IDENTIFICATION AND DISTRIBUTION OF THE POLYCHAETE FAMILY CIRRATULIDAE FROM THE LAS PERLAS ARCHIPELAGO, PANAMA

by

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This dissertation is dedicated to my dad: a man who believes strongly that education is an emporium and children should be allowed to choose their own interests and believes; a man who refused to let me do my homework in the house; and a man who now claims credit for any of my academic achievements due to his developing belief in reverse psychology.

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Abstract

Van Veen grab and trawl samples were gathered from 114 sample stations surrounding the Las Perlas Archipelago, Panama, by the R/V. "Urraca" cruises from August 2003, to October 2004. These samples were collected as part of a 3-year collaborative Darwin Project between researchers at Heriot-Watt University and the Smithsonian Tropical research Institute in Panama. From these survey results, a dataset of 361 cirratulids was generated for investigation in this study. These specimens were identified to 6 recognised genera (*Cirriformia, Aphelochaeta, Chaetozone, Monticellina, Caulleriella* and *Tharyx*) and 28 morphologically distinct taxa. The most abundant genera were *Monticellina,* and the most abundant taxa, *Monticellina A*.

The distribution patterns of all species were visualised, and compared to the results of a broader benthic study carried out by Darwin project researchers. The effects of abiotic factors, including both hydrographic conditions and sediment composition on the distribution and abundance of cirratulids were discussed.

The identified specimens are now in the care of the National Museum of Scotland, and these results will be incorporated into the ongoing work of the Darwin Initiative in Las Perlas.

1. Introduction

1.1 General Overview

Until relatively recently, studies of marine benthos were initiated for the sole purpose of satisfying scientific curiosity. The impetus for such studies was elevated by the growing concern over anthropogenic influences, most importantly the effects of oil pollution (Mackie *et al.,* 1995; Parker, 1975), and subsequently by the introduction of the Convention on Biological Diversity.

Prior to 2003, studies of the marine biodiversity of Las Perlas have focused mainly on the epifauna surrounding the 6 most northerly islands, leaving the majority of the archipelago largely undiscovered (Benfield, 2005). However, as stated in the Convention on Biological Diversity, surveys of existent biodiversity to establish presence, value, and conservational importance are essential for a successful national biodiversity strategy. Such surveys are the basis of measurable conservation targets, and sustainable use around which national strategies and management programmes must be based (United Nations, 1993).

Recognition of this need instigated the award of a Department for Environment, Food and Rural Affairs (DEFRA) funded Darwin Initiative Project for Marine Biodiversity Assessment and Development in Las Perlas Archipelago, Panama (Project 12/021): a collaboration between the Smithsonian Tropical Research Institute (STRI), the Darwin Initiative, and Heriot-Watt University (HWU). The Smithsonian Tropical Research Institute (STRI), Panama, has provided a base for research and education, whilst the Darwin Initiative has provided the motivation and funding for necessary studies to advise on the implementation of the *Zona de Manejo Especial Archipiélago de Las Perlas*: a project aiming to protect the Archipelago from anthropogenic influences whilst promoting tourism through the designation and establishment of a Marine Protected Area (MPA) (Anderson, 2005).

Historically, the designation of marine and coastal protected areas within Panama has been based on terrestrial concepts of biodiversity, (Hurtado, 1995), however, in 2003, the R/V Urraca cruises commenced an extensive

baseline survey to fully assess the benthic marine biodiversity, in terms of habitat and species type, distribution, and health (Benfield, 2005).

Benthic invertebrate communities utilize the sediment for shelter, support and as a source of food. Specific organisms tend to favour specific sediment types, subsequently, it may be hypothesized that sediment composition directly influences faunal composition. The nature of the sediment itself is under the control of other abiotic factors: anthropogenic inputs, biological inputs, factors controlling deposition, transportation and chemical transformation (Mackie *et al.,* 1995).

Low diversity and high population levels often characterize some form of historic stress, whereas high diversity with little single species dominance may denote a region of temporal stability. However, it has been shown that there is natural variability in benthic populations with alterations in community structure occurring over multiple timescales as a result of unpredictable biotic and abiotic factors: predation, competition, environmental disturbances and anthropogenic disturbances all induce community alterations (Mackie *et al.,* 1995).

Ultimately, the intention is to make the description of the marine biodiversity of the region spatially comparable with that of other regions, both locally and globally, and temporally to examine change induced naturally or anthropogenically facilitating management strategies (Benfield, 2005). The legal process to designate the Las Perlas Archipelago as a Special Management Zone is nearly complete (Mair, Pers. Comm); however, this dissertation will provide the first in-depth analysis of a benthic component through the study of the abundant polychaete family Cirratulidae.

1.2 Aims

1.2.1 Aims of the UK Darwin Initiative

The Darwin Initiative aims to assist countries with high biodiversity but limited resources in conservation and the associated implementation of the Biodiversity Convention. Projects receiving Darwin funding will draw on British expertise, whilst collaborating with local stakeholders within the host country (Mair, Pers. Comm.).

1.2.2 Aims of the Las Perlas Darwin Project

Darwin Project 12/021 aimed to establish research expertise in a team dedicated to obtain habitat and biodiversity information, whilst constructing sustainable management plans for the marine and coastal environment of the Las Perlas Archipelago, in order to facilitate the designation of a 'Marine Protected Area'. Subsequently, implementation of management plans is to be facilitated: further site and species monitoring programmes will be set up in selected areas, community workshops will be developed, educational and interest-specific material will be issued to stakeholders, and research findings will be published (Mair, Pers. Comm.).

1.2.3 Aims of Dissertation

The ultimate aim of this dissertation is to determine the composition and structure of the benthic infaunal cirratulid community of the Las Perlas Archipelago, Understanding of the family, Cirratulidae, selected for their overall abundance, will give insights into the polychaete community as a whole, and subsequently, into the marine biodiversity.

The initial objectives were to separate cirratulids from the sampled fauna, to identify specimens to genus level, and where possible, to species level. The distribution patterns of each taxonomic level would then be investigated, and the effects of certain abiotic factors examined. The precise methods utilized for these latter aims ultimately depend on the results of the initial objectives.

1.3 Cirratulidae

The R/V Urraca cruises yielded 5829 faunal specimens that researchers of the Darwin Project subdivided into phyla, highlighting that the Annelida were significantly most abundant, composing ~74% of the total fauna gathered (see Figure 1):

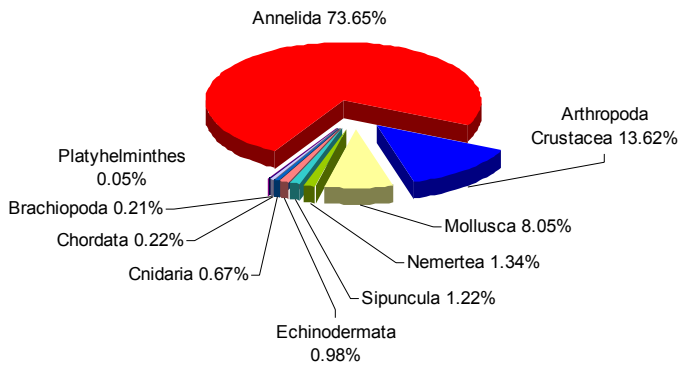


Figure 1: Percentage abundance of each phyla represented in the cumulative grab sample of 5829 specimens: Annelida are clearly most abundant with ~74%. Note that Arthropoda and Crustacea combined show less than 14% abundance, followed by Mollusca at ~8% (Mair, Pers. Comm.)

As is often the case in soft-bottomed communities, the class Polychaeta dominated within the Annelida, in terms of both individual and species abundance (Dauvin *et al*, 1994) with 1431, 960 and 326 specimens of the families Onuphidae, Spionidae and Cirratulidae respectively (see Figure 2a):

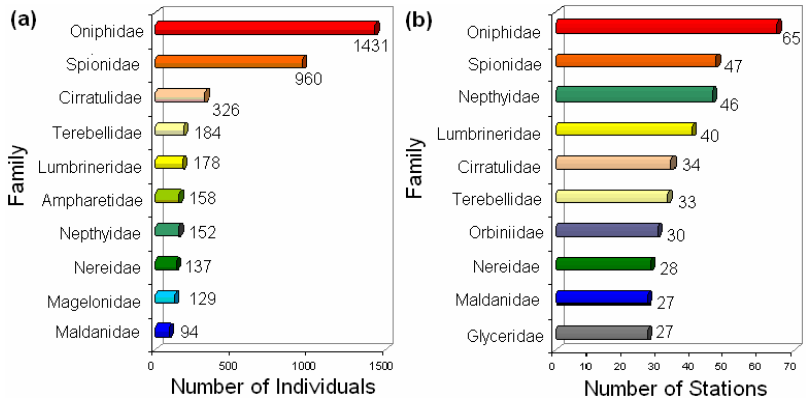


Figure 2: The most abundant and widely distributed polychaete families (a) Onuphidae, Spionidae and Cirratulidae feature 24.55, 16.47 and 5.59% of the total specimens gathered. (b)Onuphidae and Spionidae occur at 56 and 41% of the stations sampled respectively: (Mair, Pers. Comm.)

Onuphidae and Spionidae also showed the greatest distribution, occurring in 65 and 47 of the 114 stations sampled respectively (see Figure 2b). Although Cirratulidae showed a comparatively reduced distribution, they still appear widespread occurring in 34 stations.

Due to a greater volume of available literature, and expertise on the family Cirratulidae, specimen identification appeared plausible, and successive analysis of their abundance and distribution in the Las Perlas Archipelago would assist in achieving one of the aims of the Darwin Initiative Project: the quantification of biodiversity is an essential starting point to the understanding of the benthic environment, and essential to the implementation of successful management strategies.

Polychaetes in general are often considered as taxonomically problematical (Holthe, 1992), and the family Cirratulidae is no exception: recent debate stems from ignorance of their physiology, reproductive biology and systematic relationships (Blake, 1996; Woodham & Chambers, 1994). Their general biology has been recently reviewed by several authors (e.g. Blake, 1996, Chambers, 2000, 2006, George, 1963, 1964, 1967, Rouse & Pleijel, 2001). However, many of these texts differ in their emphasis reflecting both the lack of knowledge and understanding of certain morphological structures, and the associated changing taxonomy that has plagued this family.

1.3.1 Morphology and Anatomy

Cirratulids are characterised by an elongated bilaterally-symmetrical segmented body of relatively circular cross-section. Although not regionally distinct (Rouse & Pleijel, 2001), they do follow the stereotypical polychaete morphology of three fundamental sections: (i) a tapered non-segmented anterior, or head, region with a small prostomium (see Appendix 1 for nomenclature) derived from the larval episphere, followed by an annulated acheatous peristomium derived from the larval prototroch and buccal region; (ii) an elongated metamerically segmented body; and (iii) a posterior region tapering or expanding towards a non-segmented posterior pygidium (see Figure 3): In Cirratulidae, as with other families of polychaete, well-developed prostomia show a range of morphology from elongate (*Caulleriella* and some *Cirriformia*), through conical (*Chaetozone, Tharyx,* and some *Monticellina*) or semi-circular (*Aphelochaeta*), to wedge shaped (*Cirratulus, Dodecaceria* and some *Cirriformia*) (Dahl *et al.,* 1971; Fauchald, 1972; Rouse & Pliejel, 2001; Vittor *et al.,* 1984; Worsfold, 1996), featuring potentially chemosensory nuchal organs (Caullery & Mesnil, 1898) and/or eyespots: the majority of taxa feature eyes as juveniles, but may loose them as they mature (Rouse & Pliejel, 2001). Some may redevelop eyes in association with sexual maturation and epitoky (Petersen, 1999).

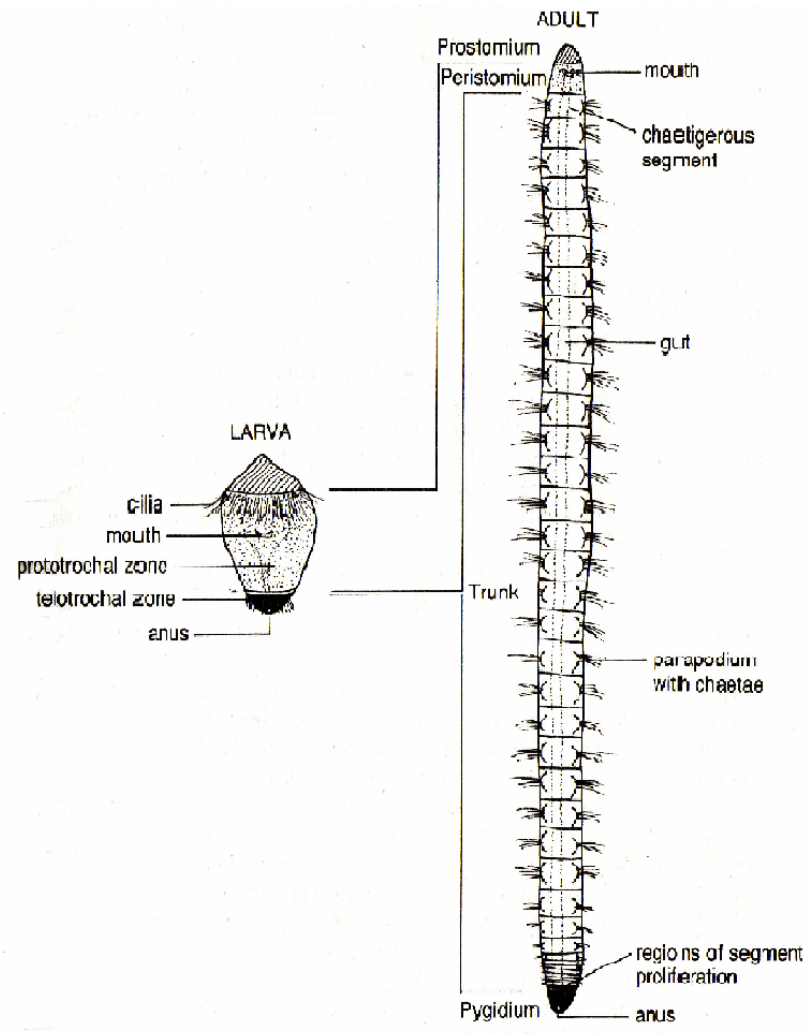


Figure 3: Illustration of basic polychaete composition showing the development of the adult composition of prostomium, peristomium, followed by chaetigerous segments, terminating in a pygidium from the larval regions: episphere, prototrochal zone and telotrochal zone respectively (George & Hartmann-Schröder, 1985)

- This diversity in structure is also prominent in the level of annulation in elongated peristomia, with some appearing as several achaetous segments: Day, 1967, through dissection, noted that these external annulations are not true segments. Additionally, variation in form is visible in the multitude and morphology of peristomial appendages: grooved tentacular palps transport food to the prostomium and occur anterior to or at the first septa (Fauchald & Rouse, 1997), directly behind which branchial gills begin to feature. Tentacular palps may arise as a single pair (*Aphelochaeta, Caulleriella, Chaetozone, Dodecaceria, Monticellina* and *Tharyx*) or numerous pairs (*Cirriformia, Protocirrineris, Timarete* and most *Cirratulus*) (Rouse & Pleijel, 2001).

Reaching from 0.7cm to over 25cm in length, adult cirratulids may feature more than 400 body segments. Segments are formed sequentially throughout maturation from paired mesodermal growth zones in the pygidium: the youngest segment is subsequently the most posterior. Each segment is a distinct entity, separated from its counterparts internally by septa, and mesenteries on the gut (Rouse & Pliejel, 2001).

Externally, with the exclusion of anterior segments, all feature both rudimentary parapodia with distinct bundles of chaetae at 2 distinct rami on each side of the body segments: a ventral neuropodium and a dorsal notopodium (Blake, 1996). Chaetae arise from small setal tori providing potentially distinctive interspecific characteristics: they are generally of simple capillary form, thin tapering cylinders often seen in the anterior or throughout the length of the body, or spine form, short thick cylinders that may be restricted to the posterior (Rouse & Pleijel, 2001). However, in some genera distinctive serrated blades, unidentate, bidentate, uncini or spatulate hooks may be visible (the differences are illustrated in Figure 4, below and elaborated on in Appendix 1, on page 82) (Blake *et al.*, 1996).

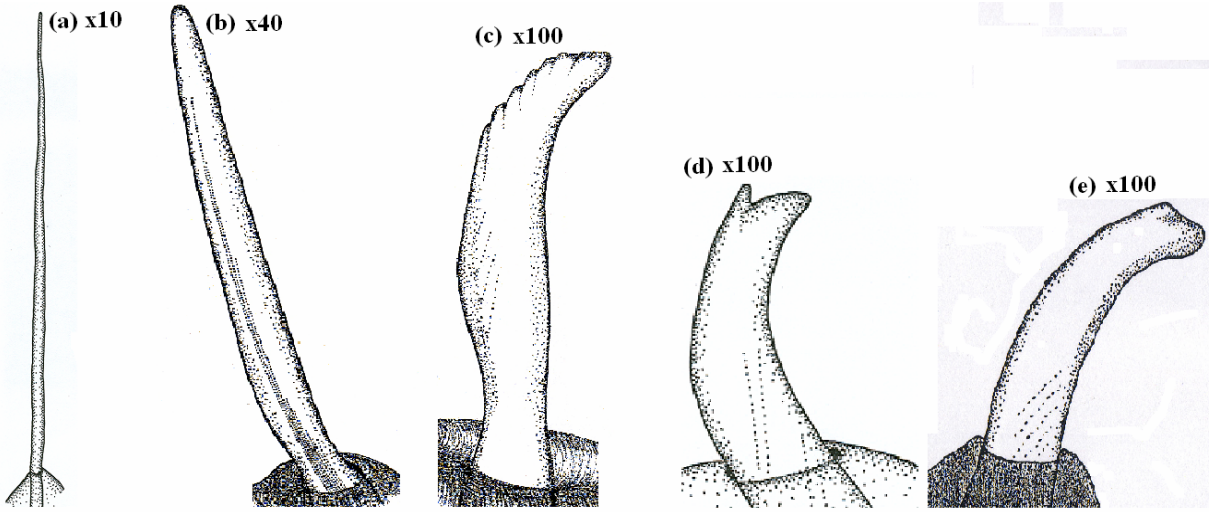


Figure 4: The chaetae of Cirratulidae take many forms. (a) A simple capillary chaetae of *Aphelochaeta B* at a magnification of x10. These are typically straight, long and relatively narrow. In some species, the fibrils of these may be splayed. (b) A spine of *Chaetozone A* at magnification of x40. These are also straight, but are shorter and thicker (c) A blade of *Monticellina G* at a magnification of x100. These are distally curved and serrated. (d) A bidentate hook of *Caulleriella A* at magnification of x100. These are distally curved featuring two distinct terminal teeth. (e) An uncini hook of *Tharyx A* at magnification of x100. These are distally curved featuring an enlarged tip. A spatulate hook is similar in appearance to an uncini hook; however the terminal bulge is indented.

1.3.2 Ecology

As with many polychaetes, cirratulids have an important role in the structuring of the benthic community, and the functioning of marine food webs: they act as an important link between the detritus and grazing food chains recycling organic matter and transferring it to higher trophic levels. In general, cirratulids are deposit-feeding organisms, embedding themselves into soft sediment, whilst extending their numerous lengthy branchial gills and tentacular palps into the water column. Members of the genus *Dodecaceria* are the known exception as physical borers of calcareous structures (Blake, 1996; Day, 1967). Burrowing and tube dwelling polychaetes often feature specialised chaetae to act as anchors.

Cirratulids have a global distribution and have been identified from the Poles to the Tropics, at a variety of depths: however, whilst they are a common component of soft benthic sediment, little is known of their ecology (Hily, 1987). *Chaetozone* diversity and abundance has been noted to increase below 500m water depth within the cold waters of the Faroe-Shetland Channel (Chambers & Woodham, 2003).

As endobenthic deposit feeders, cirratulids are often most numerous in areas of high organic enrichment, and have also been shown to respond to physical sediment disturbance. In particular the *C. setosa* 'complex' is often regarded as an indicator 'species' of perturbation (Hily, 1987; Pearson & Rosenberg, 1978). However, taxonomic confusion may lessen the value of *Chaetozone* records in environmental monitoring surveys (Telfer *et al.,* 1992): subsequently, better taxonomic definition is required.

Certain cirratulids have been linked with the uptake of metals and other pollutants: Gibbs *et al.,* 1983 reported that *Aphelochaeta marioni* was capable of bioaccumulating arsenic within its tissues with no apparent toxic affect. Milanovich *et al*, 1976 reported a similar accumulation of copper in tissues of *Cirriformia moorei.* It is possible that this metal accumulation protects from consumption by predators by making the cirratulids distasteful (Blake, 2006).

1.3.3 Reproductive Biology

Cirratulidae feature separate sexes, however, hemaphrodites have been noted in *Aphelochaeta*, *Caulleriella* (Petersen, 1994) and *Tharyx* (Blake; 1996 and Christie, 1985). In terms of sexual reproduction, females may deposit their eggs within excreted gelatinous epibenthic masses, or may excrete eggs individually. Certain species of *Cirratulus* have been observed to protect their fertilized brood with detached branchial gills and tentacular palps (Cunningham & Ramage, 1988; Stevenson, 1950; Thorson, 1950): larval development then progresses within the protective mass until the emergence of 4-5 segmented larvae (Blake; 1996).

In certain species of *Chaetozone* (e.g. *C. jubata*), exceptionally long capillary chaetae have been observed, dubbed natatory chaetae. In certain families of polychaetes (e.g. Nereidae), these are thought to be associated with epitoky, and reproductive swarming. However, there are no documented records of *Chaetozone* showing epitokous development: subsequently, the function of these chaetae must be investigated further (Chambers & Woodham, 2003).

Asexual reproduction through fission (fragmentation) may add further complexity: While species of *Dodecaceria* produce eggs and sperm for sexual reproduction, they are also capable of asexual reproduction, fragmenting into individual segments regenerating entire organisms from a single middle body segment (Clark, 1976; Day, 1967; George & Petersen, 1991; Petersen, 1991, Rouse & Pleijel, 2001). This same phenomenon has been observed more recently in species of *Cirratulus* (Curtis, 1977), *Protocirrineris* and *Timarete* (Petersen, 1991). Subsequently, it is suspected to occur widely throughout the family (Blake; 1996) and may be crucial in years with limited sexual success (Curtis, 1977).

Studies of larval cirratulidae development are few: those present suggest that cirratulid development may be direct (observed in some populations of *Cirriformia tentaculata*) (George, 1963, 1964, 1967; and Wilson, 1936), lecithotrophic (observed in *Cirratulus cirratus*, *Cirriformia moorei* and some *C. tentaculata*) (Blake, 1975; George, 1963, 1964, 1967; Okuda, 1946; Olive, 1970; Stephenson, 1950; Wilson,

1936) or vivaporous (observed in *Tharyx acutus*, *T. vivipara* and *Dodecacaria ater*) (Blake, 1996; Caullery & Mesnil, 1898; Christie, 1984).

Studies of reproductive cycles and population dynamics are also minimal, and concentrate on specimens in British waters. Gibbs, 1971; George, 1964; Olive, 1970, 1971; Oyenekan, 1987 have studied reproductive cycles and population structure in several species showing possible breeding throughout the year, with peak breeding coinciding with a seasonal peak in population density. These studies indicate that developing cirratulids do not reach breeding age until their second year. Olive reported that, after spawning, females can begin to develop another set of oocytes within 30 days, spawning up to 5 times in their lifetime, and males never fully shed their sperm, facilitating year long reproduction. Subsequently, it is possible individuals of all stages of development may occur within any one population at any one time (Olive, 1971).

1.3.4 Taxonomic Complications

Cirratulids are allocated to 10 genera and multiple species; however, as knowledge grows of the enigmatic Cirratulidae, the precise divisions between these phylogenic branches are continually queried, merged and segregated: the partial revision of the family by Blake, 1991a, has highlighted the problems in taxonomy and nomenclature of many genera and species generating further debate in recent years.

Confident identification of Cirratulidae is problematic, primarily due to limited original descriptions, followed by limited revisionary work. The pattern of taxonomic confusion was initiated by the introduction of the bitentaculate genus *Chaetozone,* for the type species *C. setosa* Malmgren, in 1867, with no generic diagnostic description: a lapse that led to taxonomic confusion throughout the following century. This single species was recorded indiscriminately throughout the world's oceans, from the intertidal to the deep sea, at depths of <4950m, inhabiting numerous benthic substrata (Chambers, 2000; Chambers & Woodham, 2003; Woodham & Chambers, 1994a) despite observations of differing external morphology (Christie, 1985). Webster and Benedict introduced a new genus, *Tharyx,* in 1887, with *T.*

acutus as the type species. Further taxonomic confusion was instigated by McIntosh's addition of 2 new species in 1911: *C. zetlandica* (a species described from a single damaged headless specimen as distinct from *C. setosa* due to partial cinctures in the posterior) and *C. dunmanni* : the latter was later redefined as *Cirratulus caudatus* Lecinsen (Woodham & Chambers, 1994b)

In 1919, Chamberlin introduced another genus, *Caulleriella*, in a dichotomous key distinguishable from *Chaetozone* and *Tharyx*: Chamberlin classified *Tharyx* by the presence of solely simple capillary chaetae, *Chaetozone* by the presence of posterior cinctures of spines, and *Caulleriella* simply by the presence of bidentate tips. Hartman, 1961, amended this distinction utilizing chaetae type alone noting that *Chaetozone* had unidentate spines. In 1991, Blake published a paper redefining the genus *Tharyx* on the basis of the discovery of uncini hooks in the type species *T. acutus*: *Tharyx* was redefined as containing uncini hooks, and a new genus, *Aphelochaeta*, was introduced to contain those with just simple capillary chaetae (Blake, 1991a).

Following Blake's partial revision of cirratulid genera, several species have been re-named and re-described: Woodham and Chambers, 1994a, re-described *Caulleriella zetlandica* whilst describing a second Atlantic species of *Chaetozone*, *C. gibber*, clearly distinctive from *C. setosa* by the presence of eyes and a humpbacked appearance. In 2000, it became clear that there was more than one Atlantic species without eyes leading to the introduction of *C. christei* (Chambers, 2000; Woodham & Chambers, 1994a). *C. setosa* is now commonly regarded as a species aggregate/complex (Chambers & Woodham, 2003). Such instability highlights the need for precise re-definitions of both *Chaetozone* and *Caulleriella* (Woodham & Chambers, 1994a). Throughout the Cirratulidae, lack of clarity in generic descriptions has lead to lapses in taxonomic characterisation. Additionally, throughout the relevant literature, there is a lack of consistency in diagnostic terms: subsequently, for the purpose of this dissertation, the terminology has been summarised within the nomenclature section.

A further complication with Cirratulidae taxonomy is that identification requires complete specimens, however, the collection fixation and preservation processes inherently damage or remove many diagnostic characters (Blake, 1996). Furthermore, specimens must be stored continuously submersed in fixative fluid in airtight containers to avoid degradation. This dissertation, as with many studies on polychaete taxonomy, is carried out on specimens collected as part of a general benthic monitoring programme. Collection, relaxation and preservation were not group specific as would be preferential since each family has specific requirements for narcotisation and preparation (Rouse & Pleijel, 2001).

It is also important that specimens are posteriorly complete for confirmation of the posterior extent of spines. Further complications arise with juveniles: the limited studies on larval development (see section 1.3.3 – Reproductive Biology) indicate that juvenile multitentaculate cirratulids feature different chaetael types and branchial distributions to their associated adults. Bidentate hooks were observed on juvenile *Cirriformia tentaculata* and *C. moorei* whilst adults featured capillary chaetae and unidentate hooks. Branchial gills were also noted on the peristomium in juveniles, whereas they usually originate on segment 1 in adults. Whilst distribution and morphology of chaetae appears vitally important in distinguishing genus and in particular species, the exact position is growth related. Subsequently, specimens must be mature for accurate identification (Blake, 1996).

1.3.5 Current Systematics

Cirratulid genera are currently categorised into three broad groups: (i) all those with many tentacular palps (*Cirratulus, Cirriformia, Protocirrineris* and *Timarete* species); (ii) those with a single pair of tentacular palps inhabiting soft-substrate (*Aphelochaeta, Caulleriella, Chaetozone, Monticellina* and *Tharyx* species); (iii) and those with a single pair of tentacular palps inhabiting hard surfaces (*Dodecacaria* species) (Blake, 1996).

Those with many tentacular palps can be easily divided further into those with tentacular palps confined to ≤3 segments (*Cirratulus* and *Cirriformia* species), and

those with tentacular palps extending over >3 segments (*Timarete* and *Protocirrineris* species). However, further classification requires closer examination of several characteristics as summarised in Table 1, below (Blake, 1996):

Genus	Distinguishing Features	
Protocirrineris	Prostomium	Bluntly conical to wedge shaped
	Peristomium	Enlarged
	Body Shape	Nearly rounded in cross-section with distinct segments
	Tentacular Palps	Relatively few tentacular palps extending over >3 segments
	Branchial Gills	May occur anterior to tentacular palps
	Chaetae	Chaetae are solely capillary chaetae
Timarete	Prostomium	Wedge shaped
	Peristomium	Relatively short; 2 annulations
	Body Shape	Nearly round in cross-section with distinct segments
	Tentacular Palps	Tentacular palps extending over >3 segments
	Branchial Gills	Branchial gills adjacent to notopodium, falling to mid-dorsum in middle sections; occur anterior to tentacular palps
	Chaetae	Capillaries & Spines
Cirriformia	Prostomium	Elongate or Blunt; eyes usually absent
	Peristomium	Relatively short; 2-3 annulations
	Body Shape	Robust; well segmented; rounded dorsally, but may be flat ventrally in cross-section.
	Tentacular Palps	Tentacular palps confined to ≤3 segments
	Branchial Gills	Branchial gills occur dorsal of notopodia throughout; generally numerous; occur anterior to tentacular palps
	Chaetae	Capillaries & Spines
Cirratulus	Prostomium	Wedge shaped, elongate or blunt; usually with eyes
	Peristomium	Relatively short; 2-3 annulations
	Body Shape	Robust; rounded dorsally and flattened ventrally in cross-section
	Tentacular Palps	Many tentacular palps confined to a single segment.
	Branchial Gills	Occur on tentaculated segment
	Chaetae	Capillaries & Spines

Table 1: Summary of characteristics useful for distinguishing different genera of multitentaculate cirratulids (Blake, 1996; Day, 1967; Fauvel, 1927; Chambers, Pers. Comm). Each genus has a very distinctive feature: *Protocirrineris* have solely simple capillary chaetae; *Cirratulus* feature tentacular palps on a single segment; *Cirriformia* feature branchial gills dorsal of notopodia, whereas *Timarete* species feature branchial gills adjacent to notopodia, becoming mid-dorsum in abdominal segments

Those with a single pair of tentacular palps gathered from hard substrate tend to be *Dodecaceria* species: they are generally dark in colouration with branchial gills limited to the anterior. However, distinguishing between other bitentaculate species can prove difficult. Blake claims that the only reliable distinguishable feature is the shape and arrangement of the chaetae (Blake, 1996), however, in the past 6

features were utilised in conjunction with one another (summarised in Table 2, below).

Genus		Distinguishing Features
Dodecaceria	Prostomium	**Bluntly rounded forming hood over mouth; eyes often absent**
	Peristomium	**Elongate and acheatous**
	Body Shape	**Body shape relatively short with few segments; dark in colouration**
	Tentacular Palps	**Single pair at setiger 1**
	Branchial Gills	**6-10 in anterior, pointing forwards**
	Chaetae	**Capillaries in anterior; spatulate hooks in posterior**
Caulleriella	Prostomium	**Elongate, sharply pointed prostomium; eyes often present**
	Peristomium	**Short to elongate**
	Body Shape	**Elongate or robust; well segmented**
	Tentacular Palps	**Usually anterior to setiger 1**
	Branchial Gills	**Numerous: extend over most of body**
	Chaetae	**Capillaries in anterior; bitentaculate hooks on posterior neuropodia that may give the impression of partial cinctures.**
Chaetozone	Prostomium	**Conical, sharply pointed or blunt; eyes may be present**
	Peristomium	**Short to elongate**
	Body Shape	**Robust; distinctive dorsal hump; segments often moniliform in middle region**
	Tentacular Palps	**Single pair from the anterior of segment 1, or peristomium**
	Branchial Gills	**Numerous: may extend along entire length of body**
	Chaetae	**Capillaries in anterior; spines in posterior; may occur from both parapodia of posterior segments, generating cinctures.**
Tharyx	Prostomium	**Conical**
	Peristomium	**Elongate**
	Body Shape	**Elongate; well segmented; sometimes moniliform in middle**
	Tentacular Palps	**Single pair anterior to or at setiger 1.**
	Branchial Gills	**Arise immediately posterior to palps; may occur on peristomium**
	Chaetae	**Simple capillaries in anterior; uncini hooks in posterior**
Aphelochaeta	Prostomium	**Conical; often with eyes**
	Peristomium	**Elongate**
	Body Shape	**Middle segments often moniliform; posterior and anterior segments often engorged**
	Tentacular Palps	**Single pair on or anterior to setiger 1**
	Branchial Gills	**Present**
	Chaetae	**Solely simple capillary chaetae**
Monticellina	Prostomium	**Short to elongate; may have eyes**
	Peristomium	**Short to elongate**
	Body Shape	**Middle segments often moniliform; anterior and posterior often enlarged**
	Tentacular Palps	**Single pair anterior to setiger 1**
	Branchial Gills	**Present throughout**
	Chaetae	**Serrated Blades**

Table 2: Summary of characteristics useful for distinguishing different genera of bitentaculate cirratulids (Blake, 1996; Day, 1967; Fauvel, 1927; Chambers, Pers. Comm). Each genus has distinctive chaetae: *Dodecacaria* have spatulate hooks, *Caulleriella* have bidentate hooks, *Chaetozone* have spines, *Tharyx* have uncini hooks, *Aphelochaeta* have solely simple capillaries and *Monticellina* have serrated blades.

1.4 The Study Area – The Las Perlas Archipelago

1.4.1 Location

The work described in this dissertation focused on specimens gathered from the Las Perlas Archipelago, Panama (shown in Figure 5 and Figure 6): a cluster of 250 basaltic rock islands, mostly uninhabited, located within the Gulf of Panama and, subsequently, within the Tropical Eastern Pacific (TEP) biogeographic zone. The TEP is one of the worlds most isolated oceanic ecosystems due to geographical boundaries: the Isthmus of Panama to the east (Figure 5), the deep expanse of the Eastern Pacific Barrier (EPB) to the west, and cold water upwellings and currents to the north and south effectively partition the TEP from the remainder of the Pacific Ocean (Cortés, 1997; Griggs & Hey, 1992)

Figure 5: The Isthmus of Panama stretches from Costa Rica to Colombia, separating the Pacific and Atlantic Oceans. The Las Perlas Archipelago is highlighted in red: it is located in the Gulf of Panama, ~70km south east of Panama City, and ~31km from mainland Panama (Baxter, 2004; Berman, 2004; Image adapted from GEsource, 2006)

The narrow Isthmus of Panama originated 3.2-3.5Mya on the American lithosphere plates: an extremely active tectonic region during the Tertiary period. The northwards movement of the South American plate collided with the eastwards movement of the Nazca and Caribbean plate effectively partitioning the American Tropical Ocean into the distinct bodies of the Pacific and the Atlantic (Glynn & Maté, 1996; Coates *et al,* 1992): to the north and east of this narrow partition lies the

Caribbean, to the south and west, the TEP (van der Spoel & Pierrot-Bults, 1979), and subsequently the Las Perlas Archipelago (see Figure 5).

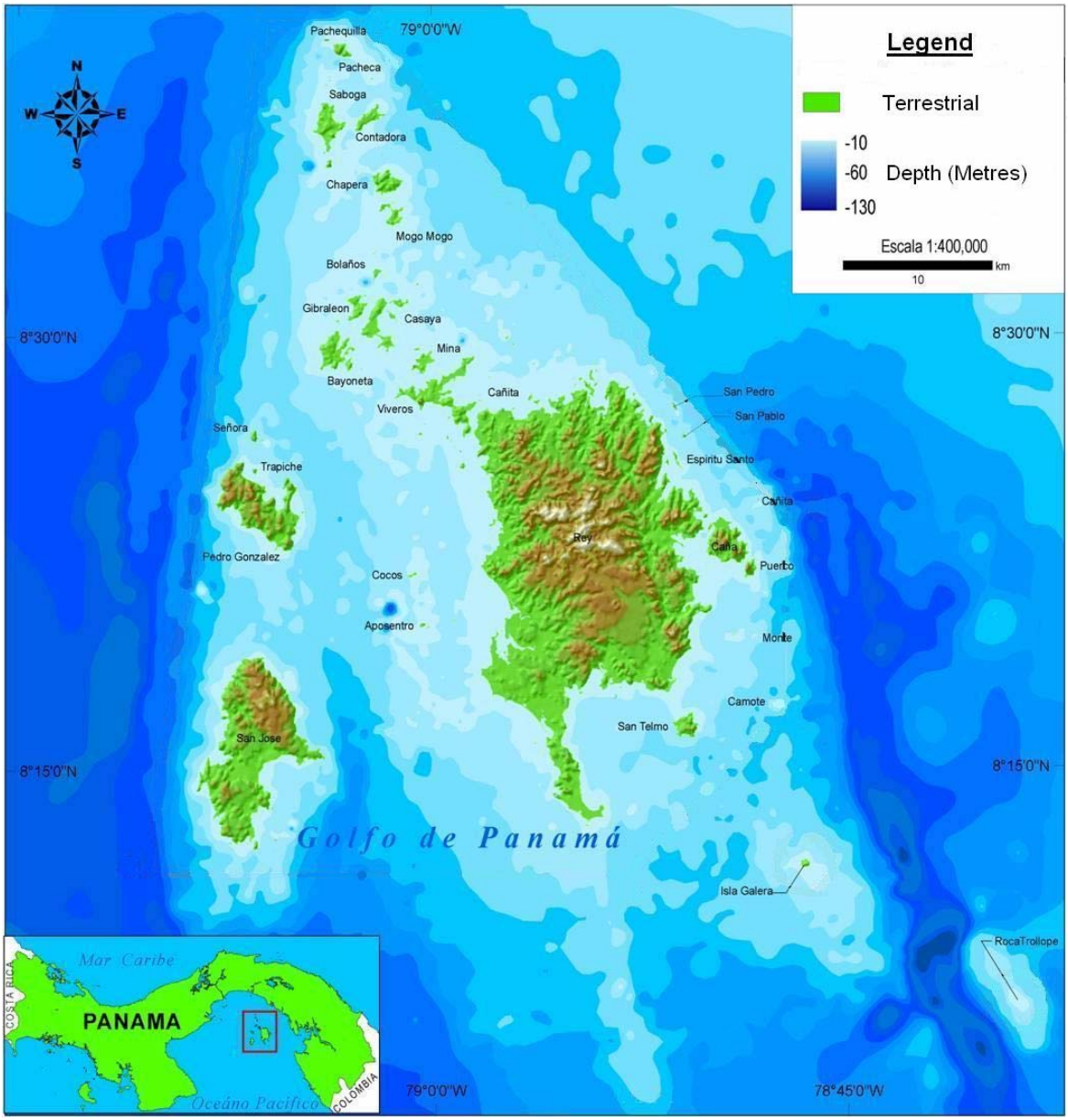


Figure 6: The Las Perlas Archipelago lies between 08°11'46''N -08°40'19''N and 78°46'31''W-79°03'49''W. The immediate marine environment is all above the 50m isobar at varying depths (adapted from Campbell, 2006).

- The relatively rapid and large-scale closure of the Boliviar Seaway had both ecological and geographical effects: previously continuous flora and fauna became effectively isolated and began to genetically evolve and adapt to new conditions.

1.4.2 Climatology and Oceanography

The creation of the physical barrier of the Panama land-mass induced marked changes in the marine environment, affecting hydromorphology, water and nutricline depth, and subsequently productivity (Kershaw, 2004): the warm equatorial Atlantic current that previously flowed westwards through the channel between the Americas was curtailed, and deflected northwards up the east coast of North America. Conversely, colder currents accumulate in the TEP resulting in a more seasonal climate (Berman, 2004; D'Croz & Robertson, 1997).

The main surface currents affecting the TEP are illustrated in Figure 7. The North and South Equatorial Currents (NEC and SEC respectively) drive surface water westwards across the Pacific to either side of the equator, whilst the Equatorial Counter-current (ECC) drives surface waters eastwards. At ~6°S, the ECC entrains the cold Humboldt, or Peruvian Coastal Current generating the cyclonic south pacific gyre to the west of Columbia at ~ 4°N:79°W, and the waters deflected northwards by Panama creating an anticyclonic eddy just south of the Costa Rica Dome at ~ 5°N:88°W (Kershaw, 2004; Hurtado, 1995).

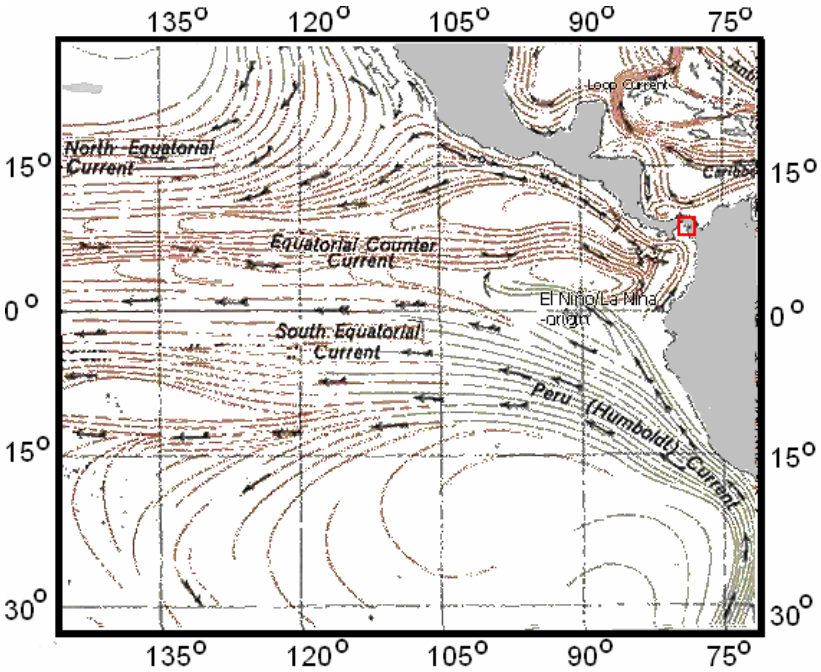


Figure 7: Illustration of the strength and direction of the main currents influencing the area of interest (highlighted in red): The NEC and SEC flow west to either side of the equator whilst the ECC flows east towards the Gulf of Panama. Here it historically passed through the Bolivar Seaway, however, it is now deflected north up the coast of Panama towards Costa Rica generating an eddy. A fraction of the Antarctic Circumpolar Current is deflected north by the tip of South America culminating in the Peruvian Current: an area of upwelling and elevated productivity, and the eastern edge of the south-pacific gyre (Image adapted from Wikipedia, 2006)

Surface circulation within the Gulf of Panama creates an anti-clockwise gyre with water exchange from the southeast. Internal currents may reach 0.5-0.6ms^{-1}, with a maximum tidal range of 6m, however mean tidal range is 3.7-3.8m (Benfield, 2005; Glynn & Maté, 1996; D'Croz & Robertson, 1997).

The marine environment surrounding the Las Perlas Archipelago is also subject to intense variation: the Gulf of Panama is a region influenced by elevated seasonal upwelling of cold nutrient enriched water, overlaid with an episodic period of surface water warming due to the El Niño Southern Oscillation (ENSO) (Anderson, 2005; D'Croz & Robertson, 1997).

The former is governed by the seasonal longitudinal migrations of a narrow area of low atmospheric pressure: the Inter-Tropical Convergence Zone (ITCZ). From January till April, during the dry season, the ITCZ travels south towards 5°N, directly below Panama: the south and north easterly trade winds converge, blowing across the Pacific Ocean (D'Croz *et al.*, 1991; Forsbergh, 1969; Glynn & Maté, 1996) and the dry north-easterlies prevail over the Gulf (Martin, 1969). This air movement displaces nutrient-poor coastal and equatorial surface waters westwards, further elevating the level of the shallow permanent thermocline in the eastern Pacific (Kershaw, 2004) allowing the wind to mix nutrient rich lower waters with the nutrient depleted surface waters. The subsequent enrichment of the surface water allows an increase in the concentration of primary producers (phytoplankton). This effect continues down the food chain elevating the concentration of higher organisms. This upwelling of cold water also cools the overlying air, making it denser: water vapour cannot condense into clouds, preventing rainfall. Conversely, from April, the ITCZ migrates as far north as 15°N, subsequently traversing the Las Perlas Archipelago: the winds over Panama become weak and intermittent; coastal surface waters are not displaced and instead become warmer and nutrient depleted with low salinity. The elevation in sea surface temperature (SST) directly influences the atmosphere. Moist air over the ocean warms, becoming less dense, rising until it creates convective clouds and the wet season sets in (D'Croz *et al.*, 1991; Forsbergh, 1969; Glynn & Maté, 1996; Summerhayes & Thorpe, 1996).

The latter, ENSO, describes an extreme oceanic eastwards shift of heat energy (El Niño) associated with an atmospheric shift in pressure (the Southern Oscillation) that occurs every 4-9 years to different degrees of severity (D'Croz & Robertson, 1997; Glynn & Maté, 1996): as noted above, anomalies in SST affect fluxes of latent heat, these in turn influence pressure. Conversely any change in pressure influences the strength of the trade winds and the level of the thermocline that, in turn, manipulate the SST. During El Niño conditions, the pressure gradient between the eastern and western Pacific levels: the trade winds over the western and central Pacific relax, and a westerly wind anomaly may occur. This creates Kelvin waves propagating eastwards along the equator (Green, 1997). Subsequently, warm SST anomalies spread eastwards towards the South American coast and Panama (Brown *et al*, 1991). As the pressure gradient is reduced, the thermocline levels out, becoming depressed in the eastern Pacific. Subsequently, any coastal upwelling cannot reach the cold, nutrient-rich waters below, and equatorial upwelling is reduced. The surface waters of the Eastern Pacific remain warm and nutrient depleted, hence primary production begins to decline (Brown *et al*, 1991; Zebiak, 1999).

D'Croz *et al* have executed long term *in-situ* measurements, from 1985 to 2001, of various water quality variables, within the Gulf of Panama. From 1993 to 1996, a site to the northeast of the Las Perlas Archipelago was sampled weekly: this sampling indicated not just a dramatic seasonal variation in water variables but also a dramatic yearly variation specifically in temperature, chlorophyll a and nutrient content (D'Croz & Robertson, 1997).

Subsequently, the Gulf of Panama is prone to strong seasonal and annual variation in physical and chemical conditions: horizontal visibility within the water column of the Gulf of Panama can fluctuate from just 1-2m during periods of high primary productivity in the dry season to 16m (Glynn & Maté, 1996), SSTs have been recorded as low as 14.7^{o}C (Maté, 2003) during seasonal upwellings, and as high as 31°C in ENSO events (Anderson, 2005), and surface salinity also varies from 30-35‰ to 24-30‰ over the same period in response to seasonal upwelling and low rainfall in the former, and increased runoff in the latter (Glynn & Maté, 1996).

1.4.3 Recent Biological Studies of the Las Perlas Archipelago

Prior to the commencement of the Darwin Project, very few studies existed on the marine biology of the Las Perlas Archipelago. Significantly, coral reef structures were only observed within the Gulf of Panama in the latter half of the C20th: Glynn & Stewart, 1973, noted that these are largely confined to the north-eastern sides of the islands where they are partially protected from upwelling currents.

In addition, although the polychaetes of the sublittoral remain unknown, Fauchald, 1977, composed a review of polychaetes of the littoral zone of Panama, reviewing the works of Monro (1928a, 1928b, 1933a, 1933b), and Hartmann, plus additional available specimens: The resultant document listed 180 named polychaetes from the littoral zone of Panama, including 9 cirratulids. Significantly, this review indicates that the eastern Pacific Ocean may be more species-rich than the western Atlantic Ocean, with many of the Pacific species restricted in distribution (Fauchald, 1977). Blake, 1991b, reviewed the polychaetes of the Galápagos Islands from his own work (1983, 1986), that of Augener (1933), Chamberlin (1919), Hartmann, Kinberg (1865), Monro (1928, 1933a, 1933b), Treadwell (1928) and other available studies. The subsequent literature featured 192 species of polychaete with 7 cirratulids. Salazar-Vallejo & Londoño-Mesa, 2004, provided the most recent and comprehensive review of polychaetes of the Tropical Eastern Pacific listing 1100 species, including 52 species of cirratulid. The majority of the species mentioned by were originally described from the Atlantic, therefore the species names are doubtful (Chambers, Pers. Comm).

In the past few years, various biological studies have been carried out within the boundaries of the Archipelago into coral, mollusc and echinoderm biodiversity, the reasons for fin and shell fisheries decline, and effect of freshwater runoff to support the designation of this important marine ecosystem as a Marine Protected Area (Mair, Pers. Comm).

Following the R/V. “Urraca” cruises of 2003-2004, Darwin researchers performed minimal statistical analysis of the quantitative faunal samples collected in an effort to

determine benthic community types (see Figure 8). This analysis indicates that there are three distinct zones in the region that can be separated in terms of their geography, fauna, particle size and depth: the northeast sector features a community with few taxa and low abundance that is mainly dominated by molluscs, with a high percentage of silt; the southwest and east sector features a community dominated by a few taxa, and a high abundance of polychaete worms, with low silt and clay percentage but high depth; and the central sector features a high abundance of crustacean and other polychaete families, with a heterogeneous sediment particle size but low depth

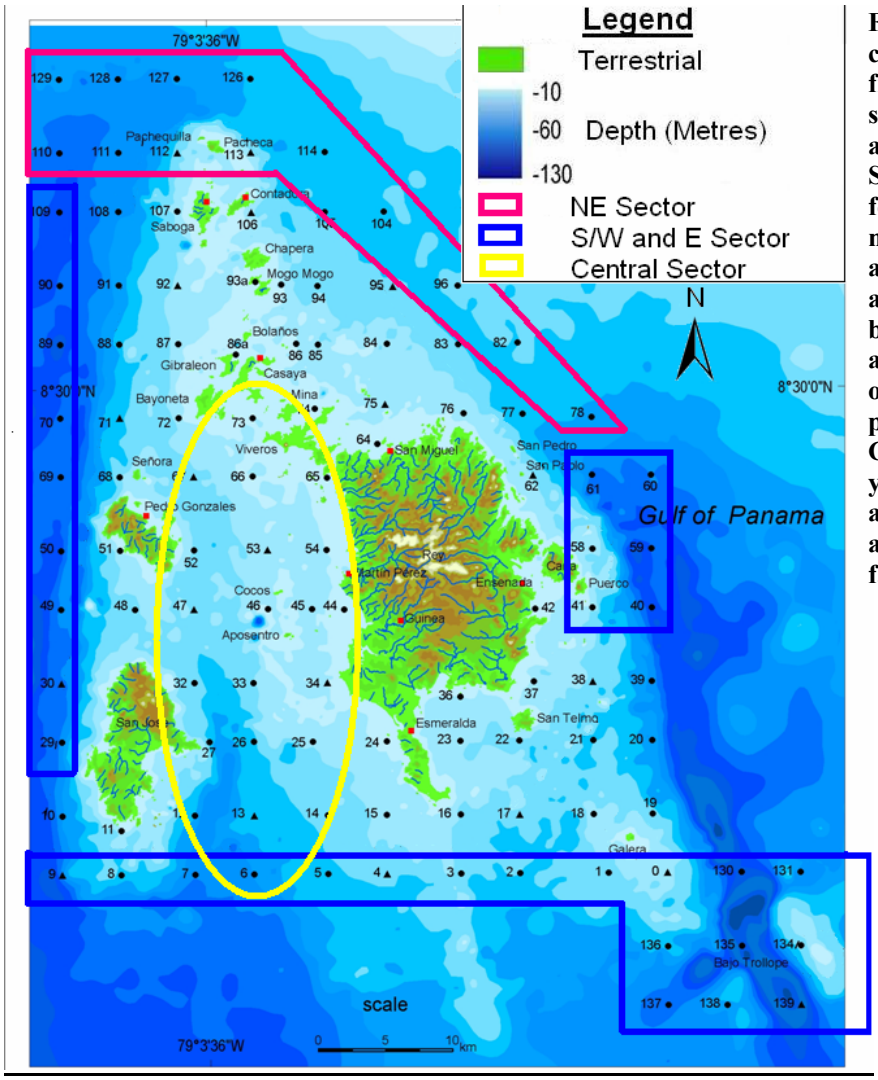


Figure 8: Illustration of community types derived from statistical analysis of sediment type and phylum abundance. The Northeast Sector, shown in pink, features few taxa, mainly molluscs, all at low abundance. The South/West and East Sector, shown in blue, feature high abundance but low number of taxa, dominated by polychaete worms. The Central Sector, shown in yellow, features a high abundance of crustaceans and other polychaete families.

2. Materials and Methods

2.1 Field Procedures on the R. V. Urraca cruise

From August 2003, until August 2004, the STRI utilised the 96 foot R/V "Urraca" to sample a regular grid of sites around the Las Perlas Archipelago (see Figure 9):

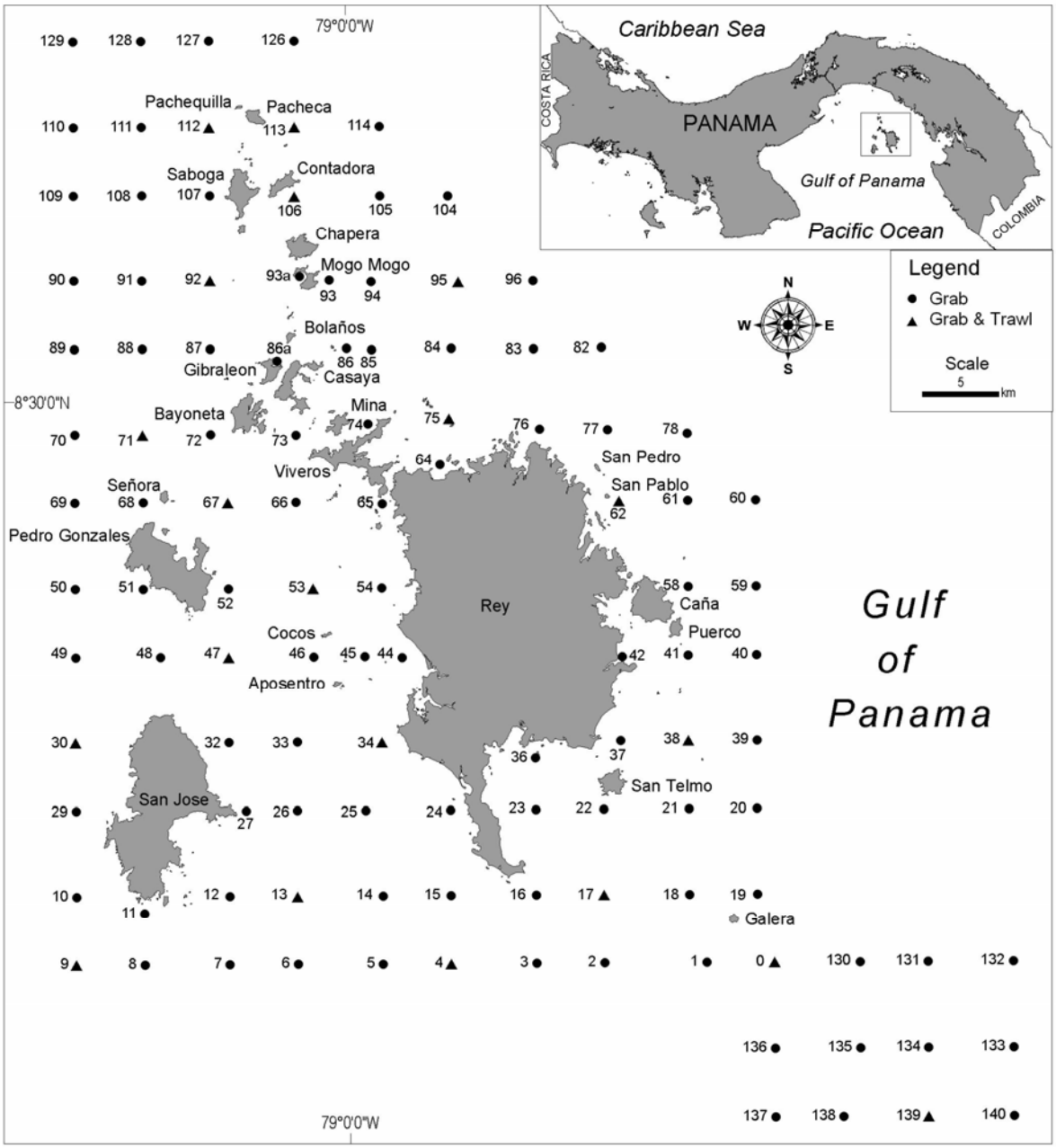


Figure 9: Illustration of the 60km by 70 km survey grid undertaken by the R/V "Urraca": 114 sites were sampled by grab, and 20 by trawl surrounding the Las Perlas Archipelago

Detailed methodology utilised will be described elsewhere in publications still in press. However, in brief, the 114 benthic sites shown were sampled by a 0.1m^2 van Veen grab (see Figure 10), of which 20 were additionally sampled qualitatively by a standard rectangular trawl (see Figure 11): 3 grab samples were taken at each site, 2 for analysis of benthic community structure and 1 for analysis of sediment composition.

Once collected, samples were rinsed through a 1mm round sieve, followed by a 500micron mesh sieve with fresh seawater. In addition, some specimens were treated with Rose Bengal. Specimens were fixed in 10% formalin solution in seawater in the field, before being brought back to the laboratory where they were washed in freshwater and then transferred to 70% ethanol

Figure 10: Hamish Mair and Hector Guzman emptying the van Veen Grab

Figure 11: Hamish Mair, Hector Guzman and the crew of the R/V Urraca survey sampling via a trawl.

2.2 Laboratory Analysis

2.2.1 Laboratory Analysis undertaken at Smithsonian Institution

Researchers at STRI carried out physicochemical analysis, via standard methods (see Holmes & McIntyre, 1984 for protocol), of the separate sediment samples gathered at each station determining organic carbon, carbonate content, and particle size composition as defined by the Wentworth Scale (shown in Appendix 6, on page 82).

In addition, the researchers undertook preliminary sorting of the faunal samples: organisms were removed from these samples, where necessary with the assistance of Rose Bengal to stain specimens, and separated to the lowest taxonomic level possible, before being stored in labelled glass vials under 70% ethanol (Mair, Pers. Comm).

Figure 12: The samples gathered by the R/V. "Urraca" cruises arrived at the NMS, Edinburgh, in mid-May in a variety of containers, lids, sealing tapes and labels.

2.2.2 Laboratory Analysis undertaken in Dissertation

The faunal samples gathered by the R/V. "Urraca" Cruises arrived at the NMS in mid-May 2006. Once unpacked, it became clear they had been divided into an assortment of vials (see Figure 12): these contained individual and assemblages of specimens, some separated as far as family, and others to phyla. Each vial featured variable degrees of labelling with some more alcohol resistant than others (see Figure 13).

The first stage of laboratory analysis involved collection of all samples containing polychaetes and ordering these by station number. Each polychaete sample was then carefully examined under a Leiza MZ6 microscope with internal magnification of up to 4, lens magnification of 10, and an associated Leica L2 light unit (see Figure 14).

Prior to arrival of samples from the STRI, specimens of Atlantic cirratulids present in the NMS were studied in order to understand and gain

Figure 13: Each container was labelled to some degree, be in on the lid, internally, externally, or a combination of all three. Unfortunately some labels were written in soluble ink.

familiarity with the family Cirratulidae: these initial specimens included representatives from all recognised genera.

From the knowledge gained, all recognisable cirratulids were removed from the polychaete assemblages and stored in airtight glass vials. Other clearly recognisable families were also separated to ease further studies. In each case, all previously associated data was preserved, and transferred to legible labels.

Figure 14: Sorting was carried out under a Leiza MZ6 microscope with an internal magnification of up to *4, and a lens magnification of *10. Sorted Cirratulids are visible in the behind left Petri-dish, sirpunculids and other small polychaetes in the behind right, large polychaetes in the front right, and unsorted specimens in the front left.

Further identification of the family of interest to the highest taxonomic level possible was facilitated by a Leitz Laborlux D Compound Microscope with magnifications of 4, 10, 40 and 100. The use of Rose Bengal, whilst often invaluable in the sorting process, can impede the identification process by dying the entirety of individuals pink and subsequently destroying any distinctive pattern or colouration, consequently, other morphological characteristics were utilised: with greater magnifications, chaetae shape could be studied to rapidly determine genus. Such magnifications were also used to examine the location and number of chaetal types on the body to assist with species separation, however, the majority of this was based on physical properties visible under the afore mentioned dissecting microscope.

Once identified, the individual specimens were stored in airtight glass vials in 70% ethanol. Specimens of the same morphological type were stored together by genus and associated species letter. These were labelled, recorded and deposited in the zoological collections of the National Museum of Scotland, Edinburgh.

2.3 Data Analysis

Illustrations of 1 representative for each identified taxon were carried out with the assistance of a 'Wild Heerbrugg M7A' microscope with a magnification of up to 30, and an attached drawing arm. An 'Ernst Leitz Eizlar' Microscope and associated drawing arm (ELW GMBH) facilitated the more precise illustrations, such as those of chaetae.

Photographs were obtained with an Asahi Pentax K100 camera, attached to a Leica MZ95 microscope with magnification of between 0.63 and 6, and a lens of 10. Several images were obtained for each species utilising a selection of Fujichrome color reversal professional super fine grain films (64, 100, 200 and 400 ASA), and light regimes (a range of below lighting, plus an additional fibre-optic light): a Kenro Lightbox was used to select the most informative photographs.

Although canonical correspondence analysis could be conducted to investigate the effects of environmental gradients on the division of cirratulids between stations, the overall cirratulid dataset generated was small, and only became smaller as further genus and species divisions were imposed restricting the potential for meaningful statistical analysis. Subsequently, analysis of distribution was restricted to visual geographical mapping through Microsoft Paint, and graphical analysis of presence and absence via Excel.

3. Results

3.1 Cirratulid Identification

3.1.1 Cirratulid Genera of the Las Perlas Archipelago

Analysis of the Las Perlas faunal samples revealed 361 cirratulids: 9 from trawls of 3 stations, and 352 from 52 grabs covering 35 stations (See Appendix 4, on page 87). These cirratulids were separated into 6 recognised genera: *Cirriformia, Aphelochaeta, Chaetozone, Monticellina, Caulleriella* and *Tharyx* as summarised in Key 1, below

Key 1: Guide to distinguish between the Genera of Cirratulidae from off the Las Perlas Archipelago in the Tropical Eastern Pacific.

1A. Anterior with many pairs of tentacular palps, or palp bases (see Figure 15a)…….. ..……... Genus *Cirriformia* (see Figure 16)

NOTE: wedge shaped prostomium; usually no visible eyes; peristomium elongate; body robust in stature (examined specimens have a length: width ratio of <6:1); tentacular palps confined to 3 most anterior segments; branchial gills dorsal to notopodia throughout.

1B. Anterior features a single pair of tentacular palps, or palp bases (see Figure 15b)……...2

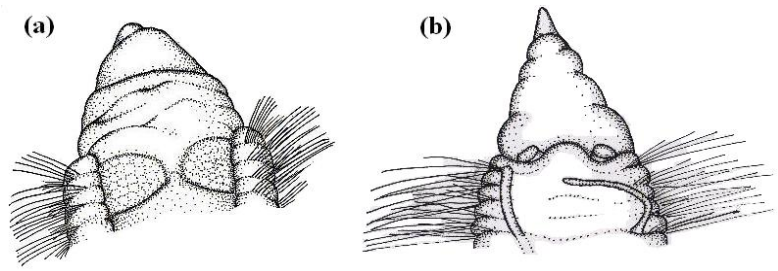


Figure 15: Cirratulidae may be bitentaculate or multitentaculate. (a) Anterior of *Cirriformia Indet (A)* featuring a series of tentacular palp bases visible as a pad. (b) Anterior of *Aphelochaeta C* featuring 2 distinct tentacular palp bases.

2A. Chaetae all capillaries (see Figure 4a, page 13)……..…….…….…… ……...……Genus *Aphelochaeta* (see Figure 17)

NOTE: prostomium conical; peristomium elongate; body elongate (examined specimens have a length: width ratio of >25:1); abdominal segments are often beadlike with enlarged posterior and anterior segments; branchial gills occur dorsal of notopodia and where present often bisect the dorsal surface.

2B. Chaetae include blades, spines, bidentate or uncini hooks in posterior regions in addition to capillaries throughout.....…… 3

3A. Short chaetae straight and blunt (spines) (see Figure 4b, page 13)……...……..… ……...……...… Genus *Chaetozone* (see Figure 18)

NOTE: prostomium conical, pointed or blunt on anterior margin; eyes may be present; peristomium no longer than prostomium; body stature elongate and robust (examined specimens have a length: width ratio of >9:1); well segmented, sometimes with beadlike middle segments; anterior chaetae are of capillary structure, with spines occurring in neuropodia and often notopodia towards the posterior; posterior chaetae may form complete cinctures.

3B. Short chaetae curved or enlarged at their external tip (blades or hooks).…… 4

4A. Short chaetae serrated (blades) (see Figure 4c, page 13)..... …….Genus *Monticellina* (see Figure 19)

NOTE: prostomium elongate or short, pointed or blunt on anterior-most margin; peristomium elongate to short; body elongate (examined specimens have a length: width ratio of >19:1); well segmented with middle segments often beadlike; external tube often visible; posterior segments may be enlarged.

4B. Short chaetae smooth and cylindrical in structure (hooks).……...…… 5

5A. Short chaetae bidentate (see Figure 4d, page 13)…..Genus *Caulleriella* (see Figure 20)

NOTE: prostomium elongate, pointed or blunt on anterior margin; peristomium short to elongate; body stature elongate and robust (examined complete specimens have a length: width ratio of >18:1, however, several incomplete specimens suggest a more robust build); well segmented.

5B. Short chaetae knob-tipped (uncini) (see Figure 4e, page 13)……..……...……. ……..Genus *Tharyx* (see Figure 21)

NOTE: prostomium elongate, pointed or blunt on anterior margin; peristomium elongate; body elongate (examined specimens have a length: width ratio of >17:1).

- Specimens within each genus were separated further depending on general morphology, specifically prostomium and peristomium shape, body segmentation and stature, and chaetae number and position. Physical characteristics suggest that the cirratulids of the Las Perlas Archipelago feature 2 species of *Cirriformia*, 5 of *Aphelochaeta* and *Chaetozone*, 8 of *Monticellina,* 6 of *Caulleriella* and 2 of *Tharyx.*

3.1.2 *Cirriformia* Species from the Las Perlas Archipelago

The 3 specimens of *Cirriformia* gathered were separated into 2 species using properties summarised in Key 2, below. Illustrations of each species are visible in Figure 16, below.

<u>Key 2: Guide to distinguish between the Species of *Cirriformia* from off the Las Perlas Archipelago in the Tropical Eastern Pacific.</u>

1A. Anterior features few capillary chaetae……...*Cirriformia A* (*c/f moorei)* (see Figure 16a)

NOTE: wedge shaped prostomium; no visible eyes; peristomium elongate and deeply annulated; body robust in stature (examined specimen has a length: width ratio of <6:1) throughout, tapering towards posterior; narrow crowded segments; ventral surface flattened; branchial gills present in posterior; neuropodal chaetae with spines posteriorly from segment 7; notopodal chaetae feature spines posterior of segment 30; dark colouration in alcohol, becoming lighter towards pygidium.

1B. Anterior features dense capillary chaetae.....…*Cirriformia Indet A* (see Figure 16b)

NOTE: short triangular prostomium; eyes absent; peristomium elongate; body robust in stature (examined specimens missing posterior region); narrow crowded segments; branchial gills dorsal to notopodia throughout; brown dorsal colouration in alcohol, becoming paler on ventral surface.

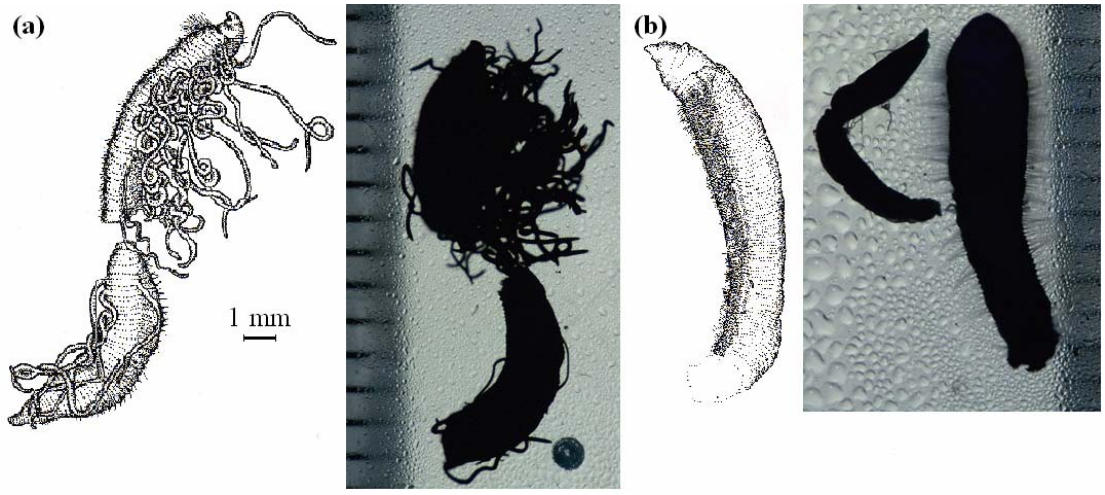


Figure 16: Illustrations of the *Cirriformia* species found, each photographed alongside a millimetre scale,, and drawn to scale (more detailed illustrations are available in Appendix 7). (a) Specimen of *Cirriformia A* from station 136, grab b that was ~15mm in length and ~2mm in width. (b) Anterior fragments of *Cirriformia Indet A* from station 9, trawl. The larger specimen was drawn to scale and was 11mm in length and 2mm in width.

- Unfortunately, whilst the species of *Cirriformia* clearly differ morphologically, the lack of a posterior in specimens of *Cirriformia Indet A* renders them unidentifiable.

3.1.3 *Aphelochaeta* Species from the Las Perlas Archipelago

The 57 specimens of *Aphelochaeta* were separated into 5 species as summarised in Key 3, below. Illustrations of each species are shown in Figure 17, on page 38.

Key 3: Guide to distinguish between the Species of *Aphelochaet*a from off the Las Perlas Archipelago in the Tropical Eastern Pacific..

1A. Abdominal segments narrow……..…….*Aphelochaeta B* (see Figure 17b)

NOTE: prostomium conical; peristomium elongate; body elongate (examined specimens have a length: width ratio of ~32:1); enlarged posterior and anterior segments; pink to purple in alcohol..

1B. Abdominal segments elongate ……..……..……...2

2A. Body segments moniliform throughout (see Figure 17a)…….…….....…..3

2B. Body segments irregular and indistinct (see Figure 17c ……...4

3A. .Prostomium conical and small; parallel to body……..……
…….*Aphelochaeta A* (*c/f. monilaris*) (See Figure 17a)

NOTE: prostomium often blunt; peristomium no longer than prostomium; body elongate (examined specimens have a length: width ratio of ~35:1); abdominal segments are long and beadlike with enlarged posterior and anterior segments; pale in alcohol.

3B. Prostomium pointed and elongate; often hooked …….*Aphelochaeta E* (See Figure 17e)

NOTE: prostomium hooked under body; peristomium elongate; body elongate (examined specimens missing posterior); abdominal segments are short and beadlike with enlarged anterior segments; pale in alcohol.

4A. Prostomium pointed and elongate…….……..*Aphelochaeta C* (See Figure 17c)

NOTE: prostomium often curled upwards at tip; eyes may be present; peristomium elongate; body elongate (examined specimens have a length: width ratio of ~40:1); abdominal segments are irregular but elongate where present; anterior segments narrow with dorsal hump; tan in alcohol.

4B. Prostomium blunt and small; parallel to body.....…….*Aphelochaeta D* (See Figure 17d)

NOTE: prostomium parallel to body; eyes may be present; peristomium elongate with dorsal hump; body elongate (examined specimens have a length: width ratio of ~35:1); abdominal segments are indistinct with enlarged posterior and anterior segments; anterior dorsal hump; pale in alcohol.

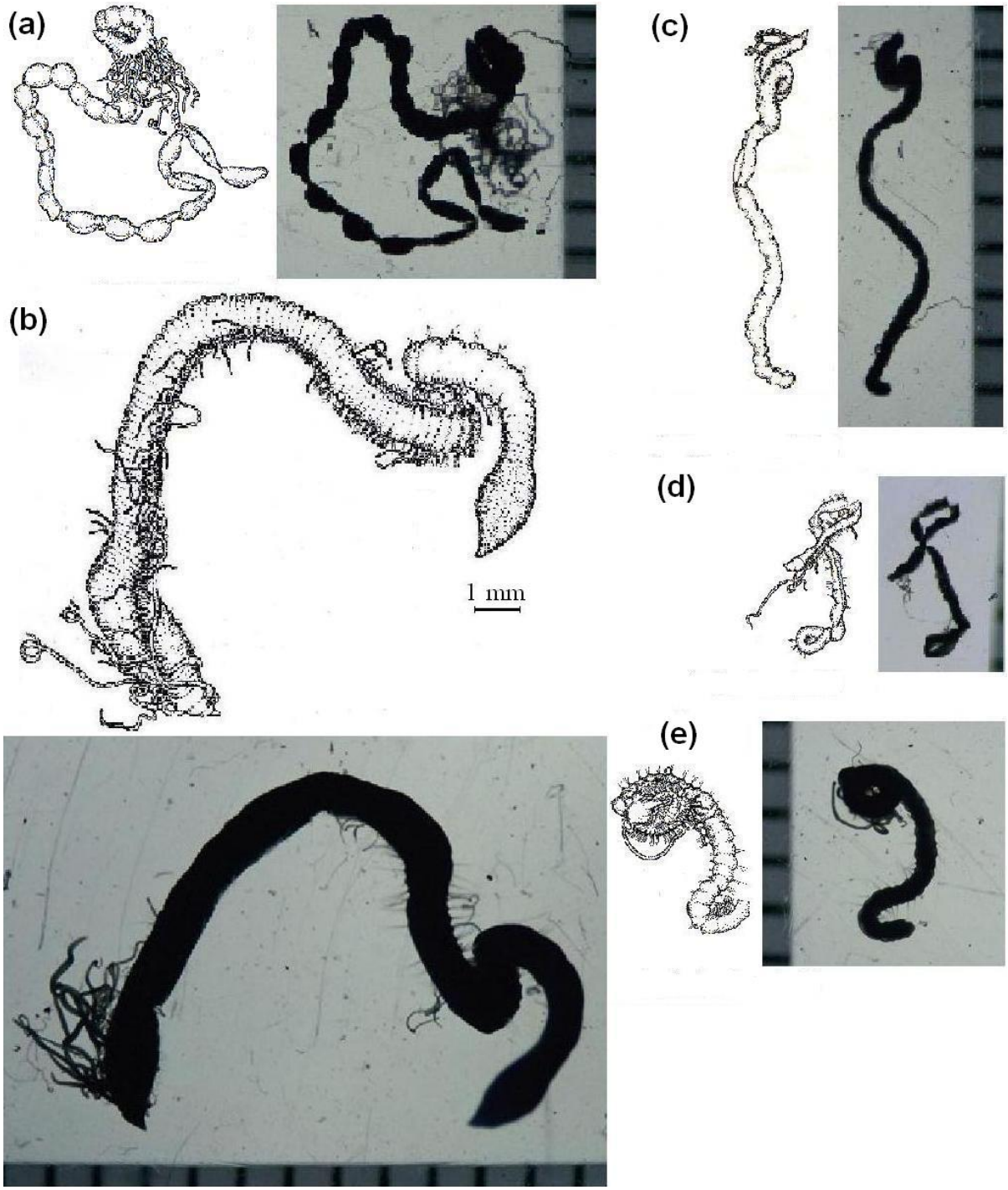


Figure 17: Illustrations of the Aphelochaeta species found, each photographed alongside a millimetre scale, and drawn to scale (more detailed illustrations are available in Appendix 7(a) A ~26mm by ~0.8mm specimen of Aphelochaeta A from station 14, grab B(b) A ~25mm by ~1.0mm specimen of Aphelochaeta B from station 14, grab B. (c) A ~12mm by ~0.3mm specimen of Aphelochaeta C from station 14, grab B. (d) A ~7.0mm by ~0.2mm specimen of Aphelochaeta D from station 29, grab B. (e) A ~12mm by ~0.3mm anterior fragment of Aphelochaeta E from station 51, grab A. From visual inspection, distinct physical characteristics are obvious.

3.1.4 *Chaetozone* Species from the Las Perlas Archipelago

The 54 specimens of *Chaetozone* were separated into 5 species as summarised in Key 4, below. Illustrations of each species are shown in Figure 18, on page 41,

Key 4: Guide to distinguish between the Species of *Chaetozone* from off the Las Perlas Archipelago in the Tropical Eastern Pacific.

1A. Body shape robust (length to width ratio <15:1) ……...2

1B. Body shape elongate (length to width ratio >15:1)……3

2A. Eyes present……...*Chaetozone A* (*c/f. corona*) (see Figure 18a)

NOTE: prostomium conical, with blunt anterior margin; eyes present; peristomium features dorsal hump but is no longer than prostomium; body stature robust (examined specimens have a length: width ratio of ~13:1); anterior cylindrical in cross-section, becoming dorsoventrally flattened towards posterior; well segmented; often curled in death; anterior chaetae feature those of capillary and spine structure; spines occur in neuropodia in all segments (3 in anterior, becoming 4 and then 5 towards posterior) and notopodia towards the posterior (~5); posterior chaetae form partial cinctures; pale in alcohol.

2B. Eyes absent……..……..…….....*Chaetozone C* (see Figure 18c)

NOTE: prostomium conical, with pointed up-curled anterior margin; eyes absent; peristomium features dorsal hump; body stature robust (examined specimens have a length: width ratio of ~9:1); dorsoventrally flattened in cross-section throughout; anterior laterally expanded; well segmented; anterior parapodia prominent, elevated over mid-dorsum creating an anterior longitudinal ridge; anterior chaetae feature elongate capillaries; spines present in very posterior parapodia, forming partial cinctures in the 6 penultimate segments; pale in alcohol.

3A. Body expanded at both anterior and posterior ends……..
……..…...……*Chaetozone E* (*c/f. bansei*) (see Figure 18e)

NOTE: prostomium conical, with pointed anterior margin; eyes absent; peristomium features dorsal hump that extends posteriorly; body stature narrow and elongate with enlarged ends (examined specimens have a length: width ratio of ~30:1); anterior features flattened ventral surface al in cross-section, becoming cylindrical towards posterior; well segmented with many narrow segments in anterior; anterior chaetae are of capillary structure becoming thickened as move towards posterior; spines occur in the posterior; extended terminal pygidium; tan in alcohol.

3B. Body expanded at anterior end only tapering towards the posterior……..4

4A. Body with ventral groove in cross-section.....
……*Chaetozone B* (*c/f. columbiana*) (see Figure 18b)

NOTE: prostomium elongate, with pointed anterior margin; eyes absent; peristomium no longer than prostomium; body stature widest in anterior, tapering towards posterior (examined specimens have a length: average width ratio of ~20:1); well segmented with many narrow segments in anterior; anterior chaetae are of capillary structure, with spines occurring in neuropodia, and notopodia towards the posterior; posterior chaetae form visible complete cinctures; pale in alcohol.

4B. Body cylindrical in cross-section.……...*Chaetozone D* (*c/f. lunala*) (see Figure 18d)

NOTE: prostomium conical, with blunt anterior margin; eyes present; peristomium features dorsal hump but is no longer than prostomium; body elongate (examined specimens have a length: width ratio of ~30:1); cylindrical in cross-section; well segmented with beadlike middle segments; anterior chaetae feature those of capillary and structure; spines occur in parapodia of posterior segments; posterior chaetae form complete cinctures; tan in alcohol.

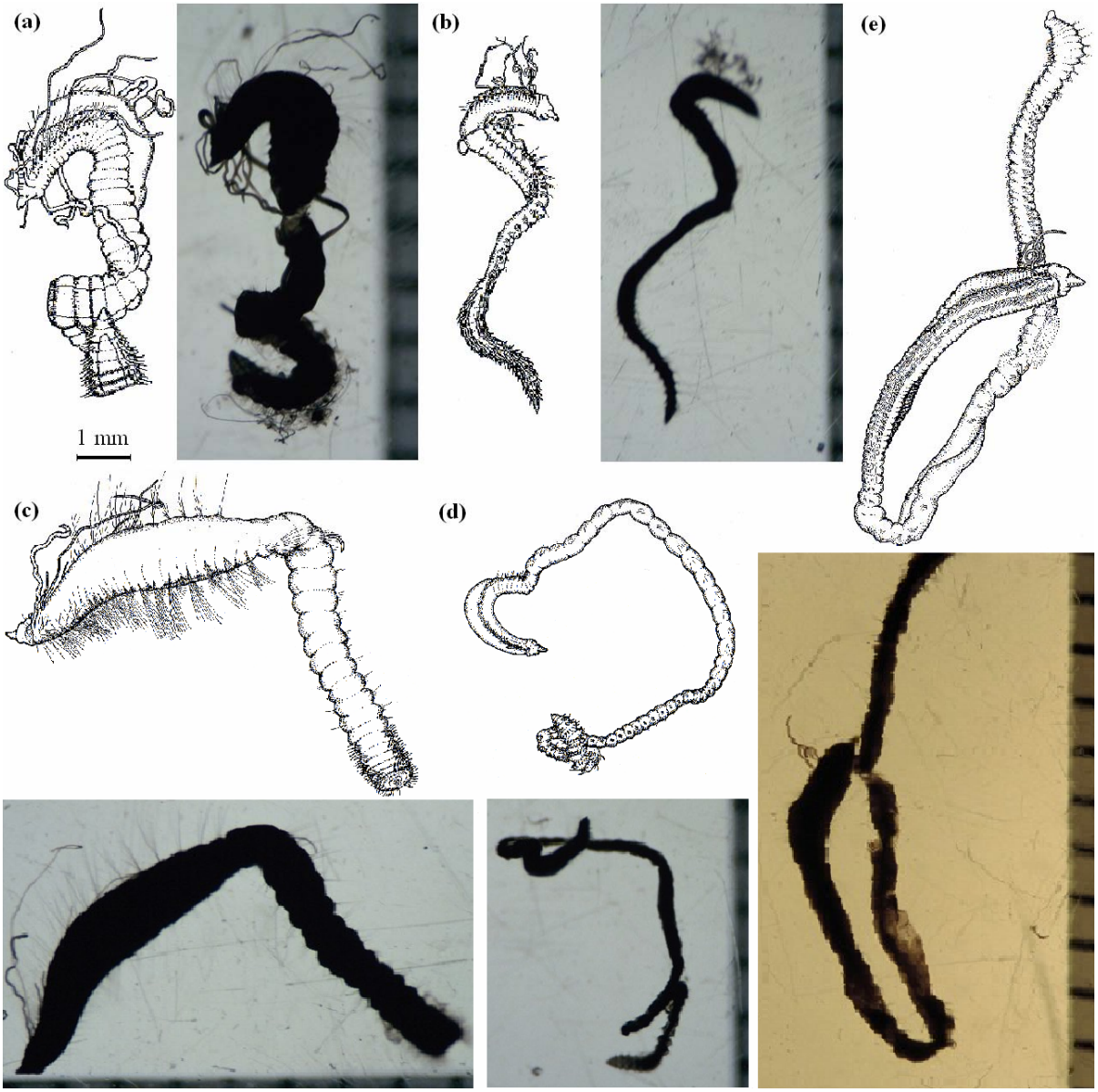


Figure 18: Illustrations of the Chaetozone species found: each photographed alongside a millimetre scale, and drawn to scale (enlarged and, subsequently, more detailed illustrations are available in Appendix 7. (a) A specimen of Chaetozone A from station 39, grab A that was ~13mm in length and ~1.5mm in width. (b) A specimen of Chaetozone B from station 41, grab A that was ~9mm long and ~0.5mm wide. (c) A specimen of Chaetozone C from station 30, grab C that was ~13mm in length and ~1.5mm in anterior and ~1mm in dorsal posterior width. (d) A specimen of Chaetozone D from station 5, grab C that was ~14mm in length and ~0.5mm in width. (e) A specimen of Chaetozone E from station 71, grab B that was ~20mm in length and ~0.7mm in width.

3.1.5 *Monticellina* Species from the Las Perlas Archipelago

The 209 specimens of *Monticellina* were separated into 8 species using properties summarised in Key 5, below. Illustrations of each species are shown in Figure 19, on page 44.

Key 5: Guide to distinguish between the Species of *Monticellina* from off the Las Perlas Archipelago in the Tropical Eastern Pacific.

1A. Body expanded at anterior and posterior ends……....2

1B. Body expanded at anterior end; tapering towards posterior …….……..3

2A. Chaetae of capillary structure dominate throughout; blade chaetae confined to very posterior …….. *Monticellina A* (see Figure 19a)

NOTE: prostomium elongate, blunt on anterior margin; eyes absent; peristomium elongate; anterior dorsal bulge; body elongate (examined specimens have a length: width ratio of ~45:1);ventral groove visible in cross-section; well segmented with middle segments more moniliform; translucent external tube often visible; anterior and posterior segments enlarged; capillary chaetae dominate; blades present in posterior; pale in alcohol, with dark dorsal stripe in anterior and middle segments.

2B. Chaetae of blade structure dominate in posterior and middle segments; capillary chaetae confined to very anterior……...*Monticellina B* (see Figure 19b)

NOTE: prostomium conical, with rounded anterior margin; eyes absent; peristomium with dorsal hump; body elongate (examined specimens have a length: width ratio of ~35:1); ventral groove in cross-section of anterior and middle segments, dorsal groove in very anterior; dorsoventrally flattened in posterior; anterior and posterior expanded; thin tube often visible; anterior often curled; well segmented; anterior parapodia prominent, creating an anterior longitudinal arc; anterior chaetae feature capillaries; blades present in posterior; pinky brown in alcohol.

3A. Peristomium more than double the length of the prostomium; extending posteriorly…....4

3B. Peristomium elongate but less than double the length of prostomium.....…5

4A. Anterior cylindrical in cross section …….*Monticellina D* (see Figure 19d)

NOTE: prostomium short, blunt on anterior margin; eyes absent; peristomium elongate; anterior dorsal bulge; body elongate (examined specimens have a length: width ratio of ~60:1) with visible ventral groove in cross-section; well segmented with middle segments wider and more beadlike; sections of external tube often visible; minimal capillary chaetae present in anterior; blades present in posterior pale in alcohol.

4B. Anterior dorsoventrally flattened in cross-section…….*Monticellina E* (see Figure 19e)

NOTE: prostomium elongate, blunt on anterior margin; eyes absent; peristomium elongate; anterior lateral bulge, and associated dorsoventral flattening; ventral groove present; specimens examined missing posterior segments; well segmented by narrow segments; capillary chaetae dominate throughout; blades present in posterior of fragments; pale in alcohol, with visible dark dorsal stripe.

5A. Body cylindrical in cross section…….. 6

5B. Body with ventral groove in cross section……. 7

6A. Prostomium pointed and conical……*Monticellina F* (*c/f. tesselata*) (see Figure 19f)

NOTE: prostomium short; eyes absent; peristomium slightly longer than wide; anterior dorsal bulge; body elongate (examined specimens have a length:width ratio of ~30:1); cylindrical in cross-section; well segmented with moniliform abdominal segments; yellow external tube often visible with numerous translucent lateral extensions through which branchial gills protrude; posterior segments enlarged; capillary chaetae dominate; blades present on posterior neuropodia; tan in alcohol.

6B. Prostomium enlarged towards anterior margin……. *Monticellina H* (see Figure 19h)

NOTE: prostomium elongate, with anterior blunt bulge; eyes absent; peristomium elongate; anterior dorsal bulge; examined specimen fragmented and incomplete; cylindrical in cross-section; well segmented in anterior; translucent external tube visible; capillary chaetae dominate with blades present in posterior; pale in alcohol.

7A. Chaetae of capillary structure dominate throughout; blade chaetae confined to very posterior……..…. *Monticellina C* (see Figure 19c)

NOTE: prostomium elongate, pointed on anterior margin; eyes may be present; peristomium no longer than peristomium; anterior dorsal bulge; body elongate (examined specimens have a length: width ratio of ~25:1); cylindrical in cross-section; well segmented with middle segments tending to moniliform; capillary chaetae dominate; blades present in posterior; pale in alcohol.

7B. Chaetae of blade structure dominate neuropodia of posterior and middle segments…… ……..*Monticellina G* (see Figure 19g)

NOTE: prostomium short, pointed and up-curled at anterior; eyes absent; peristomium slightly longer than prostomium; anterior dorsal bulge; body elongate (examined specimens have a length: width ratio of ~28:1); ventral groove visible in cross-section; well segmented; sections of external tube often visible; capillary chaetae present throughout; blades present in posterior; pinky brown in alcohol.

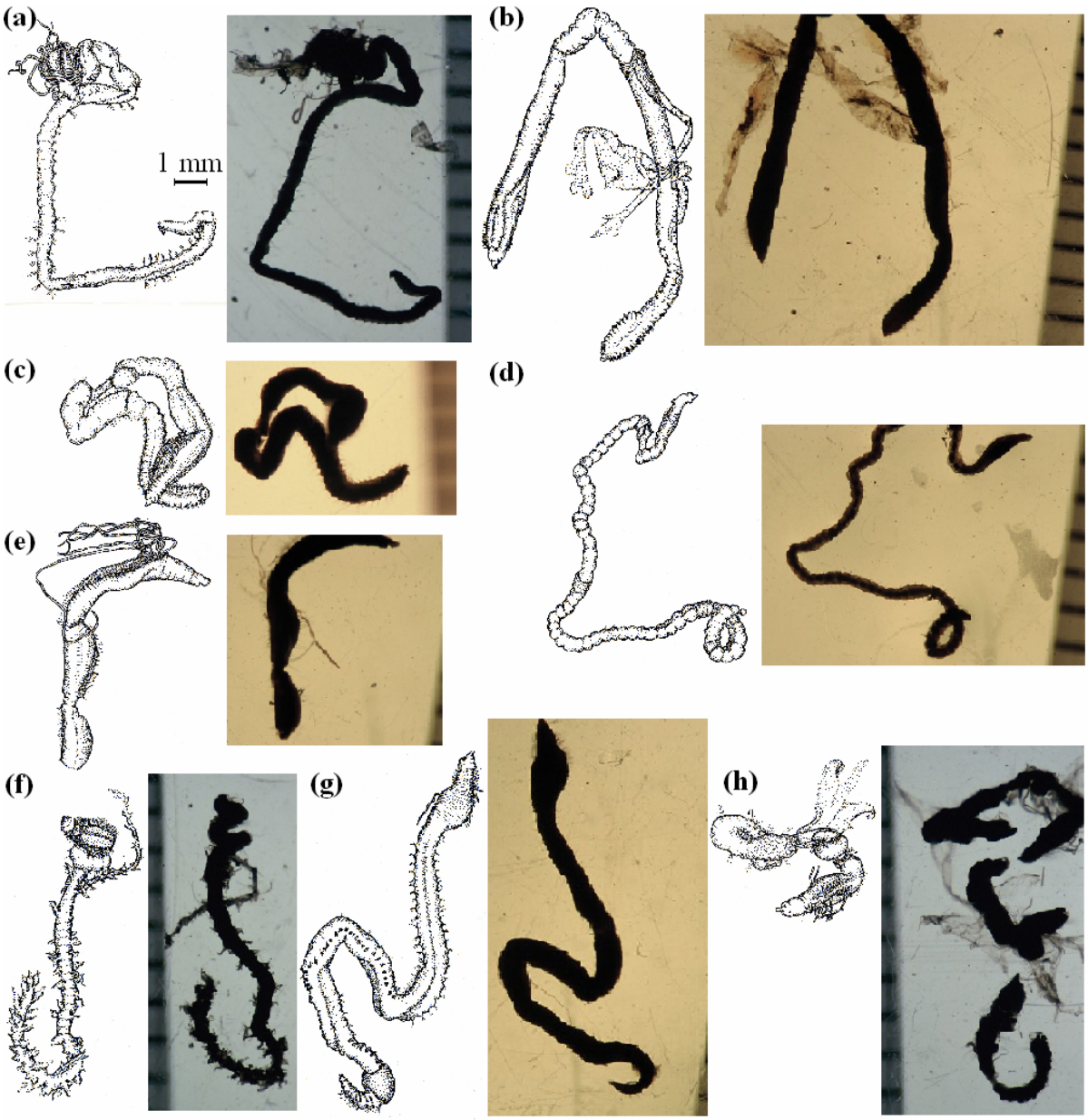


Figure 19: Illustrations of the Monticellina species found: each photographed alongside a millimetre scale, and drawn to scale (enlarged and, subsequently, more detailed illustrations are available in). (a) A specimen of Monticellina A from station 29, grab A that was ~23.0mm in length and ~0.4mm in width. (b) A specimen of Monticellina B from station 13, grab B that was ~21.0mm in length and ~0.6mm in width. (c) A fragment of Monticellina C from station 29, grab A that was ~12mm in length and ~0.7mm in width. (d) A specimen of Monticellina D from station 29, grab B that was ~20mm in length and ~0.5mm in width. (e) A fragment of Monticellina E from station 29, grab B that was ~8.0mm in length and ~1.0mm in width. (f) A specimen of Monticellina F from station 5, grab A that was ~14.0mm in length, and ~0.7mm in width. (g) A specimen of Monticellina G from station 13, grab C that was ~22mm in length and ~1.0mm in width. (h) Several fragments of a specimen of Monticellina H from station 89, grab B that total ~19.0mm in length and ~1.0mm in width.

3.1.6 Caulleriella Species from the Las Perlas Archipelago

The 33 specimens of *Caulleriella* were separated into 6 species as summarised in Key 6, shown below. Illustrations of each species are shown in Figure 20, on page 47

Key 6: Guide to distinguish between the Species of *Caulleriella* from off the Las Perlas Archipelago in the Tropical Eastern Pacific.

1A. Body shape elongate (length to width ratio >15:1); eyes absent……2

1B. Body shape robust (length to width ratio <15:1); eyes present…..……....4

2A. Prostomium short and undercurled……...*Caulleriella B* (*c/f. pacifica*) (see Figure 20b)

NOTE: prostomium short, blunt on anterior margin; eyes present, most visible from ventral side; peristomium elongate; body stature elongate (examined complete specimens have a length: width ratio of ~28:1; anterior segments rounded dorsally and flattened ventrally in cross-section, becoming dorsoventrally flattened towards posterior; well segmented; capillary chaetae dominate in anterior, and bidentate hooks in posterior; tan in alcohol.

2B. Prostomium elongate and projected from body...…….....3

3A. Peristomium longer than prostomium……*Caulleriella A* (*c/f. apicula A*) (see Figure 20a)

NOTE: prostomium elongate and wide, pointed on anterior margin; eyes present; peristomium elongate; body stature elongate (examined complete specimens have a length: width ratio of ~20:1); anterior segments rounded dorsally and flattened ventrally, becoming dorsoventrally flattened towards posterior; well segmented; capillary chaetae present in anterior, bidentate hooks present in mid and posterior segments; tan in alcohol.

3B. Prostomium same length or shorter than prostomium.....
.....*Caulleriella C* (*c/f. apicula B*) (see Figure 20c)

NOTE: prostomium elongate, pointed on anterior margin; eyes present; peristomium elongate; body stature elongate (examined complete specimens have a length: width ratio of ~30:1); anterior segments rounded dorsally and flattened ventrally, becoming dorsoventrally flattened towards posterior; well segmented; capillary chaetae present in anterior, bidentate hooks present in posterior; pale in alcohol.

4A. Body cylindrical in cross section……*Caulleriella E* (*c/f. zetlandica A*) (see Figure 20e)

NOTE: prostomium short, blunt on anterior margin; eyes absent; peristomium elongate; body stature robust (examined specimens missing posterior segments) and cylindrical;

well segmented; capillary chaetae dominate posterior segments, bidentate hooks present in posterior; pale in alcohol.

4B. Body dorsoventrally flattened in cross section...…….....5

5A. Dorsal surface well segmented……...…*Caulleriella D* (c*/f. cristata*) (see Figure 20d)

NOTE: prostomium short, blunt on anterior margin; eyes absent; peristomium elongate; body stature robust (examined specimens missing posterior segments); anterior segments rounded dorsally but flattened ventrally, becoming dorsoventrally flattened towards the posterior; well segmented; anterior parapodia prominent, elevated over mid-dorsum creating an anterior longitudinal ridge; capillary chaetae dominate throughout, bidentate hooks present in posterior; dorsal surface brown, ventral surface pale in alcohol.

5B. Dorsal surface largely smooth...……...*Caulleriella F* (*c/f. zetlandica B*) (see Figure 20f)

NOTE: prostomium short, blunt on anterior margin; eyes absent; peristomium elongate; body stature robust (examined specimens missing posterior segments); anterior segments rounded dorsally but flattened ventrally, becoming dorsoventrally flattened towards the posterior; well segmented on ventral surface; parapodia prominent, elevated over mid-dorsum creating a longitudinal ridge; elongate capillary chaetae dominate throughout, bidentate hooks present in posterior; purple in alcohol with dark dorsal line.

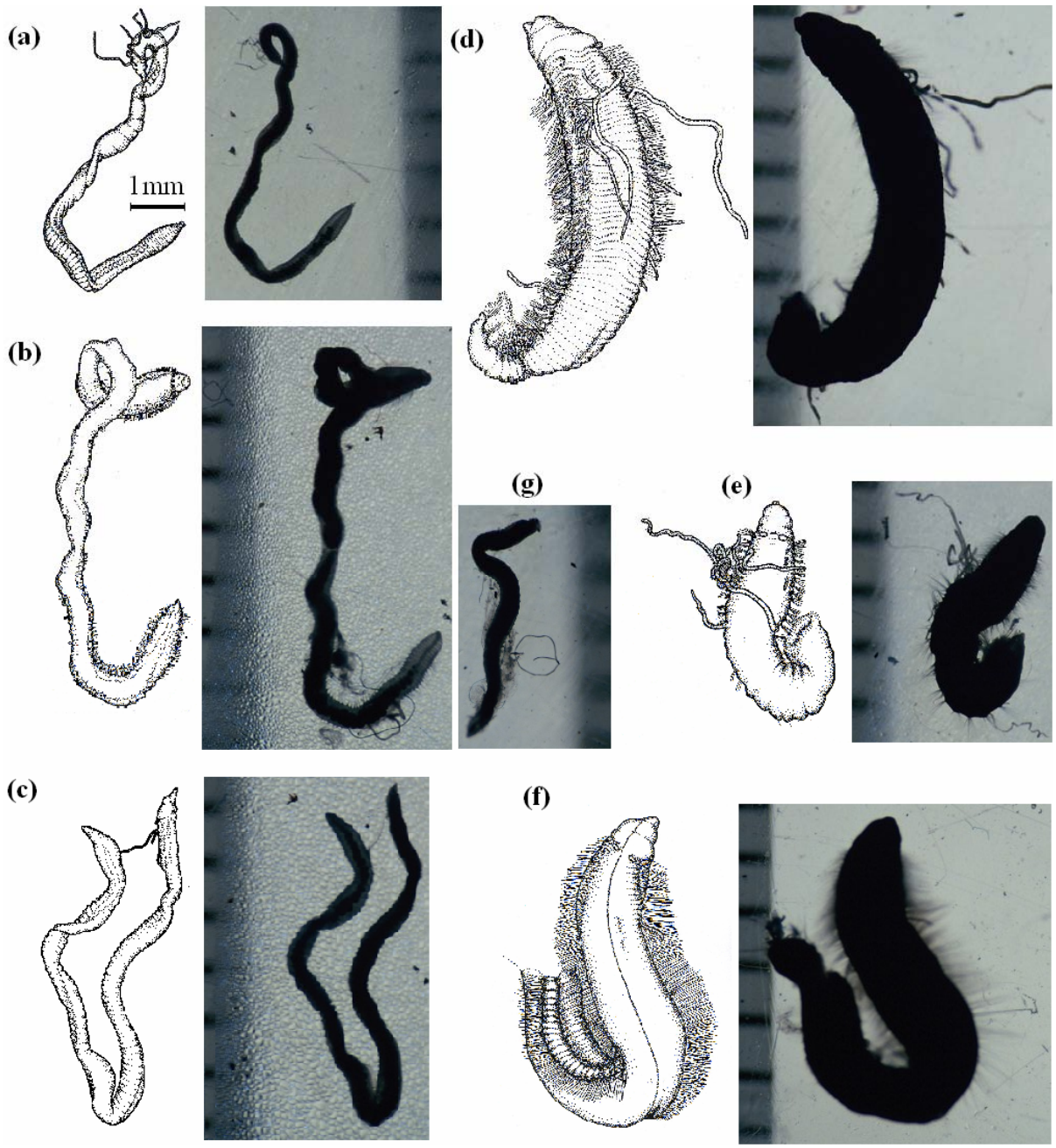


Figure 20: Illustrations of the *Caulleriella* species found, photographed alongside a millimetre scale, and drawn to scale (more detailed illustrations are available in). *Caulleriella A-C* fit the stereotypical physique of *Caulleriella* suggested by Blake, whereas *Caulleriella D-F* show a conformation similar to *Caulleriella zetlandica*. Unfortunately, all specimens in the latter group are incomplete, lacking posterior segments. (a) A ~ 9 mm by ~0.5mm specimen of *Caulleriella A* from station 59, grab B. (b) A ~14mm by ~0.5mm specimen of *Caulleriella B* from station 47, grab A. (c) A ~15mm by ~0.5mm specimen of *Caulleriella C* from station 93a, Grab A. (d) A ~9mm by ~2.0mm anterior fragment of *Caulleriella D* from station 9 (Grab A). (e) A ~5.5mm by ~1.2mm anterior fragment of *Caulleriella E* from station 70, grab A. (f) A ~10mm by ~1 anterior fragment of Caulleriella *F* from station 5, grab C. (g) A photographic image if *Caulleriella Indet B*, an unidentified posterior segment, has been included to illustrate it's similarities to *Caulleriella B*.

3.1.7 *Tharyx* Species from the Las Perlas Archipelago

The 5 specimens of *Tharyx* were separated into 2 species as summarised in Key 7, below. Illustrations of each species are shown in Figure 21, below.

Key 7: Guide to distinguish between the Species of *Tharyx* from off the Las Perlas Archipelago in the Tropical Eastern Pacific.

1A. Anterior segments dorsoventrally flattened.....*Tharyx A* (see Figure 21a)

NOTE: prostomium elongate and wide, pointed on anterior margin; peristomium elongate, roughly double the prostomium in length; body elongate (examined specimens have a length: width ratio of ~21:1); well segmented; anterior segments dorsoventrally flattened becoming rounded towards posterior; parapodia prominent creating longitudinal ridges; uncini hooks in mid and posterior, pale colouration in alcohol.

1B. Anterior segments rounded.....*Tharyx B* (see Figure 21b)

NOTE: prostomium elongate and narrow, pointed on anterior margin; peristomium elongate; body elongate (examined specimens have a length: width ratio of ~17:1); well segmented in posterior and anterior; ventral groove present; anterior segments rounded, ventral and then dorsal surface becoming flattened as move towards posterior; capillary chaetae present in anterior, uncini hooks present in mid and posterior segments; pale colouration in alcohol.

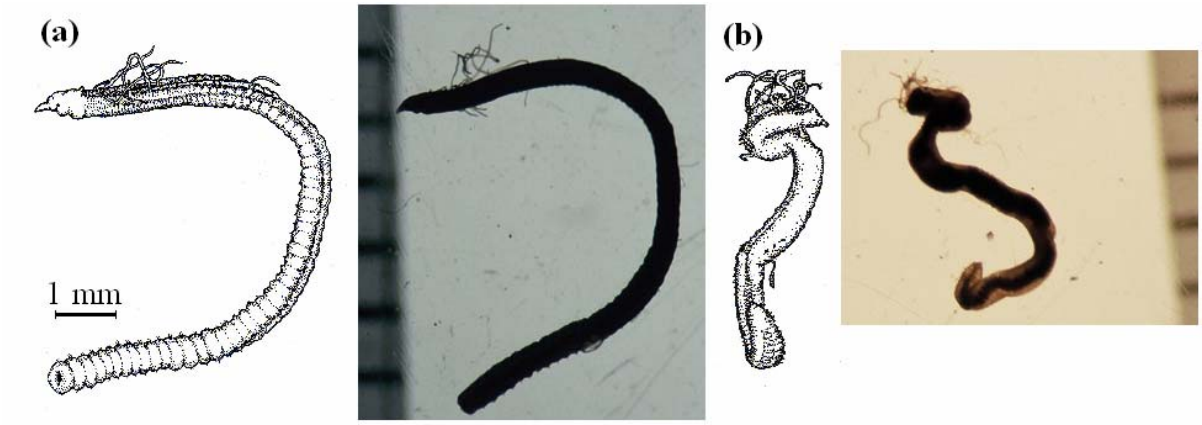


Figure 21: Illustrations of the Tharyx species found: each photographed alongside a millimetre scale, and drawn to scale (enlarged and, subsequently, more detailed illustrations are available in Appendix 7). (a) A fragment of Tharyx A from station 93a, grab A that was ~10.5mm in length and ~0.5mm in width. (b) A fragment of Tharyx B from station 5, grab C that was ~8.5mm in length and ~0.5mm in width

3.2 Cirratulid Distribution

The distribution of some cirratulids in specific locations has been studied in the past (*Dodecaceria* species by Gibson, 1996, Gibson & Clark, 1976, *Tharyx* by Gibbs, 1971 and 1983, *Chaetozone* by Hily, 1987, Southern, 1914, and Worsfold, 1996), however, there has been no prior study of the distribution of cirratulids in the Las Perlas Archipelago. Currently little is known of the habitat preferences of cirratulids, or the benthic community of the area. This dissertation will attempt to rectify this whilst contributing directly to the Darwin Initiative Project through the provision of baseline data on benthos composition of the undisturbed state essential for monitoring change.

3.2.1 Distribution of Cirratulid Genera of the Las Perlas Archipelago

361 cirratulid specimens were found at 37 stations (illustrated in Figure 22a, on page 50: raw data in Appendix 2, on page 83): 352 from 36 stations, by 52 quantitative van Veen grab samples, whilst 9 were gathered qualitatively by trawl, from 3 stations and will not be considered further (see Appendix 4, on page 87).

Stations from which cirratulids were sampled by grab are entirely absent in the north of the region, and appear to be clustered towards the southwest and east. In terms of taxa, 6 genera, covering 30 species were collected by van Veen grab. These taxa show varying patterns of distribution. *Cirriformia* specimens were only gathered from one station in the south of the survey grid, and *Tharyx* specimens from just three stations in the south and west (Figure 22b). *Aphelochaeta* specimens were entirely absent from the north, and east of the region occurring almost entirely in the south and west. The only exception to this is the presence of *Aphelochaeta* specimens at station 64 (Figure 22c). *Caulleriella* specimens were again present mainly in the south and west: the exception in this genus is the presence of specimens at station 59 in the east (Figure 22d). *Chaetozone* and *Monticellina* specimens show wider distribution: although there is a distinct clustering of stations in the south and west, specimens are also found at station 64, and several stations in the east (Figure 22e and f).

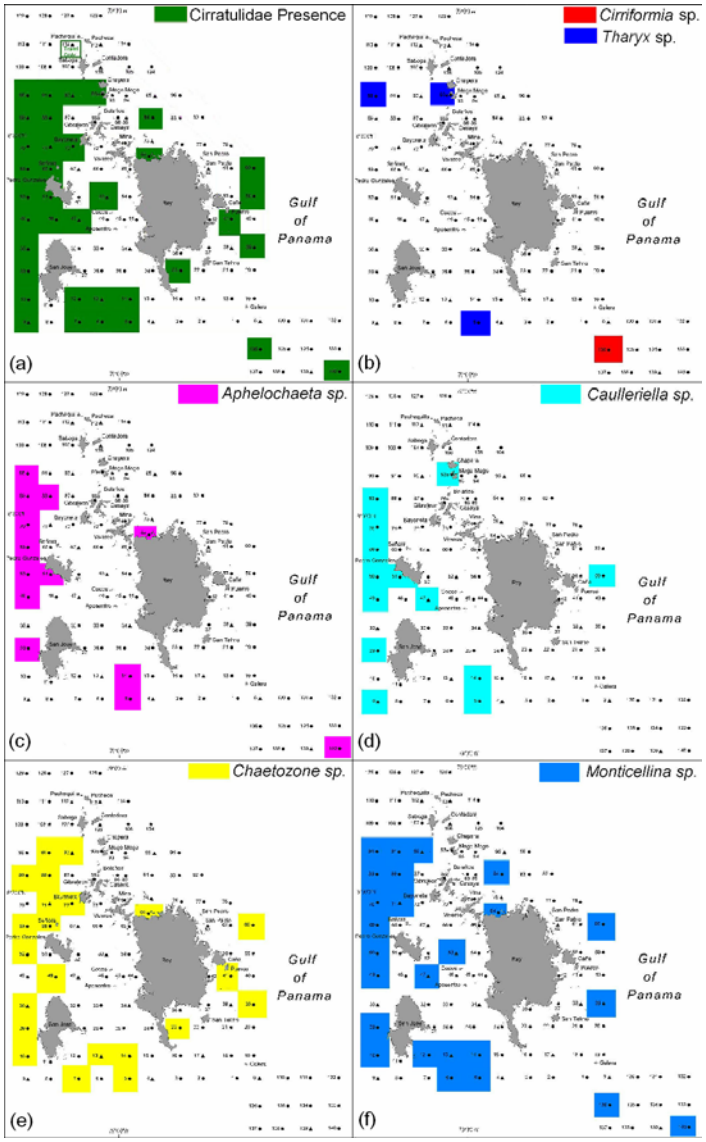


Figure 22: Illustration showing the distribution of cirratulids within the Las Perlas Archipelago. (a) The stations at which cirratulids were found by grab are highlighted in dark green (5, 6, 7, 9, 10, 12, 13, 14, 23, 29, 30, 39, 30, 39, 41, 47, 48, 49, 50, 51, 53, 59, 60, 64, 68, 69, 70, 71, 72, 83, 88, 89, 90, 91, 92, 93a, 136, 140) depicted on a small scale copy of Figure 9, on page 28 . The station in which cirratulids were found by trawl only is also outlined in green (136). The 36 stations with Cirratulids present in grabs represent almost 33% of the 114 stations sampled. However, these do not appear to be positioned at random throughout the region: rather they show a clear cluster of station in the west, east, and south, with some isolated stations presence in between. (b) The 3 stations at which *Tharyx* specimens were found are highlighted in blue, and the 1 stations at which *Cirriformia* were found by grab is highlighted in red. (c) The 13 stations at which *Aphelochaeta* specimens were found are shown in pink and are mainly in the west of the survey grid. (d) The 13 stations at which *Caulleriella* specimens were found are shown in turquoise and are mainly in the west of the survey grid. (e) The 22. stations at which *Chaetozone* specimens were found are shown in yellow, showing a wider distribution, although the majority are in the west of the survey grid. The 25 stations at which *Monticellina* specimens were found are shown in pale blue, showing a wider distribution, and are mainly in the west and south of the survey grid.

3.2.2 Distribution of Cirriformia of the Las Perlas Archipelago

Only one specimen of *Cirriformia* was sampled by grab. This individual, named *Cirriformia A.* was located at station 136 in the south of the region (see Figure 23, on page 51). However, due to the limited number of specimens of this genus (see Appendix 4, on page 87), no meaningful conclusions can be made with regards to its distribution pattern other than that this genus is scarce within the region of interest

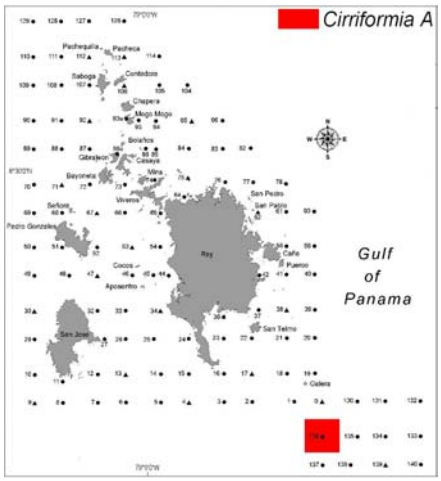


Figure 23: Location of the station at which *Cirriformia A* was gathered (station 136) depicted on a small scale copy of Figure 9, on page 28

3.2.3 Distribution of Aphelochaeta of the Las Perlas Archipelago

57 specimens of *Aphelochaeta* were gathered by grab from 13 stations, illustrated in Figure 24, on page 52. *Aphelochaeta* specimens, whilst more abundant than *Cirriformia*, are still not widespread: they are present in low numbers, (see Appendix 4, on page 87), with limited distribution. Where one species of *Aphelochaeta* occurs, others also tend to occur.

From the data gathered, *Aphelochaeta* specimens appear entirely absent from the northern stations, present mainly along the south and west boundaries of the archipelago. Although station presence is minimal for all species, each shows a similar region of distribution mirroring that suggested in section 3.2.1 for the entire cirratulidae family.

3.2.4 Distribution of Chaetozone of the Las Perlas Archipelago

48 specimens of *Chaetozone* were gathered by grab from 22 stations, illustrated in Figure 25, on page 53). *Chaetozone* specimens are relatively abundant, and widespread. Unlike *Aphelochaeta, Chaetozone* species tend to occur independently of others, with stations tending to feature fewer species but more individuals (see Appendix 4, on page 87).

Chaetozone are entirely absent from the northern stations of the Archipelago. From the data gathered it seems that *Chaetozone C, D* and *E* are again restricted to the

southwest sectors of the archipelago, whilst *Chaetozone A*, and *Chaetozone B* are more widespread, occurring in locations on the eastern side of the archipelago, suggesting adaptation to an area less favoured by this genus, and by the family as a whole. *Chaetozone A* is more numerically abundant than its counterparts suggesting that it is perhaps more tolerant to adverse conditions.

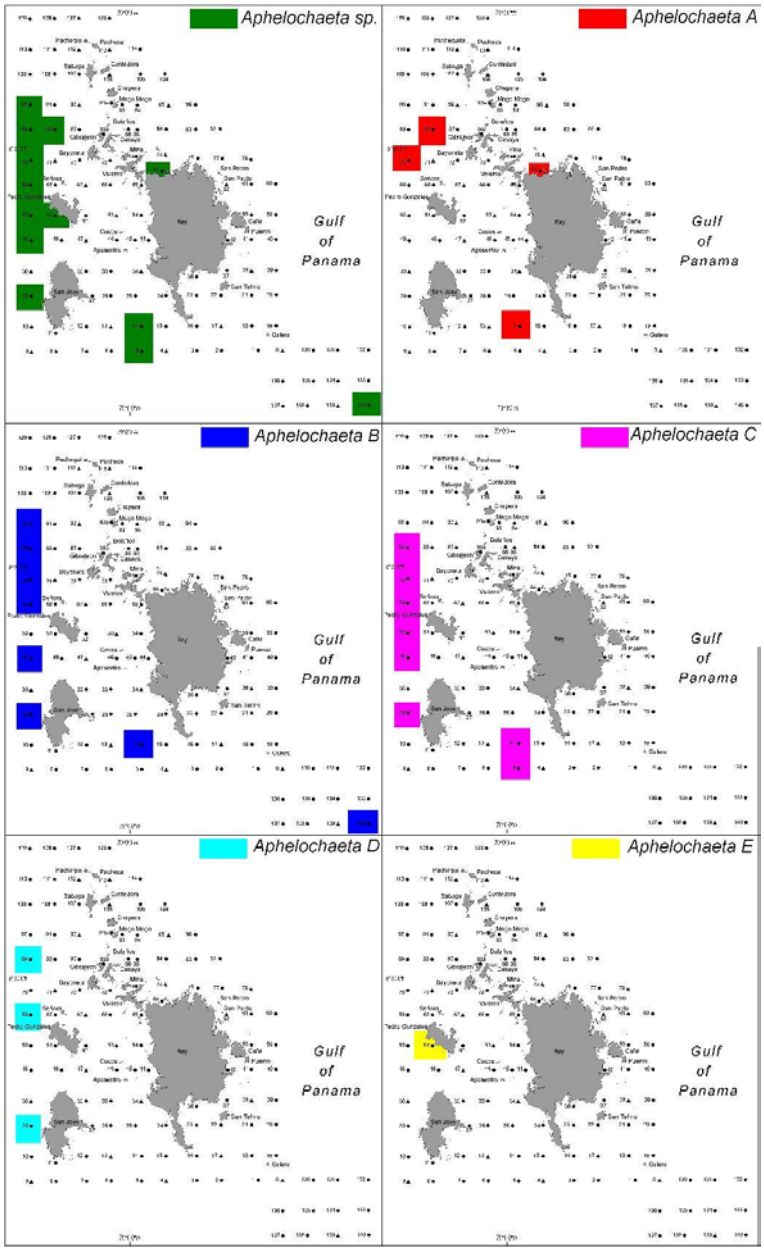


Figure 24: Locations of stations from which *Aphelochaeta* specimens were gathered by grab depicted on small scale copies of Figure 9, on page 28. Specimens of this genus were found at just 13 stations (5, 14, 29, 49, 50, 51, 64, 69, 70, 88, 89, 90 and 140). Specimens of *Aphelochaeta A* were present at just 4 stations (14, 64, 70, and 88), *Aphelochaeta B* and *Aphelochaeta C* at 8 (14, 29, 49, 69, 70, 89, 90, and 140 and 5, 14, 29, 49, 50, 69, 70, and 89 respectively), *Aphelochaeta D* at 3 (29, 69, and 89), and *Aphelochaeta E* at just 1 (51).

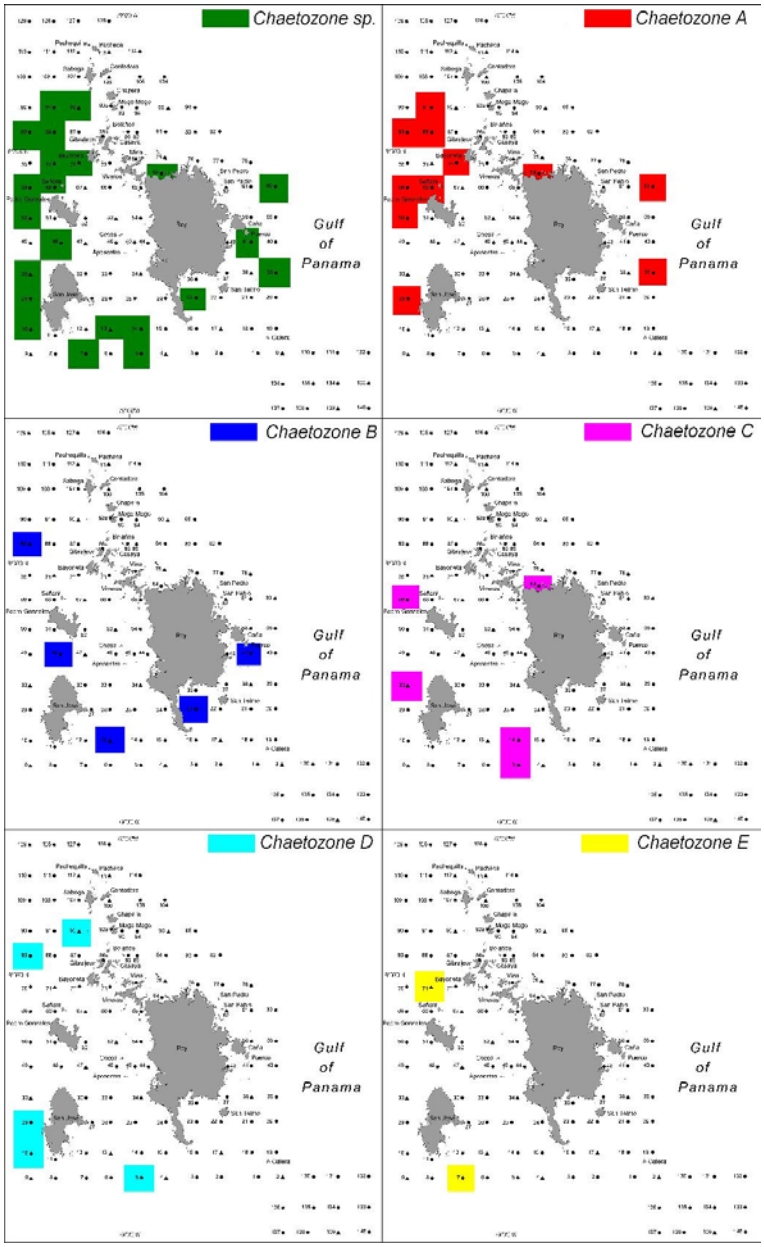


Figure 25: Locations of stations from which *Chaetozone* specimens were gathered by grab depicted on small scale copies of Figure 9, on page 28. Specimens of this genus were found at 22 stations (5, 7, 10, 13, 14, 23, 29, 30, 39, 41, 48, 50, 60, 64, 68, 69, 71, 72, 88, 89, 91, and 92). Specimens of *Chaetozone A* were present at 11 stations (29, 39, 50, 60, 64, 68, 69, 72, 88, 89, and 91), *Chaetozone B, C* and *D* at 5 (13, 23, 41, 48, and 89, 5, 14, 30, 64, and 68, and 5, 10, 29, 89, and 92 respectively), and *Chaetozone E* at just 2 (7 and 71).

3.2.5 Distribution of Monticellina of the Las Perlas Archipelago

208 specimens of *Monticellina* were gathered by grab from 25 stations (illustrated in Figure 26, on page 55), making *Monticellina* the most numerically abundant and widespread genus within the Archipelago. *Monticellina A* is also the most abundant species, with 93 specimens collected from 18 sites.

As with previous genus, *Monticellina* specimens are absent from stations in the north, with the majority of specimens of all species confined to the south and west of the region. However, some specimens were found at stations in the east of the Archipelago. This tendency is specific to 2 species: *Monticellina A* and *D*.

Monticellina species are often found in association with each other and other genus, only occurring independently at 7 stations (10, 12, 60, 71, 84, 136 and 140). At 4 (10, 60, 84, and 136)of these stations the *Monticellina* species featured is *Monticellina A*, a species seen to be most abundant.

3.2.6 Distribution of Caulleriella of the Las Perlas Archipelago

33 specimens of *Caulleriella* were gathered by grab from 13 stations (illustrated in Figure 27, on page 56). 8 distinct morphologies were distinguished suggesting 8 species, subsequently, distinct species of *Caulleriella* are not numerically abundant (see Appendix 4, on page 87) lending less meaning to any conclusions drawn with regards to their individual distributions.

As a genus, *Caulleriella* are absent from the northern stations and confined mainly to the southwest. A single specimen of *Caulleriella A,* the most numerically abundant species, was found at station 59 in the east of the region. As with *Chaetozone*, *Caulleriella* species occur independently of one another, with most stations of interest featuring one species. There are 2 stations (29 and 50) for which this generalisation is not true. These stations are not just most species abundant, but also most abundant in terms of *Caulleriella* specimens containing 10 and 11 of the 33 specimens found respectively.

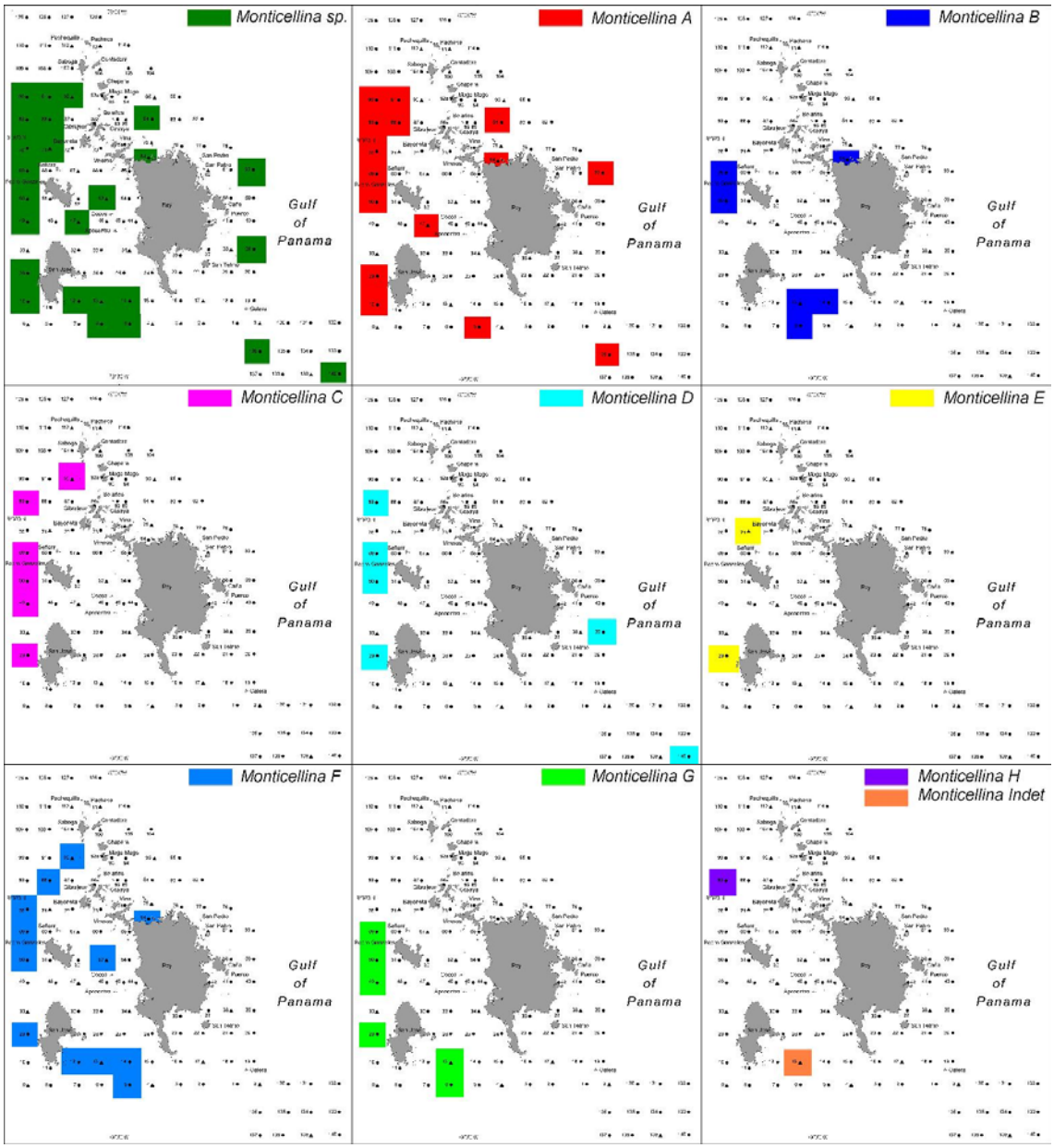


Figure 26: Locations of stations from which *Monticellina* specimens were gathered by grab depicted on small scale copies of Figure 9, on page 28. Specimens of this genus were found at 25 stations (5, 6, 10, 12, 13, 14, 29, 39, 47, 49, 50, 53, 60, 64, 69, 70, 71, 84, 88, 89, 90, 91, 92, 136 and 140). *Monticellina A* showed the greatest distribution: they were collected from 14 sites (5, 10, 29, 50, 60, 64, 69, 84, 88, 89, 90, 91, 112, and 135) as highlighted in red. Specimens of *Monticellina F* (*c/f tesselata*) were collected from a total of 12 sites (5, 10, 12, 14, 29, 50, 53, 64, 69, 70, 88, and 92) as highlighted in dark green, however, from site 112 a solitary specimen was collected by trawl only and hence cannot be used for further quantitative analysis. Specimens of *Monticellina B, C*, *D* and *G* were collected from 6 sites (6, 13, 14, 50, 64, and 70 as shown in blue, 29, 49, 50, 69, 89, and 92 as shown in pink, 29, 39, 50, 69, 89, and 140 as shown in turquoise and 6, 13, 29, 49, 50, and 69 as shown in pale green respectively). Specimens of *Monticellina E* were collected from just 2 sites (29 and 71) as highlighted in yellow, specimens of *Monticellina H* featured at from just 1 site (89) as highlighted in purple, as did an unidentified specimen (station 13) highlighted in orange

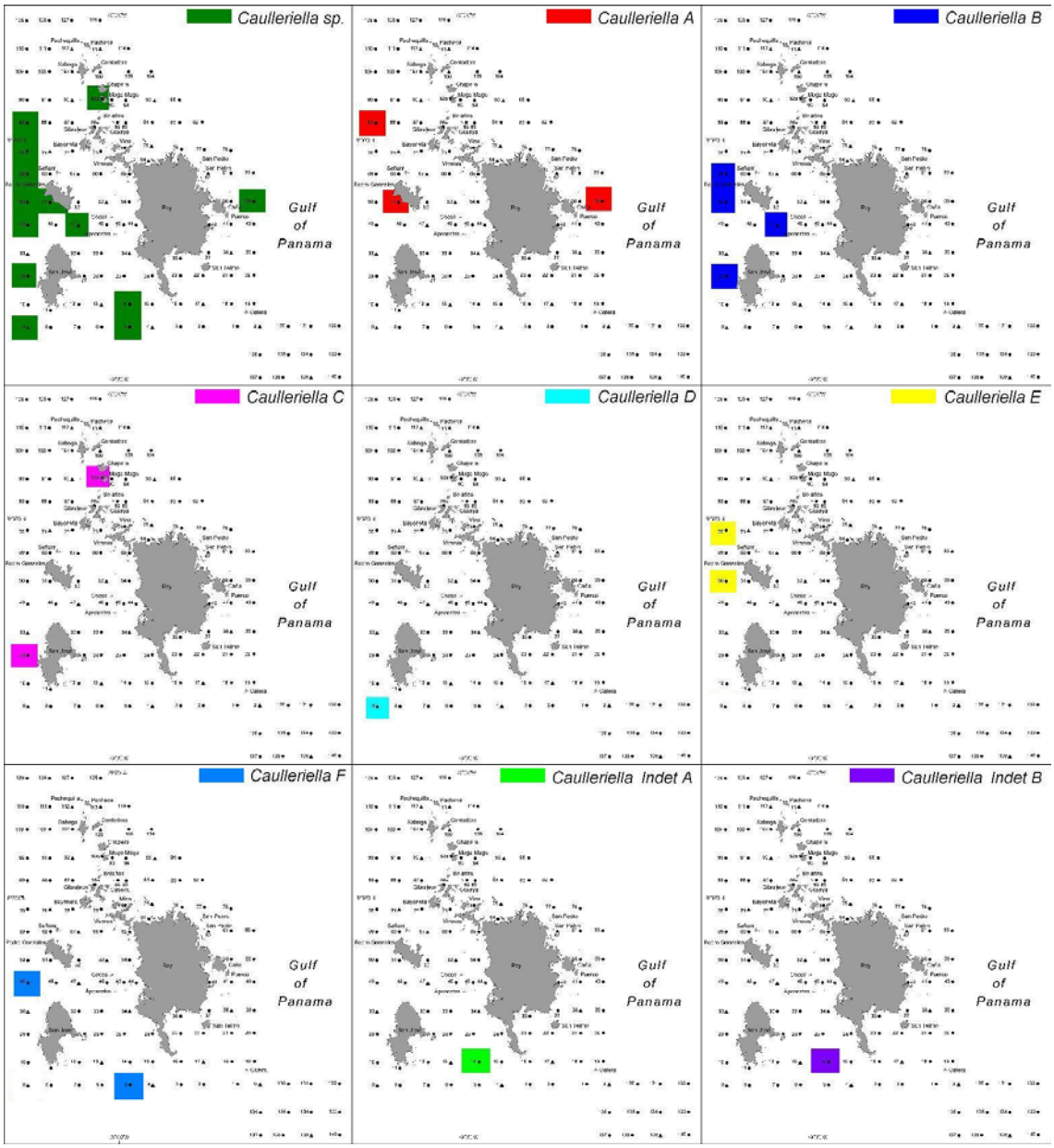


Figure 27: Locations of stations from which *Caulleriella* specimens were gathered by grab, depicted on small scale copies of Figure 9, on page 28. Specimens of this genus were found at 13 stations (5, 9, 14, 29, 47, 49, 50, 51, 59, 69, 70, 89, and 93a). All species were present in low numerical abundance, with *Caulleriella* A showed the greatest distribution, being collected from 3 isolated stations (51, 59, and 89) as highlighted in red. *Caulleriella B* was most numerically abundant being collected from 4 clustered stations (29, 47, 50, and 69) as highlighted in blue. *Caulleriella C* was collected from 2 stations (29, and 93a) as highlighted in pink. *Caulleriella D* was collected from just one stations (9), highlighted in turquoise. *Caulleriella E* was collected from 2 stations (50 and 70), as highlighted in yellow. *Caulleriella F* was collected from 2 sites (5 and 49) as highlighted in pale blue. *Caulleriella Indet A* and *Indet B* were both collected from just site (both station 14), as highlighted in bright green and purple respectively

3.2.7 Distribution of Tharyx of the Las Perlas Archipelago

5 specimens of *Tharyx* were gathered by grab from just 3 stations, illustrated in Figure 28, below) making it one of the least abundant genera gathered within the Archipelago, second only to *Cirriformia*. Consequently, few meaningful conclusions can be drawn with regards to distribution.

As with all other genera, *Tharyx* specimens are absent from the northern stations. They are also absent from all stations in the east of the region. Of additional note, however, is the stations at which each species was located are distinct: *Tharyx A* was located in 2 sites in the west of the region, whilst *Tharyx B* was located from a site in the south

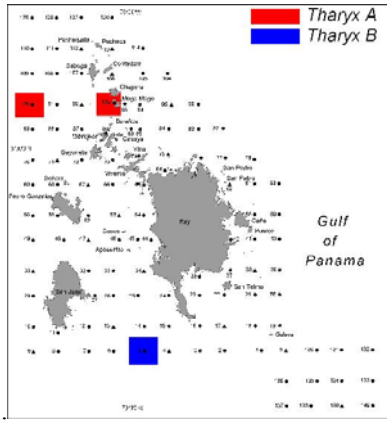


Figure 28: Position of Tharyx Species in relation to each other depicted on a small scale copy of Figure 9, on page 28. Tharyx A was collected from site 90 and 93a, as shown in red, and Tharyx B, from site 5, as shown in blue.

4. Discussion

4.1 Cirratulids as an Indicator of Community Type

From section 3.2, it can be seen that stations featuring a Cirratulid presence do cluster geographically: no cirratulids were gathered in the northern 10km of the survey grid, and relatively few were gathered in the east, southeast, south or centre. This pattern of distribution correlates, to a certain extent, with the zonation suggested by the Darwin researchers (see Figure 29,below): the northeast sector of the survey grid was deemed as a region with few taxa and low abundance, a region dominated by molluscs, with sediment high in silt and clay The results of this dissertation indicate a lack of cirratulids within this sector: cirratulid absence may be an indicator of community type 1.

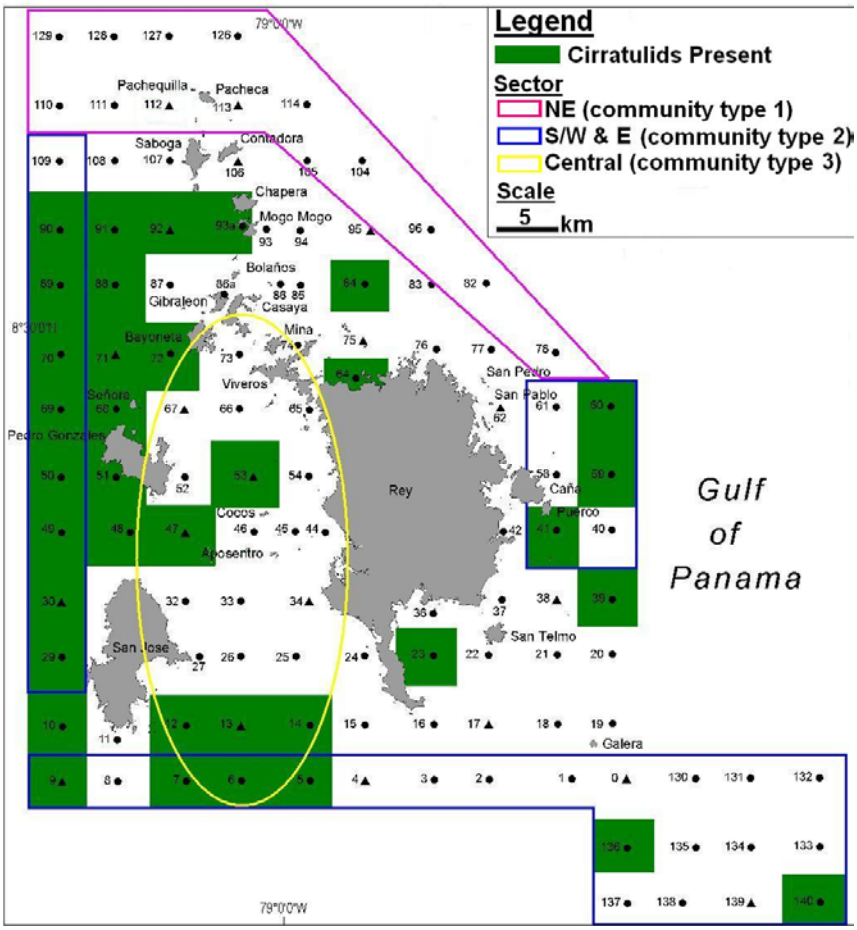


Figure 29: The zonation of community type into three distinct zones as suggested by the Darwin researchers correlates visually with the pattern of cirratulid presence generated in this dissertation. The 36 stations with cirratulid presence are highlighted in green. The suggested northeast sector is outlined in pink featuring no stations with cirratulid presence. The south, west and east sector is outlined in blue showing 17 stations with cirratulid presence, and 11 adjacent stations outwith defined sectors, in regions that represent a transition between sectors. The Central sector is outlined in yellow, and features just 6 stations with a cirratulid presence, 1 of which is station 6 and hence also falls within the south, west and east sector.

- The central sector of the Archipelago was described by Darwin researchers as a region of shallow depth, with mixed sedimentary particle size, that has a community type abundant in both crustacean, and other polychaete families. Cirratulids were located at 6 sites within this sector, 3 of which show several cirratulids (see Figure 30, below):

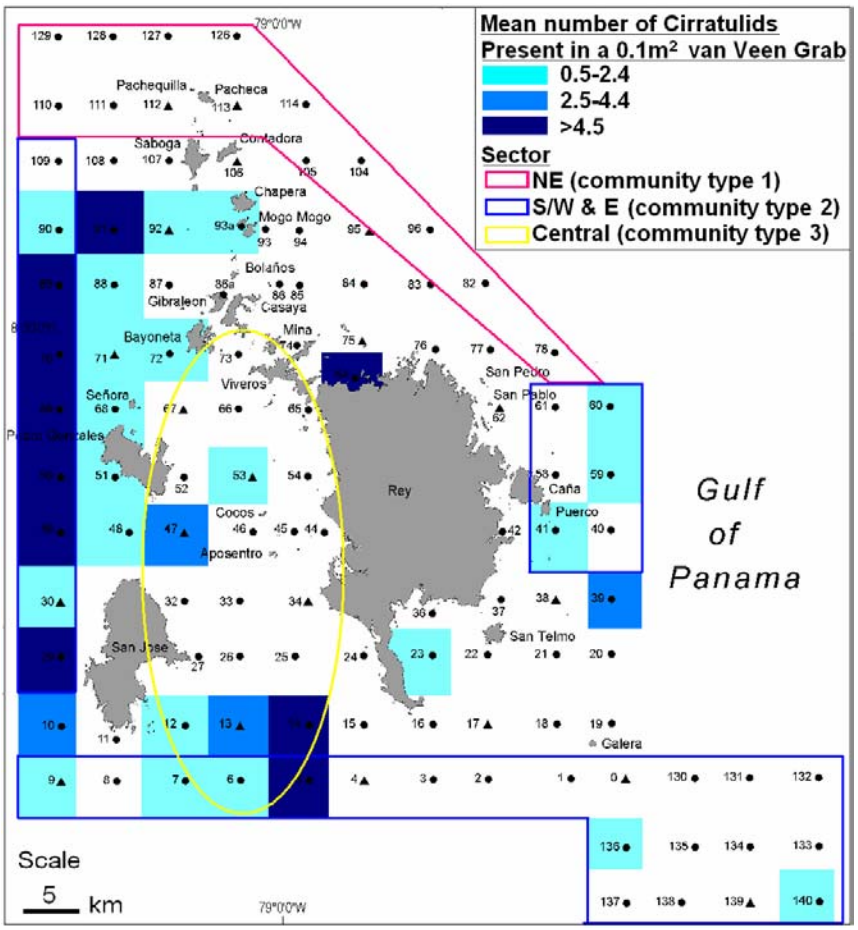


Figure 30: Illustration of the variation in cirratulid abundance across the Archipelago. Those stations with no cirratulid presence remain white, those with minimal cirratulid presence area highlighted in turquoise, those at which several cirratulids were found are highlighted in pale blue, and those stations abundant in cirratulids are highlighted in dark blue. Overlaying this pattern are the sectors specified by the Darwin researchers: northeast sector in pink, south/west and east sector in blue and central sector in yellow

- Station 14 contains an average of more than 4.5 per 0.1m^2 van Veen grab sample (18.5 per 0.1 m^2), and stations 13 and 47 feature an average of between 2.5 and 4.4 in the same sized sample(both feature 3 per 0.1 m^2).

Of note is that only *Monticellina* specimens occur in abundance within the central sector. If *Monticellina* specimens are not considered, then cirratulid presence was only noted for 3 stations within this zone: station 14 remains with an average of more

than 4.5 per 0.1m^2 van Veen grab sample (12.5 per 0.1m^2), with stations 13 and 47 featuring an average of just 0.5 per 0.1m^2 van Veen grab sample

The south, west and east sector has been described by Darwin researchers as a zone of greater depth and minimal silt and clay. This community type is dominated by few taxa, with a high abundance of polychaete worms. The results of this dissertation correlate with this, as the majority of stations with a cirratulid presence fall within this sector, or the transitional region surrounding it.

From Figure 30, on page 59, it can be seen that the majority of stations with high cirratulid abundance fall within, or adjacent to the suggested western strip of this sector (stations 29, 49, 50, 69, 70, 89 and 91). 2 abundant stations occur in and adjacent to the southern strip (5 and 14), whilst 1 station, station 64, is outwith any specified sector: station 64 was sampled off the town of San Miguel, on the north coast of the island of Rey. One explanation for this anomaly is that cirratulids have been reported to dominate in regions of high pollution; however, this should be investigated further (Hily, 1987; Pearson & Rosenburg, 1978).

Discounting station 64, visual analysis indicates that the family cirratulidae follow the zonation of community type suggested by the Darwin researchers well, absent form community type 1, present at high levels in community type 2, and at lower levels in community type 3. However, overlaying this sectorisation appears to be a strong preference for western stations. This preference may be influenced by abiotic factors.

4.2 Physicochemistry Potentially Influencing Cirratulid Distribution

Darwin researchers analysed physicochemical properties of the sediment as shown in section 2.1, and provided this information for use within this dissertation (raw data is included in Appendix 3, on page 85). The values given have all been calculated from one individual grab sample taken from the same vessel on the same day as the faunal samples. However, given that there were no replicate samples taken for this analysis, there is no data to indicate that the single sample is fully representative of the sedimentary characteristics of the stations.. This reduces the value of measurements such as organic C and Carbonate percentage, as these could be elevated by the presence of a single shell and subsequently, these are not considered. Whilst it is also entirely possible that particle size may vary within the station area, this variation is suspected to be less significant.

The stations most abundant in cirratulidae specimens, species and genus are 14, 29, 50, 69 and 89 (see Appendix 5, on page 88). Subsequently, aspects of their sedimentary composition were examined (summarised in Table 3, below):

Stations with greatest Cirratulid Abundance	Depth (m)	Sediment type	Granu-le %	VC Sand %	C Sand %	M Sand %	F Sand %	VF Sand %	Silt-Clay %
14	30	mud + shells	4.7	16.0	37.6	34.0	6.8	0.0	0.8
29	62	mud + sand	2.1	0.8	1.5	6.4	66.0	19.2	4.0
50	80	mud + sand + shells	0.7	0.4	0.8	1.1	9.4	65.8	21.8
69	66	mud + sand + shells	34.0	11.1	14.5	12.2	6.3	4.6	17.2
89	82	mud	2.2	0.3	0.6	2.6	44.4	16.3	33.6
MIN	30	mud	0.7	0.3	0.6	1.1	6.3	0.0	0.8
MAX	82	mud + sand + shell	34.0	16.0	37.6	34.0	66.0	65.8	33.6

Table 3: Summary of the physicochemical properties at the most numerically abundant stations. Depth range varies from 30 m to 82m, with a preference for deeper stations. Sediments all contain mud with a mixture of sand, and/or shell. Sedimentary particle size divisions follow the Wentworth Grade Classification (see): sediment composition varies from 0.7 to 34.0% 'Granules', 0.3 to 16.0% 'Very Coarse' sand, 0.6 to 37.6% 'Coarse' sand, 1.1 to 34.0% 'Medium' sand, 6.3 to 66.0% 'Fine' sand, 0.0 to 65.8% 'Very Fine' sand and 0.8 to 33.6% 'Silt and Clay'.

- As well as an abundance of taxa, these stations also feature a predominance of fine particulates, and have a depth range of between 30m and 82m, mainly in the deeper waters. The particle size may also influence cirratulid presence as no cirratulids were located at stations with more than 34 % granules, 16% very coarse

sand, or 37.6% coarse sand suggesting larger particle sizes may be inhibitory as suspected. The relationships between cirratulid presence and physicochemical variables, specifically depth and sediment composition are investigated in the following sections.

4.2.1 Physicochemistry Potentially Influencing the Distribution of Cirratulid Genera

Relationships between cirratulid presence and certain physicochemical properties appear to exist, however they appear to vary with respect to genera (see Figure 31, on page 63). Whilst there are too few records of all specific genera *for* any relationships to be statistically proven, especially for *Cirriformia* and *Tharyx,* some patterns are visible. Cirratulids of the Las Perlas Archipelago appear to be restricted to sediment less than 82m deep. This trait is not genus dependent and appears to be specific to the family as a whole.

From the data generated by the Darwin researchers, it appears that the quantity of granules, very coarse, coarse and medium sand and silt or clay within the sediment may also have an effect by restricting cirratulids to stations with less than 34.9% granules, less than 24.4% very coarse sand, and less than 42.9% coarse sand, whilst all stations with more than 40.6% medium sand contain cirratulids. These factors appear to influence the distribution of certain genera, with *Chaetozone* and *Aphelochaeta* limited to stations with less than 16.0% very coarse sand, *Caulleriella* restricted to stations with less than 19.7% coarse sand, *Caulleriella* and *Aphelochaeta* to stations with less than 39.1% silt or clay. *Chaetozone* appears restricted to sites with less than 70.8% silt and clay whilst *Monticellina* is present in stations with silt and clay content of 93.4%.

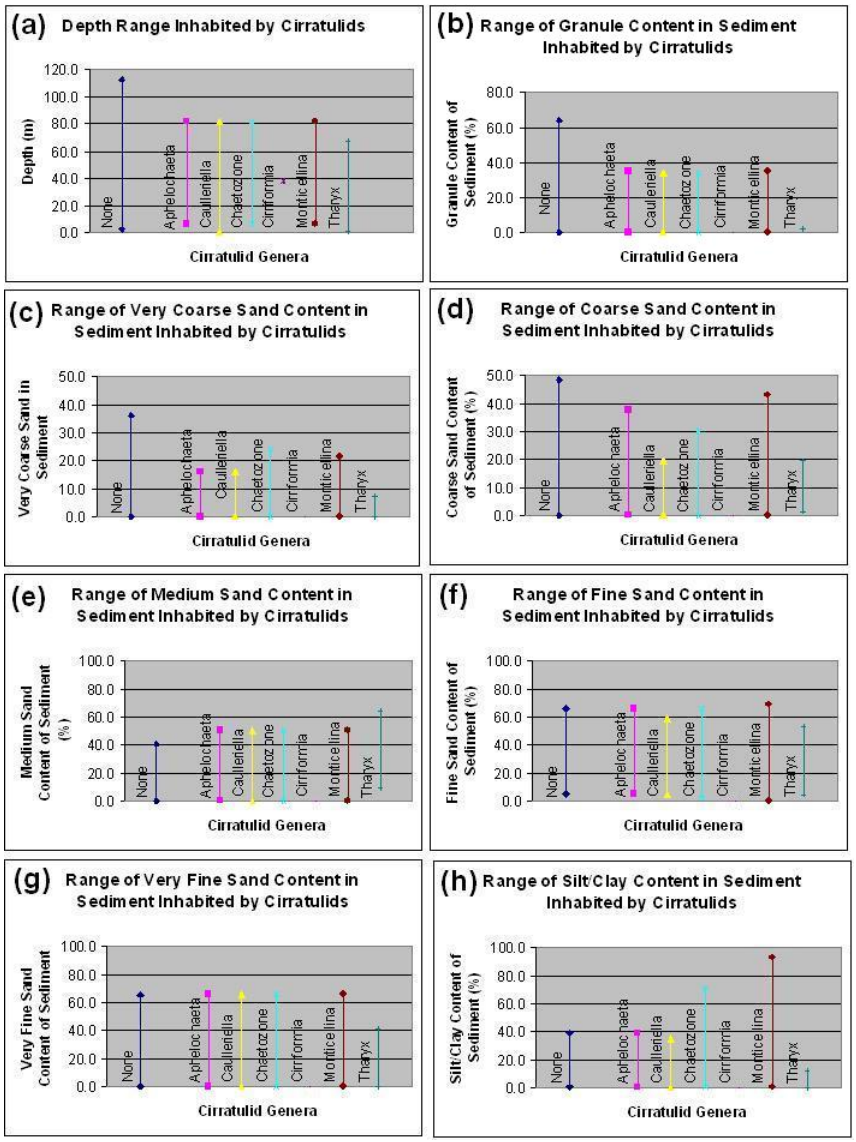


Figure 31: Graphical illustration of the physicochemical ranges of cirratulids. Those of *Cirriformia* and *Tharyx* may be restricted by numerical scarcity and, subsequently, are not considered further. Other genera are more numerically abundant. (a) Depth may influence cirratulid presence with no specimens found below 82m, however, it does not appear to effect genus presence as all occur down to 82m (b) Sedimentary 'Granule' content may effect family and genus presence: no cirratulids were gathered from stations with >34.9%. (c) Sedimentary 'Very Coarse' sand content may influence family, and genus presence: no cirratulids were gathered in sediment with >24.4%, *Caulleriella* and *Aphelochaeta* appear restricted to samples with <16.0%. (d) Sedimentary 'Coarse Sand' content may effect cirratulid presence: no cirratulids were gathered in samples with >42.9%. *Monticellina* appear least effected, whilst *Caulleriella* are restricted to sediment with <19.7% 'Coarse' sand. (e) Sedimentary 'Medium' sand content may influence cirratulid presence: cirratulids were gathered from all stations >40.6%. However, it appears to have no effect on genus presence. (f & g). Sedimentary 'Fine' and 'Very Fine' sand content may have little effect on cirratulid distribution. (h) Sedimentary 'Silt and Clay' content may effect genus distribution: only *Chaetozone* and *Monticellina* occur in stations with sedimentary 'Silt and Clay' levels >39.1%. *Chaetozone* species are absent from samples with >70.8%.

4.2.2 Physicochemistry Potentially Influencing the Distribution of Cirriformia Species

Just one specimen of *Cirriformia A* was gathered. This specimen occurred at station 136, at a depth of 30m; however no sediment data are currently available for this site. Consequently, further analyses of depth or sedimentary influences on distribution are not possible to date.

4.2.3 Physicochemistry Potentially Influencing the Distribution of Aphelochaeta Species

As shown in Figure 31, on page 63, *Aphelochaeta* are limited to depths of less than 82m. They are also limited by aspects of sedimentary composition in particular levels of sedimentary granule, very coarse sand, and silt and clay content. These properties may also be restrictive to the distribution of species.

The 57 specimens of *Aphelochaeta* were identified to 5 species: 4 specimens of *Aphelochaeta A* from 4 stations, 21 of *Aphelochaeta B* and 23 of *Aphelochaeta C* both from 8 stations, 8 of *Aphelochaeta D* from 3 stations and just 1 of *Aphelochaeta E*. Consequently, physicochemical properties of inhabited stations could be analysed for all except *Aphelochaeta E* (see Figure 32, on page 65).

Depth appears to influence species presence: *Aphelochaeta A* is present at shallower sites from 1m to 64m, whilst *Aphelochaeta B* and *C* are present in intermediate sites from 30m to 82m, and *Aphelochaeta D* is present at deeper sites between 62m and 82m (see Figure 32a). Particle size also appears to influence species presence (see Figure 32b-h) with *Aphelochaeta A* particularly sensitive to elevated levels of granules (>11.9%), very coarse (>16.0%) and fine sand (>27.0%)., and *Aphelochaeta D* particularly sensitive to high levels of very coarse (>11.1%), coarse (>14.5%) and medium sand (>12.2%) in the sediment whilst *Aphelochaeta C* appears to be the only species present in sediment with a high level of very fine sand (35.5-65.8%). For all variables, *Aphelochaeta B* and *C* show the widest tolerance.

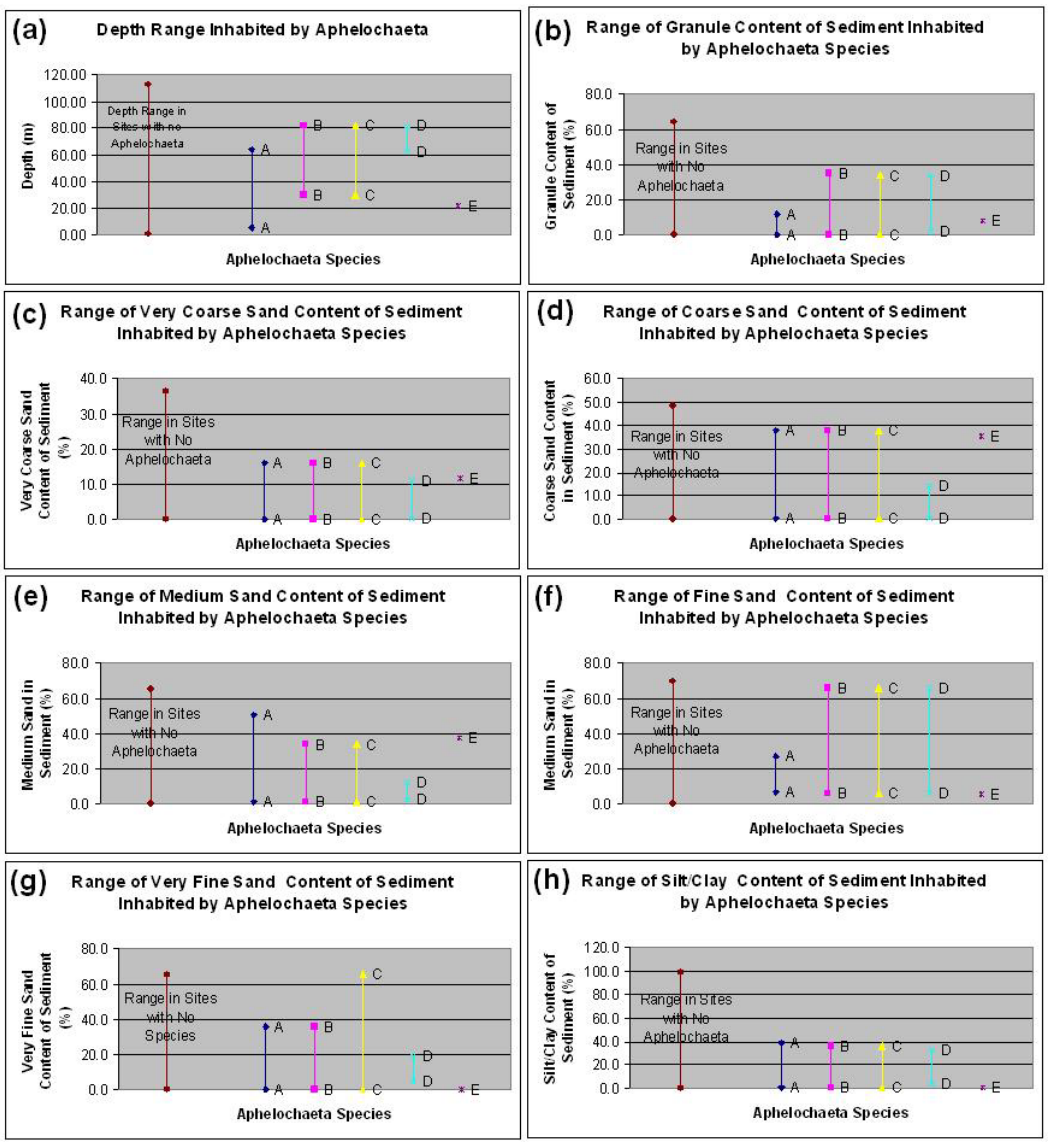


Figure 32: Graphical illustration of the physicochemical ranges that *Aphelochaeta* species inhabit. Only one specimen of *Aphelochaeta E* was located and, consequently, no conclusions can be made as to the preferred habitat of this species. Other taxa are numerically more abundant. (a) Depth may effect *Aphelochaeta* species distribution: *Aphelochaeta A* occurs at shallower sites from 1 to 64m, whilst *Aphelochaeta B* and *C* occur at depths of between 30 and 82m, and *Aphelochaeta D* at depths of 62 to 82m. (b) High sedimentary 'Granule' content may restrict the distribution of all species of *Aphelochaeta*, especially *Aphelochaeta A*, restricting it to sediment with <11.9%. (c) High sedimentary 'Very Coarse' sand content may also restrict the distribution of all species of *Aphelochaeta*, especially of *Aphelochaeta D* , restricting it to sediment with <11.1%. (d and e) High sedimentary 'Coarse' and 'Medium' sand content may be mildly restrictive to all species, but especially *Aphelochaeta D*, confining it to sediment with < 14.5% and <12.2% 'Coarse' or 'Medium' sand respectively. (f) High sedimentary 'Fine' content may effect the distribution of *Aphelochaeta A* restricting it to sediment with <27.0%. (g) High sedimentary 'Very Fine' content may be mildly restrictive to *Aphelochaeta A* and *B*, and more so to *Aphelochaeta D* confining it to sediment with <19.2%. (h) High sedimentary silt and clay content appears inhibitory to all species.

4.2.4 Physicochemistry Potentially Influencing the Distribution of Chaetozone Species

As shown in Figure 31, on page 63, *Chaetozone* are limited to depths of less than 82m. They are also limited by aspects of sedimentary composition in particular levels of sedimentary granule, very coarse, coarse and medium sand, and silt and clay content. These properties may also be restrictive to the distribution of species.

The 48 specimens of *Chaetozone* were identified to 5 species: 30 specimens of *Chaetozone A* from 11 stations, 7 of *Chaetozone B* from 5 stations, 13 of *Chaetozone C* from 7 stations, 6 of *Chaetozone D* from 5 stations and just 2 of *Chaetozone E* from 2 stations. Consequently, physicochemical properties of inhabited stations could be analysed for all except *Chaetozone E* (see Figure 33, on page 67).

Depth appears to have little effect on species presence, although *Chaetozone B* and *D* are not present at stations shallower than 16 and 23m (see Figure 33a). Particle size does appears to influence species presence (see Figure 33b-h) with *Chaetozone B* particularly sensitive to elevated levels of granules (>21.8%), very coarse (>14.1%), coarse (>13.3%), medium (>11.7%), and very fine sand (>22.6%) and silt and clay (>33.6%) and absent from all such stations. This species is also absent from stations with a fine sand content of <17.4%. *Chaetozone C* is also absent from station with a very coarse sand content of >16.0%. Another sensitive species is *Chaetozone D*, absent from all stations with an elevated granule (>26.8%), coarse sand (>9.1%), medium sand (>22.5%), very fine sand (>41.5%) and silt and clay (>33.6%). For all variables, *Chaetozone A* shows wide tolerance.

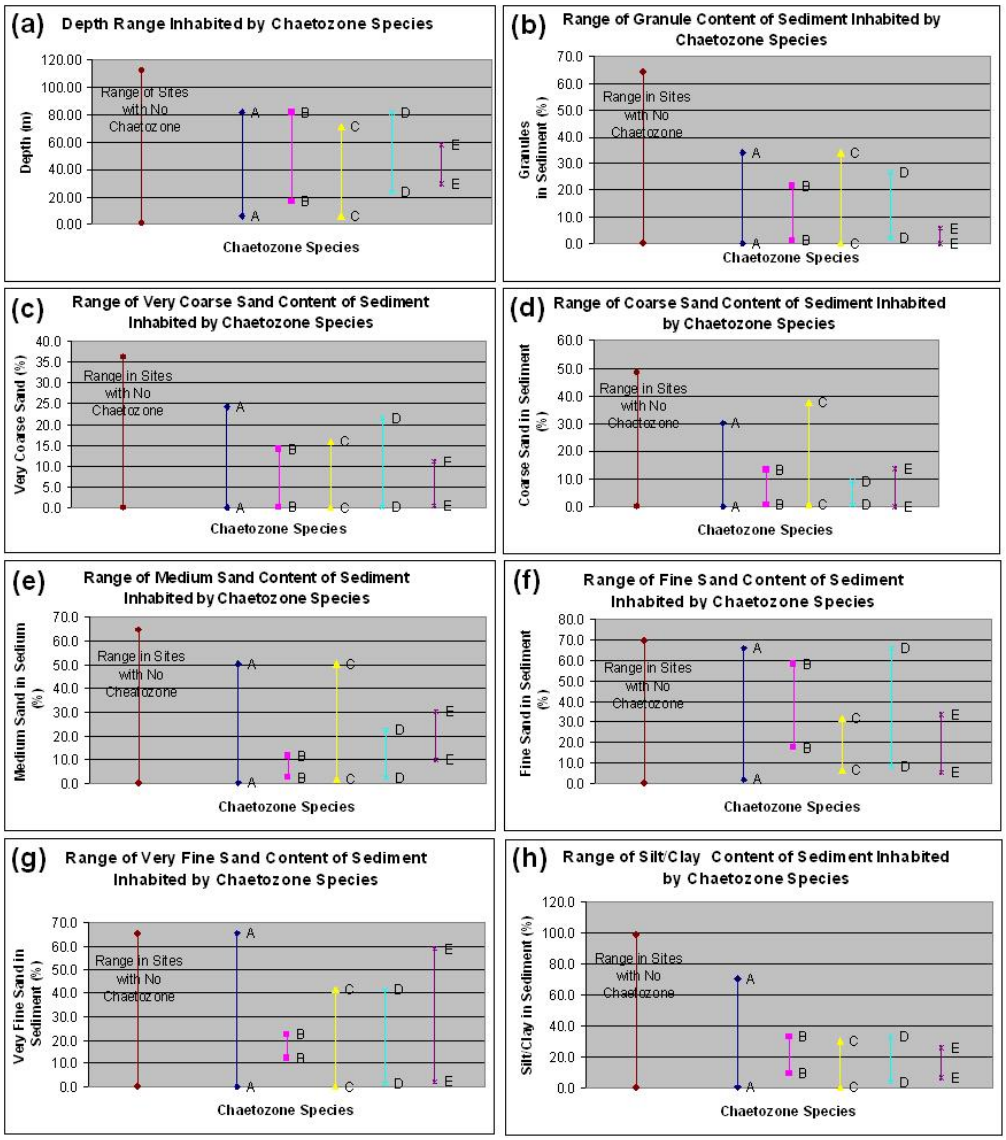


Figure 33: Graphical illustration of the physicochemical ranges that *Chaetozone* species inhabit. Only two specimens of *Chaetozone E* were located and, consequently, no conclusions can be made as to the preferred habitat of this species. Other species are more numerically abundant. (a) The possible effect of depth on *Chaetozone* distribution is not as pronounced as that on *Aphelochaeta* distribution, however, *Chaetozone B* and *D* are absent from all stations shallower than 16 and 23m respectively. Conversely, *Chaetozone C*, is not present at stations deeper than 71m. (b) High sedimentary 'Granule' content may restrict the distribution of all *Chaetozone* species, especially *Aphelochaeta B* ,absent from all stations with >21.8% . (c) High sedimentary 'Very Coarse' sand content may be restrictive to the distribution of all *Chaetozone* species, especially *Chaetozone B* and *C* , absent from all stations with >14.1% and >16.0% respectively. (d) High sedimentary 'Coarse' sand content appears to have a mildly restrictive effect on *Chaetozone A*, and a larger restrictive effect on *Chaetozone B* and *D*, with no specimens of these latter species found at >13.3% and 9.1% respectively (e) High sedimentary 'Medium' sand content appears mildly restrictive to all species of *Chaetozone* in particular *Chaetozone B* and *D*, absent from station with >11.7 and >22.5% respectively. (f). High sedimentary 'Fine' sand may effect the distribution of *Chaetozone B* and *C*, absent from all stations with >17.4% and >31.8% respectively. (g) High sedimentary 'Very Fine' sand content appears restrictive to *Chaetozone B*, absent from all station with >22.6%. (h) High sedimentary 'Silt and Clay' content appears restrictive to all *Chaetozone* species: Only *Chaetozone A* specimens are found in stations with >33.6%, and they are absent in all stations with >70.8%.

4.2.5 Physicochemistry Potentially Influencing the Distribution of Monticellina Species

As shown in Figure 31, on page 63, *Monticellina* are limited to depths of less than 82m. They are also influenced by aspects of sedimentary composition, in particular levels of sedimentary granule, very coarse, and medium sand, and silt and clay content. These properties may also be restrictive to the distribution of species.

The 208 specimens of *Monticellina* were identified to 8 species: 94 specimens of *Monticellina A* from 17 stations, 21 of *Monticellina B* from 6 stations, 13 of *Monticellina C* from 6 stations, 17 of *Monticellina D* from 6 stations, 5 of *Monticellina E* from just 2 stations, 40 of Monticellina *F* from 12 stations, 17 of *Monticellina G* from 6 stations and just 1 of *Monticellina H,* and un unidentifiable posterior fragment from just one station. Consequently, physicochemical properties of inhabited stations could be analysed for all except *Monticellina E, H* and the unidentifiable specimen (see Figure 34, on page 69).

Depth appears to have little effect on the presence of most species, however *Monticellina C, D* and G are not present at stations shallower than 23m, 59m and 36m respectively (see Figure 34a). Particle size does appears to influence species presence (see Figure 34b-h) with *Monticellina A* notably absent from stations with elevated levels of coarse sand (>14.5%), and the only species present in stations with elevated levels of silt and clay (>39.1). *Monticellina B* shows a wide tolerance for most variables whilst *Monticellina C* is absent from stations with an elevated level of very coarse (>11.1%), or medium sand (>12.2%). *Monticellina D* is absent from stations with a high elevated level of very coarse (>11.1%), coarse (>14.5%) and medium sand (>13.6). *Monticellina F* shows a wide tolerance for most variables, whilst *Monticellina G* is absent from stations with an elevated level of very coarse (>11.1%), coarse (>14.5%), or medium sand (>12.2%) or silt and clay (>28.4%).

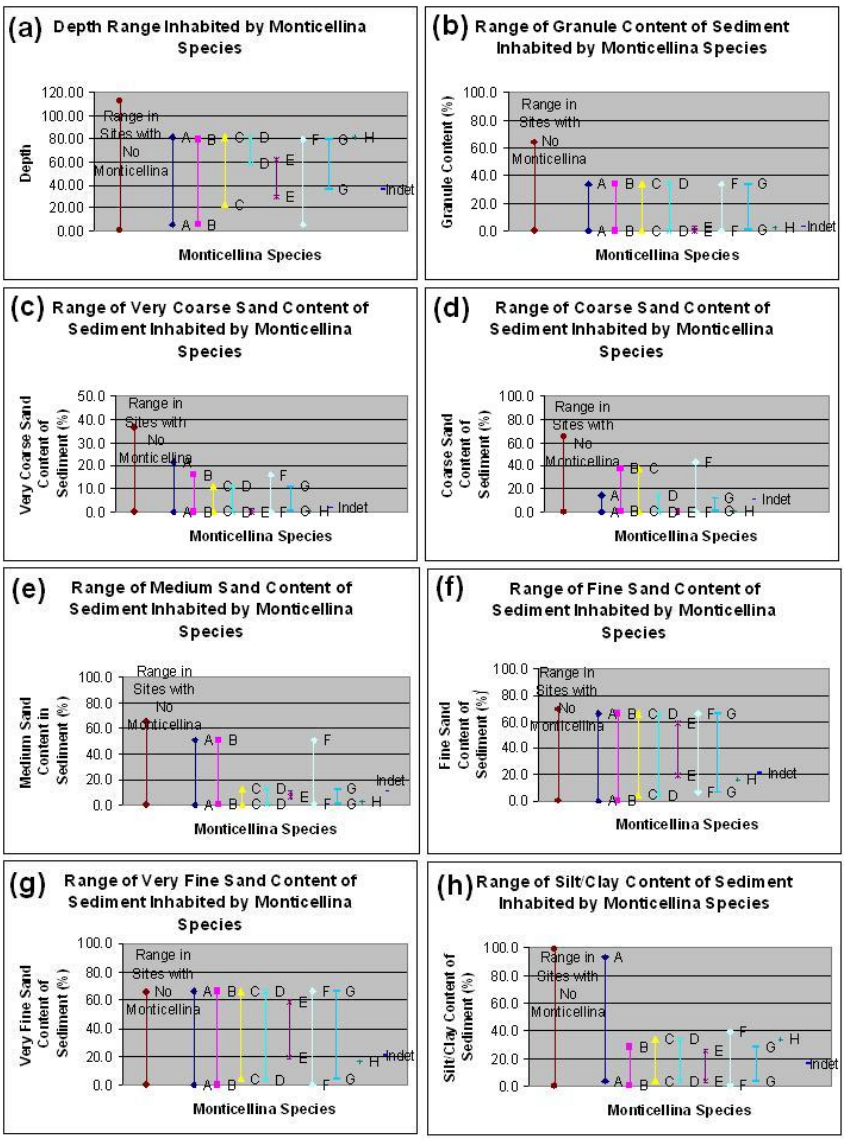


Figure 34: Graphical illustration of the physicochemical ranges that *Monticellina* species inhabit. Only 2 specimens of *Monticellina E,* and 1 of *Monticellina H* and *Indet* were located and, consequently, no firm conclusions can be made as to the preferred habitat of these species. Other species are more numerically abundant. (a) The effect of depth may be species dependent: whilst all are absent from stations deeper than 82m, *Monticellina C* and *D* are absent from stations shallower than 23m and 59m respectively, (b) High sedimentary 'Granule' content appears to effect all species similarly: all are absent in sediments with >34.9%. (c)High sedimentary 'Very Coarse' sand content may restrict the distribution of all species, in particular *Monticellina C*, *D* and *G*: absent from all stations >11.1%. (d) High sedimentary 'Coarse' sand content may restrict the distribution of *Monticellina A, C, D* and *G* to stations with <14.5%. (e) High sedimentary 'Medium' sand content may restrict the distribution of *Monticellina C, D* and *G* to stations with <12.2%, 13.6% and 12.2% respectively. (f& g). High sedimentary 'Fine' and 'Very Fine' sand content appear to have little effect on species distribution. (h) Although high sedimentary 'Silt and Clay' content did not appear to restrict the distribution of the genus *Monticellina*, this assumption may be false: The only species present in stations with a high sedimentary 'Silt and Clay' content is *Monticellina A.* All other species are absent from stations with a sedimentary silt/clay content of > 39.1%.

4.2.6 Physicochemistry Potentially Influencing the Distribution of Caulleriella Species

As shown in Figure 31, on page 63, *Caulleriella* are limited to depths of less than 82m. They are also influenced by aspects of sedimentary composition in particular levels of sedimentary granule, very coarse, coarse and medium sand. These properties may also be restrictive to the distribution of species.

The 33 specimens of *Caulleriella* were separated to 8 species: 3 specimens of *Caulleriella A* from 3 stations, 14 of *Caulleriella B* from 4 stations, 2 of *Caulleriella C* from 2 stations, 1 of *Caulleriella D*, 9 of *Caulleriella E* from 2 stations, 2 of *Caulleriella F* from 2 stations, and 1 of *Caulleriella Indet (A)* and *Indet (B)*. Consequently, physicochemical properties of inhabited stations could only be analysed for *Caulleriella B* (see Figure 35, on page 71).

Although *Caulleriella A* and *C* have limited specimens, they show a larger depth range, and are present in shallower stations than *Caulleriella B* (<28m) suggesting depth may influence distribution (see Figure 35a). Particle size may also influence species presence (see Figure 34b-h) with *Caulleriella A* and *C* present in stations with higher coarse or medium sand content than *Caulleriella B*: the latter is absent in stations with an elevated coarse (>11.1%) or medium sand content (>12.2%).

4.2.7 Physicochemistry Potentially Influencing the Distribution of *Tharyx* Species

Just 5 specimens of *Tharyx* were gathered from only 3 stations. Subsequently, the dataset is too small for any meaningful conclusions to be drawn. However, the map of species distribution patterns (Figure 28, on page 57) did highlight the distinct areas of location suggesting that some abiotic factors may influence the distribution pattern within this genus.

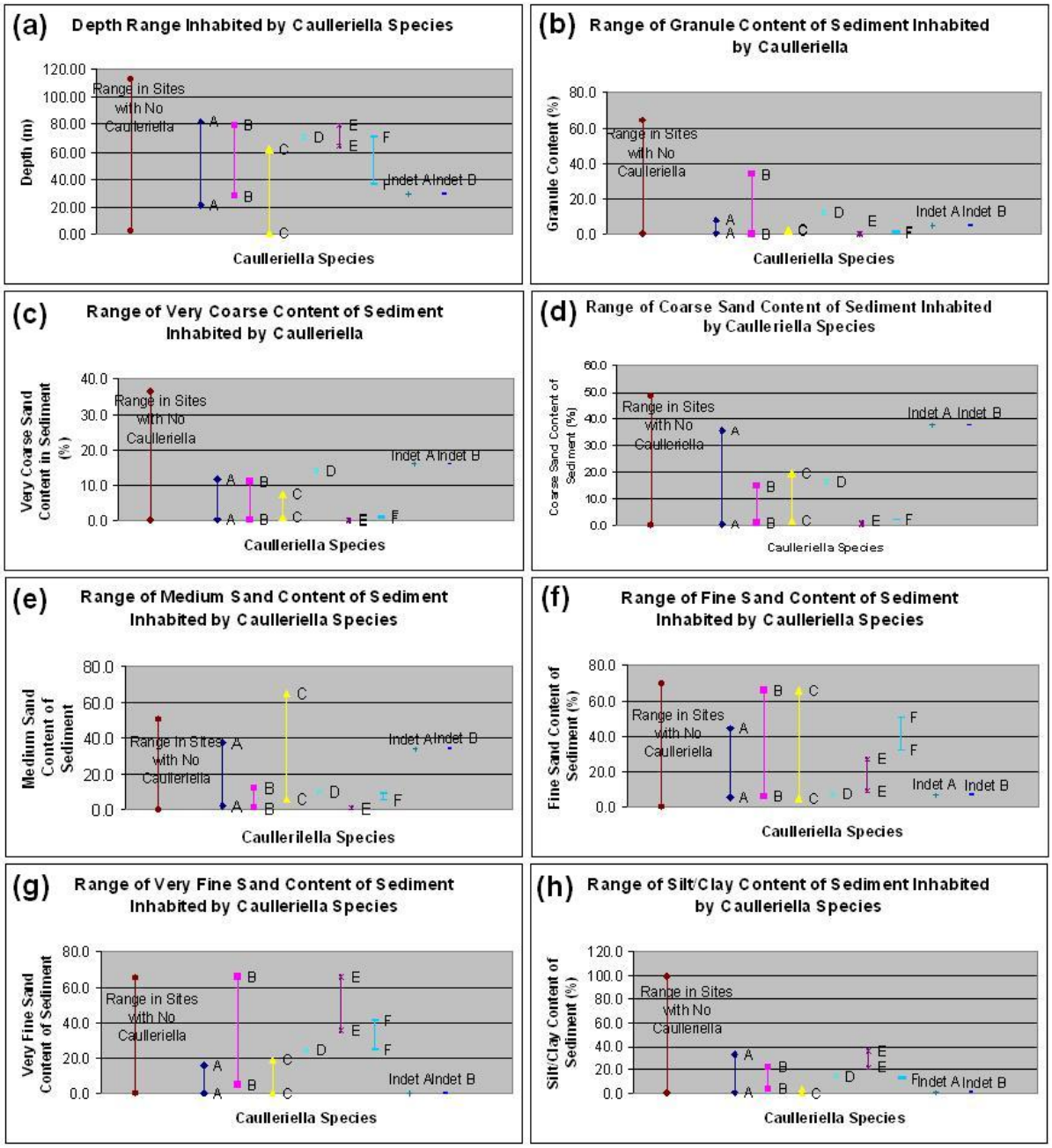


Figure 35: Graphical illustration of the physicochemical ranges that *Caulleriella* species inhabit. Only 3 specimens of specimens of *Caulleriella A*, 2 of *Caulleriella B* and *F*, and 1 of *Caulleriella D, Indet (A)* and *Indet (B)* were present. Whilst 9 specimens of *Caulleriella E* were present, they were only present from 2 stations, subsequently, just *Caulleriella B* can be analysed fully.(a) Depth may effect different species differently: whilst all are absent from stations deeper than 82m, *Caulleriella A* and *C* are present in sites shallower than the lower boundary of *Caulleriella B* of 28m. (b, c, d, f & g) Although *Caulleriella B* specimens are present at stations with a range of 'Granule', 'Very Coarse', 'Coarse', 'Fine' and 'Very Fine' sand content, it is impossible to depict if these factor influences species distribution patterns (e) High sedimentary 'Medium' sand content may effect species distribution: *Caulleriella A* and *C* are present at sites with a higher medium sand content than the upper boundary of *Caulleriella B* (>14.5%). (h) High sedimentary 'Silt and Clay' content may effect species distribution: *Caulleriella A* specimens are present at stations with higher silt and clay content than the upper boundary of *Caulleriella B* (>21.8%)

5. Conclusion

The results of this dissertation suggest that the cirratulid community within the Las Perlas Archipelago is numerically abundant, taxonomically diverse, and geographically widespread. The 361 cirratulids gathered by the R/V. “Urraca” were identified to 6 genera, and a total of 28 species. On a cautionary note, many of these specimens were damaged lacking entire chaetae, or in worst cases, sections of their body. Some may also be juveniles that, as mentioned in section 1.3.1, may have more chaetae variation than adults, hindering their identification. In addition, the benthos sampled for this dissertation has never been scientifically studied. Consequently, in the future, some of these classifications may be combined, or expanded as more becomes known of this region, and as the ambiguity surrounding Cirratulid taxonomy is resolved. However, the separation of these specimens into distinct morphs, and the provision of a description for each will greatly assist not just the Darwin Project, but also any further interest in cirratulid distribution worldwide.

Of this total count, 352 were gathered by grab from 36 stations, and 9 by trawl from 3 stations. The quantitative dataset provided by grab is too small for any meaningful statistical analysis; however, mapping does provide an insight into the distribution pattern of the cirratulids of Las Perlas. Further graphical analysis also suggests that abiotic factors such as depth and sediment composition influence family, genus and species presence; however, the sedimentary data may not be fully representative of the station. In addition, the effect of abiotic variables have been investigated separate to each other, their effects may not be independent, and they may also be influenced by biotic factors with certain genus appearing to have a preference for populated sites.

The results of this dissertation suggest that stations at depths of between 30m and 80m are most abundant, although cirratulids are present at shallower depths. In addition, larger particle sizes appear to be inhibitory throughout the family, with a preference for <35% granules, <24% very coarse sand or <43% coarse sand. Medium sand appears preferential as all stations with >40% medium sand contained

cirratulids. The sensitivity to each variable appears both genus and species dependent.

No specimens of *Aphelochaeta* or *Chaetozone* were gathered from sampled stations with >16% very coarse sand, whilst other genera were present in some. *Caulleriella* were absent from those with >20% coarse sand, whilst *Aphelochaeta* and *Monticellina* were present in sampled stations with high levels. No *Aphelochaeta* or *Caulleriella* specimens were gathered from sampled stations with a silt and clay content of >40% whilst *Chaetozone* and *Monticellina* specimens occurred in those with a very high silt and clay content. This may indicate that *Monticellina* are more tolerant to all sedimentary variables: a factor possibly determined by the predominance of *Monticellina* specimens amongst those with an external tube. However, there is still the possibility that this apparent pattern is the result of chance.

Different variables appear to affect species distribution of genera in different ways with all *Aphelochaeta* species distributed throughout the sedimentary silt and clay band inhabited by this genus, but distributed according to depth, and other sedimentary components (granule, very coarse, coarse, medium, fine or very fine sand, or silt and clay); all *Chaetozone* species were distributed throughout the depth, sedimentary granule and very coarse sand band indicated for this genus, but distributed according to other sedimentary properties (coarse, medium, fine, very fine or fine sand, or silt and clay; whilst all *Monticellina* species were distributed throughout the sedimentary granule, very fine or fine sand band indicated for this genus, but distributed according to depth, and other sedimentary components (very coarse, coarse or medium sand, or silt and clay).

Whilst attempts have been made to separate potential influences on distribution patterns from random chance, with some apparent trends, more specimens, and studies, are required to confirm any direct influences. The results of this dissertation provide potential pointers of interest for additional studies in this field, and it is hoped that the effect of both depth and particle size on the distribution of different taxonomic levels will be investigated further in the future.

References

Augener, H., 1933. Polchaeten von den Galapagos-Inseln. The Norwegian Zoological Expedition to the Galápagos Island 1925, conducted by Alf Wolleback. VI, *Medd. F. Zool. Mus., Oslo*, **25:**55-66**. In:** Matthew, J., (ed), 1991. Galapagos Marine Invertebrates. Taxonomy, Bio-geography, and Evolution in Darwin`s Islands. 1991. *Topics in Geo-biology***(8):** 75-94

Baxter, L., 2004. A study of the reef fish communities of Las Perlas Archipelago, Panama. *Unpublished document*. MSc Thesis, Heriot-Watt University, Edinburgh

Benfield, S., 2005. Mapping coral reefs and associated sublittoral habitats: A comparison of optical remote sensors and image classifiers and a study of the community structure of reef-associates fish. *Unpublished Document.* PhD thesis, Heriot-Watt University, Edinburgh.

Berman, J., 2004. Sponge diversity in coral frameworks and coral communities within the Las Perlas Archipelago, Panama. *Unpublished document*. MSc Thesis, Heriot-Watt University, Edinburgh

Blake, J.A., 1975. The larval development of Polychaeta from the northern California coast. I. *Cirriformia spirabranchia* (Family Cirratulidae). *Transactions of the American Microscopial Society*, **94:** 179-188

Blake, J. A., 1996. 8. Family Cirratulidae Ryckholt, 1851: including a revision of the genera and species of the eastern North Pacific**. In:** Blake, J. A., Hilbig, B., & Scott, P.H., (eds). 2002. Polychaeta: Orbiniidae to Crossuridae. *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and the Western Santa Barbara Channel*. Santa Barbara Museum of Natural History, Santa Barbara, California. 3rd Edition. **6(3)**:263-375

Blake, J.A., 1991a. Revision of some genera and species of Cirratulidae (Polychaeta) from the western North Atlantic. *Ophelia Supplement* **5**:17-30

Blake, J.A., 1991b. The Polychaete Fauna of the Galápagos Islands. **In:** Matthew, J., (ed) 1991. Galapagos Marine Invertebrates. Taxonomy, Bio-geography, and Evolution in Darwin`s Islands. 1991. *Topics in Geo- biology***(8):** 75-94

Brown, J., Colling, A., Park, D., Phillips, J., Rothery, D., & Wright, J., 1991. Case Studies in Oceanography and Marine Affairs. *Open University and Pergamon Press*, 179-203,

Campbell, I., 2006. The Role of Local Communities in the Designation of a Marine Protected Area in Archipelago Las Perlas. *Darwin Initiative Workshop*, Smithsonian Tropical Research Institute, Panama.

Caullery, M., & Mesnil, F, 1898. Les formes épitoques et l'évolution des Cirratuliens. *Annales de l'Université Lyon,* **39:** 1-200

Chamberlin, R., 1919. The Annelida Polychaeta. *Mem. Mus. Comp. Zool., Harvard* **48:**1-514. **In:** Matthew, J., (ed), 1991. Galapagos Marine Invertebrates. Taxonomy, Bio-geography, and Evolution in Darwin`s Islands. 1991. *Topics in Geo- biology***(8):** 75-94

Chambers, S.J., 2000. A redescription of *Chaetozone Setosa* Malmgren, 1867, including a definition of the genus, and a description of a new species of *Chaetozone* (Polychaeta: Cirratulidae) from the Northeast Atlantic. *Bulletin of Marine Science*, **67(1)**:587-596

Chambers, S.J., & Woodham, A., 2003. A new species of *Chaetozone* (Polychaete: Cirratulidae) from deep water in the northeast Atlantic, with comments on the diversity of the genus in cold northern waters. *Hydrobiologica,* **496**:41-48

Christie G., 1984. A new species of *Tharyx* (Polychaeta: Cirratulidae) from the estuaries in north-east England. *Sarsia* **69:** 69-73

Christie, G., 1985. A comparative study of the reproductive cycles of three Northumberland populations of *Chaetozone setosa* (Polychaeta: Cirratulidae). *Journal of the Marine Biological.Association, of the United.Kingdom.* **65**: 239-254

Cortés, J., 1997. Biology and geology of eastern Pacific coral reefs. *Proceedings of the 8th International Coral Reef Symposium*, **16**, Suppl.: S39—S46

Cunningham, J.T., & Ramage, G.A., 1988. The Polychaeta Sedentaria of the Firth of Forth. *Transactions of the Royal Society of Edinburgh,* **33:** 635-684

Curtis, M.A., 1977. Life Cycles and Population Dynamics of Marine Benthic Polychaetes from the Disko Bay Area of West Greenland. *Ophelia,* **16(1)** 9-58

Dahl, F., Dahl, M., & Peus, F., 1971. Annelida, Borstenwürmer, Polychaeta, *VEB Gustav Fischer Verlag, Jena.* 353-363

Dauvin, J., Kendal**, M., Paterson, G., Gentil, F., Jirkov, I., Sheader, M., and De Lange, M., 1994.** An initial assessment of polychaete diversity in the northeastern Atlantic Ocean. *Biodiversity Letters*. **2**: 171-181

Day, J.H., 1967. Sedentaria. *A Monography on the Polychaeta of Southern Africa*, British Museum of Natural History, Publication No. 656**, 2:**498-518.

D'Croz, L., Del Rosario, J., & Gomez, J., 1991. Upwelling and phytoplankton in the Bay of Panama. *Revista de Biologia Tropical*. **39(2)**:233-241

D'Croz, L.D., & Robertson, D.R., 1997. Coastal Oceanographic Conditions Affecting Coral Reefs on both sides of the Isthmus of Panama. *Proceedings of the 8th International Coral Reef Symposium,* **2**:2053-2085

Fauchald, K., 1972. Benthic polychaetous annelids from deep water off western Mexico and adjacent areas in the eastern Pacific Ocean. *Allan Hancock Monographs in Marine Biology.* **7**: 1-575

Fauchald, K., 1977. Polychaetes from the Intertidal Areas in Panama, with a review of Previous Shallow-Water Records**,** *Smithsonian Contributions to Zoology, Smithsonian Institute Press, City of Washington,* **221** : 1-2, 49-51

Fauvel, P., 1927. Polychètes sédentaires: Addenda aux errantes, archiannélides, myzostomaires. *Faune de France*, **16**,

Forsbergh, E.D., 1969. On the climatology, oceanography and fisheries of the Panama Bight. *Bulletin of the Inter-American Tropical Tuna Commission.* **14**:49-259.

George, J. D., 1963. Behavioural differences between larval stages of *Cirriformia tentaculata* (Montagu) from Drake's Island (Plymouth Sound) and from Southampton Water. *Nature,* **199:** 195

George, J. D., 1964. The life history of the cirratulid worm, *Cirriformia tentaculata* on an intertidal mudflat. *Journal of the Marine Biological Association, of the United Kingdom,* **44:** 47-65

George, J. D., 1967. Cryptic polymorphism in the cirratulid polychaete *Cirriformia tentaculata. Journal of the Marine Biological Association, of the United Kingdom* **47:**75-79

George, J.D., & Hartmann-Schröder, G., 1985. Polychaetes: British Amphinomida, Spintherida & Eunicida. **In:** Kermack, D.M., & Barnes, R.S.K., (eds), *Synopses of the British Fauna,* **32**, pp. 1-22.

GEsource, 2006. Panama**. In:** *Geography and Environmental Gateway for UK HE and FE: World Guide*, [available on-line at]: http://www.gesource.ac.uk/worldguide/html/988.html [accessed on]: 18/05/06

Green, P. M., Legler, D. M., Miranda, C. J., & O'Brien, J. J., 1997. The North American Climate Patterns Associated with the El Niño-Southern Oscillation, *COAPS Project Report*, **97(1)**,

Grigg, R.W., & Hey, R., 1992. Palaeoceanography of the tropical eastern Pacific. *Science* **255**: 172-178

Gibbs, P.E., 1971. A comparative study of reproductive cycles in four polychaete species belonging to the family Cirratulidae. *Journal of the Marine Biological Association of the United Kingdom* **51**:745-769

Gibbs, P.E., Langston, W.J., Burt, G.R., & Pascoe, P.L., 1983. *Tharyx marioni* (Polychaeta): a remarkable accumulator of arsenic. *Journal of the Marine Biological Association of the United Kingdom* **63**:313-325

Gibson, P.H., 1996. Distribution of the Cirratulid Polychaetes *Dodecaceria fimbriata, D. concharum* and *D. diceria* in European waters between latitudes 48oN and 70oN. *Journal of Marine Biology,* **76:**625-635

Gibson, P.H., & Clark, R.B., 1976. Reproduction in *Dodecaceria caulleryi* (Polychaeta: Cirratulidae). *Journal of the Marine Biological Association of the United Kingdom* **56**:649-674

Glynn, P.W., & Stewart, R.H., 1973. Distribution of Coral Reefs in the Pearl Islands (Gulf of Panama) in Relation to Thermal Conditions. *Limnology and Oceanography.* **18**: 367

Glynn, P.W., & Maté, J.L., 1996. Field Guide to the Pacific Coral Reefs of Panama. *8th International Coral Reef Symposium, Panama City, Panama,*

Guzman, H.M., Guevara, C.A., & Kaufmann, K.W. 2006. Panama Coral Reef Monitoring Network. *Smithsonian Tropical Research Institute.* [available on-line at]: http://striweb.si.edu/esp/mesp/reef_monitoring_intro.htm [accessed on]: 24/05/06

Hily, 1987. Spatio-temporal variability of *Chaetozone setosa* (Malmgren) populations on an organic gradient in the Bay of Brest, France. *J. Exp. Mar. Biol. Ecol.,* **112**:201-216

Holme, N.A., & McIntyre, A.D., (eds), 1984. Methods for the Study of Marine Benthos. *Blackwell Scientific Publications*

Holthe, T., 1992. Identification of Annelida Polychaeta from Northern European and Adjacent Arctic Waters. *Gunneria,* **66**:1-30

Hurtado, M., 1995. A Global Representative System of Marine Protected Areas- Marine Region 17: Southeast Pacific. *Biogeography and Marine Biodiversity*. 131-152. Great Barrier Reef Marine Park Authority/The World Bank/The World Conservation Union (IUCN). [available on-line at]: http://www.deh.gov.au/coasts/mpa/nrsmpa/global/volume4/chapter17.html. [accessed on]: 16/05/06

Kershaw, T., 2004. A study of Chaetognaths from the Gulf of Chiriqui, Panama. *Unpublished Document.* MSc Dissertation, Heriot-Watt University, Edinburgh

Kinberg, J.G.H., 1865. Annulata nova. *Oefv. Vet. Akad. Stockholm Förh.* **21:**59-574. **In:** Matthew, J., (ed)1 991. Galapagos Marine Invertebrates. Taxonomy, Bio-geography, and Evolution in Darwin`s Islands. 1991. *Topics in Geo- biology***(8):** 75-94

Mackie, A.S.Y., Oliver, P.G., & Rees, E.I.S., 1995. Benthic biodiversity in the southern Irish Sea. Studies in Marine Biodiversity and Systematics from the National Museum of Wales. *BIOMÔR Reports*, **1(263)**:37-131

Martin, J.H., 1969. Distribution of C, H, N, P, Fe, Mn, Zn, Ca, Sr, and Sc in Plankton Samples Collected off Panama and Colombia. *BioScience,* **19(10)**:898-901

Maté, J., 2003. Ecological, genetic, and morphological differences among three *Pavona* (Cnidaria: Anthozoa) species from the Pacific coast of Panama *I. P. varians, P. chiriquiensis*, and *P. frondifera*. *Marine Biology*, **142(3):** 427-440

Milanovich, F.P., Spies, R., Guram, M.S., & Sykes, E.E., 1976. Uptake of copper by the polychaete *Cirriformia spirabranchia* in the presence of dissolved yellow organic matter of natural origin. *Estuarine Coastal Marine Science.* **4:** 585-588

Mill, P.J., 1978. Physiology of Annelids. *Academic Press Inc. (London) Ltd*, 49-56

Monro, C.C.A, 1928a. On the Polychaeta Collected by Dr. Th. Mrtensen off the Coast of Panama. *Videnskabelige Meddelelser fre dansk naturhistorik Forening* (Copenhagen). **85:**75-103. **In: Fauchald, K., 1977.** Polychaetes from the Intertidal Areas in Panama, with a review of Previous Shallow-Water Records**,** *Smithsonian Contributions to Zoology, Smithsonian Institute Press, City of Washington,* **221** : 1-2, 49-51

Monro, C.C.A, 1928b. Polychaeta of the Families Polynoidae and Actoetidae from the Vicinity of the Panama Canal, Collected by Dr. C. Crossland and Dr. Th. Mortensen. *Journal of the Linnean Society of London,* **36:**553-576 **In: Fauchald, K., 1977.** Polychaetes from the Intertidal Areas in Panama, with a review of Previous Shallow-Water Records**,** *Smithsonian Contributions to Zoology, Smithsonian Institute Press, City of Washington,* **221** : 1-2, 49-51

Monro, C.C.A, 1933a. The Polychaeta Errantia Collected by Dr. C. Crossland at Colon in the Panama Region and the Galapagos Islands during the Expedition of the S.Y. ST. GEORGE. *Proceedings of the Zoological Society of London.* **1933(1):**1-96. **In: Fauchald, K., 1977.** Polychaetes from the Intertidal Areas in Panama, with a review of Previous Shallow-Water Records**,** *Smithsonian Contributions to Zoology, Smithsonian Institute Press, City of Washington,* **221** : 1-2, 49-51

Monro, C.C.A, 1933b. The Polychaeta Sedentaria Collected by Dr. C. Crossland at Colon in the Panama Region and the Galapagos Islands during the Expedition of the S.Y. ST. GEORGE. *Proceedings of the Zoological Society of London.* **1933(2):**1039-1092. **In: Fauchald, K., 1977.** Polychaetes from the Intertidal Areas in Panama, with a review of Previous Shallow-Water Records**,** *Smithsonian Contributions to Zoology, Smithsonian Institute Press, City of Washington,* **221** : 1-2, 49-51

Okuda, S., 1946. Studies on the development of the Annelida Polychaeta. I. *Journal of the Faculty of Sciences Hokkaido Imperial Univeristy* **9:** 115-219

Olive, P.J.W., 1970. Reproduction of a Northumberland population of the polychaete *Cirratulus cirratus. Marine Biology* **5:** 259-273

Olive, P.J.W., 1971. Ovary structure and oogenesis in *Cirratulus cirratus* (Polychaeta: Cirratulidae). *Marine Biology* **95:** 267-273

Oyenekan, J.A., 1987. Population dynamics and secondary reproduction in the Cirratulidae (Annelida: Polychaeta), with redescription of *Cirratulus gayheadius* (Hartman, 1965), new combination, and emendation or reinstatement of some cirratulid genera. *Bulletin of Marine Science* **48:** 592 (Abstract)

Parker, R.H., 1975. The Study of Benthic Communities: A Model and a Review. *Elsevier Oceanography Series,* **(9):** 1-4

Petersen, M. E., 1994. Hermaphroditic cirratulids (Annelida, Polychaeta) from Danish waters, with notes on early development, description of a new species of *Aphelochaeta* Blake and a review of hermaphroditism among the Cirratulidae. **In: Dauvin, J.-C., Laubier, L. and Reish, D.J.,** (eds.), Actes de la 4ème Conférence internationale de Polychètes. Mémoires du Muséum National d'Histoire Naturelle (Zoologie) **162: 634** (Abstract).

Petersen, M.E., 1999. Reproduction and development in Cirratulidae (Annelida: Polychaeta). **In: Dorresteijn, A.W.C., & Westheide, W., (eds) 1999.** Reproductive Strategies and Developmental Patterns in Annelids. *Hydrobiologia,* **402:** 107-128

Pearson, T.H., & Rosenberg, R., 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanogr. Mar. Bio.* **16**: 229-311

Rouse, G.W., and Pleijel, F., 2001. Polychaetes. *Oxford University Press*, 18-35 & 212-216.

Salazar-Vallejo, S.I., & Londoño-Mesa, M.H., 2004. Lista de especies y bibliografía de poliquetos (Polychaeta) del Pacífico Oriental Tropical. *Anales del Instituto de Biología, Universidad Nacional Autónoma de Móxico, Serie Zoología,* **75(1):**9-97

van der Spoel, S., & Pierrot-Bults, A.C., 1979. Zoogeography of the Pacific Ocean. **In: van der Spoel, S., & Pierrot-Bults, A.C,** Zoogeography and Diversity of Plankton. Utrecht, Bunge Scientific Publishing

Stevenson, W., 1950. The development of *Cirratulus cirratus* (O. F. Muller). *Report of the Dove Marine Laboratory for 1948,* pp.7-20.

Summerhayes, C.P., & Thorpe, S.A., 1996. Oceanography: An Illustrated Guide, *Manson Publishing*, 54-56

Telfer T.C., Woodham A., Hamilton S., & Docherty C., 1992. Problems in the Identification of Polychaeta for the Purpose of Benthic Environmental Assessment. *Polychaete Research Newsletter,* **14(1)**

Thorson, G., 1950. Reproductive and larval development of Danish marine bottom invertebrates. *Meddr Komn Danm. Fisk.- og Havunders., Ser. Plankton,* **4(1):** 523

Treadwell, A.L., 1928. Polychaetous Annelids from the Arcturus Oceanographic Expedition. *Zoologica* (New York Zoological Society), **8(8):**449-485. **In:** Fauchald, K., 1977. Polychaetes from the Intertidal Areas in Panama, with a review of Previous Shallow-Water Records**,** *Smithsonian Contributions to Zoology, Smithsonian Institute Press, City of Washington,* **221** : 1-2, 49-51

United Nations, 1993. Convention on biological diversity (with annexes). Concluded at Rio de Janeiro on 5 June 1992. *United Nations Treaty Series,* **30619:** 1-83. [available on-line] at: http://www.biodiv.org/doc/legal/cbd-un-en.pdf [accessed on 04/05/05].

Vittor, B.A., Uebelacker, J.M., & Johnson, P.G., 1984. Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico, **2**:12.1-12.30

Wikipedia, 2006. Ocean Currents. [available on-line at]: http://upload.wikimedia.org/wikipedia/en/c/c8/SurfaceCurrents.png [accessed on]: 18/05/06

Wilson, D. P., 1936. The development of *Audouinia tentaculata* (Montagu). *Journal of the Marine Biological Assocation of the United Kingdom,* B20: **567-579**

Wolf, P.S., 1984. Family Cirratulidae. **In:** Uebelacker, J.M. & Johnson, P. G. (eds), *Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico*. B.A. Vittar & Associates, Alabama **II(12)**: 1-30

Woodham, A., & Chambers, S.J., 1994a. A new species of *Chaetozone* (Polychaeta, Cirratulidae) from Europe, with a re-description of *Caulleriella zetlandica* (McIntosh). **In:** Dauvin, J.-C. Laubier, L., & Reish, D.J. (Eds). Actes de la 4ème Conférence internationale des Polychètes. *Mém. Mus. Natn. Hist. nat*. **162**: 307-316. Paris ISBN 2-85653-214-4

Woodham, A., & Chambers, S.J., 1994b. Some taxonomic problems of bi-tentaculate cirratulids. *Polychaete Research*, **16**:14-15

Worsfold, T., 1996. A Guide to the Family *Cirratulidae* including a key to anterior portions. *Unpublished document.* Unicomarine Ltd.

Zebiak, S., 1999. El Niño and the Science of Climate Prediction. *Consequences*, **5(2)**:3-15

Personal Communication:

Chambers, S., 2006. National Museums of Scotland.

Mair, H., 2006. Heriot Watt University.

Appendices

Nomenclature:

Branchial gills — *known elsewhere in literature as branchiae* (Rouse & Pleijel,2001) *branchial filaments* (Day, 1967) *or gills*: Branchial gills are long elongate cylindrical extensions of the body wall containing a double branch of the vasculature system through which oxygen can easily diffuse: deoxygenated blood enters from the ventral blood vessel, and lateral vessels return oxygenated blood to the dorsal vessel, providing an increase in surface area for gas exchange in a closed circuit circulatory system (Rouse & Pleijel, 2001). These respiratory structures are often extended into the water column.

Bitentacular — *known elsewhere in literature as bipalpate*: a single pair of tentacular palps (see below for definition) as in *Aphelochaeta, Caulleriella, Chaetozone, Dodecaceria, Monticellina* and *Tharyx* spp.

Chaetae — *known elsewhere in literature as setae* (Blake, 1996; Day, 1967)*:* segmental structures that occur at parapodial rami. These can be capillaries, spines or hooks (Blake, 1996; Mill, 1978).

Capillaries — Capillary chaetae are long cylinders: simple capillaries are smooth, whereas serrated capillaries as seen in *Dodecaceria* feature a sawlike edge. In certain species of *Chaetozone* (e.g. *C. jubata*), exceptionally long capillary chaetae have been observed: these have been dubbed natatory chaetae (Chambers & Woodham, 2003)

Cinctures — broad spreading fascicles of chaetae spanning dorsal, lateral and ventral surfaces of posterior setigers to different degrees dependent on genus: these can be complete cinctures with chaetae surrounding the entire parameter (as seen in most *Chaetozone* spp.), or partial, with hooks curving from distinct rami.

Epitoky — an unusual form of reproduction confined to polychaetes in which the organism transforms into a pelagic, sexually reproductive morph known as an epitoke.

Hooks — *known elsewhere in literature as acicular chaetae* (*Blake, 1996*)*, spines, or modified spines*: thick spine-like distally-curved chaetae that emerge from the parapodia forming a partial or full cincture dependent on the species. These can be unidentate, bidentate, uncini or spatulate (*known elsewhere as distally entire, bifid or multidentate, knob-tipped and spoon-like respectively* (*Blake, 1996*)): have a single tapered point, a double point, or an enlarged convex, or concave tip respectively.

Inter-Tropical Convergence Zone	*often abbreviated to ITCZ, or termed the Doldrums,or theT rade Wind Calm Belt:* an area influenced by the Northeast Trade-winds of the Atlantic, the South-east Tradewinds of the Pacific and the Equatorial Calm Belt (Martin, 1969)
Moniliform	*known elsewhere in literature as beaded ():* body segments are distinct and beadlike in shape
Multitentacular	multiple pairs of tentacular palps (see below for definition): *Cirratulus, Cirriformia, Protocirrineris* and *Timarete* spp
Parapodia	*known elsewhere in literature as feet:* paired lateral outgrowths of the body cavity characteristic to Polychaetes. These are divided into dorsal notopodia and ventral neuropodia and bear chaetae.
Peristomium	*known elsewhere in literature as the buccal segment*: the penultimate anterior segment of the body that bears the mouth, proboscis, tentacular palps, and often branchial gills. This structure appears to be the result of fusion of the anterior-most <3 segments giving it an annulated external structure. All parapodial rami, palps and chaetae are absent. In genus, such as *Cirriformia* and *Cirratulus*, developmental studies have shown that the peristomium extends over <7segments, however, tentacular palps and branchial gills have the appearance of emerging from body segments.
Prostomium	*known elsewhere in literature as the head* (Day, 1967)*:* the most anterior segment of the body. A well developed lobe of varying shape, that may feature eyes and nuchal slits, and is dorsal to the mouth
Pygidium	the most posterior segment of the body bearing the terminal anus.
Tentacular palps	*known elsewhere in literature as feeding appendages* (Day, 1967), , *palps, grooved palps, grooved filaments, tentacular filaments or tentacles* (Rouse & Pleijel, 2001; Blake, 1996;). *Some authors describe 2 types dependent on number: 'tentacular palps' on bitentaculate cirratulids and 'tentacular filaments' on those with multiple structures (*Wolf, 1984): grooved feeding appendages that arise from the dorsal surface of the peristomium as a solitary or multiple pairs. They contain a single blood vessel.

Appendix 1: A glossary of scientific terminology utilised throughout this literature.

Station	X Coordinate	Y Coordinate	Latitude (North)	Longitude (West)	Date Sampled
5	722553.72000	903649.39000	8 10.20 N	78 58.80 W	08/05/2003
6	717042.84000	903622.11000	8 10.20 N	79 01.80 W	08/05/2003
7	712634.25000	903600.77000	8 10.20 N	79 04.20 W	08/05/2003
9	702715.29000	903554.38000	8 10.20 N	79 09.60 W	08/05/2003
10	702695.04000	907978.69000	8 12.60 N	79 09.60 W	08/05/2003
12	712613.01000	908025.30000	8 12.60 N	79 04.20 W	08/05/2003
13	717021.15000	908046.73000	8 12.60 N	79 01.80 W	08/07/2003
14	722531.48000	908074.14000	8 12.60 N	78 58.80 W	08/07/2003
23	732421.30000	913656.48000	8 15.60 N	78 53.40 W	08/07/2003
29	702669.59000	913509.08000	8 15.60 N	79 09.60 W	08/09/2003
30	702649.12000	917933.41000	8 18.00 N	79 09.60 W	08/09/2003
39	746723.01000	918160.04000	8 18.00 N	78 45.60 W	08/07/2003
41	742284.36000	923666.97000	8 21.00 N	78 48.00 W	08/13/2003
47	712537.86000	923511.21000	8 21.00 N	79 04.20 W	08/09/2003
48	708131.37000	923489.87000	8 21.00 N	79 06.60 W	08/09/2003
49	702623.40000	923463.82000	8 21.00 N	79 09.60 W	08/09/2003
50	702602.71000	927888.17000	8 23.40 N	79 09.60 W	08/11/2003
51	707008.62000	927909.04000	8 23.40 N	79 07.20 W	08/12/2003
53	718023.84000	927963.20000	8 23.40 N	79 01.20 W	08/11/2003
59	746666.48000	928117.18000	8 23.40 N	78 45.60 W	08/13/2003
60	746634.82000	933648.95000	8 26.40 N	78 45.60 W	08/13/2003
64	726218.25800	935939.00420	8 27.70 N	78 56.71 W	8/16/2004
68	706982.06000	933439.60000	8 26.40 N	79 07.20 W	08/11/2003
69	702576.71000	933418.60000	8 26.40 N	79 09.60 W	08/11/2003
70	702555.80000	937842.96000	8 28.80 N	79 09.60 W	08/12/2003
71	706960.69000	937864.06000	8 28.80 N	79 07.20 W	08/12/2003
72	711365.68000	937885.61000	8 28.80 N	79 04.80 W	08/12/2003
84	726923.07483	943467.67750	8 31.78 N	78 56.31 W	10/09/2003
88	706933.84000	943394.64000	8 31.80 N	79 07.20 W	08/12/2003
89	702529.52000	943373.43000	8 31.80 N	79 09.60 W	08/12/2003
90	702508.39000	947797.80000	8 34.20 N	79 09.60 W	08/14/2003
91	706912.25000	947819.12000	8 34.20 N	79 07.20 W	08/14/2003
92	711316.21000	947840.89000	8 34.20 N	79 04.80 W	08/14/2003
112	711266.22000	957796.21000	8 39.60 N	79 04.80 W	10/08/2003
136	747936.73000	898251.96000	8 07.20 N	78 45.00 W	08/06/2003
140	763398.33000	893914.49000	8 04.80 N	78 36.60 W	08/06/2003
93a	717111.95120	948087.79040	8 34.32 N	79 01.64 W	8/17/2004

Appendix 2: Geographic locations of the 37 sites featuring Cirratulids The majority of these samples were taken in August 2003, however, due to limited time, 2 of the included sites (84, and 112) were sampled in October of that same year, and a further 2 (64 and 93a), the following August. Subsequently, all sites were sampled within the wet season.

Verified Stations	Depth (m)	Sediment type	organic C %	Carbonate %	Granule %	VC Sand %	C Sand %	M Sand %	F Sand %	VF Sand %	Silt-Clay %
5	36.30	sand + mud	0.5	21.4	2.7	0.7	2.1	9.2	31.8	41.5	11.9
6	52.50	mud	1.3	20.3	9.6	6.0	5.8	10.5	15.0	24.6	28.4
7	58.40	sand + mud	0.4	44.7	5.6	7.4	13.9	30.3	33.6	2.2	6.9
9	71.00	sand + mud	0.5	55.7	12.4	14.3	16.5	10.1	7.3	24.3	15.2
10	55.46	sand + mud + shells	0.4	61.1	26.8	21.6	9.1	12.2	8.4	1.2	20.6
12	39.76	sand	0.4	94.0	3.0	4.0	42.9	40.4	8.8	0.2	0.7
13	36.37	sand + mud + shells	0.3	17.6	3.2	1.7	1.9	11.2	44.5	21.3	16.1
14	29.73	mud + shells	0.5	26.9	4.7	16.0	37.6	34.0	6.8	0.0	0.8
23	16.30	sand + shells	0.2	50.0	1.3	1.1	1.0	4.2	58.4	22.6	11.5
29	62.18	mud + sand	0.8	27.1	2.1	0.8	1.5	6.4	66.0	19.2	4.0
30	66.05	mud	1.5	24.1	2.9	1.6	1.2	1.8	23.4	38.2	30.9
39	58.58	mud + sand	0.7	53.2	0.0	0.0	0.1	1.4	50.1	35.6	12.7
41	24.83	sand + shells + mud	0.5	71.9	21.8	14.1	13.3	11.7	17.4	12.2	9.6
47	27.90	sand + mud	0.5	30.0	0.2	0.4	0.9	2.3	59.2	24.7	12.2
48	28.16	sand + shells + mud	0.5	56.3	20.9	9.3	8.2	5.2	23.5	13.7	19.2
49	70.75	mud	1.0	37.4	2.3	1.3	2.0	5.3	50.4	24.9	13.9
50	79.55	mud + sand + shells	1.0	20.1	0.7	0.4	0.8	1.1	9.4	65.8	21.8
51	21.55	shells	0.2	85.9	8.1	11.8	35.6	37.5	5.5	0.1	1.3
53	12.46	sand + mud	0.4	34.4	0.1	0.1	0.3	0.7	69.4	14.1	15.3
59	66.82	mud + sand + shells	1.0	28.6	0.4	2.0	8.9	17.0	44.0	11.9	15.8
60	59.13	mud	1.5	27.3	0.0	0.1	0.8	5.6	22.7	0.0	70.8
64	6.00	Fine sand	0.2	14.2	0.0	0.1	0.9	50.6	22.0	19.0	7.4
68	17.22	sand + shells	0.3	81.2	18.5	24.4	30.2	18.0	6.6	1.5	0.7
69	66.40	mud + sand + shells	0.8	90.9	34.0	11.1	14.5	12.2	6.3	4.6	17.2
70	64.13	mud	1.9	22.9	0.0	0.1	0.3	1.4	27.0	35.5	35.6
71	29.33	mud	1.1	26.0	0.0	0.0	0.1	9.8	5.6	58.9	25.7
72	11.30	rocky	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

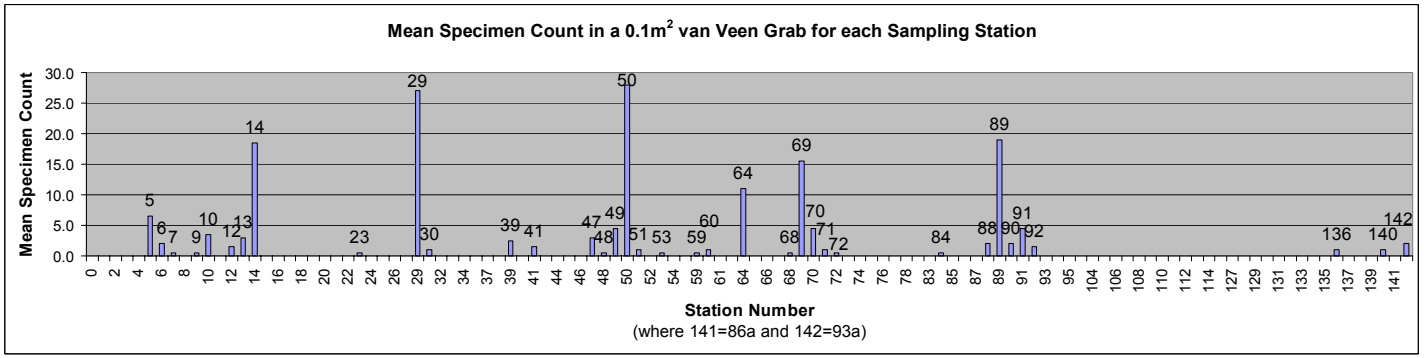
Verified Stations	Depth (m)	Sediment type	organic C %	Carbonate %	Granule %	VC Sand %	C Sand %	M Sand %	F Sand %	VF Sand %	Silt-Clay %
84	17.85	mud	1.3	14.8	0.0	0.0	0.0	0.0	0.3	6.3	93.4
88	37.65	mud	0.9	27.7	11.9	7.0	5.2	13.6	12.9	10.2	39.1
89	81.60	mud	1.8	18.5	2.2	0.3	0.6	2.6	44.4	16.3	33.6
90	67.80	mud	0.9	19.4	2.0	0.2	1.7	22.5	53.3	9.2	11.1
91	40.46	mud	1.6	26.9	0.0	0.0	0.0	0.2	2.1	39.2	58.4
92	23.36	sand + mud	0.6	48.4	0.0	0.3	0.9	2.9	30.4	37.1	28.4
112	18.64	sand + shells	0.3	83.4	8.5	18.7	16.6	22.0	2.6	0.1	31.4
136	38.40	rocky	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
140	59.40	mud+sand+shells+stones	0.5	26.3	34.9	11.0	11.5	13.6	6.5	3.8	18.7
93a	1.00	Coarse sand, few shells fragments	0.1	84.8	2.6	7.3	19.7	65.0	4.9	0.2	0.2

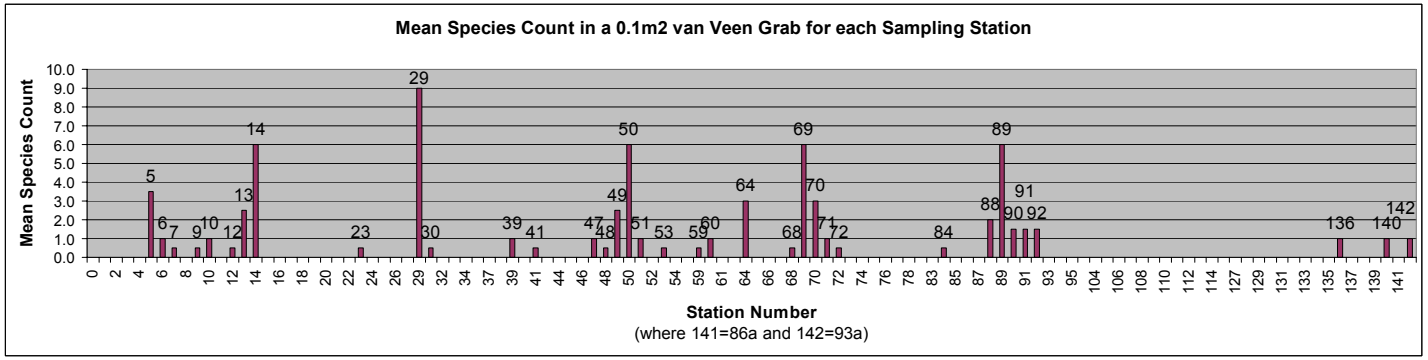
Appendix 3: Physicochemical properties of the 37 sample stations featuring Cirratulids including a broad description of sediment type and the percentage of organic carbon, carbonate, granule and very coarse, coarse, medium, fine and very fine sand, and silt and clay. These sediment categories were divided according to the Wentworth Grade Classification. Depth is also a factor that may affect the biology: It is seen to vary from 1m at site 93a to 82m at site 89.

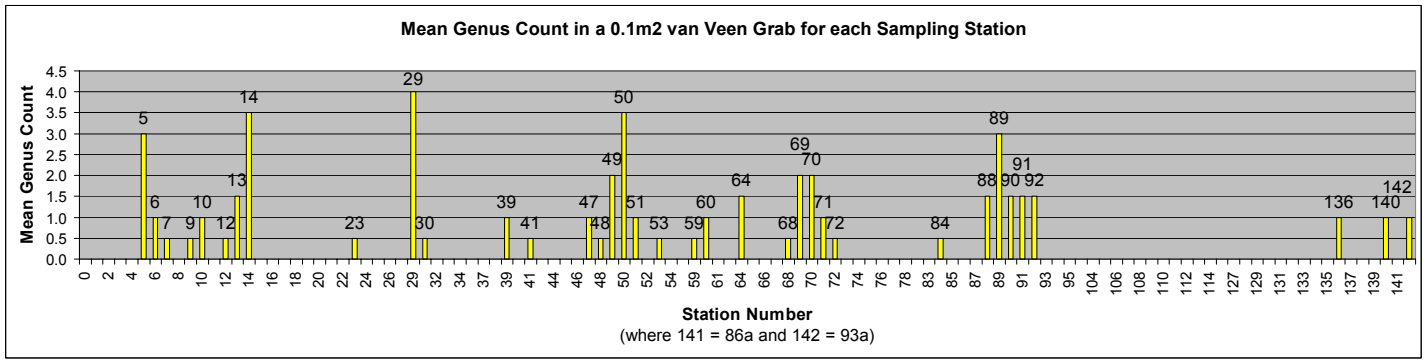
Station	Sample Method	Taxa Present																															Total Number		
		Aphelochaeta					*Caulleriella*								*Chaetozone*					*Monticellina*									*Thanyx*		*Cirrif-ormia*		Genus	Species	Specimens
		A	*B*	*C*	*D*	*E*	*A*	*B*	*C*	*D*	*E*	*F*	*Ind. A*	*Ind. B*	*A*	*B*	*C*	*D*	*E*	*A*	*B*	*C*	*D*	*E*	*F*	*G*	*H*	*Ind. A*	*A*	*B*	*A*	*Ind. A*			
5	Grab B																1																1	1	1
	Grab C			1								1						2		1					6					1			5	6	12
6	Grab C																				3					1							1	2	4
7	Grab C																		1														1	1	1
9	Grab A									1																							1	1	1
	Trawl																3															2	2	2	5
10	Grab A																	1															1	1	1
	Grab B																			6													1	1	6
12	Grab A																								3								1	1	3
13	Grab A																								1								1	1	1
	Grab B															1					2					1		1					2	4	5
14	Grab B	1	4	2									1	1			5				5				4								4	8	23
	Grab C		6	2													3								3								3	4	14
23	Grab A															1																	1	1	1
29	Grab A		2		1										2			1		5		2	1			1							3	8	15
	Grab B		2	6	1			9	1											7			3	4	3	3							3	10	39
30	Grab C																2																1	1	2
39	Grab A														4																		1	1	4
	Grab B																						1										1	1	1
41	Grab A															3																	1	1	3
47	Grab A							1												5													2	2	6
	Trawl																3																1	1	3
48	Grab A															1																	1	1	1
49	Grab B		2	1								1										1				4							3	5	9
50	Grab A			7				3			8				1					12	4		2		1								4	8	38
	Grab B																			3		6	3		3	5							1	5	20
51	Grab A					1																											1	1	1
	Grab B						1																										1	1	1
53	Grab B																								1								1	1	1
59	Grab B						1																										1	1	1

Station	Sample Method	Taxa Present																															Total Number		
		Aphelochaeta					*Caulleriella*								*Chaetozone*					*Monticellina*									*Thanyx*		*Cirrif-ormia*		Genus	Species	Specimens
		A	B	C	D	E	A	B	C	D	E	F	Ind. A	Ind. B	A	B	C	D	E	A	B	C	D	E	F	G	H	Ind. A	A	B	A	Ind. A			
60	Grab A																			1													1	1	1
	Grab B														1																		1	1	1
64	Grab A	1													3		1			10	3				5								3	6	23
68	Grab A														1																		1	1	1
69	Grab B		1	2	2			1							2		1			4	4	2	5		5	2							4	12	31
70	Grab A										1									2													2	2	3
	Grab B	1	1	1																					3								2	4	6
71	Grab A																							1									1	1	1
	Grab B																		1														1	1	1
72	Grab A														1																		1	1	1
84	Grab B																			1													1	1	1
88	Grab A	1													1																		2	2	2
	Grab B																			1					1								1	2	2
89	Grab A															1				11													2	2	12
	Grab B		1	1	4		1								1			1		14		1	1				1						4	10	26
90	Grab B		1																	2									1				3	3	4
91	Grab A														3					6													2	2	9
	Grab B																			1													1	1	1
92	Grab A																					1											1	1	1
	Grab B																	1							1								2	2	2
93a	Grab A																												3				1	1	3
	Grab B								1																								1	1	1
112	Trawl																			1													1	1	1
136	Grab A																			1													1	1	1
	Grab B																														1		1	1	1
140	Grab C		1																				1										2	2	2
Species Total		4	21	23	8	1	3	14	2	1	9	2	1	1	20	7	19	6	2	94	21	13	17	5	40	17	1	1	4	1	1	2			
Genus Total		57					33								54					209									5		3				
Family Total		361																											Total Taxa				94	145	361

Appendix 4: Samples in which Cirratulid Specimens were found, including the number of individuals of each taxa found. Note that 'Ind' stands for 'Unidentifiable' due to lack of complete specimens







Appendix 5: Variation in Specimen, Species and Genus Counts between Stations show similar trends (stations at which cirratulids are present are labelled). Those stations featuring high specimen abundance also feature high species and genus abundance: diversity is high. Such distribution patterns reinforce the hypothesis that this is not an area of great disturbance from anthropogenic or other pollution, but an area of high biodiversity

Wentworth Grade Classification

Name	Grade limits (μm)
Granule	**4000-2000**
Very Coarse Sand	**2000-1000**
Coarse Sand	**1000-500**
Medium Sand	**500-250**
Fine Sand	**250-125**
Very Fine Sand	**125-62**
Silt-Clay	**<62**

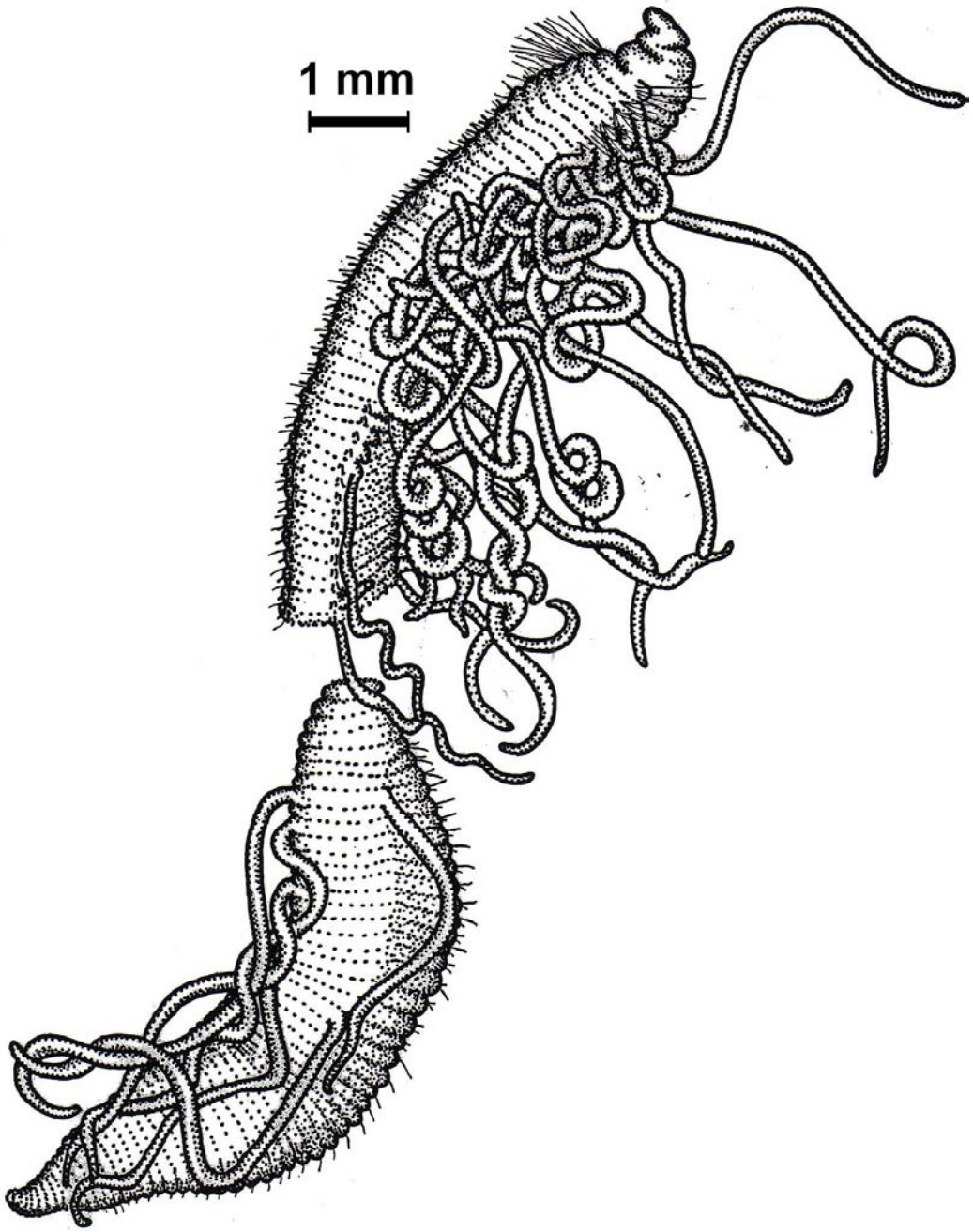
Appendix 6: The Wentworth Grade Classification as utilised in initial division of sediment

Appendix 7:

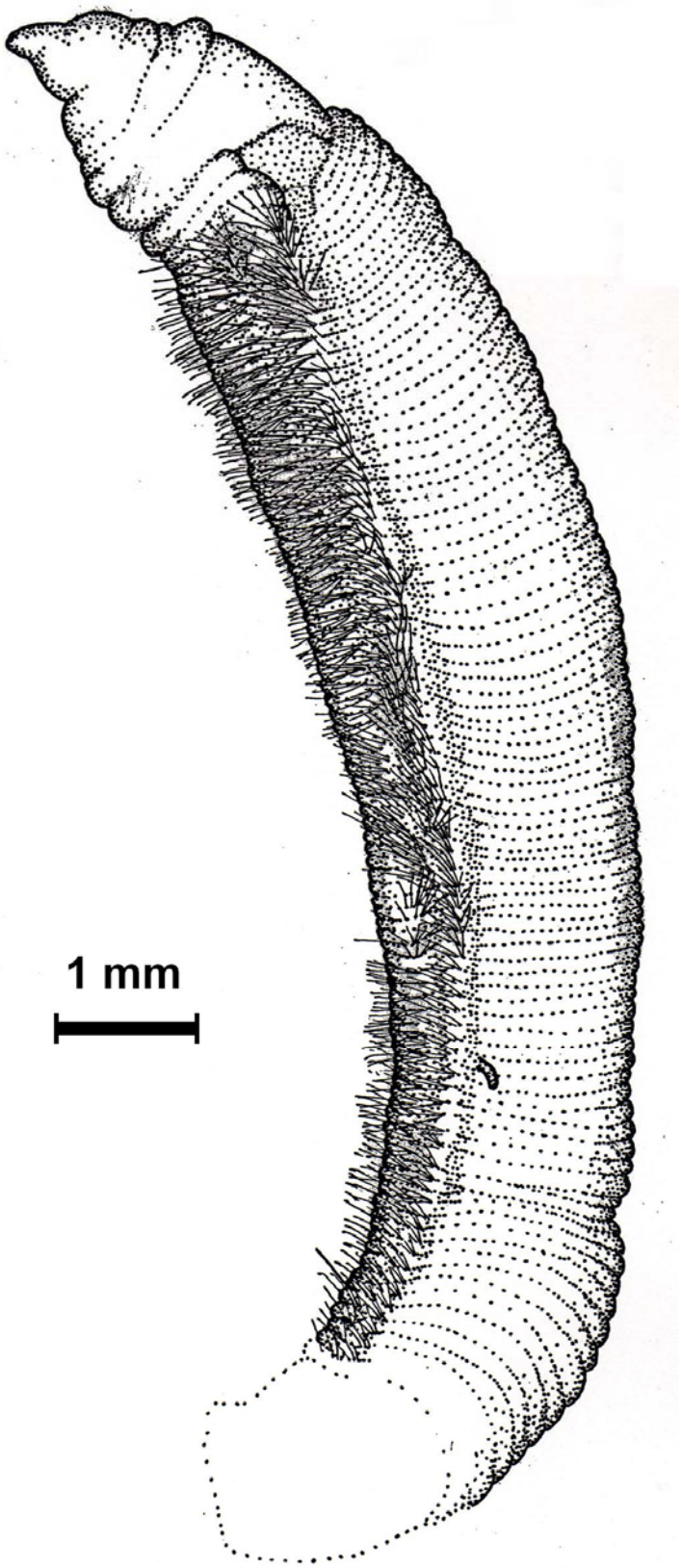
Scale drawings of Cirratulids from off the Las Perlas Archipelago in the Tropical Eastern Pacific:

Cirriformia A 91
Cirriformia Indet A 92
Aphelochaeta A 93
Aphelochaeta B 94
Aphelochaeta C 95
Aphelochaeta D 96
Aphelochaeta E 97
Chaetozone A 98
Chaetozone B 99
Chaetozone C 100
Chaetozone D 101
Chaetozone E 102
Monticellina A 103
Monticellina B 104
Monticellina C 105
Monticellina D 106
Monticellina E 107
Monticellina F 108
Monticellina G 109
Monticellina H 110
Caulleriella A 111
Caulleriella B 112
Caulleriella C 113
Caulleriella D 114
Caulleriella E 115
Caulleriella F 116
Tharyx A 117
Tharyx B 118

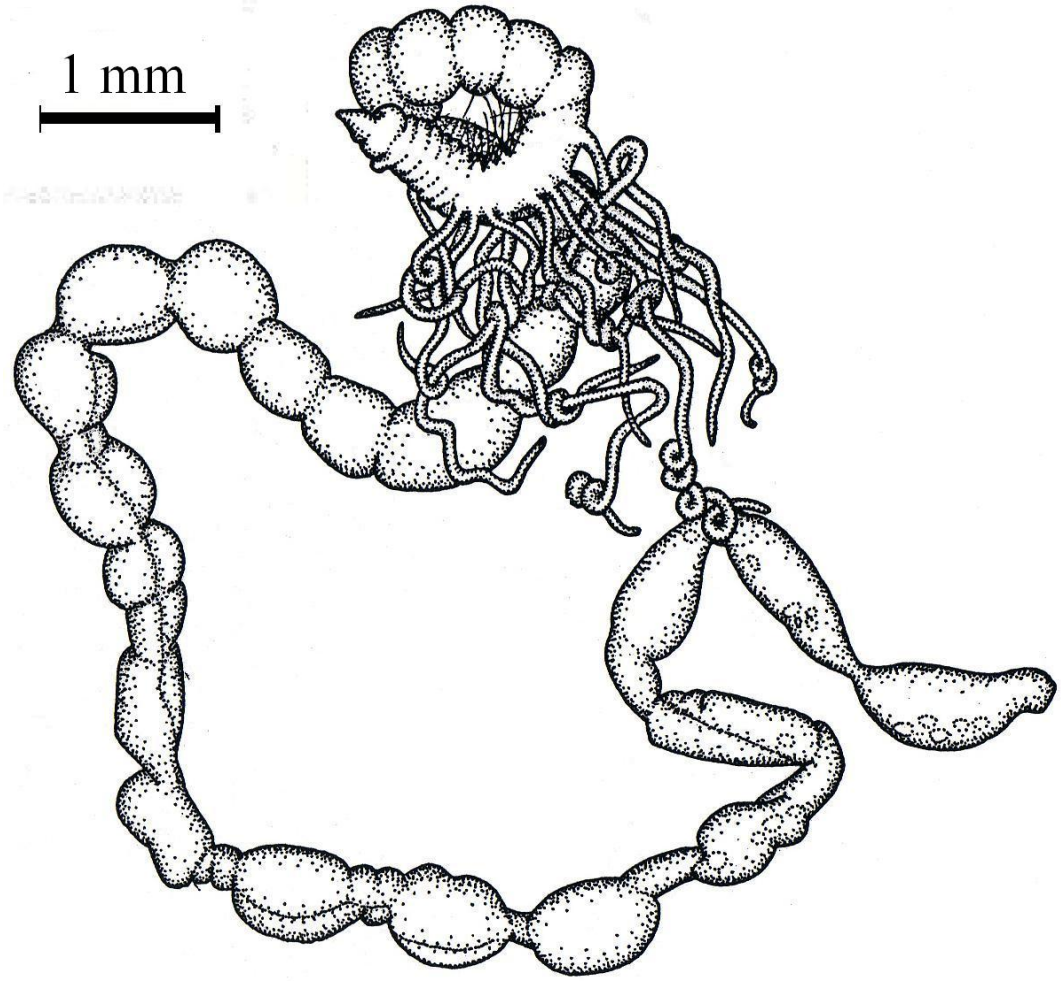
Cirriformia A



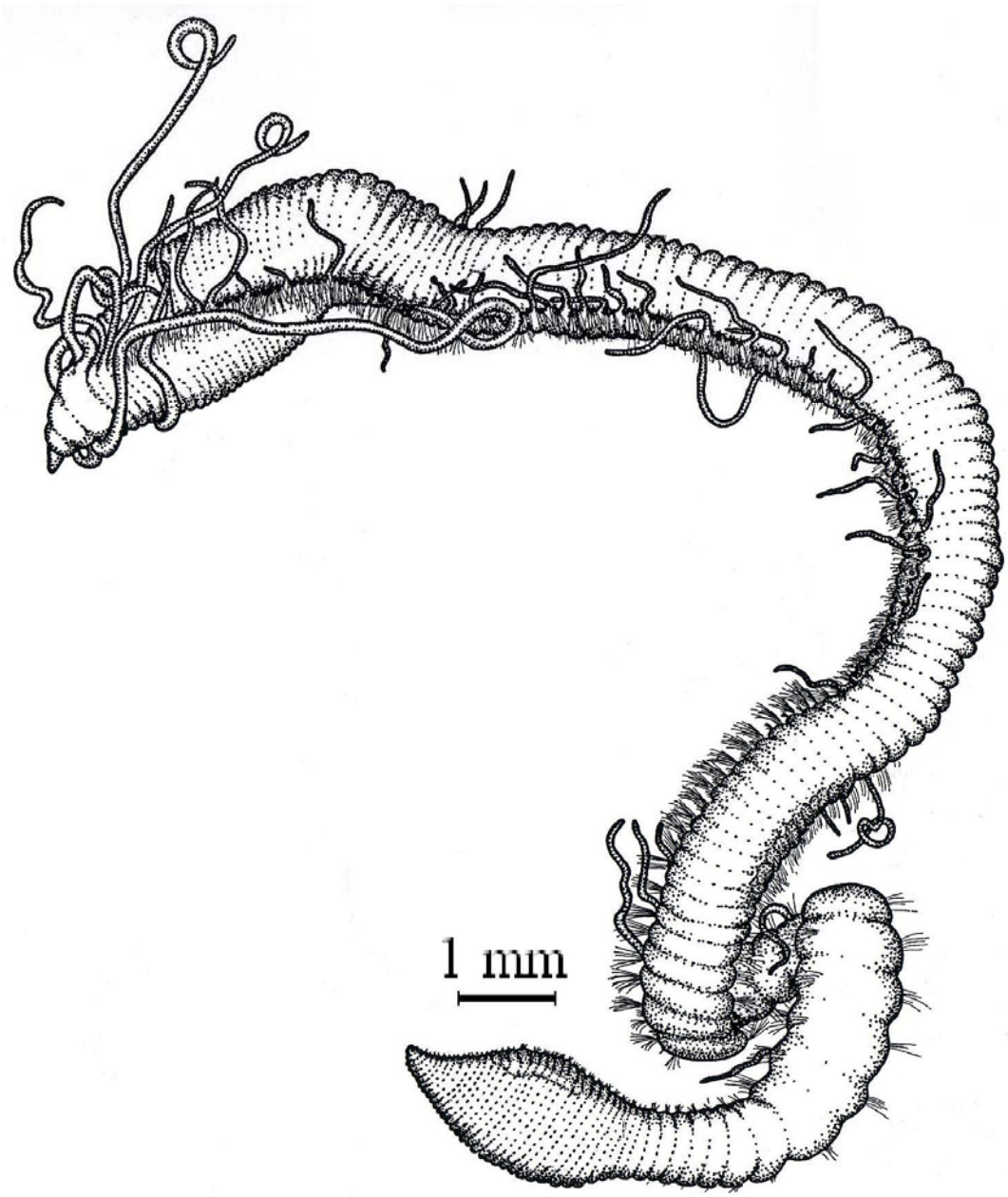
Cirriformia Indet A



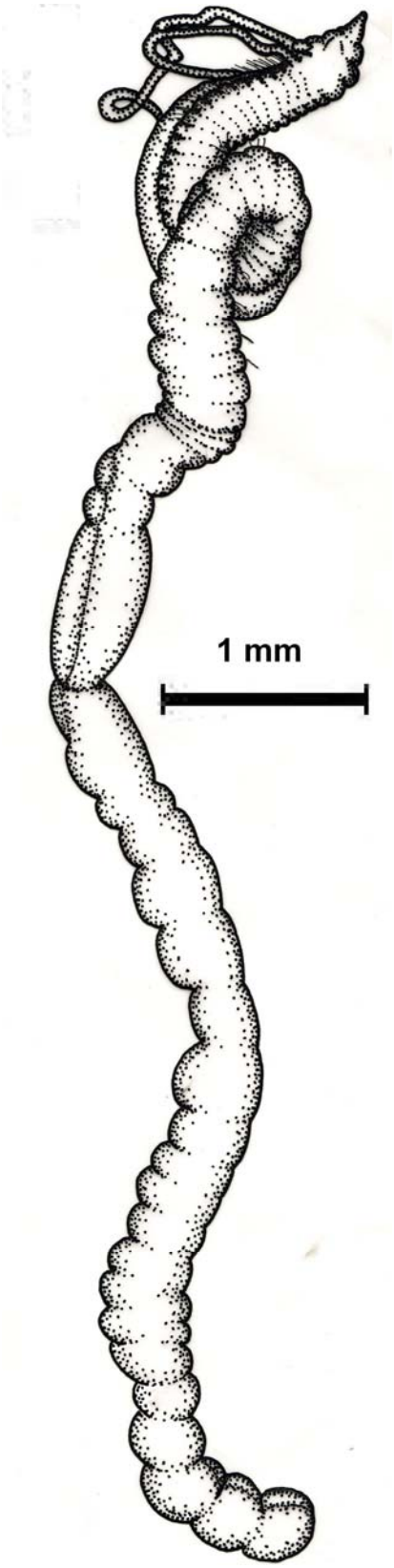
Aphelochaeta A



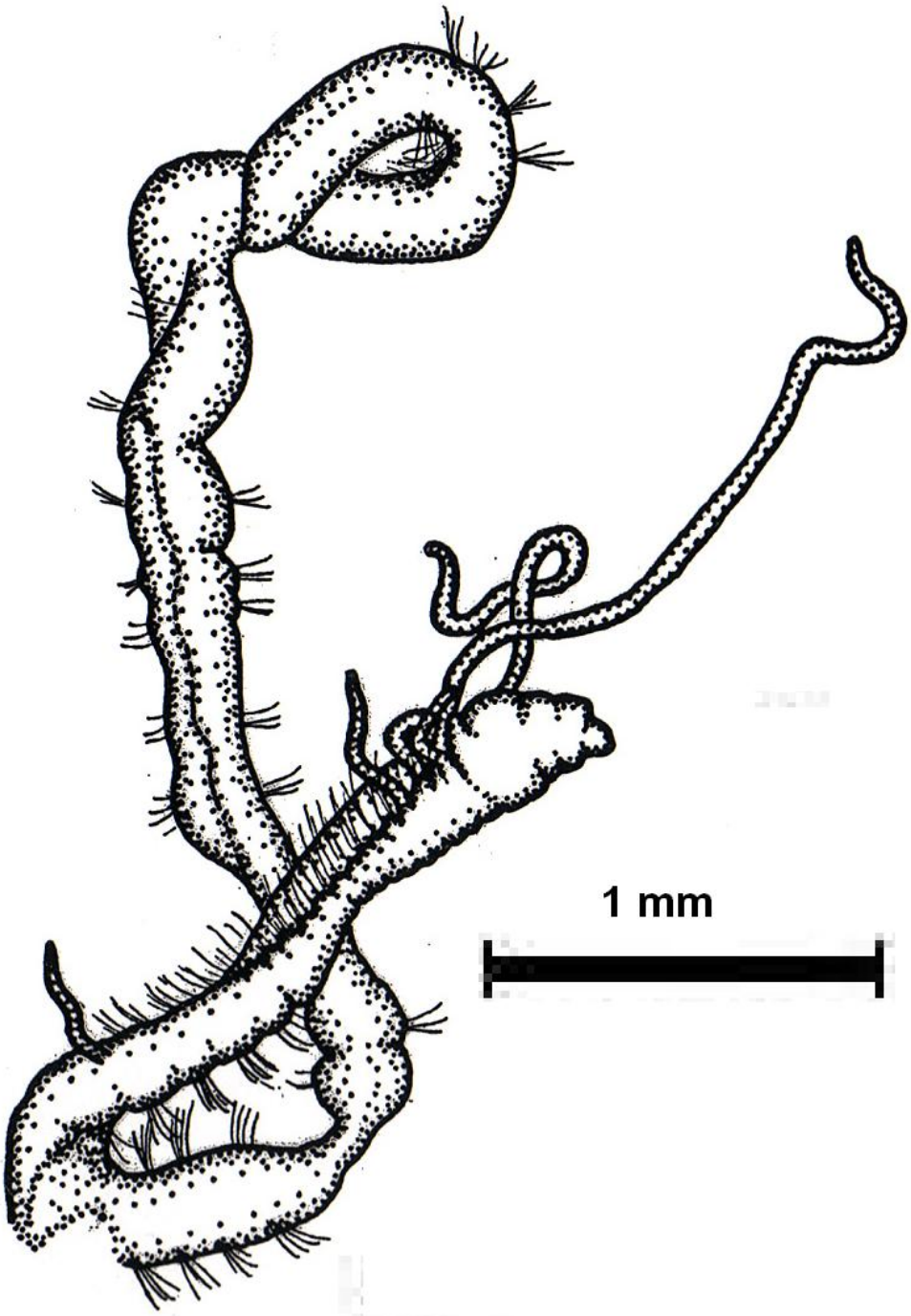
Aphelochaeta B



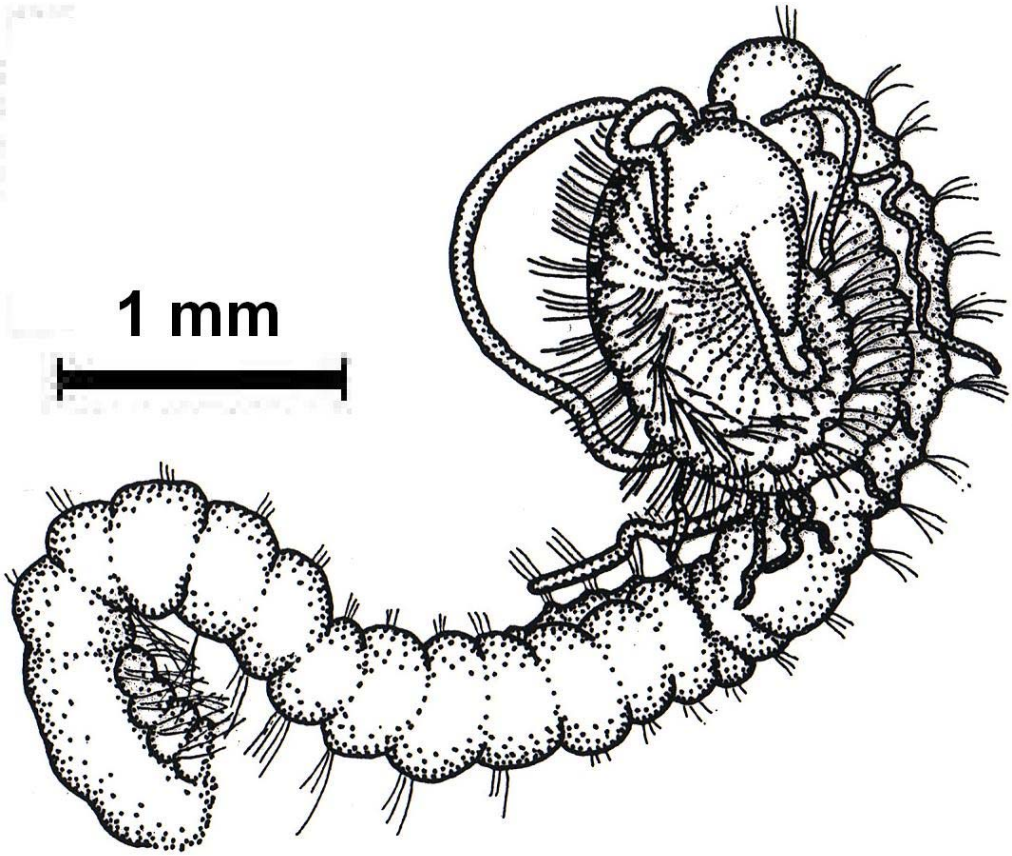
Aphelochaeta C



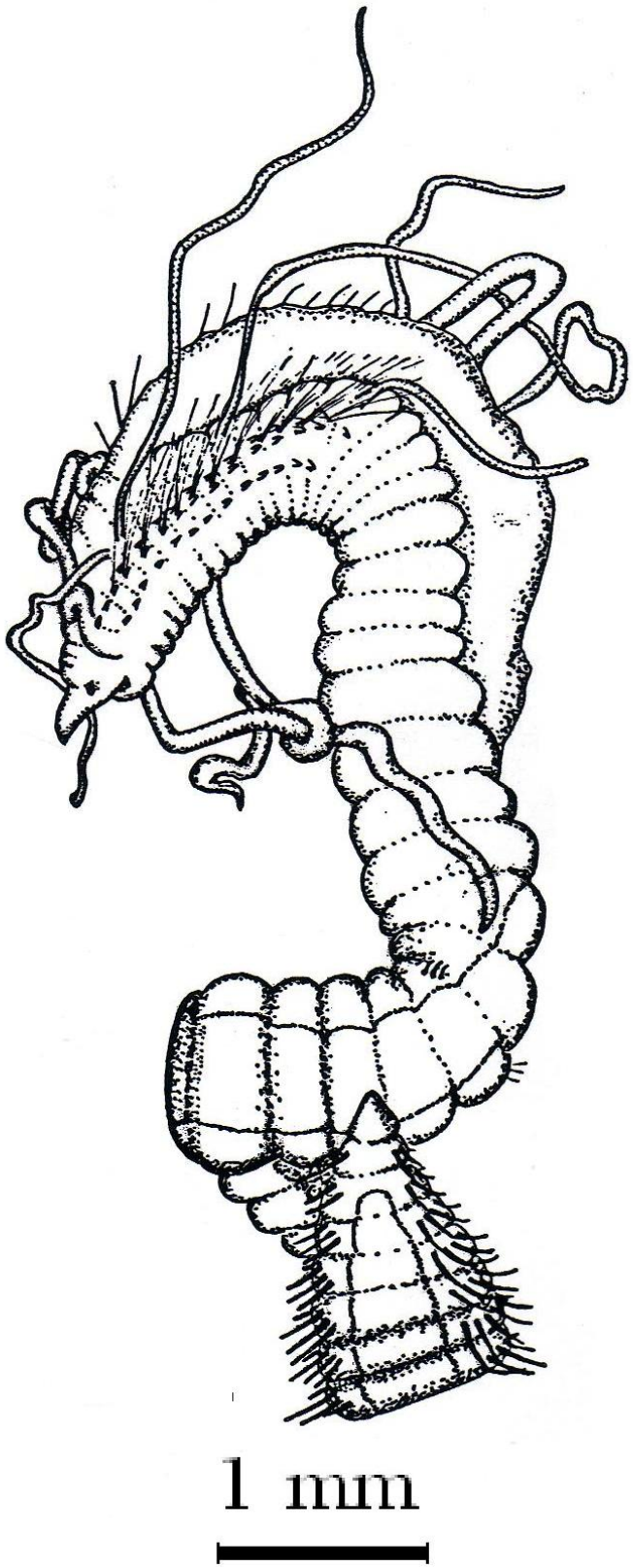
Aphelochaeta D



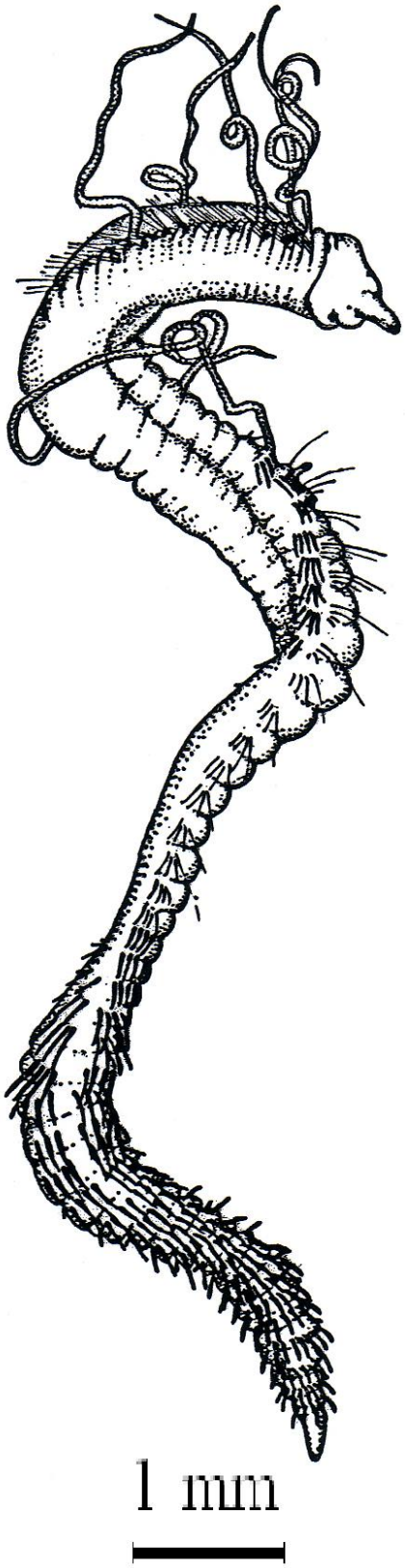
Aphelochaeta E



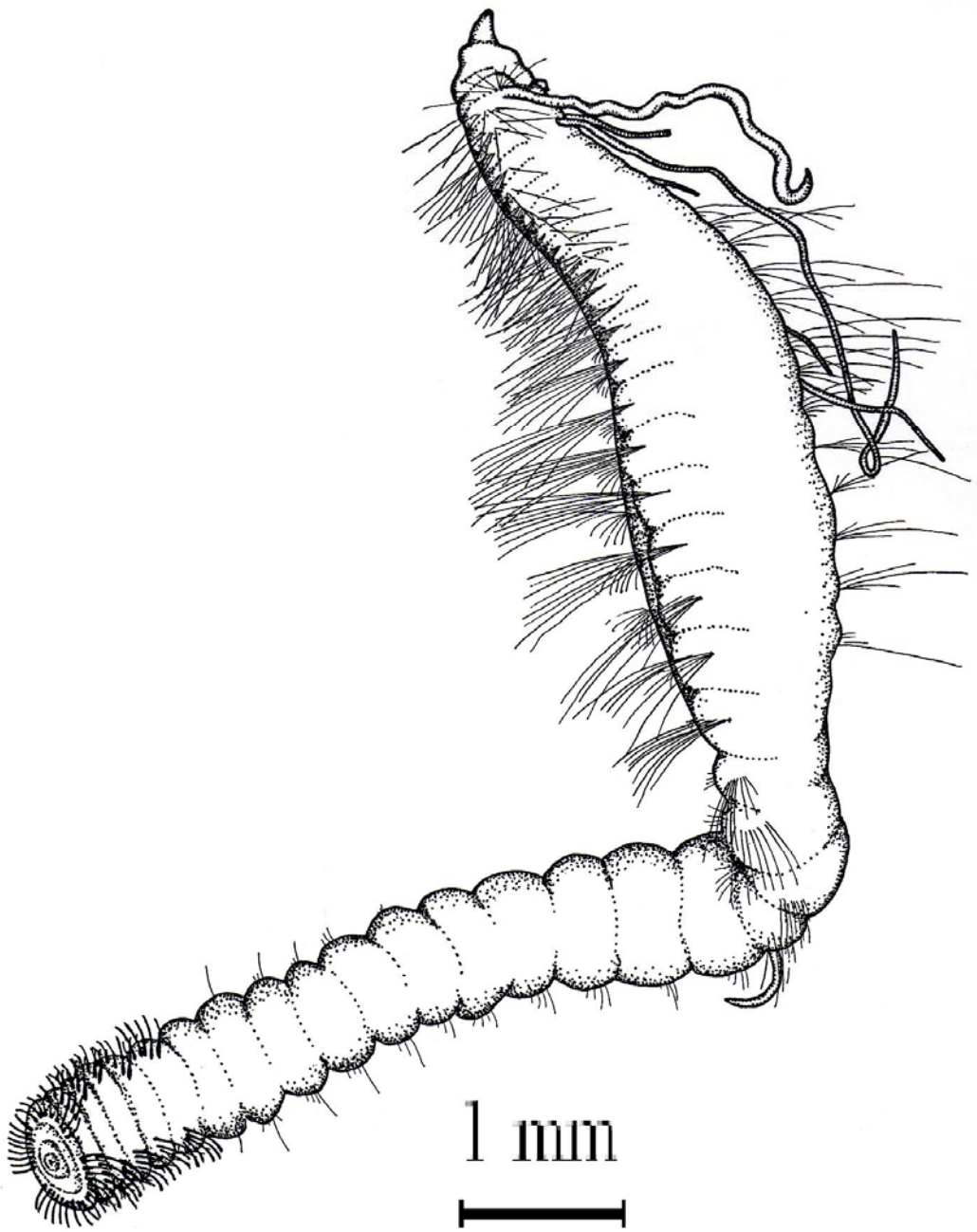
Chaetozone A



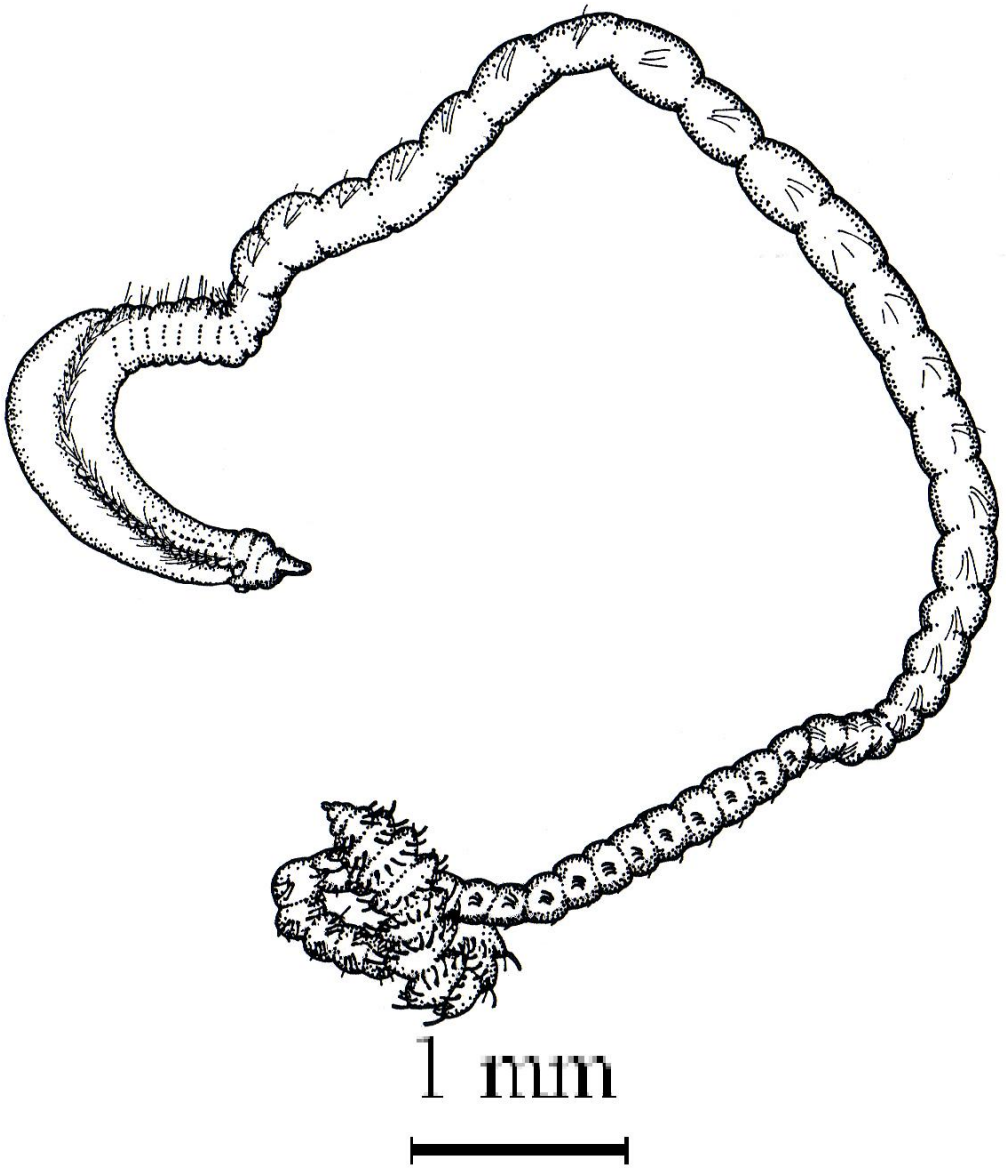
Chaetozone B



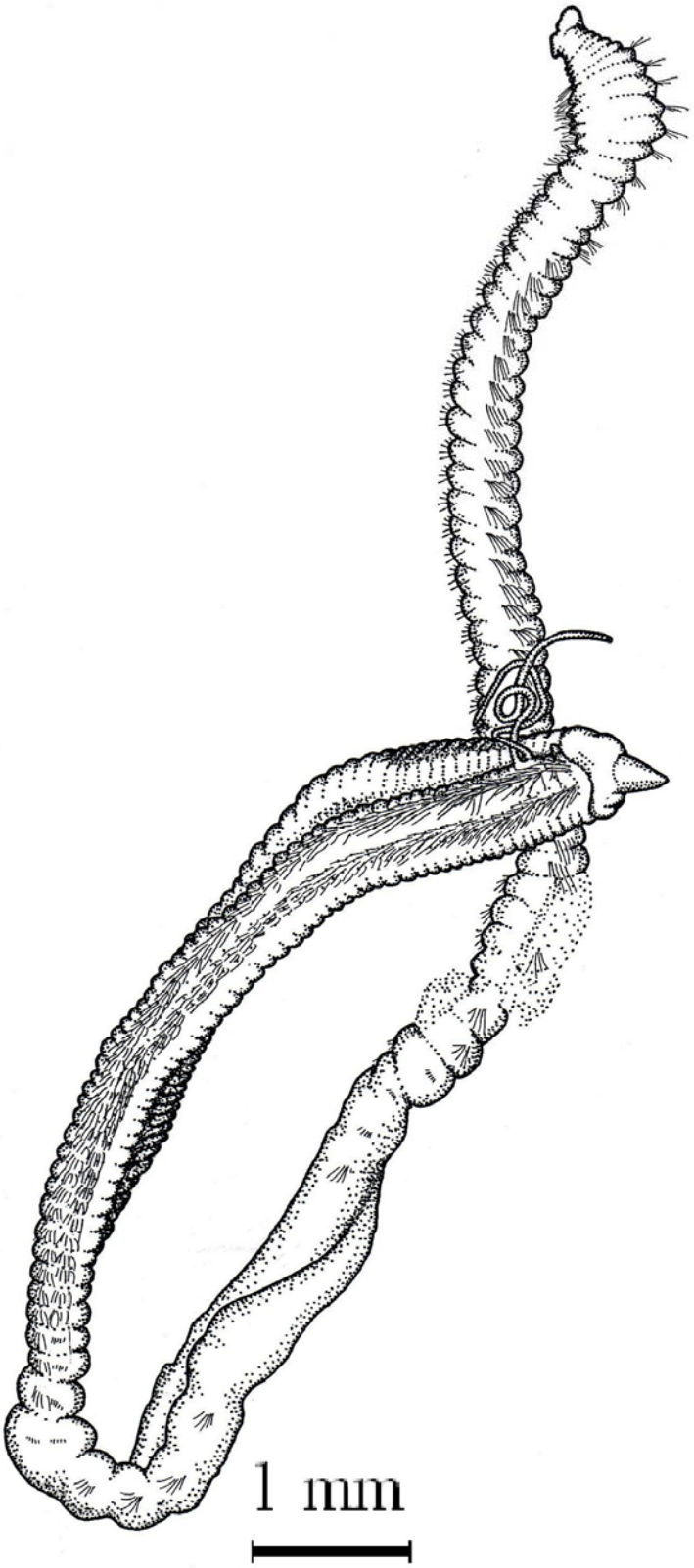
Chaetozone C



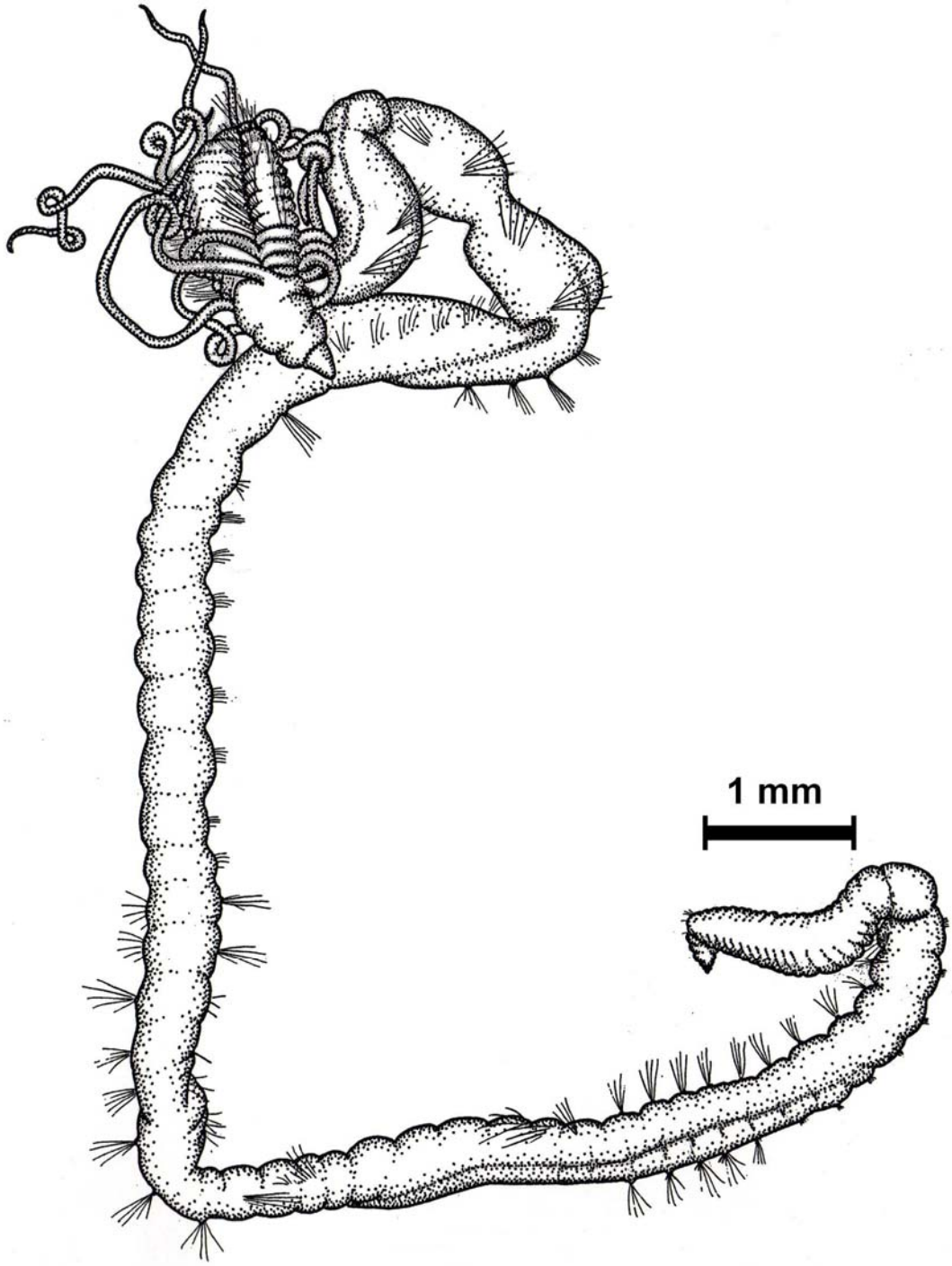
Chaetozone D



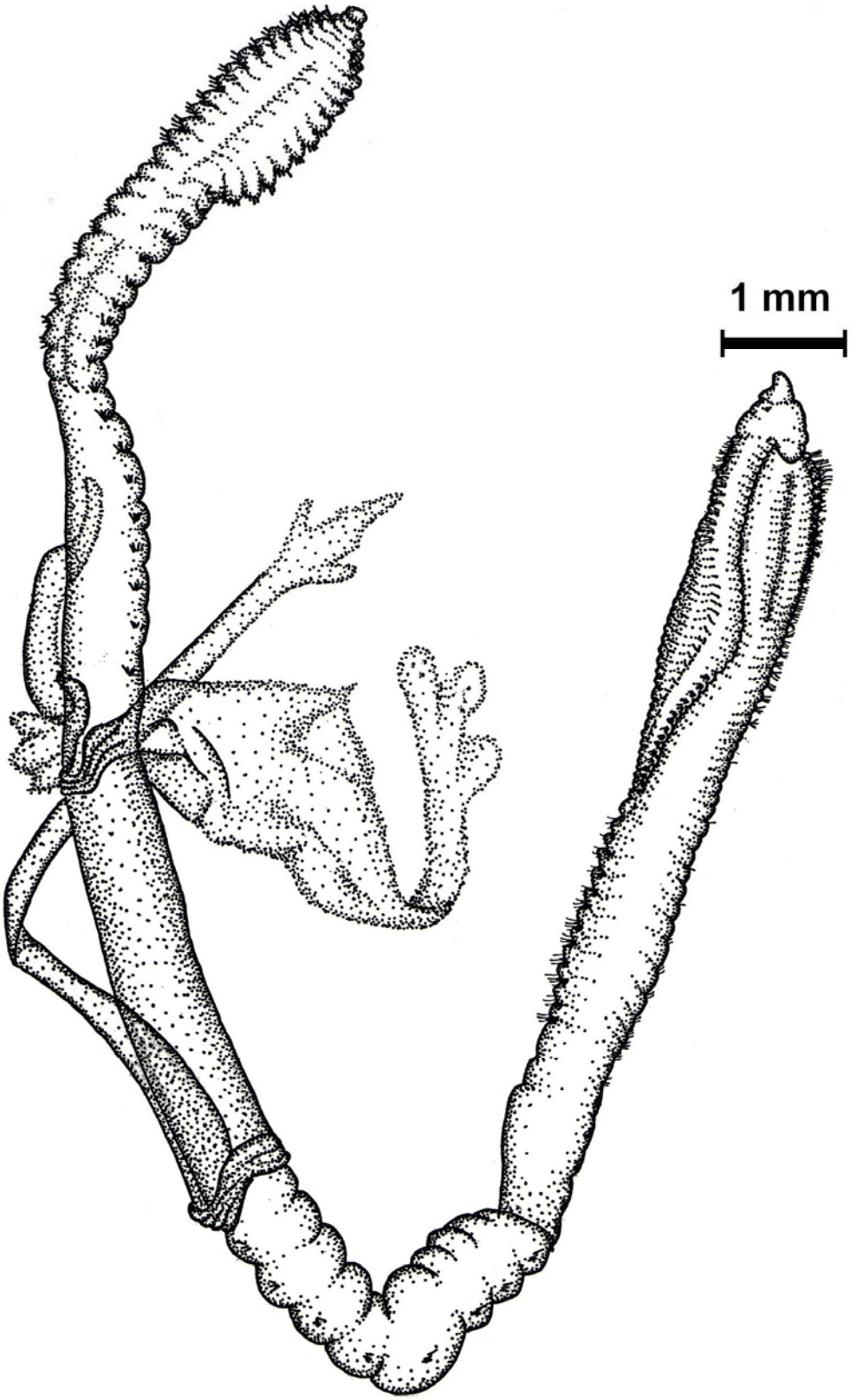
Chaetozone E



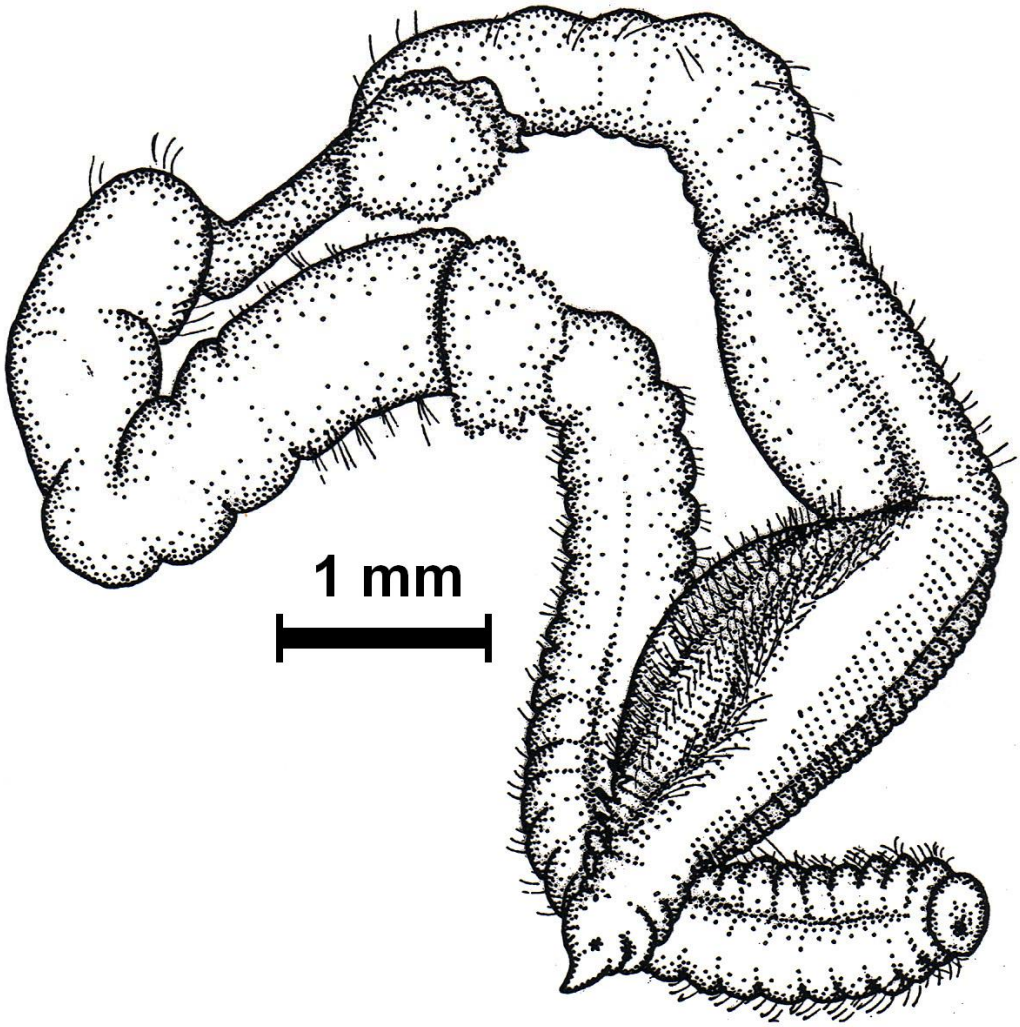
Monticellina A



Monticellina B



Monticellina C



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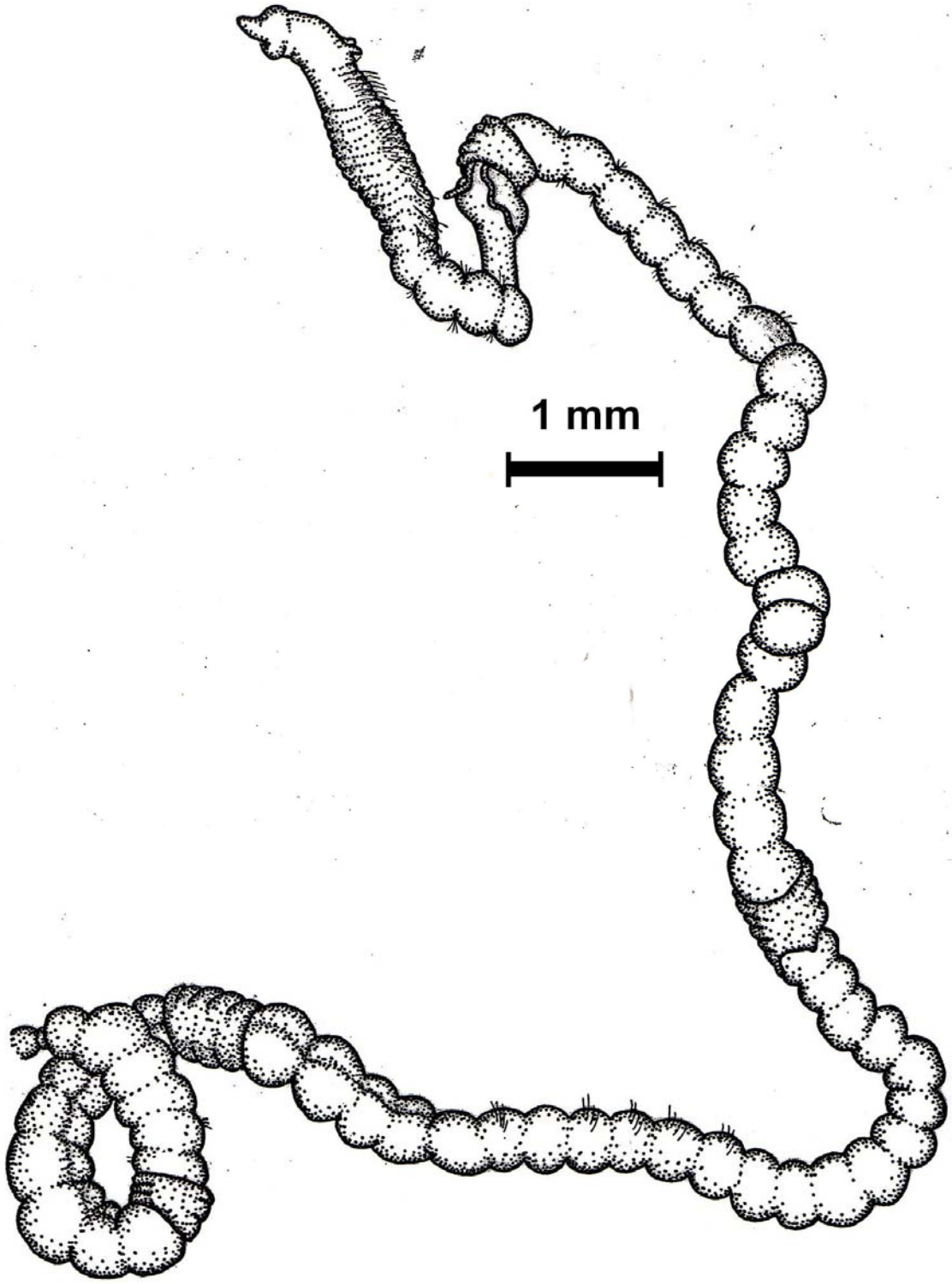

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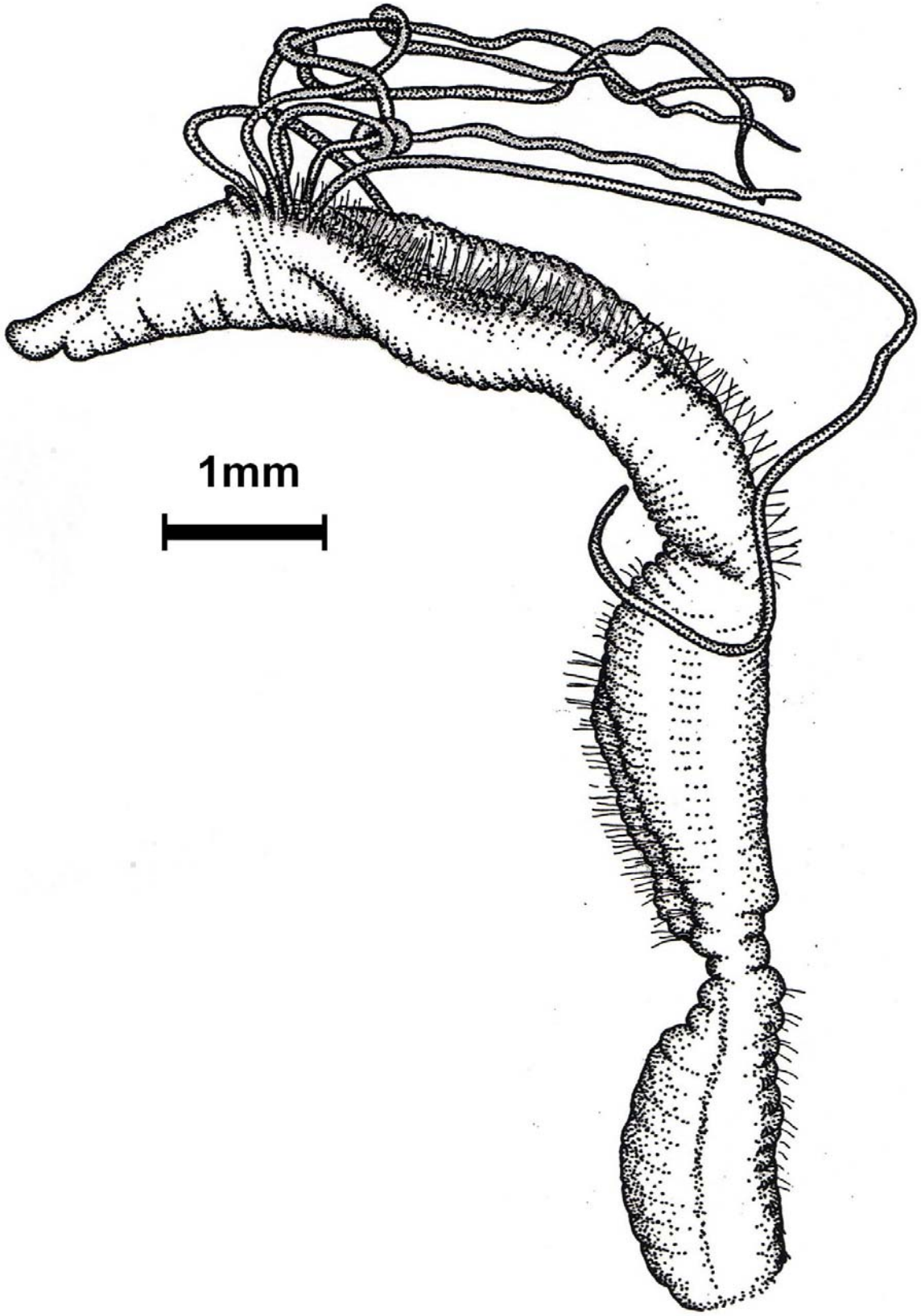

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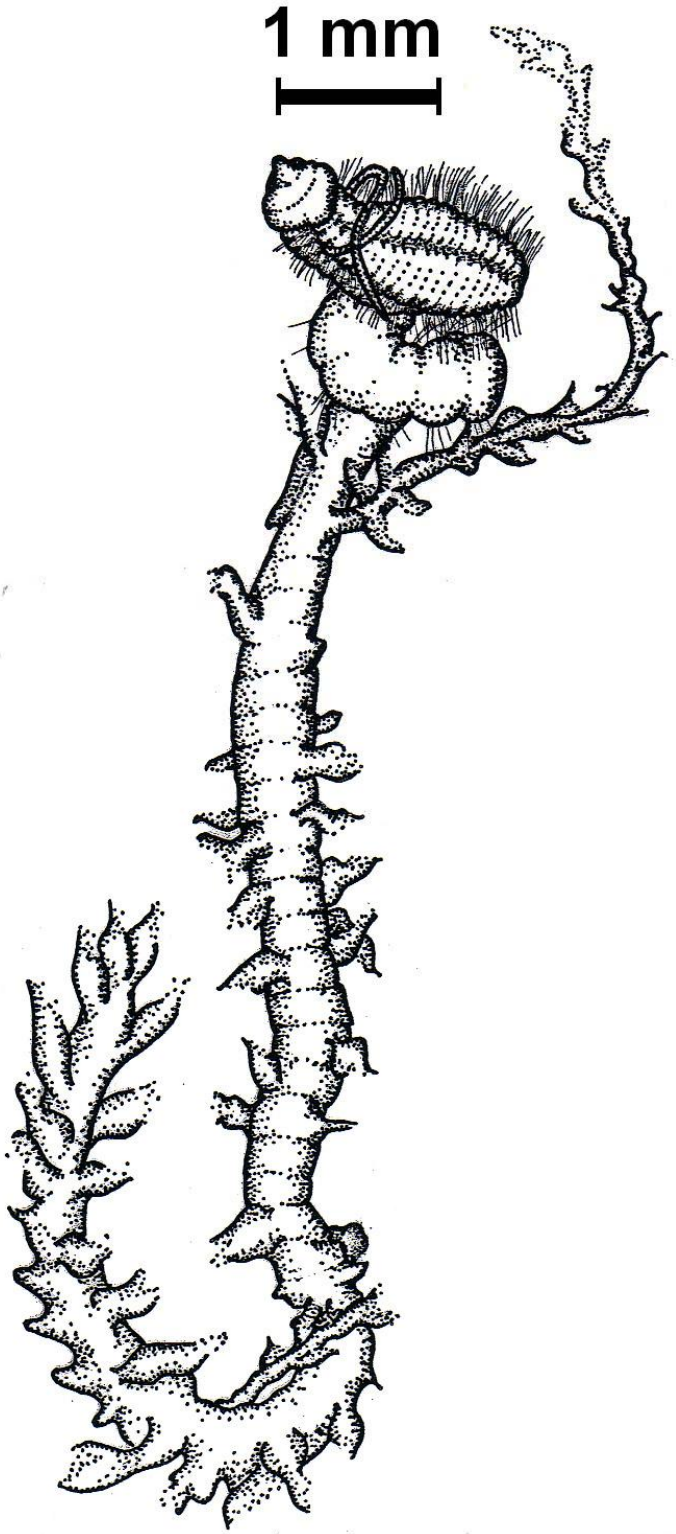

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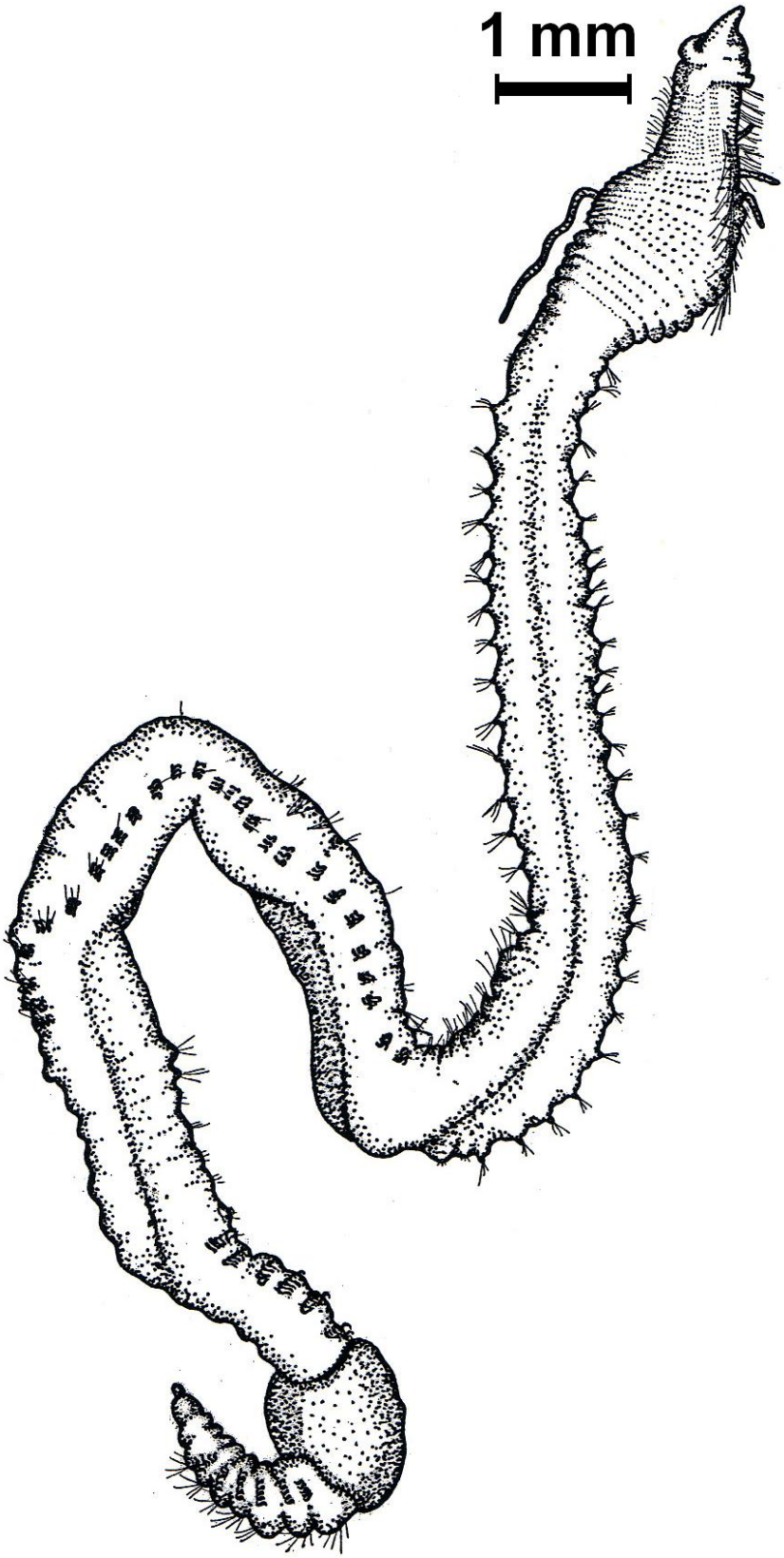

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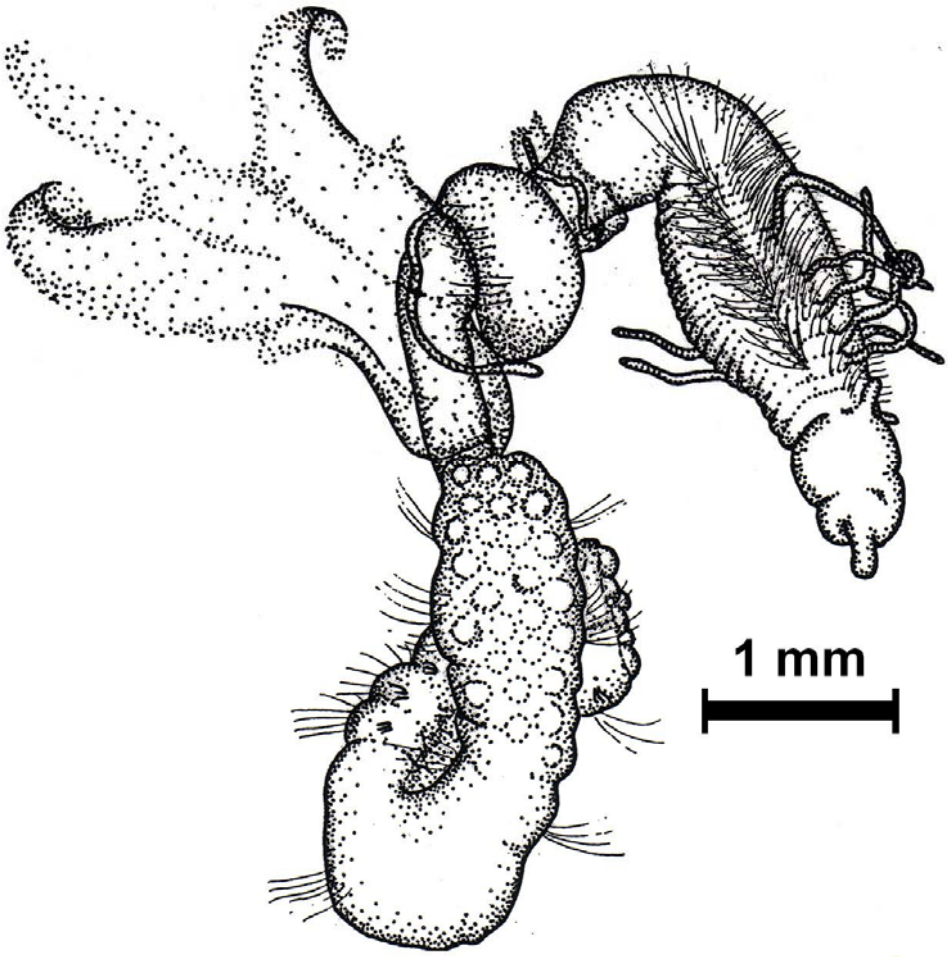

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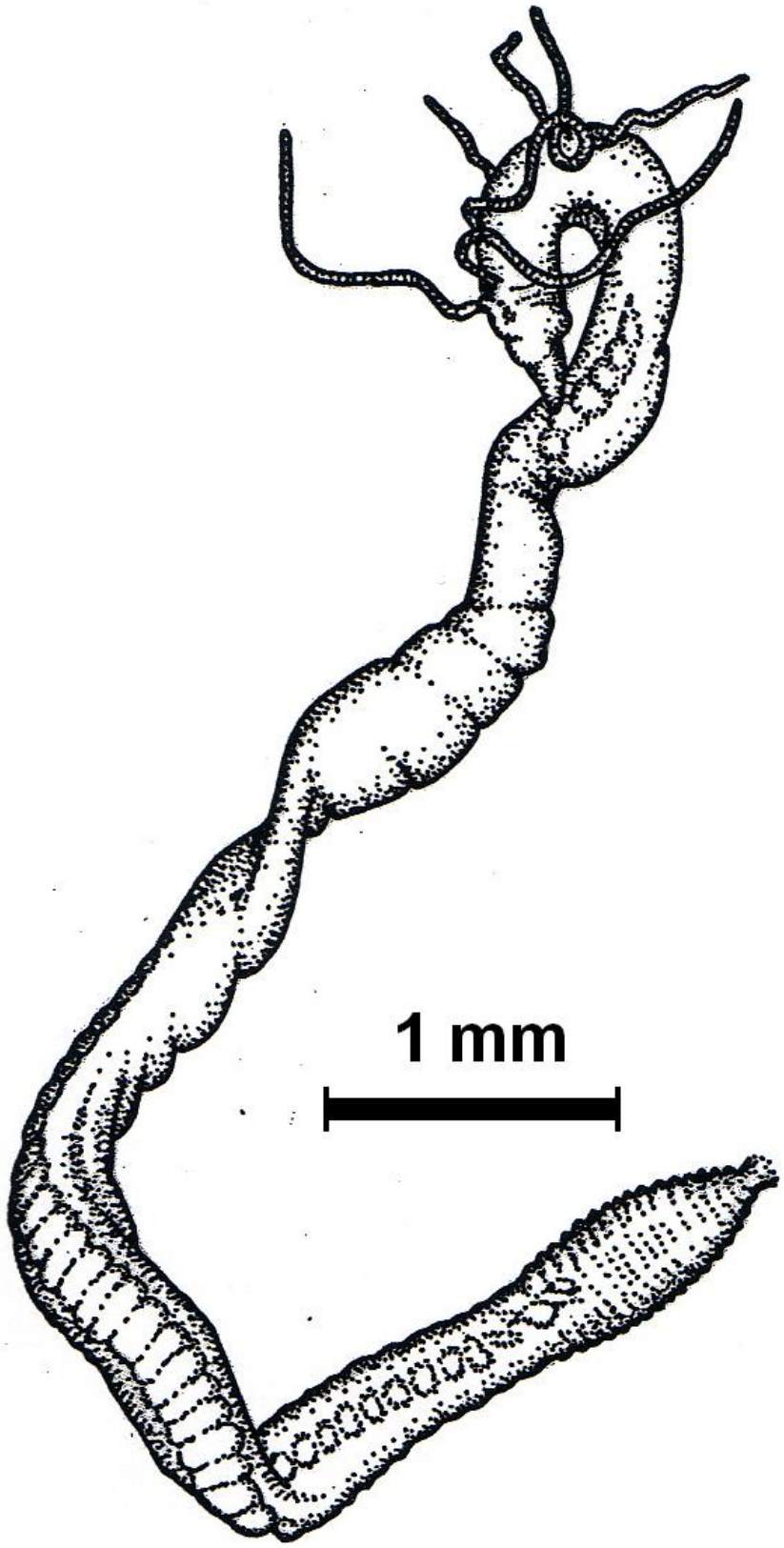

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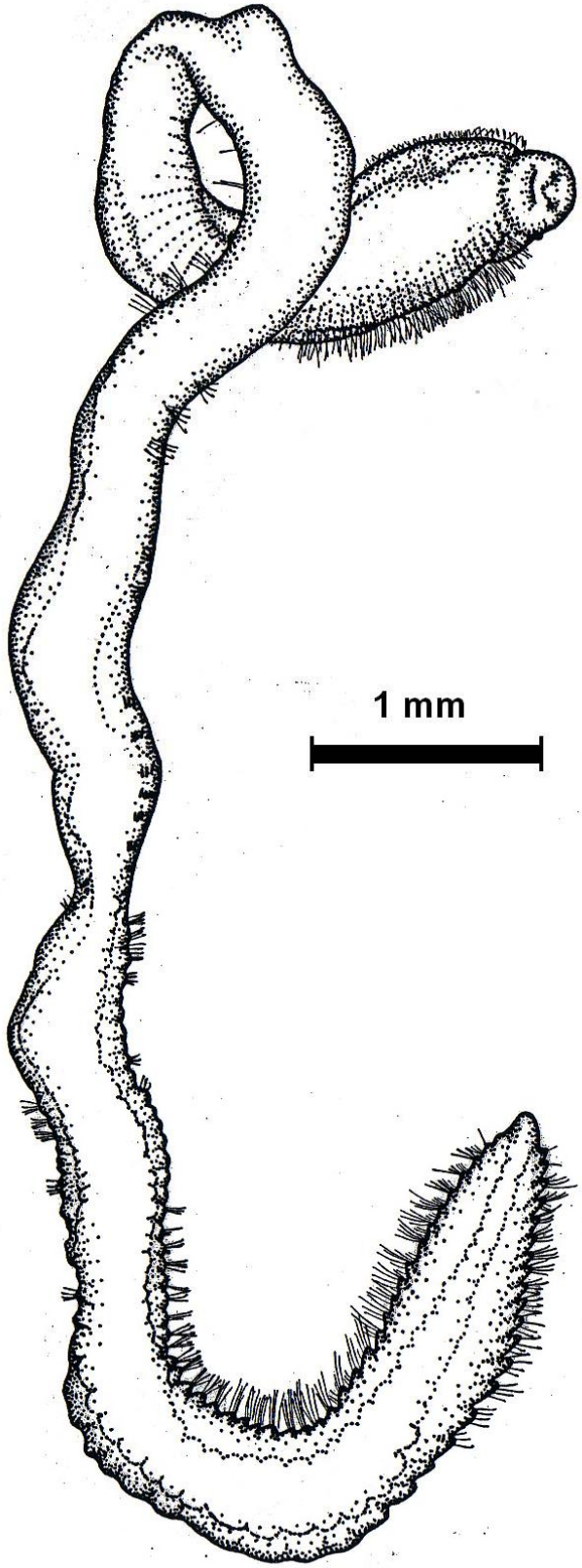

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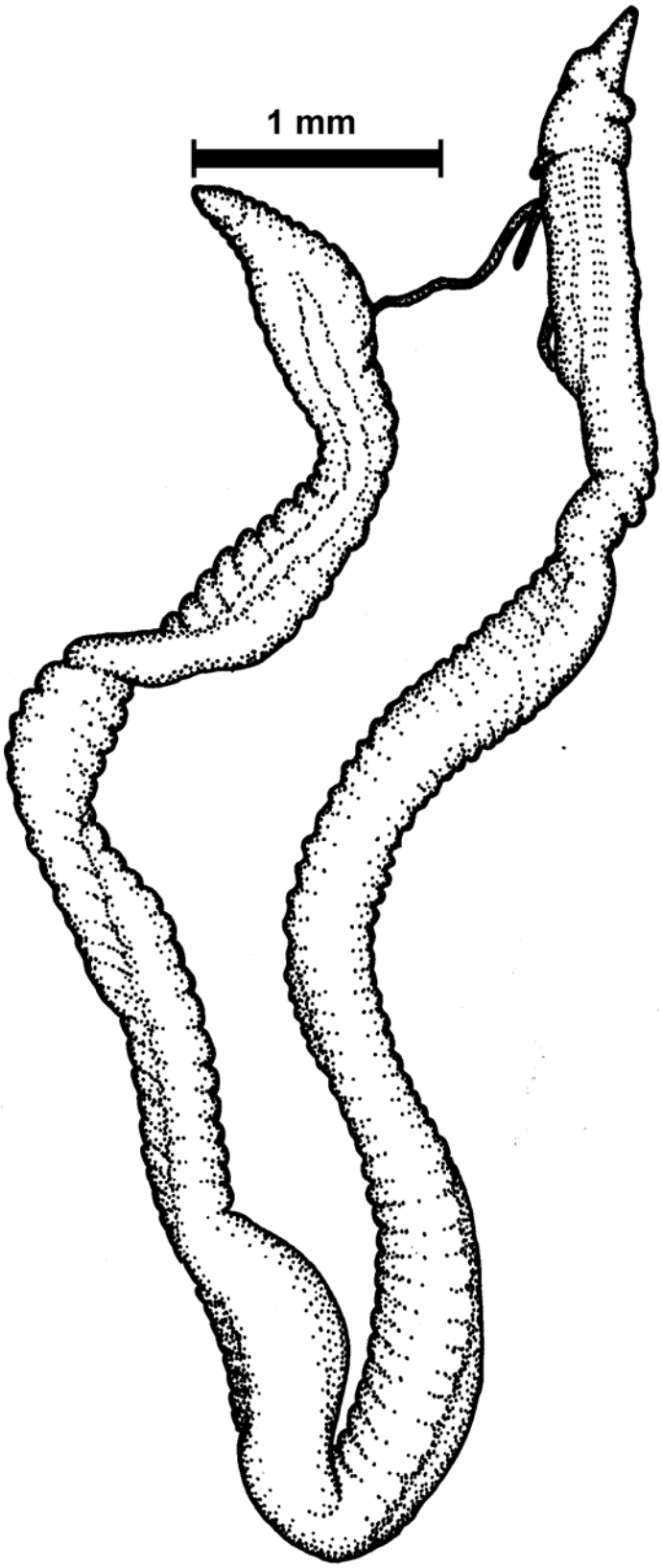

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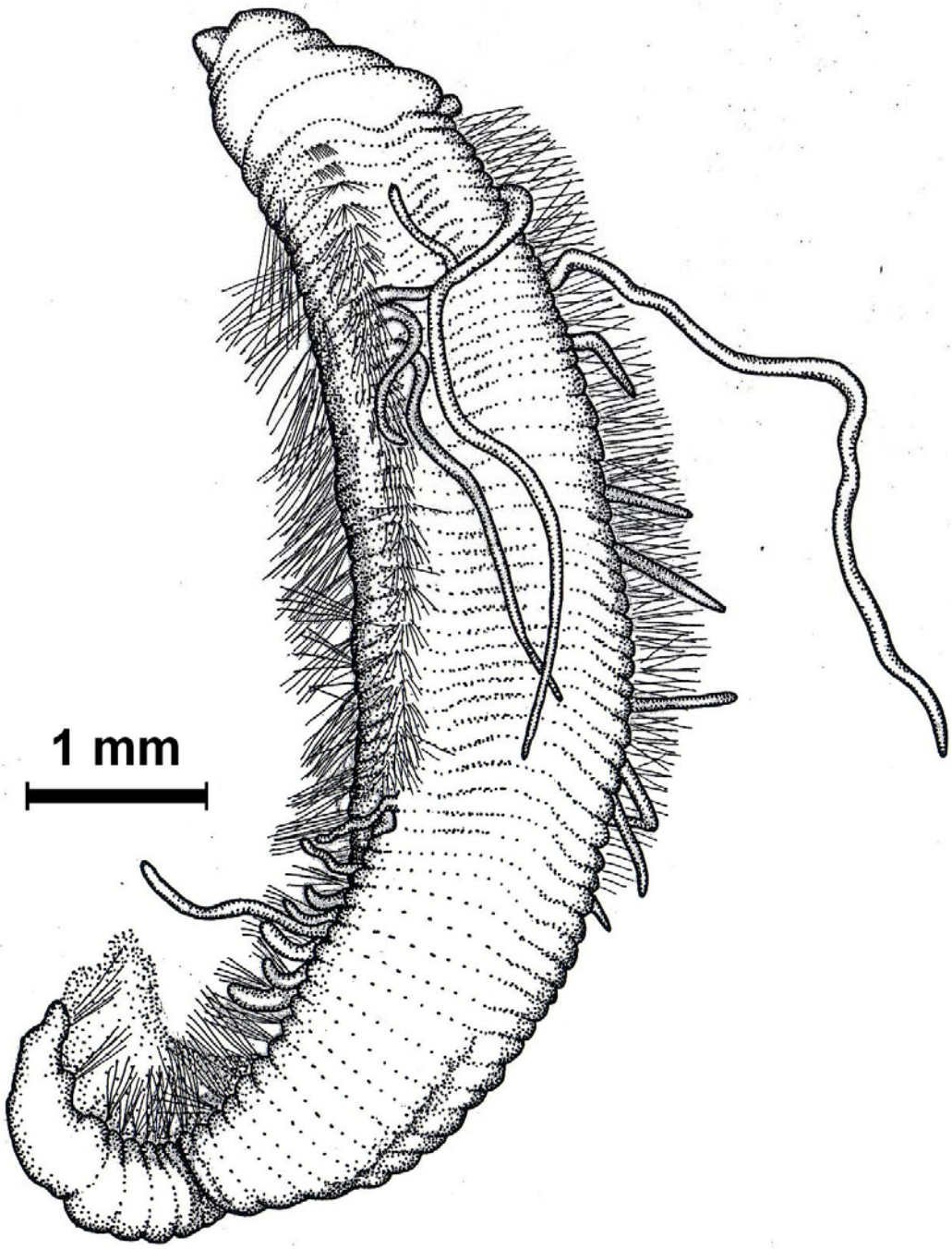

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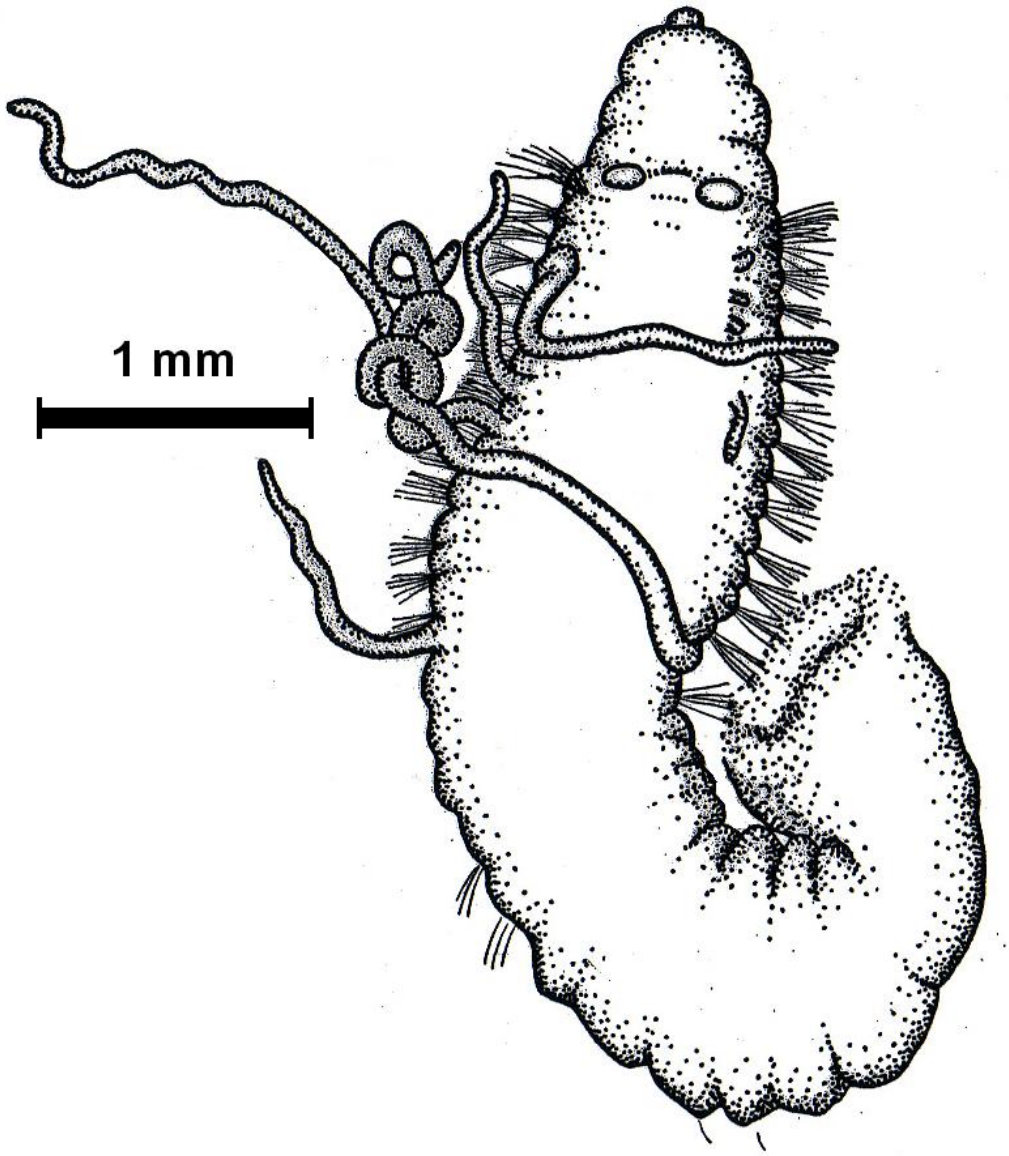

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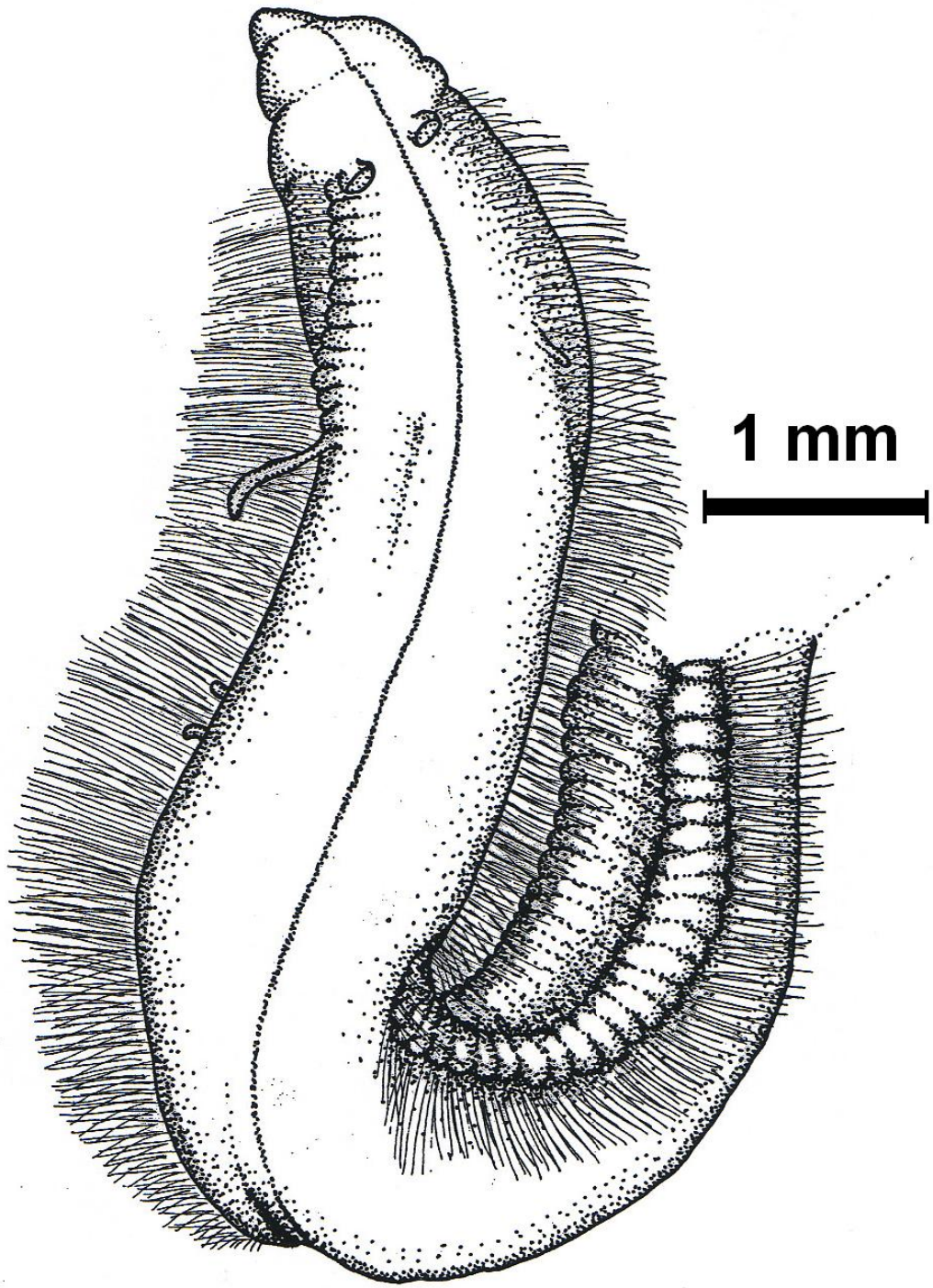

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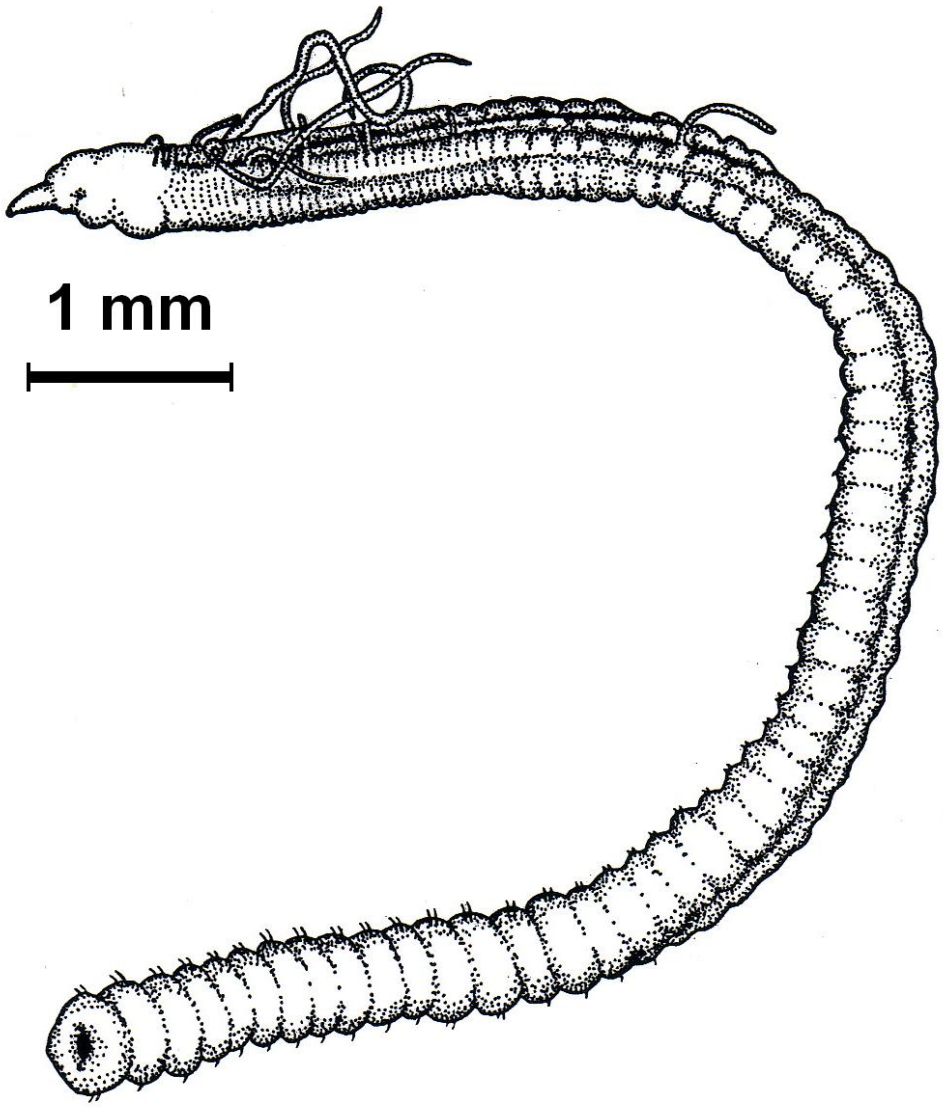
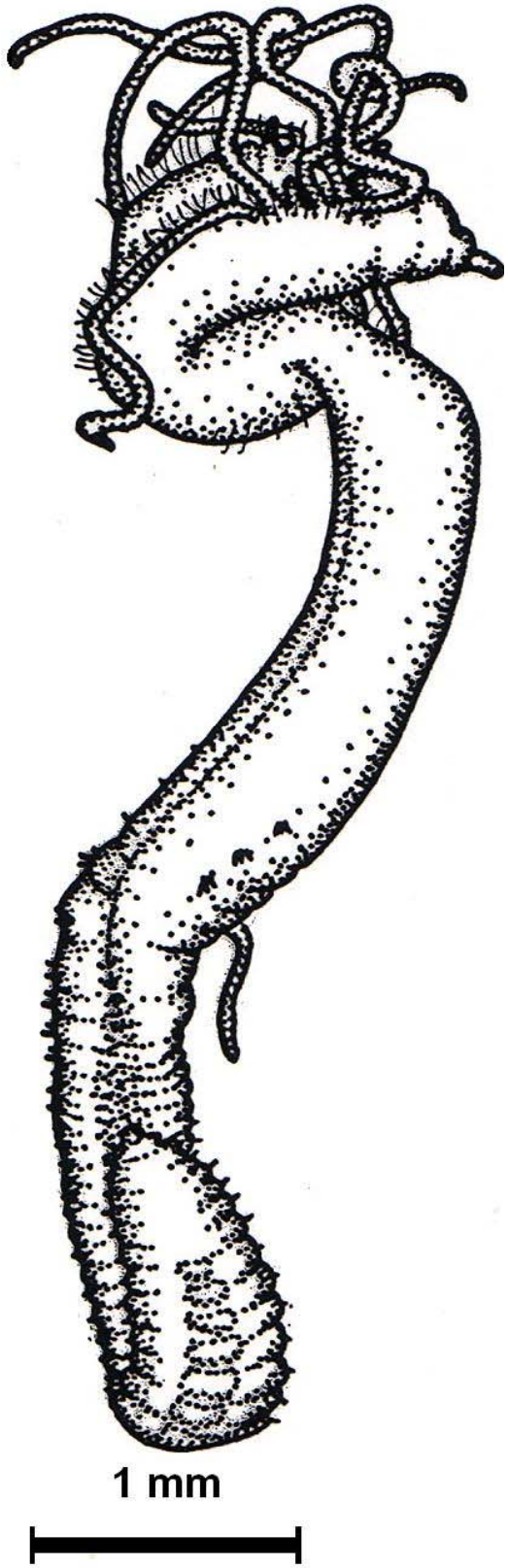
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