characters was made. An annotated list of the characters used in this chapter is given below (Table 6.3).

Table 6.3. List of characters used in the analysis.

Characters

EXTERNAL MORPHOLOGY

1. **Overall shape**: 0=body cylindrical; 1=body convex, with central thickening; 2=body flat.
2. **Tentacle shape**: 0=peltate; disc-like tentacles; 1=bushy; dendritic tentacles; 2= composite-like.
3. **Thickness of bodywall**: 0=1-5mm; 1=5-10mm; 2=more than 10mm.
4. **Ventral sole**: 0= absence, 1=presence.
5. **Position of the mouth**: 0=terminal to sub-terminal; 1=clearly ventral.
6. **Position of the anus**: 0=terminal; 1=sub-dorsal; 2=clearly dorsal.
7. **Average number of tentacles**: 0= maximum 20; 1=more than 20.
8. **Arrangement of ventral tubefeet**: 0=spread over the radial and interradial areas; 1=majority restricted to the radial areas only.
9. **Ventrolateral tubefeet**: 0=absent; 1=present.
10. **Enlarged dorsal or lateral papillae**: 0=absent; 1=present.
11. **Fusion of papillae into a brim or fringe**: 0=absent; 1=present.
12. **Fused oral brim of papillae** : 0=absent; 1=present.
13. **Rugosity of bodywall**: 0=smooth to the touch; 1=rough to the touch.
14. **Hardness of bodywall**: 0=soft; 1=hard.

CALCAREOUS RING

15. **Calcareous ring**: 0=absent, 1=present.
16. **Level of calcification**: 0=weak, 1=well developed.
17. **Radial versus interradial plates**: 0= length radial plate up to 1.5 times longer than length interradial plate; 1=length radial plate 1.5-2 times longer than length interradial plate; 2=length radial plate more than twice as long as length interradial plate.

OSSICLES

Ossicles of the bodywall

18. **Four-pillared tables**: 0=absent; 1=present; 2=pillars reduced to disc.
19. **Structure of the disc of four-pillared table**: 0=table with largely reduced disc or disc almost absent altogether; 1=table with flat disc; 2=table with raised disc.
20. **Top of spire of four pillared table**: 0=cluster or ring of spines; 1=maltese cross; 2=pillars diverging near the tip.
21. **"C" shape ossicles**: 0=absent; 1=present.
22. **Tables with four-armed disc**: 0= absent; 1=present.
23. **Tables with three-armed disc**: 0= absent; 1=present.
24. **Structure of rim of the disc table**: 0= smooth, not spinous or undulating; 1=spinous; 2=undulating.
25. **Plate ossicles**: 0= absent; 1=present.

Ossicles of the tentacles

26. **Ossicles**: 0= absent; 1=present.
27. **Tentacle rod ossicless**: 0= absent; 1=smooth; 2= spiny, elongated; spiny, stout.
28. **Cross-shaped bodies**: 0= absent; 1=present.
29. **Four-pillared table ossicles**: 0= absent; 1=present.

Ossicles of the ventral tube feet

30. **Four-pillared table ossicles**: 0= absent; 1=present.
31. **Rod ossicles**: 0= absent; 1=present.
32. **Regular, elongated plate ossicles**: 0= absent; 1=present.

Ossicles of the internal organs

33. **Ossicles in the gonads**: 0= absent; 1=present.
34. **Ossicles in the respiratory trees**: 0= absent; 1=present.

INTERNAL ANATOMY

35. **Number of Polian vesicles**: 0= 1-2; 1=3 or more.
36. **Gonad**: 0= in one tuft; 1=in two tufts.
37. **Respiratory trees**: 0= absent; 1=present.

ECOLOGY

38. **Bathymetric limits**: 0= 0-200m; 1=200-1500m; 2= from 1500m to 7000.
39. **Swimming**: 0= absent; 1=present.

6. 3. Results

Maximum parsimony analysis comprising 10 replicates (all characters equally weighted), yielded 5437 cladograms with a length of 183 steps, a consistency index (ci) of 0.452, a retention index (ri) of 0.541, a rescaled index (rc) of 0.243. Successive weighting is known to reduce the noise that originates from rapidly evolving characters (Kerr and Kim, 2001). Regardless of the rooting method or the taxa included, analyses using successive weighting produced two to four "most parsimonious" trees (Figure 6.1), while equally weighted data produced 4 to 24 "shortest" trees. Regardless of the weighting scheme or the taxa included, bootstrap values at each node were higher about twice as often under ancestor rooting, although only slightly (median=4%, range 4-11%).

Parsimony analyses that included the genera *Isostichopus*, *Stichopus* and *Holothuria* produced two different placements for the root (Figure 6.1). For both weighting procedures, *Stichopus* and *Isostichopus* rootings split the tree between the "non-synallactid" group and the apparent synallactids (Figure 6.1 A-D).

When *Hansenothuria benti* and *Paroriza pallens* were not used, all rooting by weighting schemes produced an identical strict consensus of shortest trees, but with very low resolution (Figure. 6.2).

There was strong support, via bootstrapping, for grouping the genera *Benthothuria*, *Amphigymnas*, *Bathyplotes* and *Synallactes* (Figure 6.2). These genera were joined by the synapomorphies, 1) ossicles assemblage of the tentacles, 2) position of mouth and anus and 3) bathymetric distribution.

There was always strong support for a subdivision containing *Pelopatides*, *Zygothuria*, and *Mesothuria*.

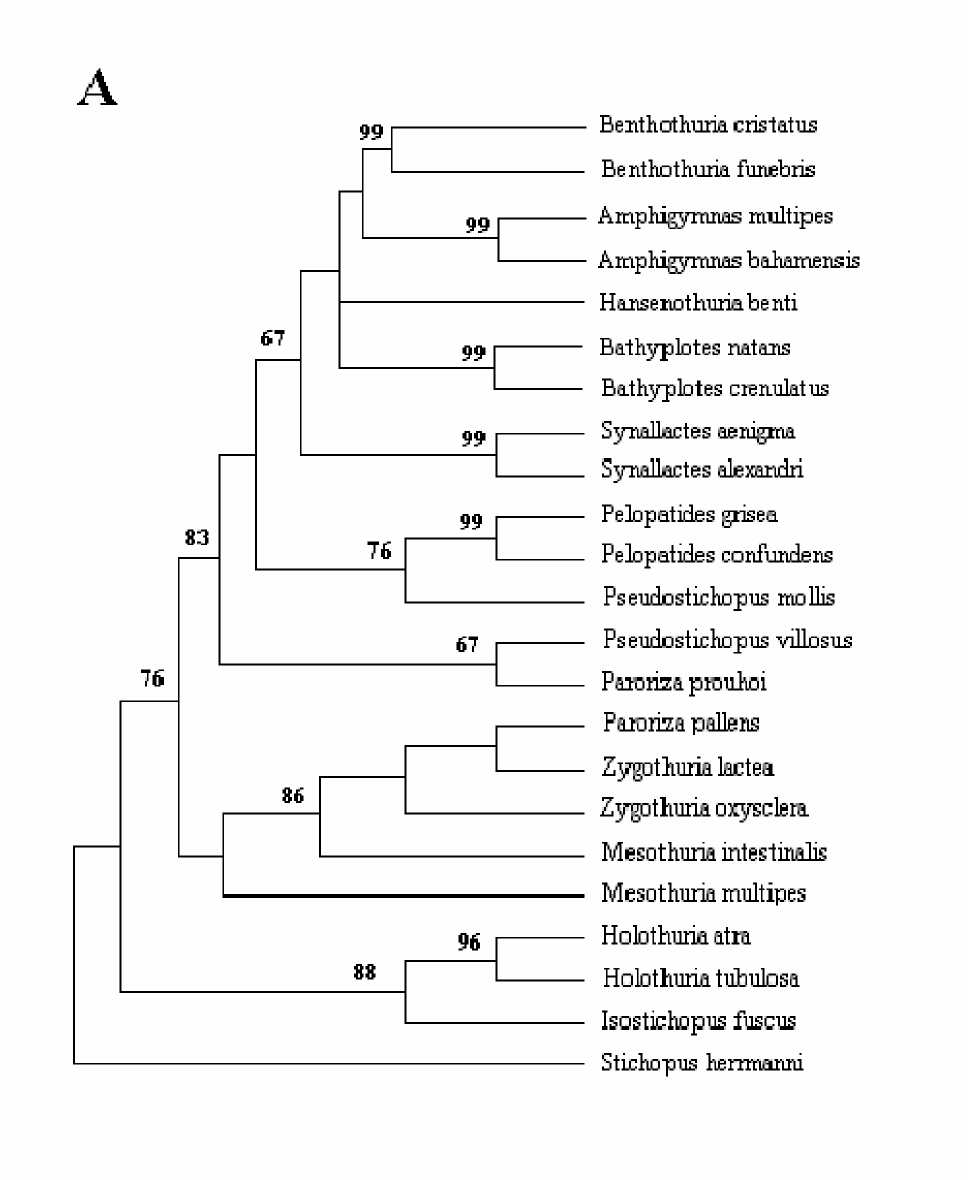

Figure 6.1.A. Most parsimonious trees for analyses of all taxa, weighting and rooting procedures. 50% majority rule consensus tree of 24 trees using equal weights plus "ancestor" rooting. Numbers above branches indicate bootstraps percentages separated by slashes, for equal and for successive weighted analyses; percentages less than 50% are not shown.

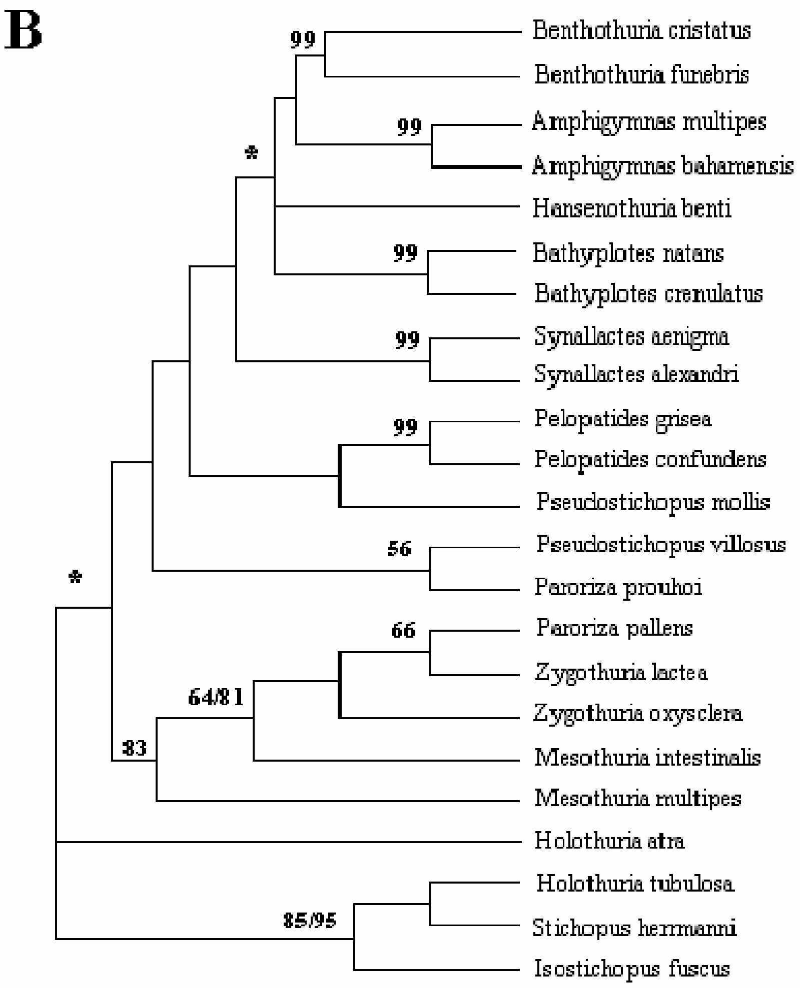

Figure 6.1.B. Most parsimonious trees for analyses of all taxa, weighting and rooting procedures. 50% majority rule consensus tree of two most parsimonious trees for successive weights and "ancestor" rooting. Numbers above branches indicate bootstraps percentages separated by slashes, for equal and for successive weighted analyses; percentages less than 50% are not shown.

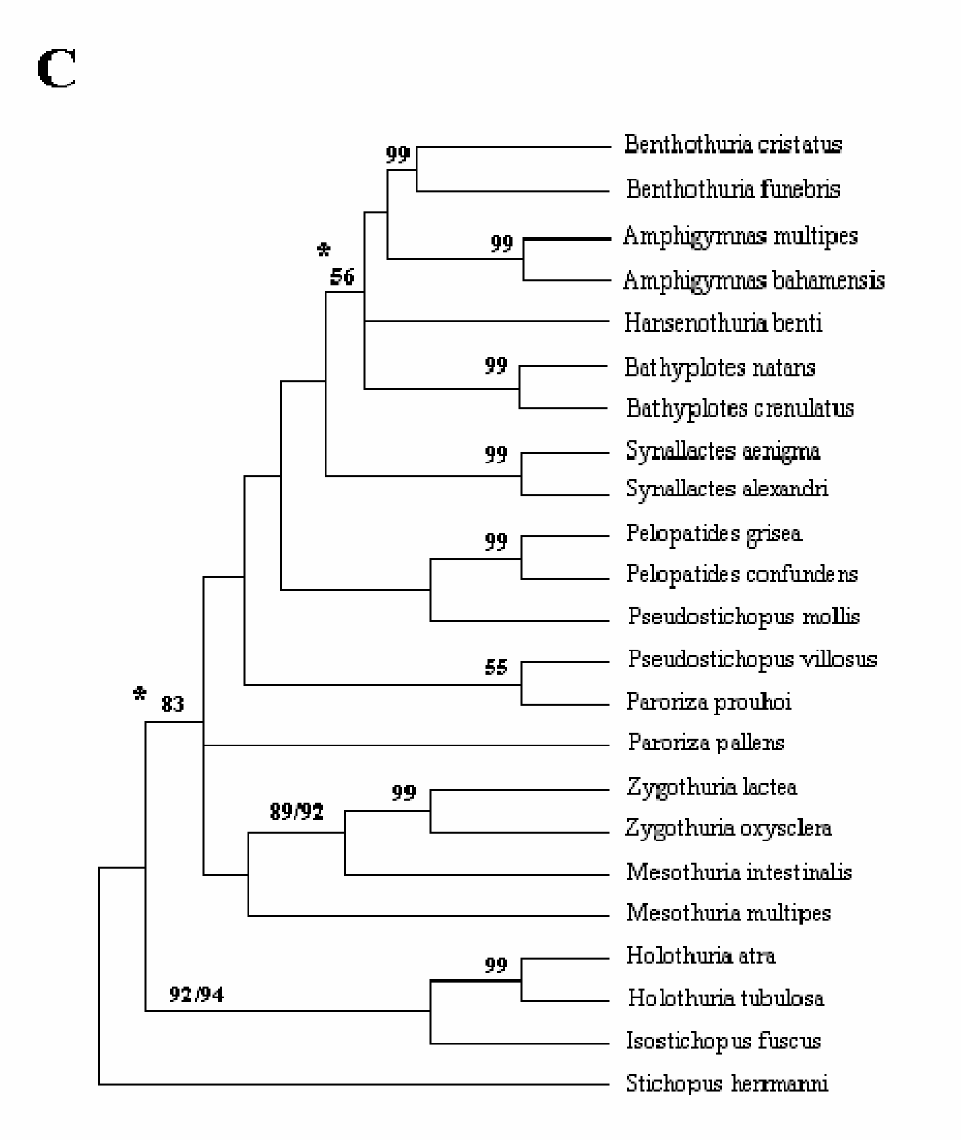

Figure 6.1.C. Most parsimonious trees for analyses of all taxa, weighting and rooting procedures. 50% majority rule consensus tree of eight trees under equal and under successive weights, using *Stichopus* outgroup each time. The asterisked nodes indicate unresolved nodes in the equally weighted analyses. Numbers above branches indicate bootstraps percentages separated by slashes, for equal and for successive weighted analyses; percentages less than 50% are not shown.

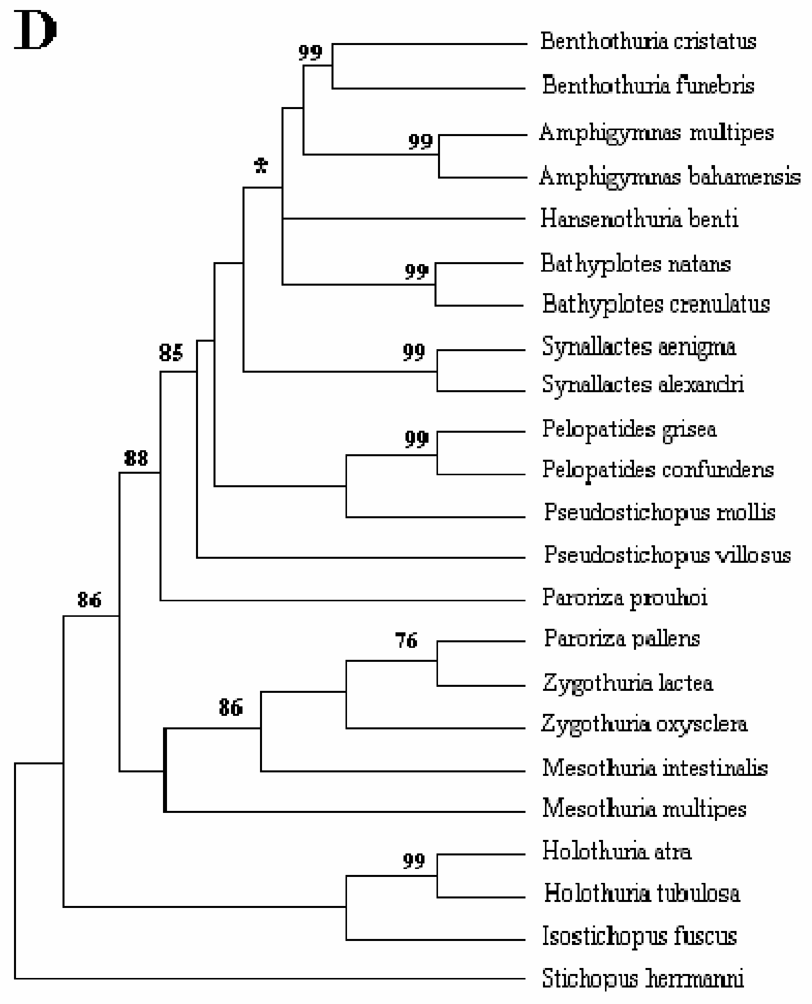

Figure 6.1.D. Most parsimonious trees for analyses of all taxa, weighting and rooting procedures. 50% majority rule consensus tree of two most parsimonious trees using successive weights and mid-point rooting. Numbers above branches indicate bootstraps percentages separated by slashes, for equal and for successive weighted analyses; percentages less than 50% are not shown.

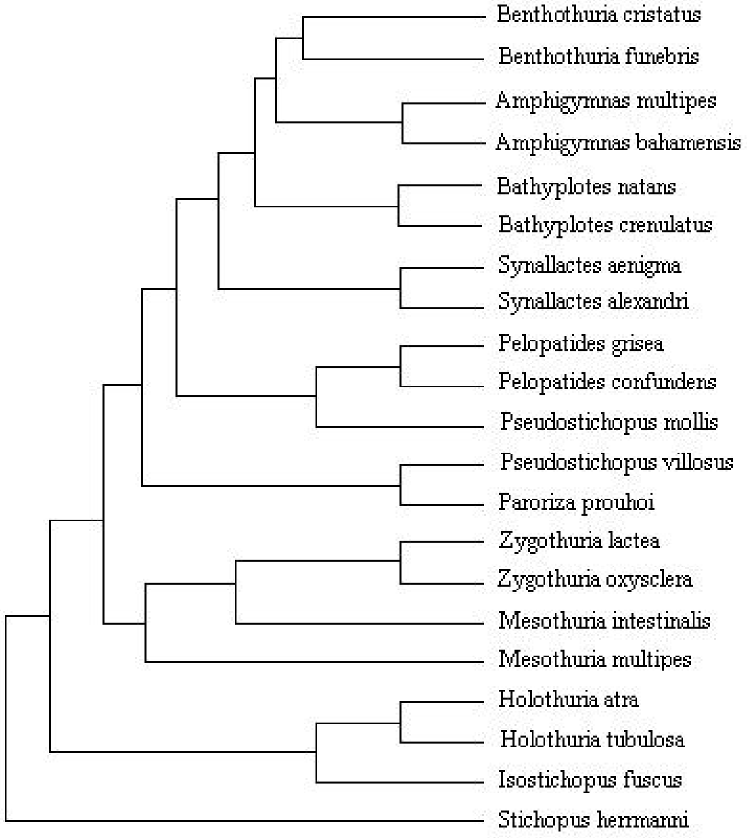

Figure 6.2. Best estimate of synallactid relationships based on the successively weighted analyses excluding *Hansenothuria benti* and *Paroriza pallens* and by collapsing all branches of the resulting single most parsimonious tree with less than 70% bootstrap support.

6.4. Molecular phylogeny of the family Synallactidae

6.4.1. Methods

Sampling, taxonomic identification, DNA extraction, 16S oligonucleotid primers sequences used, polymerase chain reactions (PCR) (preparation and performance), PCR purification, cycle-sequencing reactions, DNA sequencing methods and oligonucleotide primers used for the molecular analysis are referred in Chapters 2 and 3 of this thesis.

The samples used in this Chapter and Section are listed in Table 6

Table 6.4. List of species used in the molecular analysis procedure. In Museum donor/catalogue number, hyphen indicates no catalogue number. Note: in "No. of samples" all samples came from different individuals.

Species	Museum donor/ Catalogue No.	Locality	Collection date	Depth (m)	No. of samples
Bathyplotes bongraini	NMVF81800	Prydz Bay, Antarctica	1997	?	1
Bathyplotes bongraini	NMVF81801	Prydz Bay, Antarctica	1997	?	2
Bathyplotes moseleyi	SOC -	Antarctica	2002	?	3
Benthothuria funebris	SOC -	RRS *Discovery* St. 13914 #1, North East Atlantic, between 49º 54.84' N, 13º 34.34 'W and 49º 52.88' N, 13º 38.99' W	22-09-2000	2981-3115	10
Mesothuria sp. 1	SOC -	RRS *Discovery* St. 13919 #1, North East Atlantic, between 51º 08.89' N, 12º 03.92'W and 51º 07.34' N, 12º 00.56' W	25-09-2000	1537-1545	10
Mesothuria multipes	MNHN -	Pacific Ocean, N/O "Alis" MUSORSTOM 7, St. CP562, Tuscarora Bank, 11º 48'S, 178º 22'W	19-05-92	775-777	1
Mesothuria bifurcata	SOC -	Antarctic (58° 44.35' S, 25° 10.48' W and 65° 20.15' S, 54° 14.35' W)	??-02-2002	752-1122	2
Mesothuria multipora	MNHN -	R/V *Alis*, MUSORSTOM 7, St. DW620, Pacific Ocean, 2º 34'S, 178º 11'W	28-05-92	1280	10
Mesothuria sufflava	MNHN -	New Caledonia, N/O *Alis* HALIPRO 1, St. CH 872, 23º 02'S, 166º 52'E	30-03-94	620-700	2
Paroriza pallens	SOC -	RRS *Discovery* St. 13919 #1, North East Atlantic, between 49º 54.84' N, 13º 34.34 'W and 49º 52.88' N, 13º 38.99' W	25-09-2000	2981-3115	5
Paroriza prouhoi	SOC -	RRS *Discovery* St. 13925 #1, North East Atlantic, between 48º 53.46' N, 16º 45.82'W and 48º 56.79' N, 16º 54.73' W	07-10-2000	4835-4845	4
Pelopatides grisea	SOC -	RRS *Discovery* St. 13922 #1, North East Atlantic, between 51º 53.88' N, 11º 58.44'W and 50º 55.63' N, 12º 01.52' W	01-10-2000	1885-1933	10
Pseudostichopus sp. 1	SOC -	RRS *Discovery* St. 13925 #1, North East Atlantic, between 48º 53.46' N, 16º 45.82'W and 48º 56.79' N, 16º 54.73' W	07-10-2000	4835-4845	10
Pseudostichopus villosus	SOC -	RRS *Discovery* St. 13925 #1, North East Atlantic, between 48º 53.46' N, 16º 45.82'W and 48º 56.79' N, 16º 54.73' W	07-10-2000	4835-4845	10
Zygothuria lactea	SOC -	RRS *Discovery* St. 13919 #1, North East Atlantic, between 51º 08.89' N, 12º 03.92'W and 51º 07.34' N, 12º 00.56' W	25-09-2000	1537-1545	7
Isostichopus fuscus	LSEE	East Pacific Ocean, off the coast of Jalisco, Mexico (21ºN)	2002	15	10
Deima validum	SOC -	RRS *Discovery* St. 13925 #1, North East Atlantic, between 48º 53.46' N, 16º 45.82'W and 48º 56.79' N, 16º 54.73' W	07-10-2000	4835-4845	3

The genetic variation of the synallactid family was analysed using partial 16S sequence with all bases included. Representative consensus sequences were determined from the original sequence data of 51 individuals in which all identical sequences were collapsed.

The identity of the partial sequence of the 16S gene was confirmed by similarity of the peptide sequence to the 16S gene of the sea urchin *Strongylocentrotus purpuratus* (Jacobs *et al.*, 1988), the 16S data from holothurians published by Arndt *et al.* (1996) (GenBank Acc. Nos. U31901, U32210-U32221, U32198 and U32199) and with the same already sequenced material (see Chapters 3 and 4).

The 16S amino acid sequence was used for the best possible alignment. All sequences were aligned using Clustal X (Thompson *et al.*, 1997) and double-checked by eye. A consensus sequence for each species was drawn for the initial set. The consensus sequences retain the variable sites, which were very few in this study. Some sequences were already submitted to GenBank and the accession numbers were given in Chapter 3 (Table 3.4) and Chapter 4 (Table 4.3) of this thesis.

All phylogenetic analyses, as well as basic statistics, were performed on the nucleotide sequence data using PAUP* 4.0b 10 (Swofford, 2002).

Three methods of tree building were used: maximum-likelihood, maximum-parsimony, and neighbour-joining. For all methods, tree topology was evaluated by bootstrapping of the original data set. For maximum-likelihood and maximum-parsimony, a heuristic search was employed and starting trees were always obtained by random sequence addition. Tree visualization was carried out using TreeView version 1.5 (Page, 1996). Maximum-likelihood analysis was performed under the General Time-Reversible (GTR) model of base substitution. The modeltest 3.0 (Posada and Crandall, 1998) algorithm was used to evaluate choice of GTR model, which produced the most significant log-likelihood values, among various models tested.

The estimated values were used in searches with 1000 sequence addition replicates and in the subsequent boot-strappings, which consisted of 100 replicates with 100 sequence additions per replicate.

The trees presented were found through a search with 1000 sequence additions. Boot-strapping of the maximum-parsimony tree consisted of 1000 bootstrap replicates, each with 100 sequence addition replicates. Finally, a neighbour-joining tree was constructed from the distance calculated under the GTR+SSR model with the same parameters used for the maximum likelihood analysis. The topology of the neighbor-joining tree was evaluated by 1000 bootstraps.

6.4.2. Results

6.4.2.1. Synallactid species molecular analysis

Partial 16S mitochondrial gene sequences obtained comprised fragments of 430 to 472 bp of the 3’end of the edge. Average composition of the fragments studied were A= 31.6%, C= 17.2%, G= 19.6%, and T= 30.6%. Significant differences in base composition across all taxa were detected (X^2= 52.6; *df*= 45; *P* > 0.20).

The General Time Reversible model with G (GTR + g) was chosen above others as the most suitable model of evolution for the data set. The estimations from the hLRTs were used to refine the optimal criteria settings as follows; the proportion of invariable sites (I) was set to 0.5931, gamma distribution (the distribution of rates at variable sites) was assumed equal, the substitution model was based on the average pairwise GTR + SSR distances matrix (Table 6.5).

Table 6.5. Nucleotid substitution rate matrix.

	A	C	G	T
A	-	1.4	3.3	6.2
		-	0.2	7.0
			-	1.0
				-

The consensus DNA sequences of the amplified fragments have only 184 base pairs (Figure 6.3).

```
                                                                              50
Bathyplotes bongraini         CTTTGGTTGGGGCAACCATGGAGAAAAAATATCCTCCAGTTAAATAAGTA
Bathyplotes moseleyi          CTTTGGTTGGGGCAACCATGGAGAAAAAATATCCTCCAGTTAAATAAGAA
Mesothuria bifurcata          CTTTGGTTGGGGCAACCATGGAGCTAATTTAGCCTCCAGTTATTAAAGCT
Mesothuria multipora          CTTTGGTTGGGGCAACCATGGAGCTAACTAAGCCTCCAGTTATTAAAGTT
Mesothuria sufflava           CTTTGGTTGGGGTAACCATAGAGTAAATTAAATCTCTAGAATTTATAGAA
Mesothuria multipes           CTTTGGTTGGGGTAACCATAGAGTAAATTAAATCTCTAGAATTTATAGAA
Mesothuria sp. 1              CTTTGGTTGGGGTAACCATAGAGTAAATGAAATCTCTAGTTATTATAGAA
Zygothuria lactea             CTTTGGTTGGGGTAACCATAAAGCAAATTAAATCTCTAGTTAATATAGAA
Pseudostichopus villosus      CTTTGGTTGGGGCAACCATGGAGAAAAAATATCCTCCAGTCTAAAAAGAA
Pelopatides grisea            CTTTGGTTGGGGCAACCATGGAGAAAAAAAATCCTCCAGTTAATAGAAAA
Paroriza pallens              CTTTGGTTGGGGCAACCATGGAGAAAAAATATCCTCCAGTTAAATAAGAA
Pseudostichopus mollis        CTTTGGTTGGGGTAACCCTGGAGAAAAAATAACCTCCAGATAAATAAAAA
Pseudostichopus sp. 1         CTTTGGTTGGGGTAACCCTGGAGAAAAAATATCCTCCAGAAAAATAAAAA
Paroriza prouhoi              CATCGGTGGCGCTTTCCTTCTCGTCAATATGAGCTCTTGGAGAAGATAAC
Benthothuria funebris         CATCGATGGCGCTAACCTTCTTGTCAATATGAGCTCTTAAAGAAGATAAC
Isostichopus fuscus            CTTTGGTACCACCTTCTTTTATTTTACTTCTAGCCTCAGCTGGAAAAGA
                                                                             100
Bathyplotes bongraini         GAATACACATCACTTAAACCTAAAATATTGAACCAGAACTTCTGGAAAAC
Bathyplotes moseleyi          GAATACACATCACTTAAACCTAAAATTTTGAACCAGAACTTCTGGAAAAC
Mesothuria bifurcata          GAACTTAGCTCTCTTTAAAAATTTACATTGAACCAGTTATTCTGGAAATC
Mesothuria multipora          GAACTTAACTCTCTTTATAATTATACATTGAACCAGTTATTCTGGAAATC
Mesothuria sufflava           GAGTTTTCCTCTCTAAAAAATCTTTTATTGAACCAGTTATTCTGGAAATC
Mesothuria multipes           GAGTTTTCCTCTCTAAAAAATCTTTTATTGAACCAGTTATTCTGGAAATC
Mesothuria sp. 1              GAGTTTTACTCTCTAAAAAAGTTTTATTTGAACCAGTTATTCTGGAAATC
Zygothuria lactea             GATTATAAATCTCTATATAATCTATTATTGAACCAGTTATTCTGGAAATC
Pseudostichopus villosus      GAACTTCAATCTCTTTACATAATCATCAAGAACCAGTTATACTGGAAAAC
Pelopatides grisea            GAATTTAATTCACTTAAATATTTAATAAAGAACCAATAATTTTGGAAATC
Paroriza pallens              GAAATCAATTCACTTAAACCTTTCACAAAGAACCAGAAATACTGGTAAAC
Pseudostichopus mollis        GATACTAAATC-TTTAAACCTTTCACAAAGAACCAGAAATACTGGTAAAC
Pseudostichopus sp. 1         GATTTTTAATCTTTTAATCCTTTAACAAAGAACCAGATTTCCTGGTTAAC
Paroriza prouhoi              GCTGTTATCCCTGCGGGAACTTTTTCCGTTTACCAGTTATTCTGGTTTTC
Benthothuria funebris         GCTGTTATCCCTGCGGTAACTTTTTCTGATTACCAAAATTATTGGTTTTC
Isostichopus fuscus           GGAGCCGGAACTGGATGAACCATTTACCCTGAACCAGCTATAATATAGC
                                                                            150
Bathyplotes bongraini         GGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGCTCATA
Bathyplotes moseleyi          GGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGCTCATA
Mesothuria bifurcata          AGAACAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGTCCTAA
Mesothuria multipora          AGAACAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGTCCTAA
Mesothuria sufflava           AGAATAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTGAGAGTCCTCA
Mesothuria multipes           AGAATAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTGAGAGTCCTTA
Mesothuria sp. 1              AGAATAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTGAGAGTTCTTA
Zygothuria lactea             AGAATAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTGAGAGTTCTTA
Pseudostichopus villosus      GGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTAAGAGTTCATA
Pelopatides grisea            AGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGCTCATA
Paroriza pallens              GGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCCAAGAGTCCATA
Pseudostichopus mollis        AGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGCCCATA
Pseudostichopus sp. 1         AGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGCCCGTA
Paroriza prouhoi              ATTGAAAGTTATAAGTGAATTGATTTCTTTCTATTAAACTGGAGGATTTG
Benthothuria funebris         ATTAAAATTTATAGATGAATTAATTTCTTTCTATTAAACTGGAGGATTTA
Isostichopus fuscus           CAGCAGGAGGATCTGTAGATCTGGCCACGTTATCACTTCACTTAGCAGGT
                                                             184
Bathyplotes bongraini         TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Bathyplotes moseleyi          TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Mesothuria bifurcata          TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Mesothuria multipora          TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Mesothuria sufflava           TTGACAAGAAGGATTGCGACCTCGATGTTGGATT
Mesothuria multipes           TTGACAAGAAGGATTGCGACCTCGATGTTGGATT
Mesothuria sp. 1              TTGACAAGAAGGATTGCGACCTCGATGTTGGATT
Zygothuria lactea             TTGACAAGAAGGATTGCGACCTCGATGTTGGATT
Pseudostichopus villosus      TTGACAAGAAGGATTGCGACCTCGATGTTGGATT
Pelopatides grisea            TTGACGAGAAGGTTTGCGACCTCGATGTTGGATT
Paroriza pallens              TTGACGAGAAGGTTTGCGACCTCGATGTTGGATT
Pseudostichopus mollis        TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Pseudostichopus sp. 1         TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Paroriza prouhoi              TTTTCTCCATGGTTGCCCCAACCAAAGCTTTTCC
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Benthothuria funebris         TTTTCTCCATGGTTGCCCCAACCAAAACTTGACC
Isostichopus fuscus          CCCTCTTCAATACTTGCTTCAATCAACTTTATTAC
```

Figure 6.3. Aligned nucleotide sequence of the 3’ segment of the mitochondrial 16S gene from 16 species of sea cucumbers. Hyphens indicate missing data.

Table 6.6 presents the average pairwise GTR + SSR distances matrix for the studied 16S sequences.

Table 6.6. Holothurian Pairwise Distances Matrix[1] (Synallactidae + *Isostichopus fuscus*).

	Bb	Bm	Mb	Mm	Ms	Mmu	Mmi	Zl	Pv	Pg	Pp	Pm	Pa	Ppr	If	Bf
1 Bb	-															
2 Bm	0.010	-														
3 Mb	0.184	0.190	-													
4 Mm	0.179	0.190	0.038	-												
5 Ms	0.233	0.233	0.157	0.163	-											
6 Mmu	0.228	0.228	0.157	0.163	0.005	-										
7 Mmi	0.228	0.217	0.152	0.157	0.059	0.054	-									
8 Zl	0.201	0.201	0.163	0.152	0.086	0.081	0.081	-								
9 Pv	0.146	0.141	0.168	0.179	0.206	0.201	0.195	0.184	-							
10 Pg	0.125	0.125	0.168	0.163	0.206	0.201	0.184	0.179	0.152	-						
11 Pp	0.097	0.097	0.179	0.184	0.250	0.244	0.233	0.239	0.130	0.114	-					
12 Pm	0.125	0.125	0.197	0.202	0.235	0.230	0.230	0.219	0.158	0.136	0.076	-				
13 Pa	0.146	0.146	0.211	0.206	0.228	0.222	0.233	0.222	0.168	0.157	0.125	0.066	-			
14 Ppr	0.603	0.597	0.554	0.570	0.538	0.532	0.538	0.548	0.581	0.581	0.565	0.546	0.543	-		
15 If	0.625	0.619	0.670	0.686	0.665	0.599	0.595	0.596	0.603	0.608	0.686	0.685	0.596	0.589	-	
16 Bf	0.592	0.581	0.570	0.586	0.548	0.543	0.548	0.565	0.581	0.554	0.538	0.514	0.516	0.130	0.542	-

[1] Average pairwise GTR + SSR distances.

Abbreviations: Bb, *Bathyplotes bongraini*; Bm, *Bathyplotes moseleyi*; Mb, *Mesothuria bifurcata*; Mm, *Mesothuria multipora*; Ms, *Mesothuria sufflava*; Mmu, *Mesothuria multipes*; Mmi, *Mesothuria* sp. 1; Zl, *Zygothuria lactea*; Pv, *Pseudostichopus villosus*; Pg, *Pelopatides grisea*; Pp, *Paroriza pallens*; Pm, *Pseudostichopus mollis*; Pa, *Pseudostichopus* sp. 1; Ppr, *Paroriza prouhoi*; If, *Isostichopus fuscus*; Bf, *Benthothuria funebris*.

Two basic topologies resulted from the tree search methods described (Figure 6.4). They showed considerable agreement, the only major difference among them being the internal branching of the genus *Mesothuria*. Figure 6.4 A presents the strict consensus topology resulting from the maximum-parsimony analysis, on which two equal parsimonious trees were produced. The majority rule consensus tree resulting from neighbour-joining was identical to the maximum-parsimony tree. Maximum-likelihood produced an alternative branching for *Mesothuria* (Figure 6.4 B). Branch support followed a pattern similar to that of maximum-parsimony, with good support for *Mesothuria* and *Bathyplotes*, but poor support among species within the genera. However, GTR + g maximum likelihood bootstrap shows support for *Mesothuria*.

Summarizing information on Figure 6.4, there is strong support for *Bathyplotes* and for *Mesothuria*. Within the branch with the genera *Paroriza* and *Pseudostichopus* a lack of resolution resulted in a polytomy among *Pseudostichopus mollis-P. sp. 1, Paroriza pallens* and *Bathyplotes bongraini* and *B. moseleyi*, and the remaining species. Within the genus *Mesothuria*, the data did not resolve the relationships between the species, but *Mesothuria sufflava* and *M. multipora* clearly form a monophyletic group as well as *Bathyplotes bongraini* and *B. moseleyi.*

The genus *Paroriza* does not form a monophyletic group. *P. pallens* appears as part of a polytomy together with the genus *Bathyplotes* and *Pseudostichopus*. It is surprising how *Benthothuria funebris* and *Paroriza prouhoi* form a completly different branch in the tree with relatively high values resolving their relation. In order to probe their proximity with different taxa, such as the elasipodids, a further analysis was made.

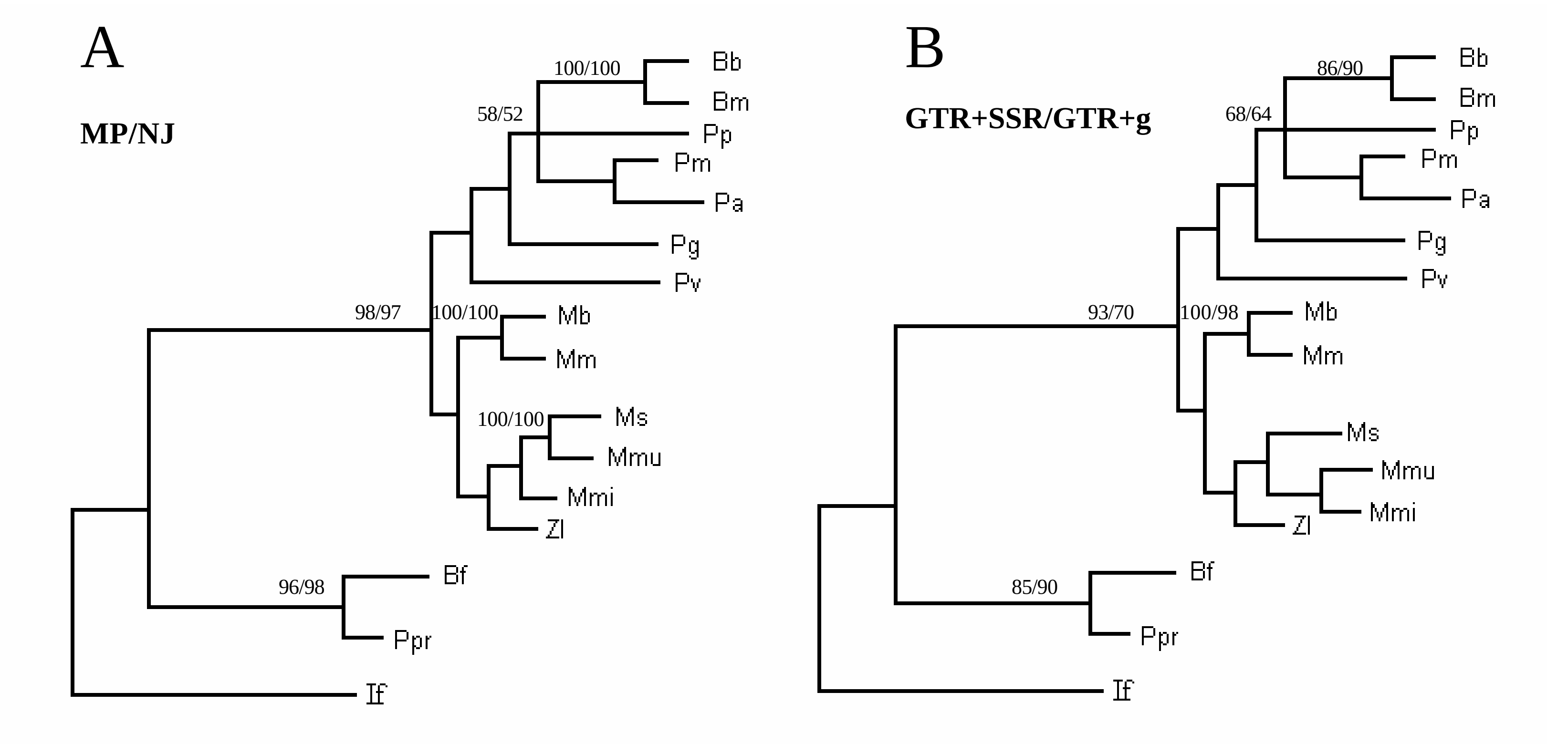

Figure 6.4. Topologies resulting from the phylogenetic methods used. A. Strict consensus tree resulting from the two most-parsimonious trees obtained through heuristic search with 1000 sequence addition replicates (L= 271; CI= 0.662; RI= 0.632; RC= 0.470). Bootstrap support shown for maximum –parsimony (MP) and neighbor-joining (NJ). Branch lengths correspond to maximum-parsimony analysis. B. Maximum-likelihood tree obtained after an heuristic search with 1000 sequence addition replicates under the GTR + SSR model. Abbreviations: Bb, *Bathyplotes bongraini*; Bm, *Bathyplotes moseleyi*; Pp, *Paroriza pallens*; Pm, *Pseudostichopus mollis*; Pa, *Pseudostichopus* sp. 1; Pg, *Pelopatides grisea*; Pv, *Pseudostichopus villosus*; Mb, *Mesothuria bifurcata*; Mm, *Mesothuria multipora*; Ms, *Mesothuria sufflava*; Mmu, *Mesothuria multipes*; Mmi, *Mesothuria* sp. 1sp. nov; Zl, *Zygothuria lactea*; Bf, *Benthothuria funebris*; Ppr, *Paroriza prouhoi*; If, *Isostichopus fuscus*.

6.4.2.2. Synallactid and elasipodid species molecular analysis.

In order to analyse the possible phylogenetic relation of some synallactid species with the elasipodids, a phylogenetic analysis was carried out using the total of the sequences used in the last analysis (excluding the outgroup *Isostichopus fuscus*) and the elasipodid *Deima validum* (see Table 6.4).

Toward this goal, the same methods as in Section 6.2.2 of this Chapter were used.

The average composition of the fragments studied were A= 31.9%, C= 17.0 %, G= 19.3%, and T= 30.8 %.

The General Time Reversible model with G (GTR + g) was chosen above others as the most suitable model of evolution for the data set. The estimations from the hLRTs were used to refine the optimal criteria settings as follows; the proportion of invariable sites (I) was set to 0.4712, gamma distribution (the distribution of rates at variable sites) was assumed equal, the substitution model was based on the rate matrix (Table 6.7).

Table 6.7. Average pairwise GTR + SSR distances matrix for the studied 16S sequences.

	A	C	G	T
A	-	1.9	3.9	6.8.3
		-	0.6	8.0
			-	1.0
				-

The consensus DNA sequences of the amplified fragments have only 184 base pairs (Figure 6.5).

Two basic topologies resulted from the tree search methods described (Figure 6.6). They showed considerable agreement with the last analysis (Figure 6.4), the only major difference among them being the internal branching of the species *Paroriza prouhoi* and *Benthothuria funebris* with the elasipodid *Deima validum*. There is strong support for this relation suggesting that *Benthothuria funebris* and *Paroriza prouhoi* are more related with *Deima validum* than with the rest of the Synallactidae as proposed above in this Chapter.

```
                                                                             50
Bathyplotes bongraini         CTTTGGTTGGGGCAACCATGGAGAAAAAATATCCTCCAGTTAAATAAGTA
Bathyplotes moseleyi          CTTTGGTTGGGGCAACCATGGAGAAAAAATATCCTCCAGTTAAATAAGAA
Mesothuria bifurcata          CTTTGGTTGGGGCAACCATGGAGCTAATTTAGCCTCCAGTTATTAAAGCT
Mesothuria multipora          CTTTGGTTGGGGCAACCATGGAGCTAACTAAGCCTCCAGTTATTAAAGTT
Mesothuria sufflava           CTTTGGTTGGGGTAACCATAGAGTAAATTAAATCTCTAGAATTTATAGAA
Mesothuria multipes           CTTTGGTTGGGGTAACCATAGAGTAAATTAAATCTCTAGAATTTATAGAA
Mesothuria sp. 1              CTTTGGTTGGGGTAACCATAGAGTAAATGAAATCTCTAGTTATTATAGAA
Zygothuria lactea             CTTTGGTTGGGGTAACCATAAAGCAAATTAAATCTCTAGTTAATATAGAA
Pseudostichopus villosus      CTTTGGTTGGGGCAACCATGGAGAAAAAATATCCTCCAGTCTAAAAAGAA
Pelopatides grisea            CTTTGGTTGGGGCAACCATGGAGAAAAAAAATCCTCCAGTTAATAGAAAA
Paroriza pallens              CTTTGGTTGGGGCAACCATGGAGAAAAAATATCCTCCAGTTAAATAAGAA
Pseudostichopus mollis        CTTTGGTTGGGGTAACCCTGGAGAAAAAATAACCTCCAGATAAATAAAAA
Pseudostichopus sp. 1         CTTTGGTTGGGGTAACCCTGGAGAAAAAATATCCTCCAGAAAAATAAAAA
Paroriza prouhoi              CATCGGTGGCGCTTTCCTTCTCGTCAATATGAGCTCTTGGAGAAGATAAC
Deima validum                 CATCGATGGCGCAAACCTTCTCGTCAATATGGACTCTTGGAGAAGATAAC
Benthothuria funebris         CATCGATGGCGCTAACCTTCTTGTCAATATGAGCTCTTAAAGAAGATAAC
                                                                             100
Bathyplotes bongraini         GAATACACATCACTTAAACCTAAAATATTGAACCAGAACTTCTGGAAAAC
Bathyplotes moseleyi          GAATACACATCACTTAAACCTAAAATTTTGAACCAGAACTTCTGGAAAAC
Mesothuria bifurcata          GAACTTAGCTCTCTTTAAAAATTTACATTGAACCAGTTATTCTGGAAATC
Mesothuria multipora          GAACTTAACTCTCTTTATAATTATACATTGAACCAGTTATTCTGGAAATC
Mesothuria sufflava           GAGTTTTCCTCTCTAAAAAATCTTTTATTGAACCAGTTATTCTGGAAATC
Mesothuria multipes           GAGTTTTCCTCTCTAAAAAATCTTTTATTGAACCAGTTATTCTGGAAATC
Mesothuria sp. 1              GAGTTTTACTCTCTAAAAAAGTTTTATTTGAACCAGTTATTCTGGAAATC
Zygothuria lactea             GATTATAAATCTCTATATAATCTATTATTGAACCAGTTATTCTGGAAATC
Pseudostichopus villosus      GAACTTCAATCTCTTTACATAATCATCAAGAACCAGTTATACTGGAAAAC
Pelopatides grisea            GAATTTAATTCACTTAAATATTTAATAAAGAACCAATAATTTTGGAAATC
Paroriza pallens              GAAATCAATTCACTTAAACCTTTCACAAAGAACCAGAAATACTGGTAAAC
Pseudostichopus mollis        GATACTAAATC-TTTAAACCTTTCACAAAGAACCAGAAATACTGGTAAAC
Pseudostichopus sp. 1....     GATTTTTAATCTTTTAATCCTTTAACAAAGAACCAGATTTCCTGGTTAAC
Paroriza prouhoi              GCTGTTATCCCTGCGGGAACTTTTTCCGTTTACCAGTTATTCTGGTTTTC
Deima validum                 GCTGTTATCCCTGCGGTAACTTTTTCCGTTTACCAGTTATTCTGGTTTTC
Benthothuria funebris         GCTGTTATCCCTGCGGTAACTTTTTCTGATTACCAAAATTATTGGTTTTC
                                                                            150
Bathyplotes bongraini         GGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGCTCATA
Bathyplotes moseleyi          GGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGCTCATA
Mesothuria bifurcata          AGAACAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGTCCTAA
Mesothuria multipora          AGAACAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGTCCTAA
Mesothuria sufflava           AGAATAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTGAGAGTCCTCA
Mesothuria multipes           AGAATAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTGAGAGTCCTTA
Mesothuria sp. 1              AGAATAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTGAGAGTTCTTA
Zygothuria lactea             AGAATAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTGAGAGTTCTTA
Pseudostichopus villosus      GGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTTTAAGAGTTCATA
Pelopatides grisea            AGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGCTCATA
Paroriza pallens              GGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCCAAGAGTCCATA
Pseudostichopus mollis        AGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGCCCATA
Pseudostichopus sp. 1         AGAAAAAGTTACCGCAGGGATAACAGCGTTATCTTCTCTAAGAGCCCGTA
Paroriza prouhoi              ATTGAAAGTTATAAGTGAATTGATTTCTTTCTATTAAACTGGAGGATTTG
Deima validum                 TTTATGAAAGTTAAGTGAATTGATTTCTTTCTATTAAACTGGAGGATTTG
Benthothuria funebris         ATTAAAATTTATAGATGAATTAATTTCTTTCTATTAAACTGGAGGATTTA
                                                             184
Bathyplotes bongraini         TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Bathyplotes moseleyi          TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Mesothuria bifurcata          TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Mesothuria multipora          TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Mesothuria sufflava           TTGACAAGAAGGATTGCGACCTCGATGTTGGATT
Mesothuria multipes           TTGACAAGAAGGATTGCGACCTCGATGTTGGATT
Mesothuria sp. 1              TTGACAAGAAGGATTGCGACCTCGATGTTGGATT
Zygothuria lactea             TTGACAAGAAGGATTGCGACCTCGATGTTGGATT
Pseudostichopus villosus      TTGACAAGAAGGATTGCGACCTCGATGTTGGATT
Pelopatides grisea            TTGACGAGAAGGTTTGCGACCTCGATGTTGGATT
Paroriza pallens              TTGACGAGAAGGTTTGCGACCTCGATGTTGGATT
Pseudostichopus mollis        TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Pseudostichopus sp. 1         TTGACGAGAAGGATTGCGACCTCGATGTTGGATT
Paroriza prouhoi              TTTTCTCCATGGTTGCCCCAACCAAAGCTTTTCC
```

Deima validum	TTTTCTCCATGGTTGCCCCAACCAAAGCTTTTCC
Benthothuria funebris	TTTTCTCCATGGTTGCCCCAACCAAAACTTGACC

Figure 6.5. Aligned nucleotide sequence of the 3’ segment of the mitochondrial 16S gene from 16 species of sea cucumbers. Hyphens indicate missing data.

Table 6.8 presents the average pairwise GTR + SSR distances matrix for the studied 16S sequences.

Table 6.8. Holothurian Pairwise Distances Matrix[1] (Synallactidae + *Deima validum*).

	Bb	Bm	Mb	Mm	Ms	Mmu	Mmi	Zl	Pv	Pg	Pp	Pm	Pa	Ppr	Dv	Bf
1 Bb	-															
2 Bm	0.010	-														
3 Mb	0.183	0.191	-													
4 Mm	0.179	0.190	0.038	-												
5 Ms	0.233	0.233	0.157	0.163	-											
6 Mmu	0.227	0.228	0.157	0.163	0.005	-										
7 Mmi	0.228	0.217	0.152	0.157	0.059	0.054	-									
8 Zl	0.201	0.201	0.163	0.152	0.086	0.081	0.081	-								
9 Pv	0.146	0.141	0.168	0.179	0.207	0.201	0.195	0.184	-							
10 Pg	0.125	0.125	0.168	0.163	0.206	0.201	0.186	0.179	0.152	-						
11 Pp	0.097	0.097	0.179	0.184	0.250	0.244	0.233	0.239	0.130	0.114	-					
12 Pm	0.125	0.125	0.197	0.202	0.235	0.230	0.230	0.219	0.158	0.136	0.076	-				
13 Pa	0.146	0.146	0.211	0.206	0.228	0.222	0.233	0.222	0.168	0.157	0.125	0.066	-			
14 Ppr	0.603	0.597	0.554	0.570	0.538	0.532	0.538	0.548	0.581	0.581	0.565	0.546	0.543	-		
15 Dv	0.604	0.517	0.572	0.585	0.565	0.581	0.585	0.582	0.512	0.502	0.585	0.565	0.576	0.089	-	
16 Bf	0.594	0.583	0.574	0.590	0.545	0.540	0.554	0.569	0.580	0.553	0.533	0.515	0.517	0.130	0.142	-

[1] Average pairwise GTR + SSR distances.

Abbreviations: Bb, *Bathyplotes bongraini*; Bm, *Bathyplotes moseleyi*; Mb, *Mesothuria bifurcata*; Mm, *Mesothuria multipora*; Ms, *Mesothuria sufflava*; Mmu, *Mesothuria multipes*; Mmi, *Mesothuria* sp. 1; Zl, *Zygothuria lactea*; Pv, *Pseudostichopus villosus*; Pg, *Pelopatides grisea*; Pp, *Paroriza pallens*; Pm, *Pseudostichopus mollis*; Pa, *Pseudostichopus* sp. 1; Ppr, *Paroriza prouhoi*; Dv, *Deima validum*; Bf, *Benthothuria funebris*.

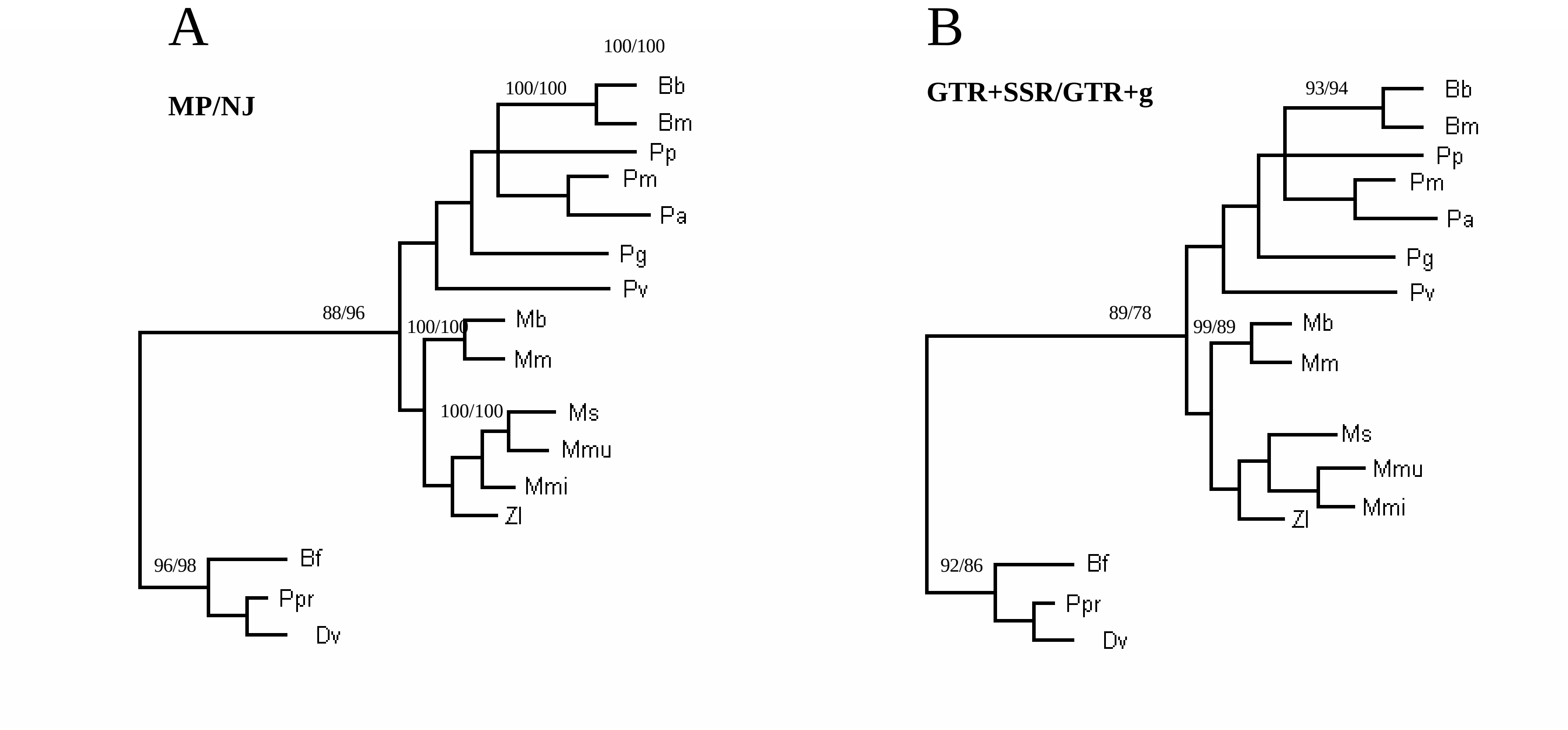

Figure 6.6. Topologies resulting from the phylogenetic methods used. A. Strict consensus tree resulting from the two most-parsimonious trees obtained through heuristic search with 1000 sequence addition replicates (L= 276; CI= 0.642; RI= 0.622; RC= 0.570). Bootstrap support shown for maximum parsimony (MP) and neighbor-joining (NJ). Branch lengths correspond to maximum-parsimony analysis. B. Maximum-likelihood tree obtained after a heuristic search with 1000 sequence addition replicates under the GTR + SSR model. Abbreviations: Bb, *Bathyplotes bongraini*; Bm, *Bathyplotes moseleyi*; Pp, *Paroriza pallens*; Pm, *Pseudostichopus mollis*; Pa, *Pseudostichopus* sp. 1; Pg, *Pelopatides grisea*; Pv, *Pseudostichopus villosus*; Mb, *Mesothuria bifurcata*; Mm, *Mesothuria multipora*; Ms, *Mesothuria sufflava*; Mmu, *Mesothuria multipes*; Mmi, *Mesothuria* sp. 1; Zl, *Zygothuria lactea*; Bf, *Benthothuria funebris*; Ppr, *Paroriza prouhoi*; Dv. *Deima validum*.

6.5. Discussion and conclusions

6.5.1. The morphological point of view

The morphological analyses with all the taxa included resulted in a low-resolution consensus tree (Figure 6.2) that excluded *Hansenothuria* and *Paroriza pallens*. Nevertheless, this preliminary tree gave some interesting insights. Of immediate importance was the observation that all the synallactid genera occurred in different clades, showing the consistency of their morphological characters. Only one genus, *Pseudostichopus*, is mixed with *Pelopatides* and *Paroriza*. The genera *Pelopatides* and *Paroriza* are also not well defined in the phylogenetic tree. This is probably because the data matrix suffers from insufficient apomorphies for *Paroriza* and *Pelopatides*.

The exclusion of *Hansenothuria* and *Paroriza pallens* from the last analysis resulted in a significant decrease of the number of most parsimonious trees. It is very important to state that *Mesothuria* and *Zygothuria* species cluster in different groups. Morphologically, both genera are well separated.

Kerr and Kim (2000) were the first to propose that the morphologically diverse family Synallactidae is probably a paraphyletic to polyphyletic group with members displaying numerous affinities to either Holothuriidae or Stichopodiidae. The results of this analyses shows that there is some morphological cohesion in the Synallactidae, but not enough to validate the monophyly in the family. Using morphological characters, and removing the monotypic genus *Hansenothuria* and the species *Paroriza pallens* the Synallactidae appears as a monophyletic group. Adding the last taxa and including some "problematic" species of the already included genera (e. g. *Pseudostichopus* species), the monophyly presented in Figure 6.2 would be easily lost.

The large amount of morphological diversity in the Synallactidae makes the use of morphological criteria of dubious value in the analysis of its phylogeny.

6.5.2. The molecular point of view

The molecular phylogenetic analysis of the Synallactidae clarified several controversial points concerning the taxonomy of this group.

1) The family Synallactidae is a polyphyletic group, as proposed by Kerr and Kim (2001). The family seems to be formed from 2 or more different taxonomic elements.

2) The species *Benthothuria funebris* and *Paroriza prouhoi* form a completely separated group from the Synallactidae suggesting the polyphyletic status of the group.

3). The group formed by the genus *Bathyplotes* (*B. bongraini* and *B. moseleyi*) is a monophyletic group and is closely related with *Paroriza pallens* and the genus *Pseudostichopus*. *Paroriza pallens* appear in a non-resolved branch together with the *Bathyplotes* group and *Pseudostichopus mollis* and *Pseudostichopus* sp. 1. It was expected in the analysis to group together the two *Paroriza* species, but one of them, *P. prouhoi* is closely related to the elasipodids (as shown in Figure 6.5).

4) *Pseudostichopus mollis* and *Pseudostichopus* sp. 1 group together into the non-resolved branch already described. This branch is not strongly support by values of maximum-parsimony and neighbor-joining.

5) *Pelopatides grisea* is related with the *Bathyplotes-Paroriza-Pseudostichopus* group. *Pseudostichopus villosus* appears to be related to this last group, but there is not strong support for any of these last relations.

6) The group *Mesothuria-Zygothuria* form a robust clade. The species *M. bifurcata* and *M. multipora* constitute a highly supported group, as well as *M. sufflava* and *M. multipes*.

In the analyses the best-supported group was the clade *Mesothuria-Zygothuria*. Although their phylogenetic relation is not fully resolved, it is significant that the two genera are closely related. As shown previously in Chapter 3, there is not enough molecular evidence to support the separation of *Zygothuria* from *Mesothuria* as different genera. *Mesothuria* is a polyphyletic group with *M. multipora* and *M. bifurcata* in one group and the other *Mesothuria* species and the genus *Zygothuria* in the other group. *Zygothuria* is the basal genus, indicating that all the species perhaps should be included in the genus *Zygothuria*. However, the morphological analysis sustains the separation of *Zygothuria* and *Mesothuria*.

In the combined analysis (synallactids+*Deima validum*) (Figures 6.6 A, B), the separation of *Benthothuria funebris* and *Paroriza prouhoi* from the synallactid group is clear. This indicates that there is a major problem with the recent organization of holothurian taxonomy. Even when the morphological analysis supports the recognition of the genus *Benthothuria* and *Paroriza*, the molecular analysis showed that *B. funebris* and *P. prouhoi* are indeed more closely related to the Elasipodida. Where should be placed in holothurian taxonomy? The Order Elasipodida is characterized by lacking respiratory trees; *B. funebris* and P. *pallens* have well developed respiratory trees, but the mitochondrial DNA (16S) showed unequivocally its close relation to the elasipodid *Deima validum*. If these genera are going to be included in the Elasipodida, a major change will need to be made in the diagnosis of the Order Elasipodida. At present I do not recommend such emendation, because it would create instability in elasipodid systematics. I recommend keeping the two genera in the Synallactidae until we understand more about their phylogenetic relationships. At the moment, there is insufficient taxonomic information (morphological and molecular) to erect new taxa to include these forms. The taxonomic position of *Benthothuria* and *Paroriza* remain uncertain. Perhaps a better approach would be to set up a new family to include these two taxa, but recognising that this may change as further work is done. It will be necessary to continue extracting DNA for different deep-sea holothurians morphotypes in order to understand more about their systematics and phylogenetic relationships.

Chapter Seven – Summary

7.1. Taxonomy

This is the second attempt since Ludwig (1894) to unite the synallactids under a unified taxonomic name. The family Synallactidae, as formally known, was believed to be composed of approximately 143 species included in 24 genera, as previously reported by Heding (1940), Hansen (1975), Miller and Pawson (1989). In the present study, on basis of morphological and molecular approaches, a few genera and species have been synonymised, removed or transferred to an *Incertae sedis* status and 3 new species have been erected. The family Synallactidae is now composed by 131 species in 10 genera.

The *Incertae sedis* group is formed by the genera *Allopatides* Koehler & Vaney, 1905; *Bathyzona* Koehler & Vaney, 1905; *Capheira* Ludwig, 1893; *Dendrothuria* Koehler & Vaney, 1905; *Filithuria* Koehler & Vaney, 1905; *Galatheathuria* Hansen and Madsen, 1952; *Perizona* Koehler & Vaney, 1905; *Pseudothuria* Koehler & Vaney, 1905; *Scotothuria* Hansen, 1978.

The species *Bathyherpystikes baculosus* Massin, 1987 is also placed in *Incertae sedis* group. There is a group of species that have been erroneously identified and/or placed as synallactids. *Bathyplotes veleronis* Domantay, 1953 is indeed a 3cm young of *Holothuria paraprinceps* Deichmann. For this reason it has been removed from the family.

Gephyrothuria europeensis Hérouard, 1923, described by Hérouard as a synallactid, was synonymised recently with *Gephyrothuria alcocki* Koehler & Vaney, 1905 and transferred to the family Gephyrothuriidae Koehler & Vaney, 1905 by O’Loughlin (1998).

Even though Clark (1922) stated that *Stichopus richardi* Hérouard, 1896 was “probably” a synallactid, Hérouard (1896) stated quite clearly that “les culs-de-sacs tentaculaires son bien developpes”. This species cannot be a synallactid because it possesses tentacular ampullae. Therefore it has been removed from the Synallactidae.

A similar problem is presented by *Stichopus torvus* Théel, 1886, which Clark (1922) also stated was a synallactid. Recently O’Loughlin (2002) placed this species into the

Synallactidae as "*Meseres torvus*". But data presented by Théel (1886) are insufficient to confirm any synonymy and in this study I have removed it from the Synallactidae.

When *Synallactes(?) dubius* Koehler & Vaney, 1905 was first described they could not provide details of the exact distribution of any external structures. The ossicles illustrated in their work are not synallactid ossicles. Rather, they look like tables from a young holothuriid. Moreover, data presented by the authors are insufficient to confirm any synonymy or placement of this species in a different group. In this thesis I have removed it from the Synallactidae.

The ossicles illustrated in Vaney (1906a) confirm that his species *Synallactes carthagei* is not a synallactid, but is closely related to the psolid genus *Staurocucumis*. Moreover, the presence of other taxonomic characters, such as the presence of 10 dendritic tentacles, anus ventral and the presence of a well-developed ventral sole, confirm this point of view. For these reasons, in this study I have removed it from the Synallactidae.

Several authors have studied the taxonomy of the genus *Pseudostichopus* (Deichmann, 1940, O'Loughlin, 2002), but all with great difficulty. In this thesis, I have reviewed the genus *Pseudostichopus* as a whole, including all the morphologically similar taxa, such as *Meseres* and *Molpadodiademas*. The genus *Pseudostichopus* is a taxon where external morphology and ossicle shape simplicities have led to uncertainties in the taxonomy at the species level. The recognition of a new species, *P. aemulatus* sp. nov., using morphological and molecular characters together allowed a better understanding on the systematics of this group.

On the basis of published descriptions and of reviewing type material in museum collections, I have synonymised the subgenera *Peristichopus* Djakonov, *Plicastichopus* Heding, *Platystichopus* Heding, and *Trachostichopus* Heding with the genus *Pseudostichopus* Théel. I have also synonymised the genus *Molpadiodemas* Heding, 1935 with the species *Pseudostichopus trachus* Sluiter, 1901a.

When the genus *Meseres* Ludwig, 1893 was erected, Ludwig did not describe its diagnostic characters well, and because of this the genus *Meseres* has been a taxonomic problem for a long time. It has been synonymised with *Pseudostichopus* by different authors, but recently O'Loughlin (2002) revived the genus. The taxonomic differentiation between

Meseres and *Pseudostichopus* proposed by O'Loughlin (2002) is confused and ambiguous. In this thesis I have synonymised *Meseres* under *Pseudostichopus* because of lack of reliable taxonomic characters.

I have reviewed the taxonomy of the genus *Synallactes*. New taxonomic combinations were created and a new species was erected, *S. laguardai* sp. nov. This is the first attempt to unify the genus since its description by Ludwig (1893). 22 species are considered to be valid, 6 new combinations have been proposed, and 7 species have been removed from the genus.

Morphologically, the genus *Zygothuria* differs from the genus *Mesothuria* in general body shape. The lack of diagnostic molecular differences between the two taxa means that they are currently identifiable only by morphological criteria. Comparative studies have shown that morphological change and molecular divergence are quite independent, responding to different evolutionary pressures and following different rules (Wilson *et al.*, 1974, 1977). Because morphologically defined taxa are still the basis for most ecological, physiological, and anatomical research, I propose to maintain *Zygothuria* and *Mesothuria* as separate genera in the family Synallactidae.

A new species of *Mesothuria* is erected in this thesis, *M. milleri* sp. nov.

7.2. General biology

As previously stated by Hansen (1975), the family Synallactidae occurs mainly at bathyal depths, rather than in hadal or shallow waters. The genera *Amphigymnas*, *Bathyplotes*, *Pelopatides*, *Synallactes* and *Benthothuria* are bathyal-abyssal. The genus *Pseudostichopus* is distributed in the bathyal, abyssal and hadal zones, but it is mainly bathyal-abyssal. The genera *Paroriza* and *Zygothuria* are distributed in the bathyal, abyssal and hadal zones. No genera are confined to the abyssal zone.

The family Synallactidae has a cosmopolitan distribution, and some individual species are distributed very widely. Many abyssal species are widespread, but only a few species are truly cosmopolitan. Bathyal synallactids have more restricted geographic distributions than abyssal forms and none are known to occur throughout the World's oceans.

The natural history, especially the reproductive biology of *Mesothuria* and *Zygothuria*, is conservative. *Z. lactea* and *M. milleri* sp. nov. are both dioecious and have a similar large egg size indicative of lecithotrophic development. No seasonality in reproduction has been found in any deep-sea holothurian.

7.3. Phylogeny

Mitochondrial DNA is a popular phylogenetic tool for marine invertebrate studies. Although there has been considerable cross-fertilization between morphological and molecular systematics, there has also been conflict of results and disagreement among practitioners of these two subfields. This has led to the perception of a battle of sorts between molecular and morphological systematics. Morphological and molecular approaches to systematics have different strengths, but also have many problems and difficulties of analysis in common. The coordinated effort between morphological and molecular systematics is necessary to make real progress in assessing the World's biodiversity.

The greatest advantage of molecular data in systematics is the large number of characters available for analysis. This contrasts with morphological studies, in which a given analysis rarely includes more than a few hundred characters and averages about three characters per taxon. The potential number of morphological characters may not be much greater than the number actually used in studies, but the potential number of molecular characters is much greater.

The greatest advantage of morphological studies is that they allow for much more thorough taxonomic sampling than is possible with molecular analyses. The greatest benefit of including additional taxa is the potential to subdivide long branches in the estimated tree, which if insufficiently subdivided can result in inaccuracies in character reconstructions and in phylogenetic estimation. Long branches can mislead all phylogenetic methods and thus can lead to answers that are strongly supported, but wrong.

Finally, in addition to phylogeny reconstruction, morphology continues to play a crucial role in alpha taxonomy. In almost all groups of organisms, species are described and identified on the basis of morphological data. Therefore, even molecular systematists depend largely on morphology to determine which species they have sampled. Given that molecular data and morphological data have distinct advantages, they can be integrated to find the best estimate of phylogeny.

This phylogenetic study is based on both morphological and molecular data. Partial DNA sequences of two mitochondrial genes; approximately 870 nucleotides of Cytochrome Oxidase subunit 1 (COI) and approximately 350 nucleotides of the large ribosomal RNA subunit (lrRNA) have been used in order to provide an accurate phylogenetic hypothesis on the phylogeny of the family Synallactidae.

The results of this study constitute the first phylogenetic test of the classification of Synallactidae. Examination of the morphology and molecular phylogenetic consensus trees reveals three main conclusions:

1) There is morphological consistency in the Synallactidae, but it is not enough to validate the monophyly of the family. The great morphological diversity of the Synallactidae makes the use of morphological criteria difficult in any phylogenetic analysis.

2) The family Synallactidae from the molecular point of view is a paraphyletic group. When analysing mitochondrial DNA sequences the family seems to be formed by 2 groups that can have different ancestors, a) a *Paroriza-Pseudostichopus-Pelopatides-Mesothuria-Zygothuria* group, b) a non-synallactid group with *Benthothuria funebris* and *Paroriza prouhoi.*

3) When combining elasipodid and synallactid mitochondrial DNA sequences in one analysis the “elasipodid clade”, is separated into two branches. One branch is formed by *Deima validum*, *Paroriza prouhoi* and *Benthothuria funebris*. These three species have no morphological relation, but their mitochondrial DNA reveals their cryptic relationship.

Even though the morphological analysis supports the recognition of the genera *Benthothuria* and *Paroriza* as synallactids, their taxonomic position remains uncertain. The molecular analysis showed that *B. funebris* and *P. prouhoi* are indeed more closely related to the Elasipodida. However, I recommend keeping these two genera, with their respective species, in the Synallactidae until we understand more about their phylogenetic relationships. At the moment, there is not sufficient taxonomic information (morphological and/or molecular) to erect new taxa to include these forms.

It is necessary to continue extracting DNA for different deep-sea holothurians morphotypes in order to understand more about its systematics and phylogenetic relations.

Even if, with the present morphological dataset, it is imprudent to discuss the paraphyletic status of the Synallactidae, it is worthwhile to consider that probably the Synallactidae needs to be split at least once (probably more) into a group with a single gonad (the "Mesothuriidae") and those with a pair of gonads (the true Synallactidae). The lack of tentacle ampullae shows convergence, so that the "Mesothuriidae" may, in effect, be deep-sea Holothuriidae, whilst the Synallactidae are deep-sea Stichopodidae, both of which have converged in their loss of tentacle ampullae by moving into deep water. In the genus *Mesothuria* some species are very closely related in ossicle shape to the Holothuriidae, but there are species, such as *M. bifurcata* and *M. crebrapedes*, that appear to be more closely related to the true Synallactidae.

This study has made a contribution to understanding the taxonomy of deep-sea synallactid holothurians. However, the scale of the problem extends well beyond what can be achieved in a 3-year study. Significant progress has been made in combining morphological and molecular approaches to taxonomy, demonstrating the need for more studies of this nature in the future.

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Appendix 1

Table 1. Examined specimens of ***Amphigymnas bahamensis*** Deichmann, 1930.

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E14718	1	Holotype	134/25	*Albatross* St. 2666, North Atlantic Ocean, Georgia, Cumberland Island, between Bahamas and Cape Fear, 30º 47’ 30” N, 79º 49’ 00” W	05-05-1886	493
USNM E53253	3	Paratypes	82/15	*Albatross* St. 2666, North Atlantic Ocean, Georgia, Cumberland Island, between Bahamas and Cape Fear, 30º 47’ 30” N, 79º 49’ 00” W	05-05-1886	493
ZMUC	1	Paratype	-	*Albatross* St. 2666, North Atlantic Ocean, Georgia, Cumberland Island, between Bahamas and Cape Fear, 30º 47’ 30” N, 79º 49’ 00” W	05-05-1886	493
USNM E18574	1	-	-	*Oregon* St. 384, North Atlantic Ocean, Gulf of Mexico, United States, Louisiana, east of Mississippi Delta, 29º 10’ N, 88º 00’ W	21-06-51	485-549
USNM E21955	1	-	-	*Oregon* St. 1507, North Atlantic Ocean, Gulf of Mexico, 27º 43’ N, 95º 05’ W	06-05-56	587
USNM E27844	3	-	-	*Columbus Iselin* St. 65, North Atlantic Ocean, United States, off E coast of Florida, 29º 13’ N, 78º 56’ W	22-09-80	802
USNM E31586	1	-	-	*VIMS*, St. VS-79-03, North Atlantic Ocean, off E coast United States	-	-
USNM E46258	1	-	-	North Atlantic Ocean, Georgia, Bahamas, Grand Bahamas Island, south of west end, 26º 34’ 54” N, 78º 59’ 06” W	-	573
USNM E46767	1	-	-	*Oregon II* St. 10844, North Atlantic Ocean, Caribbean Sea, East of St. Christopher, 17º 24’ N, 62º 28’ W	09-07-69	629
USNM E46768	1	-	-	*Oregon II* St. 10826, North Atlantic Ocean, Caribbean Sea, Leeward Islands, North East of Dominica, 15º 36’ N, 61º 09’ W	01-12-69	665
USNM E46769	1	-	-	*Oregon II* St. 10834, North Atlantic Ocean, Caribbean Sea, Anguilla, Leeward Islands, 18º 18’ N, 63º 23’ W	06-12-69	687
USNM E46770	1	-	-	*Oregon II* St. 11299, North Atlantic Ocean, Caribbean Sea, Colombia, North East of Peninsula de la Guajira, 12º 52’ N, 70º 43’ W	23-11-70	512
USNM E51993	1	-	210/34	North Atlantic Ocean, Caribbean Sea, Colombia, Bocas de Ceniza, 11º 13’ 47” N, 74º39’ 15”W	?-10-98	408

Table 2. Examined specimens of ***Amphigymnas multipes*** (Walsh, 1891)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E16616	2	-	-	*Albatross* St. 5527, North Pacific Ocean, Mindanao Sea, Philippines, Negros Oriental, Siquijor Island, Lomangcapan Point, 09º 22’ 30” N, 123º 42’ 40” E	11-08-09	716
USNM E16617	3	-	300/38.5	*Albatross* St. 5589, North Pacific Ocean, Celebes Sea, Malaysia, Sabah, South of Darvel Bay, 04º 12’ 10” N, 118º 38’ 08” E	29-09-09	475
USNM E16618	3	-	-	*Albatross* St. 5201, North Pacific Ocean, Philippines, Southern Leyte, Leyte Island, off shore of Sogod Bay, 10º 10’ 00” N, 125º 04’ 15” E	10-04-08	1013
USNM E16619	3	-	-	*Albatross* St. 5173, North Pacific Ocean, Philippines, Sulu Archipelago, Jolo Island, Candea Point, 06º 02’ 55” N, 120º 53’ 00” E	05-04-08	340
USNM E16634	1	-	-	*Albatross* St. 5625, North Pacific Ocean, Molucca Sea, Indonesia, Moluccas, Halmahera Island, Kayoa Island, 00º 07’ 00” N, 127º 28’ 00” E	19-11-09	420
USNM E16665	1	-	-	*Albatross* St. 5542, North Pacific Ocean, Mindanao Sea, Philippines, Negros Oriental, between Mindanao and Siquijor Islands, 08º 48’ 30” N, 123º 35’ 30” E	20-08-09	365
USNM E24547	1	-	-	*Albatross* St. 5587, North Pacific Ocean, Celebes Sea, Malaysia, Sabah, south of Darvel Bay, 04º 10’ 35” N, 118º 37’ 12” E	28-11-09	759
USNM E24566	1	-	302/41	*Albatross* St. 5624, North Pacific Ocean, Molucca Sea, Indonesia, Moluccas, Halmahera Island, SE of Makian Island, 00º 12’ 15” N, 127º 29’ 30” E	29-11-09	526
ZMUC -	2	-	435/37	North Pacific Ocean, Philippines, 25-26 miles E. of Zamboanga	03-04-19	360-450
ZMUC -	2	-		*The Kei* Expedition, St. 57 North Pacific Ocean, Indonesia, 5º 46’ 30”S, 132º 51’ E	07-05-22	348

ZMUC -	1	-	230/27	*The Kei* Expedition, St. 58, North Pacific Ocean, Indonesia, 5º 29’S, 132º 37’ E	12-05-22	290
NHM 1905.11.9.6	1	-	-	Marine Survey, St. 222	-	737
MNHN 7	1			*Investigator*, Indian Ocean, Andaman Islands	-	-
ZMUC -	1			Asia, Celebes Islands	?-04-14	-

Table 3. Examined specimens of ***Bathyplotes angustus*** (Cherbonnier & Feral, 1981)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN 3022	1	Holotype	-	*Valdivia* Musorstom, St. 50, 13° 49’ 2”N, 120° 01’ 08”E	25-03-76	510-515

Table 4. Examined specimens of ***Bathyplotes bongraini*** Vaney, 1914

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN 4071	1	Holotype	-	Western side of Antarctic Peninsula, 68º 00’ S, 70º 20’ W	21-01-09	250

Table 5. Examined specimens of ***Bathyplotes cinctus*** Koehler & Vaney, 1910

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	2	-	-	“St. 12”	-	660
ZMUC *	1	-	-	*Valdivia* St. 189, Indian Ocean, West of Sumatra, 0º 57’ 5”S, 99º 51’1” E	30-01-1899	768
ZMUC **	1	-	-	*Valdivia* St. 189, Indian Ocean, West of Sumatra, 0º 57’ 5”S, 99º 51’1” E	30-01-1899	768
ZMUC	4	-	-	Dr. Th. Mortensen’s Expedition St. 192, North Pacific Ocean, Philippines, 15 miles W. ½ S. of Jolo	27-03-1914	450

* Holotype of ***Bathyplotes mamillatus*** Heding, 1940

** Paratype of ***Bathyplotes mamillatus*** Heding, 1940

Table 6. Examined specimens of ***Bathyplotes crebrapapilla*** (Cherbonnier & Féral, 1981)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN	1	Holotype	-	*Valdivia* Musorstom, St. 50, Philippines, 3° 49’ 2”N, 120° 01’ 08”E	25-03-76	415-410

Table 7. Examined specimens of ***Bathyplotes imperfectus*** Cherbonnier & Féral, 1981

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN 3023	1	Holotype	-	*Valdivia* Musorstom, St. 50, North Pacific Ocean, Philippines, 13º 49.2’N, 120º 01.8’E	25-03-76	415-510

Table 8. Examined specimens of ***Bathyplotes moseleyi*** (Théel, 1886a)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
NHM 1886.10.2.136	2	Syntypes	-	HMS *Challenger* St. 306a, South Pacific Ocean, 48º 27’S, 74º 30’ W	02-01-1876	627.9
NHM 1886.10.2.137	?	Syntype(s)	-	HMS *Challenger* St. 311, South Pacific Ocean, 52º 45’ 30”S, 73º 46’ W	11-01-1876	445
NHM 1886.10.2.138	2	Syntypes	-	HMS *Challenger* St. 308, South Pacific Ocean, 50º 08’ 30”S, 74º 41’W	05-01-1876	318
ZMA E2993	1	Syntype	-	HMS *Challenger* St. 306a, South Pacific Ocean, 48º 27’S, 74º 30’ W	02-01-1876	627.9
MNHN 432	3	-	-	Antarctic, Belge 1959-1960, St. 133	30-01-1899	768

MNHN 3362	1	-	-	Antarctic Expedition, Belge 1959-1960, St. 134	-	-
MNHN 3366	1	-	-	Antarctic Expedition, Belge 1959-1960, St. 155	-	-
MNHN 4065?	1	-	-	-	-	-
MNHN 1802	2	-	-	Miss Cap. Horn, 1882-1883, St. 117, Navarin Islands?	-	-
MNHN E2011	29	-	-	*Albatross* St. 2780, South Pacific Ocean, Chile, Magallanes and Antarctica Chilena, Strait of Magellan, west mouth of straits, 53º 01’ 00”S, 73º 42’ 30”W	2-02-1888	6749
MNHN E2018	12	-	66/12	*Albatross* St. 2780, South Pacific Ocean, Chile, Magallanes and Antarctica Chilena, Strait of Magellan, west mouth of straits, 53º 01’ 00”S, 73º 42’ 30”W	2-02-1888	6749
MNHN E2020	1	-	-	*Albatross* St. 2789, South Pacific Ocean, Chile, De Los Lagos, west of Chiloe Island, 42º 36’ 00”S, 75º 28’ 00”W	12-02-1888	2454
USNM E17345	2	-	-	*Anton Brun* St. 703, South Pacific Ocean, off coast of Chile, 32º 09’ 00”S, 71º 43’ 00”W	12-08-66	960
USNM E17346	1	-	-	,*Anton Brun* St. 661-C, South Pacific Ocean, off coast of Peru, 13º 16’ 30”S, 77º 30’ 00”W	26-06-66	1730
USNM E17372	20	-	-	*Anton Brun* St. 702, South Pacific Ocean, off coast of Chile, 32º 17’ 00”S, 71º 40’ 00”W	11-08-66	580
USNM E27533	20	-	-	*Eltanin* St. 1083, Antarctic Ocean, Scotia Sea, Antarctica, South Orkney Islands, Scotia Ridge, east of islands, 60º 51’ 00”S, 42º 57’ 00”W	14-04-64	248
USNM E27534	20	-	-	*Eltanin* St. 1082, Antarctic Ocean, Scotia Sea, Antarctica, South Orkney Islands, Scotia Ridge, east of islands, 60º 50’ 00”S, 42º 55’ 00”W	14-04-64	298
USNM E27535	15	-	-	*Eltanin* St. 437, Antarctic Ocean, Antarctica, Antarctic Peninsula, South Shetland Islands, Bransfield Strait, Deception Island, 62º 50’ 00”S, 60º 40’ 00”W	9-01-63	267-311
USNM E27536	6	-	-	*Eltanin* St. 1084, Antarctic Ocean, Scotia Sea, Antarctica, South Orkney Islands, Scotia Ridge, west of islands, 60º 22’ 00”S, 46º 50’ 00”W	15-04-64	298-403
USNM E27537	3	-	-	*Eltanin* St. 441, Antarctic Ocean, Antarctica, Antarctic Peninsula, South Shetland Islands, Bransfield, south of Low Island, 63º 27’ 00”S, 62º 37’ 00”W	10-01-63	156-253
USNM E27538	5	-	-	*Eltanin* St. 439, Antarctic Ocean, Antarctica, Antarctic Peninsula, Palmer Archipelago, NW of Brabant Island, 63º 51’ 00”S, 62º 38’ 00”W	9-01-63	128-165
USNM E27539	1	-	-	*Hero* St. 511, Antarctic Ocean, Antarctica, Antarctic Peninsula, Palmer Archipelago, Wiencke Island, Port Lockroy, 64º 46’ 48”S, 63º 29’ 18”W	18-03-70	283-311
USNM E27544	4	-	-	*Hero* St. 1932, Antarctic Ocean, Antarctica, Antarctic Peninsula, Palmer Archipelago, Anvers Island, Bismarck Strait, 64º 49’ 03”S, 64º 10’ 42”W	8-03-73	255-265
USNM E27545	1	-	-	*Hero* St. 848, Antarctic Ocean, Antarctica, Antarctic Peninsula, Palmer Archipelago, Anvers Island, Arthur Harbour, 64º 47’ 24”S, 64º 06’ 54”W	26-01-72	94-165
USNM E27546	3	-	-	*Hero* St. 1887, Antarctic Ocean, Antarctica, Antarctic Peninsula, Wilhelm Archipelago, north of Quintana Island, 65º 02’ 42”S, 64º 54’ 42”W	3-03-73	340-370
USNM E27547	4	-	150/41	*Hero* St. 1825, Antarctic Ocean, Antarctica, Antarctic Peninsula, Palmer Archipelago, Anvers Island, Bismarck Strait, 64º 50’ 00”S, 63º 53’ 00”W	20-02-73	280-300
USNM E27548	3	-	-	*Hero* St. 1861, Antarctic Ocean, Antarctica, Antarctic Peninsula, Biscoe Island, South of Lovoisier Island, 66º 21’ 42”S, 66º 47’ 00”W	1-03-73	70-106
USNM E27549	1	-	-	*Hero* St. 1947, Antarctic Ocean, Antarctica, Antarctic Peninsula, Danco Coast, Flanders Bay, 65º 00’ 18”S, 63º 28’ 06”W	11-03-73	204-250
USNM E27550	1	-	-	*Hero* St. 1871, Antarctic Ocean, Antarctica, Antarctic Peninsula, Argentine Islands, Penola Strait, 65º 14’ 42”S, 64º 13’ 30”W	3-03-73	180-240
USNM E27551	5	-	-	*Hero* St. 1869, Antarctic Ocean, Antarctica, Antarctic Peninsula, Argentine Islands, Penola Strait, 65º 13’ 36”S, 64º 11’ 00”W	2-03-73	50-250
USNM E27552	1	-	-	*Hero* St. 1840, Antarctic Ocean, Antarctica, Antarctic Peninsula, Palmer Archipelago, Anvers Island, Bismarck Strait, 64º 51’ 12”S, 64º 05’ 48”W	2-02-73	250-350
USNM E27553	14	-	-	*Hero* St. 1824, Antarctic Ocean, Antarctica, Antarctic Peninsula, Palmer Archipelago, Anvers Island, Bismarck Strait, 64º 53’ 39”S, 63º 44’ 30”W	20-02-73	500-670
USNM E27554	1	-	-	*Eltanin* St. 5761, Antarctic Ocean, Ross Sea, Antarctica, Victoria Land, Pennell Bank, 76º 01’ 30”S, 179º 49’ 54”E	8-02-72	388-399
USNM E27555	1	-	-	*Eltanin* St. 5762, Antarctic Ocean, Ross Sea, Antarctica, Victoria Land, Pennell Bank, 76º 02’	9-02-72	347-358

				06”S, 179º 57’ 00”W		
USNM E27556	1	-	-	*Hero* St. 850, Antarctic Ocean, Antarctica, Antarctic Peninsula, Palmer Archipelago, Anvers Island, Arthur Harbor, 64º 47’ 18”S, 64º 06’ 42”W	26-01-72	165
USNM E27557	1	-	-	*Hero* St. 1842, Antarctic Ocean, Antarctica, Antarctic Peninsula, Biscoe Islands, west of Renaud Islands, 65º 30’ 00”S, 67º 31’ 00”W	24-02-73	180
USNM E27558	1	-	-	*Hero* St. 1143, Antarctic Ocean, Antarctica, Antarctic Peninsula, Wilhem Archipelago, Bismarck Strait, Wauwermans Island, 64º 57’ 30”S, 63º 43’ 30”W	14-03-72	230-260
USNM E27559	1	-	-	*Eltanin* St. 1521, South Atlantic Ocean, Antarctic Peninsula, Scotia Sea, east of Burdwood Bank, 54º 09’ 00”S, 52º 08’ 00”E	30-01-66	419-483
USNM E27560	1	-	-	*Eltanin* St. 1084, Antarctic Ocean, Scotia Sea, Antarctica, South Orkney Islands, Scotia Ridge, west of islands, 60º 22’ 00”S, 46º 50’ 00”W	15-04-64	298-403
USNM E27561	3	-	-	*Islas Orcadas* St. 52, South Atlantic Ocean, Scotia Sea, South Sandwich Islands, Saunders Island, 57º 39’ 24”S, 26º 26’ 42”W	26-05-75	415-613
USNM E27562	1	-	-	*Hero* St. 1947, Antarctic Ocean, Antarctica, Antarctic Peninsula, Danco Coast, Flanders Bay, 65º 00’ 18”S, 63º 28’ 06”W	11-03-73	204-250
USNM E27699	1	-	-	*Eltanin* St. 410, Antarctic Ocean, Antarctica, Antarctic Peninsula, South Shetland Islands, west of Elephant Island, 61º 18’ 00”S, 56º 09’ 00”W	31-12-62	220-240
USNM E27897	5	-	-	*Eltanin* St. 1954, Antarctic Ocean, Victoria Land, Balleny Island, Buckle Island, 66º 34’ 00”S, 163º 01’ 00”E	5-02-67	322-337
USNM E27898	2	-	-	*Eltanin* St. 2085, Antarctic Ocean, Ross Sea, Antarctica, Center of the Sea, 77º 32’ 00”S, 172º 32’ 00”E	1-02-68	468-482
USNM E27899	2	-	-	*Eltanin* St. 2012, Antarctic Ocean, Victoria Land, SE of Coulman Island, 73º 59’ 00”S, 170º 51’ 00”E	13-01-68	589-608
USNM E27908	1	-	-	*Hero* St. 764, Antarctic Ocean, Antarctica, Antarctic Peninsula, Palmer Archipelago, anvers Island, Arthur Harbour, 64º 47’ 18”S, 64º 07’ 24”W	31-01-72	110
USNM E32912	3	-	-	*Eastwind* St. EW66-029, Antarctic Ocean, Antarctica, South Orkney Islands, from 61º 00’ 36”S, 44º 57’ 48”W to 61º 00’ 48”S, 44º 57’ 00”W	11-02-66	283-329
USNM E32913	2	-	-	*Eastwind* St. EW66-023, Antarctic Ocean, Antarctica, South Orkney Islands, 60º 26’ 54”S, 45º 56’ 42”W	9-02-66	210
USNM E41758	2	-	-	*Lipps* St. SOSC-L42, Antarctic Ocean, Antarctica, Antarctic Peninsula, Palmer Archipelago, off south coast of Anvers Island, 64º 47’ 00”S, 64º 06’ 00”W	1972	-
ZMUC	3	-	-	*Terra Nova* St. 12.	-	-
NHM 1953.8.21.38	4	-	-	*Discovery* St. 1660 Antarctica, 74º 46’ 24”S, 178º 23’ 24” W	1-01-36	351
NHM 1953.8.21.37	1	-	-	*Discovery* St. 190 Bismarck Strait, Palmer Archipelago, 64º 56’ 00”S, 65º 35’ 00” W	24-03-27	93-126
NHM 1953.8.21.37	1	-	-	*Discovery* St. 187 Neumayr Channel, Palmer Archipelago, 64º 48’ 30”S, 63º 31’ 30” W	18-03-27	259
NHM 1953.8.21.42	3	-	-	*Discovery* St. 180, 1.7 miles W of N point of Gand I Schollaert Channel, Palmer Archipelago	24-03-27	160-330
NHM 1953.8.21.39	1	-	-	*Discovery* St. 1958 South Shetland Islands, 61º 17’ 54”S, 52º 50’ 54” W	5-02-37	830
NHM 1953.8.21.39	1	-	-	*Discovery* St. 1958 South Shetland Islands, 61º 17’ 54”S, 52º 50’ 54” W	5-02-37	830
NHM 1953.8.21.39	1	-	-	*Discovery* St. 1958 South Shetland Islands, 61º 17’ 54”S, 52º 50’ 54” W	5-02-37	830
NHM 1953.8.21.39	1	-	-	*Discovery* St. 1958 South Shetland Islands, 61º 17’ 54”S, 52º 50’ 54” W	5-02-37	740
NHM 1953.8.21.39	1	-	-	*Discovery* St. 1958 South Shetland Islands, 61º 17’ 54”S, 52º 50’ 54” W	5-02-37	740
NHM 1953.8.21.39	1	-	-	*Discovery* St. 1958 South Shetland Islands, 61º 17’ 54”S, 52º 50’ 54” W	5-02-37	830
NHM 1953.8.21.39	1	-	-	*Discovery* St. 1958 South Shetland Islands, 61º 17’ 54”S, 52º 50’ 54” W	5-02-37	740
NHM 1953.8.21.39	1	-	-	*Discovery* St. 1958, South Shetland Islands, 61º 17’ 54”S, 52º 50’ 54” W	5-02-37	830
NHM 1953.8.21.36	1	-	-	*Discovery* St. 1652 Antarctica, 75º 56’ 12”S, 178º 35’ 30” W	23-01-36	567
NHM 1905.3.9.120\1	1	-	-	*Discovery* St. ?	5-02-37	273
NHM 1953.8.21.41	2	-	-	*Discovery* St. 1652 Antarctica, 75º 56’ 12”S, 46º 15’ 00” W	23-01-36	567
NHM 1953.8.21.40	1	-	-	*Discovery* St. 167 Off Signy I, S Orkneys, 60º 50’ 30”S, 178º 35’ 30” W	20-02-27	244-344
NHM 1932.8.11.300	1	-	-	*Terra Nova* 1910-1913, St. 7, Antarctic		-

NHM 1932.8.11.274	1		320/ 380	*Terra Nova* 1910-1913, St. 314, Antarctic, 5 miles N. of Inaccessible Island, McMurdo Sound	23-01-11	406-441
NHM 1932.8.11.271-273	?			*Terra Nova* 1910-1913, St. 314, Antarctic, 5 miles N. of Inaccessible Island, McMurdo Sound	23-01-11	-
NHM 1932.8.11.276-277	1			*Terra Nova* 1910-1913, St. 314, Antarctic, 5 miles N. of Inaccessible Island, McMurdo Sound	23-01-11	-
PSG1/143-2 AGT	5			Antarctic	??-??-2002	-
LAC 84-243.1, R/V	1			*Polarsten* Ant. II 386, Nantucket Inlet, Lassiter Coast, Palmer Land, Antartic Peninsula, Antarctica; 74º 50'S, 61º 08'W	31-01-84	635
NHM 1953.8.21.41	2	-	-	*Discovery* St. 1652 Antarctica, 75º 56' 12"S, 46º 15' 00" W	23-01-36	567
NHM 1953.8.21.40	1	-	-	*Discovery* St. 167 Off Signy I, S Orkneys, 60º 50' 30"S, 178º 35' 30" W	20-02-27	244- 344
NHM 1932.8.11.300	1	-	-	*Terra Nova* 1910-1913, St. 7, Antarctic	-	-
NHM 1932.8.11.274	1	-	320- /380	*Terra Nova* 1910-1913, St. 314, Antarctic, 5 miles N. of Inaccessible Island, McMurdo Sound	23-01-11	406-441
NHM 1932.8.11.271-273	-	-	-	*Terra Nova* 1910-1913, St. 314, Antarctic, 5 miles N. of Inaccessible Island, McMurdo Sound	23-01-11	406-441
NHM 1932.8.11.276-277	1	-	-	*Terra Nova* 1910-1913, St. 314, Antarctic, 5 miles N. of Inaccessible Island, McMurdo Sound	23-01-11	406-441
SOC	5	-	-	PSG1/143-2 AGT, Antarctic	??-??-2002	
LAC 84-243.1	1	-	-	R/V *Polarsten* Ant. II 386, Nantucket Inlet, Lassiter Coast, Palmer Land, Antarctic Peninsula, Antarctica; 74º 50'S, 61º 08'W	31-01-84	635

?holotype of *Synallactes gourdoni* Vaney

Table 9. Examined specimens of *Bathyplotes natans* (M. Sars 1868).

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN 7137*	1	-	-	*Talisman* off Morocco	-	2210
MNHN 2461	4	-	-	*Thalassa* W. 377 (from 43º 43.3' N, 4º 27.4' W to 43º 43.2' N, 4º 29' W)	07-10-70	-
MNHN 2462	?	-	-	*Thalassa* W. 415 (from 43º 55.1' N, 6º 11.3' W to 43º 52.5' N, 6º 10.9' W)	11-10-70	1150-860
MNHN 3609	1	-	-	*Thalassa* St. 2447 (from 48º 47.3' N, 11º 12' W to 48º 47.4' N, 11º 14.3' W)	??-??-1973	1150-860
USNM E2591	1	-	150/40	*Albatross* St. 2395, North Atlantic Ocean, Gulf of Mexico, Florida, South of Pensacola, 28º 36' 15"N, 86º 50' W.	13-03-1885	634
USNM E38314	2	-	224/24	RRS *Challenger*, St. 50704, North Atlantic Ocean, SW of Ireland, 49º 40'N, 12º 07'W	13-10-79	1260-1265
ZMUC Eh 319-736	-	-	-	*Thor* St. 99, 61º 15' N, 9º 35' W	22-05-04	900
ZMUC Eh 319-737	2	-	-	*Thor* St. 166, 62º 57' N, 19º 58' W	14-07-03	957
ZMUC Eh 319-738	4	-	-	*Thor* St. 93, 49º 25' N, 12º 20' W	25-06-05	1275-1180
ZMUC Eh 319-740**	7	-	-	*Sars* Scandinavia, Lofoten	-	369-549
ZMUC Eh 319-741	2	-	-	Scandinavia, Bergen, Margerfi	??-08-23	200-300
ZMUC Eh 319-742**	16	-	-	Balestrand, Sognej	-	960
ZMUC Eh 319-743	2	-	-	Norge, Mangerfj	05-06-19	350
ZMUC Eh 319-746?	1	-	-	*Ingolf* St. 73, 62° 58'N, 23° 28'W	08-06-1896	915
NHM 1886.10.2.142	8	-	-	H.M.S *Triton* St. 10, North Atlantic Ocean, off Hebrides Islands, Scotia, West of Wyville-Thompson ridge, 59º 40'N, 7º 21' W	24-08-1882	939
NHM 1886.10.2.143	5	-	-	H.M.S. *Triton* St. 13 North Atlantic Ocean, off Hebrides Islands, Scotia, West of Wyville-Thompson ridge, 59º 51'N, 8º 18' W	31-08-1882	1037
NHM 1925.10.30.99-102	4	-	84/29	H.M.S. *Triton* St. 10 North Atlantic Ocean, off Hebrides Islands, Scotia, Isle of Wyville-Thompson ridge, 59º 40'N, 7º 21' W	-	937
NHM 1886.10.2.142	7	-	-	R.V. *Sarsia* Sognefjorden, near Hoyangsfjorden, Norway	17-07-73	1260

NHM 1889.8.31.30	1	-	-	Sogne Fiord, Norway, 1110m	-	-
NHM 1896.5.18.15	1	-	-	Bay of Biscay	-	1300
NHM 1889.5.3.401/2	1	-	39/8	Norway	-	-
NHM 1898.6.3.399	1	-	67/19	Norway	-	-
USNM E21216??	4	-	111/9	*Albatross* St. 4041, North Pacific Ocean, Hawaii Island, Malae Point, 20º 06' 10"N, 155º 59' 40"W	11-07-02	462-698
USNM E2507	2	-	-	*Albatross* St. 2395, North Atlantic Ocean, Gulf of Mexico, United States, Florida, South of Pensacola, 28º 36'15"N, 86º 50'W	13-03-1885	634
USNM E2576	3	-	-	*Albatross* St. 2398, North Atlantic Ocean, Gulf of Mexico, United States, Florida, South of Pensacola, 28º 45'N, 86º 26'W	14-03-1885	414
USNM E2591	1	-	-	*Albatross* St. 2395, North Atlantic Ocean, Gulf of Mexico, United States, Florida, South of Pensacola, 28º 36'15"N, 86º 50'W	13-03-1885	347
USNM E8584	1	-	-	Artic Ocean, North Sea, Norway, Sognefjorden	-	-
USNM E16404	1	-	-	South Pacific Ocean, New Zealand, 18'N, 30º E of Poor Knights	20-11-62	468
USNM E26069	1	-	-	*Alaminos* St. 71-A-8-67, North Atlantic Ocean, Gulf of Mexico, Mexico, Campeche, 19º 37'30"N, 92º 39'12"W	13-08-71	493
USNM E26092	1	-	-	North Atlantic Ocean, Gulf of Mexico, *Alaminos* St. 72-A-13-649	16-7-72	640
USNM E38314	2	-	-	RRS *Challenger* St. 50704, North Atlantic Ocean, South West of Ireland, West European Basin, 49º 40'N, 12º 07'W	13-10-79	1260
USNM E46771	2	-	-	*Oregon II*, St. 10899, North Atlantic Ocean, Gulf of Mexico, United States, Louisiana, east of Mississippi River Delta, 29º 10'N, 86º 46'W	04-02-70	526
USNM E46779	1	-	-	*Oregon II*, St. 11243, North Atlantic Ocean, Caribbean Sea, Colombia, North of Gulf of Morrosquillo, 10º 09'N, 76º 14'W	09-07-70	914
USNM E46780	1	-	-	*Oregon II*, St. 11276, North Atlantic Ocean, Caribbean Sea, Colombia, North West of Santa Marta, 11º 17'N, 74º 40'W	14-08-70	823
USNM E34145?	1	-	-	*Albatross* North Pacific Ocean, East China Sea, Japan, Goto Islands, South of Fukue Island	??-08-06	-
USNM E2019? ?	1	-	-	*Albatross* St. 3380, North Pacific Ocean, Colombia, North East of Malpelo Island, 4º 3'N, 81º 31'W	05-03-1891	1644
USNM E4521? ?	2	-	-	*Albatross* St. 3988, North Pacific Ocean, United States, Hawaii, Kauai Island, Papaa Bay 22º 11'10"N, 159º 18'10"W	11-06-02	301
USNM E21216?	1	-	-	*Albatross* St. 4041, North Pacific Ocean, United States, Hawaii, Hawaii Island, Malae Point 20º 6'10"N, 155º 59'40"W	11-07-02	253
USNM E21849? ?	3	-	-	*Albatross* St. 4041, North Pacific Ocean, United States, Hawaii, Hawaii Island, Malae Point, 20º 6'10"N, 155º 59'40"W	11-07-02	253
USNM E30389? ?	4	-	-	*Albatross* St. 3988, North Pacific Ocean, United States, Hawaii, Kauai Island, Papaa Bay 22º 11'10"N, 159º 18'10"W	11-06-02	301
USNM E30389? ?	1	-	-	*Albatross* St. 4021, North Pacific Ocean, United States, Hawaii, Kauai Island, Kealia 22º 7'35"N, 159º 18'W	21-06-02	523-730
USNM E30391? ?	1	-	-	*Albatross* St. 4140, North Pacific Ocean, United States, Hawaii, Kauai Island, Hanamaulu Bay 22º 3'10"N, 159º 19'40"W	02-08-02	620-799
USNM E30392? ?	1	-	-	*Albatross* St. 4014, North Pacific Ocean, United States, Hawaii, Kauai Island, East of Hanamaulu Bay 21º 59'N, 159º 19'20"W	20-06-021	662-729
USNM E30393??	1	-	-	*Albatross* St. 3994, North Pacific Ocean, United States, Hawaii, Kauai Island, North of Kee Beach 22º 18'25"N, 159º 36'50"W	12-06-02	603-698
USNM E30395? ?	1	-	-	*Albatross* St. 3824, North Pacific Ocean, United States, Hawaii, Molokai Island, Laau Point 2º 1'25"N, 157º 15'15"W	01-04-02	406-910
USNM E2508?	1	-	-	*Albatross* St. 2634, North Atlantic Ocean, Bahamas, South of Eleuthera Island; 24º 30'43"N, 76º 23'45"W	13-03-1886	1446
USNM E2590	1	-	-	*Albatross* St. 2634, North Atlantic Ocean, Bahamas, South of Eleuthera Island;	13-03-1886	1446

				24º 30’43”N, 76º 23’45”W		
USNM E26070	1	-	-	*Alaminos* St. 71-A-7-11, North Atlantic Ocean, Gulf of Mexico; 26º 32’18”N, 96º 13’18”W	??-07-71	618
USNM E26076	1	-	-	*Alaminos* St. 68-A-13-21, North Atlantic Ocean, Gulf of Mexico	19-11-68	640
USNM E26091	1	-	-	*Alaminos* St. 71-A-8-60, North Atlantic Ocean, Gulf of Mexico	??-08-71	1097
USNM E46789	2	-	-	*Oregon II*, St. 11242, North Atlantic Ocean, Caribbean Sea, Colombia, North of Gulf of Morrosquillo, 10º 10’N, 76º 14’W	09-07-96	1097
USNM E46782	2	-	-	*Oregon II*, St. 11242, North Atlantic Ocean, Caribbean Sea, Colombia, North of Gulf of Morrosquillo, 10º 10’N, 76º 14’W	09-07-96	1097
USNM E46783	2	-	-	*Oregon II*, St. 11243North Atlantic Ocean, Caribbean Sea, Colombia, North of Gulf of Morrosquillo, 10º 09’N, 76º 14’W	05-11-70	914
USNM E41404	1	-	-	Marine Lab. for Batelle-New England, St. s3:04/05, North Atlantic Ocean, Unites States; North Carolina, East of Cape Lookout, 34º 10’24”N, 75º 27’42”W	12-07-84	2908-2919
USNM E41405	2	-	-	Lab. for Batelle-New England, St. SA4:15, North Atlantic Ocean, Unites States; North Carolina, East Charleston Bump, 32º 09’43”N, 76º 42’57”W	17-05-85	2100
ZMUC ? ?	1	-	-	*Prince de Monaco* St. 1193.	??-??-1901	-

* holotype of *Bathyplotes reptans* Perrier.

** In two different jars.

? holotype of *Bathyplotes heterostylides* Heding, 1942

?? syntypes of *Bathyplotes patagiatus* Fisher, 1907

? Holotype of *Bathyplotes östergreni* Ohshima, 1915

?? Identified as *B. patagiatus* by: Fisher, W. K.

?Holotype of B. *patagiatus* Fisher, 1902

?? Paratype of *B. patagiatus* Fisher, 1902

? Identified as *B. pourtalesi* by: Fisher, W. K.

?? Paratype of *B. bipartitus* Hérouard, 1912

Table 10. Examined specimens of ***Bathyplotes punctatus*** (Sluiter, 1901a)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMA E1013	1	Syntype	-	*Siboga*, St. 65a, 7º 0’S, 120º 34.5’ E	-	400
ZMA E1005	1	Syntype	-	*Siboga*, St. 254, 5º 40’S, 132º 26’ E	-	310
ZMUC*	1	-	-	St. 194, Indian Ocean, Indonesia, Nias Channel, 0º 15.2’N, 98º 8.8’ E	01-02-1899	614
MNHN 2993	1	-	-	*Alis* Musorstom 1976, St. 50, Philippines, 13º 49'N, 120º 01.8’ E	25-03-76	415-510
USNM E24567	1	-	150/50	*Oregon*, St. 6695, North Atlantic Ocean, Caribbean Sea, St. Christopher and Nevis, Northwest of St. Christopher, 17º 41’N, 62º 50’30” E	18-05-67	549-585

*Holotype of *Kareniella gracilis* Heding, 1940, (the label inside the jar says “*Karinia gracilis*” in Heding’s handwriting)

Table 11. Examined specimens of ***Bathyplotes rubicundus*** Sluiter, 1901a

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMA E1014	1	Syntype	-	*Siboga* St. 74, South Pacific Ocean, 5º 35’S, 119º 0’E	-	450
ZMA E1016	1	Syntype	-	*Siboga* St. 2, South Pacific Ocean, 7º 25’S, 113º 16’E	-	56

Table 12. Examined specimens of ***Bathyplotes tizardi*** (Théel, 1882a)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
NHM 1900.4.1.162	1	Holotype		*Knight Errant* St. 6, Faroe Channel	-	-
ZMUC	3	-	-	North Sea, Scandinavia, North of the Byfjorden, Bergen	??-02-18	-

ZMUC Eh 319-739	-	-	-	*Ingolf* St. 89	-	-
ZMUC Eh 319-744	1	-	-	*Albatross* St. 2398	08-06-1896	915
ZMUC*	2	-	-	*Ingolf* St. 73, 62º 58' N, 23º 28' W	-	-
ZMUC Eh 319-745		-	-	*Sars* St. 76, 59º 28' N, 8º 01' W	12-08-02	1092-1297
ZMUC**	6	-	-	*Ingolf* St. 73, 62º 58' N, 23º 28' W	08-06-1896	915
ZMUC?	1	-	-	-	-	-
MNHN 958	1	-	-	Brygen Nordfjord, Gravier, No. 62	??-??-1908	400-600
MNHN 1817	1	-	-	Norway, Ostergreen	-	-

*one of them designated by Heding as paratype of *B. heterostylides* Heding

**paratypes of *B. heterostylides* Heding

? holotype of *B. heterostylides* Heding

Table 13. Examined specimens of ***Bathyplotes triplax*** (Clark, 1920)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E10557	1	Syntype	58/6	*Albatross* St. 4642, South Pacific Ocean, Galapagos Islands, South of Espanola Island, 01º 30' 30"S, 89º 35' 00"W	07-11-04	540

Table 14. Examined specimens of ***Benthothuria distortus*** Koehler & Vaney, 1905

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	1	-	-	Deutschen Tiefsee-Expedition, St. 196 , 0° 27.3' N, 98° 7.4' W	01-02-1899	646

Table 15. Examined specimens of ***Benthothuria funebris*** Perrier, 1899

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN 7801	1	Syntype	-	*Talisman* Dr. 62, 26º 20'N, 17º 13', North East Atlantic Ocean, coast of Sudan,	08-07-1883	782
MNHN 7804	1	Syntype	-	*Talisman* Dr. 62, 26º 20'N, 17º 13', North East Atlantic Ocean, coast of Sudan,	08-07-1883	782
MNHN 7805	1	Syntype	-	*Talisman* Dr. 62, 26º 20'N, 17º 13', North East Atlantic Ocean, coast of Sudan,	08-07-1883	782
USNM E38309	1	-	240/95	*Discovery* St. 9640, North Atlantic Ocean, Ireland, West European Basin, Southwest of Ireland, 1, 50º 03'N, 13º 51'W	13-11-77	3749-3757
ZMUC	1	-	-	*Ingolf* St. 36, 61º 50' N, 56º 21' E	10-06-1895	2700

Table 16. Examined specimens of ***Benthothuria fusiformis*** (Sluiter, 1901a)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	1	-		*Valdivia* St. 199, North Pacific Ocean, Indonesia, Nias Channel, 0° 15.5' N, 98° 4.0' E	02-02-1899	470

Table 17. Examined specimens of ***Benthothuria valdiviae*** Heding, 1940

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	1	Holotype		*Valdivia* St. 152, Indian Ocean, 63° 16.5' N, 57° 51'E	17-12-1898	4636

Table 18. Examined specimens of ***Hansenothuria benti*** Miller & Pawson, 1989

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E38201	1	Holotype	-	*Johnson* St. JSLII808, North Atlantic Ocean, Bahamas, Great Abaco Island, South of Cross Harbour Point, 25º 52'12"N, 77º 15'30"W	09-04-84	699
USNM E38202	1	Paratype	-	*Johnson* St. JSLII808, North Atlantic Ocean, Bahamas, Great Abaco Island, South of Cross Harbour Point, 25º 52'12"N, 77º 15'30"W	09-04-84	700
USNM E38203	1	Paratype	-	*Seward Johnson* St. JSLI2009, North Atlantic Ocean, Bahamas, San Salvador Island, East of Cockburn Town, 24º 3'12"N, 74º 33'20"W	25-04-87	694
USNM E38204	1	Paratype	-	*Edwin Link*, St. JSLI2264, North Atlantic Ocean, Bahamas, San Salvador Island, off Riding Rock, East of Cockburn Town, 24º 3'37"N, 74º 33'22"W	13-09-88	903
USNM E38205	1	Paratype	-	*Edwin Link*, St. JSLI2274, North Atlantic Ocean, Bahamas, Acklins Island, west of Plana Cays, 22º 36'30"N, 73º 38'36"W	18-09-88	814
USNM E38206	1	Paratype	-	*Edwin Link*, St. JSLI2274, North Atlantic Ocean, Bahamas, Acklins Island, west of Plana Cays, 22º 36'30"N, 73º 38'36"W	18-09-88	821
USNM E38207	1	Paratype	-	*Edwin Link*, St. JSLI2274, North Atlantic Ocean, Bahamas, Acklins Island, west of Plana Cays, 22º 36'30"N, 73º 38'36"W	18-09-88	817

Table 19. Examined specimens of ***Mesothuria abbreviata*** Koehler & Vaney, 1905

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	1	-	-	Dr. Th. Mortensen's Expeditions Java-South Africa Expedition 1929-1930, St. 7, Indian Ocean, Indonesia, Java Sea, 8º 29' S, 114º 40' E	05-04-29	240
ZMUC	1	-	-	Dr. Th. Mortensen's Expeditions Java-South Africa Expedition 1929-1930, St. 15, Indian Ocean, Indonesia, Java Sea, 07º 29' S, 114º 49' E	10-04-29	240

Table 20. Examined specimens of ***Mesothuria bifurcata*** Hérouard, 1901

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E49271	1	-	54/20	*Islas Orcadas*, St. 37, South Atlantic Ocean, Scotia Sea, South Sandwich Islands, Candlemas Island, 56° 58' 42"S, 26° 30' 36"W	22-05-75	1652-1684
NHM 1953.8.21.43	1	-	178/30	RRS *Discovery* St. 1648, Antarctic, 78º 18' 00"S, 174º 24' 00" W	18-01-36	550
NHM 1953.8.21.44	3	-	86/23	RRS *Discovery* St. 1648, Antarctic, 78º 18' 00"S, 174º 24' 00" W	26-01-36	520
SOC	5	-	-	*Andeep II*, PS61/143-2, Antarctic, 58° 44.35' S, 25° 10.48' W	25-03-2002	752.7
SOC	1	-	-	*Andeep II*, PS61/133-30, Antarctic, 65° 20.15' S, 54° 14.35' W	07-03-2002	1122

Table 21. Examined specimens of ***Mesothuria carnosa*** Fisher, 1907

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM 21215	1	Holotype	-	*Albatross* St. 4130, North Pacific Ocean, Unites States, Hawaii; Kauai Island, Hanamaulu Bay, 21º 58'15"N, 159º 20'55"W	01-01-02	517-565
USNM 30413	1	Paratype	110/30	*Albatross* St. 4130, North Pacific Ocean, Unites States, Hawaii, Kauai Island, Hanamaulu Bay, 21º 58'15"N, 159º 20'55"W	01-08-02	517-565
USNM 30409	3	-	-	*Albatross* St. 3988, North Pacific Ocean, Unites States, Hawaii, Kauai Island, Papaa Bay, 22º 11'10"N, 159º 18'10"W	11-06-02	301-857
USNM 30410	1	-		*Albatross* St. 3997, North Pacific Ocean, Unites States, Hawaii, Kaulakahi Channel, between Kauai and Niihau Islands, 21º 54'35"N, 159º 46'W	14-06-02	764-784

USNM 30411	1	-	-	*Albatross* St. 4041, North Pacific Ocean, Unites States, Hawaii, Hawaii Island, Malae Point, 20º 6’10”N, 155º 59’40”W	11-07-02	462-698
USNM E30412	7	-	120/24	*Albatross* St. 4041, North Pacific Ocean, Unites States, Hawaii, Hawaii Island, Malae Point, 20º 6’10”N, 155º 59’40”W	01-08-02	462-698
USNM 30414	2	-	-	*Albatross* St. 4131, North Pacific Ocean, Unites States, Hawaii, Kauai Island, Hanamaulu Bay, 21º 59’31”N, 159º 20’40”W	01-08-02	470-565
USNM 30415	1	-	-	*Albatross* St. 4132, North Pacific Ocean, Unites States, Hawaii, Kauai Island, Hanamaulu Bay, 22º 1’30”N, 159º 21’10”W	01-08-02	470-570
USNM 30416	8	-	107/30	*Albatross* St. 4134, North Pacific Ocean, Unites States, Hawaii, Kauai Island, Hanamaulu Bay, 22º 3’35”N, 159º 19’40”W	01-08-02	411-592
USNM 30418	1	-	-	*Albatross* St. 4139, North Pacific Ocean, Unites States, Hawaii, Kauai Island, Hanamaulu Bay, 22º 2’10”N, 159º 18’15”W	02-08-02	620-936

Table 22. Examined specimens of ***Mesothuria cathedralis*** Heding, 1940

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
ZMUC	1	Holotype	-	*Valdivia* St. 56, South East Atlantic 3º 10’ N, 5º 28.5’ E	13-09-1898	2278
ZMUC	1	Paratype	-	*Valdivia* St. 56 South East Atlantic, 3º 10’ N, 5º 28.5’ E	13-09-1898	2278
ZMUC	1	-	-	*Dana* St. 78, South East Atlantic Ocean, 8 miles W, by N. of Sugarloaf , Sant Helena	01-11-30	2400-2780
ZMUC	5	-		*Valdivia* St. 33, North East Atlantic, 24º 35.3’N, 17º 4.7’W	25-08-1898	2480
ZMUC	2	-		*Ingolf* St. 18, North East Atlantic, 61º 44’N, 30º 29’W	10-01-1896	2337
USNM E26065	1	-	55/7	*Alaminos* St. 71-A-8-10, North Atlantic Ocean, Gulf of Mexico, off coast of Louisiana, 26º 07’ 30”N, 92º 42’ 00”W	30-07-71	1998
NHM 1978.3.17.109	1	-	23/9	RRS *Challenger* St 10, North East Atlantic, 56º37’ N, 11º 04’ W	07-01-73	2540

Table 23. Examined specimens of ***Mesothuria crebrapedes*** Cherbonnier & Feral, 1981

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
MNHN 3004	1	Holotype	-	*Alis* Musorstom, St. 50, North West Pacific Ocean, Philippines, 13° 49’ 2”N, 120° 01’ 08”E	25-03-76	415-510

Table 24. Examined specimens of ***Mesothuria deani*** Mitsukuri, 1912

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
USNM E17164	25	-	(98/18)	Japan, 16 miles W. by S. of Bonomisaky	13-05-14	360
ZMUC	1		-	-	-	-
ZMUC	10		-	Th. Mortensen’s Pacific Expedition 1914-1915, Japan, Okinose, Sagami Sea	01-07-14	360-720

Table 25. Examined specimens of ***Mesothuria gargantua*** Deichmann, 1930

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
MCZ Cat. No. 449	1	Holotype	150/50	*Atlantis*, St.?	??-??-39	936
USNM E49846	3	-	550/48	-	-	-
USNM E49847	1	-	180/60	-	-	-
USNM E51998	1	-	129/15	-	-	-
NHM 1949.1.19.87	1		136/59	*Rosaura* St. 26 off British Honduras, 17º53’ N; 87º 44’ W	07-11-37	900

Table 26. Examined specimens of ***Mesothuria holothurioides*** Sluiter, 1901a

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMA E1175	10	Syntypes	-	*Siboga,* St. 173, North West Pacific Ocean, 3° 27’S, 131° 0.5’E	-	567

Note: slides coming from the Syntpes in the Museum of Monaco (Cherbonnier’s slide collection, Paris Museum).

Table 27. Examined specimens of ***Mesothuria incerta*** Koehler & Vaney, 1905

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
NHM 1991.11.15	5	-	100/28	John Murray expedition St.157 Maldives, from 04° 43’ 48” N, 072° 55’ 24” E, to 04° 44’ 00” N, 072° 54’ 18” E	06-03-34	229

Table 28. Examined specimens of ***Mesothuria intestinalis*** (Ascanius, 1805)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
UNAM -ICML 5.116.0	2	-	330/60	-	-	-
USNM E22432	2	-	59/14	*John Murray Exped.* St. 157, Indian Ocean, Maldives, East of Male Atoll, 04° 43’ 48”N, 72° 55’ 24”E	06-04-34	229
USNM E8574	1	-	142/27	Artic Ocean, Norwein Sea, Norway, Moldefjorden. “Donation from Bergen Museum”	-	-
ZMUC Eh 319-747	1	-	-	*Ingolf* St. 85, 63° 21’N, 25° 21’W	-	320
ZMUC Eh 319-748	3	-	-	“Donation from Bergen Museum “	-	-
ZMUC Eh 319-749	1	-	-	“Donation from Kgl. Museum”	-	-
ZMUC Eh 319-750	1	-	-	“Donation from Bergen Museum “	-	-
ZMUC Eh 319-751	2	-	-	Norway	-	-
ZMUC Eh 319-752	2	-	-	“Donation from Kgl. Museum”	-	-
ZMUC Eh 319-753	1	-	-	*The Minch*, Loc: England	-	-
ZMUC Eh 319-754	1	-	-	Trondhjemsj ud for Tantiva	31-07-11	200
ZMUC Eh 319-755	2	-	-	Gullmar Fjorden	14-01-10	100
ZMUC Eh 319-756	8	-	-	-	??-02-18	400
ZMUC Eh 319-757	4	-	-	-	??-07-1896	-
ZMUC Eh 319-758	3	-	-	Herlo Bergen, 1905	-	-
ZMUC Eh 319-759	2	-	-	Gullmar Fjorden	15-01-10	-
ZMUC Eh 319-760	1	-	-	*Thor* St. 134	15-07-10	-
ZMUC Eh 319-761	5	-	-	-Gullmar Fjorden	??-07-31	-
ZMUC Eh 319-762	2	-	-	Wahrberg Eliasson St. 33, Koster fjord, Boheslen	04-08-25	600
ZMUC Eh 319-763	12	-	-	Bergen Mongerfj	??-08-23	200-300
NHM 92.2.11.31/35	6	-	-	John Murray Expeditions, North of Scalpa	17-09-1891	72-109
NHM 98.5.3.342	1	-	-	Norway	-	72-109
NHM 88.6.21.1/2	2	-		Kilbrennan Sound	03-03-1888	91
NHM 98.5.3.342	1	-		Norway	-	-
NHM 97.4.4.13	1	-		Bay of Biscay	-	-
NHM 66.11.23.2	1	-		Minch, Hebrides	-	-
NHM 88.4.15.27-30	5	-	-	-	17-03-1888	54-69
NHM 98.5.3.306-8	21	-	-	Norman Expedition St. 30, Norway	??-??-1879	-
NHM	2	-	-	Norway	-	-
NHM 95.3.3.303-5	5	-	-	-	-	-

NHM 98.5.3.309-311	4	-	-	*The Minch*, Norway	-	-
NHM 1900.4.1.21/22	2	-	-	*The Minch*	-	-
ZMUC	1	-	130/29	*South Africa*	-	-
ZMUC	1	-	85/20	*South Africa*	-	-
MNHN 1103	1	-	-	*Bauguls*	??-??-63	350
MNHN 1260	5	-	-	*Bauguls*	??-??-62	-
MNHN 1261	1	-	-	*Bauguls*	??-??-63	-
MNHN 1262	1	-		-	??-??-51	280-400
MNHN 1263	2	-		*Bauguls*	??-??-63	-
MNHN 1349	2	-		*Bauguls*	14-08-62	450
MNHN 1350	2	-		*Bauguls* Mizoule	-	150
MNHN 1723	6	-		*Bauguls* Mizoule	24-08-62	-
MNHN 1755	1	-		*Talisman* Canary Islands, St. 43	26-06-1883	1180
MNHN 1756	2	-		*Travailleur* St. 38	30-07-1882	636
MNHN 1757	2	-		*Talisman* St. 49, Coast of Morocco	??-??-1883	869-927
MNHN 1811	1	-		*Princesse de Monaco* St. 1275	??-??-10	200-300
MNHN 39	1	-		*Prince Napoleon 1856*, Musee de Bergen	-	-
MNHN 40	1	-		Musee de Bergen, Loven 1852	-	-
MNHN 1776	1	-		*Talisman* off Morocco	16-06-1883	-
MNHN 2544	1	-		*Thalassa* St. U 863, 47º 11.4' N, 5º 39' W	-	450-455
MNHN 3482	1	-		*Bauguls*	23-08-68	-
MNHN 7401	3	-		*Europe*, Depro 96, St. 3,Golf du Lion, 48º 43.5' N, 4º 29.4' E	19-04-96	1129-1293
MNHN 8058	1	-		*Europe* Depro 96, St. 4, 42º 34.6' N, 4º 07.4' E	19-04-96	1179
MNHN 8059	5	-		*Europe* Depro 96, St. 6, 42º 20.7' N, 3º 58.9' E	20-04-96	1600
MNHN 8060	1	-		*Europe* Depro 96, St. 8, 42º 23.5' N, 3º 43.5' E	21-04-96	1321
MNHN 8061	2	-		*Europe* Depro 96, St. 14 , 42º 15.6' N, 3º 42.9' E	21-04-96	1153-1275
MNHN 1758	4	-		Baleares Islands	-	-
MNHN 1759	1	-		Atlantic, Coasts of Morocco, *Talisman* St. 12	02-06-1883	958
MNHN 1760	1	-		*Travuiller* St. 27	26-07-1882	470
MNHN 1761	1	-		*Travuiller* St. 33	25-07-1882	440
MNHN 1762	? fragments	-		*Talisman* St. 78, off Sahara	11-07-1883	1400-1435
MNHN 2432	1	-		*Thalassa* St. W 393, 44º 06.9' N, 04º 04.7' W	08-10-70	970-590
MNHN 2436	1	-		*Thalassa* St. W 415, from 43º 55.1' N, 06º 11.3' W to 43º 52.5'N, 6º 10.9'W	11-10-70	1150-860
MNHN 2439	2	-		*Thalassa* St. W 444, from 44º 10.5' N, 08º 38.4' W to 44º 10.1'N, 8º 38.5'W	13-10-70	580-452
MNHN 2441	1	-		*Thalassa* St. W 413 43º 50' N, 06º 08.9' W	11-10-70	500-540
MNHN 2472	1	-		*Thalassa* St. W 440 44º 11.1' N, 08º 38.8' W	13-10-70	-
MNHN 2477	1	-		*Thalassa* St. W 452, 44º 11.1' N, 08º 36' W	14-10-70	500-495
MNHN 2484	1	-	-	*Thalassa* St. W 434 44º 11.8' N, 08º 40.4' W	13-10-70	500-540
MNHN 2485	1	-	-	*Thalassa* St. W 445 44º 11.7' N, 08º 39.9' W	13-10-70	500-600
MNHN 2486	10	-	-	*Thalassa* St. W 394, 44º 04.6' N, 04º 51.5' W	08-10-70	500
MNHN 2512	3	-	-	*Thalassa* St. U 863, 47º 11.4' N, 05º 39.8' W	??-??-68	450
MNHN 2531	2	-	-	*Thalassa* St. U 862, 47º 10.3' N, 05º 41.4' W	??-??-68	630
MNHN 2536	3	-	-	*Thalassa* St. U 836, 43º 29.5' N, 09º 18' W	??-??-68	510-488
USNM E2582	1	-	-	*Albatross* St. 2754, North Pacific Ocean, Caribbean Sea, Northeast of Trinidad and Tobago, 11º 40'N, 58º 33'W	05-12-1887	1609
USNM E2587	1	-	-	*Fish Hawk* St. 7514, North Atlantic Ocean, United States, Florida, Cape Florida, Off Fowey Rocks light	25-03-031	365
USNM E2588	1	-	-	*Fish Hawk* St. 7285, North Atlantic Ocean, Gulf of México, United States, Florida, Florida Keys, west of key west, 24º 15'N, 81º 47'30"W	19-02-02	559
USNM E8574	1	-		Artic Ocean, Norwegian Sea, Norway, Moldefjorden	-	-

USNM E10591	1	-	North Atlantic Ocean or Artic Ocean, Norway	-	-
USNM E17020	4	-	Artic Ocean, North Sea, Norway, Hardangerfjorden	-	-
USNM E18292	1	-	*Pola*, St. 229, North Atlantic Ocean, Mediterranean Sea, Aegean Sea, Greece, Sporades, Samos Island, 37º 54'N, 26º 43'E	-	580
USNM E19576	8	-	North Atlantic Ocean, United States, Off Georgia, 30º 59'N, 80º 8'W	30-08-79	46
USNM E34354	1	-	*Icita* St. 13/8, North Atlantic Ocean, Gulf of Guinea, Off of Liberia, 6º 32'30"N, 11º 29'30"W	02-05-64	400
USNM E51998	1	-	*Ancon* St. C19, North Atlantic Ocean, Caribbean Sea, Colombia, Guajira, Cabo de la Vela, 12º 19'5"N, 72º 42'52"W	??-11-98	462

Table 29. Examined specimens of ***Mesothuria maroccana*** Perrier, 1899

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN 7155	1	Syntype		*Talisman*	??-??-1883	-
NHM	1	-	-	MFP-UC no catalogue number, *Atlantis* St. ?	??-05-39	1836
USNM E49839	1		(55/15)	North Atlantic Ocean, Bahamas, Tongue of the Ocean, *Columbus Iselin*, St. 044, 25º 16'N, 77º 49'W	16-09-80	2603-2768
USNM E2333	3	-	(19/6)	*Albatross* St. 2117, North Atlantic Ocean, Caribbean Sea, Venezuela, Aves Island, 15º 24' 40"N, 63º 31' 30"W	20-01-1884	1229
USNM E20808	1		(220/52)	*Gilliss*, St. 35, North Atlantic Ocean, off Virginia, 36º 57' 54"N, 73º 21' 30"W to 36º 58'N, 73º 19' 24"W	14-09-75	2915-2955
USNM E26104	1		(90/30)	*Alaminos* St. 71-A-8-8, North Atlantic Ocean, Gulf of Mexico, United States, Off the coast of Louisiana, 26º 07'N, 92º 56'W	??-??-71	2030
USNM E20808	1	-	-	*Gillis* St. 35, North Atlantic Ocean, off Virginia, from 36º 57'54"N, 73º 21'30"W to 36º 58'N, 73º 19'24"W	14-09-75	2915-2955
USNM E49844	3	-	83/33	*Columbus Iselin*, St. 010, North Atlantic Ocean, Great Exuma Island, Bahamas, 23º 54'N, 75º 33'W	03-09-80	2028-2063
USNM E49845	27	-	89/36	*Columbus Iselin*, St. 044, North Atlantic Ocean, Tongue of the Ocean, Bahamas, 25º 16'N, 77º 49'W	16-09-80	2603-2768
ZMUC	2	-	-	*Ingolf* St. 18, 61º 44'N, 30º 29'W	-	1135
ZMUC	1			*Ingolf* St. 47 Atlantic Ocean, near Iceland, 61º 32' N, 13º 40'W	??-??-1896	1789
ZMUC	1			*Ingolf* St. 76 Atlantic Ocean, near Greenland, 60º 50' N, 26º 50'W	??-??-1896	-
ZMUC	15			*Ingolf* St. 65 Atlantic Ocean, near Iceland, 61º 33' N, 19º 00'W	??-??-1896	2050
NHM 86.10.2.180	1		58/32	HMS *Challenger* St. V.	-	-
MNHN 3487	1			*Mozatlante* P. 67 B11	-	-
MNHN 6058	4			*Mozatlante*, P43B7	-	-

Table 30. Examined specimens of ***Mesothuria megapoda*** Clark, 1920

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E9847	1	Holotype	39/12	*Albatross* St. 4742, South Pacific Ocean, approx. 1600 km SW of Marquesas Islands and Acapulco, Mexico, 0º 4' 00" S, 117º 07' 00" W	15-02-05	4243

Table 31. Examined specimens of ***Mesothuria*** sp. 1.*

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN 1821	1	-	-	*Talisman* St. 75, off Sahara	10-07-1883	2325-2518

MNHN 1911	5	-	-	*Talisman* St. 81, Golfe de Gascogne	02-07-1883	1139
MNHN 1925	1	-	-	*Talisman* St. 141, Golfe de Gascogne	30-08-1883	1480
MNHN 1912	6	-	-	*Talisman* St. 122, Sud de Fayal	12-08-1883	1440
MNHN 1913	7	-	-	*Talisman* St. 45, off Morocco	26-06-1883	1440
MNHN 1914	4	-	-	*Talisman* St. 127	15-08-1883	1258
MNHN 1915	? fragments	-	-	*Talisman* St. 45, off Morocco	26-06-1883	1440
MNHN 1916	2	-	-	*Talisman* St. 50 off Morocco	27-06-1883	975
MNHN 1917	1	-	-	*Talisman* St. 127, Fayal	15-08-1883	1275
MNHN 1918	5	-	-	*Talisman* St. 40	31-07-1883	1910
MNHN 1919	4	-	-	*Talisman* St. 121	12-08-1883	1442
MNHN 1920	4	-	-	*Talisman* St. 48	26-06-1883	1180
MNHN 1921	1	-	-	*Talisman* St. 134, N. E of Azores	24-08-1883	4010
MNHN 1922	1	-		*Talisman* St. 136 between Azores and *Europe*	26-08-1883	4255
MNHN 1923	1			*Talisman* St. 136 between Azores and *Europe*	26-08-1883	4255
MNHN 1924	2	-	-	*Talisman* St. 134, N. E of Azores	24-08-1883	4010
MNHN 1925	5	-	-	*Talisman* St. 81, Golfe de Gascogne	02-07-1883	1139
MNHN 1926	4			*Talisman* St. 135	25-08-1883	4165
MNHN 1927	2			*Talisman* St. 129, Sud Fayal	16-08-1883	2220-2155
MNHN 1928	3			*Talisman* St. 127, Fayal	15-08-1883	1275
MNHN 1929	10			*Talisman* St. 48, off Morocco	26-06-1883	1180
MNHN 1930	? fragments			*Talisman* St. 127, Fayal	15-08-1883	1275
MNHN 1931	5	-	-	*Talisman* St. 127, Fayal, Azores	15-08-1883	1275
MNHN 1932	7	-	-	*Talisman* St. 121	12-08-1883	1442
MNHN 1933	1	-	-	*Talisman* St. 15, off Sahara	13-06-1883	1425
MNHN 1934	2	-	-	*Talisman* St. 121	12-08-1883	1442
MNHN 1935	2	-	-	*Talisman* St. 127, Fayal, Azores	15-08-1883	1275
MNHN 1936	? fragments			*Talisman* St. 17, Coast of Morocco	14-06-1883	550
MNHN 1937	4	-	-	*Talisman* St. 122, sud de Fayal	12-08-1883	1440
MNHN 1938	1			*Talisman* St. 83, off Sahara	12-07-1883	930

* all these material was identified as *Holothuria verrilli* or *M. verrilli*

Table 32. Examined specimens of ***Mesothuria multipes*** Ludwig, 1893

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E9942	1	Holotype	-	*Albatross* St. 3687, South Pacific Ocean, Society Islands, Tahiti, Point Venus, 17° 30'S, 149° 30'W	05-10-1899	1326
USNM E16502	1	-	-	*Yaquina*, North Pacific Ocean, United States, 44° 40'42"N, 133° 28'6"W	??-??-70	3717
USNM 18279	6	Syntypes	68/14	*Albatross* St. 3392, North Pacific O cean, Gulf of Panama, Panama, Azuero Peninsula, Southeast of Punta Mala, 7° 5'30"N, 79° 40' W	10-03-1891	2322
USNM E18280	2	Syntypes		*Albatross* St. 3362, North Pacific Ocean, Costa Rica, Cocos Island, 5° 56'N, 85° 10'30" W	26-02-1891	2149
ZMUC	1	Paratype		*Albatross* St. 3392 7° 5' 30"N, 79° 40' W	-	-
MNHN 1798	1			Donation from the USNM, no data available; 1 specimen, MNHN 1799, no data available.	-	-
USNM E9875	1			*Albatross* St. 4656, South Pacific Ocean, Peru, Lambayeque, West of Lobos de afuera Island, 6° 55'S, 83° 34' W	13-11-04	4064

Table 33. Examined specimens of ***Mesothuria multipora*** Clark, 1920

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E9942	1	Holotype	145/42	-	-	-
MNHN	5	-	113/43	*Alis* Musorstom 7, St. DW620, Pacific Ocean, 12º 34’S, 178º 11’W	28-05-92	1280
MNHN	?	-	-	*Alis* Musorstom 7, St. CP621 Ocean Pacific 12º 35’S, 178º 11’W	08-05-92	1280-1300
MNHN	17	-	-	*Alis* Musorstom 7, St. CP621 Ocean Pacific 12º 35’S, 178º 11’W	28-05-92	1280-1300
MNHN	7	-	-	*Alis* Musorstom 7, St. CP621 Ocean Pacific 12º 35’S, 178º 11’W	28-05-92	1280-1300
MNHN 3010	1	-	-	*Alis* Musorstom 7, St. CP621 Ocean Pacific 12º 35’S, 178º 11’W	28-05-92	1280-1300
ZMUC	1	-	-	Carlsbergfondets Oceanografiske Expedition Omkring Jorden 1928-1930 *Dana*, St. 3608, Pacific Ocean, Polynesia, South of Cook Islands, 20º 45.5’ S, 164º 13’ E	26-11-28	600

Table 34. Examined specimens of ***Mesothuria murrayi*** (Théel, 1886a)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
NHM 86.10.2.178.	1	Holotype	185/70	HMS *Challenger* St. 300 South East Pacific, 33º 42’ S, 78º 18’ W	17-10-1875	2502
NHM 86.10.2.176	1	Paratype	45/17	HMS *Challenger* St. 300 South East Pacific, 33º 42’ S, 78º 18’ W	17-10-1875	2502
NHM 86.10.2.179	2	Paratypes	51/21	HMS *Challenger* St. 298	17-10-1875	-
NHM 86.10.2.177	1	Paratype	56/17	HMS *Challenger* St. 219, 01º 54’ S, 146º 39’ 40” E	10-10-1875	273
MNHN 7789	1	-	-	*Alis* Musorstom III, St. CP135, 11º 58’N, 122º 02’E	-	485-551
USNM E2566	1		-	*Albatross* St. 2658, North Atlantic Ocean, United States, Florida, Blake Plateau, 28º 21’N, 78º 33’W	03-04-1886	940
USNM E4465	1	-	-	*Albatross* St. 4083, North Pacific Ocean, United States, Hawaii, Maui Island, Maliko Bay, 21º 5’25”N, 156º 20’20”W	21-07-02	435-463
USNM E27857	2	-	-	*Albatross* North Pacific Ocean, United States, Hawaii, Between Lanai and Kauai islands	??-06-02	-
USNM E30436	1	-	-	*Albatross* St. 3813, North Pacific Ocean, United States, Hawaii, Oahu Island, Diamond Head, 21º N, 157ºW	28-03-02	334-482
USNM E30437	3	-	-	*Albatross* St. 3866, North Pacific Ocean, United States, Hawaii, Pailolo Channel, Maui Island, North of Nakalele Point, 21º 10’40”N, 156º34’50”W	10-04-02	518-519
USNM E30438	8	-	-	*Albatross* St. 3883, North Pacific Ocean, United States, Hawaii, Pailolo Channel, Maui Island, Nakalele Point, 21º 9’15”N, 156º34’15”W	16-04-02	507-519
USNM E30441	4	-	26/9	*Albatross* St. 4096, North Pacific Ocean, United States, Hawaii, Maui Island, Pailolo Channel, Maui Island, Northeast of Nakalele Point, 21º 9’30”N, 156º35’5”W	22-07-02	497-523
USNM E31651	1	-	98/37	*Govenor Ray* DH50, North Pacific Ocean, 13º 13’48”N, 129º55’W	29-04-80	4925
USNM E31655	1	-	76/27	*Govenor Ray* DH47, North Pacific Ocean, 13º 13’48”N, 129º55’W	22-04-80	4880
USNM E31657	1	-	116/28	*Govenor Ray* DH33, North Pacific Ocean, 13º 13’48”N, 129º55’W	17-04-80	-
USNM E31659	1	-	65/22	*Govenor Ray* DH65, North Pacific Ocean, 13º 13’N, 129º53’W	21-02-80	4834
ZMUC	2 fragments	-	-	*Galathea* St. 497, Pacific Ocean, Banda Trench, 5° 18’ S, 131° 18’ E		6490-6550
ZMUC	1	-	-	*Princesse-Alice* (Prince de Monaco) St. 863 Atlantic Ocean, off Azores, from 39º 22’N, 29º 16’ W to 39º 19’N, 29º 15’ W	01-08-1897	1940
ZMUC	1	-	-	*Galathea* St. 497 Pacific Ocean, Banda Trench, 5º 18’ S, 131º 18’ E	1950-1952	6490-6550
ZMUC	1	-	-	*The Kei*, St. 41, 5º 28.40’S, 132º 28’ E	25-03-22	245

Table 35. Examined specimens of ***Mesothuria oktaknemus*** Sluiter, 1901a

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMA E1004	2	Syntypes	-	*Siboga*, St. 211, 5º 40.7’S, 120º 45.5’E	-	1158
ZMUC	1	-	-	*Alis* Musorstom, St. 54, Philippines, 13º 54.2’ N, 119º 57.9’ E	26-03-76	975-1125

Note: slides coming from the Syntypes in the Museum of Monaco (Cherbonnier’s slide collection, Paris Museum).

Table 36. Examined specimens of ***Mesothuria oktaknemoides*** Heding, 1940

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	1	Holotype	34/15	*Valdivia* St. 219, 0° 2.3’S, 73° 24’ E	20-02-1899	2253

Table 37. Examined specimens of ***Mesothuria regularia*** Heding, 1940

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	1	Holotype	70/30	*Valdivia* St. 203, Idian Ocean, off Sumatra 1° 47.1’ N, 96° 88.7’E	04-02-1899	660
ZMUC	1	Paratype	-	*Valdivia* St. 246 Indian Ocean, Pemba Channel 5º 24’S, 39º 19’E	22-03-1899	818
NHM 1991.11.14	1	-	-	John Murray Expedition St. 159, from 4º 47’ 30” N, 72º 45’ 18” E to 4º 48’ 00” N, 72º 46’ 42” E	07-03-34	914-1463
MNHN 3033	1	-	-	*Valdivia* Musorstom, St. 45	??-??-76	448-484

Table 38. Examined specimens of ***Mesothuria sufflava*** Cherbonnier & Féral, 1984

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN EcHh 3043	1	Holotype	110/?	New Caledonia, 22º 45’ S, 167º 14’ 5’’E	14-04-78	395-400
AM J21697*	1	-	165/57	North West tip of new Zealand, off Norfolk Island, 28º 57.9’ S, 167º 45.5’E	-	392-423

* Holotype of *M. norfolkensis* Rowe, 1989

Table 39. Examined specimens of ***Mesothuria triradiata*** Heding, 1942b

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	1	Holotype	-	*Valdivia* St. 33, North East Atlantic Ocean, Off Morocco 24° 35’ N, 17° 04’W	-	2480
ZMUC	1	-	-	*Atlantide* St. 120 02º 09’ N, 09º 27’ E, North East Atlantic Ocean, Off Africa	??-??-46	650-260

Table 40. Examined specimens of ***Mesothuria verrilli*** (Théel, 1886a)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MCZ Cat. No. 448	1	Holotype	-	-	-	-
MCZ Cat. No. 450	2	Paratypes	70/??	-	-	-
USNM E16547	1	-	180/50	*Alvin*, St. 697, North Atlantic Ocean, Bahamas, Great Bahama Bank, 23 º 54’N, 77 º 10’W	??-01-77	1337-1355
USNM E46781	1	-	210/40	*Oregon II*, St. 11242, North Atlantic Ocean, Colombia, North of Gulf of Morrosquillo, 10º 10’N, 76º 14’W	05-11-70	1097
USNM E48732	1	-	119/18	*Albatross* St. 5444, North Pacific Ocean, Philippines, Batag Island, 12º 43’ 51”N, 124º 58’ 50”E	03-06-09	563
USNM E49838	2	-	124/35	*Columbus Iselin* St. 012, North Atlantic Ocean, Bahamas, Great Exuma Island, Exuma Sound, 23º 51’N, 75º 50’W	03-09-80	1853-1858
ZMUC	1			*Albatross* St. 2379, East Atlantic Ocean	-	-
ZMUC*	1			*Caudan* Bay of Biscaya		
MNHN 7085**	2	-	-	*Caudan* St. 15, 44º 2’N, 3º 22’W	??-??-1895	1300
MNHN 7481**	1	-	-	*Caudan* St. 15, 44º 2’N, 3º 22’W	??-??-1895	1300

USNM E2593	1			*Albatross* St. 2140, North Atlantic Ocean, Caribbean Sea, Jamaica, South of Kingston Harbor, 17º 36’10”N, 76º 46’05”W	11-03-1884	1675

*it seems like material of the *Holothuria roueli* Koehler’s type series
**syntypes of *Holothuria roulei*

Table 41. Examined specimens of ***Paroriza grevei*** Hansen, 1956

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
ZMUC	1	Holotype	140/??	*Galathea* St. 495, Pacific Ocean, Banda Trench, 5° 26’ S, 130° 58’ E	-	7250-7290
ZMUC	15	Paratypes	-	*Galathea* St. 495, Pacific Ocean, Banda Trench, 5° 26’ S, 130° 58’ E	-	7250-7290
ZMUC	1	-	-	*Galathea* St. 494, Pacific Ocean, Banda Trench, 5° 36’ S, 131° 01’ E	-	7280
ZMUC	1			*Galathea* St. 497, Pacific Ocean, Banda Trench, 5° 18’ S, 131° 18’ E	-	6490-6650

Table 42. Examined specimens of ***Paroriza pallens*** (Koehler, 1895)

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
USNM E38307	1	-	220/60	RRS *Challenger*, St. 52218-1, North Atlantic Ocean, Ireland, west European Basin, 49° 25’N, 12° 50’W	26-06-85	1450-1446

Table 43. Examined specimens of ***Paroriza prouhoi*** Hérouard, 1902

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
USNM E38303	1	-	-	RRS *Challenger*, St. 50811-1, North Atlantic Ocean, SW of Ireland, 49° 39’N, 14° 34’W	02-08-80	4350-4400
MNHN 3256	1	-	346/95	*Talisman* between Azores and Europe	26-08-1883	4255

Table 44. Examined specimens of ***Pelopatides appendiculata*** Théel, 1886a

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
NHM 86.10.2.126	3	Syntypes	163/59	HMS *Challenger* St. 235, North West Pacific Ocean, Japan, 34º 7’ N, 138º 0’ E	04-06-1875	1028
USNM E17156	3	-	145/??	*Albatross* St. 5053, 34° 49’20”N, 138° 40’ 15”E: North West Pacific Ocean, Honshu Island, Omae Zaki, Suruga Bay, Japan	-	1654
USNM E2113	1	-	-	*Albatross* St. 3308, North Pacific Ocean, Bering Sea, Alaska, Pribilof Islands, 56° 12’ 00”N, 172° 07’ 00”W	-	5349

Table 45. Examined specimens of ***Pelopatides confundens*** Théel, 1886a

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
NHM 1986.10.2.121	1	Lectotype	-	HMS *Challenger* St. 299, 33º 31’ S, 74º 43’ W	17-12-1875	3931
NHM 1956.10.3.11	1	Syntype	-	HMS *Challenger* St. 300, NE Juan Fernandez Island, 33º 42’ S, 78º 18’ W	17-12-1875	2514
NHM 1986.10.2.122	2	Syntypes	220/80	HMS *Challenger* St. 298, 34º 7’ S, 73º 56’ W	17-11-1875	4049
NHM 1986.10.2.123	1	Syntype	190/60	HMS *Challenger* St. 299, 33º 31’ S, 74º 43’ W	14-12-1875	3931
NHM 86.10.2.124	4	Syntypes	145/41	HMS *Challenger* St. 300, 33º 42’ S, 78º 18’ W	17-12-1875	3931
USNM E18239	50	-	69/11	*Albatross* St. 3434, North Pacific Ocean, Gulf of California, east of San Jose Island, Mexico, 25° 29’ 30”N, 109° 48’W	21-04-1891	2904
USNM E18239*	5	-	103/25	*Albatross* St. 3434, North Pacific Ocean, Gulf of California, east of San Jose Island, Mexico, 25° 29’ 30”N, 109° 48’W	21-04-1891	2904

USNM E32015	1	-	149/50	*Albatross* St. 3434, North Pacific Ocean, Galapagos Islands, Culpepper Island, 02º 34’ 00” N, 92º 06’ 00” W	05-04-1891	2448
ZMUC	1	-		*H. Sant.* St. 3434	-	-
ZMUC	1			*Albatross* St. 3434	??-??1891	-
NHM 95.11.12.8	1		72/20	*Albatross* 3434, Gulf of California, 25º 29’ 30” N, 109º 48’ 00 ” W	21-04-1891	-
MNHN 3377	1			*Albatross* 3434, Gulf of California, 25º 29’ 30” N, 109º 48’ 00” W	21-04-1891	2904

*(note: it is the same catalogue number as the previpus one)

Table 46. Examined specimens of ***Pelopatides gelatinosa*** (Walsh, 1891)

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
NHM 1905.11.9.3	1	Holotype	140/27	Indian Ocean, Andaman Sea off Port Blair	02-01-1888	487
MNHN 3376*	1	-	-	Off Cinque Island	-	338-396

*donation of the Calcuta Museum to the MNHN

Table 47. Examined specimens of ***Pelopatides gigantea*** (Verrill,1884)

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
USNM E6313	1	-	-	*Albatross* St. 2095, North Atlantic Ocean, United States, Massachusetts, Nantucket Shoals, 39º 29’00”N, 070º 58’ 40”W	30-11-1883	2454-2653

Table 48. Examined specimens of ***Pelopatides grisea*** Perrier, 1899

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
MNHN 7144	1	Holotype	-	*Talisman* St. ?	??-??-1883	1975
MNHN 7193	3	-	-	W off Africa	-	-
MNHN 7824	1	-	-	*Talisman* St. ?	??-??-1883	1918
USNM E18930	2	-	202/90	*Gillis* St. 71, North Atlantic Ocean, off coast of Virginia, 36º 37’ 36”N, 74º 28’ 00”W	17-11-74	1695-1734
USNM E20809	1	-	234/75	*Gillis* St. 32, North Atlantic Ocean, off the coast of Virginia, From 37º 02’ 24”N, 74º 08’ 30”W to 37º 02’ 00”N, 74º 07’ 00” W	13-09-75	2130-2225
USNM E6313	1	-	245/107	*Albatross* St. 2095, North Atlantic Ocean, Massachusetts, Nantucket Shoals, 39º 29’ 00”N, 70º 58’ 40”W	30-09-1883	2454-2653
ZMUC	2	-	-	*Valdivia* St. 67, 5º 6.2’ S, 9º 58.6’ E	-	3035
ZMUC	2	-	-	*Valdivia* St. 63	26-11-1898	-
ZMUC	2	-	-	*Albatross* St. 2051, 39º 41’N, 69º 20’ 20”W	??-??-1883	1976-1990
ZMUC	1	-	-	*Albatross* St. 2232	-	-

Table 49. Examined specimens of ***Pelopatides quadridens*** Heding, 1940

Museum catalogue number	No. of specimens	Type specimen	TL/W (mm)	Locality	Date	Depth (m)
ZMUC	1	Holotype	-	*Valdivia* St. 203, Idian Ocean, Indonesia, Nias Channel, 1º 47.1’ N, 96º 58.7’E	01-02-1899	660
ZMUC	1	Paratype	-	*Valdivia* St. 203, Idian Ocean, Indonesia, Nias Channel, 1º 47.1’ N, 96º 58.7’E	01-02-1899	660
ZMUC	6*	Syntypes	-	*Valdivia* St. 186, 3º 22.1’ N, 101º 11.5’E, West Sumatra	21-01-1899	903
ZMUC	1	-	-	*Valdivia* St. 67, 5º 6.2’ S, 9º 58.6’ E	-	3035
MNHN 3029	1	-	-	*Valdivia* Musorstom, St. 49, Philippines	??-??-76	925-750m
MNHN 3032	1	-	-	*Valdivia* Musorstom, St. 49, Philippines	??-??-76	925-750m

MNHN 3035	1	-	-	*Valdivia* Musorstom, St. 49, Philippines	??-??-76	925-750m

* in three different jars

Table 50. Examined specimens of ***Pelopatides retifer*** Fisher, 1907

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E21218	1	Holotype	110/20	*Albatross* St. 4151, North Pacific Ocean, Nihoa Island, Hawaii, 23º 05'N, 161º 52'W	05-08-02	572-1463
USNM E30407	1	Paratype	90/10	*Albatross* St. 4110, North Pacific Ocean, Kaiwi, Hawaii, 21º 23' 10"N, 157º 26' 30"W	24-07-02	821-841
USNM E30364	1	-	43/9	*Albatross* St. 4039, North Pacific Ocean, Malae Point, Hawaii, 20º 08' 30"N, 56º 15' 20"W	10-07-02	1225-1274
USNM E30402	3	-	114/21	*Albatross* St. 3887, North Pacific Ocean, Maui Island, Hawaii, 21º 16' 30"N, 156º 39' 55"W	17-04-02	1009-1479
USNM E30402*	6	-	78/15	*Albatross* St. 3887, North Pacific Ocean, Maui Island, Hawaii, 21º 16' 30"N, 156º 39' 55"W	17-04-02	1009-1479

* in a different jar but with same catalogue number

Table 51. Examined specimens of ***Pelopatides suspecta*** Ludwig, 1894

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E18174	1	Holotype	94/18	*Albatross* St. 3392, North Pacific Ocean, Azuero Peninsula, Gulf of Panama, 07º 05' 30"N, 79º 40'W	10-03-1891	2322

Table 52. Examined specimens of ***Pseudostichopus echinatus*** Thandar, 1984

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
NHM 1991.11.15	1	-	51/10	John Murray Exped. St. 109, Tanzania; Zanzibar Island, 5º 10' 36" S, 39º 33' 48 E	13-01-34	640

Table 53. Examined specimens of ***Pseudostichopus lapidus*** Hérouard, 1923

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	3	-	-	*Galathea* St. 217, Indian Ocean, Mozambique Channel, 14º 20' S, 45º 09'E	27-02-51	3485

Table 54. Examined specimens of ***Pseudostichopus marenzelleri*** Hérouard, 1923

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN 6073	1	-	-	North Atlantic, P65 B1	??-??-74	-

Note: 4 slides coming from the Holotype in the Museum of Monaco (Cherbonnier's slide collection, Paris Museum).

Table 55. Examined specimens of ***Pseudostichopus mollis*** Théel, 1886a

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
NHM 86.10.2.142	3	Syntypes	-	HMS *Challenger* St. 309A, 50º 56' S, 74º 14' W	08-01-1876	254
NHM 86.10.2.143	4	Syntypes	118/30	HMS *Challenger* St. 311, 52º 30' S, 73º 46' W	11-01-1876	445.9

NHM 1956.10.3.6	2	Syntypes		HMS *Challenger* St. 311, W. end Magellan Str., 52º 45’ 30” S, 73º 46’ W	11-01-1876	445.9
NHM 86.10.2.144	2	Syntypes	165/45	HMS *Challenger* St. 144A Off Marion Island, 46º 48’S, 37º 49’ 30” W	26-12-1873	91-136.5
ZMA E2999**	1	Syntype	-	HMS *Challenger* St. 311, 52º 30’ S, 73º 46’ W	11-01-1876	445.9
UNAM -ICML 100.0	1	-	210/60	North East Pacific Ocean, Costa Rica, Coco Island	28-02-1891	245
USNM E31101	1	1	-	*Govenor* St. DH63, North Pacific Ocean, 13º 13’ 48”N, 129º 55’W	25-04-80	-
USNM E31133	1	-	-	*Govenor* St. DH32, North Pacific Ocean, 13º 13’ 48”N, 129º 55’W	17-04-80	4758
ZMUC Eh 319-415	7	-	120/??	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-416	10	-	-	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-417	4	-	-	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-419	9	-	130/??	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-420	9	-	150/??	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-421	5	-	100/??	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-422	7	-	189/??	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-423	3	-	-	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-424	6	-	82/??	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-425	4	-	-	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-426	5	-	-	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC Eh 319-427	9	-	200/??	*Galathea* St. 716, Acapulco, Mexico-Panama, 9º 23’N, 89º 32’W	06-05-52	3570
ZMUC	3	-	-	*Albatross* St. 2928	-	-
ZMUC	1	-	-	*Albatross* St. 3407	??-??-1891	-
MNHN 1750	1	-	-	*Albatross* St. 3407	??-??-1891	-
MNHN 1751*	1	-	-	-	-	-
MNHN 2142	1	-	-	MD3, St. 16/49	-	2630
SOC	1	-	-	*Discovery* Santa Isabela Island, Galapagos Islands, Dredge 58	17-09-2001	1688

* donation to the MNHN by the British Museum, no data.

**Note: This last syntype at the ZMA have a slightly different latitude position in comparison with USNM labels.

Table 56. Examined specimens of ***Pseudostichopus nudus*** Ohshima, 1915

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E10787	5	syntypes	118/33	*Albatross* St. 4774, North Pacific Ocean, Bering Sea, Alaska, Bowers Bank, 54º 33’N, 178º 45’E	04-06-06	1018-1068

Table 57. Examined specimens of ***Pseudostichopus occultatus*** Marenzeller, 1893a

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN 551	1	Holotype?	-	-	-	-
MNHN 2429	6	-	-	*Thalassa* W 391, 44º 05’N, 04º 35.5’W	08-10-70	805-730
MNHN 2483	3	-	-	*Thalassa* W 374, 43º 36.8’N, 03º 35.4’W	06-10-70	650-320
USNM E41392	4	-	43/16	*Cape Hatteras*, St. #SA4:15, North Atlantic Ocean; South Carolina; East of Charleston Bump, 32º 09’ 43”N, 76º 42’ 57”W	17-05-85	2100
ZMUC*	1			*Ingolf* St. 20, North East Atlantic Ocean, 58º 20’ N, 40º 48’ W	??-??-1895	3192
ZMUC	1			*Galathea* St. 217, Indian Ocean, Mozambique Channel, 14º 20’ S, 45º 09’E	27-02-51	3485

* holotype of *Plicastichopus ingolfi* Heding, 1940

Table 58. Examined specimens of ***Pseudostichopus profundi*** Djakonov, 1952

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E18294	4	-	-	*Pola*, St. 93, North Atlantic Ocean, Mediterranean Sea, Greece, Crete, Candia, 35º 04’N, 24º 17’E	??-??-1891	1445

Table 59. Examined specimens of ***Pseudostichopus propinquus*** Fisher, 1907

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E21217	1	Holotype	20/15	*Albatross* St. 3866, North Pacific Ocean, Hawaii, Pailolo Channel, Maui Island, North of Nakalele Point, 21 10’ 40”N, 156 34’ 50”W	10-04-02	517-519

Table 60. Examined specimens of ***Pseudostichopus trachus*** Sluiter, 1901a

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	1	-	-	*Valdivia* St. 254, 0º 29.3’S, 42º 47.6’ E	-	977
ZMUC	1	-	-	*Valdivia* St. 253, 0º 27.4’S, 42º 47.3’ E	-	638
ZMUC	33	-	-	Dr. Th. Mortensen’s Pacific Expedition 1914-1915, Sagamy Bay, Japan	??-06-14	145-182
ZMUC	1	-	-	Dr. Th. Mortensen’s Pacific Expedition 1914-1915, Sagamy Bay, Japan	06-06-14	-
MNHN 1675	1	-	-	*Valdivia* Musorstom, St. CP 56	??-??-80	970
MNHN 3037	2	-	-	*Valdivia* Musorstom, St. 43	??-??-76	484-448
MNHN 3039	1	-	-	*Valdivia* Musorstom, St. 54	??-??-76	1125
MNHN 3639	1	-	-	Sagami Bay, Japan	-	-

Table 61. Examined specimens of ***Pseudostichopus unguiculatus*** Ohshima, 1915

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E34151	2	-	-	*Albatross* St. 5083, North Pacific Ocean, Japan, Shizuoka, Honshu Island, SW of Omae Zaki, 34º 04’ 20”N, 137º 57’ 30”E	20-10-06	1141

Table 62. Examined specimens of ***Pseudostichopus villosus*** Théel, 1886a

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
NHM 86.10.2.146	1	Syntype	-	HMS *Challenger* St. 156, 62º 26’ S, 95º 44’ E	26-02-1874	3594
NHM 86.10.2.151	1	-	-	HMS *Challenger* St. 216A, 02º 56’ N, 134º 11’ E	16-02-1875	3640
NHM 86.10.2.148	1	-	-	HMS *Challenger* St. 146, 46º 46’ S, 45º 31’ E	29-12-1873	-
NHM 86.10.2.154	1	-	-	HMS *Challenger* St. 147, 46º 16’ S, 48º 27’ E	30-12-1873	2912
NHM 86.10.2.155	1	-	-	HMS *Challenger* St. 157, 53º 55’ S, 108º 35’ E	03-03-1874	3549
NHM 86.10.2.153	1	-	-	HMS *Challenger* St. 302, 42º 43’ S, 82º 11’ W	28-12-1875	2639
NHM 86.10.2.145	1	-	-	HMS *Challenger* St. 61, 34º 54’ N, 56º 38’ W	17-06-1873	5187
NHM 86.10.2.147	1	-	-	HMS *Challenger* St. 244, 35º 22’ N, 169º 53’ E	28-06-1875	5278
NHM 86.10.2.152	1	-	-	HMS *Challenger* St. 296, 38º 06’ S, 88º 02’ W	09-09-1875	3321.
NHM 86.10.2.150	1	-	-	HMS *Challenger* St. 325, 38º 44’ S, 46º 16’ W	02-03-1876	4823
NHM 86.10.2.149	1	-	232/70	HMS *Challenger* St. 298	-	5278
ZMUC	1	-	-	*Galathea* St. 186 Simokstown-Durban, 32º 33’S, 32º 01’E	31-01-51	3707
ZMUC	1	-	-	*Galathea* St. 192, 32º 00’S, 32º 41’E	-	3615

ZMUC	8	-	-	*Galathea* St. 217, Mozambique Channel, 14º 20'S, 45º 09'E	-	3485
ZMUC	2	-	-	*Galathea* St. 232, Madagascar-Mombaza, 09º 03'S, 49º 22'E	08-03-51	5082
ZMUC	2	-	-	*Galathea* St. 233, Madagascar-Mombaza, 07º 24'S, 48º 24'E	09-03-51	4830
ZMUC	1	-	-	*Galathea* St. 238, off Kenya, 03º 23'S, 44º 04'E	13-03-51	4050-4070
ZMUC	3	-	-	*Galathea* St. 282, Seychelles-Ceylon, 05º 32'N, 78º 21'E	-	4150
ZMUC	1	-	-	*Galathea* St. 474, 9º 49'S, 114º 13'E	-	3920
ZMUC	5	-	-	*Galathea* St. 651, Pacific Ocean, Kermadec Trench, 32° 10' S, 177° 14' W	-	6960-7000
ZMUC	5	-	-	*Galathea* St. 654, Pacific Ocean, Kermadec Trench, 32° 10' S, 175° 54' W	-	6002
ZMUC	31*	-	-	*Galathea* St. 658, Pacific Ocean, Kermadec Trench, 35° 51' S, 178° 31' W	-	6660-6720
ZMUC	14**	-	-	*Galathea* St. 663, Pacific Ocean, Kermadec Trench, 36° 31' S, 178° 38' W	24-02-52	4520
ZMUC	11?	-	-	*Galathea* St. 664, Pacific Ocean, Kermadec Trench, 36° 34' S, 178° 57' W		4625
ZMUC	5		-	*Galathea* St. 716, Pacific Ocean, Acapulco, Mexico-Panama, 9° 23' N, 89° 32' W	06-05-52	3680
MNHN 2772? ?	1	-	-	-	-	-
MNHN 2773?	-	-	-	-	-	-
ZMUC	10	-	-	*Eastward* St. 20099, 33º 18'N, 75º 58'W		2560-2490
ZMUC??	1	-	172/45	*Ingolf* St. 37, 60º 17'N, 54º 05'W	-	3230
ZMUC	2	-	-	RRS *Discovery* St. 1660 Antarctica, 74º 46' 24"S, 178º 23' 24" W	27-01-36	351
NHM 86.10.2.156?	1	-	-	HMS *Challenger* St. 156**,** 62º 26' S, 95º 44' E	26-02-1874	3594.5
MNHN 658? ?	1	-		*Talisman* St. 134, between Azores and Europe, 42º 19'N, 23º 36'O	28-08-1883	-
MNHN 2773?	3	-	-	*Talisman* St. 134, between Azores and France, 42º 19'N, 23º 36'O	28-08-1883	-
MNHN 2772?	1	-	-	*Talisman* St. 134, between Azores and France, 42º 19'N, 23º 36'O	28-08-1883	-
MNHN 3411	1	-	-	Kermadec Trench, 36º 31'S, 178º 38' W	-	4520
MNHN 3401	2	-	-	Kermadec Trench, 35º 51'S, 178º 31' W	-	6660
SOC	1	-	-	RRS *Discovery* St. 13907#1, North East Atlantic, 49º 55.85'N, 14º 30.34'W	20-11-2000	4220

* in five jars
**in four jars
?in two jars
?? Holotype of *P. atlanticus*
? Paratypes of *P. atlanticus*
?? holotype of *Molpadiodemas acaudum* Heding, 1940
? syntype of *Pseudostichopus villosus* var. *violaceous* Théel
?? Holotype of *Pseudostichopus atlanticus* Perrier
? paratypes of *Pseudostichopus atlanticus* Perrier

Table 63. Examined specimens of ***Synallactes aenigma*** Ludwig, 1893

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E18206	1	Syntype	29/7	*Albatross* St. 4649 South Pacific Ocean, Galapagos Islands, between Galapagos and Peru, 05º 17' 00" S, 085º 20' 00" W	10-11-04	4088
USNM E18207	1	Syntype	-	*Albatross* St. 3374 South Pacific Ocean, Colombia, Malpelo Island, 02º 35' 00" N, 83º 53' 00" W	30-03-1891	3334
USNM E9882	1	-	59/16	*Albatross* St. 4649 South Pacific Ocean, Galapagos Islands, 05º 17' 00" S, 085º 20' 00" W	10-11-04	4088
USNM E9884	1	-	75/19	*Albatross* St. 4651 South Pacific Ocean, Peru, Sechura Bay, Offshore of Bay, 05º 42' 00" S, 083º 00' 00" W	11-11-04	4064
USNM E9888	1	-	48/10	*Albatross* St. 4651 South Pacific Ocean, Peru, Sechura Bay, Offshore of Bay , 05º 42' 00" S, 083º 00' 00" W	11-11-04	4064
USNM E9908	1	-	42/??	*Albatross* St. 4651 South Pacific Ocean, Peru, Sechura Bay, Offshore of Bay , 05º 42' 00" S, 083º 00' 00" W	11-11-04	4064

USNM E9916	5	-	35/7	*Albatross* St. 4656, South Pacific Ocean, Lambayeque, Lobos de Afuera Island, Peru, , 06º 55’ 00” S, 083º 34’ 00” W	13-11-04	4064
MNHN 7123	2	-	-	*Galathea* St. 716, Acapulco, Mexico- Panama, 9º 23’N, 89º 32’ W	06-05-52	3680
ZMUC	2	-	-	*Galathea* St. 663 Kermadec Trench, 36º 31’S, 178º 38’ E	24-02-52	4520
ZMUC	44	-	-	*Galathea* St. 716 Acapulco, Mexico- Panama, 9º 23’N, 89º 32’ W	06-05-52	3680

Table 64. Examined specimens of ***Synallactes alexandri*** Ludwig, 1893

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E18185	1	Syntype	145/50	*Albatross* St. 3354, North Pacific Ocean, Azuero Peninsula, Gulf of Panama, 07º 09’ 45”N, 80º 50’W	23-02-1891	588
USNM E18212	1	Syntype	95/18	*Albatross* St. 3406, South Pacific Ocean, Galapagos Islands, 00º 16’ 00”S, 90º 21’ 30”W	03-04-1891	1007
ZMUC	1	-	-	*Galathea* St. 745 Pacific Ocean, Gulf of Panama, 7º 15’ N, 79º 25’W	16-05-52	938
LACM 301.4*	2	-	-	*Velero* St. 1400-41, 6¼ miles NE of Long. Pt. Santa Catalina Island, California, 33º 25’05”N, 118º 14’42”W	08-09-41	480
LACM 302.1	1	-	-	*Velero* St. 1306-41, 7 miles E. of Long. Point Santa Catalina Island, California, 33º 24’50”N, 118º 14’05”W	??-05-41	410-480
LACM 301.2*	4	-	-	*Velero* St. 1430-41, 7¼ miles SE of Seal Rocks, Santa Catalina Island, California , 33º 14’20”N, 118º 10’45”W	25-10-41	273

*specimens in bad condition, Paratype of *Bathyplotes hancocki* Domantay

** Holotype of *Bathyplotes maccullochae* Domantay

Table 65. Examined specimens of ***Synallactes challengeri*** (Théel, 1886a)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E47579	12	-	-	South Atlantic Ocean, South Africa, off Capetown	1929 or 1930	-

Table 66. Examined specimens of ***Synallactes chuni*** Augustin, 1908

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E46931	1	-	74/17	*Akademik Oparin*, St. 14, North Pacific Ocean, Bering Sea, Russia, Commander Islands, east of Copper Island,	02-08-91	242-569

Table 67. Examined specimens of ***Synallactes crucifera*** Perrier, 1898

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
MNHN 7162	1	Holotype	-	*Talisman* coast of Morocco, 30° 3’ N., 14° 2’ W	24-06-1883	2212
USNM E38800	3	-	40/11	*Bartlet*, St. 87, North Atlantic Ocean, Caribbean Sea, Venezuela, 13º 30’N, 64° 45’W	25-11-81	3482-3518
USNM E38801	1?*	-	-	*Bartlet*, St. 93, North Atlantic Ocean, Caribbean Sea, Venezuela, 13º 30’N, 64° 45’W	28-11-81	3411-3459
USNM E38802	1	-	-	*Bartlet*, St. 94, North Atlantic Ocean, Caribbean Sea, Venezuela, 13º 30’N, 64° 45’W	28-11-81	3428-3476
USNM E38803	1	-	14/5	*Bartlet*, St. 37, North Atlantic Ocean, Caribbean Sea, Venezuela, 15º 08’N, 69° 12’W	27-10-82	3995-4097

*destroyed specimen, only two skin fragments

Table 68. Examined specimens of ***Synallactes gilberti*** Ohshima, 1915

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E16839	9	-	88/18	North Pacific Ocean, off Oregon, 44° 42’ 18”N, 127° 23’W	-	3021

Table 69. Examined specimens of ***Synallactes heteroculus*** (Heding, 1940)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	1	Holotype	-	Ocean Pacific, Philippines, 15 miles W. ½ S. of Jolo	27-03-14	450
ZMUC	4	Paratypes	-	Ocean Pacific, Philippines, 15 miles W. ½ S. of Jolo	27-03-14	450

Table 70. Examined specimens of ***Synallactes horridus*** Koehler & Vaney, 1905

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E27893	1	-	55/19	*Anton Bruun*, St. 399C, Indian Ocean, Mozambique, 22° 30’S, 36° 07’E	01-10-64	975
ZMUC	4	-	-	*Galathea* St. 491 Indonesia, Makassar Strait, 4º 65’S, 117º 39’E	14-09-51	1600

Table 71. Examined specimens of ***Synallactes*** sp. 1.

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMUC	9	-	-	Dr. Th. Mortensen’s Expedition 1929-1930 *Pickle* St. 25, South Atlantic Ocean, South Africa, Off Durham, 29º 56’ S, 31º 19’ 30” E	26-08-29	409
ZMUC	3 (fragments)	-	-	*Galathea* St. 196, South Atlantic Ocean, South Africa, Off Durham, 29º 55’ S, 30º 20’ E	14-02-51	445-460

Table 72. Examined specimens of ***Synallactes multivesiculatus*** Ohshima, 1915

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E34143	1	Holotype	190/40	*Albatross* St. ?, North Pacific Ocean, Japan, Miyagi, Honshu Island, Kinkazan Island	10-10-06	-
USNM E16254	1	Syntype	-	*Albatross* St. 5051, North Pacific Ocean, Japan, Miyagi, Honshu Island, Kinkazan Island, 38 11’N, 142 12’E	10-10-06	729

Table 73. Examined specimens of ***Synallactes nozawai*** Mitsukuri, 1912

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E2031	4	-	70/14	*Albatross* St. 2853, North Pacific Ocean, Alaska, Trinity Islands, Kodiak Island, 56° 00’ 00”N, 154° 20’ 00”W	09-08-1888	290
USNM E2033	3	-	-	*Albatross* St. 3319, North Pacific Ocean, Bering Sea, Alaska, Aleutian Islands, Makushin Bay, 53° 40’ 30”N, 167° 30’ 00”W	18-08-1890	108
USNM E2034	1	-	39/7	*Albatross* St. 3486, North Pacific Ocean, Bering Sea, Alaska, 57° 19’ 00”N, 173° 53’ 00”W	13-07-1893	274
USNM E10626	5	-	172/28	*Albatross* St. 4986, North Pacific Ocean, Sea of Japan, Hokkaido Island 43° 00’ 00”N, 140° 10’ 30”E	19-09-06	713-785
USNM E10627	5	-	170/25	*Albatross* St. 4812, North Pacific Ocean, Sea of Japan, Sado Island 38° 33’ 00”N, 138° 40’ 00”E	18-07-06	322-366

USNM E10635	12	-	95/18	*Albatross* St. 4994, North Pacific Ocean, Sea of Japan, Hokkaido Island 45° 27’ 50”N, 140° 54’ 00”E	22-09-06	348
USNM E10636	1	-	-	*Albatross* St. 4791, North Pacific Ocean, Bering Sea, Russia, Commander Islands, Bering Island, 54° 36’ 15”N, 166° 58’ 15”E	14-06-06	132-139
USNM E17140	7	-	142/30	*Albatross* St. 4982, North Pacific Ocean, Sea of Japan, Hokkaido Island, 43° 00’ 00”N, 140° 10’ 30”E	19-09-06	713-785
USNM E17158	3	-	146/20	*Albatross* St. 4813, North Pacific Ocean, Sea of Japan, Sado Island, 38° 35’ N, 138° 41’E	18-07-06	365
USNM E17162	25	-	207/35	*Albatross* St. 4983, North Pacific Ocean, Sea of Japan, Hokkaido Island, 43° 01’ 35”N, 140° 10’ 40”E	19-09-06	787
USNM E43831	1		130/28	*Dorothy*, St. C-45, North Pacific Ocean, Gulf of Alaska, off Kodiak Island	31-05-94	182-228
USNM E46932	1	-	84/14	*Akademik Oparin*, St. 44, North Pacific Ocean, Bering Sea, Russia, Commander Islands, Bering Island, 55° 36’ 24”N, 165° 00’ 24”E	24-08-91	205
ZMUC	2	-	-	*Albatross* St. 3339	-	-

Table 74. Examined specimens of ***Synallactes profundus*** (Koehler & Vaney, 1905)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E31634	1	-	-	*Govenor Ray* DH78, North Pacific Ocean, 13º 13’N, 129º 53’W	27-02-80	4910
USNM E31636	1	-	56/22	*Govenor Ray* DH73, North Pacific Ocean, 13º 13’N, 129º 53’W	24-02-80	4849
USNM E31638	1	-	67/20	*Govenor Ray* DH32, North Pacific Ocean, 13º 13’ 48”N, 129º 55’W	14-04-80	4758
USNM E31644	1 fragment	-	-	*Govenor Ray* DH50, North Pacific Ocean, 13º 13’N, 129º 53’W	17-04-80	4925
USNM E31648	1	-	55/19	*Govenor Ray* DH1, North Pacific Ocean	14-04-80	4758
USNM E27971	6	-	34/7	*Eltanin*, St. 474, South Atlantic Ocean, Scotia Sea, South west of South Georgia Island, 55º 56’S, 44º 43’W	??-??-78	-

Table 75. Examined specimens of ***Synallactes sagamiensis*** (Augustin, 1908)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E10637	16	-	89/20	*Albatross* St. 5091, North Pacific Ocean, Honshu Island, Sagami Bay, Japan, 35° 04’ 10”N, 139° 98’ 12”E	26-10-06	360
USNM E10790	10	-	115/21	*Albatross* St. 5092, North Pacific Ocean, Joga Island, Sagami Bay, Japan, 35° 04’ 50”N, 139° 38’ 18”E	26-10-06	128
USNM E17139	12	-	103/25	*Albatross* St. 5092, North Pacific Ocean, Joga Island, Sagami Bay, Japan, 35° 04’ 50”N, 139° 38’ 18”E	26-10-06	128
USNM E17142	1	-	77/22	*Albatross* St. 5094, North Pacific Ocean, Joga Island, Sagami Bay,Japan, 35° 04’ 42”N, 139° 38’ 20”E	26-10-06	161
USNM E17144	4	-	57/18	*Albatross* St. 5048, North Pacific Ocean, Kinkazan Island, Japan, 38° 09’ 24”N, 141° 52’ 30”E	10-10-06	236
USNM E17145	1	-	201/49	*Albatross* St. 5046, North Pacific Ocean, Kinkazan Island, Japan, 38° 15’ 07”N, 141° 44’ 20”E	10-10-06	150

Table 76. Examined specimens of ***Synallactes triradiata*** Mitsukuri, 1912

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E2010	4	-	-	*Albatross* St.3331, North Pacific Ocean, Bering Sea, Alaska, Aleutian Islands, Unalaska Island, 54º 01’ 40”N, 166º 48’ 50”W	21-08-1890	640

Table 77. Examined specimens of ***Zygothuria lactea*** (Théel, 1886a)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
NHM 86.10.2.182	1*	Paratype	-	HMS *Challenger* St. 237, 35º 22' N, 169º 53' E	17-06-1875	3412
NHM 86.10.2.183	1*	Paratype	-	HMS *Challenger* St. 244, 35º 22' N, 169º 53' E	28-06-1875	5278
NHM 86.10.2.184	1*	Paratype	-	HMS *Challenger* St. ?		
NHM 86.10.2.174	1*	Paratype	-	HMS *Challenger* St. 169	10-08-1874	728
NHM 86.10.2.175	3*	Paratypes	-	HMS *Challenger* St. 78		
USNM E16924	1*	-	-	*Commando*, North Pacific Ocean, off Washington State, 45º 49'N, 125º 10'W	06-09-62	1620
USNM E18894	2	-	57/12	*Gilliss*, St. 97, North Atlantic Ocean, off Coast of Virginia, From 37º 00' 18"N, 74º 15' W to 36º 59' 54"N, 74º 24' 30"W	23-11-74	1400-1460
USNM E2572	1*	-	-			
USNM E20328	3	-	72/22	*Gilliss*, St. GS-93, North Atlantic Ocean, North of Carolina, 36º 33' 06"N, 74º 25' W to 36º 36'N, 74º 25'W	19-09-75	1795-1810
USNM E41388	1	-	114/45	*Cape Hatteras*, St. N1:05/06, North Atlantic Ocean, Massachusetts, Georges Bank, Lydonia Slope, 40º 04' 58"N, 67º 26' 35"W	06-11-84	1950-2305
USNM E46761	1	-	230/90	*Oregon II* St. 10880, North Atlantic Ocean, Gulf of Mexico, Mexico, Tamaulipas, East of Boca de Sandoval, 24º 57'N, 96º 13'W	23-01-70	1234
ZMUC	1	-	-	*Caudan* St. 15, Golfe de Gacogne, 44º 2'N, 05º 22'E	??-??-1895	1300
ZMUC	8	-	-	*Ingolf* St. 40, 62º 00'N, 21º 36'W	??-??-1895	1594
ZMUC	3	-	-	*Ingolf* St. 63, 62º 40'N, 19º 05'W	??-??-1896	1500
ZMUC	2	-	-	*Albatross* St. 2116	-	-
ZMUC	8	-	-	*Eastward* St. 20094, 31º 57'N, 76º 14'W	18-05-72	1500-1580
ZMUC	1	-	-	*Valdivia* St. 37	28-08-1898	-
ZMUC	2	-	-	*Valdivia* St. 84 South Atlantic Ocean, 25º 27'S, 6º 10.2'W	17-10-1898	936
ZMUC	2	-	-	*Valdivia* St. 87 South Atlantic Ocean	17-10-1898	5108
ZMUC	-	-	-	Th. Mortensen, South Atlantic Ocean, South Africa, Cannonier Pt., 1929-1930	1929 or 1930	-
NHM 86.10.2.181**	1	-	-	HMS *Challenger* St.158, 50º 21' S, 123º 4' E	07-04-1874	3276
NHM 96.5.18.20	1	-	-	Bay of Biscay	-	1300
NHM 1966.1.20.76	2	-	-	*Albatross* St. 2206, East Atlantic Ocean. S.of Block Dol. 39º 35'00" N, 71º 24' 30"W	20-08-1884	1908
NHM 1938.8.23.17	1	-	-	S.W. Coast of Ireland	-	1820
NHM 89.9.2.90	1	-	-	S.W. Coast of Ireland	-	1820
MNHN 1818	1	-	-	*Prince de Monaco* St. 575	??-??-1895	1165
MNHN 1644	1	-	-	*Travailleur* St. X4	31-07-1882	1900
MNHN 1645	1	-	-	*Talisman* St. 31	16-06-1883	1103
MNHN 1646	1	-	-	*Talisman* St. 59	07-07-1883	1975-2000
MNHN 1647	1	-	-	*Talisman* St. 31	16-06-1883	1103
MNHN 1939	4	-	-	*Talisman* St. 20	16-06-1883	1105
MNHN 1942	1			*Talisman* St. 34	17-06-1883	836
MNHN 1643	1	-	-	*Talisman* St. 31 coast of Morocco	16-06-1883	1535-1100
USNM E2009?	4	-	-	*Albatross* St. 2923, North Pacific Ocean, Unites States, California, San Diego, 32º 40'30"N, 117º 31'30"W	19-01-1889	1503
USNM E2013?	1	-	-	*Albatross* St. 3603, North Pacific Ocean, Bering Sea, Unites States, Alaska, south west of Pribilof Islands, 55º 23'N, 170º 31'W	11-08-1895	3239
USNM E2015?	2	-	-	*Albatross* St. 3345, North Pacific Ocean, Unites States, Oregon, Cape Falcon, 45º 39'N, 124º 53'W	22-09-1890	1388
USNM E2024?	3	-	-	*Albatross* St. 2923, North Pacific Ocean, Unites States, California, San Diego, 32º 40'30"N, 117º 31'30"W	19-01-1889	1503
USNM E2025?	1	-	-	*Albatross* St. 2929, North Pacific Ocean, Unites States, California, San Diego, 32º 27'30"N, 117º 26'30"W	26-01-1889	1139

USNM E9914?	1	-	-	*Albatross* St. 4658, South Pacific Ocean, Peru, Lambayeque, Southwest of Lobos de Afuera Island, 8º 30'S, 85º 36'W	14-11-04	4334
USNM E16459?	1	-	-	North Pacific Ocean, 45º 56'36"N, 127º 31'36"W	-	2763
USNM E16477?	1	-	-	North Pacific Ocean, 44º 42'48"N, 124º 31'12"W		150
USNM E16500?	2	-	-	North Pacific Ocean, *Cayusa* 44º 34'30"N, 128º 21'30"W	03-11-73	2820
USNM E16504?	2	-	-	North Pacific Ocean, *Cayusa* 45º 00'42"N, 127º 28'48"W	03-11-73	2848
USNM E16753?	1	-	-	North Pacific Ocean, United States, Oregon, Southwest of Mouth of Columbia River, 45º 55'N, 125º 9'W	29-05-64	1554
USNM E16754?	1	-	-	North Pacific Ocean, United States, Oregon, Southwest of Mouth of Columbia River, 45º 45'N, 125º 9'W	29-05-64	1646
USNM E16755?	2	-	-	North Pacific Ocean, *Comando*, 45º 36'N, 124º 54'W	09-06-62	1371
USNM 18163? ?	1	-	-	*Albatross* St. 3398, North Pacific Ocean, Ecuator, Cojimies, 1º 7'N, 80º 21'W	23-03-1891	2877
USNM E27540?	2	-	-	*Eltanin* St. 514, Antarctic Ocean, Weddell Sea, Antarctica, South Orkney Islands, 63º 21'S, 44º 51'W	24-02-63	3587-3660
USNM E27903?	2	-	-	*Eltanin* St. 334, South Pacific Ocean, Chile, Los Lagos, South west of Valdivia 42º 57'S, 75º 3'W	27-11-62	3651
USNM E2324	2	-	-	*Albatross* St. 2117, North Atlantic Ocean, Caribbean Sea, Venezuela, Aves Island, 15º 24'40"N, 63º 31'30" W	27-01-1884	1249
USNM E2333	1	-	-	*Albatross* St. 2117, North Atlantic Ocean, Caribbean Sea, Venezuela, Aves Island, 15º 24'40"N, 63º 31'30" W	27-01-1884	1249
USNM E2577	5	-	-	*Albatross* St. 2392, North Atlantic Ocean, Gulf of México, United States, Louisiana, east of Mississippi Delta, 28º 47'30"N, 87º 27' W	13-03-1885	1324
USNM E10534	1	-	-	*Comando* North Pacific Ocean, United States, Washington, southwest mouth of Colombia River, 45º 37'6"N, 124º 54'36" W	15-05-63	1371
USNM E10535	3	-	-	*Comando* North Pacific Ocean, United States, Washington, southwest mouth of Colombia River, 45º 54'N, 125º 9'W	17-05-62	1554
USNM E15112	4	-	-	*Albatross* St. 2706, North Atlantic Ocean, Canada, Nova Scotia, south of Browns Bank, 41º 28'30"N, 65º 35'30"W	27-08-1886	2172
USNM E28709	1	-	-	*Columbus Iselin* St. 2706, North Atlantic Ocean, Bahamas, Tongue of the Ocean, 23º 57'N, 77º 16'W	15-09-80	1378
USNM E46759	1	-	-	*Oregon II* St. 10955, North Atlantic Ocean, Gulf of Mexico, Mexico, Veracruz, Northwest part of Campeche Bay, 21º 41'N, 96º 55'W	03-06-70	896
USNM E46761	1	-	-	*Oregon II* St. 10880, North Atlantic Ocean, Gulf of Mexico, Mexico, Tamaulipas, east of Boca de Sandoval, 24º 57'N, 96º 13'W	23-06-70	1234
SOC	7	-	-	RRS *Discovery* St. 13919#1, North East Atlantic, 51º 08.89'N, 11º 03.92'W	25-10-2000	1545

* specimen(s) very deteriorated

** Syntype of *Holothuria thompsoni* var. *hyalina* Théel

? Identified at the USNM as *Capheira mollis*

?? Holotype of *Capheira sulcata* Ludwig (in poor condition)

Table 78. Examined specimens of ***Zygothuria marginata*** (Sluiter, 1901a)

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
ZMA E1028	1	Syntype		*Siboga*, St. 87, 0º 32'S, 119º 39.8'E	-	655
ZMA E1029	1	Syntype		*Siboga*, St. 170, 3º 37.7'S, 131º 26.4'E	-	924
USNM E22434	1 fragment	-	-	Indian Ocean, Tanzania, Zazinbar, off southwest coast of Pemba Island, 5º 18'6"S, 39º 24'12"E	13-01-34	786
USNM E48767	3	-	86/45	*Albatross* St.5589, North Pacific Ocean, Celebes Sea, Malaysia, Sabah, Darvel Bay, 04º 12' 10"N, 118º 38' 08"E	29-09-09	475

USNM E49850	7	-	122/41	*Albatross* St.5624, North Pacific Ocean,Molucca Sea, Indonesia, Halmahera Island, SE of Makian Island, 00º 12’ 15”N, 127º 29’ 30”E	29-09-09	526
ZMUC	1	-	-	*Valdivia* St. 203, Indian Ocean, West of Nias Island, Nias North Channel, Indonesia, 1º 47.1’ N, 96º 58.7’E	04-02-1899	660
NHM 1991.11.14	7*	-	-	John Murray, St. 108, Tanzania, Zanzibar Island, 05º 18’ 06” S, 39º 24’ 12” E to 05º 14 30” S, 39º 25’ 36” E,	13-06-34	7860

* specimens very deteriorated.

Table 79. Examined specimens of ***Zygothuria oxysclera***

Museum catalogue number	**No. of specimens**	**Type specimen**	**TL/W (mm)**	**Locality**	**Date**	**Depth (m)**
USNM E46761		-	-	*Oregon II*, St. 10880, North Atlantic Ocean, Gulf of Mexico, Tamaulipas, East of Boca de Sandoval, 24° 57’N, 96° 13’W	23-01-70	1234
MNHN 1648	1	-	-	*Talisman* St. 21	14-06-1883	1319
MNHN 1649	fragments	-	-	*Talisman* St. 31	16-06-1883	1163
MNHN 1944	2	-	-	*Talisman* St. 32 off Morocco	17-06-1883	1052
MNHN 1941	1	-	-	*Talisman* St. 36(?) off Morocco	21-06-1883	1050-1052
MNHN 1940	1	-	-	*Talisman* St. 49	27-06-1883	865

Appendix 2

Table 1. *Examined specimens of Bathyplotes natans* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
9756 #9	13-04-78	49º 47.1’	14º 1.5’	49º 48.5’	14º 2.0’	4069-4039	1
9774 #1	21-04-78	51º 4.4’	11º 59.3’	51º 5.2’	12º 3.4’	1492-1572	1
9779 #1	24-04-78	49º 22.3’	12º 49.1’	49º 20.7’	12º 49.5’	1404-1398	21
50503 #1	01-06-79	51º 37.1’	13º 14.6’	51º 35.0’	13º 15.34’	1042-992	1
50505 #1	01-06-79	51º 44.1’	12º 46.3’	51º 43.2’	12º 50.6’	1250	2
50506 #1	02-06-79	51º 55.8’	13º 36.3’	51º 58.8’	13º 34.6’	500	1
50519 #1	08-06-79	49º 29.5’	12º 48.9’	49º 29.9’	12º 43.6’	1465-1431	191
50520 #1	08-06-79	49º 33.6’	12º 08.1’	49º 36.5’	12º 06.4’	1250	1
50522 #1	08-06-79	49º 24.0’	11º 45.4’	49º 26.1’	11º 45.1’	1000-965	1
50601 #1	01-07-79	51º 19.2’	11º 41.1’	51º 21.1’	11º 42.9’	927-770	1
50606 #1	06-07-79	50º 40.4’	14º 9.8’	50º 40.1’	14º 10.8’	1120-1110	2
50606 #2	06-07-79	50º 40.8’	14º 4.1’	50º 42.1’	14º 1.3’	1080-1120	22
50606 #5	06-07-79	50º 43.1’	13º 56.1’	50º 42.7’	13º 57.0’	1140-1120	3
50607 #1	07-07-79	51º 1.7’	14º 12.1’	51º 1.4’	14º 7.3’	700-712	1
50611 #1	08-07-79	51º 19.5’	13º 15.3’	51º 15.6’	13º 20.0’	1365-1415	63
10108 #1	05-09-79	49º 20.6’	12º 49.2’	49º 19.6’	12º 48.7’	1385-1390	4
10109 #8	07-09-79	49º 11.7’	12º 19.4’	49º 10.0’	12º 18.5’	1120-1130	77
50704 #1	13-10-79	49º 40’	12º 07’	-	-	1260-1265	9
50709 #1	16-10-79	49º 23.5’	12º 21.5’	-	-	1260	10
50713 #1	20-10-79	51º 22’	13º 18’	-	-	1649-1605	1
50801 #1	30-07-80	49º 35.0’	12º 11.4’	-	-	1285-1845	27
50808 #1	01-08-80	49º 34.9’	11º 48.9’	-	-	950-965	1
50809 #1	01-08-80	49º 31.9’	12º 09.7’	-	-	1250-1260	8
50815 #1	05-08-80	51º 36.1’	13º 04.2’	-	-	1280-1344	8
50820 #1	06-08-80	51º 55.4’	13º 18.7’	-	-	725-714	1
50904 #1	08-11-80	51º 21.8’	13º 27.4’	51º 19.3’	13º 30.12’	1035-1020	15
50905 #1	08-11-80	51º 41.78’	13º 26.54’	51º 43.14’	13º 21.17’	755-820	7
50903 #1	17-11-80	51º 16.6’	13º 23.3’	51º 15.12’	13º 25.12’	1265-1250	29
51008 #1	02-05-81	51º 35.8’	13º 01.6’	-	-	1350-1370	5
51023 #1	09-05-81	49º 30.1’	12º 10.8’	-	-	1260-1275	18
51025 #1	10-05-81	49º 26.5’	11º 25.1’	-	-	460-480	5
51026 #1	10-05-81	49º 24.5’	11º 34.4’	-	-	750-730	1
51027 #1	10-05-81	49º 32.4’	11º 50.5’	-	-	970-985	1
51306 #1	19-02-82	51º 43.8’	12º 52.6’	-	-	1205-1230	5
51314 #1	22-02-82	49º 31.8’	12º 29.1’	-	-	1455-1425	4
51318 #1	24-02-82	49º 34.1’	12º 41.9’	-	-	700	2
51403 #1	25-03-82	51º 37.7’	12º 59.8’	51º 36.6’	13º 00.0’	1292-1314	8
51403 #2	25-03-82	51º 37.4’	12º 59.2’	51º 36.9’	12º 59.2’	1317-1325	17
51403 #3	25-03-82	51º 36.8’	12º 59.1’	51º 36.4’	12º 59.3’	1319-1333	4
51403 #4	26-03-82	51º 36.7’	12º 59.6’	51º 36.0’	12º 59.8’	1319-1333	8
51403 #6	26-03-82	-	-	-	-	1278-1295	5
51403 #7	26-03-82	51º 36.4’	12º 59.6’	51º 39.2’	12º 58.8’	1320-1247	22
51420 #1	02-04-82	51º 37.3’	12º 58.6’	51º 36.9’	12º 58.6’	1326-1328	19

51420 #3	02-04-82	51º 38.3’	12º 58.9’	51º 38.0’	12º 59.0’	1293-1298	6
51420 #4	02-04-82	51º 37.9’	12º 59.5’	51º 37.5’	12º 59.6’	1279-1287	8
51707 #1	12-05-83	51º 39.9’	13º 00.0’	51º 39.2’	13º 3.4’	1230-1205	7
52204 #1	16-06-85	51º 37.07’	12º 59.96’	51º 37.29’	13º 00.01’	1310-1315	9
52218 #1	26-06-85	49º 25.40’	12º 49.80’	49º 26.37’	12º 50.27’	1450-1465	12
11267 #2	22-04-86	51º 38.3’	13º 4.5’	51º 28.7’	13º 6.3’	1270-1240	8
11907 #1	20-08-89	49º 40.3’	12º 08.2’	49º 37.8’	12º 08.8’	1315-1295	4

Table 2. Examined specimens of *Benthothuria funebris* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*. In bold specimens processed for DNA extraction.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
9638 #2	08-11-77	49º 50.2’	14º 7.3’	49º 50.3’	12º 6’	4043-4104	6
9640 #1	13-11-77	50º 3.2’	13º 50.6’	50º 8.0’	13º 52.7’	3749-3757	43+
9756 #14	15-04-78	50º 4.0’	13º 55.6’	50º 4.3’	13º 53.2’	3697-3680	1
50512 #1	04-06-79	50º 13.6’	13º 44.5’	50º 10.8’	13º 36.8’	3022-3110	1
50514 #1	05-06-79	49º 43.9’	14º 02.2’	49º 38.8’	14º 00.4’	4017-4095	2
50603 #1	02-07-79	49º 46.2’	14º 1.5’	49º 44.4’	14º 0.5’	4000	1
50605 #1	05-07-79	50º 11.6’	13º 32.4’	50º 11.2’	13º 29.0’	2930-2820	3+
10115 #1	11-09-79	49º 46.3’	13º 56.0’	49º 45.6’	13º 56.6’	3900-3950	2
50701 #1	11-10-79	54º 34’	11º 54’	-	-	2870-2890	8
50811 #1	02-08-80	49º 38.6’	14º 34.2’	-	-	4400-4350	1
50812 #2	03-08-80	49º 52.7’	14º 17.3’	-	-	4140-4035	9
50813 #1	04-08-80	50º 13.6’	14º 07.9’	-	-	3640-3715	2
50906 #1	09-11-80	50º 26.2’	13º 20.8’	50º 24.10’	13º 34.91’	2585-2705	1
50907 #1	10-11-80	49º 53.7’	13º 30.4’	49º 53.19’	13º 33.5’	2820-3120	2
50910 #1	10-11-80	49º 49.6’	14º 40.5’	49º 50.56’	14º 49.63’	4265-4320	1
50913 #1	12-11-80	50º 11.9’	13º 39.8’	50º 11.3’	13º 41.3’	3000-3040	1
51012 #1	05-05-81	49º 51.0’	13º 57.8’	-	-	3880-3920	1
51214 #1	27-09-81	50º 00.9’	14º 06.8’	49º 58.0’	14º 04.3’	3820-3800	6
51216 #4	29-09-81	49º 49.1’	14º 06.6’	49º 54.3’	14º 08.8’	4000-3970	17+
51411 #1	29-03-82	50º 27.2’	12º 59.1’	50º 22.4’	13º 01.3’	2462-2510	1
51413 #1	30-03-82	50º 13.8’	13º 32.3’	50º 08.3’	13º 34.2’	2770-2940	11
51414 #1	30-03-82	49º 43.7’	14º 10.3’	49º 39.0’	14º 18.0’	4180-4310	4
51604 #1	19-07-82	50º 15.0’	13º 38.0’	50º 14.9’	13º 36.9’	2920-2890	2+
51611 #1	21-07-82	50º 17.2’	13º 24.8’	50º 21.4’	13º 17.2’	2700-2640	1
51803 #1	26-09-83	49º 37.1’	13º 48.5’	-	-	3990-3920	3
51804 #1	26-09-83	49º 55.6’	13º 26.1’	-	-	3180-3015	2
52214 #1	20-06-85	49º 51.96’	14º 14.77’	49º 52.69’	14º 19.76’	4130-4150	1
13914#1	**22-09-00**	**49º 54.84’**	**13º 34.34 ’**	**49º 52.88’**	**13º 38.99’**	**2981-3115**	**10**

Table 3. Examined specimens of *Mesothuria bifurcata* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*.

Station number	Date	Start Lat (N)	Long (W)	End Lat (N)	Long (W)	Depth (m)	No. of specimens
10111 #8	09-09-79	49º 32.7’	13º 7.1’	49º 33.5’	13º 5.9’	1630-1690	1

Table 4. Examined specimens of *Mesothuria cathedralis* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*. In bold specimens processed for DNA extraction.

Station number	Date	Start Lat (N)	Long (W)	End Lat (N)	Long (W)	Depth (m)	No. of specimens
9640 #1	13-11-77	50º 3.2’	13º 50.6’	50º 8.0’	13º 52.7’	3794-3757	1
9754 #3	09-04-78	51º 804’	12º 1.5’	51º 9.5’	12º 1.8’	1484	1
50515 #1	06-06-79	49º 43.9’	15º 04.6’	49º 46.9’	15º 08.6’	4505-4515	3
50603 #1	02-07-79	49º 46.5’	14º 1.5’	49º 44.4’	14º 0.51’	4000	1
50605 #1	05-07-79	50º 11.6’	13º 32.4’	50º 11.2’	13º 29.0’	2930-2820	1
10113 #1	10-09-79	50º 16.1’	13º 31.6’	50º 16.3’	13º 32.3’	2755-2760	1
50711 #1	18-10-79	49º 53’	15º 36’	-	-	4595-4560	1
51403 #1	25-03-82	51º 37.7’	12º 59.8’	51º 36.6’	13º 00.0’	1292-1314	2
51403 #4	26-03-82	51º 36.7’	12º 59.6’	51º 36.0’	12º 59.8’	1319-1333	1
52216 #8	25-06-85	48º 47.95’	16º 37.59’	48º 47.59’	16º 39.68’	4900-4930	2
11908 #35	03-09-89	48º 53.4’	16º 18.0’	48º 50.1’	16º 28.3’	4843-4847	3
11908 #44	05-09-89	48º 47.3’	16º 29.9’	48º 56.8’	16º 27.6’	4843-4849	7+
11908 #51	07-09-89	48º 45.5’	16º 32.2’	48º 51.0’	16º 29.4’	4839-4854	4+
11908 #55	09-09-89	48º 47.8’	16º 35.0’	48º 49.6’	16º 34.4’	4660	1
11908 #68	12-09-89	48º 52.0’	16º 24.1’	48º 47.6’	16º 36.1’	4853-4877	16+
52701 #17	18-05-91	48º 51.3’	16º 30.3’	48º 47.0’	16º 43.1’	4840-4845	31+
13200 #9	06-07-97	48º 51.96’	16º 24.61’	48º 46.21’	16º 31.63’	4844-4840	6
13200 #27	10-07-97	48º 52.50’	16º 39.31’	48º 42.44’	16º 41.00’	4848-4839	13
13200 #35	11-07-97	48º 44.03’	16º 32.82’	48º 55.85’	16º 40.22’	4842-4845	25
54301 #6	20-10-97	48º 46.9’	16º 49.7’	48º 48.6’	16º 40.5’	4837-4846	16
54301 #8	22-10-97	48º 49.1’	16º 38.4’	48º 50.5’	16º 27.0’	4839-4844	12
13368 #23	10-03-98	48º 50.7’	16º 28.34’	48º 44.84’	16º 40.44’	4844-4842	6
13925 #1	**07-10-00**	**48º 53.46’**	**16º 45.82’**	**48º 56.79’**	**16º 54.73’**	**4835-4845**	**1**

Table 5. Examined specimens of *Mesothuria intestinalis* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*.

Station number	Date	Start Lat (N)	Long (W)	End Lat (N)	Long (W)	Depth (m)	No. of specimens
50503 #1	01-06-79	51º 37.1’	13º 14.6’	51º 35.0’	13º 15.34’	1042-992	1
50505 #1	01-06-79	51º 44.1’	12º 46.3’	51º 43.2’	12º 50.6’	1250	1
50519 #1	08-06-79	49º 29.5’	12º 48.9’	49º 29.4’	12º 43.8’	1465-1431	1
50704 #1	13-10-79	49º 40’	12º 07’	-	-	1260-1265	1
50709 #1	16-10-79	49º 23.5’	12º 21.5’	-	-	1260	3

50802 #1	30-07-80	49º 39.5’	12º 36.9’	-	-	1857-1910	2
50809 #1	01-08-80	49º 31.9’	12º 09.7’	-	-	1250-1260	2
50815 #1	05-08-80	51º 36.1’	13º 04.2’	-	-	1280-1344	2
50819 #1	06-08-80	52º 04.5’	13º 29.2’	-	-	512-500	1
51025 #1	10-05-81	49º 26.5’	11º 25.1’	-	-	460-480	1
51313 #1	12-02-82	49º 32.1’	12º 11.7’	-	-	1250	1
51403 #1	25-03-82	51º 37.7’	12º 59.8’	51º 36.6’	13º 00.0’	1292-1314	1
51403 #5	26-03-82	51º 37.8’	12º 58.9’	51º 37.3’	12º 59.0’	1289-1297	1
51403 #7	26-03-82	51º 36.4’	12º 59.6’	51º 39.2’	12º 58.8’	1320-1247	7
51420 #1	02-04-82	51º 37.3’	12º 58.6’	51º 36.9’	12º 58.6’	1326-1328	1
51420 #4	02-04-82	51º 37.9’	12º 59.5’	51º 37.5’	12º 59.6’	1279-1287	1
51707 #1	12-05-83	51º 39.9’	13º 00.0’	51º 39.2’	13º 3.4’	1230-1205	1

Table 6. Examined specimens of *Mesothuria maroccana* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
50518 #1	07-06-79	49º 27.3’	13º 21.1’	49º 30.1’	13º 26.8’	2045-2110	2
50519 #1	08-06-79	49º 29.5’	12º 48.9’	49º 29.9’	12º 43.6’	1465-1431	9
10106 #1	04-09-79	50º 41.7’	12º 50.7’	50º 41.0’	12º 48.4’	2300-2315	1

Table 7. Examined specimens of *Mesothuria milleri* sp. nov. present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*. In bold specimens processed for DNA extraction.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
50301 #1	30-10-78	56º 35’	09º 38’	56º 30’	09º 45’	1500	1
50510 #1	03-06-79	51º 05.3’	13º 04.5’	51º 06.5’	12º 59.5’	1925-1945	2
50509 #1	03-06-79	51º 14.7’	13º 16.3’	51º 13.5’	13º 19.2’	1500	4
50517 #1	07-06-79	49º 30.1’	13º 19.9’	49º 27.7’	13º 17.2’	1794-1785	1
50522 #1	08-06-79	49º 24.0’	11º 45.4’	49º 26.1’	11º 45.1’	1000-965	3
50523 #1	09-06-79	49º 31.6’	11º 23.9’	48º 29.0’	11º 25.9’	455-490	2
50611 #1	08-07-79	51º 19.5’	13º 15.3’	51º 15.6’	13º 20.0’	1365-1415	7
10108 #1	05-09-79	49º 20.6’	12º 49.2’	49º 19.6’	12º 48.7’	1385-1390	2
50703 #1	13-10-79	49º 33’	12º 34’	-	-	1575-1625	2
50713 #1	20-10-79	51º 22’	13º 18’	-	-	1649-1605	1
50810 #1	02-07-80	49º 34.1’	12º 41.9’	-	-	1649-1605	1
50811 #1	02-08-80	49º 38.6’	14º 34.2’	-	-	4400-4350	1
50815 #1	05-08-80	51º 36.1’	13º 04.2’	-	-	1280-1344	7
50819 #1	06-08-80	52º 04.5’	13º 29.2’	-	-	512-500	2
51009 #1	02-05-81	51º 34.2’	12º 54.2’	-	-	1510-1535	7
51023 #1	09-05-81	49º 30.1’	12º 10.8’	-	-	1260-1275	1
51307 #1	19-02-82	51º 26.4’	13º 01.4’	-	-	1490-1415	1
51314 #1	22-02-82	49º 31.8’	12º 29.1’	-	-	1455-1425	1
51318 #1	24-02-82	49º 34.1’	12º 41.9’	-	-	700	2
51403 #2	25-03-82	51º 36.9’	12º 59.2’	51º 36.9’	12º 59.2’	1317-1325	1

51403 #5	26-03-82	49º 23.7’	11º 34.2’	51º 37.3’	12º 59.0’	1289-1297	2
51403 #7	26-03-82	51º 36.4’	12º 59.9’	51º 39.2’	12º 58.8’	1320-1247	1
51420 #1	02-04-82	51º 37.3’	12º 58.6’	51º 36.9’	12º 58.6’	1326-1328	2
51708 #2	13-04-83	51º 31.3’	12º 58.4’	51º 31.0’	13º 0.3’	1470-1430	2
52204 #1	16-06-85	51º 37.07’	12º 59.96’	51º 37.29’	13º 00.01’	1310-1315	1
13919 #1	**25-09-00**	**51º 08.89’**	**12º 03.92’**	**51º 07.34’**	**12º 00.56’**	**1537-1545**	**5**

Table 8. Examined specimens of *Paroriza pallens* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*. In bold specimens processed for DNA extraction.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
50509 #1	03-06-79	51º 14.7’	13º 16.3’	51º 13.5’	13º 19.2’	1490-1505	2
50517 #1	07-06-79	49º 30.1’	13º 19.9’	49º 27.7’	13º 17.2’	1794-1785	2
50519 #1	08-06-79	49º 29.5’	12º 48.9’	49º 29.9’	12º 43.6’	1465-1431	8
50703 #1	13-10-79	49º 33’	12º 34’	-	-	1575-1625	3
50810 #1	02-08-80	49º 34.1’	12º 41.9’	-	-	1694-1605	3
51708 #2	13-04-83	51º 31.3’	12º 58.4’	51º 31.0’	13º 0.3’	1470-1430	7
52017 #1	21-08-84	51º 31.74’	12º 58.39’	51º 31.95’	12º 57.69’	1470-1485	5
52019 #1	22-08-84	51º 24.81’	12º 46.17’	51º 25.14’	12º 45.55’	1710-1725	1
52218 #1	26-06-85	49º 25.40’	12º 49.80’	49º 26.37’	12º 50.27’	1450-1465	5
54914 #1	15-05-99	-	-	-	-	1460-1465	4
13919 #1	**25-09-00**	**51º 08.89’**	**12º 03.92’**	**51º 07.34’**	**12º 00.56’**	**1537-1545**	**5**

Table 9. Examined specimens of *Paroriza prouhoi* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*. In bold specimens processed for DNA extraction.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
9756 #3	11-04-78	49º 48.0’	114º 14.8’	49º 48.8’	14º 19.3’	4080-4156	1
50515 #1	06-06-79	49º 43.9’	15º 04.6’	49º 46.9’	15º 08.2’	4505-4515	2
50711 #1	18-10-79	49º 53’	15º 36’	-	-	4595-4580	1
50811 #1	02-08-80	49º 38.6’	14º 34.2’	-	-	4400-4350	10
50812 #2	03-08-80	49º 52.7’	14º 17.3’	-	-	4140-4035	1
50910 #1	10-11-80	49º 49.6’	14º 40.5’	49º 50.56’	14º 49.63’	4265-4320	2
51414 #1	30-03-82	49º 43.7’	14º 10.3’	49º 39.0’	14º 18.0’	4180-4310	2
51608 #1	19-07-82	49º 35.6’	14º 30.3’	49º 38.8’	14º 24.3’	4370-4270	1
52216 #8	25-06-85	48º 47.5’	16º 37.59’	48º 47.59’	16º 39.68’	4803-4832	2
52403 #25	10-12-86	48º 15.5’	16º 17.4’	49º 15.3’	16º 20.3’	4860-4880	1
11908 #44	05-09-89	48º 47.3’	16º 29.9’	48º 56.8’	16º 27.6’	4843-4849	4
11908 #51	07-09-89	48º 45.5’	16º 32.2’	48º 51.0’	16º 29.4’	4839-4854	2
11908 #55	09-09-89	48º 47.8’	16º 35.0’	48º 49.6’	16º 34.4’	4860	2
11908 #68	12-09-89	48º 52.0’	16º 24.1’	48º 47.6’	16º 36.1’	4853-4877	6
52701 #17	18-05-91	48º 51.3’	16º 30.3’	48º 47.0’	16º 43.1’	4840-4845	12
52701 #21	19-05-91	48º 50.7’	16º 32.4’	48º 50.7’	16º 42.5’	4842-4846	5
52701 #32	21-05-91	48º 48.1’	16º 32.0’	48º 45.6’	16º 40.9’	4839-4843	1

52701 #42	24-05-91	48º 52.7’	16º 38.5’	48º 51.2’	16º 28.5’	4849-4843	7
52701 #57	27-05-91	48º 51.8’	16º 25.5’	48º 51.8’	16º 24.5’	4842-4845	1
53201 #1	07-04-94	48º 51.5’	16º 41.2’	48º 46.5’	16º 51.2’	4834-4836	9
53201 #28	15-04-94	48º 55.5’	17º 0.1’	48º 52.2’	16º 51.9’	4846-4845	10
53205 #3	19-04-94	48º 54.6’	16º 47.4’	48º 50.3’	16º 35.9’	4839-4850	19
12930 #37	07-09-96	48º 50.42’	16º 41.22’	48º 49.49’	16º 26.64’	4837-4844	3
12930 #46	09-09-96	48º 47.21’	16º 43.31’	48º 49.49’	16º 32.62’	4837-4841	6
12930 #64	12-09-96	48º 47.74’	16º 15.68’	48º 49.68’	16º 28.69’	4830-4839	3
12930 #78	16-09-96	48º 53.04’	16º 30.49’	48º 50.03’	16º 41.42’	4836-4840	26
13078 #29	04-04-97	48º 56.20’	16º 22.77’	48º 47.35’	16º 33.23’	4844-4847	15
13078 #31	05-04-97	48º 52.80’	16º 21.48’	48º 49.88’	16º 30.34’	4850-4844	6
13078 #37	07-04-97	48º 52.16’	16º 35.32’	48º 49.63’	16º 28.30’	4842-4844	7
13200 #60	17-07-97	48º 52.11’	16º 26.66’	48º 48.34’	16º 42.01’	4847-4843	25
13200 #99	27-07-97	48º 51.36’	16º 43.42’	48º 52.27’	16º 48.67’	4847-4850	2
13368 #23	10-03-98	48º 50.70’	16º 28.34’	48º 44.84’	16º 40.44’	4844-4842	5
13368 #24	11-03-98	48º 50.31’	16º 37.30’	48º 57.01’	16º 46.02’	4802-4844	19
13368 #51	18-03-98	48º 49.71’	16º 28.42’	48º 48.88’	16º 20.61’	4840	1
13369 #1	22-03-98	48º 55.79’	15º 44.66’	48º 52.33’	15º 38.85’	4826-4841	4
13369 #2	23-03-98	48º 54.37’	15º 39.93’	48º 50.72’	15º 31.82’	4828-4838	1
54901 #2	26-04-99	48º 42.2’	16º 51.6’	48º 48.0’	16º 50.4’	4811-4837	22
54901 #5	28-04-99	48º 44.9’	16º 40.5’	48º 48.2’	16º 36.2’	4835-4838	9
54901 #7	29-04-99	48º 47.4’	16º 48.9’	48º 50.8’	16º 46.0’	4836-4838	9
54901 #9	30-04-99	48º 46.9’	16º 41.6’	48º 50.6’	16º 36.4’	4837-4841	13
54903 #1	03-05-99	49º 32.1’	15º 56.0’	49º 28.1’	15º 56.5’	4810-4817	9
54905 #1	04-07-99	50º 32.7’	16º 57.8’	50º 28.7’	16º 59.5’	4764-4786	2
13925 #1	**07-10-00**	**48º 53.46’**	**16º 45.82’**	**48º 56.79’**	**16º 54.73’**	**4835-4845**	**4**

Table 10. Examined specimens of *Pelopatides gigantea* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
9753 #7	08-04-78	50º 54.5’	12º 10.9’	50º 54.8’	12º 11.4’	1942	3
9753 #8	08-04-78	50º 54.6’	12º 11.1’	50º 55.6’	12º 12.7’	1942	1
9754 #3	09-04-78	51º 8.4’	12º 1.5’	51º 9.5’	12º 1.8’	1484	1
9775 #3	22-04-78	50º 56.8’	12º 22.4’	50º 55.7’	12º 19.8’	2019-2012	61
50510 #1	03-06-79	51º 05.3’	13º 04.5’	51º 06.5’	12º 59.5’	1925-1945	20
50517 #1	07-06-79	49º 30.1’	13º 19.9’	49º 27.7’	13º 17.2’	1794-1785	24
50703 #1	13-10-79	49º 33’	12º 34’	-	-	1575-1625	5
50715 #1	21-10-79	51º 19.5’	12º 57’	-	-	1635-1720	2

Table 11. Examined specimens of *Pelopatides grisea* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*. In bold specimens processed for DNA extraction.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
9774 #1	21-04-78	51º 4.4’	11º 59.3’	51º 5.2’	12º 3.4’	1492-1572	1
50511 #1	04-06-79	50º 32.4’	13º 01.4’	50º 31.4’	12º 55.6’	2410-2440	1
50602 #2	01-07-79	51º 1.0’	13º 5.9’	51º 1.1’	13º 8.4’	1980	4
50602 #3	02-07-79	51º 6.8’	13º 16.7’	51º 6.9’	13º 24.4’	1930-1815	11
10106 #1	04-09-79	50º 41.7’	12º 50.7’	50º 41.0’	12º 48.2’	2300-2315	16
10111 #8	09-09-79	49º 32.7’	13º 7.1’	49º 33.5’	13º 5.9’	1630-1690	2
10108 #1	05-09-79	49º 20.6’	12º 49.2’	49º 19.6’	12º 48.7’	1385-1390	2
50802 #1	30-07-80	49º 39.5’	12º 36.9’	-	-	1857-1910	1
50810 #1	02-08-80	49º 34.1’	12º 41.9’	-	-	1694-1605	4
50822 #1	07-08-80	50º 56.7’	13º 11.6’	-	-	2150-2095	5+
51010 #1	02-05-81	51º 19.1’	12º 29.5’	-	-	1780-1800	3
51011 #1	03-05-81	50º 44.6’	12º 14.8’	-	-	2180-2165	1
51021 #1	09-05-81	49º 38.6’	12º 40.9’	-	-	1860-1875	3
51022 #1	09-05-81	49º 33.0’	12º 38.8’	-	-	1575-1600	1
51201 #1	16-09-81	51º 05.4’	12º 55.8’	51º 06.8’	12º 52.9’	1980-1995	37
51214 #1	27-09-81	50º 00.9’	14º 06.8’	49º 58.0’	14º 04.3’	3820-3800	1
51308 #1	20-02-82	51º 13.0’	13º 02’	-	-	1715-1770	1
51311 #1	21-02-82	49º 50.7’	12º 22.9’	-	-	2020-1940	7
51314 #1	22-02-82	49º 31.8’	12º 29.1’	-	-	1455-1425	1
51801 #1	24-09-83	51º 20.8’	12º 31.4’	-	-	1700-1740	1
52019 #1	22-08-84	51º 24.81’	12º 46.17’	51º 25.14’	12º 45.55’	1710-1725	1
52211 #1	18-06-85	51º 10.57’	13º 14.71’	51º 09.84’	13º 15.15’	1715-1760	5
13922 #1	**01-10-00**	**51º 53.88’**	**11º 58.44’**	**50º 55.63’**	**12º 01.52’**	**1885-1933**	**10**

Table 12. Examined specimens of *Pseudostichopus aemulatus* sp. nov. present in the RRS Discovery Collections at the Southampton Oceanography Centre. RRS Challenger and RRS Discovery. In bold specimens processed for DNA extraction.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
52216 #8	25-06-85	48º 47.5’	16º 37.59’	48º 47.59’	16º 39.68’	4803-4832	1
52403 #12	04-12-86	48º 56.6’	15º 45.4’	48º 58.0’	15º 42.5’	4810-4820	5
52403 #13	05-12-86	48º 52.0’	15º 57.0’	48º 59.0’	16º 04.4’	4839-4844	10
52403 #25	10-12-86	48º 15.5’	16º 17.4’	49º 15.3’	16º 20.3’	4860-4880	4
52602 #3	03-05-88	48º 50.39’	16º 31.36’	48º 52.87’	16º 31.51’	4850	1
11908 #35	03-09-89	48º 53.4’	16º 18.0’	48º 50.1’	16º 28.3’	4843-4847	10
11908 #38	04-09-89	48º 46.8’	16º 34.3’	48º 49.6’	16º 34.1’	4844-4846	4
11908 #40	04-09-89	48º 47.6’	16º 35.9’	48º 50.4’	16º 35.5’	4850	6
11908 #44	05-09-89	48º 47.3’	16º 29.9’	48º 56.8’	16º 27.6’	4843-4849	26
11908 #51	07-09-89	48º 45.5’	16º 32.2’	48º 51.0’	16º 29.4’	4839-4854	7
11908 #55	09-09-89	48º 47.8’	16º 35.0’	48º 49.6’	16º 34.4’	4860	11
11908 #68	12-09-89	48º 52.0’	16º 24.1’	48º 47.6’	16º 36.1’	4853-4877	8
52701 #6	17-05-91	48º 50.7’	16º 31.8’	48º 50.7’	16º 29.1’	4843-4844	10

52701 #21	19-05-91	48º 50.7’	16º 32.4’	48º 50.7’	16º 42.5’	4842-4846	15+
52701 #32	21-05-91	48º 48.1’	16º 32.0’	48º 45.6’	16º 40.9’	4839-4843	7
52701 #48	25-05-91	48º 51.7’	16º 33.4’	48º 51.3’	16º 31.5’	4846	9
52701 #52	26-05-91	48º 50.4’	16º 31.4’	48º 51.9’	16º 27.4’	4839-4847	1
53201 #1	07-04-94	48º 51.5’	16º 41.2’	48º 46.5’	16º 51.2’	4834-4836	46
53201 #24	13-04-94	48º 53.7’	16º 36.8’	48º 51.7’	16º 19.2’	4846-4843	38
53201 #28	14-04-94	48º 55.5’	17º 0.1’	48º 52.2’	16º 51.9’	4846-4843	40
53205 #3	15-04-94	48º 54.6’	16º 47.4’	48º 50.3’	16º 35.9’	4829-4850	106
12930 #37	07-09-96	48º 50.42’	16º 41.22’	48º 49.49’	16º 26.6’	4837-4844	39
12930 #60	12-09-96	48º 50.33’	16º 32.99’	48º 48.96’	16º 20.61’	4838-4841	2
12930 #64	12-09-96	48º 47.74’	16º 15.68’	48º 49.68’	16º 28.69’	4836-4839	26
13078 #31	05-05-97	42º 52.80’	16º 21.48’	48º 49.88’	16º 30.34’	4850-4844	68
13078 #37	07-05-97	48º 52.16’	16º 35.32’	48º 49.63’	16º 28.30’	4842-4844	39
13200 #9	06-07-97	48º 51.96’	16º 24.61’	48º 46.21’	16º 31.63’	4844-4840	71
13200 #27	10-07-97	48º 52.50’	16º 39.9’	48º 42.44’	16º 41.00’	4848-4839	75
13200 #35	11-07-97	48º 44.03’	16º 32.82’	48º 55.85’	16º 40.22’	4842-4845	99
13200 #60	17-07-97	48º 52.11’	16º 26.66’	48º 48.34’	16º 42.01’	4847-4843	145
13200 #99	27-07-97	48º 51.36’	16º 43.42’	48º 52.27’	16º 48.67’	4847-4850	10
54301 #6	20-10-97	48º 46.9’	16º 49.7’	48º 48.6’	16º 40.5’	4837-4846	95
54301 #8	22-10-97	48º 49.1’	16º 38.4’	48º 50.5’	16º 27.0’	4839-4844	71
13368 #23	10-03-98	48º 50.70’	16º 28.34’	48º 44.84’	16º 40.44’	4844-4842	61
13368 #24	11-03-98	48º 50.31’	16º 37.30’	48º 57.01’	16º 46.02’	4802-4844	150
13368 #51	18-03-98	48º 49.71’	16º 28.42’	48º 48.88’	16º 20.61’	4840	68
13369 #1	22-03-98	48º 55.79’	15º 44.66’	48º 52.33’	15º 38.85’	4826-4841	143
13369 #2	23-03-98	48º 54.37’	15º 39.93’	48º 50.72’	15º 31.82’	4828-4838	109
13370 #3	24-03-98	48º 50.48’	16º 27.91’	48º 48.54’	16º 34.53’	4839	5
13925 #1	**07-10-00**	**48º 53.46’**	**16º 45.82’**	**48º 56.79’**	**16º 54.73’**	**4835-4845**	**10**
54901 #2	26-04-99	48º 42.2’	16º 51.6’	48º 48.0’	16º 50.4’	4811-4837	62
54901 #7	29-04-99	48º 47.4’	16º 48.9’	48º 50.8’	16º 46.0’	4836-4838	50
54902 #1	02-05-99	48º 26.4’	15º 39.7’	48º 24.3’	15º 34.9’	4843-4845	2
54905 #1	04-07-99	50º 32.7’	16º 57.8’	50º 28.7’	16º 59.5’	4764-4786	1

Table 13. Examined specimens of *Pseudostichopus villosus* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*. In bold specimens processed for DNA extraction.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
9638 #2	08-11-77	49º 50.2’	14º 7.3’	49º 50.3’	12º 6’	4043-4104	1
10115 #1	11-09-79	49º 46.3’	13º 56.0’	49º 45.6’	13º 56.6’	3900-3950	1
50910 #1	10-11-80	49º 49.6’	14º 40.5’	49º 50.56’	14º 49.63’	4265-4320	3
52602 #1	01-05-88	48º 48.6’	16º 31.7’	48º 50.51’	16º 40.28’	4850	4
11908 #44	05-09-89	48º 47.3’	16º 29.9’	48º 56.8’	16º 27.6’	4843-4849	20
11908 #68	12-09-89	48º 52.0’	16º 24.1’	48º 47.6’	16º 36.1’	4853-4877	48
52701 #42	24-05-91	48º 52.7’	16º 38.5’	48º 51.2’	16º 28.5’	4849-4843	132+
53201 #1	07-04-94	48º 51.5’	16º 41.2’	48º 46.5’	16º 51.2’	4834-4836	86
53201 #24	13-04-94	48º 53.7’	16º 36.8’	48º 51.7’	16º 19.2’	4846-4843	9
53201 #28	14-04-94	48º 55.5’	17º 0.1’	48º 52.2’	16º 51.9’	4846-4843	44+

53205 #3	15-04-94	48º 54.6’	16º 47.4’	48º 50.3’	16º 35.9’	4829-4850	143+
12930 #37	07-09-96	48º 50.42’	16º 41.22’	48º 49.49’	16º 26.6’	4837-4844	49+
12930 #46	09-09-96	48º 47.21’	16º 43.31’	48º 49.49’	16º 32.62’	4847-4841	34
12930 #60	12-09-96	48º 50.33’	16º 32.99’	48º 48.96’	16º 20.61’	4838-4841	1
12930 #64	12-09-96	48º 47.74’	16º 15.68’	48º 49.68’	16º 28.69’	4836-4839	31+
12930 #78	16-09-96	48º 53.04’	16º 30.49’	48º 50.03’	16º 41.42’	4836-4840	141
13078 #29	04-04-97	48º 56.20’	16º 22.77’	48º 47.35’	16º 33.23’	4844-4847	181
13078 #31	05-05-97	42º 52.80’	16º 21.48’	48º 49.88’	16º 30.34’	4850-4844	77
13078 #37	07-05-97	48º 52.16’	16º 35.32’	48º 49.63’	16º 28.30’	4842-4844	56
13200 #9	06-07-97	48º 51.96’	16º 24.61’	48º 46.21’	16º 31.63’	4844-4840	45
13200 #27	10-07-97	48º 52.50’	16º 39.9’	48º 42.44’	16º 41.00’	4848-4839	90
13200 #35	11-07-97	48º 44.03’	16º 32.82’	48º 55.85’	16º 40.22’	4842-4845	214
13200 #60	17-07-97	48º 52.11’	16º 26.66’	48º 48.34’	16º 42.01’	4847-4843	186
13200 #88	23-07-97	48º 52.10’	16º 25.47’	48º 48.52’	16º 36.01’	4852-4845	8
13200 #99	27-07-97	48º 51.36’	16º 43.42’	48º 52.27’	16º 48.67’	4847-4850	10
54301 #6	20-10-97	48º 46.9’	16º 49.7’	48º 48.6’	16º 40.5’	4837-4846	89+
54301 #8	22-10-97	48º 49.1’	16º 38.4’	48º 50.5’	16º 27.0’	4839-4844	75+
13368 #23	10-03-98	48º 50.70’	16º 28.34’	48º 44.84’	16º 40.44’	4844-4842	101+
13368 #51	18-03-98	48º 49.71’	16º 28.42’	48º 48.88’	16º 20.61’	4840	43
13369 #1	22-03-98	48º 55.79’	15º 44.66’	48º 52.33’	15º 38.85’	4826-4841	214
13627 #10	30-09-98	48º 53.64’	16º 42.65’	49º 01.98’	16º 53.26’	4837-4835	59
13627 #23	05-10-98	48º 58.93’	16º 45.22’	49º 03.88’	16º 40.66’	4837-4814	83
54901 #2	26-04-99	48º 42.2’	16º 51.6’	48º 48.0’	16º 50.4’	4811-4837	64
54901 #5	28-04-99	48º 44.9’	16º 40.5’	48º 48.2’	16º 36.2’	4835-4838	118+
54901 #7	29-04-99	48º 47.4’	16º 48.9’	48º 50.8’	16º 46.0’	4836-4838	59+
54902 #1	02-05-99	48º 26.4’	15º 39.7’	48º 24.3’	15º 34.9’	4843-4845	2
54903 #1	03-05-99	49º 32.1’	15º 56.0’	49º 28.1’	15º 56.5’	4810-4817	254+
13907 #1	**20-09-00**	**49º 55.85’**	**14º 30.34’**	**50º 02.64’**	**14º 36.04’**	**4128-4220**	**1**
13925 #1	**07-10-00**	**48º 53.46’**	**16º 45.82’**	**48º 56.79’**	**16º 54.73’**	**4835-4845**	**10**
13925 #1	07-10-00	48º 53.46’	16º 45.82’	48º 56.79’	16º 54.73’	4835-4845	80+
50514 #1	06-06-79	49º 43.9’	14º 02.2’	49º 38.8’	14º 00.4’	4017-16054095	1
50515 #1	06-06-79	49º 43.9’	15º 04.6’	49º 46.9’	15º 08.2’	4505-4515	12
50711 #1	18-10-79	49º 53’	15º 36’	-	-	4595-4580	6
50812 #2	03-08-80	49º 52.7’	14º 17.3’	-	-	4140-4035	4
51414 #1	30-03-82	49º 43.7’	14º 10.3’	49º 39.0’	14º 18.0’	4180-4310	2
52216 #8	25-06-85	48º 47.5’	16º 37.59’	48º 47.59’	16º 39.68’	4803-4832	1
52403 #25	10-12-86	48º 15.5’	16º 17.4’	49º 15.3’	16º 20.3’	4860-4880	1

Table 14. Examined specimens of *Zygothuria lactea* present in the RRS *Discovery* Collections at the Southampton Oceanography Centre. RRS *Challenger* and RRS *Discovery*. In bold specimens processed for DNA extraction.

Station number	**Date**	**Start Lat (N)**	**Long (W)**	**End Lat (N)**	**Long (W)**	**Depth (m)**	**No. of specimens**
9754 #3	09-04-78	51º 8.4’	12º 1.5’	51º 9.5’	12º 1.8’	1484	9
9774 #1	21-04-78	51º 4.4’	11º 59.3’	51º 5.2’	12º 3.4’	1499-1572	1
9779 #1	24-04-78	49º 22.3’	12º 49.1’	49º 20.7’	12º 49.5’	1404-1398	5
50510 #1	03-06-79	51º 05.3’	13º 04.5’	51º 06.5’	12º 59.5’	1925-1945	7

50511 #1	04-06-79	50º 32.4’	13º 01.4’	50º 31.4’	12º 55.6’	2410-2440	7
50513 #1	05-06-79	50º 07.6’	13º 58.3’	50º 04.2’	14º 02.0’	3400-3620	3
50517 #1	07-06-79	49º 30.1’	13º 19.9’	49º 27.7’	13º 17.2’	1794-1785	1
50519 #1	08-06-79	49º 29.5’	12º 48.9’	48º 29.9’	12º 43.6’	1465-1431	8
50602 #3	02-07-79	51º 6.8’	13º 16.7’	51º 6.9’	13º 24.4’	1930-1815	36
10108 #1	05-09-79	49º 20.6’	12º 49.2’	49º 19.6’	12º 48.7’	1385-1390	2
10111 #8	09-09-79	49º 32.7’	13º 7.1’	49º 33.5’	13º 5.9’	1630-1690	15+
50703 #1	13-10-79	49º 33’	12º 34’	-	-	1575-1625	1
50715 #1	21-10-79	51º 19.5’	12º 57’	-	-	1635-1720	4
50902 #1	07-11-80	51º 17.4’	12º 45.2’	51º 15.74’	12º 49.19’	1825-1865	1
51009 #1	02-05-81	51º 34.2’	12º 54.2’	-	-	1510-1535	1
51307 #1	19-02-82	51º 26.4’	13º 01.4’	-	-	1490-1415	1
51308 #1	20-02-82	51º 13.0’	13º 02’	-	-	1715-1770	1
51403 #1	25-03-82	51º 37.7’	12º 59.8’	51º36.6’	13º 00.0’	1292-1314	5
51403 #4	26-03-82	51º 36.7’	12º 59.6’	51º 36.0’	12º 59.8’	1319-1333	5
51403 #5	26-03-82	49º 23.7’	11º 34.2’	51º 37.3’	12º 59.0’	1289-1297	2
51403 #6	26-03-82	-	-	-	-	1278-1295	1
51403 #7	26-03-82	51º 36.4’	12º 59.9’	51º 39.2’	12º 58.8’	1320-1247	1
51409 #1	28-03-82	51º 16.5’	13º 00.2’	51º 19.0’	12º 56.6’	1660-1740	28+
51411 #1	29-03-82	50º 27.2’	12º 59.1’	50º 22.4’	13º 01.3’	2470-2500	1
51419 #1	01-04-82	51º 19.0’	13º 05.4’	51º 16.8’	13º 07.4’	1500-1555	25
51420 #1	02-04-82	51º 37.3’	12º 58.6’	51º 36.9’	12º 58.6’	1326-1328	2
51708 #2	13-04-83	51º 31.3’	12º 58.4’	51º 31.0’	13º 0.3’	1470-1430	10
52018 #1	21-08-84	51º 42.36’	13º 05.76’	51º 31.39’	12º 46.97’	1095-1620	6
52019 #1	22-08-84	51º 24.81’	12º 46.17’	51º 25.14’	12º 45.55’	1710-1725	9
52203 #1	16-06-85	51º 25.91’	13º 00.60’	51º 25.48’	13º 00.38’	1540-1550	11
52204 #1	16-06-85	51º 37.07’	12º 59.96’	51º 37.29’	13º 00.01’	1310-1315	2
52211 #1	18-06-85	51º 10.57’	13º 14.71’	51º 09.84’	13º 15.15’	1715-1760	19
52213 #1	20-06-85	50º 33.04’	12º 59.21’	50º 32.41’	12º 58.53’	2440-2405	1
13919 #1	**25-09-00**	**51º 08.89’**	**12º 03.92’**	**51º 07.34’**	**12º 00.56’**	**1537-1545**	**7**

Appendix 3

Table 1. Index of *Synallactes* species, including new synonymies and new combinations.

Original name	Current combination or validity
anceps, Synallactes Koehler & Vaney, 1910	*Synallactes rigidus* Koehler & Vaney, 1905
angustus, Synallactes, Cherbonnier & Féral, 1981	*Bathyplotes angustus* (Cherbonnier & Féral, 1981)
cartagei, Synallactes, Vaney, 1906	Not a synallactid, its is probably a psolid related with *Staurocucumis*.
crebrapapilla, Synallactes, Cherbonnier & Féral, 1981	*Bathyplotes crebrapapilla* (Cherbonnier & Féral, 1981)
dubius, Synallactes(?), Koehler & Vaney, 1905	Not a *Synallactes*
elongata, Paradeima, Heding, 1940	*Synallactes elongata* (Heding, 1940)
gourdoni, Synallactes, Vaney, 1914	*Bathyplotes moseleyi* (Théel, 1886a)
heteroculus, Bathyplotes, Heding, 1940	*Synallactes heteroculus* (Heding, 1940)
ishikawi, Synallactes, Mitsukuri, 1912	*Synallactes sagamiensis* (Augustin, 1908)
monoculus, Bathyplotes, Heding, 1940	*Synallactes monoculus* (Heding, 1940)
moseleyi, Stichopus, Théel, 1886a	*Bathyplotes moseleyi* (Théel, 1886a)
moseleyi, Synallactes, (as referred by Perrier 1902)	*Bathyplotes moseleyi* (Théel, 1886a)
pellucidus, Synallactes(?), Koehler & Vaney, 1905	*Bathyplotes*(?) *pellucidus* (Koehler & Vaney, 1905)
profundus, Bathyplotes, Koehler & Vaney, 1905	*Synallactes profundus* (Koehler & Vaney, 1905)
reticulatus, Synallactes, Sluiter, 1901	*Amphigymnas multipes* Walsh, 1891
sagamiensis, Stichopus, Augustin, 1908	*Synallactes nozawai* Mitsukuri, 1912
sp., *Synallactes*, Augustin, 1908	*Bathyplotes moseleyi* (Théel, 1886a)
triplax, Synallactes, Clark, 1920	*Bathyplotes triplax* (Clark, 1920)
woodmasoni, Synallactes, Koehler & Vaney, 1905	*Amphigymnas multipes* Walsh, 1891

Table 2. Check list of the *Synallactes* species.

Species	Geographic and bathymetric distribution
Synallactes aenigma Ludwig, 1894	Pacific Ocean, Gulf of Panama; Sechura Bay, Peru (2404-4334m).
Synallactes alexandri Ludwig, 1894	Gulf of Panama, Galapagos Islands (585-1018m).
Synallactes challengeri (Théel, 1886a)	Indian Ocean, Crozet Islands (990m). Ocean Pacific records need corroboration.
Synallactes chuni Augustin, 1908	North Pacific Ocean, Bering Sea, Russia, Commander Islands, east of Copper Island (242-600m).
Synallactes crucifera Perrier, 1898	Atlantic Ocean, coast of Morocco (2212m).
Synallactes discoidalis Mitsukuri, 1912	Pacific Ocean, Sagami Bay and Sagami Sea, Japan (491.4-728m).
Synallactes elongata (Heding, 1940)	Indian Ocean (614m).
Synallactes gilberti Ohshima, 1915	Pacific Ocean, South of Totomi, Honshu, Japan (918-943m).
Synallactes heteroculus (Heding, 1940)	Indian Ocean (371m).
Synallactes horridus Koehler & Vaney, 1905	Indonesia, Makassar Strait, (1600-3181m).
Synallactes laguardai sp. nov.	South Atlantic Ocean, South Africa, off Cape Town (409.5 to 460m).
Synallactes longipapillata Sibuet, 1978	Atlantic Ocean, Bay of Biscay (3345m).
Synallactes mollis Cherbonnier, 1952	Atlantic Ocean, Off Morocco (364m).
Synallactes monoculus (Sluiter, 1901)	Indonesia, Java Sea (310-462m).
Synallactes multivesiculatus Ohshima, 1915	Pacific Ocean, South of Hokkaido, off Ojika Peninsula, Honshu, Japan (194-844m).
Synallactes nozawai Mitsukuri, 1912	Pacific Ocean, Hokkaido, Japan. Bering Sea; north of Sado Island, west of Hokkaido; off Cape Terpyeniya, Sakhalin.
Synallactes profundus Koehler & Vaney, 1905	Indian Ocean (2992m).
Synallactes rigidus Koehler & Vaney, 1905	Indian Ocean, Bay of Bengal (3501m).
Synallactes robertsoni Vaney, 1908	Antarctic (4413m).
Synallactes sagamiensis (Augustin, 1908)	Pacific Ocean, Sagami Bay, Japan (180-4297m).
Synallactes triradiata Mitsukuri, 1912	Pacific Ocean, Sagami Bay and Sagami Sea, Japan (728-1092m).
Synallactes viridilimus Cherbonnier, 1952	Atlantic Ocean, Off Morocco (527m).

Appendix 4

Class Holothuroidea
Subclass Aspidochirotacea
Order Aspidochirotida Grube, 1840
Family Synallactidae Ludwig, 1894

Genus ***Amphigymnas*** Walsh, 1891 (2 valid species)
Amphigymnas bahamensis Deichmann, 1930
Amphigymnas multipes (Walsh, 1891)

Genus ***Bathyplotes*** Östergren, 1896 (19 valid species)
Bathyplotes angustus (Cherbonnier & Féral, 1981)
Bathyplotes bigelowi Deichmann, 1940
Bathyplotes bongraini Vaney, 1914
Bathyplotes cinctus Koehler & Vaney, 1910
Bathyplotes crebrapapilla (Cherbonnier & Féral, 1981)
Bathyplotes crenulatus Koehler & Vaney, 1905
Bathyplotes goldenhindi Mitsukuri, 1912
Bathyplotes imperfectus Cherbonnier & Féral, 1976
Bathyplotes moseleyi (Théel, 1886)
Bathyplotes natans (M. Sars, 1808)
Bathyplotes pellucidus (Koehler & Vaney, 1905)
Bathyplotes phlegmaticus (Sluiter, 1901)
Bathyplotes punctatus (Sluiter, 1901)
Bathyplotes roseus Koehler & Vaney, 1910
Bathyplotes rubicundus Sluiter, 1901
Bathyplotes sulcatus Sluiter, 1901a
Bathyplotes tizardi (Théel, 1882)
Bathyplotes triplax (Clark, 1920)
Bathyplotes variabilis (Koehler & Vaney, 1905)

Genus ***Benthothuria*** Perrier, 1898 (5 valid species)
Benthothuria cristatus Koehler & Vaney, 1905
Benthothuria distortus Koehler & Vaney, 1905
Benthothuria funebris Perrier, 1899
Benthothuria fusiformis (Sluiter, 1901)
Benthothuria valdiviae Heding, 1940

Genus ***Hansenothuria*** Miller & Pawson, 1989 (1 valid species)
Hansenothuria benti Miller & Pawson, 1989

Genus ***Mesothuria*** Ludwig, 1894 (27 valid species)
Mesothuria abbreviata Koehler & Vaney, 1905
Mesothuria bifurcata Hérouard, 1901
Mesothuria carnosa Fisher, 1907
Mesothuria cathedralis Heding, 1940

Mesothuria crebrapedes Cherbonnier & Féral, 1981
Mesothuria deani Mitsukuri, 1912
Mesothuria edwardensis Massin, 1992
Mesothuria gargantua Deichmann, 1930
Mesothuria grandipes (Hérouard, 1923)
Mesothuria holothurioides Sluiter, 1901
Mesothuria incerta Koehler & Vaney, 1905
Mesothuria intestinalis (Ascanius, 1805)
Mesothuria magellani (Ludwig, 1883)
Mesothuria maroccana Perrier, 1902
Mesothuria megapoda Clark, 1920
***Mesothuria* sp. 1**
Mesothuria multipes Ludwig, 1894
Mesothuria multipora Clark, 1920
Mesothuria murrayi (Théel, 1886a)
Mesothuria oktaknemus Sluiter, 1901a
Mesothuria oktaknemoides Heding, 1940
Mesothuria regularia Heding, 1940
Mesothuria rugosa Hérouard, 1912
Mesothuria squamosa Koehler & Vaney, 1905
Mesothuria sufflava Cherbonnier & Féral, 1984
Mesothuria triradiata Heding, 1942b
Mesothuria verrilli (Théel, 1886a)

Genus ***Paroriza*** Hérouard, 1902 (4 valid species)
Paroriza grevei Hansen, 1956
Paroriza pallens (Koehler, 1895)
Paroriza prouhoi Hérouard, 1902
Paroriza verrucosa Massin, 1987

Genus ***Pelopatides*** Théel, 1886a (19 valid species)
Pelopatides appendiculata Théel, 1886a
Pelopatides atlantica Hérouard, 1902
Pelopatides confundens Théel, 1886a
Pelopatides dissidens Koehler & Vaney, 1910
Pelopatides gelatinosa (Walsh, 1891)
Pelopatides gigantea (Verrill, 1884)
Pelopatides grisea Perrier, 1899
Pelopatides illicitus Sluiter, 1901a
Pelopatides insignis Koehler & Vaney, 1905
Pelopatides mammillatus Koehler & Vaney, 1905
Pelopatides megalopharynx Sluiter, 1901a
Pelopatides modestus Koehler & Vaney, 1905
Pelopatides mollis Koehler & Vaney, 1905
Pelopatides ovalis (Walsh, 1891)
Pelopatides quadridens Heding, 1940

Pelopatides retifer Fisher, 1907
Pelopatides solea Baranova, 1955
Pelopatides suspecta Ludwig, 1894
Pelopatides verrucosus Koehler & Vaney, 1905

Pseudostichopus Théel, 1886a (26 valid species)
***Pseudostichopus* sp. 1**
Pseudostichopus aleutianus Ohshima, 1915
Pseudostichopus arenosus Ohshima, 1915
Pseudostichopus depressus Hérouard, 1902
Pseudostichopus dilatorbis Imaoka, 1978
Pseudostichopus echinatus Thandar, 1984
Pseudostichopus hyalagerus (Sluiter, 1901a)
Pseudostichopus involutus (Sluiter, 1901a)
Pseudostichopus japonensis Imaoka, 1978
Pseudostichopus lapidus Hérouard, 1923
Pseudostichopus macdonaldi (Ludwig, 1894)
Pseudostichopus marenzelleri Hérouard, 1923
Pseudostichopus mollis Théel, 1886a
Pseudostichopus molpadioides Ohshima, 1915
Pseudostichopus nudus Ohshima, 1915
Pseudostichopus occultatus Marenzeller, 1893a
Pseudostichopus papillatus (Djakonov, 1952)
Pseudostichopus peripatus (Sluiter, 1901)
Pseudostichopus profundi Djakonov, 1952
Pseudostichopus propinquus Fisher, 1907
Pseudostichopus pustulosus Sluiter, 1901a
Pseudostichopus spiculiferus (O'Loughlin, 2002)
Pseudostichopus tachimaruae Imaoka, 1978
Pseudostichopus trachus Sluiter, 1901a
Pseudostichopus unguiculatus Ohshima, 1915
Pseudostichopus villosus Théel, 1886a

Genus ***Synallactes*** Ludwig, 1893 (22 valid species)
Synallactes aenigma Ludwig, 1893
Synallactes alexandri Ludwig, 1893
Synallactes challengeri (Théel, 1886a)
Synallactes chuni Augustin, 1908
Synallactes crucifera Perrier, 1898
Synallactes discoidalis Mitsukuri, 1912
Synallactes elongata (Heding, 1940)
Synallactes gilberti Ohshima, 1915
Synallactes heteroculus (Heding, 1940)
Synallactes horridus Koehler & Vaney, 1905
***Synallactes* sp. 1**
Synallactes longipapillata Sibuet, 1978

Synallactes mollis Cherbonnier, 1952
Synallactes monoculus (Sluiter, 1901a)
Synallactes multivesiculatus Ohshima, 1915
Synallactes nozawai Mitsukuri, 1912
Synallactes profundus (Koehler & Vaney, 1905)
Synallactes rigidus Koehler & Vaney, 1905
Synallactes robertsoni Vaney, 1908
Synallactes sagamiensis (Augustin, 1908)
Synallactes triradiata Mitsukuri, 1912
Synallactes viridilimus Cherbonnier, 1952

Genus *Zygothuria* Perrier, 1898 (6 valid species)
Zygothuria candelabri (Hérouard, 1923)
Zygothuria connectens Perrier, 1898
Zygothuria lactea (Théel, 1886a)
Zygothuria marginata (Sluiter, 1901a)
Zygothuria oxysclera (Perrier, 1902)
Zygothuria thomsoni (Théel, 1886a)