Universidade de Aveiro Departamento de Biologia
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FAUNA DE ANÉMONAS (ANTHOZOA: ACTINIARIA) DE OCEANO PROFUNDO DO NORTE ATLÂNTICO.

SEA ANEMONES (ANTHOZOA: ACTINIARIA) FAUNA OF THE NORTH ATLANTIC DEEP SEA.

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Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Ciências das Zonas Costeiras, realizada sob a orientação científica do Prof. Dr. Pablo López-González, Professor Associado do Departamento de Fisiologia e Zoologia da Universidade de Sevilha, e da Prof. Dra. Maria Marina Pais Ribeiro da Cunha, Professora Auxiliar do Departamento de Biologia da Universidade de Aveiro

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Dedico este trabalho à minha família pelo incansável apoio.

o júri

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palavras-chave

Actiniaria, taxonomia, mar profundo, bentos, biogeografia, Norte Atlântico

resumo

A dissertação da Tese de Mestrado enquadra-se no âmbito do estudo do material recolhido durnte as expedições realizadas na Planície Abissal de Porcupine e no Talude Noroeste Irlandês. Estas expedições integram, respectivamente, três programas: BENGAL financiado pela UE com o Programa de Tecnologia e Ciência Marinha (MAST III), PROSPEC e CARACOLE coordenados pelo IFREMER.

O objectivo deste trabalho centra-se principalmente no estudo da fauna de actiniários recolhidos nas campanhas efectuadas durante a época de 1996 a 2001 (PROSPEC- 96; BENGAL - 97/98; CARACOLE - 2001), e na análise biogeográfica desta fauna profunda do Atlântico Nordeste.

Este estudo contribui com informação sobre 1) novos registos e redescrições do material recolhido no Nordeste Atlantico; 2) a variabilidade dos caractéres utilizados para a identificação das espécies, 3) a distribuição geográfica e batimétrica destas espécies, 4) análises da distribuição dentro da área de estudo atendendo às variáveis ambientais disponíveis; 5) actualização de dados taxonómicos e biogeograficos das especies que compõem a fauna do Ártico, o Norte Atlântico (Nordeste e Noroeste Atlântico, Lusitâneo e Mauritâneo) e o Mediterrâneo; e 6) a composição e afinidades faunísticas na comparação com outras áreas biogeográficas do Norte Atlântico. Neste contexto, foi discutida a origem da fauna de anemonas de oceano profundo.

keywords

Actiniaria, taxonomy, deep-sea, benthos, biogeography, North Atlantic

abstract

This Master thesis is integrated in the study of the deep-sea fauna collected during expeditions carried out in the Porcupine Abyssal Plain and the Irish North-western Slopes. These campaigns integrate, respectively, three programs: BENGAL sponsored by the Marine Science and Technology Program (MAST III) from the EU, PROSPEC and CARACOLE coordinated by IFREMER.

This work focus mainly the study of the actiniarian fauna collected in the mentioned campaigns during the years 1996 to 2001 (PROSPEC-96; BENGAL- 97/98; CARACOLE-2001), and the biogeographical approach of the deep-sea fauna of the Northeast Atlantic.

This study contributes with information on: 1) new records and redescriptions of material collected in the Northeast Atlantic; 2) the variability of the used characters for the species identification; 3) the geographic and bathymetric distribution of these species; 4) the distributional analyses in the study area in relation to the environmental variables available; 5) an update of taxonomic and biogeographic data of the Arctic, North Atlantic (Northeast and North-west Atlantic, Lusitanian and Mauritanian) and Mediterranean areas; and 6) the composition and faunistic affinities in comparison to other biogeographical areas of the North Atlantic. In this context, the origin of the North Atlantic deep-sea anemones fauna is discussed.

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GENERAL INTRODUCTION

Brief history of Actiniaria (Cnidaria: Anthozoa)

The history of Cnidarians' classification system is made of successive drastic transformations depending on the criteria used in each period of knowledge. Independent studies recognizing new characters were subsequently introduced, altered the arrangement between groups of organisms and created controversy among different authors. The particular study subject in this contribution is the order Actiniaria and therefore I will focus on this group. In a first comprehensive review by the end of the nineteenth century McMurrich (1893) considered "three periods in the history of the Anthozoan's classification". More than one century after, due to their strong historical value it is still extremely interesting to remind briefly these periods that somehow lead to the contemporary classification of the Actiniaria.

Initially, old naturalists supposed that corals, sea anemones and similar forms had a vegetable character. Accordingly to these thoughts the term "animal-flowers" was coined. This term, commonly used, is an etymologically precursor of the old Greek words "Zoophyta" and "Anthozoa" (phyta=plant; anthos=flower; zoo, zoa=animal). In addition, the term "anemone" is a reference to a vascular plant genus (Family Ranunculaceae) that means "wind". Actually, the term "*sea anemone",* is commonly used for the hexacoral anthozoans without skeleton and includes the orders Actiniaria, Corallimorpharia, Ceriantharia and Zoantharia.

The first period of "Anthozoan's classification", begins with Linnaeus (1758) who, in his "Systema Naturae", classified cnidarians together in Mollusca, Litophyta and Zoophyta. In this period, characters as the presence or absence of a hard skeleton (stony or proteinaceous) and division between solitary or colonial forms are considered characters of high-level distinction. Later, Cuvier (1817) founded the Radiata bringing a new concept of radially symmetrical polyps, which is the base of the actual system. The Cuverian system gave considerable weight to the character of hardness or softness but the separation of the actiniarians from the Mollusca (creating the class Acalephs in the order Zoophyta; containing the genera Actina and Zoanthus) was, nevertheless, a considerable step forward. Ehrenberg (1834) replaced the term Zoophyta for Anthozoa and erected two orders: Zoocorallia and Phytocorallia. Even after this change, Dana (1846), describing material of the Charles Wilkes Exploring Expedition, re-uses the term Zoophytes. However, Dana (1846) established a better and clear division between groups, delimiting the suborders Actiniaria and Alcyonaria (were he includes tribes), grouping together actiniarians and madreporarians in the same order, and down-weighing the importance to the skeleton. Their taxonomy was based in external characters (coloration, column form and tentacles).

In 1857, Milne-Edwards provided another classification recognizing groups of genera, families and sub-families among the Actiniaria, and started the second period of Anthozoan's classification. Instead of considering this new arrangement, Gosse (1860) followed the classification proposed by Dana, but went a little further dividing certain tribes of Actiniaria into families. Furthermore, other authors followed Milne-Edwards current, introducing several changes or additions (Verrill, 1865; Andres, 1883).

Because of the impossibility of using only external characters, the brothers Hertwig (1879, 1882) introduced a new classification of the Anthozoa based on the internal anatomy and histology. Instead of relying entirely on variable characters, prone to alterations according to external conditions, fixed characters, specially the musculature, were used. This step was extremely important, and marks the third period based in more reliable taxonomic characters. Subsequently, several other authors (Haddon, 1889; Danielssen, 1890; McMurrich, 1893) adopted Hertwig's vision. McMurrich (1893) added some more anatomical characters (embryological data, mesenteries succession and tentacles ordination) incrementing the Anthozoa tribes. He criticizes other authors from his generation but, modestly sugests that his classification is open to any changes as future observations would confirm.

Indeed, since his early work in 1891, Prof. Oskar Carlgren progressively provided descriptions of 424 species and 42 families of Anthozoans, incorporated new characters (cnidae types and dimensions) and, finally in 1949, assumed the establishment of a new classification. Carlgren was a prolific researcher until 1959, and he is actually considered the "father" of actiniarian taxonomy in the twentieth century. He completed the first global study of actiniarian species descriptions in a biogeographic context. His classification (Carlgren, 1949) was traditionally used worldwide until nowadays and is the result of series of publications and book volumes (Carlgren, 1921; 1941). This "fourth period" of Anthozoan's classification, it preferentially mentioned as the "Carlgren period" due to the huge importance of the author. Carlgren's work is stills very useful and even contemporary works follow the same rational assessment of the material. Stephenson (1920 and 1922) also created a classification, that was in fact incorporated in Carlgren's scheme, once they were in close contact, sharing ideas and solving problems together (see Stephenson *Preface* in Carlgren, 1949). Carlgren's assumptions and theoretical lineage are the base of the actiniarian systematic strategy using morphological characters. Because of their uniform body shape, anemones have few diagnostic characters, and their systematics relies basically in the histology and morphology of the polyp. Few things changed since Carlgren's manuscripts. Only some misinterpretations of material observations were corrected (for instance, absence or presence of acontia or other anatomical features, not so easily noticed because of their small size or even material maceration), adaptations of the diagnoses of some genera were made and of course the importance to some characters in different groups of species is always subject for discussion in diverse publications.

Unexpectedly, Schmidt (1972) made a drastic revision of the subgroups within Actiniaria in his "Prodromus" and proposed a new model for the evolution in the group. He considered novel characters such as the form of reproductive tissues (development of gonads and filaments occurs distally or proximally), and created a different interpretation of nematocyst types (*p*-rhabdoids A and B). His classification stands on the nature of sphincter (endodermal - Endomyaria or mesogleal - Mesomyaria, elevating former Sub-tribes to Tribe level as the Boloceroidaria). Schmidt also considers new evolution assumptions like evolution of nematocysts and regression or progress of basilar muscles and acontia. According to the latter he eliminated the Tribes Athenaria and Thenaria, fused Acontiaria into Mesomyaria and divided Athenaria in Endo- and Mesomyaria (Schmidt, 1974). One of the advantages of Schmidt's new system is the fact that it is simpler than the one currently in use (see also brief revision by Hand, 1974). After all, the need of a large number of histological characters do not results very practical and requires a wide knowledge of the histology and anatomy of the species. Although working with a large number of characters (the nematocyst forms) increases the knowledge of species and facilitates the understanding of the phylogenetic and evolutionary relationships of the group. It is unbelievable how the absence of a skeleton produces such a big morphological variability, both external and internal, especially due to the flexibility caused by the environment.

Fautin *et al.* (2007), did not adopt Schmidt classification, based on the fact that just the new nematocysts classification would generate a global revision of all species. The nomenclatural assumptions of these authors are available through the on-line database "Hexacorallians of the World" (Fautin, 2009).

The composition and delimitation of the taxonomic groups and their phylogenetic relations is still very controversial and far from an complete resolution. Recently, Daly *et al.*, (2008) in their phylogenetic study about the relationships among sea anemones, suggests that Carlgren (1949) distinction between Athenaria, Boloceroidaria and Thenaria is not well supported. The authors interpret basilar muscles as a labile feature among Actiniaria. Moreover they propose a dichotomy between taxa with an endodermal (or no) marginal sphincter and those with mesogleal (or no) marginal sphincter. However they still do not have basis for inferring the ancestral type of marginal sphincter, and can not determine homology of endo and mesogleal muscles in Nynantheae. In this manner, they can not refute Carlgren (1942) interpretation of the origin of the sphincter. Their results are also incompatible with Schmidt (1974) hypothesis that forms with an endodermal sphincter are most derived. Daly et al

(2008) recommend that ranks and taxonomic categories above family should be abandoned for Nynantheae pending further phylogenetic investigations. For the resolution of these issues it is necessary to include members of the actinian suborders Endocoelantheae and Protantheae, both of which are characterized by the absence of both marginal sphincter and basilar muscles (Daly *et al*., 2008).

The systematic problems that subsist in the order Actiniaria are the creation of a large number of families and genera mainly monogeneric and monospecific, the great variability in the diagnoses provided by different authors and the absence of features rather than synapomorphies (Daly *et al*., 2008). Studies integrating morphology and molecular data are in order but it will be impossible to examine genetic markers before a comprehensive morphological update and a most needed review of the knowledge of species. Taking into account the reduced number of species in comparison with other invertebrate groups, it first step is necessary: to create a framework of morphological investigation for the revision of all species, genera and families in order to clarify their taxonomy using accurate and standardized diagnostic characters. This basic work will facilitate, in a near future, more detailed phylogenetic studies to understand actiniarian evolution and diversification.

Another recurrent problem is that species from particular habitats, (poles, abyss, deep-trenches, canyons, seamounts, hydrothermal vents, etc) are rarely sampled. Sometimes the area is very well covered but few specimens are collected. Besides, frequently there are only poor descriptions of the material, depending on the “historical period” of their collection. This makes the identification and classification of Actiniaria difficult due to the lack of information available for comparisons with the type species (if wherever they exist).

Characteristics of Actiniarians

Cnidarians can be found throughout the world oceans to the greatest depth of the sea, and also include some fresh water species (Fautin, 1999). The Phylum comprises nearly 9000 species (Ruppert and Barnes, 1994), from which only 1103 species are included in the order Actiniaria and presently considered valid (Fautin 2007). This relatively small taxon is part of the simplest animals within the Eumetazoa (Nielsen, 2001). They are a very ancient group with a fossil record that comes from the Precambric (Conway Morris, 1993).

As it was previously documented, in the beginning cnidarians represented a low grade of animal existence (Gosse, 1960). Even nowadays, they are considered primitive because they are at the tissue level of organization; they are solitary individuals, without skeleton, lack of organs and central nervous system (Fautin, 1999). Their cells are organized into discernible tissues having specialized functions, but the tissues are not further grouped into organs having multiple tissue types (see Fautin and Mariscal, 1991). Their remarkable feature is the cnidom, one the most complex secretion product ever known (Mariscal, 1974, Fautin, 1999). Weill’s (1934) proposal for using the cnidae was followed by Carlgren (1940) and numerous authors incremented their value as taxonomic character, exploiting new characters such as cnidom types and sizes, and their distribution and statistic significance to recognize species.

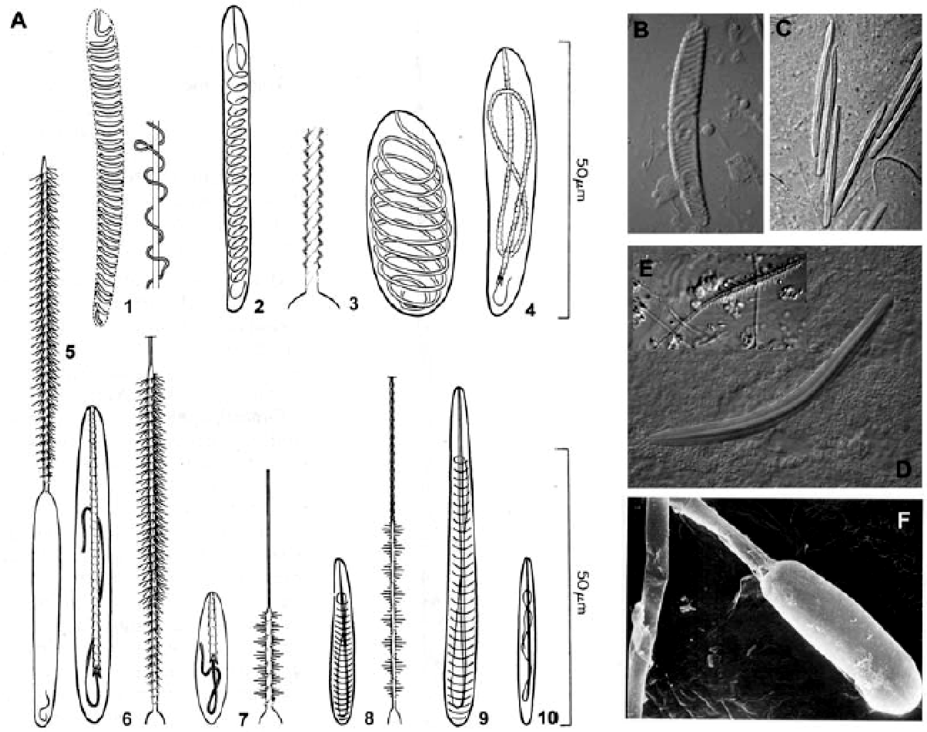

Figure I.— Cnidocysts: A) scheme representation of an cnidocysts selection: 1, spirocyst; 2, nematocyst (holotrich); 3, nematocyst (holotrich); 4, nematocyst (macrobasic p-mastigophore); 5, nematocyst (microbasic p-mastigophore); 6, nematocyst (microbasic p-mastigophores); 7, nematocyst (microbasic p-mastigophore); 8, nematocyst (basitrich); 9, nematocyst (microbasic b-mastigophore), nematocyst (basitrich); B) spirocyst photo; C) nematocyst (basitrich); D) nematocyst (microbasic p-mastigophore); E) discharged nematocyst detail (microbasic p-mastigophore); F) electronic microscopy of an pticocyst.

Basically, a cnidocyst, in the unfired state, is a microscopic capsule provided with an eversible tubule strongly rolled whose thread is the extension of the wall of the capsule. When, driven by a variety of physical and chemical stimuli, the nematocysts responds (having special receptors for its detention) and fires ejecting the shaft that consists in the reversion of the thread (Mariscal, 1974).There are there types of cnidocysts (Mariscal, 1984): spirocysts (exclusively of Hexacorallia), nematocysts, and pticocysts (exclusively of Ceriantharia) (Fig. I).

Sea anemones (*s.l.*), settle on a variety of substrates (rocks, corals, mollusc shells, sediments, algae) where they attach their pedal discs (Fig. II). Usually they are considered sessile benthic invertebrates that keep on at the same place their entire life. However, they are much more versatile in their mobility than commonly thought, both as adults and post-metamorphic juveniles (Riemann-Zürneck, 1998). The distribution patterns of sea anemones are variable spatially and numerically (abundant, scarce, patchy or isolated) depending on environmental factors.

Figure II.— Some images of sea anemones, with different pedal disc forms, attached or burrow on diverse types of substrates.

Actiniarians play an important role in the trophic web. They are suspension feeders that capture a wide range of preys, and they are considered voracious animals with a high predation capacity, however they are dependent of the water movement or prey locomotion. The most common strategy of these sessile consumers is “settle and wait”, thus minimizing the energetic costs. Sebens (2002) made comparisons between optimal energetic sizes and mechanical limits using sea anemones, in intertidal and subtidal environments, concluding that polyp and population sizes and their distribution are directly dependent on biological (e.g. predation, food) and physical stress (e.g. temperature, hydrography). In deep-sea waters, food availability may determine their activity rhythms, metabolic rates and reproductive patterns. With increased water depth, different specific morphological adaptations overcome: some increase in size (gigantism) and have a sessile life style (Ammons and Daly, 2008) and others show a trend towards body size miniaturization, a hemisessile lifestyle, moving over the bottom by currents (Riemann-Zürneck, 1979 and 1997a).

The reproduction in actiniarians can be sexual or asexual. In the same habitat they can display different patterns: longitudinal fission, basal laceration, some incubate small polyps inside the gastrovascular cavity, and, depending on species, they can have only sexual reproduction, only asexual reproduction or both (see revision by Shick, 1991). Several authors tried to explain the advantages and disadvantages of distinct reproductive strategies although many of these empirical and experimental studies may not be ecologically significant (see revision by Fautin, 2002). The knowledge on the reproduction of deep-sea actiniarians although some reproductive features have been reported (e.g. Van Praët *et al*., 1990; Bronsdon *et al*., 1993 and 1997).

Due to their sessile or hemisessile character, monitoring impact assessment of the benthic actiniarian communities is easy to study. Being suspension feeders, actiniarians accumulate chemical substances and are ideal indicator species for contamination studies, offering excellent opportunities to detect changes in general. The production of secondary metabolites is also extremely interesting for the chemical and pharmaceutical industries, and some of the applied research was directed to these resources exploitation point of view.

Deep-sea expeditions in the North Atlantic

The study of the actiniarian deep-sea fauna of the North Atlantic began with the first expeditions of the *Challenger* led by Charles Wyville Thomson during the second half of the XIX century (1872-76) which laid the foundations of the modern science of oceanography (Murray, 1895; Doumenc, 1975; Perry and Fautin, 2004). The pioneers who studied these samples were H. N. Moseley, D.C. Danielssen, A.E. Verrill, O. and R. Hertwig and J. P. McMurrich. All these authors approached the study of actiniarians from a purely systematic point of view and often using poorly preserved samples (Doumenc, 1975).

Two navy ships, H.M.S. *Lightning's* and H.M.S. *Porcupine* (1868-1870) were provided for the use of a team of scientists to explore the depths off Western Europe (off Ireland and Scotland) in the search for life, and established the base for the so-called "Atlantic Frontier" (Gage, 2001). The previous accepted assumption of absence of any life at great depths was promptly rejected. Also the actiniarians collected by the U.S. Fish Commission Steamer Albatross during 1887-1888 (McMurrich, 1893) provided some interesting biological and distribution remarks (Doumenc, 1975). Moreover, the *Travailleur* and *Talisman* dredging of the Gulf of Gascoigne (Marion, 1882) gave some records of actiniarians in this zone while Gravier studied the actiniarian fauna collected by the expeditions of Prince Albert of Monaco with *Princesse Alice* and *Hirondelle* (1888-1913). The *Michael Sars* North Atlantic Deep Sea Expedition – 1910 (Murray and Hjort, 1912 and 1914), the *Godthaab* Expedition 1928, the Swedish Deep-Sea Expedition 1947-1948, numerous Norwegian, Greenlandic and Icelandic Arctic Expeditions and the *Galathea* expedition (1950-52) were challenged to confirm the existence of deep abyssal life and documented the rich diversity of benthic fauna previously unknown to science. Identifications and descriptions of the Actiniaria, and some Corallimorpharia and Zoantharia taxonomic groups of the above mentioned expeditions were carried out by Prof. Oskar Carlgren.

In the last decade, various expeditions were carried out by the French Oceanographic Centres (IFREMER) such as the Noratlante (1969), Biogas (1972-1975) and Biaçores (1971); by British surveys of the R.R.S. *Discovery* and numerous German vessels, in special the R.V. *Meteor*, R.V. *Walther Hertwig*, and more recently the R.V. *Polarstern*. New advanced techniques emerged with remotely operated vehicles (VICTOR, etc) and manned submersibles (ALVIN, NAUTILE, etc) which provided more information about actiniarians *in vivo* morphology and biological activity in their natural habitat.

OBJECTIVES

The main goal of this thesis is to contribute to the knowledge on the Actiniaria deep-sea fauna of the North Atlantic. The specific objectives include the following:

1. Identification and taxonomic description of the deep-sea actiniarian species from the Atlantic Frontier provided from IFREMER expeditions: BENGAL, PROSPEC and CARACOLE.

2. Detection of intraspecific variations, redescription of poorly-known species, and whenever needed, revision of their taxonomic “status”, as well as, description of new species.

3. Analysis of the faunistic composition, geographical and bathymetric distribution patterns in relation to other regions and other benthic organisms.

CHAPTER I: DESCRIPTION OF THE STUDIED SPECIES

INTRODUCTION

The central subject of this study is justified by the fact that the taxonomic state of knowledge of the class Actiniaria is far behind other taxa of comparable importance. The causes of this gap are the many previous doubtful identifications, the absence of synthesis work in the literature and the lack of taxonomic expertises and specialist researchers. Also the habitats surveyed for this study were not easily accessed and sampled in the past.

The present study focus on the taxonomic descriptions and some revisions of the deep sea actiniarian species found during several campaigns of the nineties decade on the Atlantic Frontier, lead by the IFREMER. By reviewing the available literature on biodiversity assessments and ecological studies of this region, some inaccuracy and gaps were noticed regarding the Actiniaria group. Thus, the study of actiniarians is imperative once they are one of the most neglected marine taxonomic groups.

Nowadays, the search for new hydrocarbon reserves shifted from the North Sea and continental shelf off Norway to the exploration of the deep sea (conventionally taken as seabed deeper than the 200m isobath) in the Atlantic margin off the north and west of Scotland, Ireland and UK. Also, activities such as deep-sea trawling fisheries (Gage, 2001), sewage-sludge and radioactive waste disposal (Vobach and Kellermann, 2001) remain poorly legislated. For these reasons, the knowledge of the taxonomy, community structure, biogeography and natural history of deep-sea organisms is of utmost important since it promotes an accurate risk assessment of species extinctions and habitat destruction that may result from large scale anthropogenic impact, which in turn can be detectable, and predictable (Glover and Smith, 2003).

This contribution is expected to constitute a practical comprehensive and feasible guide to the knowledge of deep sea actiniarian fauna of the so-called “Atlantic Frontier”..

MATERIAL AND METHODS

Description of the study area

The study area, the so-called “Atlantic Frontier”, was surveyed during three oceanographic campaigns: PROSPEC (1996), BENGAL (1997-98) and CARACOLE (2001).

The PROSPEC program covered the Hébrides Terrace, at stations located between 55-56ºN and 10-9ºW, at 1000 and 2000m depth (Fig. III).

The BENGAL (High resolution temporal and spatial study of the BENthic biology and Geochemistry of a north-eastern Atlantic abyssal Locality) program comprehended six cruises in the area of the Porcupine Abyssal Plain (PAP) in the north-eastern Atlantic (see Fig. III), centred on 48°50 N-16°30 W, southwest of Ireland with a depth of about 4840m (Billett and Rice, 2001). This location is known to be subjected to a regular seasonal deposition of aggregated particulate organic matter (POM) which normally reaches the seafloor in May/June. This seasonal input characterizes this deep-sea plain as relatively eutrophic (Rice *et al*., 1994). The survey sampling program in the PAP area was conducted by the R.R.S. *Meteor* in October 1996 and the R.R.S .*Discovery*, in March–April 1997 and July 1997, respectively.

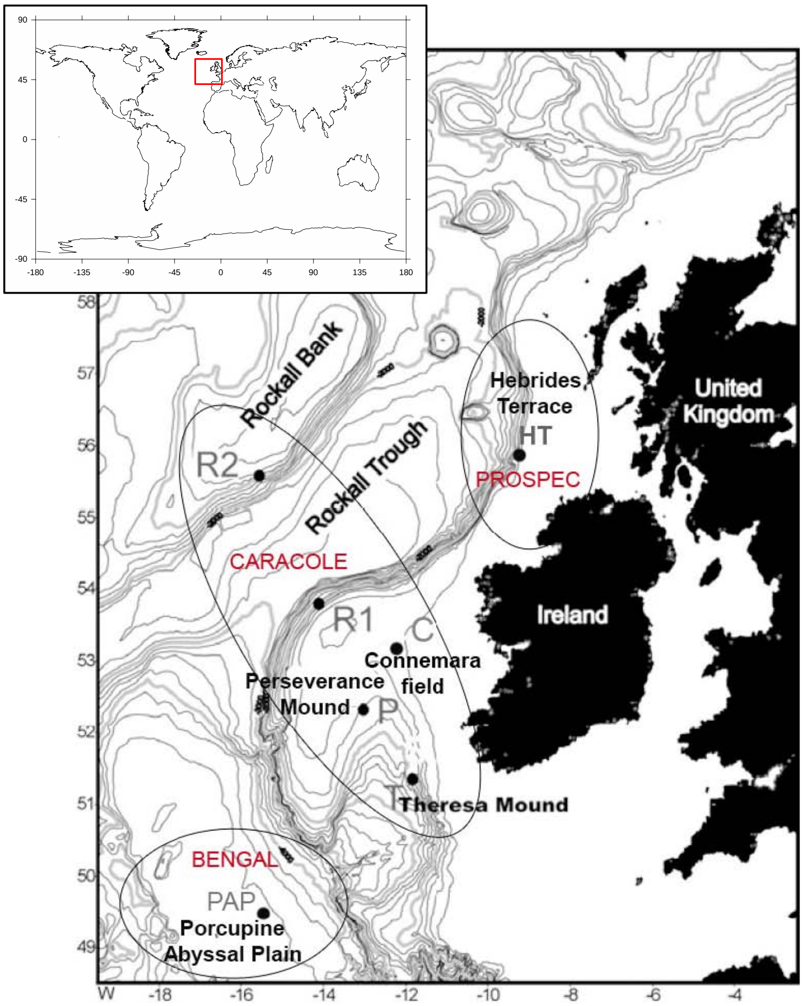

Figure III.— Study area: Atlantic Frontier; Stations: BENGAL, Porcupine Abyssal Plain (PAP: 4000-5000m); PROSPEC: Hébrides Terrace (HT: 1000-2000m); CARACOLE: Rockall Bank (R1: 640m; R2: 1000m), Thérèse Mound (T: 875m), Perseverance Mound (P: 640m) and Connemara field (C: 380m). Adapted from Olu-Le Roy (2004), IFREMER.

The CARACOLE program (Olu-Le Roy, 2004) surveyed the Rockall Bank, the Connemara field and the Thérèse Mound. The Connemara field area is located at the northern end of the Main Porcupine Basin, offshore Ireland (Fig. III). The area is characterized by vertical fluid migration pathways (‘‘seismic chimneys’’ or ‘‘gas chimneys’’) that extend from the top of the Jurassic sequence, cross-cutting the entire Cretaceous sequence to the Upper Tertiary deposits over a vertical distance of up to 1.5km. These vertical chimneys indicate important pathways of fluid and gas migration from the deep subsurface to the shallow subsurface and seemingly to the sea floor.

Material origin and sampling methods

Material origin and recollection

A total of 1254 actiniarian specimens belonging to 16 species collected from BENGAL, PROSPEC and CARACOLE cruises were examined for this study. The sampling methods and gear varied between campaigns (see on Appendix I.A). During BENGAL and PROSPEC Agassis trawl was used to sample along transects (BENGAL at 4810 to 4850 m depth, PROSPEC at 1000 to 1579 m), randomly covering the study area. The sampling method is qualitative or semi-quantitative, once the area covered by each trawling transect could not be estimated. The samples from BENGAL and PROSPEC cruises were sieved with a mesh size of 500 µm. Later, the organisms were sorted and preliminary labelled.

During CARACOLE (at 380 to 875m) sampling was carried out using several strategies and different gears: the material was also randomly caught by the USNEL corer or directionally selected using video cameras associated to the ROV. Occasional sampling was also provided by the fouling on some instruments (e.g. CTD) that were recovered with organisms attached.

Fixation and preservation of the material

On board the basic classical conservation methods were applied for all fauna. Sea anemones were therefore fixed on board using formaldehyde diluted in seawater at 4%. Later, the specimens were washed and kept in ethanol (70%) at IFREMER laboratories.

Actiniarians require special attention during fixation because most of the material becomes very contracted and, in some cases, with the interior macerated. To prevent this type of damage, there are some recommendations to follow in future expeditions and collection of actiniarians elsewhere. As actiniarians get stressed with capture techniques and handling, especially out of their natural habitat, they usually arrive at the deck strongly contracted. Therefore, specimens must be maintained in cold sea water with diluted menthol crystals during the sufficient time to reach anaesthesia. The relaxed state is achieved when it is possible to observe the expanded tentacles and oral disc. There are distinct techniques available to narcotise sea anemones, although this one, with menthol crystals is the most simple and effective (Moore, 1989). Pictures must be taken preferentially when the material is alive or at least freshly collected to reveal natural pigmentation that will be lost when the traditional fixation methods are used. To prevent maceration, it is also recommended to inject some formalin inside the body with a syringe; this will fix immediately the internal tissues preventing further damage. When molecular analyses are planned tissue must be collected prior to fixation with formaldehyde. A sterile blade must be handled with care in order to take a small piece of tissue from the specimen that should be fixed in 99% ethanol (Dawson *et al.*, 1998). In the actiniarians, it is not adequate to fix all the specimen in ethanol once this chemical induces the nematocysts to discharge, and these capsules are needed for measurements and for the correct species identification (*in* López-González, 1993, not published).

Deposit of the material

All material was stored at the IFREMER (Brest) during several years, and was later sent to the "Biodiversidad y Ecologia de Invertebrados Marinos" (BEIM) laboratory, Universidad de Sevilla to be identified. After the conclusion of the study, a small reference collection will be stored in BEIM and the remainder specimens will be deposited in the Museum National d'Histoire Naturelle in Paris.

Taxonomic Methodology

Anatomic external and internal study

The species descriptions were based in the external and internal observations of the polyps (see scheme example of an actinia polyp, Fig. IV). Three body layers (ectoderm, endoderm and a connective mesoglea between these two epithelia) form these simple organisms. An individual polyp consists of a sac-like body (the space of which is named the gastrovascular cavity of coelenteron) that connects to the outside through a single opening, the oral disc which is surrounded by tentacles and acts both as feeding and excretory orifice (Fautin and Mariscal, 1991).

The base of the polyp, the zone in contact with the substrate which attaches the animal, can be more or less plain or adherent and is named the pedal disc. In burrowing anemones, the base is modified to form a conical physa that penetrates and anchors the anemone in the substrate via hydrostatic action (Ansell and Trueman, 1968). The limit between the column and the base is denominated limbus.

The column can be continuous or differentiated in two regions: scapus and scapulus. The scapus is the most proximal part of the column, it may show a chitinous cuticle, be smooth or ornamented. There are diverse structures present at the scapus: the tenaculi (a modification of the cuticle development, sometimes with adherent capacity); striation or longitudinal or transversal furrows; tubercles (which imply epidermis and mesoglea); vesicles (non-adhesive evaginations of the column that imply the three layers - ectoderm, mesoglea and gastrodermis - with more or less numerous nematocysts of various categories); verrucae (evaginations with adhesive properties); cinclides (perforations that cross the epidermis, mesoglea and gastrodermis, enabling the escape of water); and acontia, among others. The nomenclature of these structures is not always very clear.

The scapulus, the most distal part of the column extending to the base of the tentacles, lacks cuticle. Sometimes, it presents a parapet (a fold of the column in the oral disc border) or a fosse (a concavity surrounded by the parapet that forms between the oral disc and the tentacles). The scapulus can yield acrorhagi (ectodermal marginal structures exclusively endocoelic, with great abundance of certain nematocysts in the epidermis). Sometimes when the fosse is present, the capitulum (a space between the fosse and the tentacles base) can be differentiated (*in* Rodriguez, 2007, not published).

The column presents a longitudinal ectodermal musculature and a circular endodermal musculature with different development in the different actiniarian groups. At the most distal part of the column, where the endodermal circular muscles accumulate, it is commonly found a marginal sphincter, which can be mainly endodermic, or mesogleal, when the fibbers are embedded on the mesoglea. In some cases, a transitory state of both may occur, and this can be endo-mesogleal or meso-endodermic. The sphincter can have different shapes at the histological sections; diffuse, when is long and softly anchored to the column; restricted, when the muscular fibbers are more concentrated; and circumscript, when the fibbers are very concentrated (*in* Rodriguez, 2007, not published).

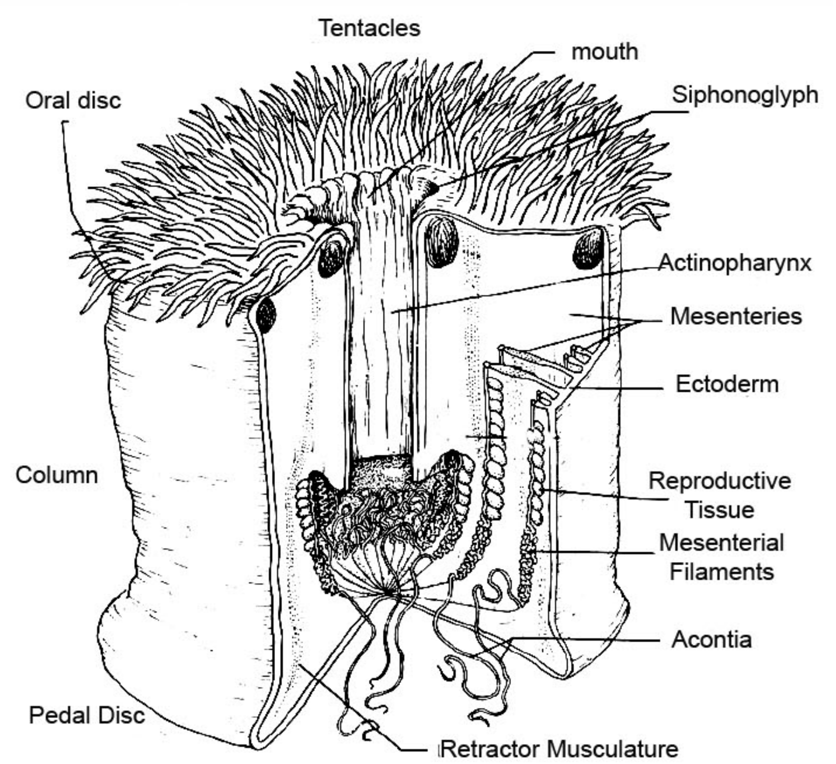

Figure IV.— Scheme of an actiniarian polyp, adapted from Fautin and Mariscal (1991).

The tentacles are located at the oral disc and are empty structures, physical prolongations of the polyp; their arrangement in cycles is connected to the mesenteries arrangement, normally there is one tentacle for each endocoel and exocoel. The older cycles of tentacles are located closer to the mouth and the younger around the oral disc margin. The tentacles may be classified as short (longitude inferior or equal to the distance between the border of the oral disc and the mouth), moderate (reaching the opposite border of the oral disc) or large (larger than the oral disc diameter). When the external tentacles are larger than the internal they are named ectameric and, if the opposite happens, entameric. Normally, tentacles are simple, although they can also be ramified, ending with the apex acuminate or capitate, rarely with a marginal spherule. When expanded their surface must be smooth although when contracted they may appear wrinkled or reticulate. The musculature of the tentacles, as in the oral disc, is double. At the endodermic face, the mesoglea has circular musculature and at the ectodermic face, the mesoglea has longitudinal epithelium muscular cells, typically more developed than the endodermic; the fibbers of the ectodermal musculature, seemingly as the marginal sphincter, can be embedded within the mesoglea (*in* Rodriguez, 2007, not published).

The actinopharynx, usually longitudinally folded, appears towards the interior of the mouth. Generally, the actinopharynx has one or two ciliate furrows named siphonoglyphs that help in the water circulation from the outer and inside cavity.

The radial perpendicular line insertions correspond to the mesenteries, normally, hexamerously arranged in pairs and in a sequence of cycles. The mesenteries comprise a mesogleal layer flanked by gastrodermis from both sides. When a mesentery is connected to the actinopharynx it is designated perfect, when not, it is imperfect. The space between a pair of mesenteries is named endocoel and the space between adjacent pairs of mesenteries is the exocoel. New pairs of mesenteries may occur between the exocoels or endocoels depending on the suborder. The pairs of mesenteries connected to the siphonoglyphs are named directives. Proximally they can be connected to the base, externally to the internal face of the body of the body wall, distally to the oral disc, and in its maximal development also to the gastrovascular cavity of the actinopharynx. The axial border of the mesentery, when proximally free, is composed by a thickened cord running downwards, named cnidoglandular filament, that can be unilobate or trilobate. The entire cord is also denominated cnidoglandular tract. Sometimes, below the filaments, long thin threads, named acontia, may occur attached to the end of mesenteries. The acontia can also extend to the exterior by the mouth or by the cinclides.

Each side of the mesenteries presents musculature: one longitudinal layer that extends from the disc to the base, in which the fibbers concentrate forming more or less thickened bands - the retractor musculature. The retractors can be diffuse, restricted or circumscript depending on the grade of concentration of the muscular fibbers. There are other diagonal muscular fibbers, which form a triangular area in the angle between the base and the body wall, named parietobasilar musculature. There are also basilar muscles running both sides of the base of the mesentery. Sometimes the mesenteries are differentiated in macrocnemes and microcneme; the macrocnemes are perfect, they have a very well developed retractor musculature, cnidoglandular filament and gametogenic tissue; instead, the microcnemes are small with poorly developed retractors that lack mesenterial filament and gametogenic tissue (in Rodriguez, 2007, unpublished Phd thesis).

Histological study

For the internal anatomic study, it is essential to prepare histological sections, enabling the observation of the internal structures. To obtain these sections it is necessary to proceed by three successive processes: i) paraffin inclusion, ii) sectioning and slide preparation and iii) staining (Gabe, 1968).

Previously to the paraffin inclusion three other steps are necessary:

1. Selection of the specimens. To accomplish the study, they must be in the best relaxed and fixed conditions; most times, especially in old material, this is impossible to obtain, but necessarily the material has to be worked even in poor conditions.

2. Pre-treatment. The fragments of the specimen (longitudinal and transversal sections, tentacle, etc) are selected. If the organism presents incrustations at the cuticle or epidermal structures, it has to be treated previously with Fluorhidric acid at 40% (for sand) or Chloridric acid (for calcareous remains, including foraminifera) during the sufficient time to dissolve these particles. After this, it is recommended to wash carefully the sample because of the possible affinity of the acid with the chemicals during staining.

3. Dehydration of the selected material. The actiniarians are preserved in 70% ethanol, so dehydration is necessary before the hydrophobic paraffin is used. The dehydration methodology selected in this study (see Table 1) was the one recommended by Johansen (1940). In this technique, the samples were included in various steps of a Tertiary Butyric Alcohol (TBA: 2-Metil-2, $(CH_3)3COH$, Panreac) increasing series. The objective is to gradually replace the water of the tissues by alcohol. At the final step of this process, the sample was submitted to a mixture of TBA and paraffin oil, which facilitates the paraffin infiltration. All these steps were performed at room temperature and using a vacuum glass to avoid the permanent contact with air bubbles in the sample.

Table I.– Composition (ml) of each TBA in Johansen series and minimal times of permanence of each sample in each step**.**

	Alcohol Tertiary Butyric	Ethanol 100%	Ethanol 90%	H2O	Paraffin Oil	Time (Hours)
TBA1	**10**	**-**	**40**	**50**	**-**	**1**
TBA2	**20**	**-**	**50**	**30**	**-**	**1**
TBA3	**35**	**-**	**50**	**15**	**-**	**1**
TBA4	**50**	**-**	**50**	**-**	**-**	**1**
TBA5	**75**	**25**	**-**	**-**	**-**	**1**
TBA pure	**100**	**-**	**-**	**-**	**-**	**12**
TBA-Paraffin Oil	**50**				**50**	**1**

Paraffin inclusion. The process was carried out in a heater at the temperature of 55-60%, to maintain all samples inside a paraffin (Paraplast Plus, Sherwood Medical) liquid medium for tissue inclusion. Four successive changes of paraffin were made: the first of one hour, the second of at least 12 hours, and the last two changes of one hour each. Once the impregnationprocess was finished paraffin blocks with the samples inside were prepared and left to cool and solidify.

Sectioning and slide preparation.— the blocks were kept in a refrigerator, because low temperatures facilitate the sectioning. The blocks were sliced with the microtome (Leitz 1512), in order to obtain sections of 7-10 µm thick. The sections were placed in warm water till their complete stretch. Each slide was previously impregnated with a gelatine adhesive and once the sections were fixed to the slide, all the water excess was removed (the slides were left to dry for a couple of days).

Staining.— the Ramón y Cajal Triple Stain (Gabe, 1968) with modifications adapted to the actinarian material was used in this study. This method clearly differentiates the epithelium, musculature and mesoglea; ideally, the epithelium should be pink in colour, the musculature of a green shade and the mesoglea of a soft blue. The nematocysts and granular cells of an intense red, the spirocysts of green or blue and the cuticles of yellow and green shades. The gametogenic tissue, such as the oocyts and spermatic quistes were coloured with intense pink. The protocol is detailed below:

- Phenic Fuchsine of Ziehl (1gr, basic Fuchsine, 5 gr of Phenol, 10 ml of Ethanol 96%, 90 ml of distilled water.
- Picric –indigocarmine (0.4 gr of indigocarmine, 100 ml of saturate solution of Picric acid.
- Acetidified Water at 0.3-0.5% (100ml of distilled water, one drop of Acetic acid)
- Remove the paraffin of the cuts: three steps of xilol (10 min each one)
- Hydration of the sections: three steps of ethanol (100%, 90% and 70% respectively, of five minutes each one)
- Stain the sections, three steps: 1) Stain with a solution of Fuchsina of Ziehl and distilled water of 1:9, some five or ten minutes depending of the sample. 2) Remove the colour excess with Acetidified water one our two times. 3) Stain with the solution of “picric-indigocarmine” of 6 and 15 minutes, depending on the sample.
- Differentiation and fast dehydration of the sections, the excess of the colouration was removed with three more steps of ethanol (70%, 100% and 100% respectively). Afterwards, the sections were carefully inserted in xilol.

- For preservation, all sections were fixed with a synthetic resin (DPX) and then air dried at room temperature. Finally, the slides were labelled for further study and manipulation.

All histological sections were observed and studied under a stereomicroscope (Leica MZ12) for general observation and under a compound microscope (Leica DNLB) at different magnifications (10x, 20x, 40x and 100x) for detailed observation. Photographs of the histological details were taken with a digital camera (Nikon E-4500), in order to document the different characters with taxonomic value for species identification (sphincter, mesenteries, musculature, etc).

Study of cnidocysts

As it was already mentioned before, the type and size of cnidocysts present at distinct parts of the body are a character of utmost importance for the taxonomy of the actiniarians. Cnidae measurements were taken from preserved material in squash preparations at 1000X magnification with Nomarski differential interference contrast optics (Leica DMLB). The Mariscal (1974) and Östman (2000) nomenclature with modifications was adopted for this study: the nomenclature followed for basitrichs and *b*-mastigophores is the one from Carlgren (1940) and Mariscal (1974) in order not to comply with the majority of the literature and also because of the obscure distinction between both categories (Östman, 2000). Presence of cnidae was first confirmed in the histological sections of the tissues. For each analysed specimen at least 20 undischarged capsules (in height and length) from each part of the body (scapus, scapulus, tentacle, actinopharynx, filament, acontia and pedal disc, etc) were measured. The given frequencies are subjective estimates based on the following criteria: (+++) = very common, (++) = common, (+) = poorly common, (---) = sporadic. The average and standard deviation of the size ranges of cnidae measurements are provided. Photographs of each category of nematocyst found in each tissue were also taken.

Structure of the taxonomic description

For this study the classification proposed by Schmidt (see Schmidt, 1972) was adopted:

- Placement of the taxon in the different taxonomic categories with their respective diagnoses (order, suborder, tribe, family, genus, species).
- The type species followed by the enumeration of all species in the genus is included after the genus diagnosis.
- The description of the species includes: material examined; species diagnosis; description (external anatomy; internal anatomy; cnidom; colour)
- Geographic and bathymetrical distribution.
- Etymology (in case of a new species).
- Discussion

The list of citations and synonyms has been placed at the end of this work, in the APPENDIX.

RESULTS AND DISCUSSIONS

List of species studied

The list of the species included in this study and the highr taxon at which they were ascribed is presented below. The classification adopted is the one proposed by Schmidt (1972), with modifications by Cappola & Fautin (2000).

CLASS ANTHOZOA

SUBCLASS HEXACORALLIA

ORDER ACTINIARIA

SUBORDER ENDOCOELANTHEAE Carlgren, 1925

FAMILY HALCURIIDAE Carlgren, 1032
    Genus *Carlgrenia* Stephenson, 1918
        Carlgrenia desiderata Stephenson, 1918

SUBORDER NYNANTHEAE Carlgren, 1899

TRIBE ENDOMYARIA Stephenson, 1921

FAMILY EDWARDSIIDAE Andres, 1881
    Genus *Edwardsia* de Quatrefages, 1842
        Edwardsia tuberculata Dueben and Koren, 1847
FAMILY ACTINIIDAE Rafinesque, 1815
    Genus *Bolocera* Gosse, 1860
        Bolocera tuediae (Johnston, 1832)
FAMILY CONDYLANTHIDAE Stephenson, 1822
    Genus *Segonzactis* Riemann-Zürneck, 1979
        Segonzactis platypus Riemann-Zürneck, 1979
FAMILY IOSACTIIDAE Riemann-Zürneck, 1997
    Genus *Iosactis* Riemann-Zürneck, 1997
        Iosactis vagabunda Riemann-Zürneck, 1997

TRIBE MESOMYARIA Carlgren, 1899

- FAMILY ACTINOSCYPHIIDAE Stephenson, 1920
  - Genus *Actinoscyphia* Stephenson, 1920
    - ***Actinoscyphia aurelia*** (Stephenson, 1918)
- FAMILY ACTINOSTOLIDAE Carlgren, 1932
  - Genus *Actinostola* Verrill, 1883
    - ***Actinostola callosa*** (Verrill, 1882)
  - Genus *Parasicyonis* Hertwig, 1882
    - ***Parasicyonis biotrans*** Riemann-Zürneck, 1991
- FAMILY BATHYPHELLIDAE Carlgren, 1932
  - Genus *Daontesia* Carlgren, 1942
    - ***Daontesia porcupina*** Riemann-Zürneck, 1997
- FAMILY HORMATHIIDAE Carlgren, 1932
  - Genus *Actinauge* Verrill, 1883
    - ***Actinauge abyssorum*** (Gravier, 1918)
    - ***Actinauge richardi*** (Marion, 1882)
  - Genus *Caracolactis* gen. nov.
    - ***Caracolactis maternalis*** sp. nov.
  - Genus *Amphianthus* Hertwig, 1882
    - ***Amphianthus bathybium*** Hertwig, 1882
  - Genus *Phelliactis* Simon, 1892
    - ***Phelliactis hertwigi*** Simon, 1892
- FAMILY KADOSACTIDAE Riemann-Zürneck, 1991
  - Genus *Kadosactis* Danielssen, 1890
    - ***Kadosactis commensalis*** (Gravier, 1918)
- FAMILY ANTIPODACTIDAE Rodríguez *et al.*, 2009
  - Genus Antipodactis Rodríguez *et al.*, 2009
    - ***Antipodactis ifremeri*** sp. nov.

Description of the studied species

ORDER ACTINIARIA HERTWIG, 1882

Anthozoa (Hexacorallia) with flat pedal disc more or less developed, or well developed rounded base, in physa-like shape. Column smooth or with verrucae, tenaculi, vesicles, marginal spherules or pseudospherules or other specializations of variable structure. Column often divided into different regions, sometimes with spirocysts and with nematocyst batteries, rarely with ectodermal muscles. Margin tentaculate, sometimes distinct, others with a more or less developed fosse. Tentacles arranged hexamerously in alternating cycles, occasionally ordered in radial series (endocoels); normally simple, however can be ramified, ending in knobs or branched or provided with papillae, exceptionally absent. Sphincter absent or present, endodermal or mesogleal. Oral disc usually circular, but sometimes drawn out into lobes of varying appearance. Actinopharynx shorter or longer usually with siphonoglyphs, typically two but varying from one to several. Siphonoglyphs usually connected with mesenteries, but very exceptionally the single siphonoglyph is more or less wholly separated from the actinopharynx. Pairs of mesenteries usually arranged in hexamerous cycles, with a variable number of pairs of perfect mesenteries. From the stage with six pairs of mesenteries or later, the subsequent mesenteries grow either from the pedal disc to the distal limit, or from the oral disc to the proximal limit, or simultaneously from the proximal and distal limits. Retractor muscles diffuse or circumscript. Parietobasilar muscles more or less developed, often differentiated in a lobule. Basilar muscles absent or present. Ciliated tract of the filaments normally present. Acontia absent or present. Distribution of the fertile mesenteries variable.

SUBORDER ENDOCOELANTHEAE Carlgren, 1924

Diagnosis (adapted from Carlgren, 1949 and Fautin & den Hartog, 2003)

Actiniaria with well developed pedal disc but without basilar musculature. Column without vesicles and verrucae, nearly always with spirocysts. Margin tentaculate. No sphincter. Tentacles in variable number, often with their aboral side thickened, in two cycles or, owing to the particular development and arrangement of the mesenteries, ordinate in an atypical form, as the position of the last ones. Longitudinal muscles of tentacles and radial muscles of oral disc ectodermal, with a slight mesogleal tendency. Oral disc sometimes lobed. One or two siphonoglyphs. Normally more than one pair of mesenteries (directives) attached to the siphonoglyphs. Arrangement of the mesenteries particular, after the development of the 12 first mesenteries (six pairs), all the subsequent pairs appear in the lateral endocoels and have their longitudinal muscles oriented as in the directives. Without acontia.

Observations

As mentioned in the diagnosis above, the suborder Endocoelantheae Carlgren, 1928 is characterized by the peculiar mesenteric arrangement. The mesenteries developed from the six pairs of the first cycle of mesenteries appear regularly in the lateral endocoels, in contrast with the other Actiniarians that show posterior cycles developed in exocoels, with few exceptions of irregular arrangements due to accidental regenerations or asexual longitudinal fission. This peculiarity was first mentioned by Carlgren (1897) from his observations of several specimens from Korean Strait, Hirado Strait and Japan (Uchida, 2004).

This suborder includes only two families, Halcuriidae and Actinernidae. The family Halcuriidae differs from Actinernidae by the following charaters: in the former, the mesenteries are differentiated between macro and microcnemes, the retractor musculature is restricted and presents a single siphonoglyph, in the latter the mesenteries are not differentiated in macro-microcnemes, and the retractor musculature is diffuse and presents two siphonoglyphs. In various taxa from the order Actiniaria mesenterial arrangements different from the "regular" patterns may occur (Carlgren, 1949). In the family Exocoelactiidae (tribe Mesomyaria), after the state of 12 pairs of mesenteries, the next ones appear bilaterally between the secondary exocoels, being of equal development. In the family Minyadidae (tribe Endomyaria) the endocoels are very well developed while the exocoels are less developed.

Family Halcuriidae Carlgren, 1918

Diagnosis (adapted from Carlgren, 1949)

Endocoelantheae with elongate, not lobed body. Column with small groups of nematocysts. Tentacles few, up to 70 in more than two cycles, without basal swellings on their aboral side, atypical arrangement. One or two siphonoglyphs. Mesenteries divided into macro-and microcnemes. Six or 10 pairs of macrocnemes; some of the microcnemes are perfect. Retractors of the macrocnemes rather strong, restricted.

Genus *Carlgrenia* Stephenson 1918

Diagnosis (adapted from Carlgren, 1949)

Halcuriidae with distinct base, slight parapet and fosse and no distal lobbing. Ectoderm of column, at least in upper part, with nematocyst batteries. No sphincter. Tentacles few. Macrocnemes six pairs, fertile, filamented with reniform retractors strongly restricted. In the lateral endocoels four pairs of perfect microcnemes which run down the whole length of the body; beyond these first ten pairs (six pairs macrocnemes and four pairs microcnemes). Basilar musculature absent.

Type species

Carlgrenia desiderata Stephenson, 1918

Species included in the genus

Carlgrenia desiderata Stephenson, 1918; monospecific genus

Carlgrenia desiderata Stephenson, 1918

(Fig. 1.1-1.3; Table 1)

Material examined

CARACOLE: Stn. PL 132-10 (R2) (2 specimens)

Description

External anatomy (Fig.1.1).— Pedal disc small, 0.9 cm diameter. One specimen attached to a carbonate structure of dead coral of *Lophelia pertusa*. Body cylindrical, elongate. Column measures 2.5 cm. Scapus wrinkled or striate, but do not form verrucae or tubercles. Oral disc open, tentacles visible. Ectoderm present nematocyst batteries, forming solid masses of spots along the scapus varying in size and density. Tentacles short, more than 32 in number. Slight fosse and parapet.

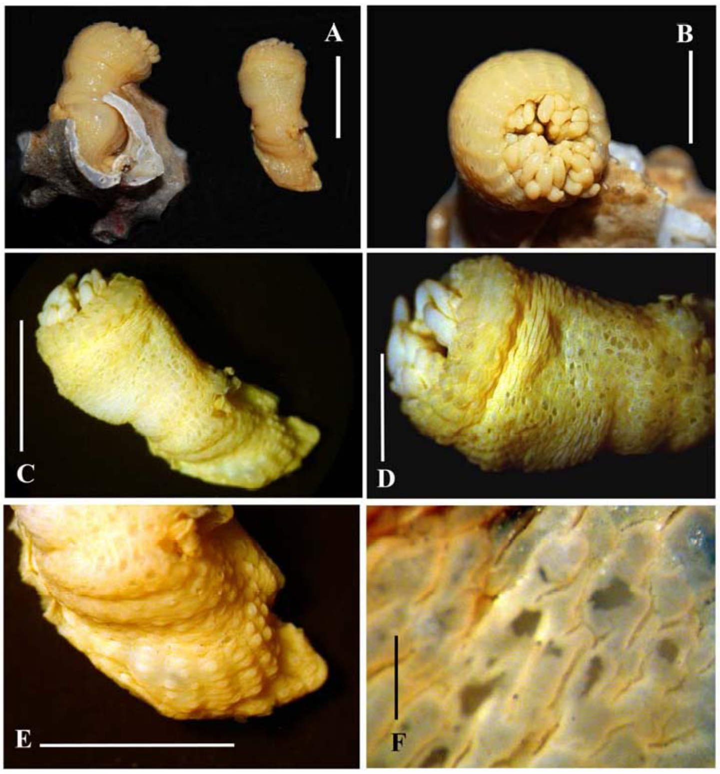

Figure 1.1.– *Carlgrenia desiderata* Stephenson, 1918. External anatomy [PL 132-10 (R2)]: A) Lateral view of two specimens; B) Oral disc open and tentacles view; C) Column detail; D) Column distal margin showing a slight fosse and parapet; E) Pedal disc detail; F) Ectoderm detail showing spots of dense nematocysts solid mass. Scale: A, 9 mm; B, 4 mm; C, 9 mm; D, 5 mm; E, 7mm; F, 0.5 mm.

Internal anatomy (Fig.1.2).— Two cycles of mesenteries divided into six pairs of macrocnemes and four pairs of microcnemes. Retractor musculature of the macrocnemes restricted, reniform, carrying filaments. Gametogenic tissue absent. Mesenterial filaments trilobate. Each pair of microcnemes develops between the endocoels of the macrocnemes. These four pairs run down the whole length of the body and reach the actinopharynx in its upper part. There are no additional microcnemes. Sphincter absent. Microcnemes small, without retractor muscles, filaments and gametogenic tissue either. Retractors circumscript. Parietobasilar weak, poorly developed. Longitudinal musculature and tentacles and radial muscles of the oral disc ectodermal with a slight mesogleal tendency. Column ectoderm with batteries of nematocysts (including spirocysts), varying in size and density, more abundant at the distal part and more scattered at the proximal part. Numerous batteries of spirocysts at the actinopharynx.

Cnidom (Fig. 1.3; Table 1).— An summary of the cnidom characteristics is given at Table 1. Spirocysts, basitrichs and microbasic *p*-mastigophores present.

Colour.— Yellowish white in preserved state.

Geographic and bathymetric distribution

The first capture of *Carlgrenia desiderata* Stephenson 1918 was recorded between 1247-1333 m depth at the SW coast of Ireland. This species has the deepest distribution in the family Halcuriidae (Uchida, 2004). The two specimens described in this work are the first record since its original description. The specimens examined herein were found in the Rockall Bank at a slightly shallower depth (690 m). As in the first record, these specimens were also attached to *Lophelia pertusa* branches.

Discussion

The observed material of *Carlgrenia desiderata* Stephenson, 1918 (two specimens and several young immature ones) allowed the redescription of this species.

Stephenson (1918) hypothesised that this species might possibly be a juvenile stage of a *Halcurias*, if the microcnemes can become macrocnemes. However, he considered that the observed specimen was not far from the adult stage (developed gametogenic tissue in the observed specimens is indicative of a mature form). Because of these findings, Stephenson created a new genus for this species. The specimen observed in this study was not in the reproductive stage. Although it showed the same characters used to recognise the genus (Uchida, 2004), which are the presence of six macrocnemes and four pairs of perfect microcnemes that appear along the whole body. Additional microcnemes beyond these first ten pairs (as in the genus description by Carlgren (1949)) were not found. Any other small microcnemes in the distal-most part of the body as it was reported by Stephenson were also not seen in the material examined herein. In the genus *Halcurias* (McMurrich, 1893) there are 10 macrocnemes, and the microcnemes appear only in the distal-most part of the body.

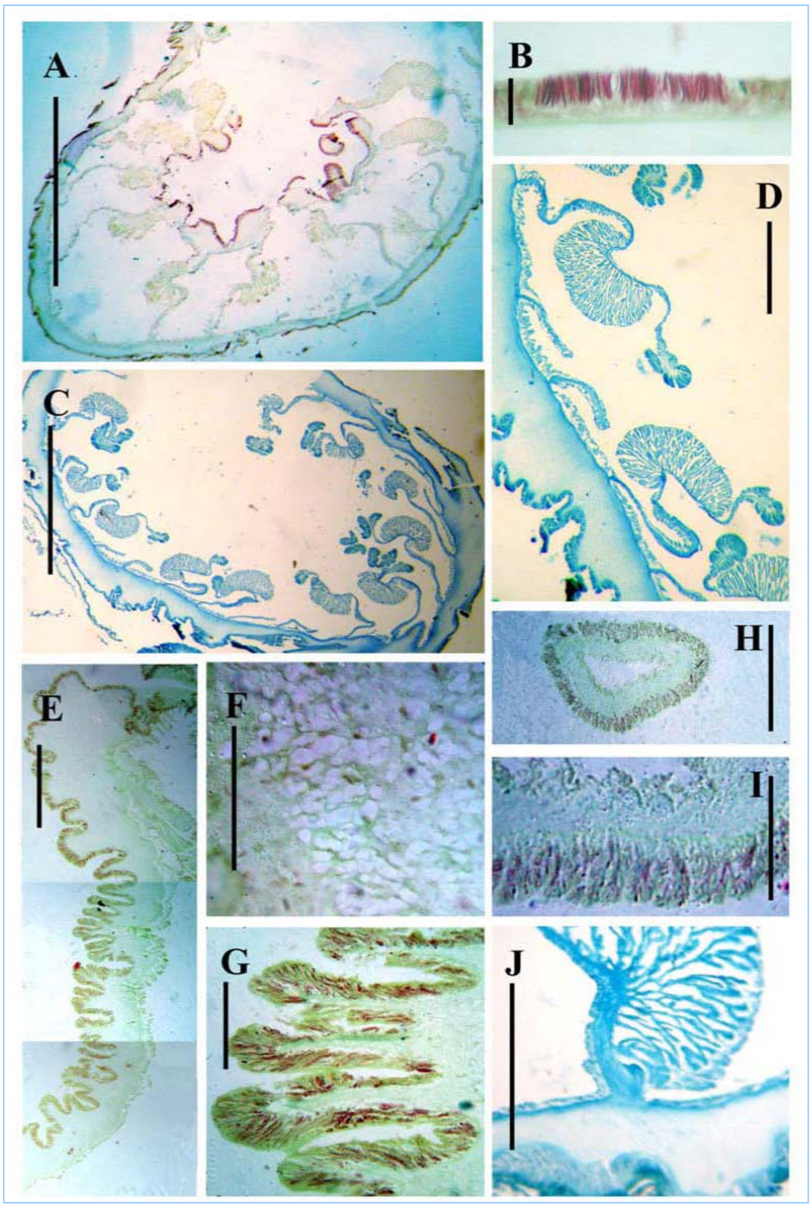

Figure 1.2.– *Carlgrenia desiderata* Stephenson 1918. Internal anatomy [PL 132-10 (R2)]: A) Transversal section at actinopharynx level showing 1st cycle perfect (macrocnemes) and pairs of microcnemes appearing in the lateral endocoels; B) Ectoderm detail with nematocyst batteries; C) Transversal section of the aboral region; D) Detail of macrocnemes retractor musculature and filaments, E) Longitudinal section of the column distal margin showing sphincter absence; F) Longitudinal musculature detail of the oral disc ectoderm with a slight mesogleal tendency; G) Column detail with nematocyst batteries; H) Transversal section of tentacle; I) Tentacle detail showing longitudinal musculature ectodermal; J) Longitudinal section of the pedal disc showing the absence of basilar musculature. Scales: A, 3mm; B, 0.5mm; C, 3mm; D, 1mm; E, 2mm; F, 0.07mm; G, 0.8mm; H, 0.75mm; I, 0.2mm; J, 0.3mm.

Table 1.– Dimensions of cnidae of *Carlgrenia desiderata* Stephenson, 1918. Specimens: [PL 132-10 (R2)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --sporadic. Abbr. Mic. Microbasic. (*) Average based on measures of less than 40 capsules, which is considered the meaningful minimum (Williams, 1996; 1998).

Category	**Fig. 1.3**	**Range of length and width of capsules in µm**	**X ± SD**	**S**	**N**	**F**	***Halcurias carlgreni* McMurrich, 1901 data (Uchida, 2004)**	**X**	**F**
PEDAL DISC									
Basitrichs	**A**	**(10-13) x 2**	**10.8±0.9 x 2±0.0**	**2/2**	**40**	**+++**	**–**	**–**	**–**
COLUMN									
Basitrichs	**B**	**(24-39) x (2-3)**	**31.8±3.3 x 2.1±0.2**	**2/2**	**40**	**++**	**20-27 x 1.9-2.6**	**24 x 2.2**	**++**
Mic. *p*-*m*astigophores	**C**	**(16-31) x (4-6)**	**25.2±3.2 x 5.8±0.5(*)**	**2/2**	**24**	**+**	**–**	**–**	**–**
Spirocysts	**–**	**–**	**–**	**–**	**–**	**–**	**23-32 x 5.2-6.5**	**29 x 5.9**	**+++**
							22-31 x 2.9-3.0	**28 x 5.5**	
TENTACLES									
Spirocysts	**D**	**(20-45) x (3-8)**	**32.1±5.1 x 6.1±1.7**	**2/2**	**40**	**+++**	**32-48 x 5.0-7.0**	**37 x 6.3**	**+++**
							22-31 x 2.8-4.0	**24 x 3.4**	**++**
Basitrichs	**E**	**(20-29) x (2-3)**	**24.0±2.2 x 2.5±0.4**	**2/2**	**40**	**++**	**24-33 x 2.4-3.8**	**28 x 2.7**	**++**
PHARYNX							**24-36 x 2.6-3.7**	**28 x 2.8**	**++**
Spirocysts	**F**	**(22-38) x (5-7)**	**30.1±3.9 x 6.0±0.6**	**2/2**	**40**	**+++**	**20-42 x 4.8-7.7**	**28 x 3.0**	
Basitrichs	**G**	**(22-35) x (2.5-7)**	**29.5±2.9 x 4.3±1.6**	**2/2**	**40**	**++**	**24.5-31 x 2.9-3.0**	**28 x 3.0**	**++**
Mic. *p*-mastigophores	**H**	**(16-32) x (4-7)**	**26.7±2.9 x 5.6±0.8**	**2/2**	**40**	**++**	**25-31 x 4.3-5.8**	**28 x 5.8**	**++**
FILAMENTS									
Basitrichs	**I**	**(26-31) x (2-3)**	**28.9±1.4 x 2.8±0.3**	**2/2**	**40**	**+++**	**21-29 x 3.0-3.2**	**No data**	**+**
Mic. *p*--mastigophores	**J; K**	**(14.5-25) x (4-7)**	**20.3±3.7 x 5.6±0.8**	**2/2**	**40**	**+++**	**22.5-32 x 4.8-6.0**	**26 x 60**	**++**
Spirocysts	**–**	**–**		**–**	**–**	**–**	**16-30 x 5.0-6.7**	**25 x 5.6**	

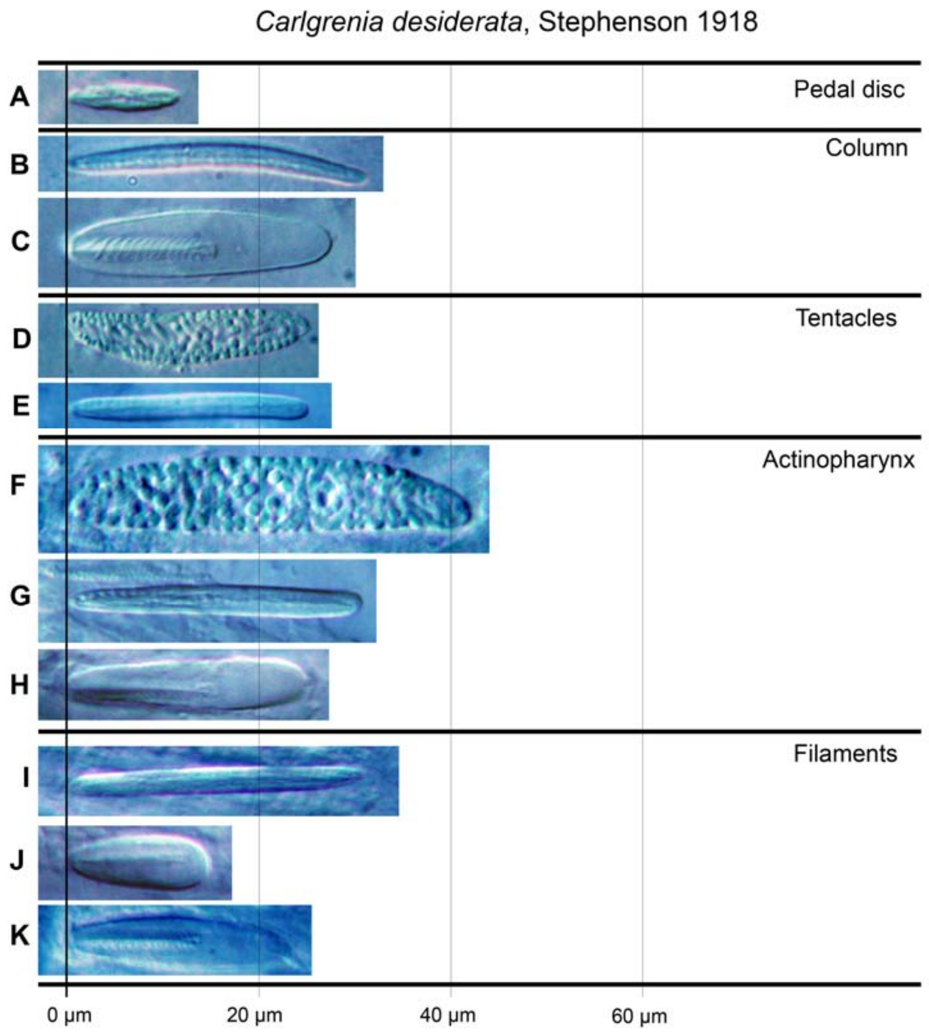

Figure 1.3.– *Carlgrenia desiderata* Stephenson, 1918. Cnidae: A) basitrich; B) basitrich; C) microbasic p-mastigophore; D) spirocyst; E) basitrich; F) spirocyst; G) basitrich; H) microbasic p-mastigophore; I) basitrich; J) microbasic *p*-mastigophore 1; K) microbasic *p*-mastigophore 2.

There is no previous data on nematocyst types and sizes. The only information available reports the presence of numerous batteries of nematocysts in the column. In this work it was possible to measure and identify all categories of nematocysts in the different tissues of all parts of the body. Moreover, the presence of spirocysts in other tissues than tentacles is considered of high relevance. The presence of spirocysts in the actinopharynx was observed in both *Carlgrenia* and *Halcurias* (see Table 1.3; example with *H. carlgreni;* McMurrich, 1901). Uchida (2004) also noticed the presence of spirocysts on scapus and filaments of *Halcurias*. However, this feature was not seen in *Carlgrenia*. The presence or absence of spirocysts in such tissues is a distinctive character to determine species. Despite the similarities on sizes and types of nematocysts, *Carlgrenia* has a unique cnidom when compared with *Halcurias* species (see key *in* Uchida, 2004).

The number of captures of these species (Family Halcuriidae) recorded globally is in fact so small that makes these organisms very special and extremely rare. According to the few records of captures the monotypic genus *Carlgrenia* has the deepest distribution, and also, exceptionally is the only Boreal North Atlantic species within the Halcuriidae; the *Halcurias* species were found only in the Southern Hemisphere (see Uchida, 2004). Presently *Carlgrenia desiderata* maintains the same distributional area since its first record in 1918. However, this restricted distribution may be due to the lack of sampling or because the species may have been overlooked in previous collections; it would be very interesting to be aware in future expeditions, especially in *Lophelia* habitats, of the possible presence of this species in order to clarify its possible endemism. However, the rare occurrence of the species in previous trawl samples suggests that this species wiil be rarely collected in the future since this type of destructive sampling methods were abandoned due to the conservation status of the *Lophelia* habitats.

SUBORDER NYANTHEAE Carlgren, 1899

Diagnosis (adapted from Carlgren, 1949)

Actiniaria with a round or flat base with or without basilar muscles. Column smooth or with growths of one sort or another, rarely (and then especially in the uppermost part) provided with ectodermal muscles. Sphincter absent or present, endodermal or mesogleal. Tentacles simple or complex, commonly arranged in cycles, sometimes in radial rows. Siphonoglyphs usually attached to directives, rarely to non directives, when directives are absent. Mesenteries, as a rule, arranged in cycles, commonly hexamerously. Secondary mesenteries always develop in exocoels. The pairs of non-directives consist of two mesenteries which retractors face one another, rarely unpaired mesenteries occur. Mesenterial filaments always with ciliated tracts.

TRIBU ENDOMYARIA STEPHENSON, 1921

Diagnosis (adapted from Stephenson, 1935)

Nynantheae with well defined base, normally adherent and with or without basilar musculature. Column smooth, with vesicles or verrucae, sometimes with cinclides, and usually acrorhagi. Tentacles simple or modified, normally one tentacle for each endocoel and exocoel, rarely more than one tentacle for each endo- and exocoel. Without sphincter or with endodermal sphincter that occasionally shows a strong tendency to be more or less mesogleal. Without acontia.

Family Edwardsiidae

Diagnosis (adapted from Carlgren, 1949)

Nynantheae (Endomyaria) with elongate, vermiform body, usually divided at least into two regions, a long scapus with cuticle and a short upper scapulus. Often there is also a rounded, naked physa at the aboral end and a very short, thin capitulum immediately below the tentacles. No sphincter or acontia. Mesenteries divisible into eight macro- and at least four microcnemes. Of the macrocnemes there are two pairs of directives and four lateral mesenteries, two on each side with retractors that face the ventral directives. Retractors diffuse to strongly restricted. Parietal muscles always distinct.

Genus *Edwardsia* Quatrefages, 1842

Diagnosis (England, 1987; adapted from Carlgren, 1949)

Body divided into physa, scapus, scapulus and capitulum; physa short, ampullaceous, without nemathybomes or cuticle. Scapus long with batteries of nematocysts (nemathybomes) sunk in the mesoglea. Nemathybomes always containing two types of nematocysts. Siphonoglyph weak, ventral. Mesenteries comprising eight macrocnemes (perfect) and at least four microcnemes (imperfect), which are very weak and in the capitulum only; first four microcnemes always paired with macrocnemes. Gonads, filaments, and parietal and retractor muscles on macrocnemes only. Parietal muscles well developed, retractors strong-diffuse to restricted-reniform. Cnidom: spirocysts, basitrichs, pterotrichs, microbasic amastigophores and t- mastigophores.

Type species

Edwardsia beautempsii de Quatrefages, 1842

Species included in the genus

Edwardsia beautempsii de Quatrefages, 1842; *E. timida* de Quatrefages, 1842; *E. clavata* (Rathke, 1843); *E. tuberculata* Dueben and Koren, 1847; *E. sipunculoides* (Stimpson, 1853); *E. collaris* Stimpson, 1856; *E. rubricollum* Stimpson, 1856; *E. sulcata* Verrill, 1864; *E. allmani* M'Intosh, 1865; *E. goodsiri* M'Intosh, 1865; *E. elegans* Verrill, 1869 (?); *E. coriacea* Moseley, 1877; *E. arenosa* Klunzinger, 1877; *Edwardsianthus pudica* (Klunzinger, 1877); *E. claparedii* Andres, 1881; *E. meridionalis* Williams, 1981; *E. scabra* Marion, 1882 (?); *E. flaccida* Marion, 1882; *E. rigida* Marion, 1882; *E. grubii* Andres, 1883; *E. octoplax* (Sluiter, 1888); *E. tecta* Haddon, 1889; *E. fischeri* Chevreux et de Guerne, 1889; *E. vitrea* (Danielssen, 1890); *E. fusca* Danielssen, 1890; *E. costata* Danielssen, 1890; *E. andresi* Danielssen, 1890; *E. intermedia* McMurrich, 1893; *E. neozelanica* Farquhar, 1898; *E. californica* (McMurrich, 1913); *E. tinctrix* Annandale, 1915; *E. willeyana* Bourne, 1916; *E. mammillata* Bourne, 1916; *E. rugosa* Bourne, 1916; *E. vegae* Carlgren, 1921; *E. incerta* Carlgren, 1921; *E. arctica* Carlgren, 1921; *E. islandica* Carlgren, 1921 (?); *E. carlgreni* Carlgren, 1921; *E. longicornis* Carlgren, 1921; *E. finmarchica* Carlgren, 1921; *E. danica* Carlgren, 1921; *E. incerta* Carlgren, 1921 (*nomen dubium* in Williams, 1981)*;* *E. kameruniensis* Carlgren, 1927; *E. delapiae* Carlgren and Stephenson, 1928; *E. octoradiata* Carlgren, 1931; *E. maroccana* Carlgren, 1931; *E. japonica* Carlgren, 1931; *E. duodecemtentaculata* Carlgren, 1931; *Edwardsianthus gilbertensis* (Carlgren, 1931); *E. callianthus* Rawlinson, 1935*;* *E. capensis* Carlgren, 1938; *E. sanctaehelenae* Carlgren, 1941; *E. norvegica* Carlgren, 1942; *E. annamensis* Carlgren, 1943; *E. vivipara* Carlgren, 1950; *E. jonesii* Seshaiya and Cuttress, 1969 (?); *E. ivelli* Manuel, 1975; *E. meridionalis* Williams, 1981; *E. hantuensis* England, 1987; *E. athalyei* England, 1990, *E. handi* Daly & Ljubenkov, 2008; *E. juliae* Daly & Ljubenkov, 2008; *E. mcmurrichi* Daly & Ljubenkov, 2008; *E. olguini* Daly & Ljubenkov, 2008; *E. profunda* Daly & Ljubenkov, 2008.

Observations

The taxonomic ranking of Edwardsiidae has been changed from genus (Andres, 1883) to family (Carlgren, 1921), and it has been even considered as equivalent to a group containing the modern orders Actiniaria, Corallimorpharia and Scleractinia (Hertwig, 1882; Stephenson, 1921). Recent molecular phylogenetic analyses have confirmed that edwardsiids belong within Actiniaria (Daly, 2002a and 2002b) and that the current rank of family within the Actiniaria is suitable.

Edwardsia tuberculata Dueben and Koren, 1847

(Fig. 2.1-2.3, Table 2)

Material examined

CARACOLE (St. KGS11): 1 specimen for histological analyses, 3 specimens for cnidae measurements.

Additional examined material

Edwardsia tuberculata Dueben and Koren, 1847. Bergen Museum: "Koren" determ. Carlgren (2 specimens); "Thor" determ. Carlgren (3 specimens); "Norge" determ. Carlgren; "Lütken" determ. Carlgren. Copenhagen Museum: Specimen 32998 determ. Grieg; Specimen 32992 determ. Grieg.

Description

External anatomy (Fig. 2.1).— Column long, 15 to 20mm in contracted state. divided into three regions: physa, scapus and scapulus. Nemathybomes in eight rows, prominent (visible to the naked eye), along the column. Physa well developed, without periderm or nemathybomes, invaginated. Centre of aboral end introvertable. Scapular rugae. Oral disc retracted. Tentacles contracted, 12 in number. Tentacles filiform.

Figure 2.1.– *Edwardsia tuberculata* Dueben and Koren, 1847. External anatomy [KGS11]: Lateral view of three specimens. Scale: 2cm.

Internal anatomy (Fig. 2.2).— Mesenteries ordered in 8 perfect macrocnemes and 4 imperfect microcnemes. Microcnemes present at the most distal part of pharynx, disposed individually coupled with macrocnemes in lateral and ventrolateral compartment and one pair in dorsolateral compartment. Ciliated tracts continuous, extending into reproductive region. Retractor muscles circumscribed, in palmate and convex shape, with close branch spacing.

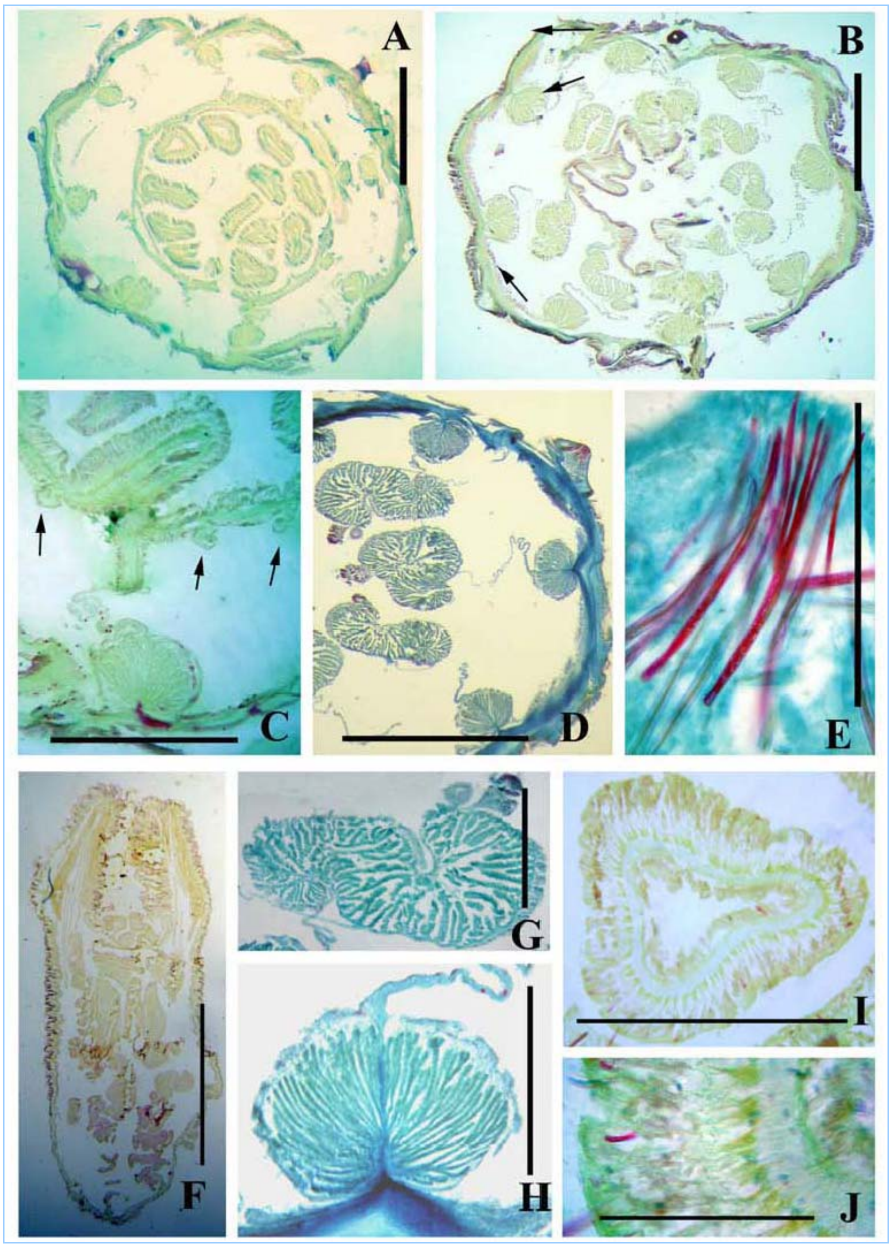

Figure 2.2.– *Edwardsia tuberculata* Duben and Koren, 1847. Internal anatomy [KGS11]: A) Transversal section at the actinopharynx level, showing 12 tentacles inside; B) Transversal section at actinopharynx level showing 8 individual mesenteries with parietal and retractor musculature; C) Transversal section detail at uppermost distal part, showing one macrocneme and microcnemes at ventrolateral compartment (reversed); D) Mesenteries at proximal part with filaments; E) Nemathybome with Pterotrichs; F) Longitudinal section of the entire body showing the absence of sphincter; G) Detail of macrocneme with circumscribed retractor; H) Detail of macrocneme showing the parietobasilar musculature; I) Transversal section of an tentacle; J) Detail of tentacle ectodermal musculature. Scale: A, 2mm; B, 2mm; C, 1mm; D, 2mm; E, 0.15mm; F, 3.5mm; G, 0.4mm; H, 0.3mm; I, 0.4mm; J, 0.1mm.

Table 2.– Dimensions of cnidae in *Edwardsia tuberculata* Duben and Koren, 1847. Specimens: [KGS11]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic.

Category	Fig. 2.3	Range of length and width of capsules in µm	X ± SD	S	N	F	Data of *E. tuberculata* Dueben & Koren, 1847 from Carlgren, 1921	Data of *E. claparedii* (Panceri, 1869) syn. *E. callimorpha* (Gosse, 1853) from Stephenson, 1935
NEMATHYBOMES								
t-mastigophores	**A**	**(55-89) x (2.5-3)**	**72.2±8.6 x 3±0.1**	**3/3**	**60**	**+++**	**(60-96) x (2-2.5)**	**69-95 x about 3**
Pterotrichs	**B**	**(90-168) x (5-8)**	**132.8 ±18.2 x 6.2±0.5**	**3/3**	**60**	**++**	**(72-190) x (4-7)**	**97-154 x 5-7**
TENTACLES								
Spirocysts	**C**	**(16-30) x (2-5.5)**	**23.5±2.7 x 4.1±0.8**	**3/3**	**59**	**+++**	**(14-23) x (1.5-2.5)**	**–**
Basitrichs	**D**	**(20-29) x (2-3.5)**	**24.4 ±2.1 x 2.4±0.3**	**3/3**	**60**	**+++**	**(18-26) x (1.5)**	**17-26 x 2-2.5**
PHARYNX								
Basitrichs 1	**E**	**(15-20) x (2-3)**	**16.9±1.2 x 2.4±0.4**	**3/3**	**79**	**++**	**–**	**15-39 x 2-4**
Basitrichs 2	**F; G**	**(25-41) x (2.5-3)**	**17.8±3.8 x 3±0.2**	**3/3**	**80**	**+++**	**(22-34) x 2.5**	
Mic. *p*-mastigophores	**H**	**(26-37) x (5-8.5)**	**30.6±2.8 x 6.4±0.6**	**3/3**	**70**	**++**	**(29-34) x (5-6)**	**27-37 x 5-7.5**
FILAMENTS								
Mic. b-mastigophores	**I**	**(23-25) x (4-6)**	**29.3±2.8 x 4.4±0.5**	**3/3**	**58**	**+**	**–**	**25-27 x 4-6**
Basitrichs	**J; K**	**(16-30) x (2-3)**	**20±3.5 x 2.9±0.2**	**3/3**	**60**	**++**	**–**	**16-34 x 2-3**
Mic. *p*-mastigophores	**L**	**(18-32) x (4-7)**	**25.8±3.8 x 5.7±0.6**	**3/3**	**60**	**+++**	**–**	**19-33 x 4-7**
PHYSA								
Basitrichs	**No image**	**(10-15) x (2-3)**	**12.8±1 x 2.5±0.3**	**3/3**	**60**	**++**	**(11-16) x 1.5**	**–**

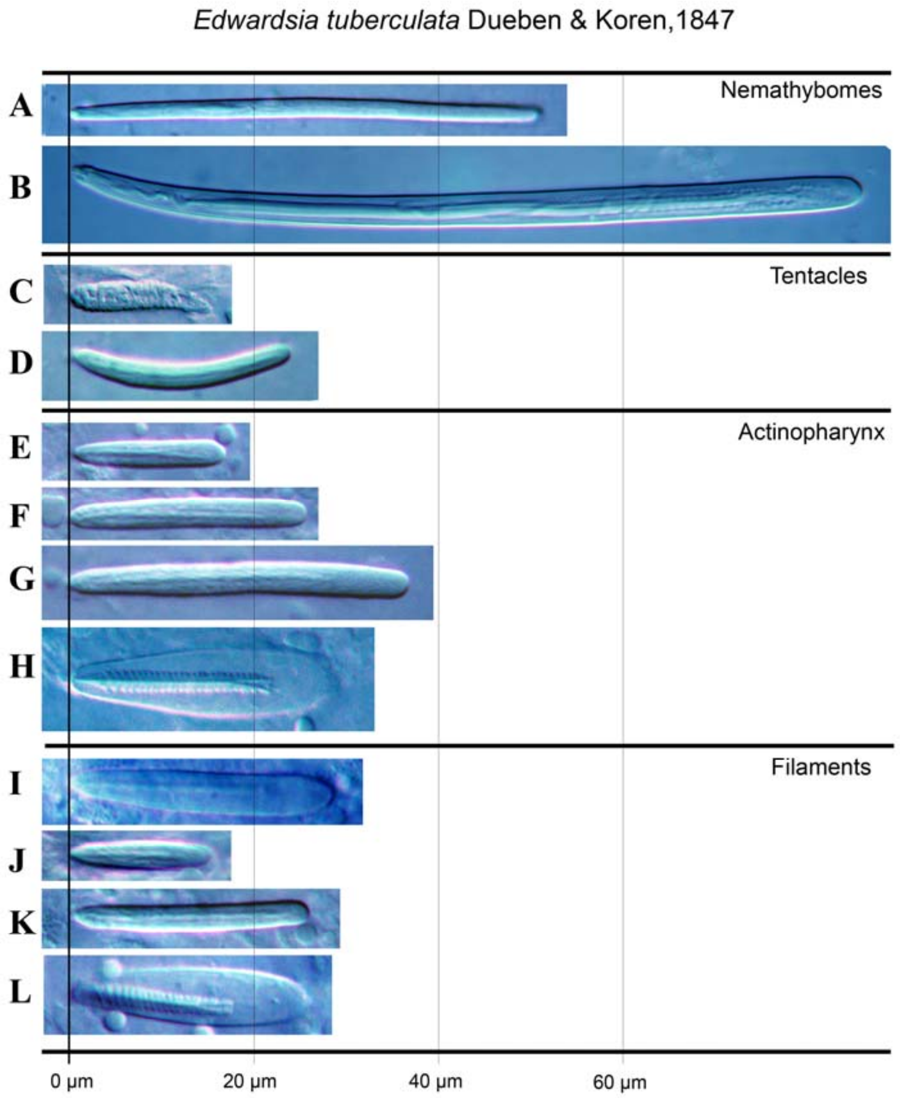

Figure 2.3.– *Edwardsia tuberculata* Dueben and Koren, 1847. Cnidae: A) t-mastigophore; B) pterotrich; C) spirocyst; D) basitrich; E) basitrich 1; F) basitrich 2a; G) basitrich 2b; H) microbasic *p*mastigophore; I) microbasic b-mastigophore; J) basitrich 1; K) basitrich 2; L) microbasic *p*mastigophore.

Cnidom (Fig. 2.3; Tab. 2). — Nemathybomes with very large "Pterotrichs", between 120-150µ, and microbasic t-mastigophores of 70-80 µm. Basitrichs, microbasic *p*-mastigophores and spirocysts.

Colour.— Beige, opaque

Geographic and bathymetric distribution

The locations were *Edwardsia tuberculata* was collected previously to this work are: Norway, Sweden, Denmark, Iceland (Carlgren, 1921; Daly, 2002) and also the Faroe Islands (Fautin, *et al.*, 2005). The maximum depth was recorded at the lowest latitudes in Iceland (216-326m) and at the BIOFAR station (503m) all the other specimens were found at shelf depths (Carlgren, 1921; Fautin *et al,* 2005). The material collected in CARACOLE station St. KGS11, in the Rockall area (R1), was found at 702m depth, which means that *E. tuberculata* extends its distribution to the Boreal sub-region, although at deeper habitats.

Discussion

One of the most important differences between *Edwardsia tuberculata* Duben and Koren, 1847 specimens collected in CARACOLE stations and the type material described by Duben and Koren (1847) from Bergen and re-examined by Carlgren is the basitrich thickness of the tentacles. In CARACOLE material it has nearly 2.5-3 µm instead of 1.5 µm measured by Carlgren. However, from the observations observations of "Koren" specimens made during this study, nemathybomes are similar (Pterotrichs: 114-138 x 5.5-6µ; t-mastigophores: 68-73 x 2,5-3µ), and also the spirocysts and basitrichs from tentacles. On the other hand, it was impossible to measure nematocysts from the filaments due to the poor conservation (macerated tissue) of the specimens. We had not access to "Sars"'s material (from Bergen - Manger) nor to Sweden material (from Väderöarne and Kosterfiord N. Hellsö) which are the other specimens with thin basitrichs measured by Carlgren in 1921. Contrarly, in "Thor"'s material, filaments nematocysts are very similar to our measurements. In the "Norge"'s material the analysis of these features was not possible because all specimens were dehydrated. In "Lütken"'s material the observed nemathybomes agreed fairly well. However, in specimens from the Copenhagen Museum (two specimens determined by Grieg), t-mastigophores were not seen and pterotrichs were smaller (5084 x 4-5µ). Probably these specimens are not *E. tuberculata*, but a more detailed study is needed to clarify their identity.

The cnidom of the actinopharynx is composed by two basitrich sizes, one large and other small, in opposition to *E. tuberculata* Carlgren data, which mentions only the large basitrich. Carlgren did not found microbasic b-mastigophores at the filament, however we suspect this was due to the poor conservation condition of the material (has he complained). Daly (2002) observed microbasic b-mastigophores in all *Edwardsia* species examined in her work. Manuel (1977) presented data of microbasic b-mastigophores which are similar to our observations.

Comparatively to Daly's key (2002), our observations fit better in *E. tuberculata* than in any of the other species, except for internal anatomy, where there is some ambiguity due to the parietal muscle core thickness (Appendix 2: character 32 *in* Daly, 2002) and the existence (or not) of ramification at upper lateral branches (Appendix 2: character 35 *in* Daly, 2002). In the CARACOLE material, the parietal muscle core thickness is a little bit thicker than lateral branches, and dichotomous ramification in few upper lateral branches was observed. Also Carlgren presented similar observations in his work (Carlgren, 1921: pp. 31; Fig. 14). Inexplicably, Daly (2002) considered "beautempsii clade" using characters 32 and 35 as unambiguous morphological synapomorphies. Daly (2001), presented the characters list and data of the museum specimens examined, although this information remains published only in a Phd dissertation, which we could not access. In her revision (Daly, 2002), the species close to *E. tuberculata* is *E. claparedii* (Panceri, 1869). The latter is distinguished by the lack of a introverted physa, absence of reproductive tissue on filaments and presence of a disorganized scapular ectoderm. In fact, we compared *E. tuberculata* cnidom with *E. claparedii* syn. *E. callimorpha* in Stephenson, 1935, and they seem very similar to each other (see Table 2.). In this case the cnidom analysis is not sufficient. Daly (2002) showed the importance of the analysis of combined morphological and molecular data to assess Edwardsiidae systematics classification and provided new characters to be applied in species identification and taxonomic problems.

Family Actiniidae Rafinesque, 1815

Diagnosis (adapted from Carlgren, 1949)

Nynantheae (Endomyaria) with basilar musculature. Column smooth or with projections, verrucae, marginal acrorhagi, pseudacrorhagi or vesicles but never with macrobasic *p*amastigophores. Sphincter endodermal, diffuse to circumscript or absent. Tentacles simple, ordered in cycles. Never more than one tentacle communicating with each endo- and exocoel. Mesenteries not divided in macro- and microcnemes. Pairs of mesenteries perfect rarely only six, as a rule more than six.

Genus *Bolocera* Gosse, 1860

Diagnosis (adapted from Carlgren, 1949)

Actiniidae with pedal disc well developed. Column short, smooth without spherules or verrucae. Sphincter diffuse. Large tentacles, hexamerous, each one with an endodermal sphincter in its base that can be liberated with their contraction. Pairs of perfect mesenteries more or less numerous, two pairs of directives. Retractor musculature diffuse. Proximal mesenteries in similar or higher number than distal.

Type species

Bolocera tuediae (Johnston, 1832)

Species included in the genus

Bolocera africana Pax, 1909; *B. kerguelensis* Studer, 1879; *B. maxima* Carlgren, 1921; *B. norvegica* Pax, 1909; *B. pannosa* McMurrich, 1893; *B. somaliensis* Carlgren, 1928; *B. tuediae* (Johnston, 1832).

Observations

Along its taxonomic history the genus *Bolocera* suffered numerous events of misinterpretation of type species and crossed information involving northern and southern species. These misinterpretations originated successive synonymies. In the North Hemisphere, *B. tuediae* was confounded with *B. longicornis* (Stephenson, 1918; and Carlgren 1891); also *Liponema multicornis*, presently in the family Liponematidae, was identified as *Bolocera multicornis* Verrill 1879 and *B. brevicornis* McMurrich, 1893. At the moment, the only valid species cited in the literature for the North Hemisphere are *B. tuediae* (Johnston, 1832) and *B. maxima* Carlgren, 1921. For the South Hemisphere, several species were synonymised as *B. kerguelensis* Studer, 1879 (*B. longicornis* of Stephenson (1918) and Carlgren (1949), *B. occidua* McMurrich, 1893, *B. capensis* Carlgren, 1928, *B. patens* Carlgren, 1949, *B. paucicornis* Dunn, 1983 and *B. tudiae* spp. *kerguelensis* of Riemann-Zürneck, 1986).

Bolocera tuediae (Johnston, 1832)

(Fig. 3.1-3.3; Table 3)

Material examined

PROSPEC: stn. CPH-03 (BEIM: 3129, 1 specimen); stn. 1 (CPH-02) (BEIM: 3132, 3 specimens).

Description

External anatomy (Fig. 3.1).— Body cylindrical. Pedal disc well developed, 30mm in diameter. Limbus very well pronounced. Column short, firm, funnel shape, with 30mm length and breadth in preserved material. Column smooth with remarkable mesenteric insertions and with irregular circular furrows caused by contraction.

Figure 3.1.– *Bolocera tuediae* (Johnston, 1832). External anatomy [BEIM (3129)]: A) Lateral view; B) Oral disc view; C) Pedal disc view. Scale: A, 30 mm; B, 20 mm; C, 30 mm.

Broad oral disc, plane not contracted with a very big mouth. One larger specimen of the Stn. (CPH-02) PROSPEC, in preserved conditions shows the actinopharynx in a reverse state. Numerous tentacles hexamerously arranged in 5 cycles, with longitudinal furrows and more straight in its distal part. They occupy half oral disc and normally they auto-discharge due to the strong endodermal sphincter at the base. Oral disc frequently with holes that are marked by the place of such tentacles. Tentacles are of different sizes due to the regeneration process at different times.

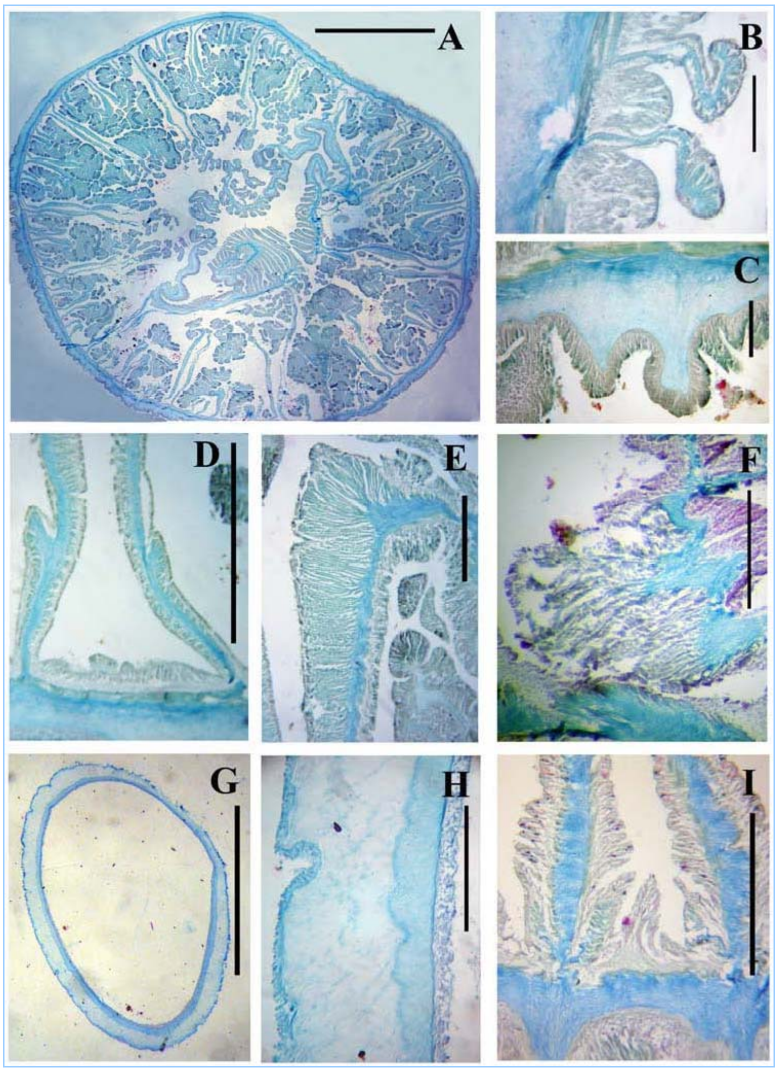

Figure 3.2.– *Bolocera tuediae* (Johnston, 1832). Internal anatomy [BEIM (3132)]: A) Transversal section at actinopharynx level showing mesenteries cycles; B) Detail of a pair of microcnemes; C) Detail of ectoderm; D) Detail of macrocnemes parietobasilar muscles; E) Detail of macrocneme retractor musculature; F) Longitudinal section of the margin distal part showing the sphincter endodermal diffuse; G) Transversal section of tentacle; H) Detail of tentacle ectodermal musculature; I) Longitudinal section of the pedal disc showing basilar musculature. A, 7.5 mm; B, 1.5 mm; C, 0.25 mm; D, 0.55 mm; E, 0.4 mm; F, 0.4 mm; G, 3.5 mm; H, 0.3 mm; I, 0.45 mm.

Internal anatomy (Fig.3.2).— Hexamerous mesenteries, five cycles, 1st and 2nd perfects. Last cycle incomplete poorly developed, without mesenteric filaments, sterile. Sphincter endodermal circumscript. First three cycles fertile, except for the two pairs of directives. Retractor musculature diffuse and strong. Parietobasilar muscles well developed. Basilar musculature well developed.

Cnidom (Fig. 3.3; Table 3).— Spirocysts, basitrichs; microbasic *p*-mastigophores.

Table 3.– Dimensions of cnidae in *Bolocera tuediae* (Johnston, 1832). Specimens: [BEIM (3132)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic. (*) Average based on measures of less than 40 capsules, which is considered the meaningful minimum (Williams, 1996; 1998).

Category	Fig. 3.3	Range of length and width of capsules in µm	X ± SD	S	N	F	Data from Carlgren 1921
PEDAL DISC							
Basitrichs	**A**	**(15-42) x (2.5-4)**	**32.8 ±6.1 x 3.6±0.5**	**3/3**	**60**	**+++**	**–**
COLUMN							
Basitrichs 1	**B**	**(15-24) x (2-3)**	**19.1±1.6 x 2.6±0.3**	**3/3**	**50**	**++**	**14-19 x 1.5**
Basitrichs 2	**C**	**(31-49) x (3-4.5)**	**39.1±4.4 x 4.0±0.2**	**3/3**	**60**	**+++**	**26-48 x 2.5-3.5**
TENTACLES							
Spirocysts	**No image**	**(30- 75) x (2-6)**	**46.8±12.1x 3.8±0.6**	**3/3**	**60**	**+++**	**22 x 1-2 77 x 4-5**
Basitrichs	**D**	**(52-104) x (3.5-5)**	**75.1±9.4 x 4.1±0.3**	**3/3**	**60**	**+++**	**Apex: 60-82 x 2.5-3 (small) 70-127 x 3-3.5 (large); Proximal: 36-60 x 2.5-3 (small) 53-72(86) x 2.5-3 (large)**
PHARYNX							
Basitrichs	**E**	**(47-70) x (4-6)**	**55.7±5.0 x 4.7±0.5**	**3/3**	**60**	**---/+**	**(30)43-62 x 3-4**
Mic. *p*-mastigophores	**F**	**(21-30) x (5-7)**	**24.6±2.5 x 5.6±0.5(*)**	**3/3**	**25**	**---/+**	**–**
FILAMENTS							
Basitrichs 1	**G**	**(18-27) x (2-3)**	**21.5±2.0 x 2.9±0.3**	**3/3**	**60**	**+/++**	**–**
Basitrichs 2	**H**	**(51-82) x (4-6)**	**69.4±5.4 x 4.7±0.5**	**3/3**	**60**	**++**	**–**
Mic. *p*-mastigophores	**I**	**(25-37) x (4-7)**	**30.3±2.5 x 5.8±0.7**	**3/3**	**60**	**++**	**–**

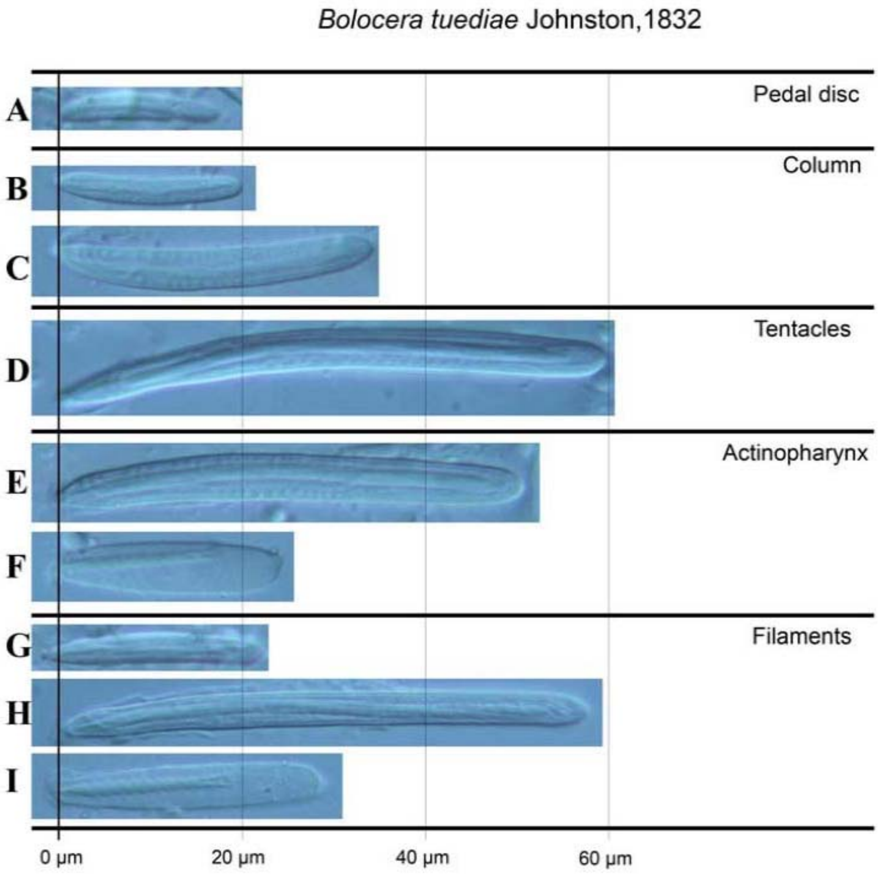

Figure 3.3.– *Bolocera tuediae* (Johnston, 1832). Cnidae: A) basitrich; B) basitrich 1; C) basitrich 2; D) basitrich; E) basitrich; F) microbasic p-mastigophore; G) basitrich 1; H) basitrich 2; I) microbasic pmastigophore.

Geographic and bathymetric distribution

This species is considered to have a wide boreal distribution in the North Hemisphere. Its distribution extends from West Greenland to Cape Fear along the east coast of America, northern part of N Atlantic, the Faroes, Norway, North Sea, S and SW of Ireland and probably more southwards. Its bathymetrical distribution is between 40 and 1844 m (Carlgren, 1939).

Discussion

According to the data provided above, the analysed material appears to conform with the description of *Bolocera tuediae* (in Carlgren, 1921, p. 140). In the present study, the observation of nematocysts from filaments and pedal disc was also possible. Carlgren suggests that *B. maxima* (found in Davis Strait; see Carlgren, 1921, p. 145) differ from *B. tuediae* based only on the large size of the nematocysts, and he gave their dimensions in the apex (96-192 x 3.3-4.5µ) and in the proximal part (68-120 x 3.5 -4µ). In our opinion, this suggestion is totally doubtful due to the high variability of sizes caused by the autodischarge and consequently different development stages.

Riemann-Zürneck (1986a) suggested that all the austral species are synonyms of *B. tuediae* with distinct subspecies. She also recommended the observation of ecological characters (reproduction season, viviparity) to detect subspecies variability. However, the available material was not at the reproductive period. Morphological constraints make the differentiation between *Bolocera* species (if they really exist) complex; Genetic studies to clarify the possible existence of subspecies of *B. tuediae* and compare distinct populations are in need.

Family Condylanthidae Stephenson (1922)

Diagnosis (according with Carlgren, 1949 with corrections of Riemann-Zürneck, 1979)

Endomyaria possess a column that is usually divided into scapus and scapulus. Marginal pseudospherules sometimes present. Sphincter absent, diffuse or circumscript. Tentacles few. Longitudinal muscles of tentacles and radial muscles of oral disc ectodermal or mesogleal. One or two siphonoglyphs. Mesenteries divided into macro- and microcnemes, the latter often present only in the lowermost part of the body. Microcnemes few, with strong retractors, which may be circumscript or strongly restricted. Parietobasilar muscles often very strong. Basilar muscles present or absent.

Genus *Segonzactis* Riemann-Zürneck, 1979

Condylanthidae with broad pedal disc but without basilar muscles. Column divided in scapus and scapulus, scapus short, with cuticle. Scapulus with membranous appendages of the mesoglea (pseudospherules). Sphincter endodermal, very weak. Only eight tentacles, short and thick. Longitudinal muscles of the tentacles mesogleal, at the oral sides of the tentacles stronger than at the aboral sides. Radial muscles of the oral disc meso-ectodermal. Mesenteries in five cycles, arranged hexamerously, several pairs of the fifth cycle often lacking. Only eight mesenteries developed as macrocnemes, with circumscript retractors, reproductive tissue and mesenterial filaments. Mesenteries from the third up to the fifth cycle only present in the lowermost part of the body. Only one very strong (ventral) siphonoglyph. Parietobasilar muscles strong. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Type species

Segonzactis platypus Riemann-Zürneck, 1979

Species included in the genus

Segonzactis hartogi Vafidis and Chintiroglou, 2002; *Segonzactis platypus* Riemann-Zürneck,

Segonzactis platypus Riemann-Zürneck, 1979

(Fig. 4.1-4.3; Table 4)

Material examined

BENGAL 2: stn. 13078 (27) (BEIM: 3043, 2 specimens); stn. 13078 (11) (BEIM: 3054, 2 specimens); stn. 13078 (6) (BEIM: 3056, 1 specimen); BENGAL 3: stn. 13200 (93) (BEIM: 3117, 2 specimens); stn. 13200 (94) (BEIM: 3039, 7 specimens); stn. 13200 (84) (BEIM: 3031, 6 specimens); stn. 13200 (70) (BEIM: 3037, 2 specimens). BENGAL 5: stn. 13368 (48) (BEIM: 3035, 6 specimens); stn. 13368 (53) (BEIM: 3038, 14 specimens); stn. 13368 (47) (BEIM: 3046, 1 specimen); stn. 13368 (52) (BEIM: 3047, 4 specimens). BENGAL 6: 13627 (11) (BEIM: 3018, 7 specimens); stn. 13627 (24) (BEIM: 3032, 5 specimens).

In total 59 specimens from Porcupine Abyssal Plain were studied. Seven specimens were used for the histological study: two specimens from BENGAL 3, Stn 13200(94); three specimens from BENGAL 5, Stn 13368 (53) and two specimens from BENGAL 6, Stn 13627(24).

Description

External Anatomy (Fig. 4.1).— Body shape like a disc, oral disc contracted. Usual morphology for all specimens of these expeditions. Pedal disc 15mm in diameter, scapus 10mm. Pedal disc smooth; transparent making visible the insertions of the mesenteries. No trace of adhesion to firm objects. Scapus provided by a cuticle easily deciduous that contains small foreign particles attached. Scapulus is packed with slight appendages of mesoglea.

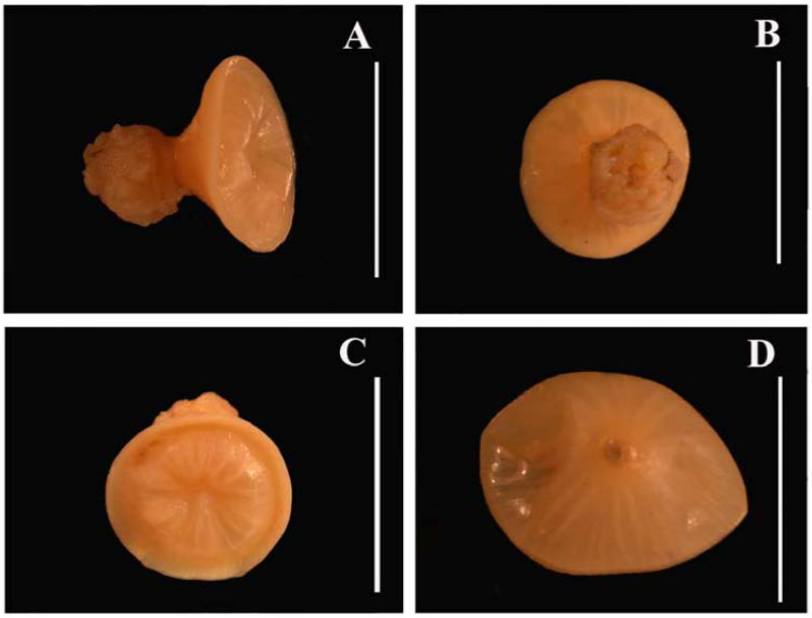

Figure 4.1.– *Segonzactis platypus* Riemann-Zürneck, 1979. External anatomy [BEIM (3039)]: A) Lateral view; B Oral disc view showing some tentacles; C) Pedal disc view; D) Oral view. Scale: A) 2cm; B) 2cm; C) 2cm; D) 2cm.

Internal anatomy (Fig. 4.2).— Five cycles of mesenteries, several pairs of the 5th septa are lacking. One ventral siphonoglyph. Longitudinal musculature of the tentacles mesogleal stronger at the oral side. Radial muscles of the oral disc weak, meso-ectodermal. Sphincter endodermal, very weak. Only eight macrocnemes of the first cycle provided with reniform retractors, strong parietobasilar muscles, mesenterial filaments and reproductive tissue. The other macrocnemes of the first cycle are not connected with the actinopharynx and do not present filaments nor reproductive tissue but they have strong parietobasilar muscles. Mesenteries from the third up to the fifth cycle only present in the lowermost part of the body. Without basilar muscles. Reproductive tissue present, very well developed (examined material: male).

Cnidom (Fig.4.3; Table 4).— Basitrichs, microbasic *p*-mastigophores, spirocysts. The material is strongly contracted so it is very difficult to obtain good preparations of nematocysts without contamination of various tissues. For instance, it is very hard to distinguish the pharynx from the mesenterial filaments.

Colour.— pale white.

Geographical and bathymetric distribution

Abyssal region of the Gulf of Biscay, between 4237 and 4850 depth (Riemann-Zürneck, 1979) and Porcupine Abyssal Plain at 4845m (Riemann-Zürneck, 1998).

Discussion

The family Condylanthidae Stephenson, 1922 consists of five genera, divided in two groups: first group -*Condylanthus* Carlgren, 1899 and *Pseudhormathia* Carlgren, 1928; second group *Macrocnema* Carlgren, 1928; *Charisea* Torrey, 1902; *Charisella* Carlgren, 1949. They differ from each other by the division of the body, the presence of tubercles of the column, presence or absence of the pseudospherules, and by the number of the macrocnemes (Carlgren, 1949). Riemann-Zürneck (1979) discussed the taxonomic position of *Segonzactis* within the family Condylanthidae, referring that it is close to the first group of the key, especially to *Condylanthus* (Carlgren, 1899), once it has the body divided in scapus and scapulus, endodermal sphincter, longitudinal muscles of the tentacles mesogleal and a stronger development on the oral side. It is also close to other genera of the second group, *Macrocnema* Carlgren (1928) and *Charisella* Carlgren (1949), because of the presence of some kind of appendages on the scapulus, probably, pseudospherules.

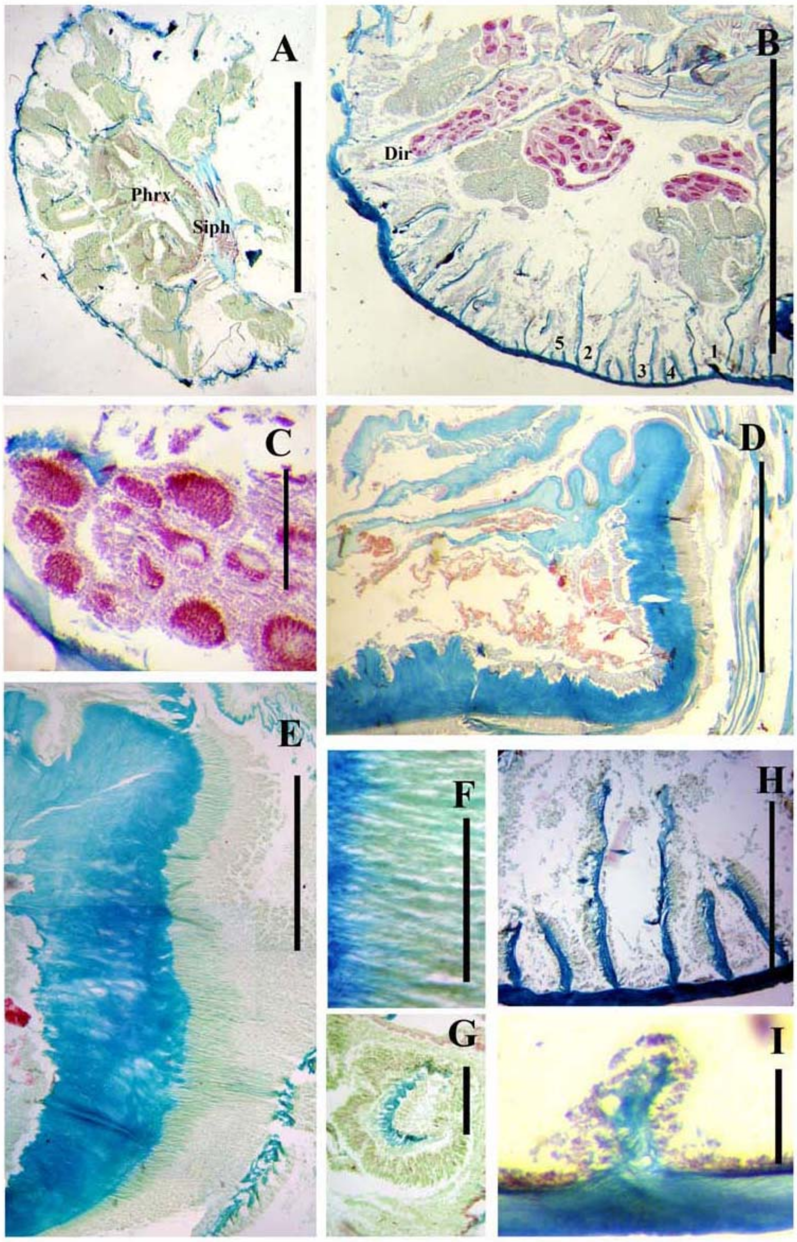

Figure 4.2.– *Segonzactis platypus* Riemann-Zürneck, 1979. Internal anatomy [BEIM (3032)]: A) Transversal section at oral disc level showing some tentacles; B) Transversal section at actinopharynx level; C) Detail of gametogenic tissue; D) Longitudinal section of the scapulus with pseudospherules; E) Longitudinal section of the distal part of the column showing the endodermal sphincter; F) Detail of sphincter diffuse; G) Transversal section of tentacle; H) Detail of pairs of mesenteries showing retractor musculature; I) Longitudinal section at pedal disc level showing absence of basilar musculature. Scale: A, 5.5mm; B, 4.5mm; C, 0.1mm; D, 2mm; E, 0.8mm; F, 0.1mm; G, 0.4mm; H, 0.5mm; I, 0.15mm.

Table 4.– Dimensions of cnidae in *Segonzactis platypus* Riemann-Zürneck, 1979. Specimens: [BEIM (3038)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic. (*) Average based on measures of less than 40 capsules, which is considered the meaningful minimum (Williams, 1996; 1998).

Category	**Fig. 4.3**	**Range of length and width of capsules in µm**	**X ± SD**	**S**	**N**	**F**	***Segonzactis platypus* Riemann-Zürneck, 1979**	***S. hartogi* Vafidis & Chintiroglou, 2002**
COLUMN								
Basitrichs	**A, B**	**(12-23) x (3-5)**	**18.4±2.5 x 3.7±0.5**	**3/3**	**59**	**++/+++**	**14.5-23 x 3-3.5**	_
TENTACLES								
Spirocysts	**D**	**(34-65) x (3-10)**	**46.5±6.8 x 4.9±1.0**	**3/3**	**46**	**+++**	**81 x 3.5-4.5**	**6-21.8 x 1-4**
Basitrichs	**C**	**(13-26) x (3-4)**	**18.8±3.2 x 3.3±0.5**	**3/3**	**42**	**---/+**	**27-32 x 3-4**	**7-13 x 1-3**
ACTINOPARYNX								
Basitrichs	**E**	**(12-18) x (3)**	**15.9±1.8 x 3±0(*)**	**1/3**	**8**		_	_
Mic. *p*-mastigophores	**F**	**(24-31) x (4-7)**	**28.1±2.3 x 5.7±1.1(*)**	**1/3**	**7**		_	_
FILAMENTS								
Basitrichs 1	**G**	**(12-20) x (2.5-4)**	**16.3±1.4 x 3.2±0.4**	**3/3**	**60**	**+++**	**14-18 x 3-3.5**	**10-24 x 1.5-4**
Basitrichs 2	**H**	**(24-37) x (3-4)**	**31.5±3.1 x 3.7±0.5(*)**	**3/3**	**28**	**+**	**32-33 x 4-4.5**	_
Mic. *p*-mastigophores 1	**I**	**(20-35) x (5-6)**	**29.3±2.5 x 5.7±0.4**	**3/3**	**60**	**++**	**25-30 x 5-5.5**	**9-9.5 x 3-4**
Mic. *p*-mastigophores 2	_	_	_	_	_	_	_	**14-29.5 x 2.5-7**

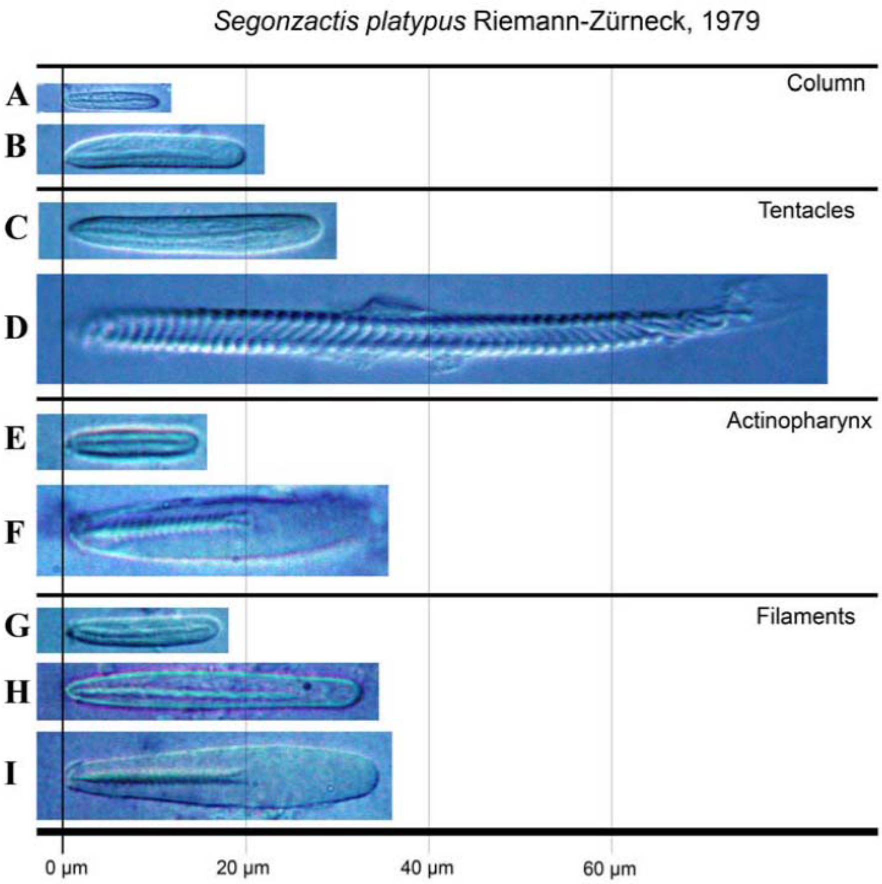

Figure 4.3.– *Segonzactis platypus* Riemann-Zürneck, 1979. Cnidae: A) basitrich 1; B) basitrich 2; C) basitrich; D) spirocyst; E) basitrich; F) microbasic *p*-mastigophore; G) basitrich 1; H) basitrich 2; I) microbasic p-mastigophore.

However, *Segonzactis* taxonomic position is still much debated. The absence of basilar musculature, the presence of eight macrocnemes similar to *Edwardsia* arrangement, and its peculiar body form differ from all the family genera. Riemann-Zürneck, 1979 included *Segonzactis* in the family Condylanthidae because of common features such as: mesenteries differentiated in macro and microcnemes, with strong macrocnemes carrying filaments and gametogenic tissue and thin microcnemes. *Segonzactis platypus* Riemann-Zürneck, 1979 and *S. hartogi* Vafidis and Chintiroglou, 2002 are distinguished only by the cnidae biometry (see Table 4.), although they have the same shape and internal morphology, and by their geographical and bathymetric distributions, altough both were found in soft silty bottom (Vafidis and Chintiroglou, 2002). Being so delicate and small, with a flat disc-shaped body and the ability to contract the upper part, they can be carried into low current through the semi-fluid sediment surface or in no-motion areas, where sedimentation of potential food may be higher (Riemann-Zürneck, 1979 and 1998). In addition, the presence of gametogenic tissue in the macrocnemes of both *Segonzactis* species in abyssal and bathyal benthos suggests a good reproduction capacity of these species and consequently the existence of an impotantl population in deep sea habitats (Vafidis and Chintiroglou, 2002).

Family Iosactiidae Riemann-Zürneck, 1997

Diagnosis (adapted from Riemann-Zürneck, 1997)

Burrowing endomyarians with undifferentiated, smooth body and rounded aboral end. No basilar muscles. Two perfect cycles of mesenteries. Tentacles non-retractile, easily deciduous. Circular endodermal musculature of body wall strong, with girdle-like concentration. Mesenteries with strong parietal muscles and weak diffuse retractors.

Type species

Iosactis vagabunda Riemann-Zürneck, 1997

Species included in the genus

Iosactis vagabunda Riemann-Zürneck, 1997, monospecific genus

***Iosactis vagabunda* Riemann-Zürneck, 1997**

(Fig. 5.1-5.3; Table 5)

Material examined

BENGAL 2: stn. 13078 (11) (BEIM: 3048, 19 specimens); stn. 13078 (27) (BEIM: 3113, 2 specimens); stn. 13078 (21) (BEIM: 3034, 2 specimens); BENGAL 3: stn. 13200 (70) (BEIM: 3044, 7 specimens); stn. 13200 (84) (BEIM: 3097, 6 specimens); stn. 13200 (94) (BEIM: 3102, 16 specimens); stn. 13200 (93) (BEIM: 3108, 8 specimens). BENGAL 5: stn. 13368 (48) (BEIM: 3028, 9 specimens); stn. 13368 (47) (BEIM: 3029, 2 specimens); stn. 13368 (53) (BEIM: 3098, 14 specimens); stn. 13368 (52) (BEIM: 3074, 33 specimens). BENGAL 6: stn. 13627 (24) (BEIM: 3052, 14 specimens); stn. 13627 (11) (BEIM: 3100, 12 specimens).

In total 144 specimens from Porcupine Abyssal Plain were studied. Four specimens from BENGAL 5, stn. 13368(52) were used for the histological study.

Description

External anatomy (Fig. 5.1).— Small and relatively long body, between 2 and 2.5cm in height, and 0.5 and 1cm in diameter. Smooth body and rounded aboral end. In all specimens 24 longitudinal lines of mesenterial insertions are visible. Aboral end with a small pit invaginated in its centre. All observed specimens had lost their tentacles, and had the oral disc damaged with ruptures.

Internal anatomy (Fig. 5.2).— 12 pairs of perfect mesenteries. Two pairs of directives and respective well developed siphonoglyphs. 24 tentacles, however the observed specimens have only few tentacles inside. Endodermal marginal sphincter at the upper part of the body. Mesenteries with strong parietobasilar muscles and weak diffuse retractors. Well developed circular musculature in the column. Longitudinal mesenterial musculature changes character, shape and size along the longitudinal extension. Close to the oral disc retractors are weak and diffuse. Retractors become stronger along the actinopharynx where they are close the column wall and a small parietobasilar muscle appears at the opposite side. Retractors are strongest around the region where the actinopharynx ends, and have a strong parietobasilar musculature developed on both sides of the mesentery. Below the actinopharynx, retractors disappear, and a bilateral symmetrical parietobasilar musculature becomes even stronger. Close to the basal end they become smaller. Tentacles' musculature ectodermal, with weak mesoglea at the oral side. Lumen of tentacles contains some granular matter. At the proximal lower part of the body only six of the 12 pairs of mesenteries have filaments and gametogenic tissue. Spermatocysts are well developed, round and mature. Accumulation of unilobate filaments below the actinopharynx. Basilar muscles absent.

Cnidom (Fig. 5.3; Table 5).— One of most curious feature of *Iosactis vagabunda* cnidom is the absence of spirocysts on the tentacles. Basitrichs, b- and *p*-mastigophores and spirocysts.

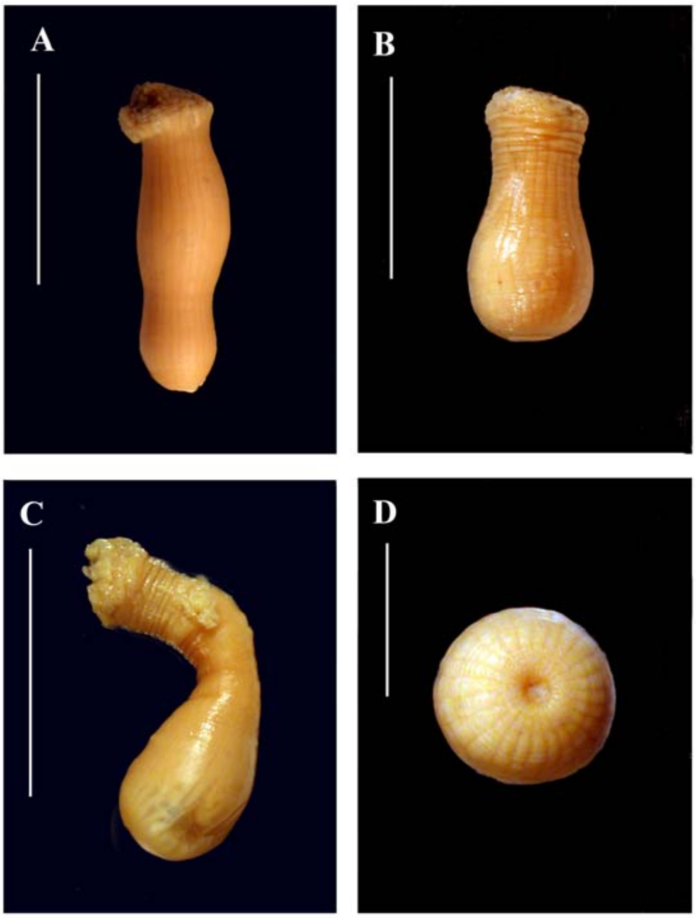

Figure 5.1.– *Iosactis vagabunda* Riemann-Zürneck 1997. External anatomy [BEIM (3074)]: A) Lateral view; B) Lateral view; C) Lateral view; D) Basal view. Scales: A, 2cm; B, 2cm; C, 2cm; D, 1cm.

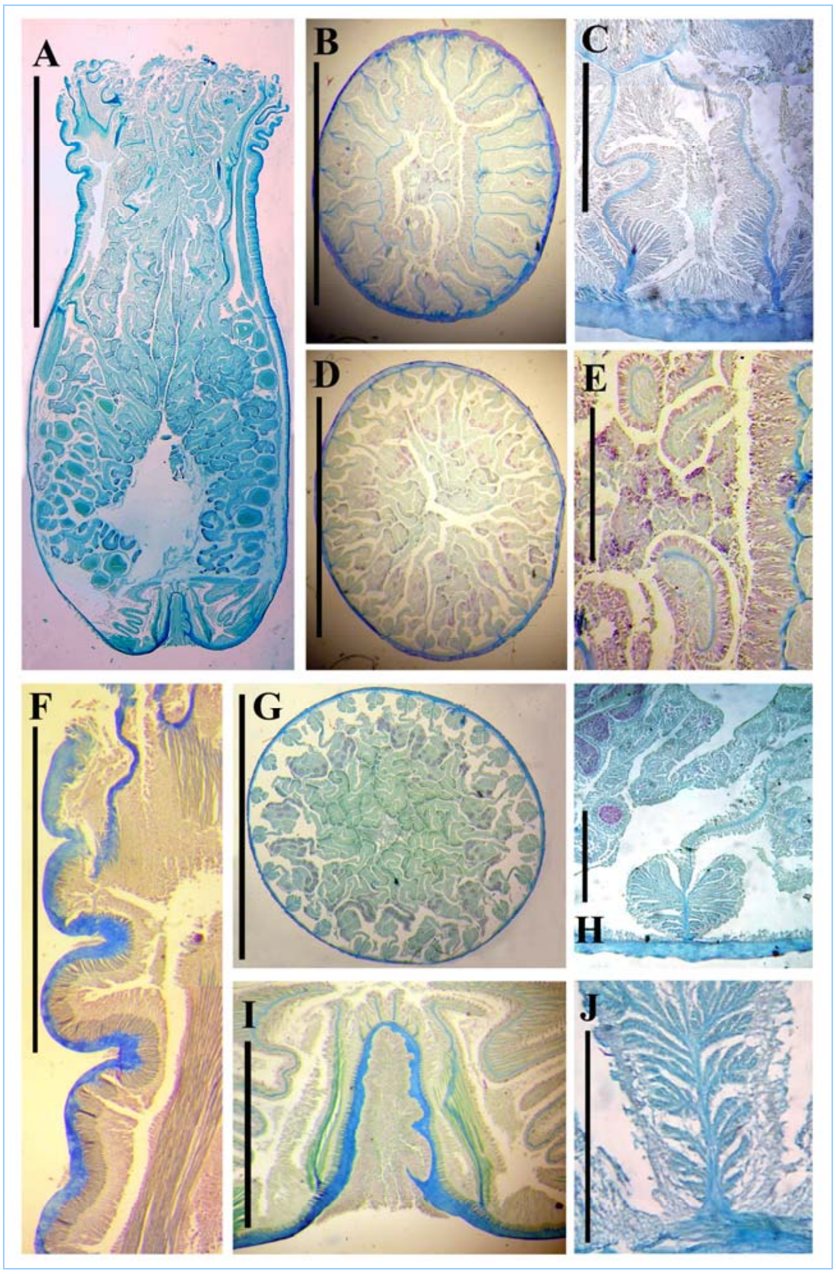

Figure 5.2.– *Iosactis vagabunda* Riemann-Zürneck, 1997. Internal anatomy [BEIM (3074)]: A) Longitudinal section of entire body; B) Transversal section at actinopharynx level, showing pairs of perfect mesenteries; C) Detail of one pair of mesenteries; D) Transversal section at proximal part, showing filaments and strong parietobasilar muscles; E) Detail of actinopharynx, showing tentacles transversal sections with ectodermal musculature; F) Longitudinal section of the column showing endodermal sphincter; G) Transversal section at lower proximal part; H) Detail of a mesentery carrying gametogenic tissue; I) Aboral pit detail; J) Longitudinal section at pedal disc level showing parietobasilar muscle. Scales: A) 10mm; B) 5.2mm; C) 0.75mm; D) 6mm; E) 0.8mm; F) 4mm; G) 7,1mm; H) 0.4mm; I) 1.5mm; J) 0.3mm.

Table 5.– Dimensions of cnidae in *Iosactis vagabunda* Riemann-Zürneck, 1997. Specimens [BEIM (3074)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic.

Category	Fig. 5.3	Range of length and width of capsules in µm	X ± SD	S	N	F	Data from Riemann-Zürneck, 1997
COLUMN							
Basitrichs 1	A	(19.2-27.3) x (2.5-3.5)	22.4 ±2.04 x 3.1 ±0.2	2/3	40	++	(Bs2?) 10.5-13 x 2.5-3
Mic. b-mastigophores	B	(32.3-49.5) x (5-7)	36.3 ±3.2 x 5.7 ±0.5	2/3	40	++	(Bs1?) 23.5-30 x 3.5-4.5
TENTACLES							
Basitrichs 1	C	(14.1-26.3) x (3-3.5)	19.4 ±2.8 x 3 ±0.14	3/3	60	+	19-25 x 3-3.5
Basitrichs 2	D	(29.3-51.5) x (3.5-5)	37.9 ±4.12 x 4.7 ±0.38	3/3	60	++	39-45 x 3.5-4.5
PHARYNX							
Basitrichs 1	E	(15.1-26.3) x (2-3.5)	20.4 ±4.2 x 3.1 ±0.5	3/3	45	---/+	13.5-26 x 3-3.5
Basitrichs 2	F	(33.3-52.5) x (3-5)	41.5 ±7.2 x 4.2 ±0.6	3/3	45	---/+	33-43 x 4-4.5
FILAMENTS							
Basitrichs	G	(18.2-26.3) x (3-4)	22.5 ±1.8 x 3.3 ±0.31	3/3	60	+/++	15-22 x 3
Mic. b-mastigophores	H	(28.3-37.4) x (4.5-7)	33.2 ±2 x 5.45 ±0.5	3/3	60	++	33-40 x 5-6
Mic. *p*-mastigophores	I	(27.3-41.4) x (4.5-6)	35.2 ±3.1 x 5.5 ±0.44	3/3	60	++	30-35 x 4.5-6
ABORAL PIT							
Spirocysts	J	(26.3-42.4) x (5-9)	35.5 ±3.7 x 7.9 ±0.77	3/3	60	+	27-33 x 7-8.5
Basitrichs 1	K	(10-18.2) x (2.5-3)	13.15 ±1.3 x 2.7±0.25	3/3	60	+	11-12 x 2.5-3
Basitrichs 2	L	(22.2-32.3) x (3.5-5)	27.1 ±2.2 x 4.14 ±0.28	3/3	60	++/+++	21-26 x 3.5-4

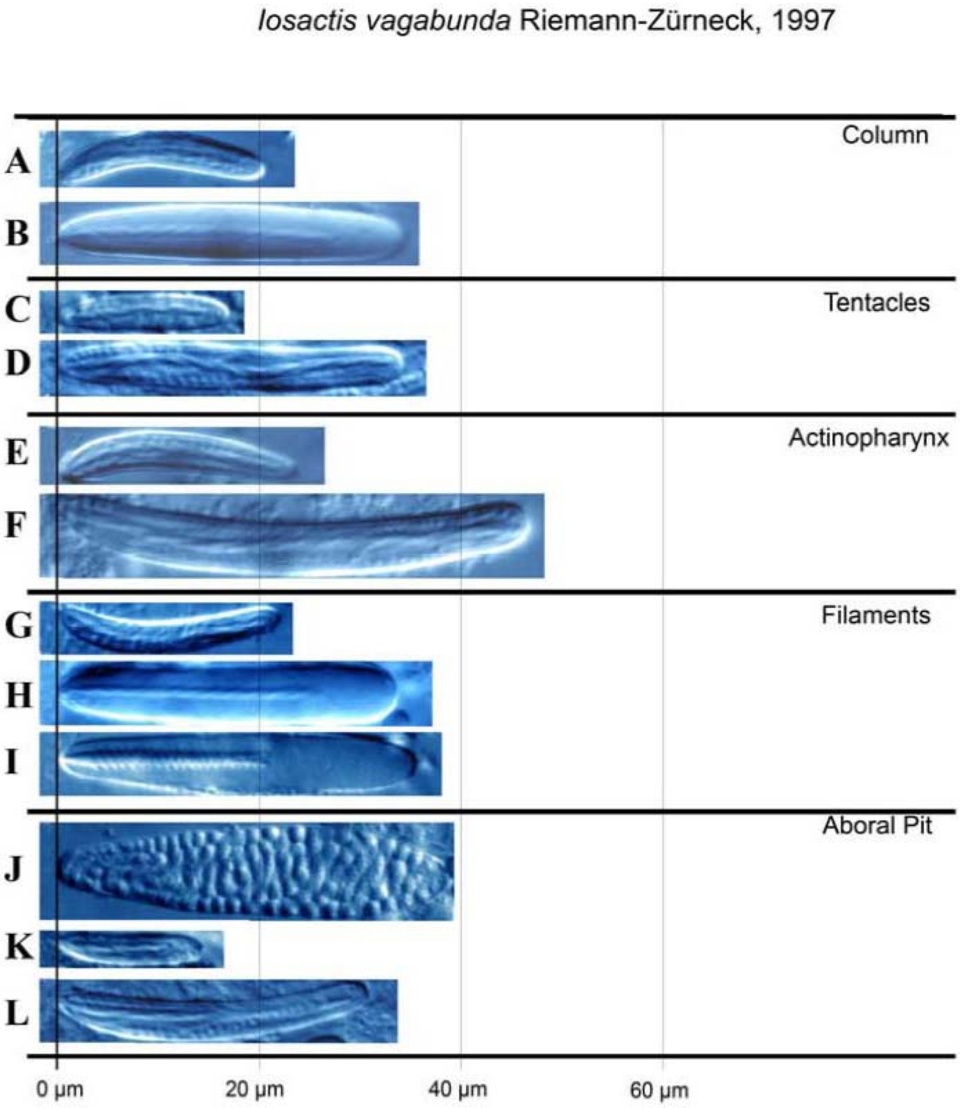

Figure 5.3.– *Iosactis vagabunda* Riemann-Zürneck 1997. Cnidae: A) basitrich; B) microbasic b-mastigophore; C) basitrich 1; D) basitrich 2; E) basitrich 1; F) basitrich 2; G) basitrich; H) microbasic b-mastigophore; I) microbasic *p*-mastigophore; J) spirocyst; K) basitrich 1; L) basitrich 2.

Geographical and bathymetric distribution

Holotype and paratypes of *Iosactis vagabunda* Riemann-Zürneck, 1997 were found at the Porcupine Sea Bight and the Abyssal Plain between 4595 and 4877m depth. This anemone has a burrowing habit on mud sediments at abyssal depths at PAP region, and till the present seems endemic of this area. The material analysed in this study was collected more than 15 years after Riemann-Zürneck's material (1979-1991 period, IODSL Deep sea programme; see Rice *et al*, 1994), and therefore it seems that the population is very stable.

Discussion

Riemann-Zürneck (1997a) established the new family Iosactiidae with a single genus/species, *Iosactis vagabunda*, within the Endomyaria based on the high systematic ranking of characters such as: endodermal sphincter, two perfect cycles of mesenteries, large b-mastigophores in the filaments and round spermatocysts.

Differences between the observed material and Riemann-Zürneck statements are few, for instance it was not possible to observe the trilobate filaments on the lower level of the actinopharynx, neither the presence of a basal sphincter on tentacles which makes them easily deciduous. These particular features were not seen probably because of some inaccuracy on histological methods or due to the bad condition of tentacles. Other differences observed include the cnidae size (larger basitrichs) and type (b-mastigophore instead of basitrichs) on scapus.

Riemann-Zürneck (1997a) discussed the taxonomic position of Iosactiidae, and according to her interpretation the new family is placed somewhere between the "deep-sea actiniids" (such as *Bolocera* and *Liponema*) and the Andresiidae (Stephenson, 1921). However, their burrowing habit, the relatively small and long body, the presence of only 24 mesenteries and 24 tentacles, the very strong parietobasilar muscle, the "*Edwardsia*-condition" of the parietobasilar musculature and the presence of an aboral pit (with ectodermal spirocysts) makes them very different from the "actiniids". They are also different from Andresiidae because *Andresia* is much larger, lacks a tentacle sphincter, has large and numerous spirocysts on tentacles. Also, *Andresia* is known from warm sublittoral Mediterranean areas. Regarding the phylogenetic position, Iosactiidae morphological characteristics are close to the hypothetical ancestral forms of Endomyarian sea anemones (Riemann-Zürneck, 1997a). It could be very interesting to do molecular research to prove it.

Iosactis vagabunda is probably endemic, confined to the particular habitat of the Porcupine Abyssal Plain (known for seasonal inputs of phytodetritus) and even nowadays it was not found in any other area. This anemone has an opportunistic burrowing lifestyle, waiting for the deposition of phytodetritus, extending their tentacles to trap it. This species is "hemissesile" and has the capacity to leave its burrow and move over the seafloor using near-bottom currents (see *in situ* camera observations, Riemann-Zürneck, 1997a).

TRIBU MESOMYARIA STEPHENSON, 1921

Diagnosis (adapted from Stephenson, 1921)

Nynantheae with mesogleal sphincter or (rarely) without sphincter. Base disc–shaped, adherent or with physa, with basilar musculature present or absent. Column sometimes divided in regions, rarely with ectodermic longitudinal musculature . Tentacles normally in alternate cycles. Mesenteries hexamerous, with or without acontia. Retractor muscles rarely circumscript.

Family Actinoscyphiidae Stephenson, 1920

Diagnosis (adapted from Riemann-Zürneck, 1978 and Rodríguez et al., 2008)

Nynantheae (Mesomyaria) with basilar muscles and mesogleal marginal sphincter. Pedal disc flat sometimes small, grasping. Column commonly smooth, often with distal row of cinclides and sometimes verrucae. Tentacles usually marginal on wide oral disc, their aboral sides sometimes thickened. Oral disc sometimes lobed. Mesenteries not divisible into macro- and microcnemes. At least six pairs of perfect and fertile mesenteries. No acontia. Cnidom: robust spirocysts, basitrichs, holotrichs, and microbasic *p*-mastigophores.

Genus *Actinoscyphia* Stephenson, 1920

Diagnosis

Pedal disc small, transformed, involving; can be concave, secreting cuticle and agglutinating mud, polychaete tubes or sponge spicules. Column smooth, thick. Without cinclides or verrucae. Tentacles in two cycles, with their bases thickened on the aboral side. Oral disc broad, undulated, bilobed. Mesenteries more numerous than tentacles. Six pairs of perfect fertile mesenteries. All mesenteries delicate and thin, with their retractor musculature diffuse, weak. Well developed siphonoglyphs. Sphincter mesogleal, weak in comparison to the body size.

Type species

*Actinernus saginat*a Verrill, 1882

Species included in the genus

Actinoscyphia aurelia (Stephenson, 1918); *A. japonica* (Wassilief, 1908); *A. plebeia* (McMurrich, 1893); *A. saginata* (Verrill, 1882).

Observations

Stephenson (1918) provided a meticulous redescription of *Actinernus saginatus* Verrill, 1882 and added the diagnosis of a new type species, *Actinernus aurelia* Stephenson, 1918. In an attempt to reorganize the heterogeneous family Paractidae Verrill, 1882, Stephenson (1920) and Carlgren's (1918) confirmed the already recognized special status of the two *Actinermus* species, and created a new genus *Actinoscyphia* Stephenson, 1920. Furthermore, Stephenson (1920) erected a new family Actinoscyphiidae to accommodate these genera removed from the family Paractidae. Carlgren (1921, p. 188) disagreed with this systematic upgrading, and re-established the genera back into the

Paractidae (from Carlgren 1932: Actinostolidae), so that the Actinoscyphiidae is a synonym of Actinostolidae.

The resurrection of Stephenson's family Actinoscyphiidae by Riemann-Zürneck (1978) is essentially based on the cnidae re-categorization of the two *Actinermus* species of *A. aurelia* and *A. saginata*. Thus, Riemann-Zürneck considered as the most important characters the presence of thick walled *p*-mastigophore in the actinopharynx and mesenterial filaments, or "*p*-rhabdoids B" *sensu* Schmidt, typical of "early" Mesomyaria, instead of thin walled *p*-mastigophores or "*p*-rhabdoids A", typical of "late" Mesomyaria) found in actinostolids. The terms "*p*-rhabdoids B" and "*p*-rhabdoids A" were used by Schmidt (1972) for the classification of cnidae, but it is preferable not to use this terminology in family definition because it is much commonly used than the one by Mariscal (1974), and also because the differences between these types are not always clear (Rodríguez, *et al.* 2008). Riemann-Zürneck (1978) also elucidated the loss of the acontia on Actinoscyphiidae, proposing their closer relation to the Acontiaria (*in* Carlgren, 1949 classification) than to other Mesomyaria. Recent phylogenetic studies proved this hypothesis, because even being a non-acontiate taxa, *Actinoscyphia* nests within the Acontiaria-Boloceroidaria-Mesomyaria clade (Daly, *et al.* 2008), being more distant from *Actinostola-Stomphia-Hormosoma* group and closer to *Hormathia*. Acontiaria is polyphyletic and distributed between Endomyarians and Mesomyarians clades and therefore it makes no sense to give this taxon an high taxonomic rank as it is in the classic system created by Carlgren (1949).

Actinoscyphia aurelia (Stephenson, 1918)

(Fig. 6.1-6.3; Table 6)

Material examined

PROSPEC: stn. Arrow 15 (BEIM: 3012, 1 specimen); stn. 7 (Arrow 7) (BEIM: 3016; 2 specimens).

Description

External anatomy (Fig. 6.1).— Pedal disc very small, transformed in a tiny tube, secreting cuticle and agglutinating silt. No other type of substrate. Medium sized (50 to 70mm). Body flattened in a longitudinal direction. Bilaterally divided in two lobes from which one is always bigger than the other. Column firm, thick and smooth.

Figure 6.1.– *Actinoscyphia aurelia* (Stephenson, 1918). External anatomy [BEIM (3016)]: A) Lateral and oral view; B) Lateral and oral view; C) Lateral view; D) Pedal disc view. Scale: A, 5cm; B, 5cm; C, 5cm; D, 5cm.

Internal anatomy (Fig. 6.2).— Mesenteries thin, hexamerously arranged in five cycles. Equal number of proximal and distal mesenteries. First cycle perfect and fertile, except for the two pairs of directives with respective siphonoglyphs; 2nd to 4th cycles imperfect and fertile; 5th cycle imperfect, incomplete and sterile. All mesenteries with filaments, except the last cycles, from 4th to 5th. Mesenteries more numerous than tentacles. Ectoderm very vulnerable, always missing in observed specimens. Tentacles numerous, small and short (5 to 8mm), without aboral thickenings at the base. Column with thick mesoglea (1cm). Preserved animals possess a dark brown pigment at the endoderm, which is more evident on the oral disc and actinopharynx. Endoderm of the column and a thin layer surrounding mesenteries is also pigmented. Mesogleal alveoles from sphincter also pigmented, making sphincter longitudinal layer easily recognizable. Sphincter inconspicuous, longitudinally is a short narrow band (6mm long, 0.35mm wide) separated from the endoderm by a thin mesogleal layer (0.15 and 0.2mm). Retractors musculature diffuse and short. Parietobasilar musculature well developed and differentiated. Basilar musculature well developed. Gametogenic tissue present on second to fourth cycles. Without acontia.

Cnidom (Fig. 6.3; Table 6).— spirocysts, basitrichs and microbasic p-mastigophores thick walled ("p-rhabdoids B" sensu Schmidt, 1969).

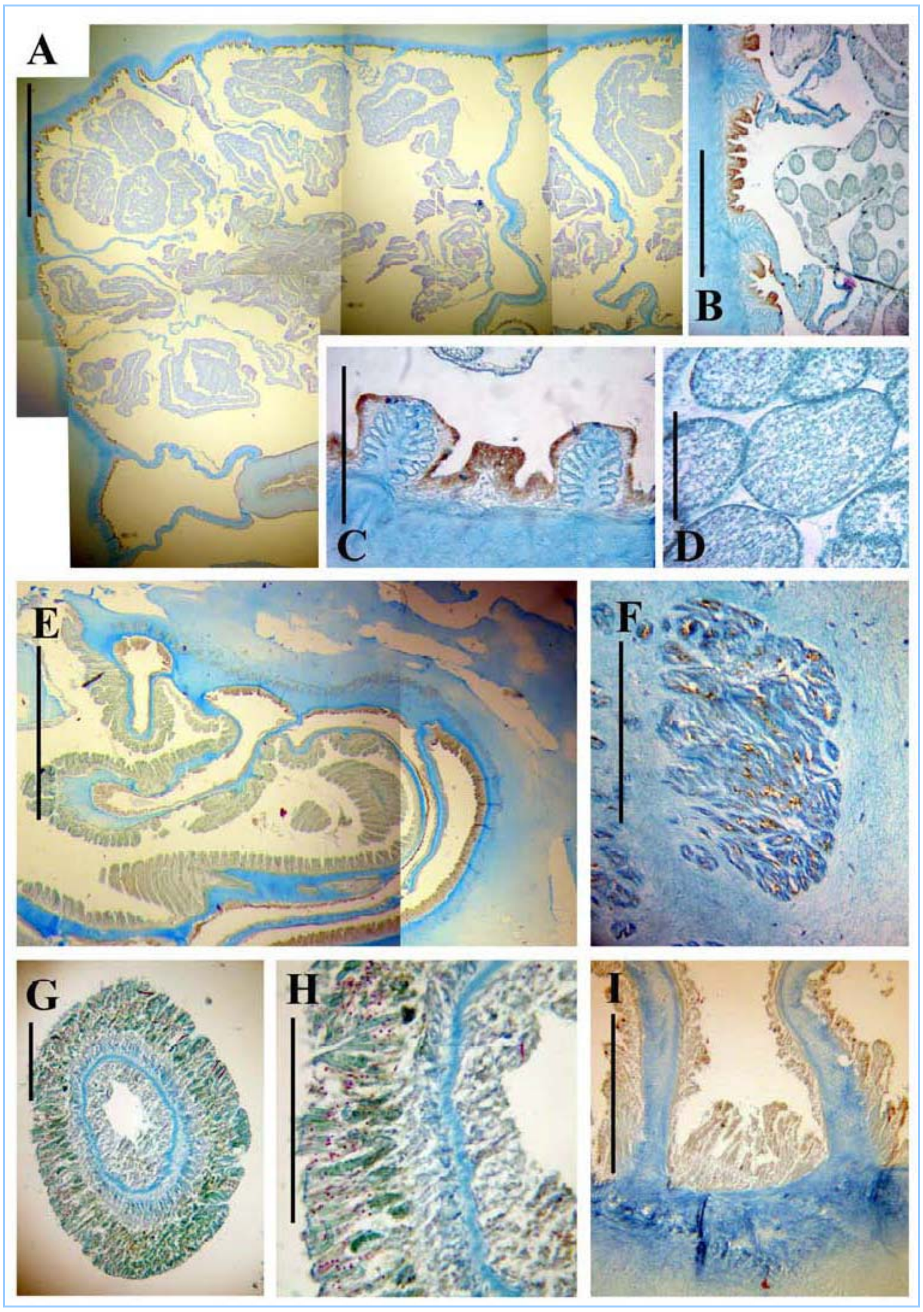

Figure 6.2.– *Actinoscyphia aurelia* (Stephenson, 1918). Internal anatomy [BEIM (3016)]: A) Transversal section at actinopharynx level showing mesenteries cycles; B) Detail of a pair of mesenteries from 3rd cycle; C) Detail of a pair of mesenteries from 4th cycle; D) Detail of gametogenic tissue; E) Longitudinal section of the distal part of the margin showing the sphincter; F) detail of sphincter, mesogleal; G) transversal section of the tentacle; H) Detail of tentacle ectodermal musculature; I) Longitudinal section of the pedal disc showing basilar musculature. Scales: A) 9mm; B) 0.2mm; C) 0.07mm; D) 0.1mm; E) 5mm; F) 0.1mm; G) 0.1mm; H) 0.1mm; I) 5.4mm.

Table 6.– Dimensions of cnidae in *Actinoscyphia aurelia* (Stephenson, 1918). Specimens [BEIM (3012; 3016)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic.

Category	Fig. 6.3	Range of length and width of capsules in µm	X ± SD	S	N	F	Data from Doumenc, 1975	Riemann-Zürneck, 1978
PEDAL DISC								
Basitrichs 1	**A**	**(12.1-16.2) x (2-3)**	**13.5 ±1.1 x 2.3 ±0.26**	**3/3**	**48**	**---/++**	**–**	**–**
Basitrichs 2	**B**	**(18.2-27.3) x (3-5)**	**23.8 ±2.1 x 4 ±0.4**	**3/3**	**51**		**–**	**–**
COLUMN								
Basitrichs 1	**–**	**No data**	**No data**				**–**	**11.5-13.5 x 2-2.5**
Basitrichs 2	**–**	**No data**	**No data**				**–**	**21-27.5 x 3-3.5**
TENTACLES								
Spirocysts	**E**	**(27.3-65.7) x (3-11)**	**43.8 ±9.4 x 6.6 ±2.1**	**3/3**	**60**	**+++**	**40-55 x 3.5-5**	**57 x 9**
Basitrichs 1	**C**	**(11.1-17.2) x (2-2.5)**	**14.4 ±1.6 x 2.3 ±0.2**	**3/3**	**49**	**---/++**	**_**	**13.5-16 x 2-2.5**
Basitrichs 2	**D**	**(22.2-33) x (3-5)**	**26.6 ±3.1 x 3.9 ±0.4**	**3/3**	**60**	**++**	**22-25 (28) x 2.3-3.5**	**19-27.5 x 3-3.5**
PHARYNX								
Basitrichs 1	**H**	**(28.3-39.4) x (3-5)**	**33.5 ±2.5 x 4.2 ±0.45**	**3/3**	**60**	**++**	**(Bs?) 30-34 x 3.2-5**	**22-33 x 3-4**
Basitrichs 2	**–**	**–**	**–**	**–**	**–**	**–**	**–**	**13.5 x 2-2.5**
Mic p-mastigophores	**F;G**	**(26.3-36.4) x (4-5.5)**	**32.2 ±2.3 x 4.7 ±0.45**	**3/3**	**60**	**++/+++**	**–**	**26-32 x 4.5-5**
FILAMENTS								
Basitrichs	**I**	**(12.1-19.2) x (2-3)**	**15.5 ±1.47 x 2.41 ±0.3**	**3/3**	**60**	**+/++**	**(Bs?) 13-17 x 2-3**	**14.5-17.5 x 2-2.5**
Mic. *p*-mastigophores 1	**J**	**(27.3-35.4) x (3.5-5)**	**30.7 ±1.7 x 4.3 ±0.37**	**3/3**	**60**	**++**	**32-34 x 5-7**	**26-32 x 4.5-5**
Mic. *p*-mastigophores 2	**–**	**–**	**–**	**–**	**–**	**–**	**24-28 x 3-4**	**–**

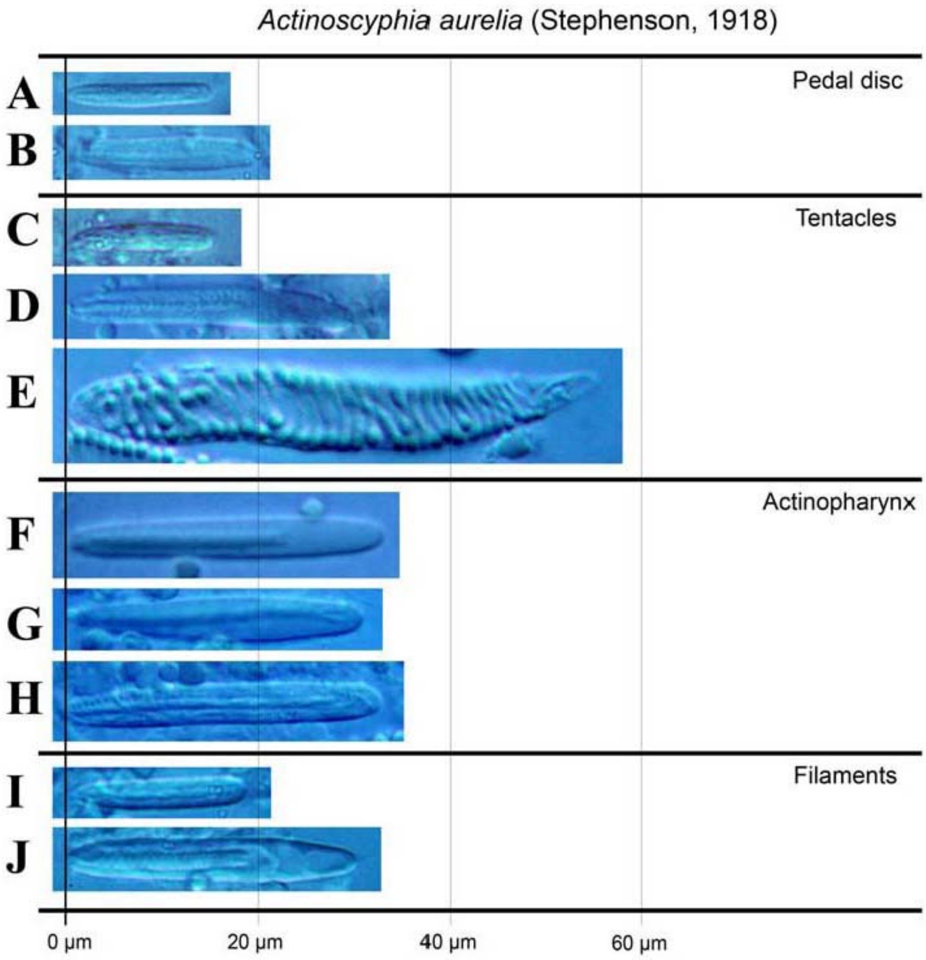

Figure 6.3.– *Actinoscyphia aurelia* (Stephenson, 1918). Cnidae: A, basitrich 1; B, basitrich 2; C, basitrich 1; D, basitrich 2; E, spirocyst; F, microbasic *p*-mastigophore 1; G, microbasic *p*mastigophore 2; H, basitrich; I, basitrich; J, microbasic *p*-mastigophore.

Geographical and bathymetric distribution

This taxon occurs only on bathyal muddy bottoms at depths from 900 to 2160m. It was recorded previously off SW Ireland, the Azores, in Canary Islands (it was only recorded off northern Lanzarote) and the Sahara -Mauritania coast.

Discussion

The genus *Actinoscyphia* was more correctly studied since Riemann-Zürneck (1978a) redescribed the two North Atlantic species (*A. aurelia* and *A. saginata*). Rodríguez (2007, unpublished) re-described *A. plebeia* for the South Hemisphere. The studied material agrees with the original and following descriptions of *A. aurelia* (Stephenson, 1918; Doumenc, 1975; Riemann-Zürneck, 1978a).

Actinoscyphia aurelia Stephenson, 1918 lives in large populations in silty to sandy soils. Live collections and video images show that *A. aurelia* is a “Venus fly-trap” form on the sediment, with a very small pedal disc firmly attached at the sediment surface.

Differences between *A. aurelia* and *A. saginata* are: the type of substrate and pedal disc shape, *A aurelia* as a tiny pedal disc attached to sediments while *A. saginata* seems to need solid objects to settle and shows a preference for other organisms (glass spicules of *Hyalonema*, Pennatulaceans or polychaete tubes); the bilateral furrows in *A. aurelia* with regular shape present a lobe larger than the other. *A. saginata* is much more irregular. *A aurelia* has short tentacles without aboral thickenings while *A. saginata* has long ones with aboral mesogleal thickenings; pigmentation is present, on *A. aurelia* at the endoderm of mesenteries and on the sphincter alveoli, in *A. saginata* pigments occur only on upper section of the margin, tentacles’ oral disc, actinopharynx and mesenterial filaments; also the sphincter is close to the longitudinal endoderm and not marginal approaching to the base as in *A. saginata*.

The distributions of these two species are very close to each other. *A. aurelia* has been reported from material collected off the coast of Ireland between 1400 to 1600 m depth (Stephenson, 1918), but there are also records of specimens collected in the Azores (Doumenc, 1975), and material collected off the Northwest African coast in unusual high densities (Riemann-Zürneck, 1978a and Aldred, et al. 1979). *A. saginata* is more widely distributed and has been recorded several times from both sides of the Atlantic in depths ranging from 700 to 2200m, from the North America coast, to Ireland, Bay of Biscay (Doumenc, 1975) and Moroccan coast (Carlgren, 1934) not far away from the stations where specimens of *A. aurelia* were found (see Riemann-Zürneck, 1978a).

Family Actinostolidae Carlgren, 1932

Diagnosis (modified from Carlgren 1949, by Rodríguez et al.,2008)

Nynantheae with basilar muscles and mesogleal marginal sphincter; column commonly smooth, rarely tuberculate or with papillae. Tentacles regularly arranged, their aboral sides sometimes with nematocyst batteries, sometimes thickened. Mesenteries not divided into macro and microcnemes. Younger mesenteries not bilaterally arranged. Retractor muscles diffuse, rarely circumscript. No acontia. Cnidom: spirocysts, basitrichs, and microbasic b- and p-mastigophores.

Genus *Actinostola* Verrill, 1883

Diagnosis (adapted from Carlgren, 1949 and Haussermann, 2004)

Actinostolidae with the body sometimes short, sometimes cup-like, sometimes long, cylindrical. Column usually thick, firm, slightly rough or smooth, or with flat tubercles produced by mesogleal thickenings. Sphincter mesogleal, so that the upper part of the column can cover completely the tentacles. Tentacles short, the inner probably longer than the outer; sometimes with mesogleal thickening on their aboral sides at the base; sometimes with microbasic b-mastigophores in their aboral distal extreme side. Longitudinal muscles of tentacles mesogleal; radial muscles of the oral disc endodermal to mesogleal. Two well developed siphonoglyphs each one connected with a pair of directive mesenteries. Mesenteries hexamerously arranged. Two mesenteries of the same pair, from the 3rd or 4th, developed unequally, but, as a rule, orientated so that the mesentery, which turns its longitudinal muscle towards the nearest mesentery of the preceding cycle, is more developed than its partner (*Actinostola* rule). Retractors of mesenteries diffuse, parietobasilar and basilar strong. Mesenteries of the two first cycles sterile. Cnidom: spirocysts, basitrichs, microbasic p-and b-mastigophores.

Type species

Urticina callosa Verrill, 1882

Species included in the genus

Actinostola abyssorum (Danielssen, 1980); (?) *A. bulbosa* (Carlgren, 1928); *A. callosa* (Verrill,1882); (?) *A. capensis* (Carlgren, 1928); *A. carlgreni* Wassilieff, 1908; (?) *A. clubbi* Carlgren, 1927; *A. crassicornis* (Hertwig, 1882); A. chilensis McMurrich, 1904; *A. georgiana* Carlgren, 1927; *A. groenlandic*a Carlgren, 1899; (?) *A. intermedia* Carlgren, 1899; (?) *A. kerguelensis* Carlgren, 1928; *A. spetsbergensis* Carlgren, 1893; *A. walteri* Kwietniewski, 1898.

Actinostola callosa Verrill, 1883

(Fig. 7.1-7.3; Table 7)

Material examined

PROSPEC: stn. CPH-10 (BEIM: 3010, 1 specimen); stn. CPH-09 (BEIM: 3013, 2 specimens); stn. 1 (CPH-01) (BEIM: 3078, 5 specimens); stn. CPH-03 (BEIM: 3127, 3 specimens); stn. Arrow 27 (BEIM: 3130, 1 specimen); stn. 1 (CPH-02) (BEIM: 3133, 1 specimen).

In total 12 specimens from “Hébrides Terrace” were studied. Four specimens from stn. CPH-09 and CPH-01 were used for the histological study.

Description

External anatomy (Fig.7.1).— Body in contracted state cylindrical or somewhat cup-like, higher than broad. Pedal disc nor larger than the breadth of the column, excavated (contracted). Column firm, thick, rather flat, with thickenings of mesoglea in the upper part. Tentacles rough with large thickenings of mesoglea at the outside of the base. Inner tentacles much thicker and longer than the outer.

Internal anatomy (Fig. 7.2).— Occurrence of mesogleal thickening at the edge of the mouth. Mesenteries very thin and delicate. Four cycles hexamerously arranged, two pairs of perfect mesenteries (directives) connected respectively with two very well developed siphonoglyphs. First and second cycles perfect, sterile. Third to fourth cycle incomplete and fertile. Mesenteries of the fourth cycle irregular, following *Actinostola* rule (mesentery that turns its longitudinal muscle towards the nearest mesentery of the preceding cycle is more developed than its partner). Mesenterial filaments trilobate well developed with cnidoglandular cells at the border. Tentacles hexamerously arranged in four cycles. Occurrence of large mesogleal thickenings at the aboral base of tentacles. Sphincter longitudinal mesogleal, stratified in a very thin layer and weak. Retractors diffuse. Parietobasilar musculature and basilar musculature strong.

Cnidom (Fig. 7.3; Tab. 7).— basitrichs, microbasic b- and *p*- mastigophores, spirocysts.

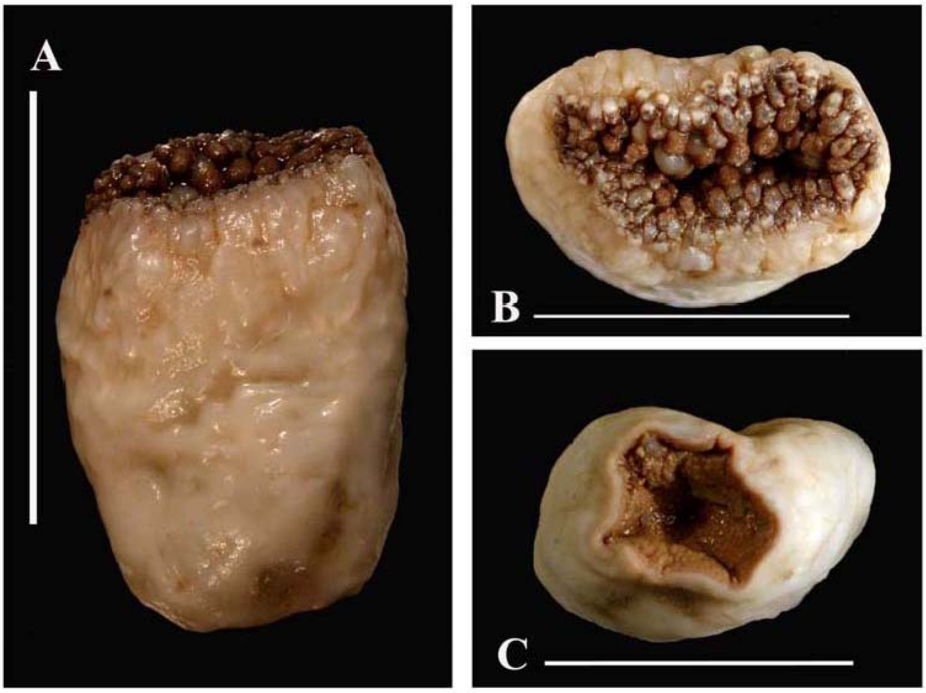

Figure 7.1.– *Actinostola callosa* Verrill, 1883. External anatomy [BEIM (3010)]: A) Lateral view of an preserved specimen; B) Oral view; C) Pedal disc view. Scale: A, 5cm; B, 4cm; C, 4cm.

Geographic and bathymetric distribution

Actinostola callosa Verrill, 1883 was initially found in the North American coast (Massachusetts, Gulf of Maine and Southern New England). It was described for several localities from Norway to the North Sea and also the from the South Western coast of Ireland (Carlgren, 1921; Gravier, 1922).

After synonymy recognition of *A. abyssorum* by Riemann-Zürneck, 1971 the distribution was extended to higher latitudes (North of Norway). There is also the possibility (see Riemann-Zürneck, 1971) of synonymy from Carlgren (1921) material, of *A. groenlandica* and *A. spetsbergensis*, and in this way, the distribution would reach to the Arctic (Greenland, Arctic Sea, and Behring Sea). There is also a Pacific (Japan) record by Uckida and Soyama (2001), and another in the South Atlantic (West Falkland Islands, King George's Bay) by Rees (1913). Although, the status of this species is still uncertain. The bathymetric range can vary from shelf cold waters at high latitudes (Arctic and North of Norway) to high depths (more than 1000m) at lower latitudes. The PROSPEC station [CPH-10] is the deepest record (1579m) known for *A. callosa* untill now, at least from published data available.

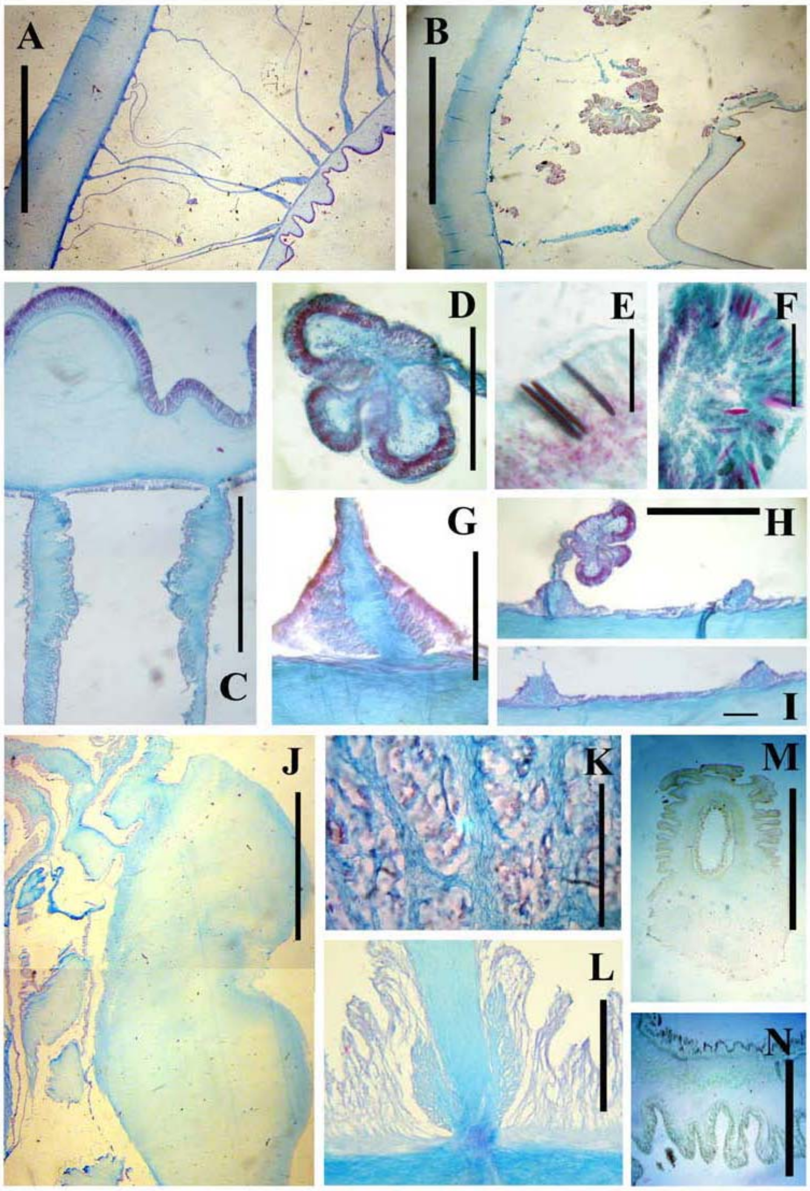

Figure 7.2.– *Actinostola callosa* Verrill, 1883. Internal anatomy [BEIM (3010)]: A) Transversal section at actinopharynx level showing mesenteries cycles; B) Transversal section at actinopharynx level showing a siphonoglyph and mesenteries with filaments; C) Detail of pharynx and a pair of perfect mesenteries; D) Detail of trilobate filaments; E) Detail of nematocysts of siphonoglyph; F) Detail of nematocysts of filament; G) Detail of parietobasilar musculature of mesentery of 3rd cycle; H) Pair of mesenteries of 4th cycle with filaments; I) Pair of mesenteries of the 4th cycle without filaments; J) Longitudinal section at distal part showing sphincter; K) Detail of sphincter mesogleal alveolar; L) Longitudinal section of pedal disc showing basilar musculature; M) Transversal section of tentacle showing mesogleal longitudinal musculature; N) Detail of tentacle musculature. Scale: A, 6.5mm; B, 6.5mm; C, 0.67mm; D, 0.2mm; E, 0.03mm; F, 0.02mm; G, 0.2mm; H, 0.15mm; I, 0.1mm; J, 4mm; K, 0.1mm; L, 0.2mm; M, 2.5mm; N, 0.2mm..

Table 7.– Dimensions of cnidae in *Actinostola callosa* Verrill, 1883. Specimens [BEIM (3010; 3078)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic.

Category	Fig. 7.3	Range of length and width of capsules in µm	X ± SD	S	N	F	Data from Carlgren, 1940	Riemann-Zürneck, 1971
PEDAL DISC								
Basitrichs	**A**	**(17.2-24.3) x (2.5-3.5)**	**19.45 ±1.4 x 2.1 ±0.25**	**3/3**	**60**	**++**	**–**	**–**
COLUMN								
Basitrichs	**B**	**(18.2-24.3) x (2.5-3.5)**	**20.5 ±1.3 x 3 ±0.5**	**2/3**	**40**	**---/+**	**22-24 x 2.5**	**18.5-28-5**
TENTACLES								
Spirocysts	**C**	**(24.3-67.7) x (3-6)**	**46.2 ±11 x 4.5 ±0.2**	**3/3**	**60**	**+++**	**–**	**–**
Basitrichs	**E**	**(26.3-39.4) x (2-3)**	**34.4 ±2.5 x 3 ±0.23**	**3/3**	**60**	**++/+++**	**31-36 x 2**	**30-42**
Mic. b-mastigophores	**D**	**(40.4-54.5) x (6-8)**	**48.5 ±3 x 6.95 ±0.5**	**3/3**	**60**	**+**	**41 x 6.5**	**42.5-60**
Mic. *p*-mastigophores	**–**	**–**	**–**	**–**	**–**	**–**	**21.26 x 4-5**	**–**
PHARYNX								
Basitrichs	**F**	**(23.2-31.3) x (2.5-3.5)**	**274 ±2.2 x 3 ±0.2**	**3/3**	**60**	**++/+++**	**26-31 x 2**	**22-42.5**
Mic. *p*-mastigophores	**G**	**(20.2-27,3) x (4-6)**	**23.5 ±1.7 x 4.9 ±0.42**	**3/3**	**60**	**---/+**	**24 x 4**	**18-26.5**
FILAMENTS								
Mic. b-mastigophores	**H**	**(17.2-28.3) x (3.5-5)**	**24 ±2.63 x 4.5 ±0.34**	**3/3**	**60**	**++/+++**	–	–
Mic. *p*-mastigophores 1	**I**	**(18.2-27.3) x (4-6)**	**23.3 ±2 x 5.7 ±0.5**	**3/3**	**60**	**---/++**	**22-26 x 5**	**18.5-28.5**
Mic. *p*-mastigophores 2	**–**	**–**	**–**	**–**	**–**	**–**	**23-31 x 3.5**	**19-27**

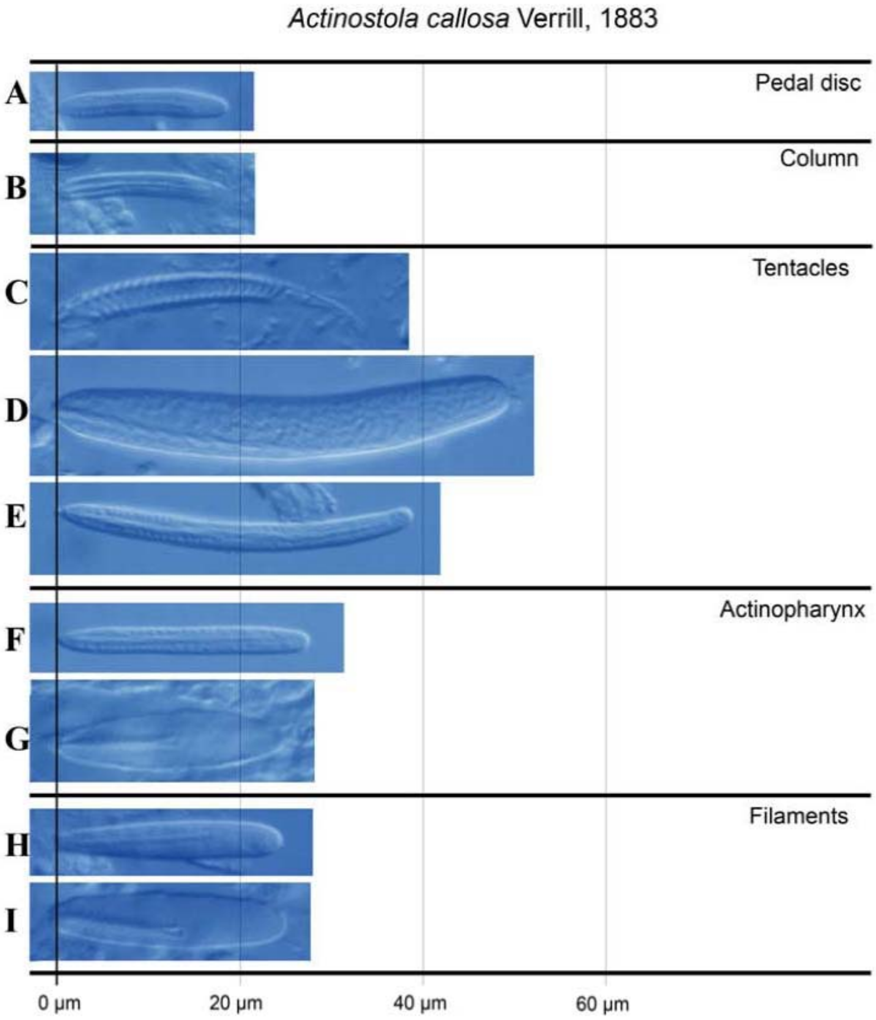

Figure 7.3.– *Actinostola callosa* Verrill, 1883. Cnidae: A) basitrich; B) basitrich; C) spirocyst; D) microbasic b-mastigophore; E) basitrich; F) basitrich; G) microbasic *p*-mastigophore; H) microbasic b- mastigophore; I) microbasic *p*-mastigophore.

Discussion

At the present, the *Actinostola* species described for the North Atlantic are: *A. abyssorum* (Danielssen, 1980); *A. callosa* (Verrill, 1882) syn. *A. atrostoma* (Stephenson, 1918); *A. spetsbergensis* Carlgren, 1893; *A. walteri* Kwietniewski, 1898 and *A. groenlandica* Carlgren, 1899. *Actinostola* species can vary intraspecifically in relatively wide limits and the distinction between *Actinostola* species by anatomical characters traditionally used is complex in preserved specimens. The present material fits the preceding descriptions of *A. callosa* Verrill, 1883 (Carlgren, 1921; Riemann- Zürneck, 1971).

Riemann-Zürneck (1971) presented a detailed study of *A. callosa* and documented the great variability of the anatomical characters used for species diagnosis. The list of additional characters to distinguish the genus species included: 1) cnidom; 2) occurrence of b-mastigophores in the apex of tentacles; 3) occurrence of marginal stomata; 4) dimension of the mesoglea of tentacles; 5) occurrence of mesogleal thickenings at the aboral base of tentacles; 6) occurrence of a mesogleal thickening at the edge of the mouth; 7) structure of the mesogleal sphincter; 8) structure of the longitudinal mesogleal muscles of the tentacles. In this study, Riemann-Zürneck (1971) analysed 9 specimens of *A. callosa* and mentions that the comparison between nematocysts of different animals of a particular body section seems very stable in its dimensions and quality. However, the b-mastigophore of the tentacles varies in frequency of “very often” to “non-existent”. Also the longitudinal musculature and the mesogleal thickness of tentacles vary between animals and from one tentacle to another in the same animal.

Carlgren (1921) in his description of *A. abyssorum* explains his doubts about the relation of this species to *A. callosa*. His assumptions were based in relatively small specimens of *A. abyssorum*. Riemann-Zürneck (1971), compared characters of *A. callosa* Verrill, 1882 and *A. abyssorum* (Danielssen, 1980), and based on Carlgren manuscripts of 1893 (a single animal from Northern Norway) and 1921 (examination of material after Danielssen) found that these two species show high variability of tentacles thickness, type of contraction and size and are therefore synonyms. Another synonym of *A. callosa* is *A. atrostoma* (Stephenson, 1918). The four specimens described by Stephenson (1918) are from 1000 to 1500m depth and present marginal stomata and unusual strong thickenings of the tentacles’ aboral base. Riemann-Zürneck (1971) suggests that perhaps there is a relation between the occurrence of these findings and each community at different depths.

In 1978, Riemann-Zürneck proposed new criteria for the taxonomic evaluation of *Actinostola* comparing the species of the northern and southern Hemispheres (Riemann-Zürneck, 1978b). She described three sphincter types that can be useful for the identification: A) Sphincter with very long stretches in relation to the thin mesoglea belt; alveolar, several mesogleal bands in layers; alveoli not linked in meshes; B) Long stretches, but marginally broad and about half of the mesoglea of the column engaging; alveoles arranged in layers within the layers together in groups, sometimes even reticulate; C) Sphincter relatively short and wide, marginally less than half of the mesogleal column engaging, without stratification and meshed with associated mesogleal alveoles.

Riemann-Zürneck (1978b), also fixed the cnidom of the filament as a good discernable indicator between *Actinostola* species. We do not consider valid the use of cnidom on filaments, once our specimens do not show a second microbasic *p*-mastigophore in the filaments contrarily to Carlgren (1940) and Riemann-Zürneck (1971) data (see Tab. 7). We did not found microbasic p-mastigophores in tentacles either, contrarily to Carlgren (1940) data. Concerning Riemann-Zürneck (1971) data, the microbasic b-mastigophores vary in frequency of “very often” to “absent” (see Tab. 2 in Riemann-Zürneck, 1971). She refers that different phases could be varying in shape and shaft length, like intermediate stages, and thus could not distinguish distinct types of cnidae. She also mentions that this feature was also observed by Carlgren (1921) in *A. spetsbergensis* and *A. groenlandica*. So neither types nor sizes are useful. The proposed synonymy of *A. spetsbergensis* and *A. groenlandica* Carlgren (1921) as *A. callosa* stands unclear. In fact, Riemann-Zürneck in 1978, created a new genus, *Glandolactis*, for *A. spetsbergensis* (Carlgren, 1893), giving taxonomic significance to reproductive type, gametogenic tissue and embryonic development. However, it seems that it was not widely accepted (see Fautin *et al*, 2007).

Redescribing *A. spetsbergensis* is not the objective of the present work. However, in a future research it is necessary to compare *A. callosa* with these high latitude actinostolids to solve this taxonomic problem and to know the zoogeographical limits of this “species complex”.

Genus *Parasicyonis* Hertwig, 1882

Diagnosis (adapted and changed from Carlgren, 1949)

Actinostolidae with well developed pedal disc. Body usually broader than long. Column thick, smooth without tubercles. Margin tentaculate. Tentacles rather short, robust, wrinkled in the contracted state, the inner longer than the outer. Sphincter mesogleal weak or fairly well developed, in some cases, able to cover wholly the tentacles. Two deep siphonoglyphs. Numerous perfect mesenteries. Mesenteries often slightly irregularly arranged, so that, in the last sterile cycle the partner of a pair is sometimes differently developed, one mesentery being larger than the other, but not as in *Actinostola*. Number of mesenteries about twice as many as the tentacles. Only the mesenteries of the last cycle fertile. These mesenteries do not reach the oral part of the column and are like all other mesenteries, provided with filaments. Retractors diffuse, rather weak. Cnidom: spirocysts, basitrichs and microbasic *p*-mastigophores.

Type species

Parasicyonis sarsi Carlgren, 1921

Species included in the genus

Parasicyonis maxima (Wassilief, 1908); *Parasicyonis actinostoloides* (Wassilief, 1908); *Parasicyonis groenlandica* Carlgren, 1933; *Parasicyonis ingolfi* Carlgren, 1942; *Parasicyonis antartica* Carlgren, 1949.

Observations

Reviewing the diagnosis of genus *Parasicyonis* Hertwig, 1882, a modification in the form of the sphincter (text underlined) was introduced, due to the controversy on the descriptions of species *P. groenlandica* Carlgren, 1933 and *P. ingolfi* Carlgren, 1942 and the later diagnosis of the genus (Carlgren, 1949). Obviously, the character given to the type species *P. sarsi* Carlgren, 1921 was maintained. Even in the description of this species, Carlgren also mentions that “it is however questionable if the tentacles may be totally covered, as the sphincter is weak in comparison to the size of the animals”. However, the following descriptions and also the material observed herein, confirm that *Parasicyonis* Hertwig, 1882 presents considerable variability in the oral disc contraction and sphincter strength.

Nevertheless, the genus *Parasicyonis* prevails with an uncertain status. Carlgren in his diagnosis (1921) argues that *Parasicyonis* is in fact closely related to *Sicyonis*, from which it is mainly distinguished through the fertile mesenteries (last cycle) that have well developed filaments, while in *Sicyonis* they are absent. However, Carlgren also considers that this separation is rather practical, and refers that further studies may merge the two genera in only one. At this state of knowledge, it is better to follow the classification initiated by Carlgren (1949) instead of t reformulating completely the genera since, till the present moment, nothing disapproves entirely his statements. It is preferable to wait for a more detailed study, that carries out complete descriptions of the type species and includes more specimens for evaluation.

Parasicyonis biotrans (Riemann-Zürneck, 1991)

(Fig. 8.1-8.3; Table 8)

Material examined

BENGAL 2: stn. 13078 (6) (BEIM: 3090, 1 specimen); stn. 13078 (11) (BEIM: 3091, 1 specimen). BENGAL 3: stn. 13200 (94) (BEIM: 3092, 1 specimen); stn. 13200 (70) (BEIM: 3089, 1 specimen); stn. 13200 (93) (BEIM: 3087, 3 specimens). BENGAL 5: stn. 13368 (53) (BEIM: 3123, 6 specimens); stn. 13368 (52) (BEIM: 3088, 1 specimen); stn. 13368 (48) (BEIM: 3125, 3 specimens). PROSPEC: stn. Arrow 20 (BEIM: 3001, 1 specimen).

In total 17 specimens from Porcupine Abyssal Plain and 1 from “Hebrides Terrace” were studied. Three specimens were taken from BENGAL 5, Stn. 13368(48) for the histological study.

Description

External anatomy (Fig. 8.1).— Pedal disc forming a shallow cavity. Large species, in contracted and preserved condition about 5 to 8cm high and 5cm broad. Column smooth, without tubercles, formed with firm and thick mesoglea (4.5-5.5mm). Tentacles short, partially enclosed (inner tentacles), arranged at the periphery of the wide oral disc. Base of tentacles with mesogleal thickenings.

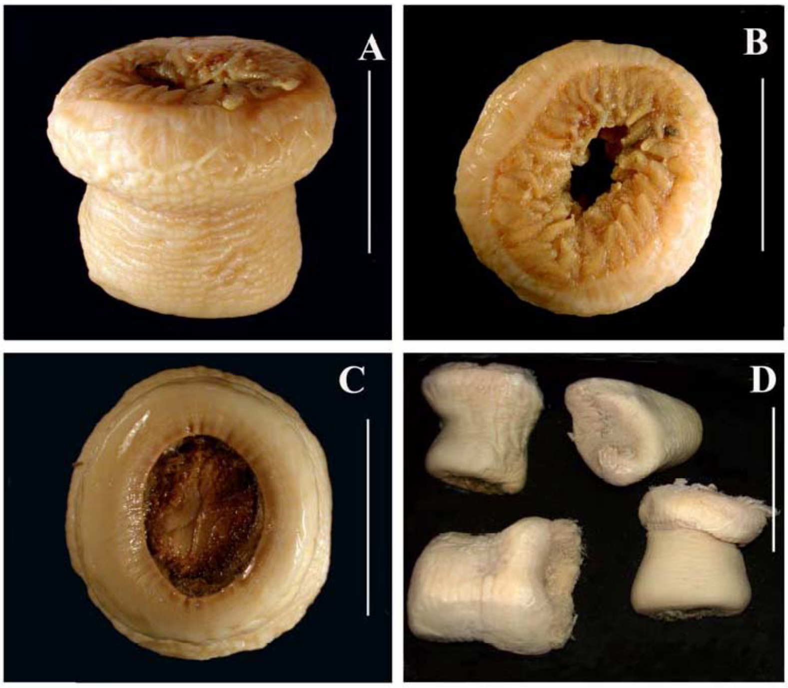

Figure 8.1.– *Parasicyonis biotrans* (Riemann-Zürneck, 1991). External anatomy [BEIM (3125; 3123)]: A) Longitudinal view of entire body of one specimen; B) Oral view; C) Pedal disc view; D) Four specimens in preserved conditions. Scale: A, 5cm; B, 5cm; C, 5cm; D, 8cm.

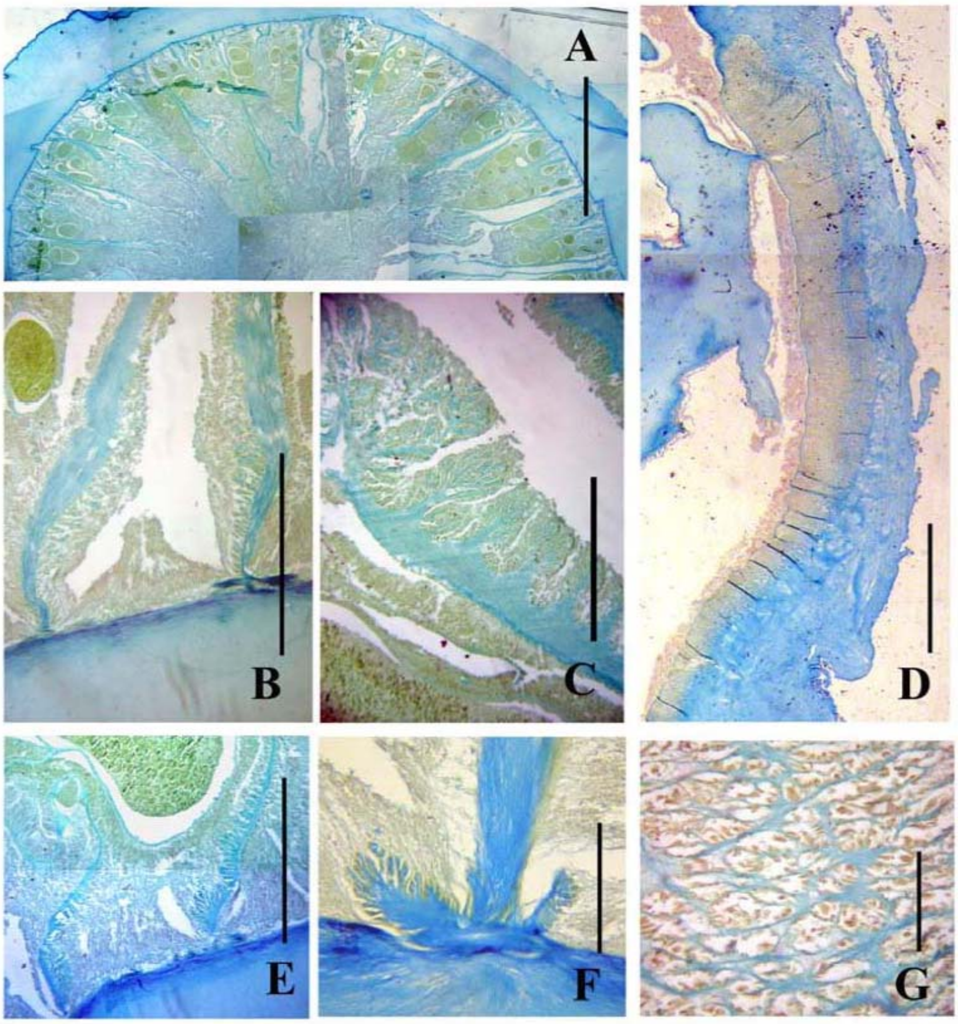

Figure 8.2.– *Parasicyonis biotrans* (Riemann-Zürneck, 1991). Internal anatomy [BEIM (3125)]: A) Transversal section showing mesenteries cycles; B) Detail of a pair of mesenteries showing parietobasilar musculature; Detail of a mesentery showing retractor musculature; D) Longitudinal section at distal part showing mesogleal sphincter; E) Detail of a pair of mesenteries from 4th cycle showing gametogenic tissue; F) Longitudinal section of pedal disc showing basilar musculature; G) Detail of sphincter showing alveoli. Scale: A) 15mm; B) 1mm; C) 1mm; D) 5mm; E) 0.5mm; F) 0.5mm; G) 0.2mm.

Internal anatomy (Fig. 8.2).— Column mesoglea firm and thick. Mesenteries arranged in four cycles, hexamerously arranged. First two cycles are perfect, and maybe also the next cycle, although the observation was difficult because fairly macerated pharynx. Fourth cycle with different development of the mesenteries of the same pair. Directives respectively connected with two well developed siphonoglyphs. Filaments present in all mesenteries. Only the last cycle carries the gametogenic tissues, very well developed large mature oocyts, which can reach 2.5mm in diameter. Tentacle musculature mesogleal. Retractors strong and diffuse. Parietobasilar musculature diffuse and weak. Basilar musculature diffuse in small pennons. Sphincter musculature not strong in relation to the size of the species; mesogleal, reticulated, but without capacity to enclose all the tentacles. Gametogenic tissue very well developed, can reach 1.5mm in diameter, with a bright yellow colour...

Table 8.– Dimensions of cnidae in *Parasicyonis biotrans* (Riemann-Zürneck, 1991). Specimens [BEIM (3125)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic. (*) Average based on measures of less than 40 capsules, which is considered the meaningful minimum (Williams, 1996; 1998).

Category	Fig. 8.3	Range of length and width of capsules in µm	X ± SD	S	N	F	Data from Riemann-Zürneck, 1991
PEDAL DISC							
Basitrichs	A	(19-29) x (2.5-4)	24.2 ± 2.3 x 3.1 ± 0.3	3/3	60	++/+++	(24-34) x (2.5-3.5)
COLUMN							
Basitrichs	B	(26-29) x (3)	26.8 ± 1.1 x 3 ± 0.0(*)	1/1	7		(24-34) x (2.5-3.5)
TENTACLES							
Spirocysts	C	(35-84) x (3-6)	59.7 ± 12.0 x 4.5 ± 0.6	3/3	60	+++/+++	(81) x (4-4.5)
Basitrichs	D	(39-60) x (3-4)	51. 0 ± 4.5 x 3.4 ± 0.4	3/3	60	+++/+++	(42-60) x (3-3.5)
PHARYNX							
Basitrichs	E, F, G (probably 3 size ranges)	(15-46) x (2.5-4)	29.9 ± 7.1 x 3.1 ± 0.2	3/3	60	+++/+++	(26-40.5) x (3-3.5) (probably 2 size ranges)
Mic p-mastigophores	H	(27-40) x (3-8)	33.6 ± 2.7 x 5.7 ± 1.1	3/3	60	+++/+++	(28-31) x (4.5-6.5)
FILAMENTS (trilobate)							
Basitrichs 1	I	(15-24) x (2.5-3)	19.0±2.5 x 2.9 ± 0.2(*)	2/3	30	+/---	(14.5-20) x (2.5-3)
Basitrichs 2	J						(26-30.5) x (2.5-3)
Mic p-mastigophores	K	(25-40) x (3.5-7.5)	31.1±3.2 x 5.6±1.1(*)	2/3	30		(28-31) x (4.5-6)

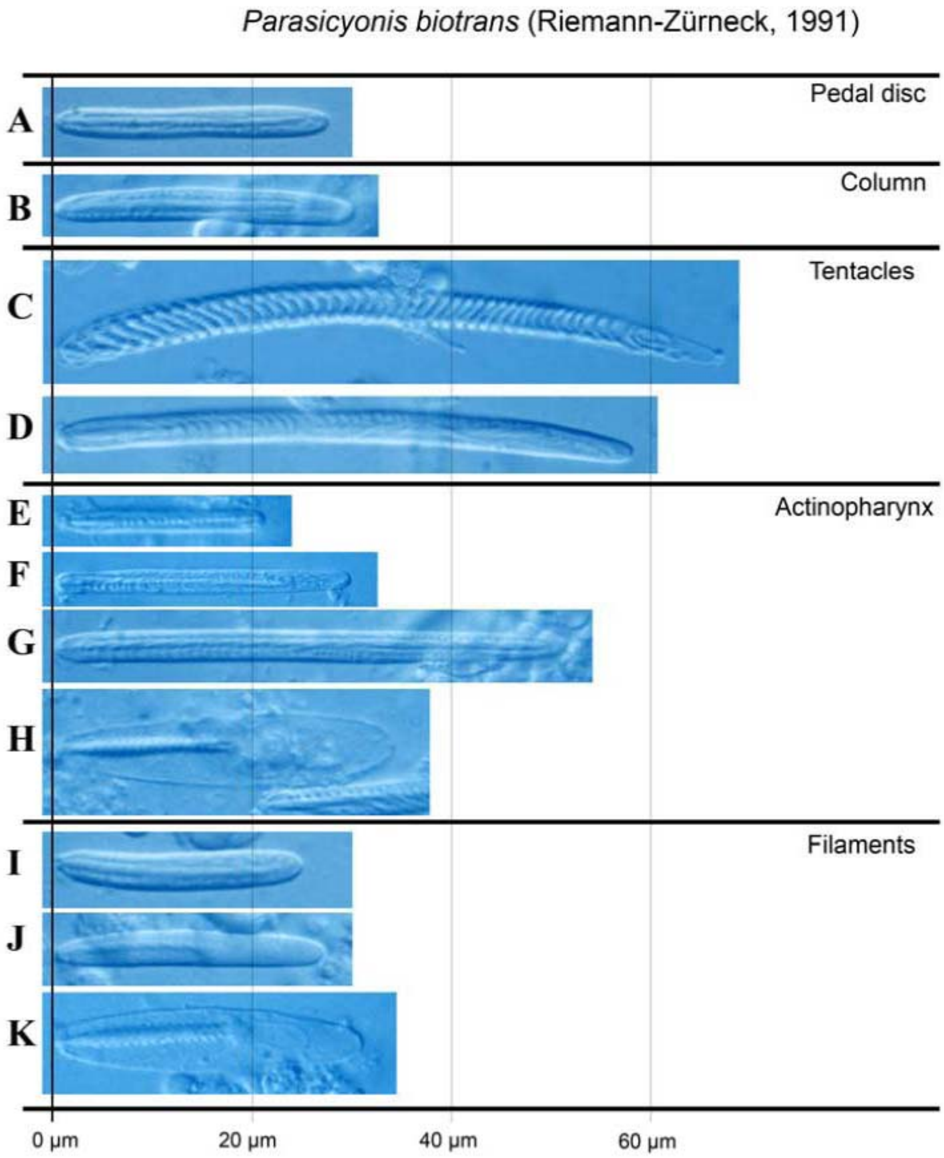

Figure 8.3.– *Parasicyonis biotrans* (Riemann-Zürneck, 1991). Cnidae: A) basitrich; B) basitrich; C) spirocyst; D) basitrich; E, G and G) basitrichs (three size ranges); H) microbasic p-mastigophores; I) basitrich 1; J) basitrich 2; K) microbasic p-mastigophores.

Cnidom (Fig. 8.3; Table 8).— Cnidae of tentacle ectoderm at least 10µm larger than in any other related species (large basitrichs 50-59µm, and large spirocysts of 80 µm).

Colour.— In preserved condition without pigmentation, white.

Geographic and bathymetric distribution

The studied specimens were collected from depths between 4806-4844m. All *Parasicyonis biotrans* (Riemann-Zürneck, 1991) specimens are known from North Atlantic deep-sea, and it seems that they are confined to the abyssal plains (Porcupine Abyssal Plain and deep sea areas near the Mid Atlantic Ridge).

Discussion

The examined species was fairly well described by Riemann-Zürneck (1991a) in its original description of *Sicyonis biotrans*. There is evidence that the specific shape and structure of its body in the preserved condition (which state of contraction it is a unique form that shows little variation), the large dimensions of the oocytes in mature females, the large sizes of the tentacle cnidae and the arrangement of those close to the margin are the most significant discriminating characters. However, as Riemann-Zürneck also refers, it is necessary to include in the discussion of the genus *Sicyonis* the genus *Parasicyonis*, due to Carlgren (1921) separation based on the presence of filaments in the fertile cycle of mesenteries. The author proved the presence of this character in the examined material, although he persisted in assigning the new species to the genus *Sicyonis*. At present this character seems more stable than any other feature, so it is preferred to accept this generic division instead of creating a new taxonomic problem. According to this point of view *Sicyonis biotrans* is a synonym of *Parasicyonis biotrans*. In this manner, the *Parasicyonis* species nominated for the North Atlantic are: *P. maxima* (Wassilieff, 1908), *P. sarsi* Carlgren, 1921, *P. groenlandica* Carlgren, 1933, *P. ingolfi* Carlgren, 1942, and now *P. biotrans* (Riemann-Zürneck, 1991).

Riemann-Zürneck (1991) documented that tentacles are thickened with mesoglea all around their bases, not only on their aboral sides. This is equivalent to say that the tentacles are "not thickened" if the mesogleal ring measures the same at both sides. Accordingly, that character places this species in the genus *Parasicyonis.* However, Carlgren (1949) includes it in the genus *Sicyonis*, *S. variabilis* which did not have thickenings in tentacles base, creating again another contradiction.

In Carlgren's (1949) diagnosis of the genus *Sicyonis* there is a gaffe, instead of "mesenteries differentiated into stronger, fertile mesenteries with well developed filaments and into weaker fertile mesenteries without filaments", there should be (text underlined) "sterile mesenteries". The number of cycles of perfect mesenteries is an important feature to differentiate the two genera, according to Carlgren's descriptions and our data, it is assumed that *Sicyonis* has two perfect cycles and some more perfect mesenteries of the next cycle differing from *Parasicyonis* which has at least three perfect cycles (or four) and some more perfect mesenteries of the next cycle. Although, comparing with *Parasicyonis, s*pecimens of genus *Sicyonis* (Carlgren, 1921) are smaller, some of them in a not totally developed state (at instance, *S. variabilis*), suggesting that this parameter might possibly be related to growth.

An additional equivocal occurrence is the question of the filaments type (unilobate or trilobate). Riemann-Zürneck (1991) alleged that Carlgren (1949) in his diagnosis of genus *Sicyonis* found unilobate filaments in the fertile mesenteries*,* to which she opposes revealing that *S. biotrans* (syn. *P. biotrans*) carry trilobate filaments in the smallest septa and never unilobate ones. Reviewing the text, we confirmed that Carlgren never referred the filaments type in 1949, and simply says that filaments are "*well developed*" at stronger mesenteries side. Besides, we found unilobate filaments in the last cycle of fertile mesenteries and not trilobate filaments as Riemann-Zürneck explicit. Even though, the cnidom present in filaments comprises one small basitrich and two different microbasic *p*-mastigophores (one large with thin membrane and the other narrow with a thicker membrane), and not two different basitrichs (one with short shaft and other with long one) as assumed Riemann-Zürneck (1991).

Family Bathyphelliidae Carlgren, 1932

Diagnosis (adapted from Fautin, 1983)

Mesomyaria with broad base and generally elongate column that may be divided into scapus and scapulus. Mesenteries divided into macro- and microcnemes. Retractors diffuse to circumscript. Sphincter mesogleal. Acontia carrying only basitrichs

Genus *Daontesia* Carlgren, 1942

Diagnosis (modified from Riemann-Zürneck, 1997)

Column divided into scapus and scapulus. Scapus with tenaculi which produce a soft, dense, squamous multistratified cuticle. Cinclides sometimes present. Tentacles not numerous, hexamerously arranged in number as the mesenteries. Tentacle ectoderm with a peculiar b-mastigophores. Sphincter strong. Six or 12 pairs of macrocnemes with strong but diffuse retractors. Two siphonoglyphs and two pairs of directives. At least the mesenteries of the first cycle fertile. Retractors diffuse, strong. Cnidom: spirocysts, microbasic *p*-mastigophores, microbasic b-mastigophores, basitrichs.

Type species

Daontesia praelonga (Carlgren, 1928).

Species included in the genus

Daontesia mielchei Carlgren 1956; *Daontesia australis* (Dunn, 1983) syn. *Bathyphellia australis* Dunn, 1983. *Daontesia porcupina* Riemann-Zürneck, 1997

Daontesia porcupina Riemann-Zürneck, 1997

(Fig. 9.1-9.3, Table 9)

Material examined

BENGAL 2: stn. 13078 (6) (BEIM: 3120, 2 specimens); stn. 13078 (27) (BEIM: 3007, 3 specimens); stn. 13078 (11) (BEIM: 3020, 6 specimens). BENGAL 3: stn. 13200 (70) (BEIM: 3104, 7 specimens); stn. 13200 (94) (BEIM: 3065, 16 specimens); stn. 13200 (84) (BEIM: 3106, 4 specimens); stn. 13200 (93) (BEIM: 3112, 3 specimens). BENGAL 5: stn. 13368 (53) (BEIM: 3000, 11 specimens); stn. 13368 (47) (BEIM: 3105, 1 specimen); stn. 13368 (48) (BEIM: 3099, 3 specimens); stn. 13368 (52) (BEIM: 3042, 4 specimens); stn. 13627 (24) (BEIM: 3103, 1 specimen).

In total, 61 individuals from the Porcupine Abyssal Plain were studied. Four specimens from stn. 13200(94) at 4814m depth and another four specimens from stn. 13368(53) at 4810m were used for histological analyses.

Description

External Anatomy (Fig. 9.1).— Body shape conical or hemispherical in preserved condition depending on the state of contraction or/and natural blown up, consequence of sampling methods. Detached cuticle, in some specimens, reveals a transparent pinkish ectoderm with longitudinal rows along the body.

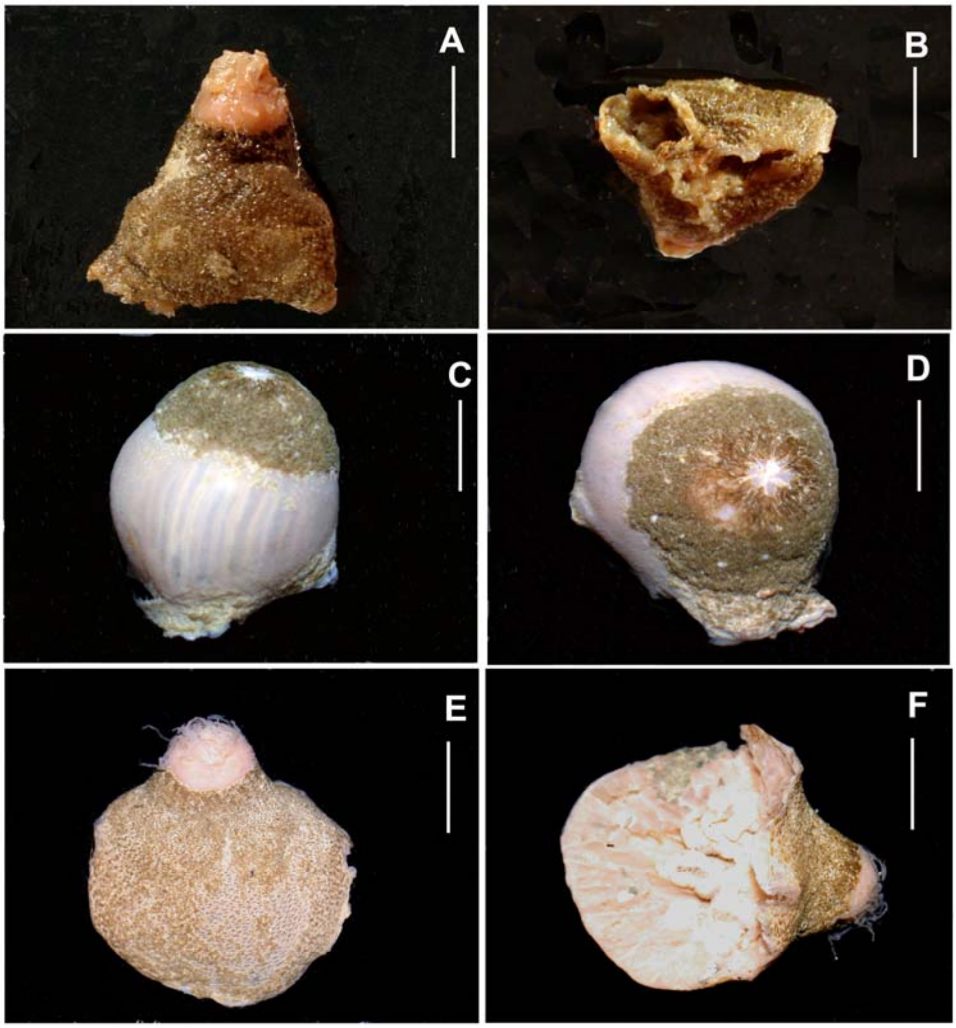

Figure 9.1.– *Daontesia porcupina* Riemann-Zürneck, 1997. External anatomy [BEIM (3065, 3000)]: A) Lateral view of a contracted specimen; B) Basal view of the specimen; C) Lateral view of a inflated specimen; D) Oral view of the specimen enclosing al tentacles; E) Oral view of the specimen showing some tentacles out; F) Basal view of the specimen distended. Scale: A, 10 mm; B, 10 mm; C, 10 mm; D, 10 mm; E, 10 mm; F, 10 mm.

Medium sized species, to 1.5 cm diameter and 2.0 cm height. Broad pedal disc (3.5 cm in large specimens) usually extended with adherent foreign sediment particles showing evidence of being attached to stones, boulders or clinker. Column divided into scapus and scapulus without cinclides. Scapus covered with a dense squamous and multistratified cuticle. Some specimens lost part of their coat due to sampling methods. Scapulus turned inside covering all the tentacles. In less contracted specimens the scapulus can be noticed by a pale pinkish colour and some damaged tentacles out.

Internal Anatomy (Fig. 9.2).— Mesenteries divided in macrocnemes (first cycle, 6 pairs) and microcnemes (second and third cycle, six and 12 pairs respectively), hexamerous arranged in three regular cycles. Only first cycle perfect. Two pairs of directives connected with two poorly differentiated siphonoglyphs. Actinopharynx with thickened mesoglea. About 48 tentacles (same number of mesenteries). Filament gonads and acontia are present on the macrocnemes. Acontia are distinctly marked, appearing in small spirals on the most proximal parts of the macrocnemes.

Sphincter musculature mesogleal strong, alveolar. Macrocnemes retractor musculature diffuse and strong. Microcnemes rise firmly over the endoderm with diffuse and strong retractors. Parietobasilar muscles diffuse and weak. Without basilar muscles.

Column wall of similar thickness along entire length. In longitudinal section, mesogleal structure of the column is fibrilar. Scapus is multistratified presenting tenaculi, which form several layers of concentric cuticle sheets with a granular substance besides tenaculi.

Cnidom (Fig. 9.3; Table 9).— An analysis of cnidom is given in Table 9. Spirocysts, basitrichs, microbasic *b*-mastigophores (?), and microbasic *p*-mastigophores.

Colour.— All specimens in the preserved state show a cuticle with a brownish dark colour.

Geographic and bathymetric distribution

Daontesia porcupina seems to be endemic of the Porcupine Abyssal Plain. The specimens available for this study were all collected in the Porcupine Abyssal Plain (4808-4814 m) and are apparently common in places where hard substrates are available.

Discussion

The type species of the genus *Daontesia* occurs in different biogeographical areas, *D. praelonga* and *D. porcupina* are from the Northern Hemisphere and *D. mielchei* is from the Southern Hemisphere but all are confined to the deep-sea. (Riemann-Zürneck, 1997b).

D. praelonga was found in the transition of North Atlantic to Arctic waters (Iceland, Faroe Islands) and also in the North Sea (Denmark) at 1041-1960 m depth. Instead *D. porcupina* is an abyssal North Atlantic species collected between 4556 and 4855 m depth (Riemann-Zürneck, 1997b).

D. mielchei is represented only by one exemplar found during Galathea expedition (St. 495) in Banda Trench (South Pacific) at 7250 m depth (Carlgren, 1956).

Carlgren (1942), classified the Bathyphelliidae within the Acontiaria. In his classification, he considered the basilar muscles and the acontia as high-ranking taxonomic characters. Although Stephenson (1920), criticized these purposes explaining that the opposition of the Acontiaria to the Mesomyaria is “unnatural” and acontia should not be made more important than and the other characters. Schmidt (1972), stated that the acontia can be reduced and, in a evolutionary perspective, all the Acontiaria came from the Mesomyaria.

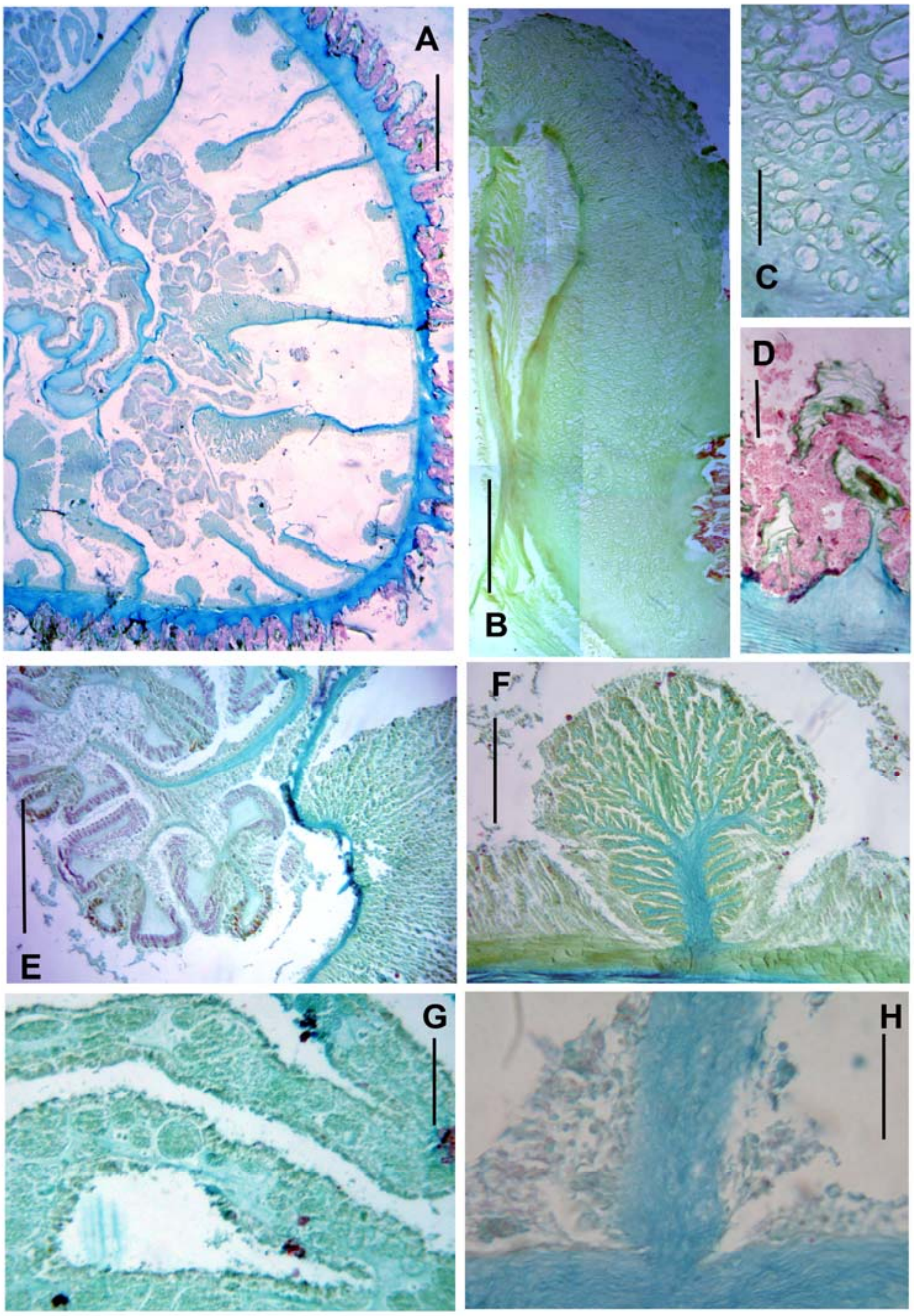

Figure 9.2.– *Daontesia porcupina* Riemann-Zürneck, 1997. Internal anatomy [BEIM (3065, 3000)]: A) Transversal section at actinopharynx level showing mesenteries cycles; B) Longitudinal section of the column distal margin showing the mesogleal sphincter; C) Detail of sphincter mesogleal musculature (alveolar); D) Detail of the multistratified cuticle; E) Detail of filament and macrocneme retractor musculature; F) Detail of microcneme retractor musculature. G) Detail of reproductive tissue; H) Longitudinal section of the pedal disc showing the absence of basilar musculature. Scale: A, 2 mm; B, 2.5 mm; C, 0.4 mm; D, 1.1 mm; E, 1.25 mm; F, 1.0 mm; G, 1.4 mm; H, 0.5 mm.

Table 9.– Dimensions of cnidae of *Daontesia porcupina* Riemann-Zürneck, 1997. Specimens: [BEIM (3065, 3000)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic. (*)Average based on measures of less than 40 capsules, which is considered the meaningful minimum (Williams, 1996; 1998).

Category	Fig. 9.3	Range of length and width of capsules in µm	X ± SD	S	N	F	Data from Riemann-Zürneck, 1997	F
PEDAL DISC								
Basitrichs	**A**	**(12-17.5) x (2-2.5)**	**14.8 ± 1.6 x 2.3 ± 0.3(*)**	**3/1**	**10**	**---**	**–**	**–**
SCAPULUS								
Basitrichs	**B**	**(22-27) x (3-4)**	**24.5 ± 1.4 x 3.5 ± 0.4**	**3/2**	**40**	**++**	**(24-27) x (3-5)**	
SCAPUS								
Basitrichs 1	**C**	**(7-10) x (2-3)**	**8.1 ± 1.0 x 2.3 ± 0.4(*)**	**3/2**	**10**	**---**	**(8.5-10) x 1.5**	**---**
Basitrichs 2	**D**	**(15-19) x (3-4)**	**17.1 ± 1.2 x 3.5 ± 0.4(*)**	**3/1**	**10**	**---**	**(15.5-18) x (3-3.5)**	**---**
TENTACLES								
Spirocysts	**E**	**(30-93) x (4-11)**	**57.2 ± 11.2 x 7.4 ± 1.5**	**3/3**	**59**	**+++**	**(72-87) x (9-10)**	
b-mastigophores	**F**	**(25-39) x (4-5)**	**35.1 ± 2.3 x 4.6 ± 0.5**	**3/3**	**60**	**+++**	**(35-41.5) x (4-4.5)**	
basitrichs	**–**	**–**	**–**	**–**	**–**	**–**	**13.5 x 2**	**---**
PHARYNX								
Basitrichs 1	**G**	**(15-28) x (2-3)**	**18.9 ± 2.6 x 2.3 ± 0.3**	**3/3**	**60**	**++/+++**	**(16.5-18) x 2**	**---**
Basitrichs 2	**H**	**(28-36) x (3-4)**	**32.0 ± 2.1 x 3.5 ± 0.3**	**3/3**	**53**	**++**	**No Data**	
Mic *p*-mastigophores	**I**	**(27-36) x (3.5-6.5)**	**32.2 ± 2.0 x 5.1 ± 0.5**	**3/3**	**60**	**+/++**	**(27.5-32) x (3.8-4.3)**	
FILAMENTS								
Basitrichs	**J**	**(14-19) x (2-2.5)**	**16.0 ± 2.2 x 2.3 ± 0.2**	**3/3**	**60**	**---**	**(13-16.5) x 2**	**---**
Mic *p*-mastigophores	**K**	**(26-35) x (2.5-6)**	**30.6 ± 2.0 x 5.0 ± 0.6**	**3/3**	**60**	**++**	**(28-31) x (3.8-4.3)**	
ACONTIA								
Basitrichs 1	**L**	**(13-18) x (2- 3)**	**15.2 ± 1.6 x 2.2 ± 1.3(*)**	**3/3**	**28**	**---**	**(13-17.5) x 2**	
Basitrichs 2	**M**	**(22.5-35) x (2-3.5)**	**28.5 ± 2.4 x 2.8 ± 0.3**	**3/3**	**60**	**+++**	**(28-33) x 2.5**	

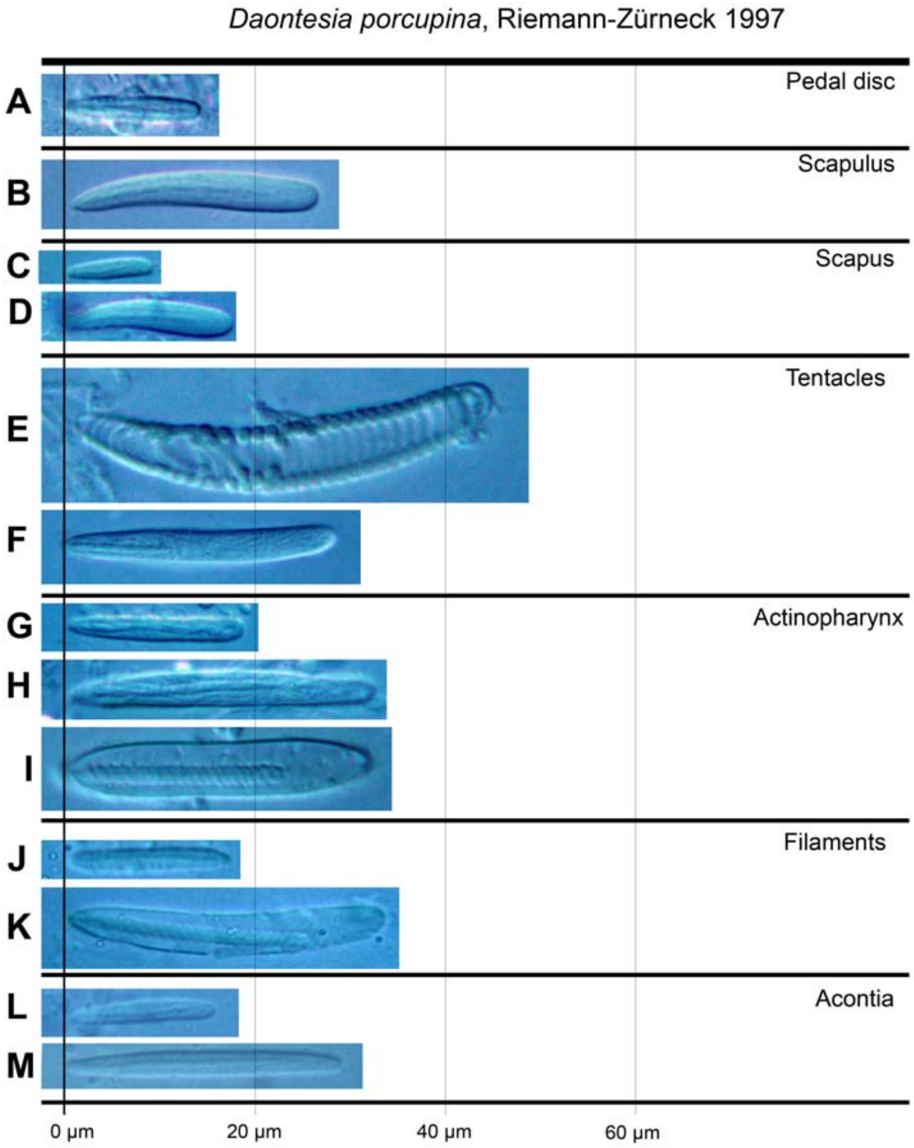

Figure 9.3.– *Daontesia porcupina* Riemann Zürneck, 1997. Cnidae: A) basitrich; B) basitrich; C) basitrich 1; D) basitrich 2; E) Spirocyst; F) microbasic b-mastigophore; G) basitrich 1; H) basitrich 2; I) microbasic p-mastigophore; J) basitrich; K) microbasic b-mastigophore; L) basitrich 1; M) basitrich 2.

Bathyphelliidae is one of these families in which the reduction of the acontia has been suspected, due to their poor development, unconspicuous state or even absence as in the case of *Bathyphellia margaritacea* (Danielssen, 1890) which is the type species of the genus and family (Riemann-Zürneck, 1997b). However, observations of *Daontesia porcupina* Riemann-Zürneck, 1997 specimens, argue contrarily to this statement because acontia are easily discernible forming spirals.

Schmidt (1972, 1974) did not recognize acontiarian anemones as a group, instead he grouped them with non-acontiate species in either “early” or “late” Mesomyaria. Following Schmidt’s (1972, 1974) classification, “early” and “late” mesomyarians differ by the latter having a type of nematocyst (which he termed *p*-rhabdoids A) absent in the early lineage. However, as England (1991) advised, from taxonomist’s point of view, it is not always possible to identify Schmidt’s categories (including ultrastructure features such as: length of spines, density and the angle that spines make with the shaft on discharge). Usually the condition in which the material was preserved do not allow geting discharged capsules because only formalin-fixed material is available.

Riemann-Zürneck (1997), considered *D. porcupina* an “early” Mesomyaria due to its cnidom, based on the presence of only *p*-rhabdoids B (*sensu* Schmidt, 1974). However it is not very clear how she noticed “*p*-rhabdoids A and B” in the actinopharynx, because no images were provided nor a diagnosis explanation to differentiate them in detail and showing the ultrastructure features mentioned above. Riemann-Zürneck (1997) proposed the evolutionary state of acontia in her discussion using the argument that *p*-rhabdoids A are “thin walled” and *p*-rhabdoids B are “thick walled”. Recent molecular phylogenetic studies (Daly *et al*, 2008) found Acontiaria as a polyphyletic group, however these results failed to support the distinction between “early” and “late” Mesomyaria and do not support the value of *p*-mastigophores as a phylogenetic character.

A main characteristic of bathypheliids is the presence of only basitrichs in the acontia (Carlgren, 1949). However molecular evidence suggests that the ancestral cnidom of the acontiarian actiniarians included both basitrichs and *p*-mastigophores, and that one or both of these types have been lost several times (Rodríguez *et al,* 2009).

Although, cnidom in *Daontesia porcupina* is very peculiar, the tentacle ectoderm possesses an uncommon microbasic *b*-mastigophore with a short shaft, the scapus presents a rare nematocyst slightly curved which is a basitrich and the acontia have a characteristic basitrich with a somewhat bottle-like neck. Riemann-Zürneck (1997) observed a small basitrich in the tentacles that could not be confirmed in the specimens observed during the present work. However Riemann-Zürneck (1997) also stated that these features were very rare. Additionally, in our results, a large basitrich was found frequently in the actinopharynx but this feature was not mentioned by Riemann-Zürneck (1997).

Daontesia porcupina is most distinguishable from the type species, *D. praelonga* Carlgren, 1942, because it lacks cinclides at the limbus; It is also distinguishable from *D. praelonga* and *D. mielchei* Carlgren, 1956 because it has six pairs of macrocnemes instead of 12. So it is questionable why Riemann-Zürneck did not ascribed *D. porcupina* to the genus *Bathyphellia*.

In Riemann-Zürneck’s (1997) opinion, the most significant feature of the genus *Daontesia* is the peculiar multistratified cuticle coating. The author argues that *D. porcupina* is more closely related to *Bathyphellia australis* Dunn, 1983 since it has a very similar multistratified cuticle with tenaculi, the same number of macrocnemes and most types of cnidae. For this reason, Riemann-Zürneck (1997) synonymised *B. australis* to *Daontesia australis* and adapted Carlgren diagnosis of the genus. She also questioned the possibility to elevate *Daontesia* to family status, considering the unique structure of the cuticle and the peculiar diverse cnidom as high-ranking taxonomic features.

In our opinion, the multistratified cuticle is not a so high-ranking feature because, contrarily to Riemann-Zürneck statement, *B. margaritacea* has also a cuticle considerably thicker in tenaculi, which is sometimes stratified (Carlgren, 1942; M. Ramos personal observations). Other fact is that the four known species of bathypheliids of the genus *Bathyphellia* and *Daontesia* are confined to the deep sea, in opposite the other two genera of the family, *Phelliogeton* and *Acraspedanthus* occur in shallow (less than 20 m) austral waters.

The full resolution of this question can only be achieved upon collection of new specimens of both genus, preserved in ethanol in order to conduct molecular studies, and assess their real dissimilarities.

Family Hormathiidae Carlgren, 1925

Diagnosis (adapted from Carlgren, 1949)

Nynantheae (Mesomyaria) with acontia and strong mesogleal sphincter. Mesenteries not divided into macro- and microcnemes. Usually six pairs of perfect mesenteries, sometimes more, but never numerous. Perfect mesenteries usually sterile, rarely fertile. Nematocysts of the acontia basitrichs only. Usually the spirocysts are large and broad.

Genus *Actinauge* Verrill, 1883

Diagnosis (adapted from Carlgren, 1949)

Well developed pedal disc, often cup-like, enclosing sand, mud or other objects. Column divided into scapus and scapulus, the former with rows or tubercles, provided with a weaker or stronger cuticle. Arrangement of the tubercles variable; tendency to form longitudinal furrows, or reduced to a single corona in its uppermost part (mostly 12 or multiple of 12). No cinclides. Sphincter strong, mesogleal. Tentacles hexamerously arranged, usually 96 or some more, clearly with thickenings on their aboral sides. Longitudinal muscles of tentacles ectodermal, radial muscles of oral disc ectodermal or more or less mesogleal. Six pairs of perfect mesenteries; about the same number of mesenteries distally and proximally. Two well developed siphonoglyphs. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Type species

Urticina longicornis Verrill, 1882.

Species included in the genus

Actinauge abyssorum Gravier, 1918; *Actinauge bocki* Carlgren, 1943; (?)*Actinauge chilensis* Carlgren, 1959; *Actinauge cristata* Riemann-Zürneck, 1986; *Actinauge granulata* Carlgren, 1928; *Actinauge longicornis* (Verrill, 1882); *Actinauge richardi* (Marion, 1882); *Actinauge verrillii* McMurrich, 1893.

Actinauge richardi (Marion, 1882)

(Fig. 10.1-10.2; Table 10)

Material examined

PROSPEC: stn. CPH 9 (BEIM: 3014, 1 specimen). CARACOLE: PL 128-06 (3 specimens)

In total four specimens were used for the histological study.

Description

External anatomy (Fig.10.1).— Pedal disc deeply excavated, forming a cup-shaped concavity filled with sand or mud that serves as an anchor; the animal is not adherent to a firm substratum. Column variable depending on state of contraction, cylindrical to ovoid in general. Cartilaginous consistence. Divided in scapus and scapulus.

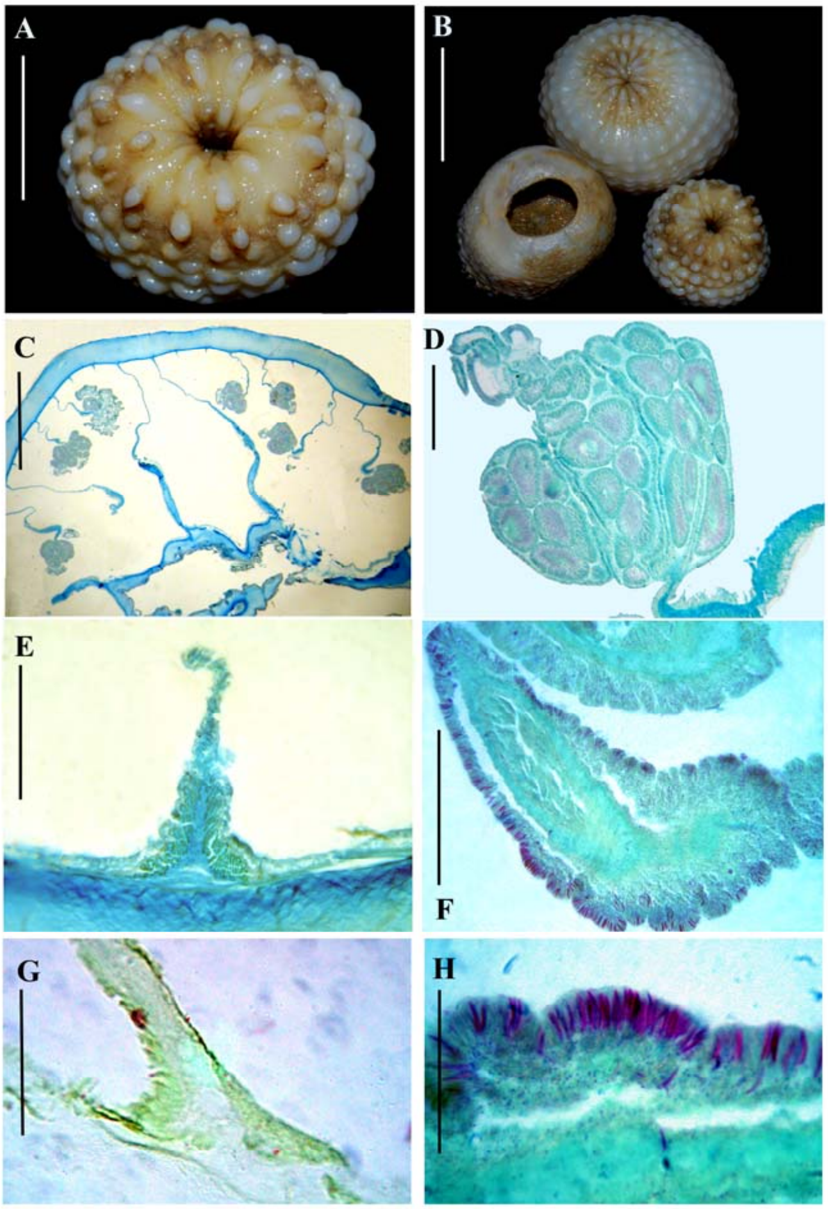

Figure 10.1.– *Actinauge richardi* (Marion, 1882). External and internal anatomy [PL 128-06]: A) Oral disc view of one specimen showing strong tubercles; B) Oral and pedal disc view of three specimens, pedal disc deeply excavated; C) Transversal section view showing four cycles of mesenteries; D) Filament detail; E) Detail of microcneme of the third cycle, poorly developed; F) Transversal section of the tentacle showing aboral mesogleal thickenings; G) Longitudinal section of the pedal disc showing basilar musculature, H) Detail of tentacle ectoderm showing nematocyst batteries. Scale: A, 11 mm, B, 20 mm; C, 3.5 mm; D, 0.35 mm; E, 0.01 mm; F, 0.4 mm; G, 0.25 mm; H, 0.09 mm.

Scapus provided with tubercles arranged in vertical and longitudinal rows, variable in thickness and appearance (large, rounded or acuminate). At the upper part, scapulus usually with 12 strong tubercles where almost 24 longitudinal ridges start. Covered with a thin cuticle, easily deciduous, usually in the interspaces between the tubercles. Oral disc strongly contracted, tentacles introverted. Number of tentacles 96, arranged in five cycles.

Table 10.– Cnidae of *Actinauge richardi* (Marion, 1882). Specimens: [PL 128-06]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic. (*)

Category	Fig. 10.3	Range of length and width of capsules (µm)	X ± SD	S	N	F	Data from Carlgren 1928	Data from Doumenc *et al*, 1985	Pablo López-González, 1993
PEDAL DISC									
Basitrichs	_	(13-20) x (2-3)	15.6±1.6 x 2.5±0.2(*)	2/3	29	---	–	–	–
Basitrichs	A	(8-13) x (1-2)	10.1±1.4 x 1.6±0.2	2/3	40	---	–	–	–
COLUMN									
Basitrichs	–	(13.5-16.5) x (2-3)	15 ± 0.9 x 2.3±0.3(*)	3/3	15	---	–	8.82-17.64 x 1.46-2.93 (13.55 ± 2.56)	15.3 x 2.2
Mic *p*-mastigophores 1	–	–	–	–	–	–	–	20-23.5 x 1.43-4.41 (22.5 ± 2.1)	–
Mic *p*-mastigophores 2	–	–	–	–	–	–	–	14-17 x 1.43-4.41 (15.5 ± 1.3)	–
TENTACLES									
Spirocysts	B, C	(22-40) x (3-8.5)	33.2±4.1 x 5.7±1.3	3/3	60	+++	6 x 5.5	16.6-30.86 x 2.2-4.41 (21.85 ± 3.25)	31.4 (29-34.3) x 3.2 (2.9-3.6)
Basitrichs 1	D	(9-14) x (1.5-2)	11.3±1.2 x 1.5 ±0.1	3/3	60		11.3 x 1.5-2 (rare)	19.1-19.9 x 2.2-2.93 (19.5 ± 0.7)	13 (12.5-13.8) x 1.3 (1.2-1.6)
Basitrichs 2	E	(22-34) x (2-3)	25.3 ±2.4 x 2.5±0.3	3/3	60		18.3-26.8 x 2.5-2.8	22-23.35 x 2.2-2.93 (23.5 ± 1.15)	27.5 (24.4-32.3) x 2.4 (2.3-2.6)
PHARYNX									
Basitrichs 1	F	(10-14) x (1.5-2)	12.0 ±1.1 x 1.5±0.1(*)	2/3	35	+/-	–	14-16 x 1.46 (15 ± 1.2) rare	15.3 x 2.7
Basitrichs 2	G	(27-32) x (3-3.5)	29.9±1.6 x 3±0.1(*)	2/3	27	+/-	22-36 x 2.8-4	26-32.33 x 2.5-3.67 (30.5 ± 3.1)	31.4 (29-34.3) x 3.2 (2.9-3.6)
Mic p-mastigophores	H, I	(17-25) x (2.5-3.5)	20.7± 1.8x 3.1±0.2	3/3	59	++	19.7 x 3 (very rare)	14.69-24.98 x 2.93-3.67 (20.13 ± 2.05)	20.8 (18.4-22.4) x 3.6 (2.9-3.9)
FILAMENTS									
Basitrichs	J	(8.5-15) x (1.5-2)	10.3±1.2 x 1.5±0.1	3/3	60	+++	10-11.3 x 1.5-2	8.82-20.57 x 1.46-2.2(11.93±2.3)	16.6 x 1.8
Mic *p*-mastigophores	K	(16-22) x (3-4)	19.0 ± 1.7x 3.3±0.3	3/3	60	+++	16.2-20 x 3-4.2	14.69-17.64 x 2.93 (16.69±1.32)	17.8 (15.8-19.8) x 3.4 (2.9-4.3)
ACONTIA									
Basitrichs	–	–	–	–	–	–	10 x 1.5-2	–	–
Basitrichs	L	(19-35) x (2.5-4)	31.1 ±2.5 x 3.0±0.1	3/3	60	+++	24-34 x 3-3.5	24.98-32.33 x 2.57-3.3 (28.9±1.55)	29.7 (26.1-31.5) x 2.7 (2.2-3.6)

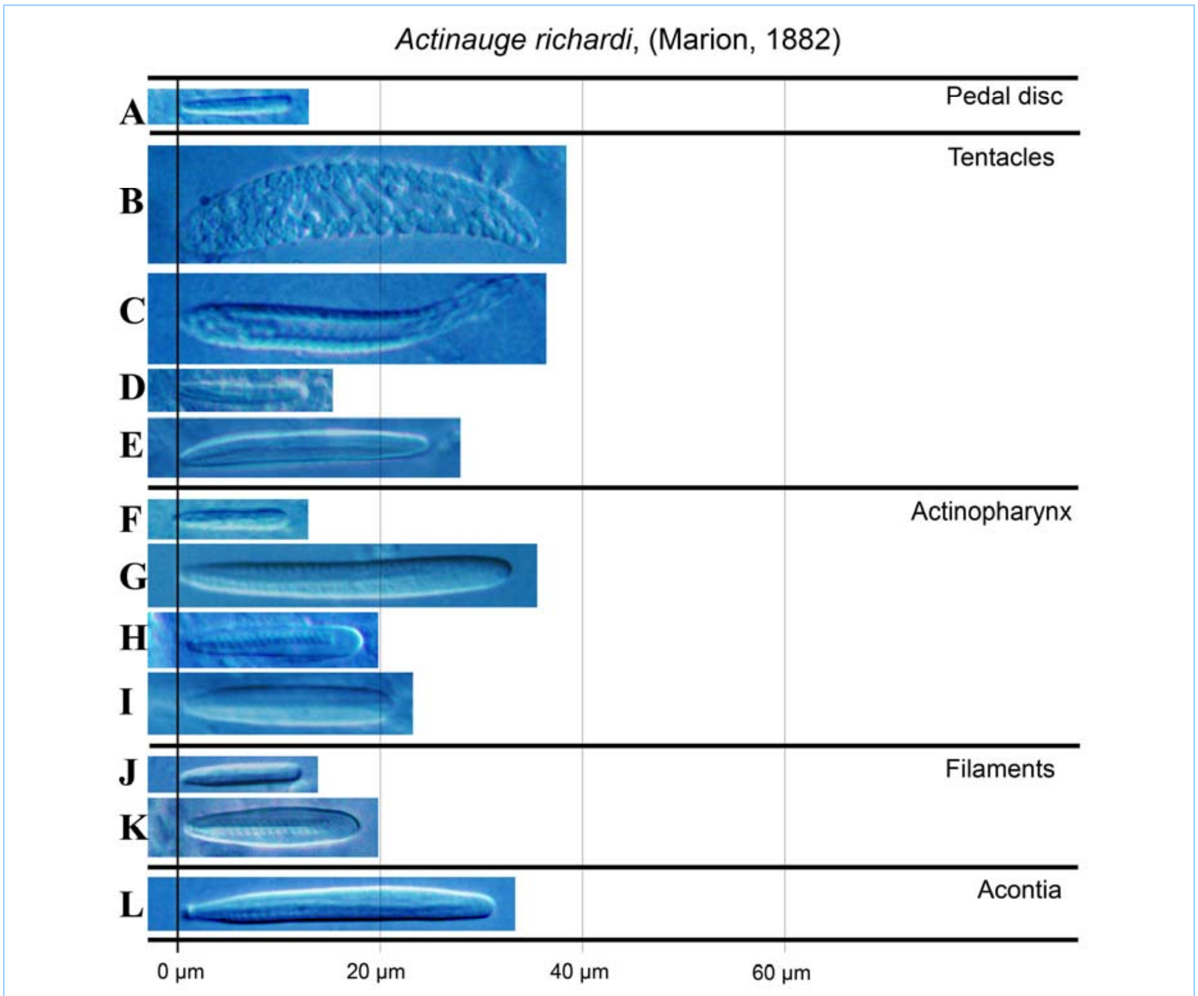

Figure 10.2.– *Actinauge richardi* (Marion, 1882). Cnidae: A) basitrich; B) spirocyst 1; C) spirocyst 2; basitrich 1; D) basitrich 2; F) basitrich 1; G) basitrich 2; H) microbasic *p*-mastigophore 1; I) microbasic *p*-mastigophore 2; J) basitrich; K) microbasic *p*-mastigophore; L) basitrich.

Internal anatomy (Fig.10.1).— Four cycles of mesenteries. Similar number of mesenteries at distal and proximal part. Only the first cycle of mesenteries is perfect. Two siphonoglyphs and two pairs of directives. The second and third cycles have fertile mesenteries carrying gametogenic tissues (spermatocysts in the analysed specimen) and the cnidoglandular tract of trilobate filaments is carrying batteries of nematocysts. Fourth cycle is complete but poorly developed, forming merely tiny ridges along the internal side of the body wall.

Mesoglea of the body wall thick and tough, somewhat thicker in scapulus containing a large mesogleal sphincter. Musculature of the mesogleal sphincter strong and reticular (M. Ramos personal observations, no image available). Retractors are diffuse and poorly developed. Parietobasilar muscles weak, diffuse. Basilar muscles are poorly developed and diffuse. Numerous acontia without spiral form. Some tentacles with basal mesogleal thickenings.

Cnidom (Fig. 10.3; Table 10).— Spirocyst, basitrichs, and *p*-mastigophores.

Colour.— Dirty white.

Geographic and bathymetric distribution

Actinauge richardi is a circalittoral and bathyal species. The three specimens caught during the CARACOLE cruise were taken in Connemara field at 380 m depth, were cold seeps occur at the sea floor and vertical gas fluids flow in the subsurface. The other specimen was collected at the Hébrides at greater depth (990 m). All specimens were anchored in soft sediments. *A. richardi* has a wide distribution; it is very common in the East coast of the North Atlantic from Norway to Biscay (Manuel, 1981). The species was found at the West and South coast of Ireland (Stephenson, 1935; O'Riordan, 1973), Arcachon (Durègne, 1890) at the Gulf of Biscay (Marion, 1882), in the West (Gravier, 1922a) and East Mediterranean (Doumenc, *et al.* 1985) and, finally, at the Atlantic Moroccan coast (Carlgren, 1928 and 1942; Patriti, 1970). The bathymetric range varies between 60 to 2000 m (Carlgren, 1949).

Discussion

Actinauge richardi was described by Marion (1882) as *Chitonactis richardi*, from material collected in the Gulf of Biscay; it was included in *Actinauge* by Haddon (1889) because of the thickenings at the base of the tentacles.

Stephenson (1935), examining 205 specimens from the collections of the Irish Fisheries Department, remarked the great variability of the *A. richardi* in respect to the tubercles of the scapus, which vary both in extent and in development from one specimen to another. In fact, *A. richardi* presents a considerable constancy in its major features when it has the globose form with the cavity of the pedal disc filled with mud. However, in this collection Stephenson (1935) has also noticed some specimens adherent to gastropod shells by the pedal disc, which was enlarged and flattened instead of cup-form. Even the type of sphincter varied within the examined specimens, it can be alveolar or reticular. The retractors vary from diffuse to circumscript diffuse.

Stephenson questioned: "can all these specimens be genuine examples of *A. richardi*"? His answer was yes, there are two types of sphincter and two types of retractors both linked by intermediate forms. In addition, he refers that one truly distinctive character from other British anemones is the possession of basal thickenings on the aboral side of the tentacles inner cycles. However, the author also states that these swellings are sometimes very large and others very reduced, but "apparently" always present. As this sentence shows, this character is also very variable. The other stable features are characteristic of the whole *Hormathia* genus; these are: the coronate tubercles (which may be more or less rounded, acuminate, large or small) usually organized in groups of 12 (exactly or approximately); the five cycles of mesenteries and tentacles (never more than 96 in number).

In this work, we gave more importance to the nematocysts anatomy, and we verified the constancy in their types and dimension in three analysed specimens. Comparing with Carlgren (1942) diagnosis, the small basitrichs on the acontia could not be observed, only the larger one (see Table 10.). There are also differences between our observations and the cnidom equipment of *A. richardi* specimens found at the Aegean sea (Doumenc *et al*, 1985); these include the size of basitrich (2) from tentacles and the two types of *p*-mastigophores on scapus (inexistent in the observed material). This fact may be due to the collection and preservation methods which remove the fine cuticle layer with nematocysts.

Other important feature is the reproduction type of *A. richardi* which seems to be only sexual and, as a rule, never asexual (Stephenson, 1935).

Actinauge abyssorum (Gravier, 1918)

(Figs. 11.1-11.3; Table 11)

Material examined

BENGAL 2: Stn. 13078 (6) (BEIM: 3025, 12 specimens); Stn. 13078 (11) (BEIM: 3002, 16 specimens); Stn. 13078 (27) (BEIM: 3057, 13 specimens). BENGAL 3: Stn. 13200 (70) (BEIM: 3027, 9 specimens); Stn. 13200 (84) (BEIM: 3081, 11 specimens); Stn. 13200 (93) (BEIM: 3021, 15 specimens), Stn. 13200 (93) (BEIM: 3062, 1 specimens); Stn. 13200 (94) (BEIM: 3066, 1 specimen); Stn. 13200 (94) (BEIM: 3073, 1 specimen); Stn. 13200 (94) (BEIM: 3075, 55 specimens). BENGAL 5: Stn. 13368 (47) (BEIM: 3109, 4 specimens); Stn. 13368 (48) (BEIM: 3093, 41 specimens); Stn. 13368 (52) (BEIM: 3005, 1 specimen); Stn. 13368 (52) (BEIM: 3006, 25 specimens); Stn. 13368 (53) (BEIM: 3096, 71 specimens); Stn. 13368 (53) (BEIM: 3060, 15 specimens). BENGAL 6: Stn. 13627 (11) (BEIM: 3095, 49 specimens); Stn. 13627 (11) (BEIM: 3064, 1 specimen); Stn. 13627 (24) (BEIM: 3069, 21 specimens).

In total, 362 specimens from the Porcupine Abyssal Plain were available. Four specimens were used for the histological study: three specimens were taken from BENGAL 5, Stn 13368 (48) and one specimen from BENGAL 3 Stn. 13200 (94).

Description

External anatomy (Fig. 11.1).— Pedal disc is extended laterally to embrace objects of biogenic origin (polychaete tubes and siliceous spicules of glass sponges). Diameter of pedal disc can diverge between specimens, measuring 10 to 60 mm.

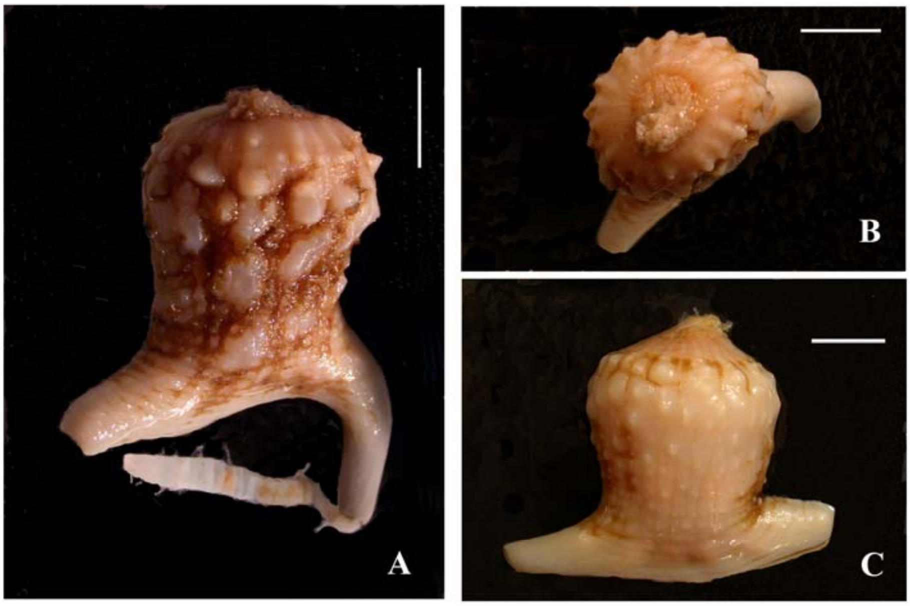

Figure 11.1.– *Actinauge abyssorum* (Gravier, 1918). External anatomy [BEIM (3066, 3093)]: A) Lateral view of a “rough” morphotype; B) Oral view; C) Lateral view of a “smooth” morphotype. Scales: A, 10 mm; B, 10 mm; C, 10 mm.

Column firm, usually with a stretched shape if attached to stick-like objects but depending on the way the animal is clasped to the substratum,. The column height varies between 18 to 45 mm. The structure of the column is variable, although the observed specimens have 24 longitudinal furrows and a varying number of transversal furrows creating regular squares on the surface of the column. This feature is more evident in animals with cuticle debris adhering to the furrows.

Scapus with tubercles extremely variable both in form and size; however there are always 24 medium-sized tubercles surrounding the scapulus; with a dark brown chitinous cuticle, easily deciduous. Scapulus clearly differentiated from scapus by the different shade of colour, even when cuticle is lacking. Despite the wide morphological variability observed in this collection, it can be simplified to two distinct morphotypes: one usually of larger size, with large round tubercles and a dark chitinous cuticle, and the other smaller, with a rather smooth pale white appearance because it is almost devoid of cuticle. However transitional forms involving the two morphs are also present. The oral disc was not observed in expanded state; in preserved material the diameter can reach 0.8 to 2.5 cm. The tentacles are contracted in preserved specimens, although approximately 96 tentacles could be observed.

Internal anatomy (Fig. 11.2).— Four cycles of mesenteries. Similar number of mesenteries at distal and proximal part. Only first cycle of mesenteries is perfect and sterile. The second cycle has six pairs of fertile mesenteries carrying gametogenic tissue; cnidoglandular tract of trilobate filaments carrying batteries of nematocysts; one pair of the third cycle also carrying gametogenic tissue. Mesenteries of the third and fourth cycles are complete but poorly developed, forming merely tiny ridges along the internal side of the body wall.

Mesoglea of the body wall thick and tough, somewhat thicker in scapulus, containing a large mesogleal sphincter. Musculature of the mesogleal sphincter strong and reticular. Retractors are diffuse and poorly developed. Parietobasilar muscles are diffuse. Basilar muscles are well developed and diffuse. Numerous acontia without spiral form. Tentacles without basal mesogleal thickness.

Cnidom (Fig. 11.3; Table 11).— Spirocyst, basitrichs, and *p*-mastigophores.

Geographic and bathymetric distribution

The general distribution of *A. abyssorum* is mainly in the North and Northwest Atlantic; it was found on the French and Iberian deep sea abyssal plains, between 4400 and 5200 m depth (Riemann-Zürneck, 1986b). Riemann-Zürneck also refers one specimen found in Venezuela margin, but recommends caition because of the uncertainty of its taxonomic status. Another contribution was the note of Doumenc (1975) who found *A. abyssorum* on the Mid-Atlantic Ridge, at 2900 m depth. The specimens available for this study were collected in the Porcupine Abyssal Plain (North Eastern Atlantic), between 4806 and 4842 m.

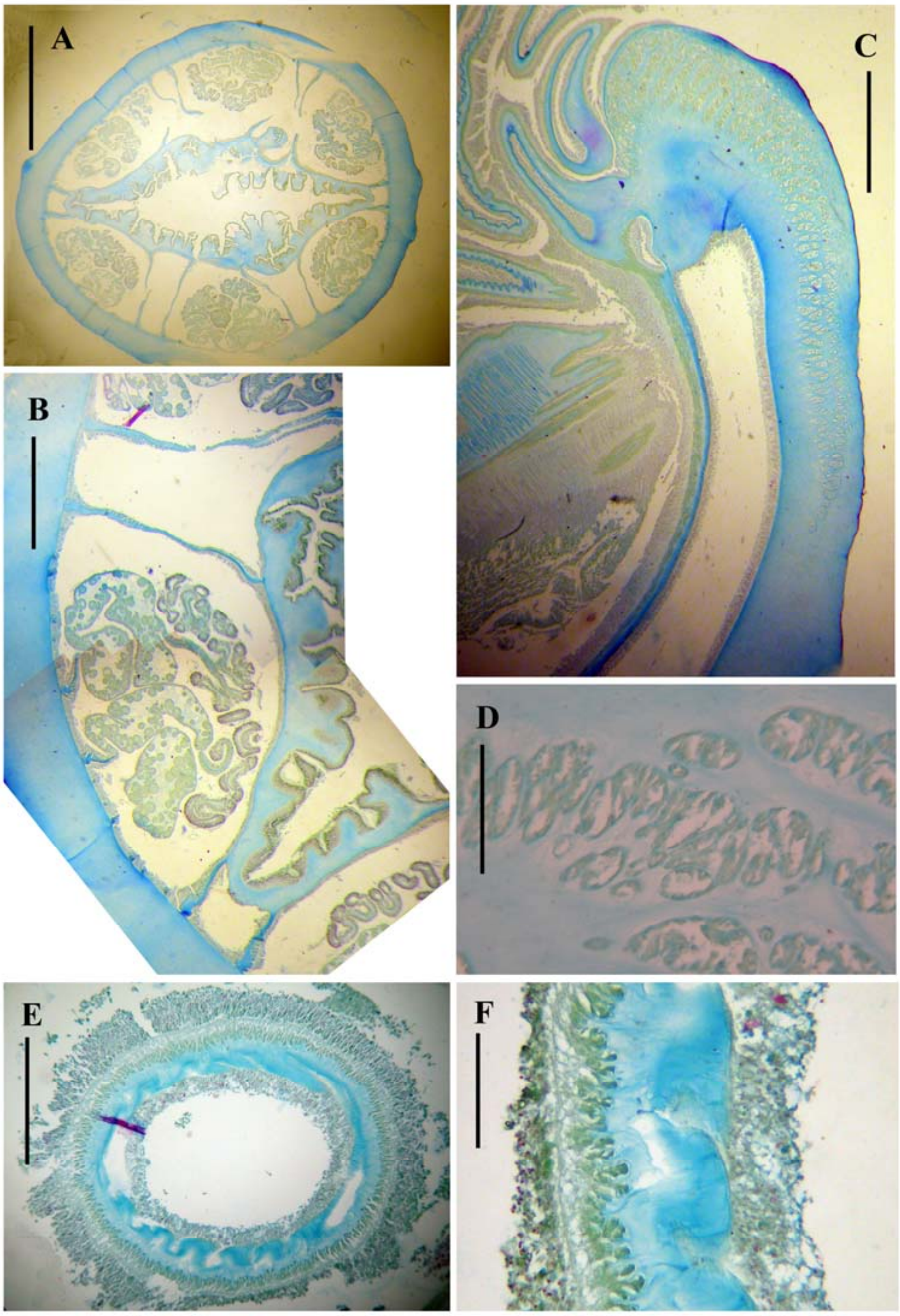

Figure 11.2.– *Actinauge abyssorum* (Gravier, 1918). Internal anatomy [BEIM (3093)]: A) Transversal section, 4 cycles of mesenteries; two siphonoglyphs and directives, 2nd cycle fertile; B) Transversal section detail showing 3rd and 4th cycles of microcnemes C) Longitudinal section of marginal distal column showing the mesogleal sphincter; D) Sphincter detail, alveolar; E) Tentacle transversal section; G) Tentacle detail. Scales: A, 15 mm; B, 5 mm; C, 5 mm; D, 0.1 mm; E, 0.5 mm; F, 0.1 mm.

Table 11.– Cnidae of *Actinauge abyssorum* (Gravier, 1918). Specimens: [BEIM (3066, 3093)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic.

Category	Fig. 11.3	Range of length and width of capsules in µm	X ± SD	S	N	F	*A. abyssorum* sensu Carlgren, 1934	*A. abyssorum* sensu Riemann-Zürneck (1986)	*A. longicornis* data by Riemann-Zürneck (1973)	*A. cristata* Riemann-Zürneck, 1986
COLUMN										
Basitrichs 1	A	(10-18.1) x (2-2.5)	14.2 ±1.5 x 2 ±0.5	3/3	60	+	–	11.5-14.5 x 2-2.5	9.1-13 x 1-1.5	10-13 x 1.5-2
Basitrichs 2	B	(25-36.4) x (3.5-4.5)	30 ±2.38 x 4 ±0.22	3/3	60	++	–	26-30.5 x 3.5-4	13-19.5 x 2.5-3	19-22 x 3.5
Mic. *p*-mastigophores	C	(30.3-43.4) x (4-6)	35.6 ±2.49 x 5 ±0.39	3/3	60	---	–	31-36 x 4.5-5	18-28.6 x 3-3.5	22-28 x 4-5
TENTACLES										
Spirocysts	D	(32.3-78) x (4-11)	52.4 ±12.8 x 7 ±2.1	3/3	60	+++	31 x 3 – 77 x 8-10	72 x 10 (max. size)	32-42 x 5-7	52 x 8.5
Basitrichs 1	E	(13.1-22.2) x (2-3)	18.7 ±1.66 x 2.36 ±0.3	3/3	60	+/++	–	18 x 2 (rare)	9.1-18.2 x 1-1.5	13-16 x 1.5-2
Basitrichs 2	F	(32.3-47.5) x (3-4.5)	40 ±3.3 x 3.6 ±0.33	3/3	60	++	30-46 x 2.5-3 (3.5)	32-45 x 4-4.5	19.5-29.9 x 3-3.5	29-33.5 x 3-3.5
Mic *p*-mastigophores	G	(33.3-48.5) x (4-6)	38.5 ±2.7 x 5.3 ±0.59	3/3	60	---/+	(29) 31-42 x 4-4.5	32-42 x 4-5	–	–
PHARYNX										
Basitrichs 1	H	(17.2-25.3) x (2-3)	21.6 ±2 x 2.4 ±0.3	2/3	40	---		20-23 x 2.5-3	10.4-18.2 x 1-1.5	16-17.5 x 2-2.5
Basitrichs 2	I	(33.3-44.5) x (3.5-4.5)	37.3 ±2.7 x 4 ±0.22	3/3	60	+/++	31-37 x 3	35-41 x 3.5	22.1-39 x 3-4	35-40.5 x 3.5
Mic. *p*-mastigophores	J	(29.3-41.4) x (4-6)	34.8 ±3 x 4.75 ±0.5	3/3	60	++	26-36 x 4-4.5	35-38 x 4-4.5	16.9-28.6 x 3	27-32 x 3.5-4.5
FILAMENTS										
Basitrichs 1	K	(16-26.3) x (2-3)	21 ±2.5 x 2.5 ±0.28	3/3	60	+/++	–	17.5-20.5 x 2.5	7.8 x 18.2 x 1-1.5	10-19 x 2-2.5
Basitrichs 2	L	(38.4-46.5) x (3.5-4)	42.1 ±2 x 3.8 ±0.25	3/3	60	+/++	–	38-40.5 x 3-3.5	26-33.8 x 3-4	29-32 x 4-4.5
Mic. *p*-mastigophores	M	(25.3-39.4) x (4-6)	32.3 ±3.1 x 5 ±0.59	3/3	60	++	–	29-35 x 3.5-4.5	16.9-24.7 x 3	–
ACONTIA										
Basitrichs 1	N	(18.2-27.3) x (2-3)	22.4 ±2 x 2.6 ±0.3	3/3	60	+	–	20.5-24.5 x 2-2.5	10.4-19.5 x 1-1.5	17.5-22.5 x 2-2.5
Basitrichs 2	O	(34.3-49.5) x (3.5-4.5)	42.8 ±3.2 x 4 ±2.2	3/3	60	+++	34-43 x 3-3.5	38-43.5 x 3.5-4	26-37.7 x 3-4	38-42.5 x 3.5-4

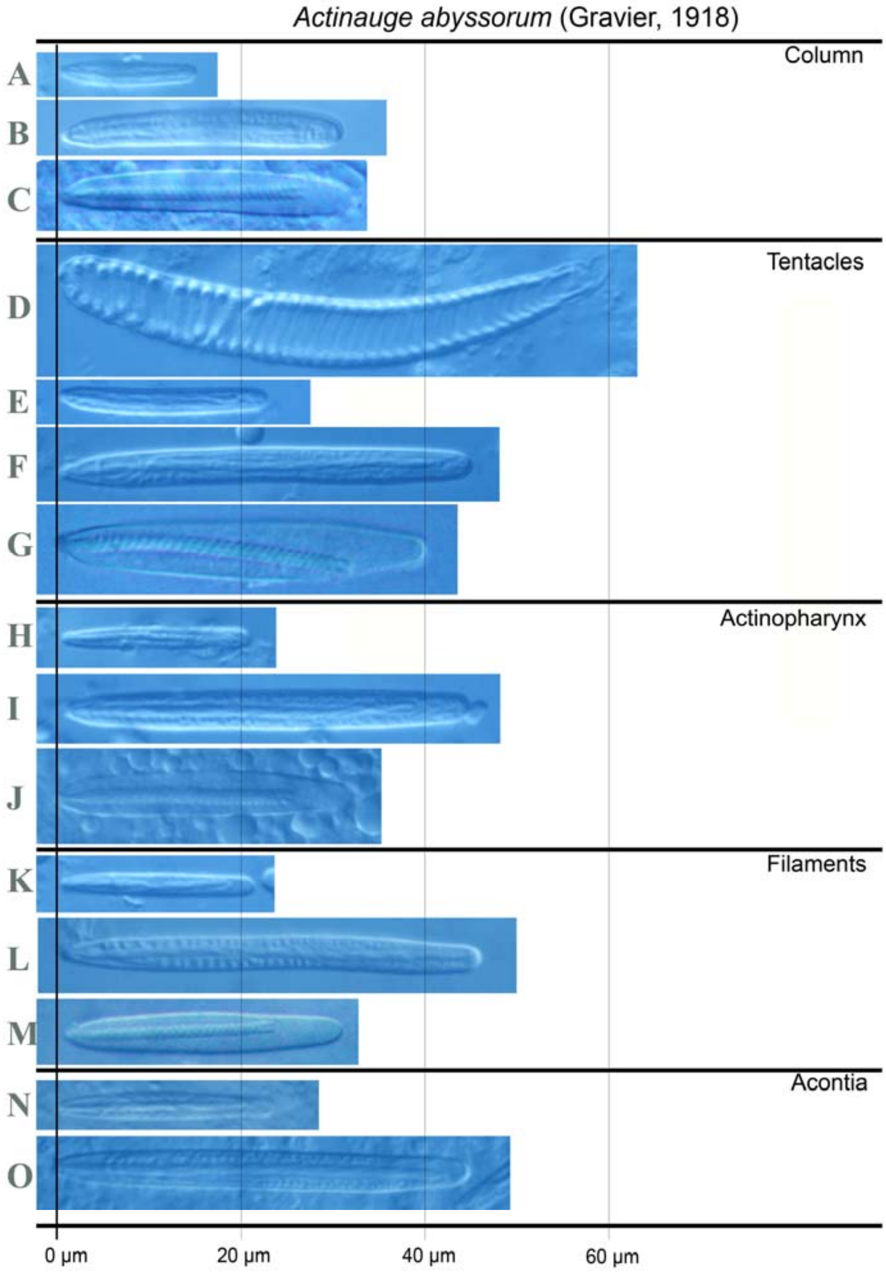

Figure 11.3.– *Actinauge abyssorum* (Gravier, 1918). Cnidae: A) basitrich 1; B) basitrich 2; C) microbasic *p*-mastigophore; D) spirocyst; E) basitrich; F) basitrich; G) *p*-mastigophore; H) basitrich; I) microbasic *p*-mastigophore; J) microbasic *p*-mastigophore; K) basitrich; L) basitrich; M) microbasic *p*-mastigophore; N) basitrich; O) basitrich.

Discussion

The original description of *Chitonanthus abyssorum* Gravier, 1918, mainly concerning the external anatomical appearance of the characteristic corona of tubercles and the pedal disc embracing tubes of polychaetes, is very close to the observations of the specimens collected during the BENGAL program. Also the external/internal anatomy and cnidom agrees with the description of *Actinauge abyssorum* sensu Riemann-Zürneck (1986b).

Although this species seems to be morphologically well known, its taxonomic position among the other hormathids is still unstable, and remains unsolved. According to the reviewed literature, the diagnostic characters of the species currently included in the genus *Actinauge* are not always clearly delimited. All this uncertainty produced erroneous citations in the past of similar species with wide distribution, and it has hidden the existence of other biological species through out decades.

The specific binomial combination *Actinauge abyssorum* was first given by Carlgren (1934) for two specimens collected from the Iberian abyss (45º26'N, 9º20'W at 4700m). According to Carlgren's description, this material seems different from *Chitonanthus abyssorum* Gravier, 1918 and *Actinauge abyssorum* sensu Riemann-Zürneck, 1986. Carlgren refers that such material agrees in appearance with *Actinauge verrilli* McMurrich, 1893: pedal disc deeply excavated, enclosing a stone; tentacles with distinct mesogleal thickenings at the aboral base (although not very pronounced). However, it is distinguished by the large size of the nematocysts.

For a long time, *A. verrillii* was cited in the North Hemisphere but with a wide distribution including the South Eastern Pacific (see McMurrich, 1893; Carlgren, 1933; Riemann-Zürneck, 1973). Dunn (1983) demonstrated that South Hemisphere specimens should retain the name *A. verrilli*, whereas the North Atlantic material was assigned to a different species, *A. cristata* Riemann-Zürneck, 1986.

Consequently, besides *Actinauge abyssorum*, three other *Actinauge* species are present in the North Atlantic: *A. longicornis, A. cristata* and *A. richardi.* However, the basic morphologic differences between them remain difficult to elucidate. Nevertheless, according to Carlgren (1942) and Riemann-Zürneck (1973 and 1986), *A. longicornis* differs by its weak cuticle and lack of the typical coronial tubercles; *A. cristata* differs from *A. richardi* mostly in the cnidom equipment, such as the presence of large microbasic *p*-mastigophores on the filament and a second category of basitrichs in the acontia (Carlgren also found a small basitrich [10x1.5-2µm] in *A. richardi*, contrarily to all other authors). Besides this, *A. abyssorum* differs from other congeners by the unusually large size of cnidae and the presence of microbasic *p*-mastigophores in their tentacles (see, for comparisons: Table 10 and Table 11).

The only *Actinauge* species with microbasic *p*-mastigophores in their tentacles are *Actinauge verrilli* McMurrich, 1893 (cnidae data in Rodríguez, 2007, not published), and *Actinauge abyssorum* sensu Carlgren, 1934 ("penicili", see for comparison Table 11).

One of the most interesting aspects of *A. abyssorum* is the fact that this species differs from all its congeners by the absence of thickenings in the tentacles aboral base (which does not agree with the genus diagnosis), it never forms a cup-shaped base enclosing sand (listed as one of the diagnostic characters in the genus), and microbasic *p*-mastigophores are present in the tentacles (a feature which is quite uncommon in the family Hormathiidae). These characters do not support the inclusion of this species in the genus *Actinauge*. Riemann-Zürneck (1986) introduced variability in the description of the genus *Actinauge*, but did not solved the question of the identity of *A. abyssorum* sensu Carlgren (1934), creating an homonymy. Also, Doumenc (1975) cited *A. abyssorum* Carlgren, 1934 (with material from "Noratlante" stations) with an Azorean distribution.

As *Chitonanthus* McMurrich, 1893 is actually a synonym of *Hormathia*, one solution might be a combination such as *Hormathia abyssorum*, keeping also the first author name (Gravier, 1918). This was already proposed by Stephenson (1918). However, none of the *Hormathia* species has microbasic *p*-mastigophores on tentacles. So, this action also introduces variability in the genus.

The generic placement of this species (either in *Actinauge* or *Hormathia*) is controversial and should be solved in the near future to ensure the taxonomic stability of the generic units involved. Further detailed studies, such as molecular analysis concerning the genetic variability of this and related species are also recommended. At the moment, the species name should be retained instead of making modifications on genera diagnoses without more plausible data.

Genus *Caracolactis* gen. nov.

Diagnosis

Hormathiidae with well developed pedal disc often elongated in the transversal plan. Flattened, broader than the column and oral disc diameter. Column divided in scapus and scapulus. Scapus with cuticle and tubercles not clearly arranged in longitudinal rows, scattered, varying in dimension, with denticulate aspect. Sphincter well developed, mesogleal reticular. Tentacles about 100 in number; short and conical, with mesogleal thickenings at the base on their outer sides. Longitudinal muscles of the tentacles ectodermal. 1-2 siphonoglyphs. Four cycles of mesenteries, some times irregularly arranged. 12 perfect pairs of mesenteries at the uppermost part of the actinopharynx. More mesenteries distally than proximally. No cinclides. Retractor and parietobasilar muscles weak. Asexual reproduction by basal laceration. Acontia few. Cnidom: spirocysts, basitrichs and microbasic *p*-mastigophores.

Etymology

The genus is named after the cruise where the type material was collected.

Caracolactis maternalis sp. nov.

(Fig. 12.1-12.3; Table 12)

Material examined

CARACOLE: PL 129-07 (12 specimens)

Etymology

The specific epithet *maternalis,* from Latin *māternus* "maternal, of a mother," from *māter* "mother". Pertaining to a mother and having the characteristics of a mother because of the evidence of asexual reproduction by basal laceration.

Description

External anatomy (Fig. 12.1).— Pedal disc broader than the cylindrical column, prolonged in transverse plan of the body and clasping dense stalks of the octocoral *Acanella arbuscula*. Very enlarged base (the larger specimen with 4 cm), much larger in area than the oral disc, distended and embracing the octocoral. Specimens near all together with their lateral basal lobes coming into contact with each other. Body small and soft. Diameter of the oral disc 1-2cm, and column almost 2cm height. Scapus provided with a thin cuticle, in its upper part, especially on the tubercles. Arrangement of the tubercles somewhat scattered, varying in number and dimension (according to the contraction and height of each specimen). Slight tendency to an arrangement in longitudinal rows, but never structured in straight furrows. Oral disc open, circular, slightly contracted in some specimens. Tentacles conical, short, and probably more numerous than mesenteries, hexamerously arranged in four cycles.

Asexual reproduction by basal laceration was observed; one small propagule extended from the base of a single individual. Possibly all specimens were originated asexually because they are all connected by their bases.

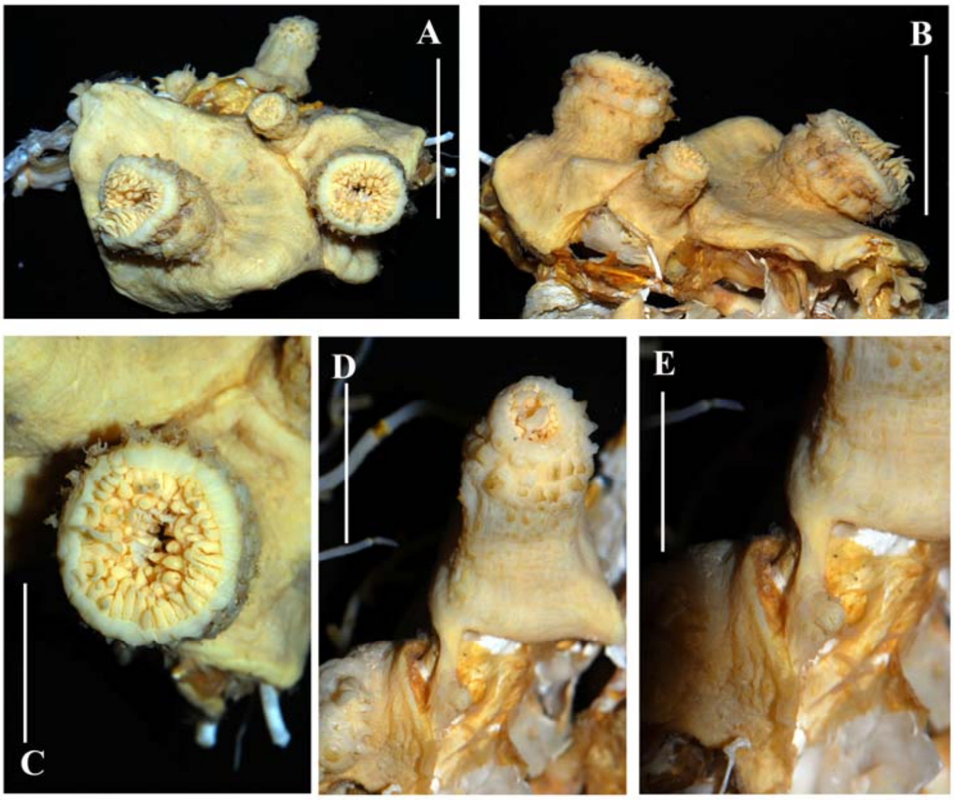

Figure 12.1.– *Caracolactis maternalis* sp. nov. External anatomy [PL 129-07]: A) Colony attached to *Acanella arbuscula*, B) Lateral view, pedal disc distended embracing the octocoral, C) Oral view showing tentacles, D) Small specimen showing irregular tubercles E) Detail showing asexual reproduction by basal laceration. Scale: A, 4cm; B, 3cm; C, 2cm; D, 2cm; E, 1cm.

Internal anatomy (Fig. 12.2).— 4 cycles of mesenteries, last cycle incomplete. 12 pairs (or more) perfect mesenteries. First cycle perfect, second cycle perfect at the uppermost part of the actinopharynx. One siphonoglyph. Mesenteries at the limbus fewer than at the margin. Arrangement at proximal level irregular, 7 perfect pairs and one pair of which one mesentery is perfect and its partner imperfect (Fig. 12.2.- F). Second and some mesenteries of the third cycle with trilobate filaments. Retractor musculature weak diffuse. Parietobasilar muscles very weak and diffuse. Basilar muscles poorly developed and diffuse. Sphincter mesogleal well developed, reticular. Transversally stratified, filling up most of the breath of the mesoglea. Longitudinal musculature ofe tentacles ectodermal. No cinclides observed. Acontia few. It was not possible to appreciate gametogenic tissue. Asexual reproduction.

Cnidom (Fig. 12.3; Table 12).— Spirocyst, basitrichs, and *p*-mastigophores.

Colour.— pale white.

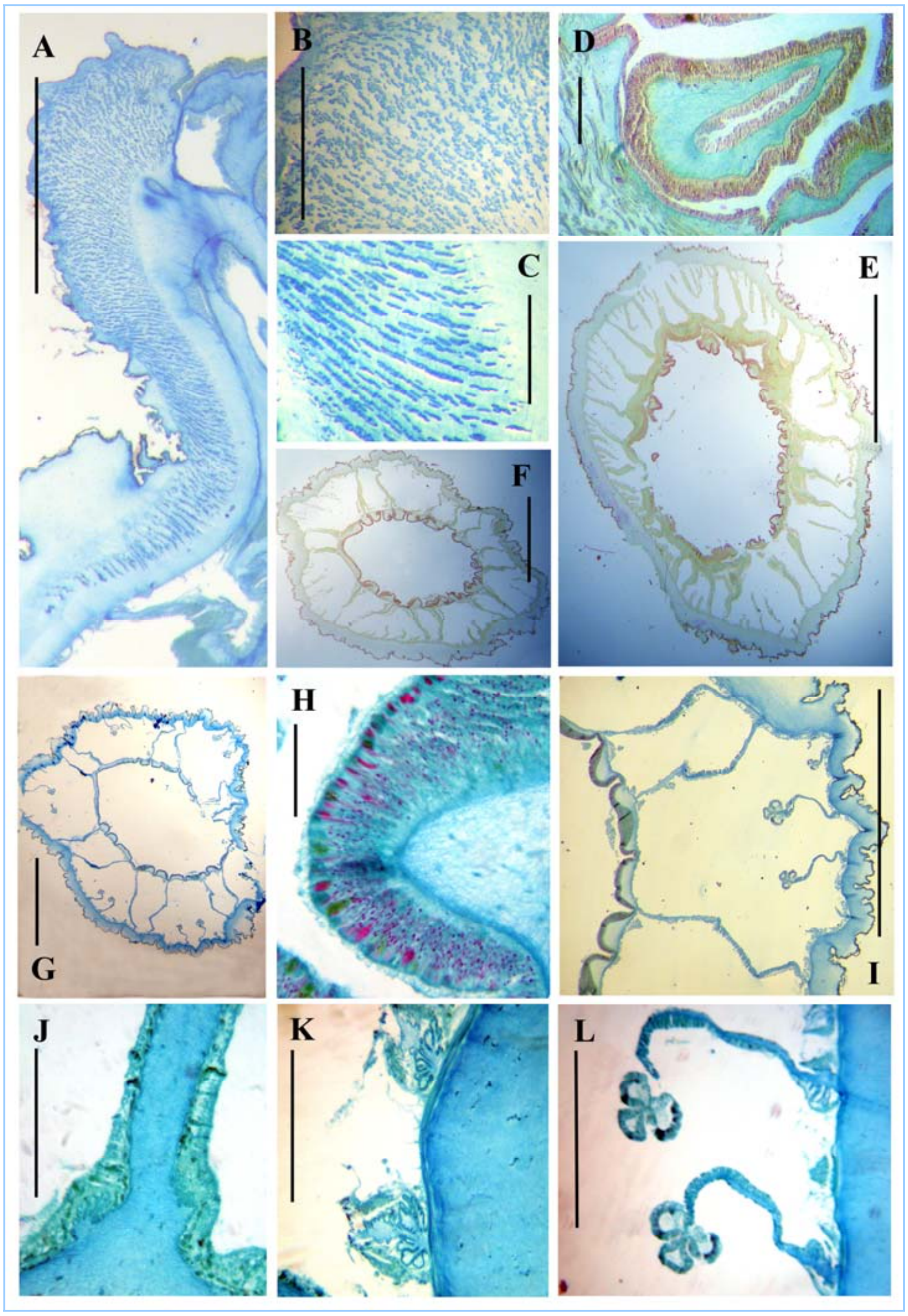

Figure 12.2.– *Caracolactis maternalis* sp. nov. Internal anatomy [PL 129-07]: A) Longitudinal section of the distal part of the column showing the sphincter, B) Detail of sphincter at higher part; C) Detail of sphincter at lower part; D) Transversal section of tentacle showing ectodermal musculature and aboral thickenings; E) Transversal section of the body at actinopharynx level (1st and 2nd cycles perfect), F) Transversal section showing three cycles of mesenteries; G) Transversal section three cycles of mesenteries, one siphonoglyph; H) Actinopharynx detail with nematocyst spots; I) Detail of 1st and 2nd cycles at proximal part; J) Longitudinal section of the pedal disc showing the basilar musculature; K) Pair of microcnemes from the 4th cycle with weak parietobasilar muscles; L) Detail of 2nd cycle showing trilobate filaments, weak retractors and parietobasilar muscles. Scales: A, 8.5 mm; B, 4 mm; C, 2 mm; D, 2.5 mm; E, 4 mm; F, 4.5 mm; G, 3 mm; H, 0.04 mm; I, 3 mm; J, 0.1 mm; K, 0.2 mm; L, 0.7 mm.

Table 12.– Cnidae of *Caracolactis maternalis* sp. nov. Specimens: [PL 129-07]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic. (*) Average based on measures of less than 40 capsules, which is considered the meaningful minimum (Williams, 1996; 1998).

Category	Fig. 12.3	Range of length and width of capsules in µm	X ± SD	S	N	F	Data from Actinauge richardi in Carlgren, 1941
PEDAL DISC							
Basitrichs	No image	(17-29) x (2.5-3)	21 ± 2.2x 3±0.1	3/3	60	++	–
COLUMN							
Basitrichs 1	No image	(9-11) x (1.5)	9.4±0.8 x 1.5±0.0(*)	2/3	7	---	–
Basitrichs 2	A	(16-19) x (3)	17.25±1.0 x 1.0±0.0(*)	2/3	8	---	–
TENTACLES							
Spirocysts	B	(20-53) x (2.5-8.5)	37.3±5.8 x 5.4±1.4	3/3	60	+++	36 x 5.5
Basitrichs 1	No image	(12-17) x (1.5-2)	14.2±1.2 x 1.6 ±0.2(*)	3/3	13	---	11.3x1.5-2 (rare)
Basitrichs 2	C	(21.5-36) x (2-3.5)	28.2 ±2.6 x 2.7±0.3	3/3	60	+++	18.3-26.8 x 2.5-2.8
PHARYNX							
Basitrichs 1	D	(12-17) x (1.5-2)	14.2 ±1.2 x 1.6±0.2	3/3	40	+	
Basitrichs 2	E	(22-34.5) (2.5-3.5)	27.2±2.3 x 2.9±0.2	3/3	59	++	22-36 x 2.8-4
Mic. p-mastigophores	F	(18-26) x (3-4)	22.3± 1.9x 3.4±0.4	3/3	46	+	19.7 x 3 (rare)
FILAMENTS							
Basitrichs	G	(10-18) x (1.5-2)	14.4±1.5 x 1.8±0.2	3/3	60	+++	10-11.3 x 1.5-2
Mic. p-mastigophores	H	(20-25) x (3-4)	22.3± 1.3x 3.1±0.3	2/3	40	+/-	16.2-20 x 3-4.2
ACONTIA							
Basitrichs	I	(29-37) x (2.5-3)	31.5 ±1.4 x 2.9±0.2	3/3	60	+++	24-34 x 3-3.5

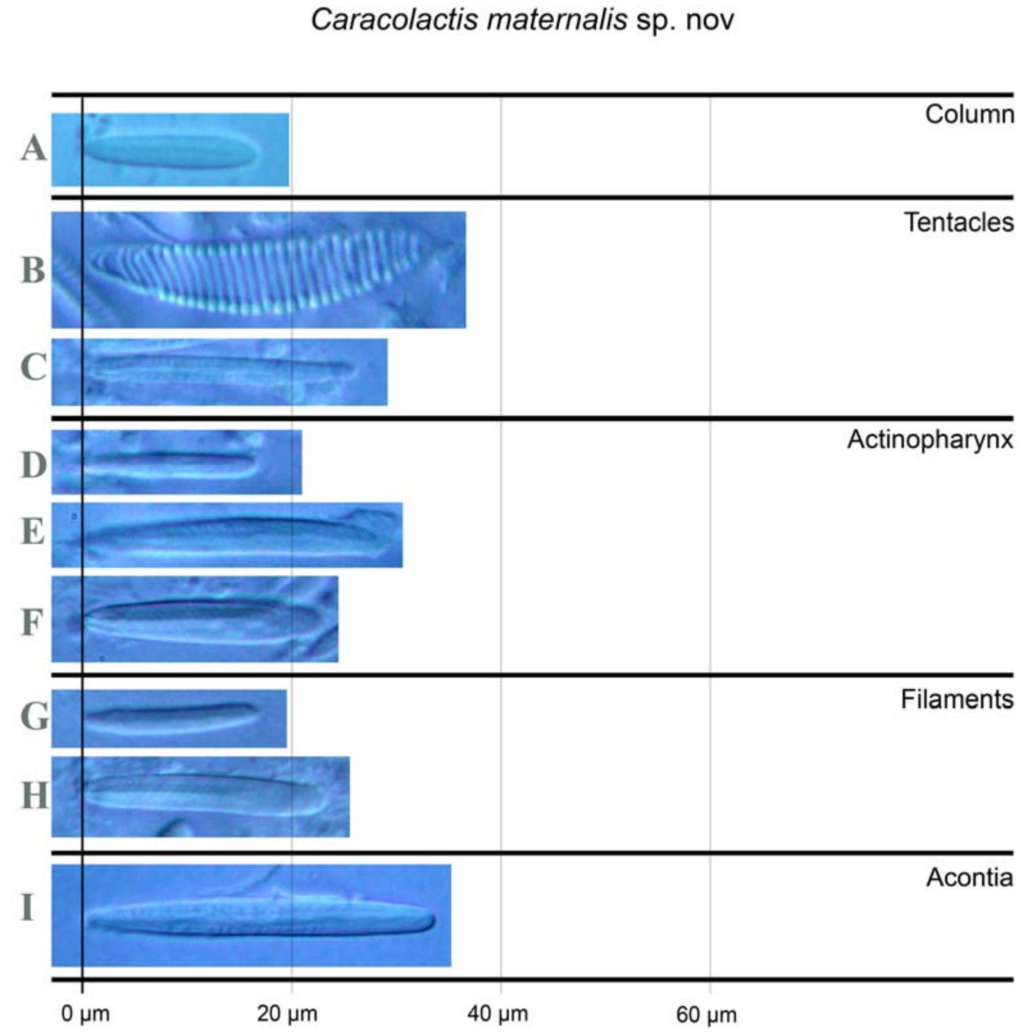

Figure 12.3.– *Caracolactis maternalis* sp. nov. Cnidae: A) basitrich 2; B) spirocyst; C) basitrich 2; D) basitrich 1; E) basitrich 2; F) microbasic *p*-mastigophore; G) basitrich; H) microbasic *p*-mastigophore; I) basitrich.

Geographic and bathymetric distribution

These organisms were found by the IFREMER expedition, during CARACOLE cruise in the Rockall bank station R1. This station is located at the position 53º 46'N and 15º55W, at 777m depth (see appendix 1.A). This location is characterised by the occurrence of deep-sea cold water coral reefs of *Lophelia pertusa* .

Discussion

Frequently, the diagnosis of some genus are totally based on the description of the type species, and other species have to follow the same distinguishable characters in order to be included in the genus. The family Hormathiidae emcompasses 16 genera, in which most of the species present a great variability of the column and pedal disc. This makes their determination difficult, and consequently the number of synonyms and *incertae sedis* species is high (Stephenson, 1918; Riemann-Zürneck, 1986). On the other hand, five other genus of the family contain only one species. Following Carlgren (1949), the main differences between groups of hormathids are the number of perfect mesenteries (6 or 12), the number of mesenteries proximally and distally, and the presence or absence of gametogenic tissue on perfect mesenteries (and if they are fertile or sterile). In the case of these specimens, the last assumption is very difficult to apply, because asexual reproduction was observed in one specimen; some kind of laceration of the base created a propagule and all individuals seem to have an asexual origin once their bases are all joined together. Probably, most of these specimens are juveniles and we cannot assure if they reproduce sexually and which mesenteries are fertile. If we ignore this sentence, the presence of 12 perfect mesenteries at the uppermost part of these specimens allows us to allocate them to the *Chondrophellia-Amphianthus-Stephanauge* group (see 92 pp, Carlgren, 1949). However, they differ from *Chondrophellia* because they do not have corona, neither only six pairs of perfect mesenteries; they differ from *Amphianthus* because they have more mesenteries distally than proximally and cinclides were not detected in any part of the body; and they differ from *Stephanauge* because the column is not smooth and the pedal disc is not prolonged in the transversal axis circling only one stem. The analysed specimen has four cycles of mesenteries, has prominent scapular tubercles never arranged in structural furrows, and the pedal disc is very enlarged, not filled with mud or stones, but covering the octocoral in an unusual adherent type. Maybe these facts are sufficient to create a new genus for this species. However, in Carlgren's classification system the pedal disc and the column contraction are not good characters due to their high variability. However, the number of mesenteries, their irregular arrangement and also the presence of only one siphonoglyph are probably irregular features due to the asexual propagation. The same questions were promoted by Carlgren in 1925, differentiating the amphiantiids from *Stephanauge* and *Actinauge* genera.

In addition, the nematocysts equipment of the analysed specimens is very different from *Chondrophellia-Amphianthus-Stephanauge* group of species and much closer to *Actinauge* species. Nevertheless, Stephenson (1918) stated that the reproduction of the *Actinauge* species is absolutely sexual, and also they present only six pairs of perfect mesenteries, they have the same number of mesenteries distally and proximally and they present 12 coronal tubercles merging into ridges of the scapulus.

Instead of modifying the classification of the family Hormathiidae done by Carlgren (1949), or making genus adaptations it is better to wait for molecular studies, to obtain more information on the similarities between these groups of genus/species. At this state of knowledge we think it is preferable to create a new genus than to discuss the importance of the characters which are higher ranking.

Genus *Amphianthus* Hertwig, 1882

Diagnosis (adapted from Carlgren, 1949)

Hormathiidae with the pedal disc often prolonged in the transverse plan and clasping branches of octocorals, sponges or other objects. Column rather low, mostly thick, sometimes smooth, sometimes provided with small tubercles, commonly arranged in more or less distinct longitudinal rows. Cinclides very variable in number, indistinct or absent. At least six pairs (often more) of perfect and fertile mesenteries. Considerably more mesenteries at the base than at the margin. Retractors of the mesenteries weak. Asexual and sexual reproduction.

Type species

Amphianthus bathybium (Hertwig, 1882)

Species included in the genus

Amphianthus dohrnii (Koch, 1878); *Amphianthus bathybium* Hertwig, 1882; *Amphianthus minutus* (Hertwig, 1882); *Amphianthus mirabilis* (Verrill, 1879) *nomen dubium* according to Andres, 1883; *Amphianthus margaritaceus* (Danielssen, 1890); *Amphianthus mopseae* (Danielssen, 1890); *Amphianthus lacteus* (McMurrich, 1893); *Amphianthus caribaea* (Verrill, 1899); *Amphianthus nitidus* (Verrill, 1899); *Amphianthus rosaceus* Wassilieff, 1908; *Amphianthus brunneus* (Pax, 1909); *Amphianthus armatus* Carlgren, 1928; *Amphianthus capensis* Carlgren, 1928; *Amphianthus radiatus* Carlgren, 1928; *Amphianthus valdiviae* Carlgren, 1928; *Amphianthus michaelsarsi* Carlgren, 1934; *Amphianthus californicus* Carlgren, 1936; *Amphianthus laevis* Carlgren, 1938; *Amphianthus natalensis* Carlgren, 1938; *Amphianthus sanctaehelenae* Carlgren, 1941; *Amphianthus ingolfi* Carlgren, 1942; *Amphianthus islandicus* Carlgren, 1942; *Amphianthus norvegicus* Carlgren, 1942; *Amphianthus verruculatus* Carlgren, 1942.

Amphianthus bathybium (Hertwig, 1882)

(Figs. 13.1-13.3; Table 13)

Material examined

BENGAL 2: stn. 13078 (6) (BEIM: 3026, 6 specimens); stn. 13078 (11) (BEIM: 3003, 14 specimens) BENGAL 3: stn. 13200 (84) (BEIM: 3111, 6 specimens); stn. 13200 (70) (BEIM: 3118, 10 specimens); stn. 13200 (94) (BEIM: 3077, 2 specimens); stn. 13200 (93) (BEIM: 3061, 31 specimens); stn. 13200 (94) (BEIM: 3072, 59 specimens). BENGAL 5: stn. 13368 (52) (BEIM: 3004, 60 specimens); stn. 13368 (47) (BEIM: 3022, 18 specimens); stn. 13368 (53) (BEIM: 3059, 104 specimens); stn. 13368 (48) (BEIM: 3094, 24 specimens). BENGAL 6: stn. 13627 (11) (BEIM: 3063, 23 specimens); stn. 13627 (24) (BEIM: 3070, 1 specimen); stn. 13627 (24) (BEIM: 3071, 8 specimens).

In total 368 specimens from the Porcupine Abyssal Plain were studied. Four specimens, taken from BENGAL 5 Stn 13368 (52), were used for histological purposes.

Description

External anatomy (Fig. 13.1).— Pedal disc wide, always prolonged in the transversal plane and measures 2.5 to 4.5cm. Firmly attached by its base, rounding a tube of polychaets or spicules of sponges, so that the margins of the pedal disc clasp as one together. Column in the contracted state with a distinct circular wall, to 2.8cm diameter 1.8cm height in preserved and retracted specimens. Presents small and numerous mesogleal papillae, next to the tentacles, arranged in 24 longitudinal rows. Lowest part of the column smooth. Oral disc strongly retracted in all preserved specimens. Approximately 50 tentacles, always contracted, however some of them appears visible in the top of the oral disc.

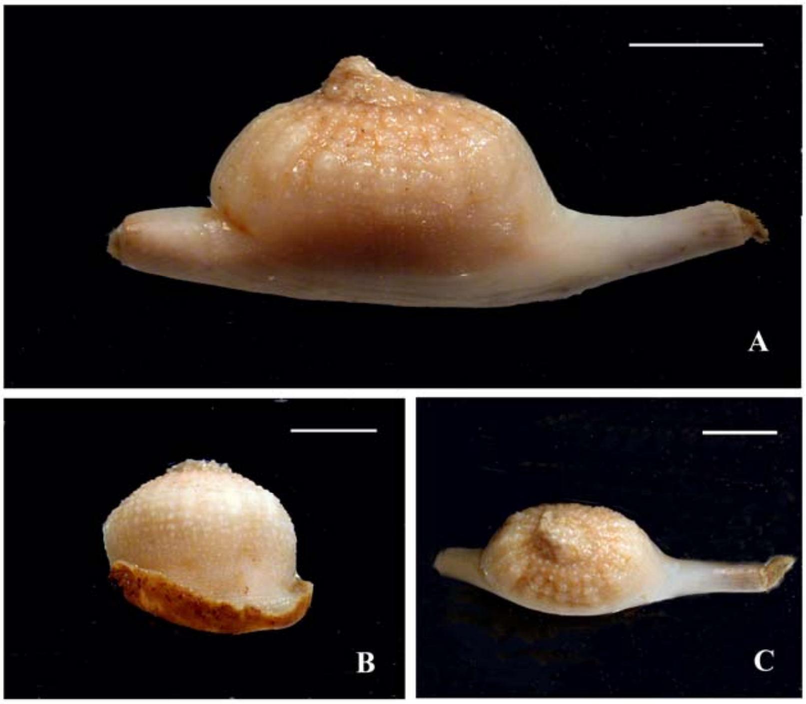

Figure 13.1.– *Amphianthus bathybium* (Hertwig, 1882). External anatomy [BEIM (3004)]: A) Lateral view; B) Ventral view; C) Oral view. Scales: A, 10 mm; B, 10 mm; C, 10 mm.

Internal anatomy (Fig.13.2).— Mesenteries hexamerously arranged in four cycles (6+6+12+24=48 pairs), 96 septa in total. Only the first cycle perfect. Six pairs of perfect mesenteries. Directives connected with two well developed siphonoglyphs, mesoglea and gastrodermis. All cycles (excluding the fourth) carrying gonads and filaments. First cycle also fertile, excluding the directives. Fourth cycle is incomplete, mesenteries are very small and appear at the lower part of the body. Filaments trilobate.

Retractor musculature weak and diffuse. Parietobasilar musculature poorly developed and diffuse. Basilar musculature distinct but also poorly developed.

Sphincter strong, broad, extended over almost the whole breadth of the mesoglea (alveolar).

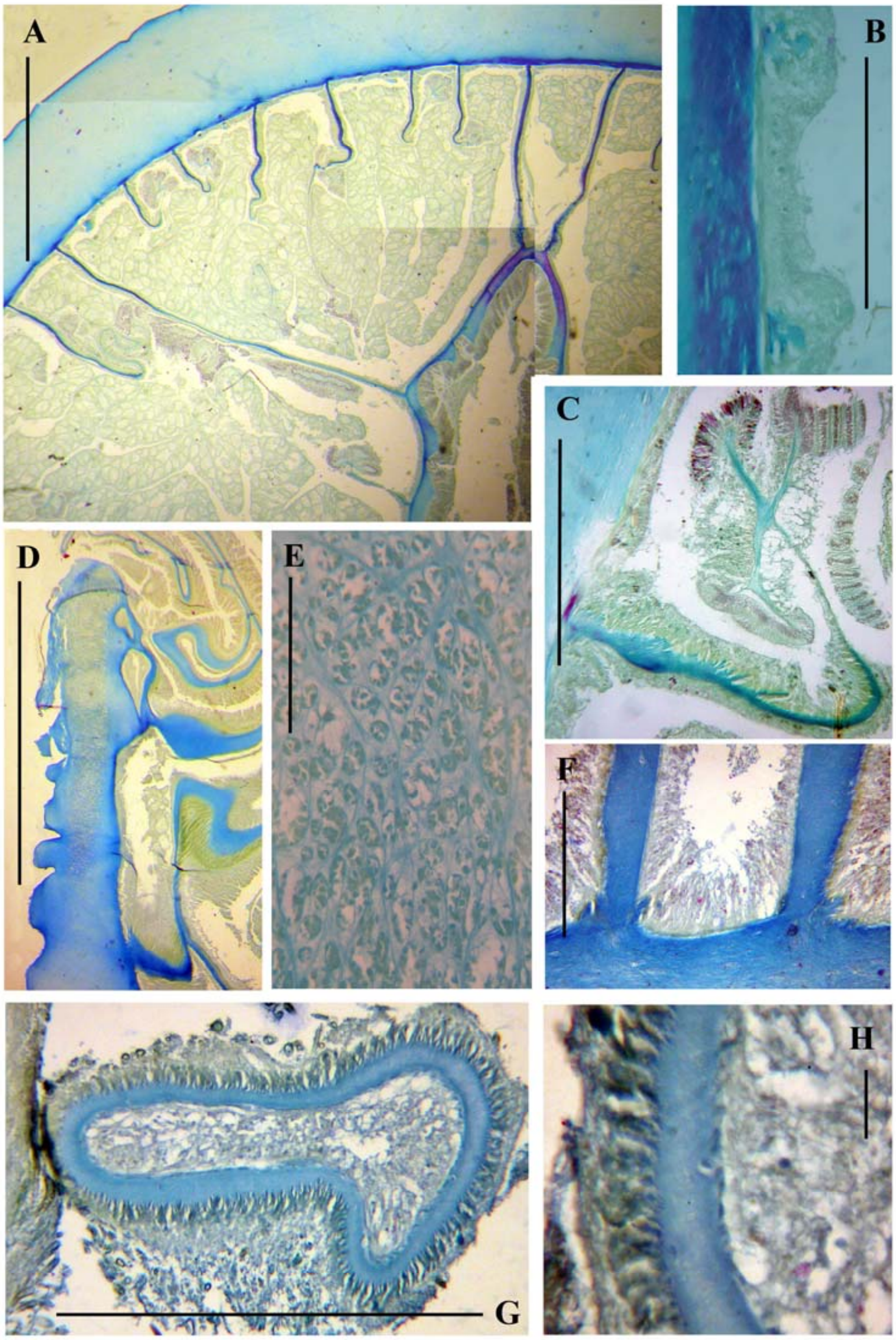

Figure 13.2.– *Amphianthus bathybium* (Hertwig, 1882). Internal anatomy [BEIM (3004)]: A) Transversal section at actinopharynx level showing four mesenteries cycles; B) Detail of microcnemes of 4th cycle; C) Detail of mesentery with trilobate filament; D) Longitudinal section of the column distal part showing mesogleal sphincter ; E) detail of alveolar sphincter; F) Longitudinal section of pedal disc showing basilar musculature; G) Transversal section of a tentacle; H) Tentacle detail showing ectodermal musculature. Scales: A, 24mm; B, 2.5mm; C, 4.5mm; D, 35mm; E, 0.9mm; F, 2.5mm; G, 6mm; H, 1mm.

Table 13.– Dimensions of cnidae in *Amphianthus bathybium* (Hertwig, 1882). Specimens: (BEIM: 3004). X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic.

Category	Fig. 13.3	Range of length and width of capsules in μm	X ± SD	S	N	F	Data from Riemann-Zürneck, 1987
COLUMN							
Basitrichs	A	(22.2-29.3) x (3.5-5.0)	25.4 ±1.4 x 4.2 ±0.3	3/3	60	+/++	23.5-25 x 3-3.5
Mic p-mastigophores	B	(21.2-28.3) x (4.0-5.5)	25.1 ±1.5 x 4.7 ±0.3	3/3	60	+/++	21-23 x 3.5-4
TENTACLES							
Spirocysts	C, D	(29.2-79.5) x (3.5-11.1)	51.6 ±14 x 6.67 ±2.83	3/3	60	+++	70 x 7-9 (max)
Basitrichs	E	(22.2-33.3) x (3.5-5)	28.15 ±2.4 x 4.4 ±0.45	3/3	60	---/+	22-28 x 3.5
Holotrichs 1	F	(23.2-36.3) x (4.5-9)	30.88 ±2.8 x 6.2 ±0.65	3/3	60	++	29.5-34 x 5-7
Holotrichs 2	–	–	–	–	–	–	35-41 x 3.5-4 (only in 2 sp.)
Mic p-mastigophores	G	(20.2-29.3) x (3.5-6)	24.1 ±2.12 x 4.33 ±0.6	3/3	60	++	20-26 x 3.5
PARYNX							
Basitrichs	H	(24.2-34.3) x (3-5)	29.6 ±2.32 x 3.91 ±0.4	3/3	60	++/+++	27-28.5 x 3
Mic p-mastigophores	I	(24.2-32.3) x (3.5-6)	24.1 ±2.12 x 4.33 ±0.6	3/3	60	+/++	23.5-28 x 3.5
FILAMENTS							
Basitrichs	J	(11.1-16.1) x (2-3)	13.5 ±1.2 x 2.5 ±0.34	3/3	60	---	13-16 x 2
Mic p-mastigophores	K	(23.2-32.3) x (3.5-5.5)	27.9 ±1.9 x 4.43 ±0.4	3/3	60	++	23.5-28 x 3.5
ACONTIA							
Basitrichs 1	L	(13.1-20.2) x (2-3)	15.38 ±1.35 x 2.6 ±0.3	3/3	60	+/++	14.5-19 x 2
Basitrichs 2	M	(39.4-51.5) x (4-5)	45.6 ±2.5 x 4.5 ±0.39	3/3	60	+++	41-48 x 3.5-4

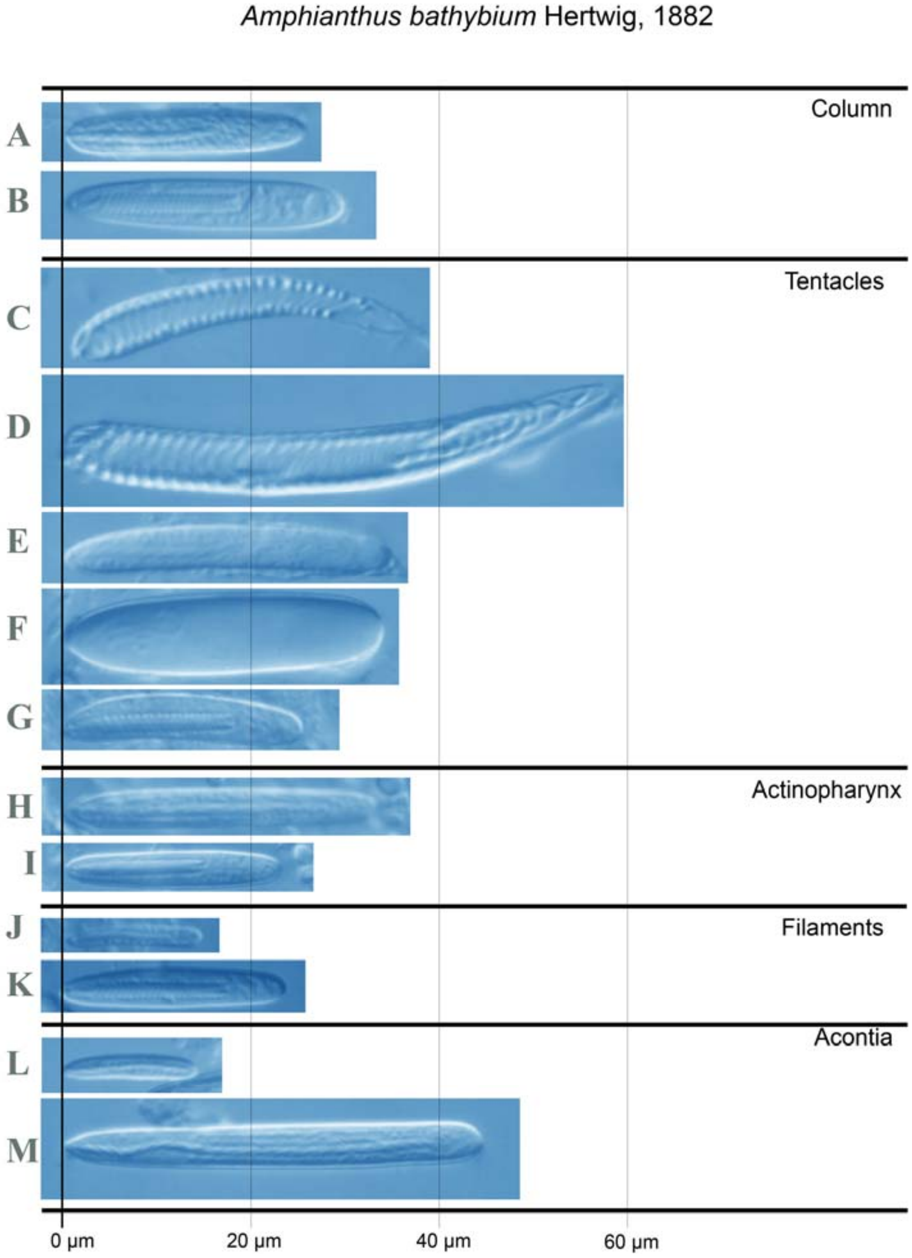

Figure 13.3.– *Amphianthus bathybium* (Hertwig, 1882). Cnidae: A) basitrich; B) microbasic *p*-mastigophore; C) Spirocyst 1; D) Spirocyst 2; E) basitrich; F) Holotrich; G) microbasic *p*-mastigophore; H) basitrich; I) microbasic *p*-mastigophore; J) basitrich; K) microbasic *p*-mastigophore; L) basitrich 1; M) basitrich 2.

Oral disc and tentacles with ectodermal longitudinal musculature. Musculature of tentacles with similar development in aboral and oral sides. Column wall of similar thickness along the entire length. Acontia well developed. No cinclides.

Cnidom (Fig.13.3; Table 13).— A survey of the cnidae is presented: Spirocysts, basitrichs, microbasic *p*-mastigophores and holotrichs.

Colour.— Preserved material has a rose pale white colour and little more darker around the oral disc.

Geographic and bathymetric distribution

Amphianthus bathybium is known for the North West Pacific (35º 41'N 157º 42'E; 35º 22'N-169º53'E) deep sea between 4192-5285m depth (Hertwig, 1888; Carlgren, 1949), and for the North Atlantic on the French and Iberian deep sea (see Meteor 15, Biogas V and VI, Walther Herwig 45 stations) between 3850-5315m depth (Riemann-Zürneck, 1987). All exemplars in this study were collected rather Northern, also in abyssal areas of the Porcupine, between 4839 and 4851m.

Discussion

Genus *Amphianthus* Hertwig, 1882 is very problematic due to the variability of the generic ranking status within their intra and inter-specific characters. Therefore, the 28 nominal species are uncertain.

Amphianthus bathybium Hertwig, 1882 is the type species of the genus and was poorly known until Riemann-Zürneck's (1987) re-description. In this paper it was confirmed that *A. abyssorum* is a synonym of *A. ornatum* Hertwig, 1888.

In the genus *Amphianthus,* cinclides are a systematic rule as stated by Carlgren (1942). However they do not occur in *A. bathybium* which is the type species of the genus. Contrarily to other deep-sea amphiantiids (*A. inornata* (Gravier, 1918), *A. impeditus* (Gravier, 1918), *A. radiatus* Carlgren, 1928 and *A. michaelsarsi* Carlgren, 1934), all possess cinclides (Riemann-Zürneck, 1987). As this character seems to be very variable it is better to exclude it from the generic rank status.

Strong mesenteries carrying gametogenic tissue was present in the observed specimens that therefore did not present asexual reproduction. In opposition to Hertwig and according to Carlgren, 1925 we could see that perfect mesenteries, excluding the directives, are fertile.

Our analysis of the nematocysts equipment agreed fairly well with *A. bathybium* description by Riemann-Zürneck (1987), although this author has noticed a second holotrich from the tentacle in two animals that was not found in our examined specimens.

Possibly during decades, *A. bathybium* was collected without perception of their identity, maybe mixed together with *Actinauge abyssorum*, as these two species share the same habitat and have a similar clasping tubes habit (Riemann-Zürneck, 1986 and 1987).

Genus *Phelliactis* Simon, 1892

Diagnosis (adapted from Carlgren, 1949 and Riemann-Zürneck, 1973)

Hormathiidae with well developed pedal disc. Body often asymmetrical. Arrangement of the column not recognised in scapus and scapulus (often indistinct). Column very thick with tubercules which can be arranged regularly or irregularly, stronger in the margin (except for some individuals with smooth column). Cuticle present, however easily deciduous. Tentacles more than 100 (six cycles), relatively short, with aboral thickness in their base. Mesenteries hexamerously arranged in five cycles, rarely six. Perfect mesenteries: six to 12 pairs (in some cases a few more). Smallest cycle of mesenteries (5th) usually incomplete, these mesenteries in neighbourhood of certain pairs of septa of the third cycle are sometimes missing. Ectodermal musculature of the body wall weak. Longitudinal musculature of the tentacle ectodermal over the aboral side. Sphincter mesogleal usually very weak, alveolar. Arrangement of the gametogenic tissue different, perfect mesenteries always sterile. No asexual reproduction, no parental care. Acontia numerous. Cinclides absent. Nematocysts comparatively large.

Type species

Phelliactis hertwigi Simon, 1892; Syn. *Paraphelliactis* Carlgren (1928), Type: *Paraphelliactis spinosa* Carlgren (1928).

Species included in the genus

Phelliactis hertwigi Simon, 1892; *Phelliactis crassa* (Wassilieff, 1908); *Phelliactis magna* (Wassilieff, 1908); *Phelliactis japonica* (Wassilieff, 1908); *Phelliactis algoaensis* Carlgren, 1928; *Phelliactis robusta* Carlgren, 1928; *Phelliactis siberutiensis* Carlgren, 1928; *Phelliactis somaliensis* Carlgren, 1928; *Phelliactis spinosa* (Carlgren, 1928); *Phelliactis incerta* Carlgren, 1934; *Phelliactis michaelsarsi* (Carlgren, 1934); *Phelliactis capensis* Carlgren, 1938; *Phelliactis gigantea* (Carlgren, 1941); *Phelliactis callicyclus* Riemann-Zürneck, 1973; *Phelliactis americana* Widersten, 1976; *Phelliactis capricornis* Riemann-Zürneck, 1973; *Phelliactis carlgreni* Doumenc, 1975; *Phelliactis lophohelia* Riemann-Zürneck, 1973; *Phelliactis pelophila* Riemann-Zürneck, 1973; *Phelliactis hydrothermala* Sanamyan and Sanamyan, 2007.

Observations

Riemann-Zürneck (1973), found Carlgren's diagnosis of the genus *Phelliactis* very variable in some points and strict in others. She made the revision of the genus *Phelliactis* defending that the diagnosis of Carlgren was limited regarding the exercise of the radial musculature of the oral disc. Instead she developed a new identification key, in which the principal feature to distinguish species (or groups) is the number of perfect mesenteries in the first cycles. However she introduces a new concept on the genus *Phelliactis* finding "aberrant" species with 12 pairs of perfect mesenteries, and in some cases more (*P. capricornis*). This suggests that *Phelliactis* should be excluded from the Hormathiidae group I (in controversy with the statement "usually six pairs of perfect mesenteries, sometimes more, but they are never numerous") and the Hormathiidae key should be restructured and updated.

Riemann-Zürneck (1973) described four new species (*P. callicyclus*, *P. capricornis*, *P. lophohelia*, *P. pelophila*) for the SW Atlantic, provided three redescriptions of the "Walter Herwig" Expedition material (*P. hertwigi*, *P. robusta* and *P. magna*), discussed the concerned information in literature and synonymised *Phelliactis incerta* (Carlgren, 1934) to *P. hertwigi*. Doumenc (1975) regarded the number of perfect mesenteries as one of the main features and reconsidered *Phelliactis incerta* as accepted species due to the more regular arrangement of the tubercules, the less developed sphincter, the stronger radial muscles of the oral disc and the smaller nematocysts size of the tentacles and actinopharynx. He described a new species, *P. carlgreni* Doumenc, 1975 based on the very large conical tubercles. At present and considering the objectives of this manuscript, Riemann-Zürneck differentiation regarding mesenteries, dividing *Phelliactis* genus in two large groups is accepted: *P. hertwigi* group has six pairs of mesenteries and two additional mesenteries; and *P. robusta* group has only six pairs of perfect mesenteries in the first cycle.

***Phelliactis hertwigi* Simon, 1892**

(Fig. 14.1-14.4; Table 14)

Material examined

PROSPEC: stn. CPH-08 (BEIM: 3008, 3 specimens); stn. CPH-10 (BEIM: 3009, 6 specimens); stn. Arrow 15 (BEIM: 3011, 2 specimens); stn. CPH-09 (BEIM: 3015, 2 specimens); stn. 7 (Arrow 7) (BEIM: 3017, 2 specimens); stn. Arrow 10 (BEIM: 3024, 1 specimen); stn. Arrow 14 (BEIM: 3124, 4 specimens); stn. CPH-03 (BEIM: 3128, 1 specimen); stn. 1 (CPH-02) (BEIM: 3134, 9 specimens).

In total 30 specimens from “Hébrides Terrace” were available. Four specimens from PROSPEC, stn.1(CPH-02) were used for the histological study.

Description

External anatomy (Fig. 14.1).— Well developed pedal disc, sometimes enclosed (specimens from samples 3134 and 3015) or enlarged (specimen 3009). Specimens large, up to 12 cm height. Column in its upper part asymmetric, very variable in shape depending on type of contraction. Bilobed oral disc. Numerous large and prominent tubercles in the distal region. Irregular and regular furrows transversal and longitudinal. Sometimes smooth with large tubercles. No sharp difference between scapus and scapulus. Cuticle very thin and easily deciduous; some specimens loose the most part of it, in others it can be found between furrows of tubercles. Column very thick but variable along it length. Tentacles more than 100, hexamerously arranged in six cycles; in all specimens they are retracted, very short, moderately thickened at the base.

Internal anatomy (Fig. 14.2).— Mesenteries arranged hexamerously in five cycles (the last cycle incomplete), with more than six pairs of perfect mesenteries in the first cycle. Presence of imperfect mesenteries forming pairs with perfect mesenteries. Two directives connected with two well developed siphonoglyphs. No cinclides. Longitudinal musculature of the tentacles and oral disc ectodermal. Sphincter well developed, mesogleal, alveolar, very strong in its upper part with thick mesoglea meshes between the muscles and gradually diminishing downwards. Retractor musculature diffuse (stronger in the upper part of the column than in the lower part). Parietobasilar muscles poorly developed, weak. Gametogenic tissue in mesenteries of the 2nd and 3rd cycles.

Cnidom (Figs. 14.3-14.4; Tables 14.1-14.2).— Spirocysts, basitrichs and microbasic *p*-mastigophores.

After revision of Carlgren’s (1942) nematocysts description, we noticed that his data is nearly similar to our measurements, although in specimen 3134 we found one more basitrich in the tentacles (Fig. -F). Specimen 3009 do not have this basitrich. Another difference encountered was the existence of a small basitrich in the filament of the examined specimens that was not recorded by Carlgren. The nematocysts from scapus and pedal disc were also determined.

Colour.— Preserved material of a dirty white colour.

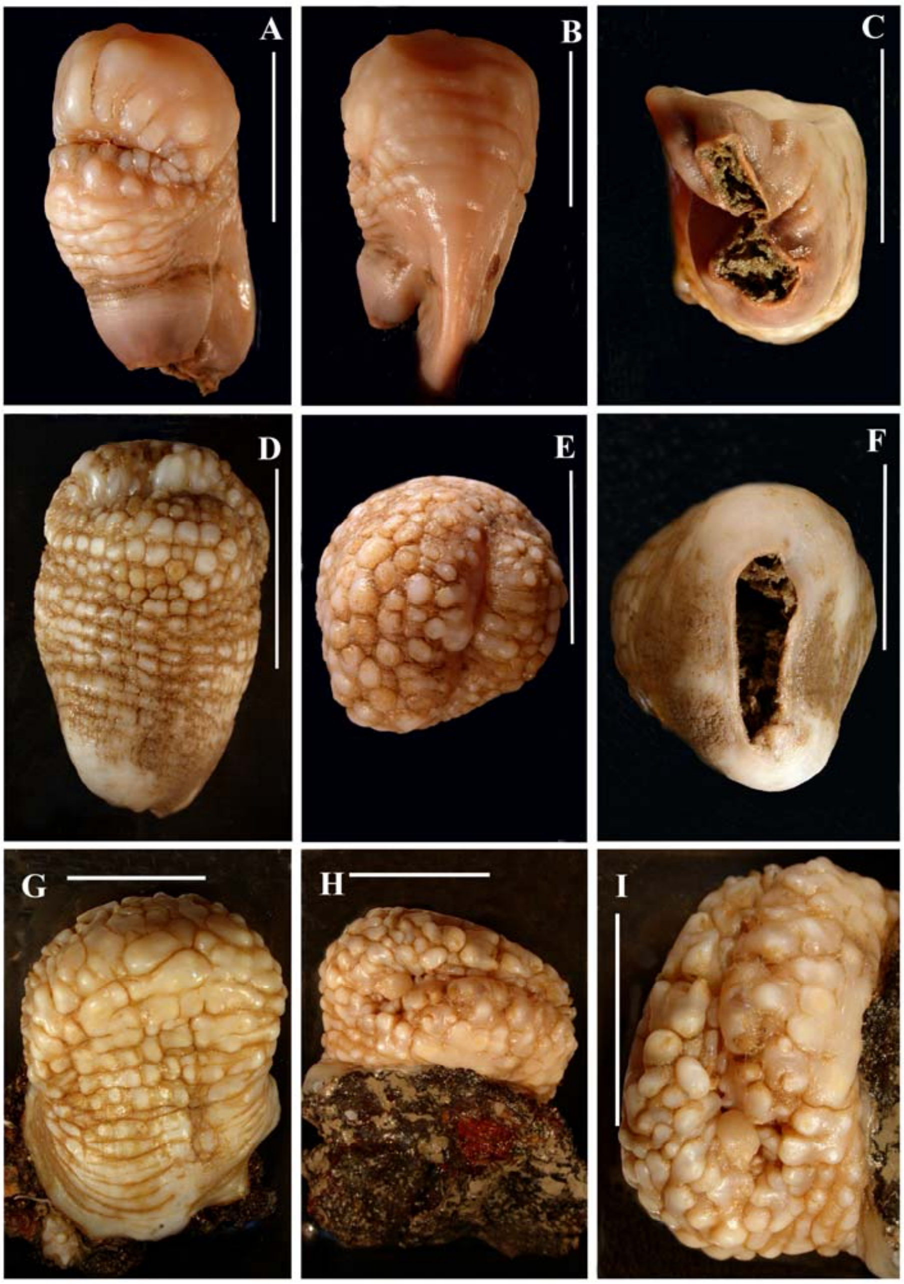

Figure 14.1.– *Phelliactis hertwigi* Simon, 1892. External anatomy: A) Lateral view showing oral disc with large tubercles (BEIM-3134); B) Lateral view showing column (BEIM-3134); C) Basal view showing pedal disc (BEIM-3134); D) Lateral view showing numerous tubercles (BEIM-3015); E) Oral view showing bilobed disc strongly retracted (BEIM-3015); F) Basal view showing pedal disc (BEIM-3015); G) Lateral view (BEIM-3009); H) Basal view (BEIM-3009); I) Oral view (BEIM-3009). Scales: A, 50 mm; B, 50 mm; C, mm; D, 50 mm; E, 50 mm; F, 50 mm; G, 50 mm; H, 50 mm; I, 50 mm.

Geographic and bathymetric distribution

Norwest Atlantic: (Davis Strait, Greenland). Between 923-1960 m depth (see Carlgren, 1942) and East side of North Atlantic (Ireland) nearly between 500-1500 m.

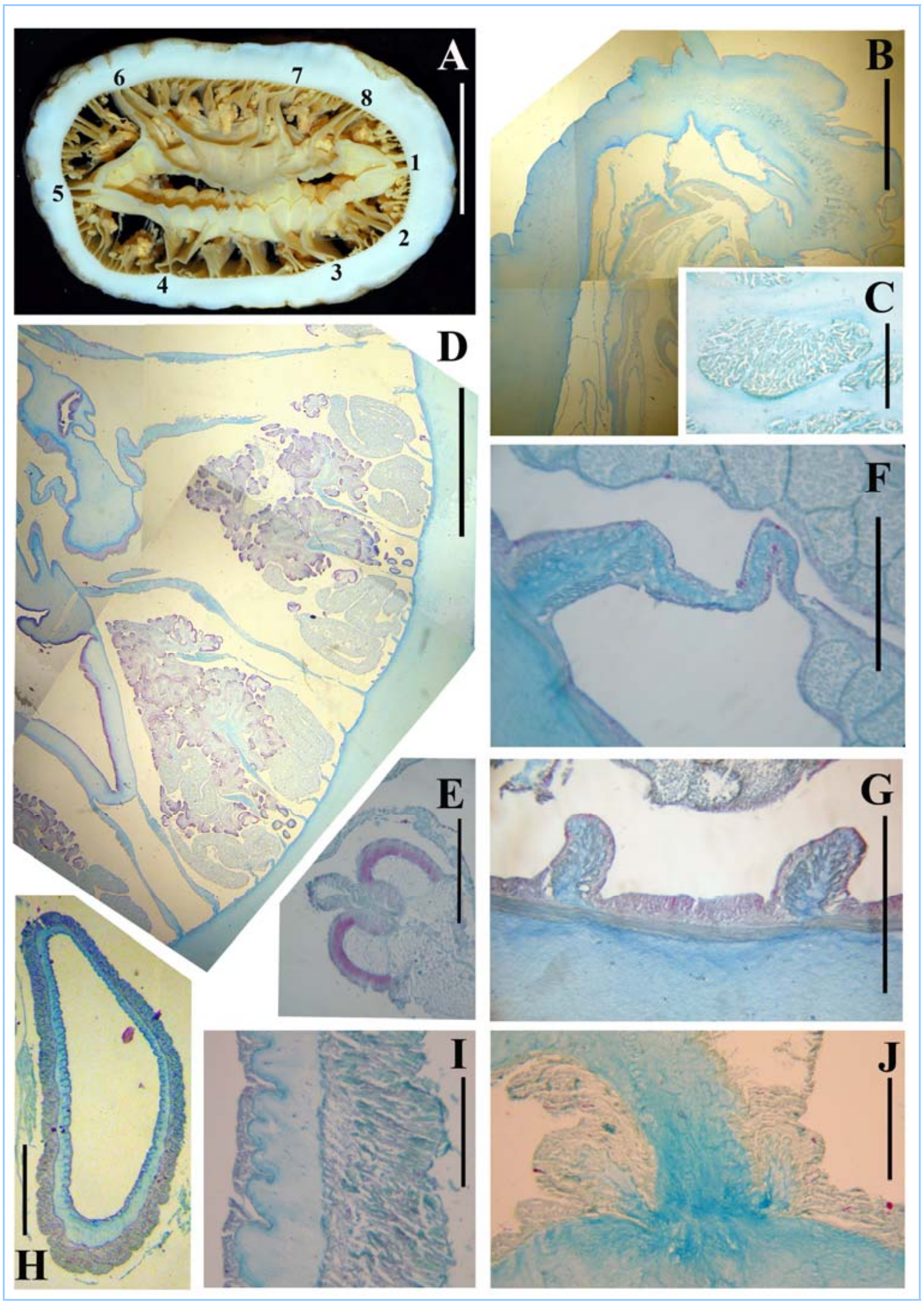

Figure 14.2.– *Phelliactis hertwigi* Simon, 1892. Internal anatomy [BEIM (3134)]: A) Transversal section at actinopharynx level showing 7 pairs of perfect mesenteries; B) Longitudinal section of the distal part of the column showing the mesogleal sphincter; C) Detail of the sphincter alveolar; D) Transversal section at actinopharynx level showing one pair of directives and filaments on 2nd and 3rd cycles; E) Detail of trilobate filaments; F) Detail of parietobasilar muscles of a mesentery of the 3rd cycle, with gametogenic tissue; G) Detail of a pair of microcnemes from the 5th cycle; H) Transversal section of a tentacle with aboral thickenings; Detail of tentacle showing ectodermal musculature; J) Longitudinal section of the pedal disc showing basilar musculature. Scale: A, 25 mm; B, 6 mm; C, 0.1 mm; D, 5.5 mm; E, 0.3 mm; F, 3 mm; G, 3.1 mm; H, 2 mm; I, 0.1 mm; J, 0.4 mm.

Table 14.1.– Dimensions of cnidae on *Phelliactis hertwigi* Simon, 1892. Specimens: [BEIM (3134)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic. (*) Average based on measures of less than 40 capsules, which is considered the meaningful minimum (Williams, 1996; 1998).

Category	Fig. 14.3	Range of length and width of capsules in µm	X ± SD	S	N	F	Carlgren, 1949	K. Riemann-Zürneck, 1973	Doumenc, 1975
PEDAL DISC									
Basitrichs	A	(24.2-30.3) x (3-4)	26.9 ±2 x 3.4 ±0.3(*)	2/3	11	---	_		_
COLUMN									
Basitrichs 1	B	(10.5-15.2) x (2)	12.3 ±1.1 x 2 ±0	3/3	42	---/+	_	18-22x2.5-3	_
Basitrichs 2	C	(18.2-26.3) x (2.5-4)	21.7 ±1.8 x 3.2±0.4	3/3	60	-/++	_	_	_
Mic. p-mastigophores	D	(29.3-46.5) x (5-7)	39.7 ±3.7 x 5.6 ±0.5	3/3	60	+	_	38x4 (only 2 animals)	_
TENTACLES									
Spirocysts	E	(28.3-75.8) x (3-12)	54 ±13.7 x 6 ±2	3/3	60	+++	75 x 8-10	55-65 x ca.8	70-80 x 10
Basitrichs 1	F	(14.1-25.5) x (2-2.5)	17.8 ±2 x 2.2 ±0.2	3/3	60	+	_	15.5 (very rare)	_
Basitrichs 2	G	(36.8-46.5) x (3-5)	41.6 ±2.2 x 3.7 ±0.4	3/3	60	++	32.4-46 x 2.8(3.5)	31-41.5x3	30-44 x 3
PHARYNX									
Basitrichs 1	H	(16.2-25.3) x (2-3)	20 ±1.7 x 2.3 ±0.3	3/3	60	+	31-39.5 x 4.2 (4.5)	18-23.5x1.5	_
Basitrichs 2	I	(34.4-46.5) x (3-4)	41.5 ±2.2x 3.7 ±0.4	3/3	60	+/++		39-41.5x3	35-50x2-3
Mic. p-mastigophores	J	(30.3-43.4) x (4-6)	37.4 ±2.8 x 4.6 ±0.4	3/3	60	++	35.2-48 x 2.8	31-39x4	30-40x4-5
FILAMENTS									
Basitrichs 1	K	(16.2-27.3) x (2-2.5)	21.3 ±2.6 x 2.3 ±0.3	3/3	60	+/++	_	15-24x1.5	_
Basitrichs 2	L	(35.4-44.5) x (3-4)	40.8 ±2 x 3.5 ±0.4	3/3	60	++	32.4-38 x 2.8	34-40x3	30-37x3
Mic. p-mastigophores	M	(30.3-43.4) x (4-5)	36.8 ±2.4 x 4.5 ±0.4	3/3	60	++	26.6-31 x 3.5	30-38x4	24-31x3
ACONTIA									
Basitrichs 1	N	(17.2-24.2) x (2-2.5)	20.5 ±2 x 2.3 ±0.3	3/3	60	+	14-22 x 1.5 (sparse)	15-24x1.5	14-20x2
Basitrichs 2	O	(37.4-47) x (3-4.5)	42 ±2.2 x 3.7 ±0.3	3/3	60	+++	36-50 x 2.8	34-45.5x3.5	36-45x3

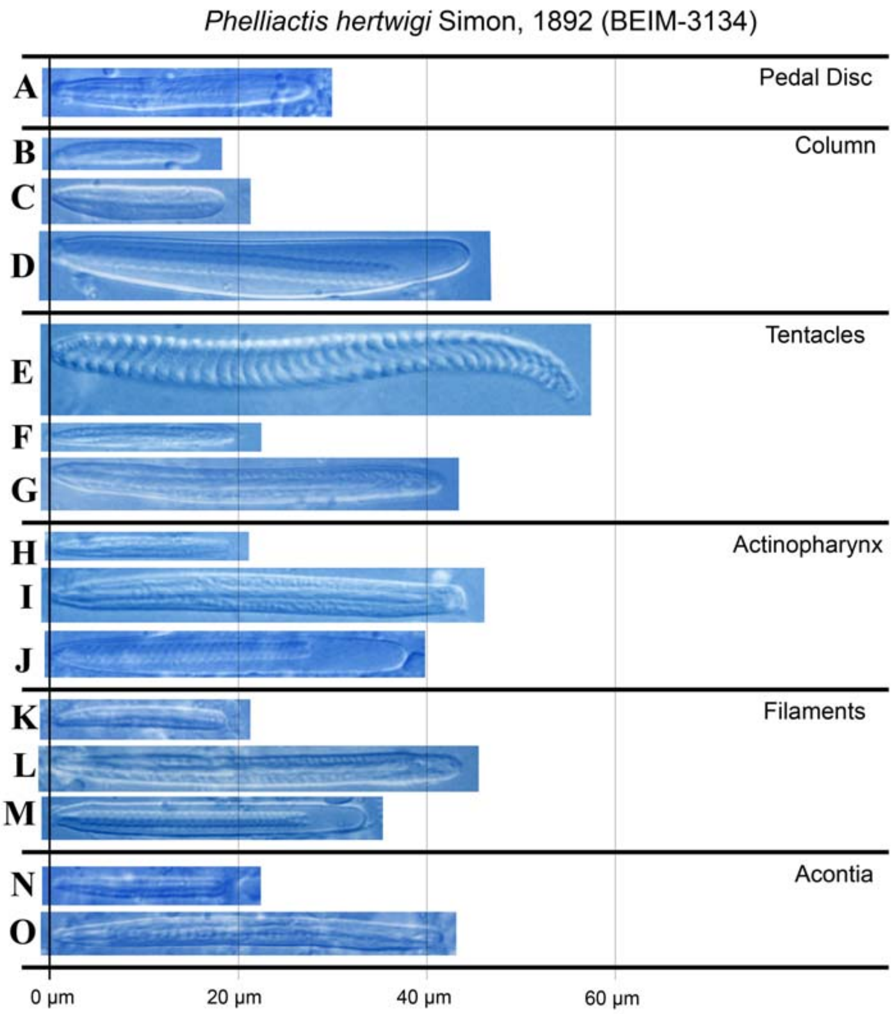

Figure 14.3.– *Phelliactis hertwigi* Simon, 1892. Cnidae [BEIM (3134)]: A) basitrich; B) basitrich 1; C) basitrich 2; D) microbasic *p*-mastigophore; E) spirocyst; F) basitrich 1; G) basitrich 2; H) basitrich 1; I) basitrich 2; J) microbasic *p*-mastigophore; K) basitrich 1; L) basitrich 2; M) microbasic p-mastigophore; N) basitrich 1; O) basitrich 2.

Table 14.2.– Dimensions of cnidae from *Phelliactis hertwigi* Simon, 1892. Specimens: [BEIM (3009)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic. (*) Average based on measures of less than 40 capsules, which is considered the meaningful minimum (Williams, 1996; 1998).

Category	Fig. 14.4	Range of length and width of capsules in µm	X ± SD	S	N	F	Carlgren, 1949	K. Riemann-Zürneck, 1973	Doumenc, 1975
COLUMN									
Basitrichs 1	**A**	**(11.1-15.2) x (2.0)**	**13.5 ±1.1 x 2.0 ±0**	**3/3**	**44**	**---/++**	_	_	_
Basitrichs 2	**B**	**(15.2-25.3) x (3.0-4.6)**	**20.9 ±2 x 3.7 ±0.3**	**3/3**	**50**	**++**	_	**18-22x2.5-3**	_
Mic p-mastigophores	**C**	**(30.3-43.5) x (4.0-5.6)**	**37.1 ±3.5 x 4.8 ±0.5(*)**	**3/3**	**22**	**---**	_	**38x4 (only 2 animals)**	_
TENTACLES									
Spirocysts	**E**	**(30.3-73.7) x (3.0-11.1)**	**50.9 ±13.5 x 6.1 ±2.2**	**3/3**	**60**	**+++**	**75 x 8-10**	**55-65 x ca.8**	**70-80 x 10**
Basitrichs 1		_	_	_	_	_	_	**15.5 (very rare)**	_
Basitrichs 2	**F**	**(32.3-49.5) x (3.0-4.0)**	**42.3 ±4.0 x 3.5 ±0.4**	**3/3**	**52**	**+++**	**32.4-46 x 2.8(3.5)**	**31-41.5x3**	**30-44 x 3**
PHARYNX									
Basitrichs 1	**G**	**(16.2-25.3) x (2.0-3.5)**	**20.2 ±2 x 2.2 ±0.3**	**3/3**	**60**	**+**	_	**18-23.5x1.5**	_
Basitrichs 2	**H**	**(37.4-49.5) x (3.0-4.0)**	**42.7 ±2.6 x 3.6 ±0.4**	**3/3**	**60**	**++**	**31-39.5 x 4.2 (4.5)**	**39-41.5x3**	**35-50x2-3**
Mic. p-mastigophores	**I**	**(32.3-41.4) x (3.5-6.0)**	**36.5 ±2.1 x 4.9 ±0.4**	**3/3**	**60**	**++/+++**	**35.2-48 x 2.8**	**31-39x4**	**30-40x4-5**
FILAMENTS									
Basitrichs 1	**J**	**(16.16-25.3) x (2.0-2.5)**	**19.5 ±2.2 x 2.2 ±0.3**	**3/3**	**60**	**++**	_	**15-24x1.5**	_
Basitrichs 2	**K**	**(37.4-48.5) x (3.5-4.5)**	**41.8 ±2.6 x 3.9 ±0.3**	**3/3**	**45**	**+**	**32.4-38 x 2.8**	**34-40x3**	**30-37x3**
Mic. p-mastigophores	**L**	**(29.3-41.4) x (4.0-6.1)**	**34.2 ±2.5 x 4.8 ±0.5**	**3/3**	**60**	**++**	**26.6-31 x 3.5**	**30-38x4**	**24-31x3**
ACONTIA									
Basitrichs 1	**M**	**(16.2-26.3) x (2.0-2.5)**	**21.4 ±2.3 x 2.3 ±0.3**	**3/3**	**60**	**+/++**	**14-22 x 1.5 (sparse)**	**15-24x1.5**	**14-20x2**
Basitrichs 2	**N**	**(34.3-51.5) x (4.0-5.1)**	**46.8 ±3.2 x 4.2 ±0.3**	**3/3**	**60**	**+++**	**36-50 x 2.8**	**34-45.5x3.5**	**36-45x3**

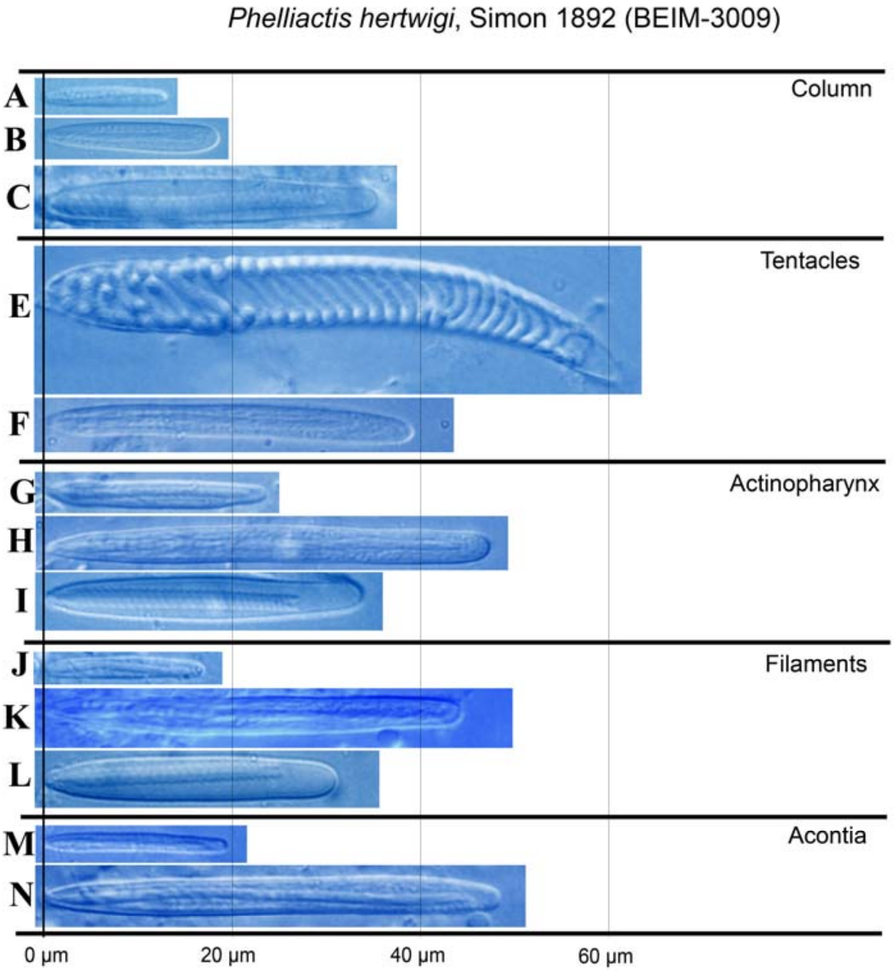

Figure 14.4.– *Phelliactis hertwigi* Simon, 1892. Cnidae [BEIM (3009)]: A) basitrich 1; B) basitrich 2; C) microbasic *p*-mastigophore; D) spirocyst; E) basitrich; F) basitrich 1; G) basitrich 2; H) microbasic *p*-mastigophore; I) basitrich 1; J) basitrich 2; K) microbasic p-mastigophore; L) basitrich 1; M) basitrich 2.

Discussion

Phelliactis Simon, 1892 genus is characterized by the asymmetry of the oral disc: the bilobed aspect, in most cases of unequal size. The asymmetric appearance is the principal element to distinguish *Phelliactis* from the genera *Actinauge* and *Hormathia*. However, some *Phelliactis* species have a very similar shape due to their external form always with many tubercles of different sizes (more irregular or plane) depending on the animal contraction. For that reason, this character is not good to discern *Phelliactis* species (except for instance, *P. carlgreni* Doumenc, 1975).

Table 14.3. Comparison of cnidae dimensions between *Phelliactis* species from North Atlantic, within data of different authors.

	Riemann-Zürneck, 1973 and 1986				Doumenc, 1975				Carlgren, 1942	
	P. hertwigi	P. robusta	P. magna	P. michaelsarsi	P. hertwigi	P. robusta	P. incerta	P. carlgreni	P. hertwigi	P. robusta
PEDAL DISC										
Basitrichs				24.5-27.5x3-3.5						
SCAPUS										
Basitrichs 1	18-22 x 2.5-3	14–16 x 2	13.5-15x2	12-14.5x2-2.5 (limbus)						
Basitrichs 2		21–26 x 3	39-45.5 x 4.5-5	23-26x3.5-4.5 (limbus) 30.5-36.5x3.5-4.5 (margin)						
Mic p-mastigophores	38x4 (only 2 animals)	Not found	39-45.5 x 4.5-5	28-32 x 4-4.5 (margin, rare)						
TENTACLES										
Spirocysts	55-65 x ca.8		55	81x13 (max)	70-80 x 10	61-68x5.5-10	42-60x5.2-6.5	40-52x4.5(6.5)	75 x 8-10	60 x 7
Basitrichs 1	15.5 (very rare)		41 (only one found)	17.5-23x2.5						
Basitrichs 2	31-41.5x3	large		36-43.5x3-3.5	30-44 x 3	36-47.6 (54) x3-3.5	33-36x2.6-3	30-33x3.2	32.4-46 x 2.8(3.5)	35-46 x 2.8
PHARYNX										
Basitrichs 1	18-23.5 x 1.5			23 x 2.4-3 (rare)					31-39.5 x 4.2 (4.5)	17-22 x 2
Basitrichs 2	39-41.5x3		35-41.5	40.5-45x3.5	35-50x2-3	26-40x2-3	34-38x4	35-40x2-3		26.8-43 x 2.8-3.5
Mic p-mastigophores	31-39x4		34-40.5	29-33.5x3.5 (rare)	30-40x4-5	35.7-37.4x5	35-39x4-5	30-40x4	35.2-48 x 2.8	25.5-36 x 4
FILAMENTS										
Basitrichs 1	15-24x1.5		18	20.5-24.5x2.5				25-28x3.4-5		
Basitrichs 2	34-40x3			35-41x3-3.5	30-37x3	17-21x2	39-41x3.1	28-35x3.2	32.4-38 x 2.8	18.3-21 x 2
Mic p-mastigophores	30-38x4		34-40.5	27.5-35x3.5-4	24-31x3	22-29x3-4	33-36x3.2-3.9		26.6-31 x 3.5	23.3-28.2 x 3.5-4
ACONTIA										
Basitrichs 1	15-24x1.5		21-23.5	22-29x2.5-3	14-20x2				14-22 x 1.5 (sparse)	19-22 x 2 (rare)
Basitrichs 2	34-45.5 x3.5	large	39-48	46.5-52x3.5-4	36-45x3	35-45x2.8	36-42x2.8-3.2	39.1-42.5x1.7-2.3	36-50 x 2.8	35-46(49) x 2.8-3.5

In addition, the bilobed oral disc, very peculiar within the *Phelliactis* genus, is very variable; more or less asymmetrical in most species, or in other cases without asymmetry within the same species. This was observed in the *Phelliactis hertwigi* collected for the present study: some individuals were very asymmetrical and others more symmetrical and regular. The features of two animals studied (specimens 3134 and 3009) are the same, they show variability but do not fit in the features of *Phelliactis* that have a very high taxonomic level such as the number of mesenteries and the position of the mesenteries of the 5th cycle.

Although somewhat confuse, Riemann-Zürneck considerations about *P. hertwigi* ("aberrante Individuen") refer to the 5th cycle of mesenteries missing at the side of the 1st and 2nd cycles. However, the author was concerned about the possible variability within *P. hertwigi* species, even when her comments were based on the observation of a single specimen with these characteristics.

The observed species of PROSPEC campaigns were ascribed to *P. hertwigi* group because of the six pairs plus two pairs of mesenteries at the first cycle and the incomplete 5th cycle. All the other species are mainly distinguished by the tubercular shape, bilobed asymmetrical or not. Also the localities where they were found are biogeographically distant (large scale), from the Pacific to the South Atlantic (Brazil, Argentina, Cape Town), so it is considered that they are different species. However, it is probable that many specimens were wrongly ascribed to only a few widely distributed species of this genus and in fact many other species also occur.

In relation to *P. incerta* it is very difficult to decide if it is a *P. hertwigi* synonym or not, without further observation of the type specimen described by Carlgren (1918) from Michael-Sars Expedition 1910 Sta.23 (deposited in Bergen Museum), which was also observed by Riemann-Zürneck (1973) and Doumenc (1975). Moreover, the four specimens seen by Doumenc (1975) of the Biaçores st.254 should be accessed for comparison. More studies on this genus should be carried out, in future expeditions samples for molecular analyses should be acquired, as their genetic assessment could probably reveal more valid differences between *Phelliactis* species.

Family Kadosactidae Riemann-Zürneck, 1991

Diagnosis (adapted from Riemann-Zürneck, 1991 by Rodríguez, 2007)

Nynantheae (Mesomyaria) with basilar muscles. Body with well developed pedal disc. Column divided into scapus and scapulus, usually cinclides at borderline between these two regions. Scapus usually with a cuticle that can be easily vanished and with tenaculi. Sphincter strong, mesogleal. Tentacles of variable length, conical, hexamerously arranged. Tentacles of variable longitude, conical, hexamerously arranged. External tentacles with (sometimes without) basal thickenings in its aboral part. Three cycles of mesenteries. Same number of septa and tentacles (about 48). Longitudinal muscles of tentacles and oral disc ectodermal. Two siphonoglyphs, two pairs of directives. Hexamerous mesenteries. 12 pairs of perfect mesenteries. Perfect mesenteries, and sometimes also the imperfects, are strong, including the directives with strong diffuse retractor muscles. Parietobasilar muscles weak. Strong mesenteries are fertile (including directives). Acontia poorly developed. Cnidom: spirocysts, basitrichs and microbasic *p*-mastigophores (*p*-rhabdoids B *sensu* Schmidt, 1969)

Genus *Kadosactis* Danielssen, 1980

Diagnosis

The same as the family.

Type species

Kadosactis rosea, Danielssen, 1890

Species included in the genus

Kadosactis rosea Danielssen, 1890, *Kadosactis antartica*, (Carlgren 1928), *Kadosactis sulcata*, Carlgren 1934, *Kadosactis commensalis* (Gravier, 1918).

Observations

The genus Kadosactis was firstly placed in the family Paractidae Hertwig, 1918 (see Danielssen, 1890). Later it was inserted in the family Sagartiidae Gosse, 1858 by Haddon (1898). Carlgren reviewed the family Sagartiidae as "Thenaria (Acontiaria) with mesogleal sphincter, normally strong, with mesenteries not differentiated in macro and microcnemes, and typical acontia with numerous nematocysts, basitrichs and microbasic amastigophores". However, Riemann-Zürneck (1991b) argued that the position of the genus Kadosactis in the family Sagartiidae was based on the observation of an archaic cnidom, when according to Schmidt's terminology, these are big "p-rhabdoids B" which are considered typical of "early Mesomyaria". In this way, she established the family Kadosactidae once Kadosactis has to be excluded from Sagartiidae. Later, Rodríguez and González (2005), found microbasic p-mastigophores and not microbasic *p*-amastigophores in *Kadosactis antartica* (Carlgren, 1928). This occurrence further supports the exclusion of the genus *Kadosactis* from Sagartiidae, and the erection of the family Kadosactidae.

Presently the family Kadosactidae Riemann-Zürneck, 1991 comprises two genera (*Kadosactis* Danielssen, 1890 and *Seepactis* Sanamyan and Sanamyan, 2007) including four valid species, all from deep-sea (Daly *et al*., 2007). In this contribution, and according to Carlgren (1934), we confirm the addition of another deep-sea species, *Sicyopus commensalis* Gravier, 1918 in the genus *Kadosactis*.

The genus name *Sicyopus* Gravier, 1918, is a junior primary homonym of *Sicyopus* Gill T., 1864, since it was first described has a gobioid genus of the western coast of temperate North America. This homonymy invalidates the genus *Sicyopus* and family name Sicyopidae Gravier, 1918. Since Carlgren, 1934 considered Gravier's species a *Kadosactis*, *Sicyopus commensalis* is rejected in favour of *K. commensalis* (Gravier, 1918).

In the note published by Fautin *et al*. (2007) the authors consider the genus name as valid, In our opinion, this is a "gaffe", the genus must be rejected and an *errata* of the paper should be requested.

***Kadosactis commensalis* (Gravier, 1918)**

(Fig.15.1-15.3; Table. 15)

Material examined

BENGAL 2: 13078 (11) (BEIM: 3049, 1 specimen); stn. 13078 (27) (BEIM: 3041, 7 specimens); stn. 13078 (6) (BEIM: 3033, 5 specimens). BENGAL 3*:* stn. 13200 (70) (BEIM: 3045, 13 specimens); stn. 13200 (94) (BEIM: 3058, 25 specimens); stn. 13200 (84) (BEIM: 3030, 6 specimens). BENGAL 5: stn. 13368 (48) (BEIM: 3040, 5 specimens); stn. 13368 (52) (BEIM: 3051, 1 specimen); stn. 13368 (53) (BEIM: 3053, 12 specimens); stn. 13368 (47) (BEIM: 3019, 3 specimens). BENGAL 6: stn. 13627 (24) (BEIM: 3036, 1 specimen); stn. 13627 (11) (BEIM: 3107, 16 specimens).

In total 95 specimens from the Porcupine Abyssal Plain were available. In total eight specimens were used for the histological study: 4 specimens were taken from BENGAL 3, Stn 13200(94), and 4 specimens from BENGAL 3 Stn 13200 (70).

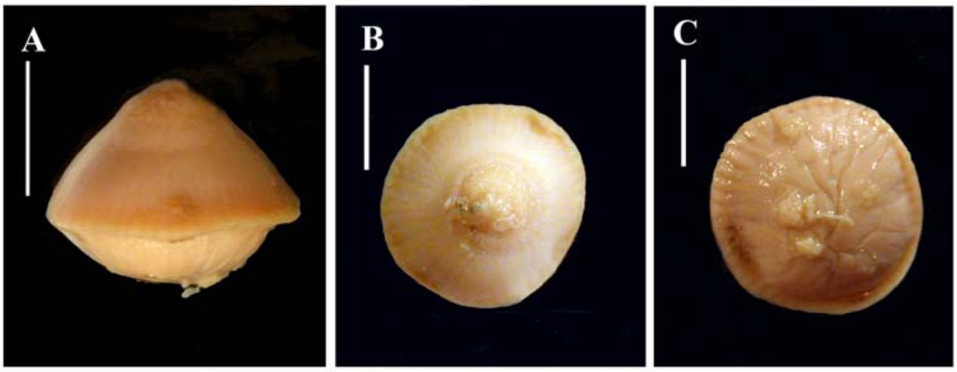

Figure 15.1.– *Kadosactis commensalis* (Gravier, 1918). External anatomy [BEIM (3058)]: A) Lateral view of contracted specimen; B) Oral disc view; C) Pedal disc view. Scale: A) 10mm; B) 10mm; C) 10mm.

Description

External anatomy (Fig. 15.1).— Pedal disc well developed, convex, round and measures 0.5-2.3cm in breadth. Limbus prominent. Column firm, inverted cone shape (1.5-2.0cm height). Fine longitudinal folds in the column which radiate from the centre, delimited by a lob margin, towards the upper part which indicate insertions of septa. Body strongly retracted in conical form. Oral disc encloses all the tentacles inside the body. The number of tentacles are about 48.

Internal anatomy (Fig. 15.2).— 3 cycles of mesenteries (6+6+12=48). 12 pairs (1st and 2nd cycles) perfect. Two directives connected with two siphonoglyphs. 3rd cycle incomplete. Mesenteries not divided in macrocnemes and microcnemes. Currently it is not possible to confirm existence of cinclides. Further examination, more exemplars in good conditions, required to confirm if there is any cinclides ring between the scapus and scapulus (family/genus rule). Stratified cuticle but easily deciduous. Sphincter strong mesogleal, alveolar. Longitudinal muscles of tentacles and oral disc ectodermal without aboral thickness of mesoglea. Strong retractors. Parietobasilar muscles strong, diffuse. Basilar muscles present (however no image available because of the bad histological samples).

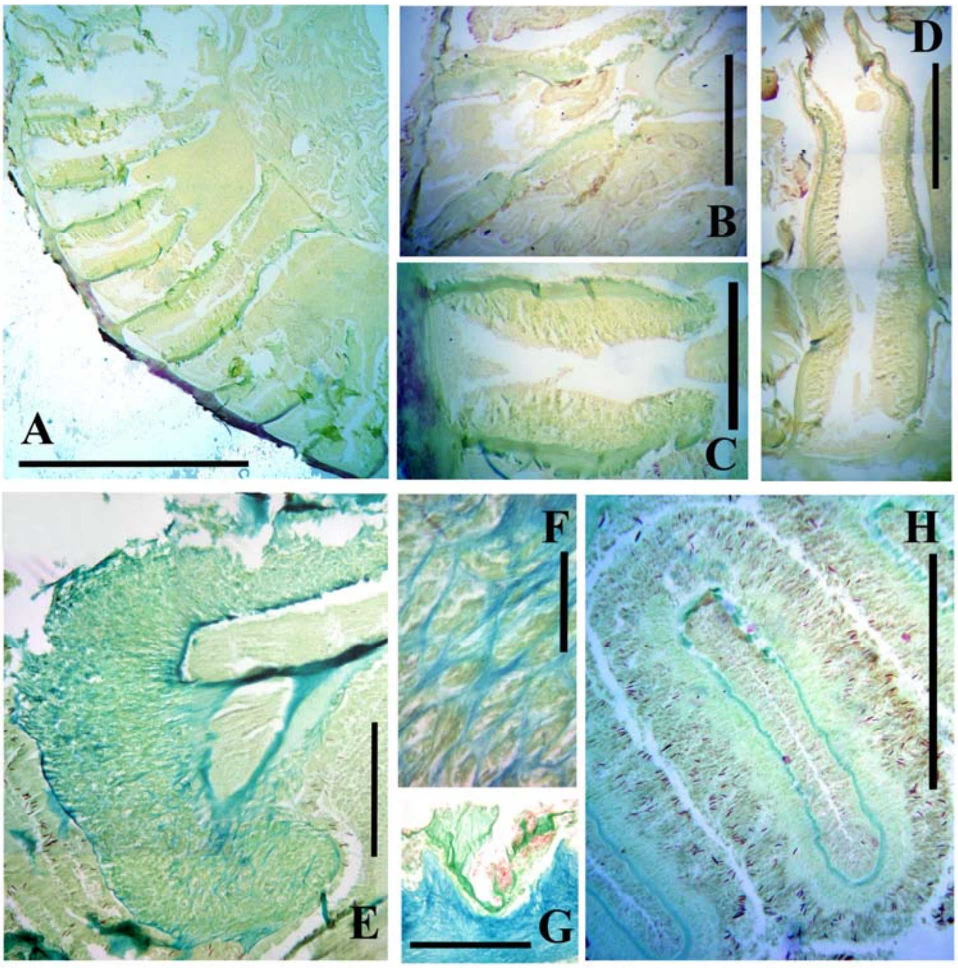

Figure 15.2.– *Kadosactis commensalis* (Gravier, 1918). Internal anatomy [BEIM (3045)]: A) Transversal section at actinopharynx level showing three cycles of mesenteries; B) Detail of one pair of directives and respective siphonoglyph; C) Detail of a pair of mesenteries from 3rd cycle showing retractor musculature; D) Detail of a perfect mesentery showing retractor musculature; E) Longitudinal section of distal margin of the column showing sphincter; F) Detail of sphincter; G) Detail of cuticle; H) Transversal section of tentacle showing ectodermal musculature. Scale: A, 5.5mm; B, 1.4mm; C, 1.2mm; D, 1.5mm; E, 5.5 mm; F, 0.1mm; G, 0.35mm; H, 7mm.

Table 15.– Dimensions of cnidae in *Kadosactis commensalis* (Gravier, 1918). Specimens: [BEIM (3058, 3045)]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic. (*) Average based on measures of less than 40 capsules, which is considered the meaningful minimum (Williams, 1996; 1998).

Category	Fig. 15.3	Range of length and width of capsules (µm)	X ± SD	S	N	F	Data from Carlgren, 1934	Gravier, 1918
PEDAL DISC								
Basitrichs	A	(17.2-28.3) x (3-4)	22.75 ±3 x 3.3 ±0.3	3/3	60	+++	–	–
Holotrichs	B	(20.2-33.3) x (4-5.5)	24.6 ±3.3 x 4.9 ±0.4	3/3	60	+++	–	–
Mic p-mastigophores	C	(27.3-35.3) x (3.5-4)	32.5 ±2.7 x 4 ±0.2(*)	3/3	11	---	–	–
COLUMN								
Basitrichs	D	(10.1-21.2) x (2-3.5)	15.5 ±2.3 x 2.8 ±0.3	3/3	60	+++	–	–
Mic p-mastigophores	E	(20.2-38.4) x (3-4)	28.5 ±6.6 x 3.9 ±0.3	3/3	44	+	–	–
TENTACLES								
Spirocysts	F	(19.2-48.5) x (3-8.1)	37.2 ±7 x 5.95 ±1.1	3/3	60	+++	13 x 1.5 – 36 x 5	26 x 5
Basitrichs	G	(17.2-29.3) x (3-4)	23.75 ±2.4 x 3.2±0.3	3/3	54	+	15-21 x 1.5(2)	–
Holotrichs	H	(41.4-57.6) x (5-7)	54.4 ±3.3 x 6 ±0.5	3/3	60	+++	–	–
Mic p-mastigophores	I	(28.3-42.4) x (4-5)	35.4 ±0.5 x 4.4 ±0.6(*)	3/3	22	---	31-36 x 5	–
PHARYNX								
Basitrichs 1	J	(18-25) x (2-3)	21.2 ±2.2 x 2.5±0.3(*)	3/1	10	---	–	23-24 x 2
Basitrichs 2	K	(30-38) x (2.5-3)	33.4±2.1 x 2.9±0.1(*)	3/1	20	+	–	–
Mic p-mastigophores	L	(35-41) x (4-4.5)	38.3±1.8 x 4.0±0.1(*)	3/1	20	+	–	–
FILAMENTS								
Basitrichs	M	(14-26) x (2-4)	18.2 ± 2.6 x 2.6±0.5	3/3	60	+++	together with the acontia	–
Mic p-mastigophores	N	(29-43) x (3.5-4.5)	36.9±3.0 x 4.1±0.1	3/3	60	+++		–
ACONTIA								
Basitrichs	O	(16.2-29.3) x (2.5-4)	20.8 ±2.7 x 3.2 ±0.3	3/3	60	+++	sp. 1: 17-23 x 1.5 sp. 2: 16-22 x 1.5-2	–
Mic p-mastigophores	P	(35.3-55.5) x (4-5.5)	49.5 ±4 x 4.7 ±0.5	3/3	60	+++	sp. 1: 47-53x5 and 29x3 sp. 2: 45-53 x 4-5.5	–

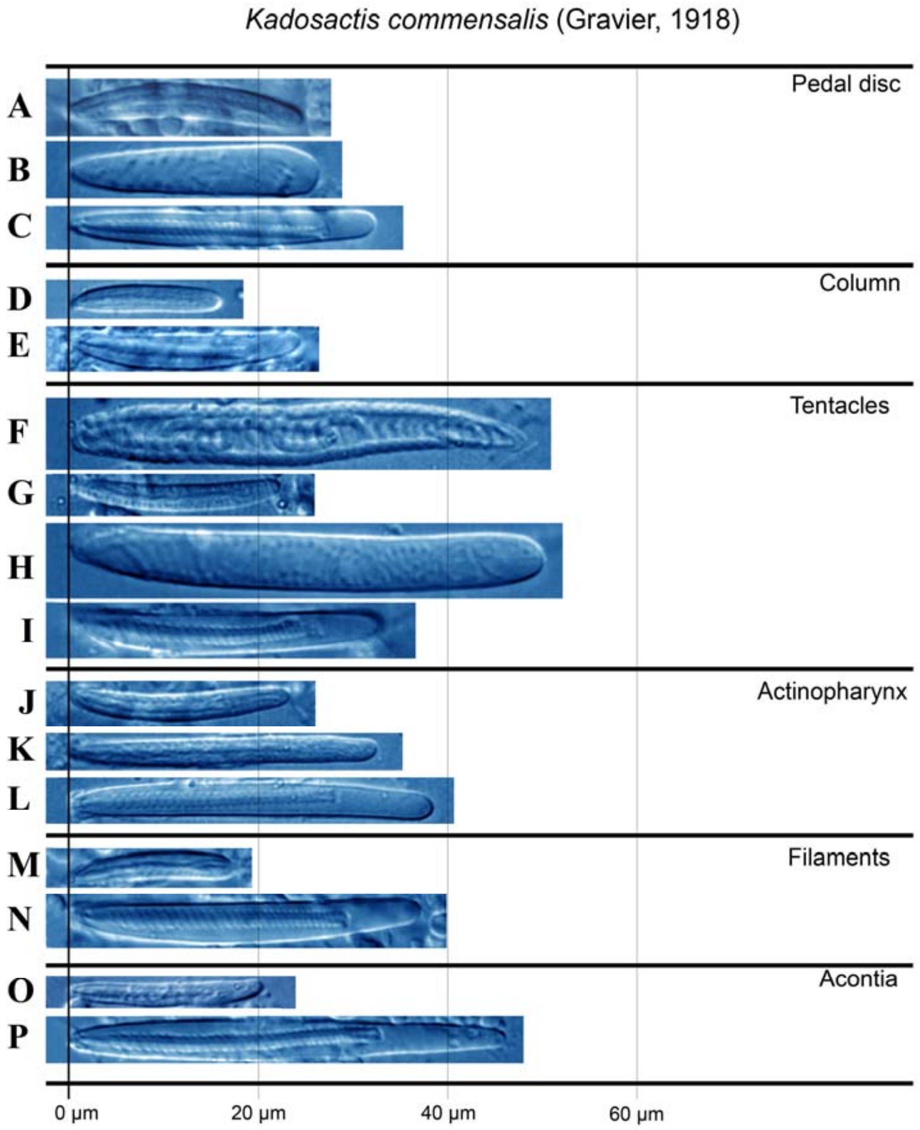

Figure 15.3.– *Kadosactis commensalis* (Gravier, 1918). Cnidae: A) basitrich; B) holotrich; C) microbasic *p*-mastigophore; D) basitrich; E) microbasic *p*-mastigophore; F) spirocyst; G) basitrich; H) holotrich; I) microbasic *p*-mastigophore; J) basitrich 1; K) basitrich 2; L) microbasic *p*-mastigophore; M) basitrich; K) microbasic *p*-mastigophore; O) basitrich; P) microbasic *p*-mastigophore.

Cnidom (Fig. 15.3; Table 15).— Measurements of the nematocysts are resumed below. basitrichs, holotrichs, microbasic *p*-mastigophores and spirocysts.

Colour.— Preserved material in ethanol pale rose.

Geographic and bathymetric distribution

The first report (Gravier, 1918) of this speciesis from the North Atlantic at 37º28’N and 20º21’W at 4275m depth (St. 1306). In this work itis reported also in the North Atlantic, but at higher latitude, for the Porcupine Abyssal Plain (more or less 48º50N and 16º40'W), at depths between 4810-4849m. It was also reported by Bronsdon (1997) for the same area. It is probably, a North Atlantic (Boreal and Lusitanian) abyssal species

Discussion

Due to the bad preservation (maybe also the depth pressure and sampling methods), the material was not in adequate conditions for histological purposes. In all specimens the body was extremely compressed and some tissues were totally macerated. However, based only in the material that was available, no differences were observed between the specimens collected in the different expeditions (BENGAL 2, 3, 5 and 6) probably because the same treatment (direct fixation in formaldehyde) was applied in all cases. In future expeditions to this area, we recommend to follow the protocol rules of Actiniaria preservation (see menthol technique *in* Moore, 1989).

Carlgren (1934) re-examined the two specimens of *Sicyopus commensalis* Gravier, 1918 and he suggested, with some doubts however, that this species belongs to genus *Kadosactis*, because of the presence of a pedal disc, strong mesogleal sphincter, 48 tentacles (evidence of 3 cycles of mesenteries), and acontia with numerous nematocysts (see Table 15) with basitrichs ("spirulae") and *p*-mastigophores ("penicili"). However Riemann-Zürneck (1991), does not agree with Carlgren's classification of *Kadosactis commensalis* (Gravier, 1918), arguing that the most important characters of these specimens are the inexistence of pedal disc, the presence of an aboral end rounded and their "regularly arranged apertures". This author further suggests that *K. commensalis* has more affinities to the family Andvakiidae because of the presence of a strong mesogleal sphincter and acontia with both basitrich and *p*-mastigophores. However, Riemann-Zürneck (1991) judgment is inconsistent because she did not examine Gravier's material. In fact, studying Gravier (1922) manuscript, we found some coincidence with our specimens. First of all, the pedal disc exists, in a convex and rounded form which is similar to Gravier's (1922) figure (Pl. VI, Fig. 67), however we failed to illustrate the basilar muscles because of some inaccuracy in the histological processing of our material. In the observed material, the pedal disc shows indication of attachment but there is no undoubted evidence of its occurrence, or information about its nature. First, *K. antartica* (Carlgren, 1928) also presents a convex pedal disc (see Rodríguez and López-González, 2005). Second, the analysed material has 12 perfect mesenteries, the retractors are strong and diffuse and the mesenteries are not differentiated in macro and microcnemes. Instead Andvakiidae has only 6 perfect mesenteries, the retractors are circumscript, and mesenteries are divided into macro and microcnemes. It must be taken into account that in Carlgren's (1949) Athenaria key the author incorrectly, and in contradiction to family diagnosis (Pg. 38), describes Andvakiidae with 12 perfect mesenteries (Pg. 22),. Third, we found the type of sphincter represented by Gravier (Pl. XIII, Fig. 127) very similar to our observations (Fig. 15.2), principally in the contracted form and the special kind of mesoglea mesh ("ses fibres musculaires qui le constituient sont groupées en fascicules isolés les unes des autres par des travées de mésoglée, (…) un aspect que rapelle un peau les îlots de cellules cartilagineuses au milieu de la substance interstitielle."). In Andvakiidae, the sphincter is elongated with scattered meshes. Finally, Andvakiidae has acontia with basitrichs and microbasic amastigophores, on the contrary, the analysed material has basitrichs and microbasic *p*-mastigophores. However, it is very difficult to observe them, we found some exploded capsules (Fig. 15.4) and there are also some doubts about their terminology.

The type species *Kadosactis* (*Sicyopus*) *commensalis* (Gravier, 1918) was collected in the Iberian abyss (at 4275m depth), attached to an holothuria (*Pseudostichopus villosus*). Gravier also took picture of the holothuria with a round hole (Pl. VI, Fig. 66). Moreover, in the Porcupine Abyssal Plain at a depth of 4850m on 48º50N 16º30W (Rice *et al*, 1994), commensalism of *K. commensalis* on holothurians, predominantly *Paroriza prouhoi* and, less frequently, on *Pseudostichopus villosus* was also documented (Bronsdon *et al*, 1993 and 1997; Iken *et al*, 2001). Surprisingly, the taxonomist who identified this material was Riemann-Zürneck (see "acknowledgments" at the end *in* Bronsdon *et al*, 1993) who changed her opinion since 1991 (personal communication in Bronsdon *et al*, 1993).

The re-assessment of Gravier's type specimen must be achieved, but it was not possible in the framework of the present study. The observed specimens belong to the family Kadosactidae because they possess a strong mesogleal sphincter, 12 pairs of perfect mesenteries and acontia with numerous nematocysts containing basitrichs and microbasic *p*-mastigophores. Even if the differentiation of macro- and microcnemes character was not included in generic diagnosis, our specimens do not show distinction between them (similarly as *K. antartica*, see Rodríguez and López-González, 2005).

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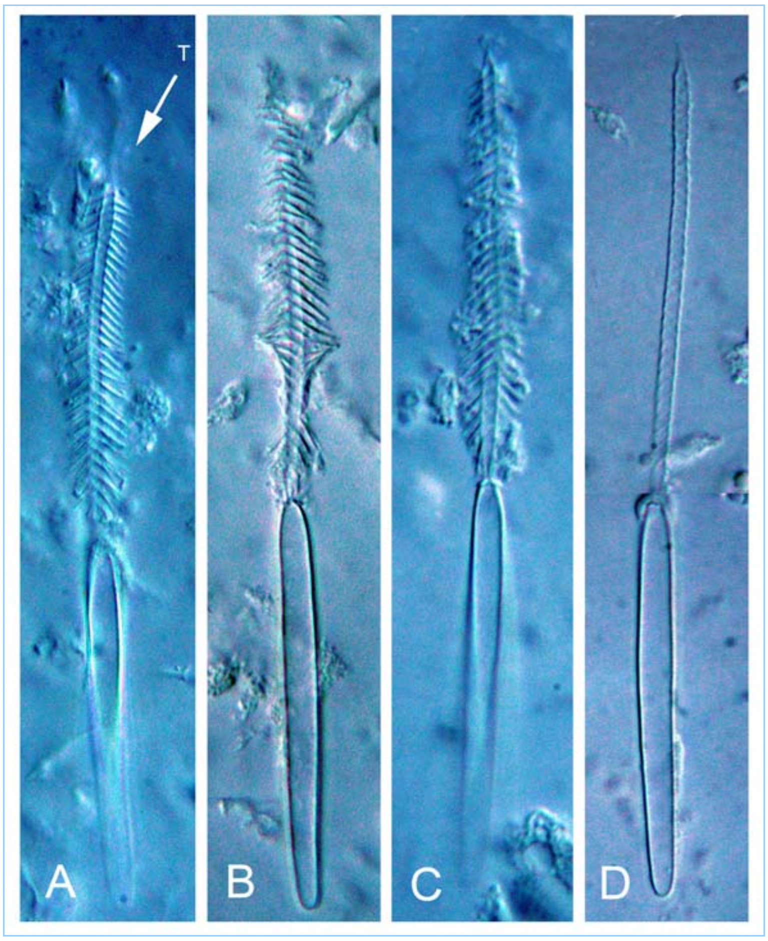

Figure 15.4.– Exploded capsules of the microbasic *p*-mastigophores (*p*-rhabdoids B *sensu* Schmidt, 1974) from the acontia. A) Detail of the distal tubule (T) beyond the shaft. B) Shaft without final tubule (microbasic *p*-amastigophore?); C) Shaft with a small thin tubule at the end; D) Shaft without large spines.

The observed material differs in some details from Carlgren's (1934) examination; basitrichs of the filaments and acontia have a larger breadth (2.5-4µ instead of 1.5-2µ, Table 15); tentacles are not thickened at the aboral side (or maybe it was not possible to obtain good histological sections), and the presence of cinclides was not confirmed.

There are slight differences between the well known species of the family Kadosactidae. *K. rosea* does not have microbasic *p*-mastigophores on its tentacles and it is an arctic bathyal species. *K. antartica* has a globular cylindrical column, and it is an antartic bathyal and abyssal species (Rodríguez and López-González, 2005). *K. sulcata* has a globular column with a tuberculate scapus without cuticle nor tenaculi, the pedal disc is concave and it is a North Atlantic species from bathyal and abyssal waters. All these three species show very large microbasic *p*-

mastigophores on the acontia, more than 100µ while in our material the maximum length observed was 55.5µ (Fig. 15.3.-P).

Also Carlgren's (1934) measurements agree with the ones from our material (see Table 15). *K. commensalis* has also holotrichs on tentacles and pedal disc which were not observed in the other species. The peculiar shape of their column and pedal disc (possibly due to the adaptation to commensalism) and the fact of being known only from abyssal area (PAP and Iberian abyss) are the most distinguishable specific characters, however still very subjective.

In previous studies, Carlgren (1932; 1933) first distinguished and then synonymised the genera *Kadosactis* and *Sagartiogeton* (*K. (Sagartiogeton) antartica* and *K. (Sagartiogeton) sulcata*) Carlgren (1949) distinguished *Kadosactis* from *Sagartiogeton* because of the number of distal and proximal mesenteries. He established that in *Kadosactis,* mesenteries grow proximal to distal part (so there are more mesenteries proximally than distally) and in *Sagartiogeton* they grow equally proximally and distally, but originate first proximally (so there are more mesenteries proximally). However, due to the condition of the material it was not possible to verify this character.

Another difference is the mesogleal thickness of the aboral base of tentacles, a generic character for *Kadosactis;* however in the analysed species this feature was not observed, so it is recommended to revise the genus diagnosis accordingly. *Kadosactis* species do not have restricted or circumscript retractors and in general they have a similar homogenous nematocyst equipment which is totally different from *Sagartiogeton* species.

Family Antipodactidae

Diagnosis (from Rodríguez *et al*., 2009)

Nynantheae with basilar musculature. Mesogleal marginal sphincter muscle. One tentacle connecting to each endo- and exocoel. Mesenteries regularly arranged, not differentiated into macro- and microcnemes. Acontia with macrobasic *p*-amastigophores and basitrichs. Cnidom: spirocysts, basitrichs, holotrichs, microbasic *p*-mastigophores and macrobasic *p*-amastigophores.

Genus *Antipodactis* Rodríguez, *et al.* 2009

Diagnosis (adapted from Rodríguez *et al*., 2009)

Antipodactidae with elongated or strongly compressed body. Aboral end slightly rounded or expanded. Column divisible into scapus and scapulus; scapus bears tenaculi with cuticle. Scapulus with cinclides (sometimes absent?) irregularly arrayed. Tentacles not numerous: about as many tentacles as mesenteries at the margin. Longitudinal muscles of tentacles and radial muscles of oral disc ectodermal. Strong mesogleal marginal sphincter muscle. Mesenteries regularly arranged, not differentiated into macro- and microcnemes, first three cycles fertile. More mesenteries proximally than distally. At least 12 pairs of perfect mesenteries at mid-column; two pairs of fertile directives each attached to a siphonoglyph. Retractor muscles of older mesenteries strong, restricted. Parietobasilar muscles well developed. Acontia with macrobasic *p*-amastigophores and basitrichs. Cnidom: spirocysts, basitrichs, holotrichs, microbasic *p*-mastigophores, and macrobasic *p*-amastigophores.

Type species

Antipodactis scotiae Rodríguez *et al*., 2009

Species included in the genus

Antipodactis awii Rodríguez *et al.,* 2009; *Antipodactis scotiae* Rodríguez *et al*., 2009

Observations

Antipodactidae family includes at the moment only the genus *Antipodactis* which was recently created for two new polar deep-sea species, *A. scotiae* and *A. awii*. These two species have bipolar distributions, *A. scotiae* from Scotia Sea (Antarctica) and *A. awii* from the Norwegian Sea (Arctic). They are mainly characterized by the presence of macrobasic *p*-amastigophores sensu England (1991) in the acontia (Rodríguez *et al*., 2009).

Antipodactis ifremeri sp. nov.

(Fig.16.1-16.3; Table 16)

Material examined

CARACOLE: stn. PL 130-08: 41 specimens.

Description

External anatomy (Fig.16.1).— Pedal disc broad, very well developed, undulated (probably were attached to mollusc shells), diameter 2.5cm. Cinclides were not observed on scapus, nor on scapulus because it is totally invaginated.

All exemplars were in contracted state. Column height more or less 1cm. Diameter variable depending on specimen size and contraction. Column divided in scapus and scapulus (reversed). A few of them were not totally contracted, however they were in bad state. Margin differentiated, extended. Oral disc strongly contracted, tentacles (more than 60 in number) totally inverted. Scapus with cuticle and tenaculi (small papillae).

Internal anatomy (Fig.16.2).— Mesenteries hexamerously arranged in five cycles. More mesenteries proximally than distally. First and second cycles perfect; third cycle with both perfect and imperfect mesenteries; fourth and fifth cycles imperfect, incomplete. Three initial cycles fertile. Directives fertile. Fourth cycle sterile. Fifth cycle only present proximally, sterile. Retractor muscles of initial three cycles of mesenteries strongly restricted, reniform.

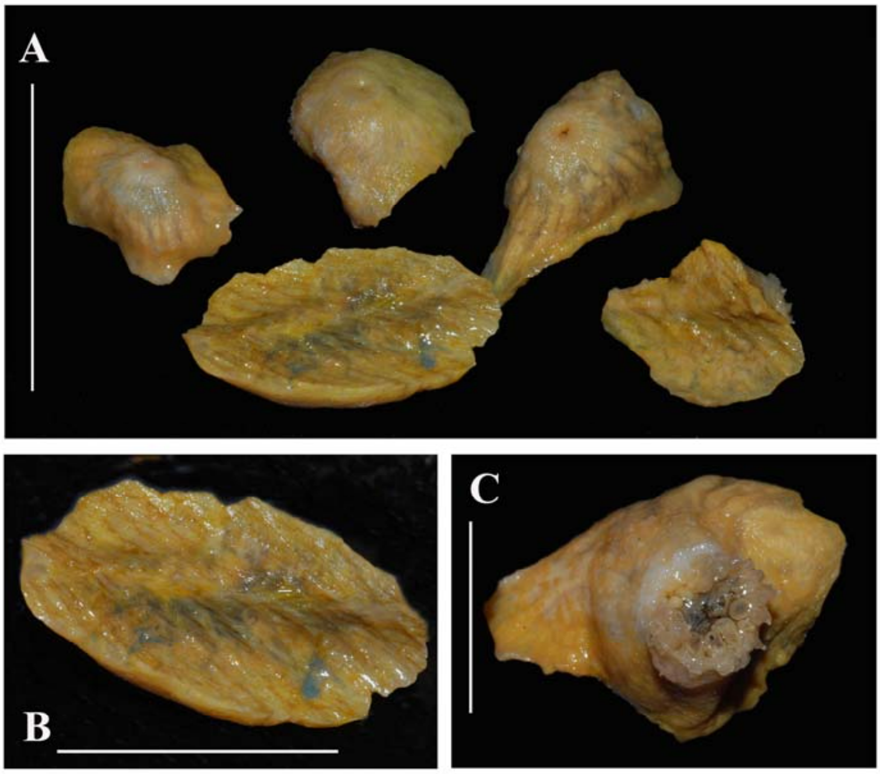

Figure 16.1.- *Antipodactis ifremeri* sp. nov.. External anatomy [PL 130-08]: A) Specimens in contracted form; B) Pedal disc view; C) Oral disc view showing tentacles insertions. Scale: A, 3cm; B, 2 cm; C, 2cm.

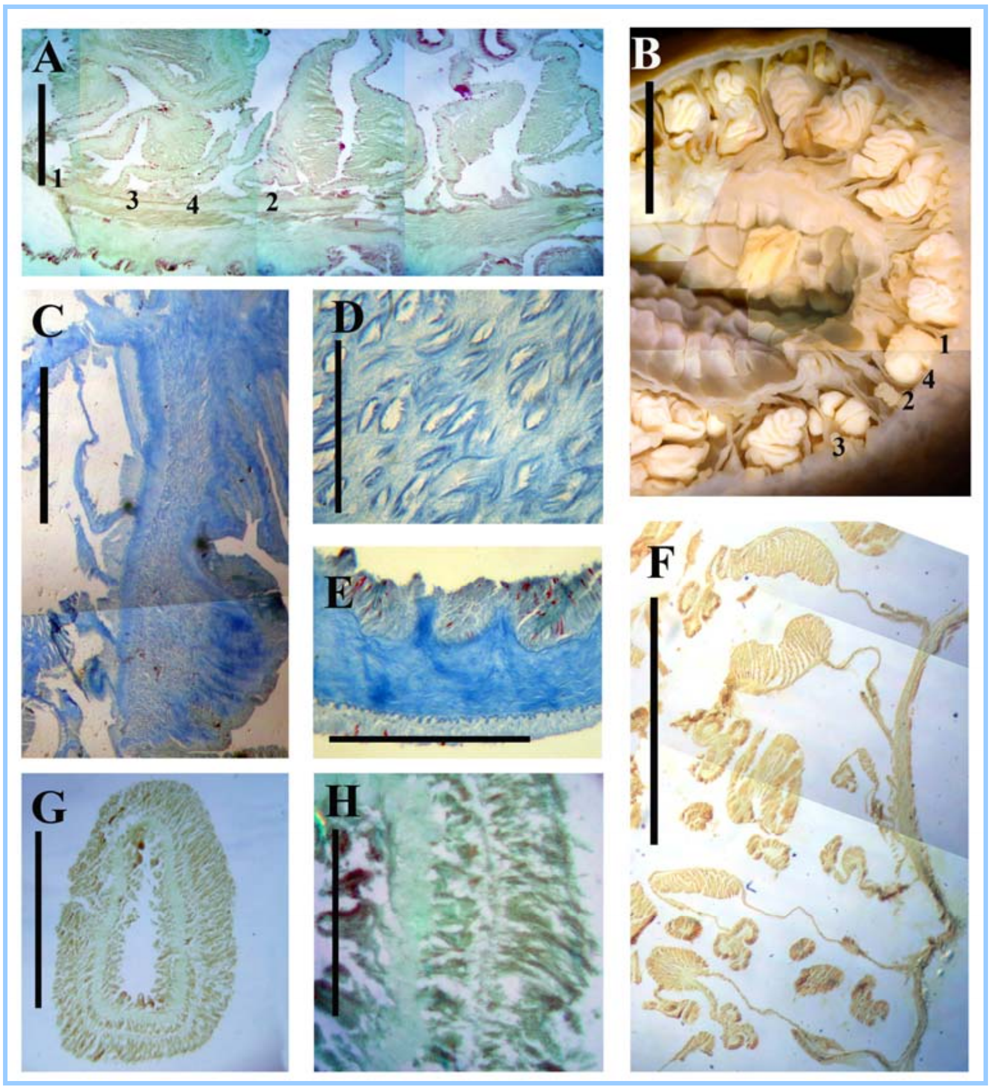

Figure 16.2.– *Antipodactis ifremeri* nov. sp. Internal anatomy [PL 130-08]: A) Transversal section at actinopharynx level showing cycles of mesenteries [130-8 (1)]; B) Transversal section actinopharynx level, without histology [130-8 (4)]; C) Longitudinal section at distal part showing sphincter; D) Detail of sphincter mesogleal; E) Detail of column; F) Transversal section at proximal level showing retractors and parietobasilar musculature; G) Transversal section of tentacle; J) Detail of tentacle musculature ectodermal. Scale: A, 3mm ; B, 4mm; C, 4mm; D, 0.1mm; E, 1mm; F, 6mm; G, 0.7mm; H, 0.3mm; F, 2.5mm.

Mesenteries of third cycle differentially developed, some pairs with slightly restricted retractors and some with poorly developed muscle. Mesenteries of last two cycles poorly developed.

Gametogenic tissue well developed. Parietobasilar musculature well developed. Basilar musculature weak. Tentacles longitudinal musculature ectodermal. Acontia present. Sphincter musculature mesogleal, well developed, reticulate.

Cnidom (Fig. 16.3; Table 16).— Spirocysts, basitrichs, holotrichs, microbasic *p*-mastigophores and macrobasic *p*-amastigophores.

Colour.— All organisms were preserved in ethanol; pale yellow.

Table 16.– Dimensions of cnidae in *Antipodactis ifremeri* sp. nov. Specimens: [PL 130-08]. X: average; SD: standard deviation; S: sample; N: number of measured capsules; F: frequency: +++ very common; ++ common; + less common; --- sporadic. Abbr. Mic. Microbasic; Mac. Macrobasic. (*) Average based on measures of less than 40 capsules, which is considered the meaningful minimum (Williams, 1996; 1998).

Category	Fig. 16.3	Range of length and width of capsules in µm	X ± SD	S	N	F	A. awii Rodríguez et al., 2009	X ± SD	F
PEDAL DISC									
Basitrichs 1	A	(7-11) x (1.5-2)	9.1±1.1 x 1.8±0.2	3/3	60	++	(11.3-15.3) x (2.1-3.3)	13.4 ± 1.1 x 2.8 ± 0.3	++/+++
Basitrichs 2	B	(14-24) x (3-4)	18.8±2.2 x 3.1±0.2	3/3	60	+++	(20.3-29.9) x (3.1-5.0)	25.4 ± 2.0 x 4.0 ± 0.4	++
Mic p-mastigophores	C	(12.5-22) x (4-4.5)	15.0±1.7 x 4.0±0.1	3/3	60	+++	(20.1-35.3) x (4.0-6.0)	27.5 ± 4.0 x 5.2 ± 0.5	+/++
Holotrichs	–	–	–				(16.4–23.2) 9 (6.8–7.2)	Contamination??	---
COLUMN									
Basitrichs 1	D	(5-10) x (1-2)	8.1±1.2 x 1.4±0.2	3/3	60	+++	(10.5-16.1) x (1.8-3.3)	13.3 ± 1.3 9 2.6 ± 0.4	++
Basitrichs 2	E	(13-27) x (2.5-3.5)	16.5±1.8 x 3.0±0.1	3/3	60	+++	(19.1-27.9) x (2.5-4.7)	23.7 ± 2.2 x 3.9 ± 0.4	++/+++
Mic. p-mastigophores	F	(23-36) x (4-6)	31.3±3.1 x 4.9±0.3	3/3	60	+++	(23.8-37.4) x (4.4-5.5)	29.3 ± 6.0 9 5.0 ± 0.4*	±
Holotrichs	G	(19-23) x (6)	20.6±1.2 x 6.0(*)	1/3	8	---	(19.0-25.6) x (5.9-7.9)	22.3 ± 1.9 x 7.2 ± 0.6*	±
TENTACLES									
Spirocysts	H	(18-40) x (2.5-7)	28.7±6.1 x 4.6±1.3	3/3	58	+	(23.0–43.5) x (3.5–9.6)	35.2 ± 5.0 x 5.9 ± 1.7	+++
Basitrichs	I	(18-25) x (2-3)	21.6±1.6 x 2.9±0.3	3/3	60	+++	(22.3–31.3) x (3.0–4.7)	27.0 ± 2.6 x 3.7 ± 0.5*	+/++
Mic. p-mastigophores	J	(24-45) x (4-5)	32.7±4.1 x 4.2±0.4	3/3	60	+++	(36.1–50.0) x (5.1–7.6)	42.1 ± 2.4 x 6.1 ± 0.6	++/+++
PHARYNX									
Basitrichs 1	K	(10-15) x (1.5-2)	12.8±1.4 x 1.8±0.2	3/3	60	+++	(12.8–23.2) x (2.0–4.1)	15.6 ± 1.9 x 2.9 ± 0.4	+/++
Basitrichs 2	L	(19-37) x (2-3.5)	26.8±3.1 x 2.9±0.2	3/3	60	+++	(28.5–44.1) x (3.6–5.3)	37.5 ± 3.4 x 4.5 ± 0.4	++/+++
Mic. p-mastigophores	M	(19-39) x (3.5-5)	27.1±3.5 x 4.2±0.4	3/3	60	+++	(34.4–48.0) x (4.8–6.5)	41.6 ± 3.1 x 5.8 ± 0.4	++/+++
FILAMENTS									
Basitrichs	N	(9-13) x (1.5-2)	11.3±1.4 x 1.6±0.2(*)	2/3	22	--	(12.8–19.1) x (2.0–3.3)	15.6 ± 1.4 x 2.7 ± 0.3	++/+++
Mic. p-mastigophores 1	O; P	(9.5-16) x (3-4)	12.3±1.8 x 3.5±0.4	3/3	47	++	(12.9–22.6) x (3.2–5.5)	18.2 ± 1.7 x 4.3 ± 0.6	+/++
Mic. p-mastigophores 2	Q	(20-40) x (4-5)	27.6±4.2 x 4.4±0.5	3/3	59	+++	(33.6–47.3) x (4.9–7.0)	41.0 ± 2.6 x 5.8 ± 0.4	+/++
ACONTIA									
Basitrichs 1	R	(13-20) x (2)	16.1±1.6 x 2(*)	3/3	24	--	(12.6–24.1) x (2.0–3.6)	18.0 ± 2.6 x 2.9 ± 0.4	++/+++
Basitrichs 2	S	(34-44) x (3-3.5)	38.2±2.4 x 3.1±0.2	3/3	60	+++	(40.3–49.9) x (3.1–5.3)	44.9 ± 2.4 x 4.3 ± 0.5	++/+++
Mac. p-amastigophores	T	(59-66) x (6-7)	59.6±3.3 x 6.2±0.4	3/3	60	+++	(64.2–78.0) x (6.4–8.8)	70.4 ± 3.2 x 7.4 ± 0.6	++/+++

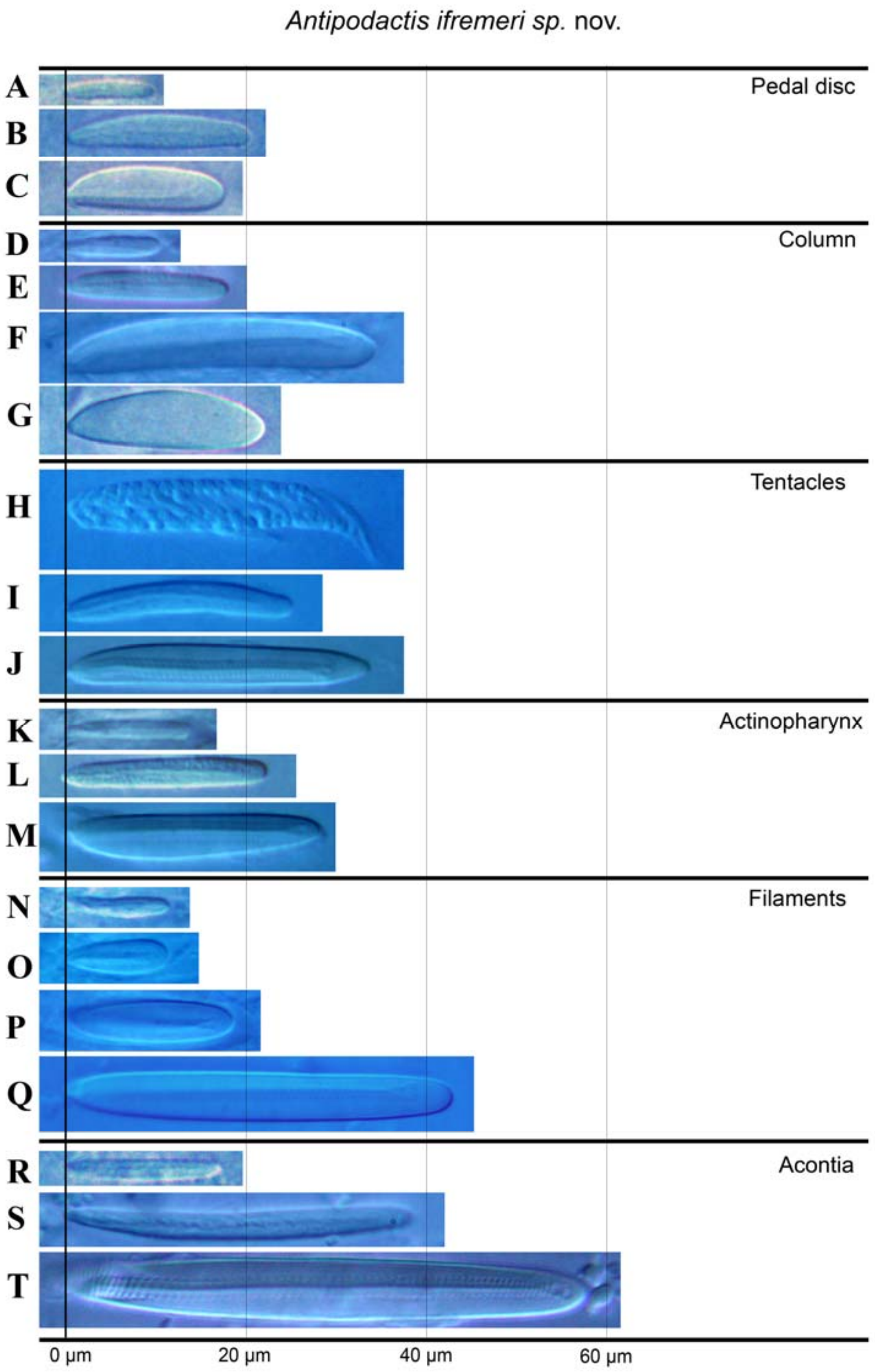

Figure 16.3.– *Antipodactis ifremeri* sp. nov. Cnidae: A) basitrich 1; B) basitrich 2; C) microbasic *p*-mastigophore; D) basitrich 1; E) basitrich 2; F) microbasic *p*-mastigophore; G) Holotrich; H) spirocyst; I) basitrich; J) microbasic *p*-mastigophore; K) basitrich 1; L) basitrich 2; M) microbasic *p*-mastigophore; N) basitrich; O and P) microbasic *p*-mastigophore 1; Q) microbasic *p*-mastigophore 2; R) basitrich 1; S) basitrich 2; T) macrobasic *p*-amastigophore.

Geographic and bathymetric distribution

The two *Antipodactis* species have polar distributions, *A. scotiae* from Antarctica and *A. awii* from the Arctic. The examined material was found on the Rockall Bank at 777m depth. With this new distribution, the genus *Antipodactis* is not strictly polar neither abyssal, once the new specie was found in the Boreal area at bathyal depth.

Etymology

The specific epithet honours the Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER, France), who gave the opportunity to study this extraordinary organism.

Discussion

All specimens became very contracted, because of the immediate formaldehyde preservation. It was very difficult to obtain clear information about characters as sphincter, length of the column, basal musculature and to make the adequate transversal sections to observe mesenterial arrangement.

The new specie is corroborate with *Antipodactis* genus principal features: aboral bases of tentacles are not thickened; mesenteries are more numerous proximally than distally; at least some of the mesenteries of the third cycle are perfect; the retractor muscles are restricted; the parietobasilar muscles are differentiated and strong and comprises macrobasic p-amastigophores in their acontia. The presence of cinclides was not seen probably because of the inverted state of the scapulus, once in *Antipodactis* they are distributed along scapus only.

The principal differences between *Antipodactis* species are the internal anatomy, cnidae, and geographic distribution. However, *Antipodactis ifremeri* sp. nov. also differs externally, because all observed specimens are strongly contracted of 10mm height and large diameter (20-30mm) and their bases extended, whereas *A. scotiae* and *A. awii* have the body elongate (36mm and 25mm, respectively) and small diameter (13mm and 10mm, respectively).

A. ifremeri sp. nov. is somewhat an intermediate specie, because *A. scotiae* has only four cycles of mesenteries, *A. awii* has a fifth and a partial sixth cycle (Rodríguez *et al*., 2009) whereas *A. ifremeri* sp. nov has four and a partially fifth cycle proximally. The retractor muscles of the perfect mesenteries differ: at distal part are less reniform showing variable sizes and shapes, and at proximal part are strongly reniform and densely packed. Also the diameter vs. number of mesenteries differs: *A. scotiae* has 13mm of diameter and only four cycles; *A. awii* has shorter diameter (10mm) and six cycles; and *A. ifremeri* nov. sp has a larger diameter (between 10 to 30mm, depending on specimen size) but do not have more mesenteries than the other two species (only five).

Regarding Table 16, the examined material has different ranges of nematocysts, which differ from *A. awii* because, in general, are smaller or overlaps. However, all types of capsules are very close to *Antipodactis* species descriptions. One of the most important characters found was the presence of types of nematocysts in the acontia extremely similar to those *Antipodactis* species, which were diagnosed as being large "macrobasic" *p*-amastigophores and two sizes of basitrichs (see Rodríguez*, et al.* 2009).

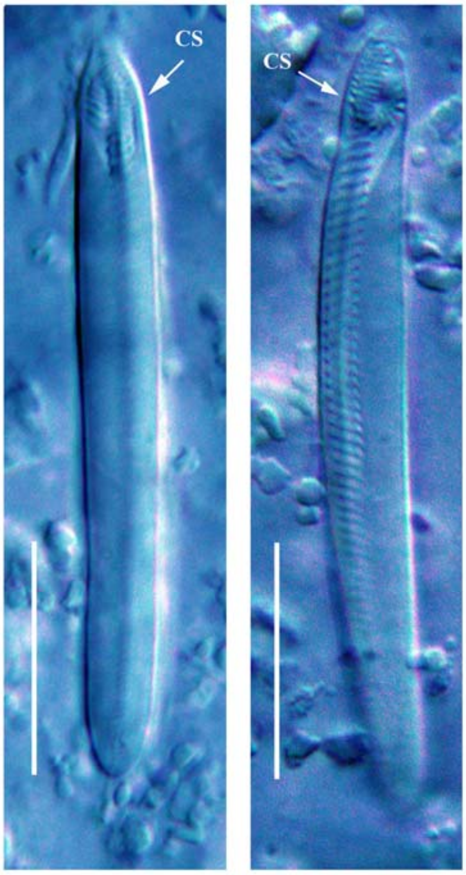

Figure 16.4.**–** Images of macrobasic *p*-amastigophores of the acontia from *Antipodactis ifremeri* sp. nov. showing the differentiated basal part. cs: coiled shaft. Scale: 20µm.

The distinction between "macrobasic" and "microbasic" varies between authors. Weill (1934) states that they differ by the greater length (at least four times longer) of the thickened proximal shaft in the "macrobasic" type. It was not possible to observe the shaft fired because only formalin-fixed material was available. Moreover, these nematocysts have a distinct appearance and agree with England (1991) definition, who says that the "macrobasic" has a long, differentiated basal part of the shaft that coils within the undischarged capsule (see Fig. 16.4).

The size of the macrobasic *p*-amastigophore is slightly smaller when compared with the other two *Antipodactis* species as well (see comparison with *A. awii*, Table 16).

The presence of macrobasic *p*-amastigophores and basitrichs in the acontia in actiniarian is very uncommon, and presently it is totally exclusive of *Antipodactis* genus.

Many abyssal species of the genus *Sagartiogeton* have also very long *p*-amastigophores and basitrichs in the acontia, however these were diagnosed as "microbasic" (Carlgren, 1942), and none of these species has more than 12 pairs of perfect mesenteries. A review of *Sagartiogeton* abyssal species is necessary, to prove the type of nematocysts of the acontia (if they present or not the same shape, coiled shaft at the base and ultrastructural studies of the discharged capsules).

CHAPTER II: BIOGEOGRAPHY

INTRODUCTION

The geological history of North Atlantic biogeographic regions

The Arctic-North Atlantic domain is an extremely relevant area for biogeographical studies. The area covered in this compilation includes the Arctic (Canada and Eurasian basins, Norwegian-Greenland Sea, Labrador Sea and Baffin Bay), the North-western Atlantic (North America), the North-eastern Atlantic (Faroes-Shetland Channel, Celtic-Irish Sea, English Channel and Iberian Sea), the northern part of North Africa (Mauritanian Sea), and the "Western Tethys realm" which embraces the Mediterranean Sea (Briggs, 1995; Ziegler, 1999).

Several lines of evidence suggest that ecological and historical phenomena are very interrelated and implicated at large scales. To understand the actual biogeography and the distribution limits of benthic organisms in the North Atlantic it is essential to know the geological eras of the Earth (position of continents) and their climatic latitudinal changes.

In the Jurassic, Cretaceous, and Paleogene, the richest marine fauna was characteristic of part of the Tethys Sea that included southern Europe and northern Africa. The high taxonomic capacity of this region was apparently determined by its tropical climate and a complex system of semiclosed seas between converging continents (Mironov, 2006). Since the late Paleogene to the recent evolution of the Arctic-North Atlantic and Western Tethys domains, families and genera which where originated at that time have many recent representatives widely distributed in cold and temperate waters in the North Atlantic (Golikov, *et al.* 1990).

The formation of the Atlantic boreal biogeographical areas began with the occurrence of a mountainous glaciation in the Northern high latitudes and also an intensified glaciation in the southern pole (Golikov, *et al.* 1990). The temperature of surface waters in the North Atlantic fell to 8ºC in winter and 20 to 21ºC in summer. The initial boreal species, characteristic of the region off the European shores had a Mediterranean-Lusitanian origin (Golikov, *et al.* 1990).

In the Neogene the trans-Arctic exchange of marine organisms, established many species of Pacific boreal origin in the North Atlantic, mainly through the Bering Strait which, according to recent data (Gladenkov *et al*., 2002), took place 5.32 million years ago. Like most other biotic interchanges, the direction of interchange was highly asymmetric (Vermeij, 1991). The abyssal North Atlantic and Arctic fauna had origin in the Antarctic abyssal fauna which had spread along meridians, mainly at depths exceeding 3000m (Mironov, 2006).

Approximately 1.8 million years ago, as a result of marked lowering of the sea level the Arctic Ocean became completely isolated from the Pacific and North Atlantic Oceans. One of the most important stages on the formation of the North Atlantic was the geological processes that occurred in the Faroes-Greenland district. Also the strong weakening or cessation of the inflow of the North Atlantic current into the Arctic seems to have been the major cause of the surface glaciation and the formation of a saline cold pseudoabyssal Arctic water mass and the emergence of Arctic endemic genera and species took place (Golikov, *et al.* 1990).

The relative warm saline Atlantic-Arctic water mass occupied an intermediate position (at depths 200 to 800m). Freshening of surface water during the beginning of the first interglacial period served as a base for the formation of estuarine-arctic water mass and its characteristic species (Golikov, *et al.* 1990). Further glacial and interglacial changes of climate of sea level accompanied by migration of organisms completed the youngest Arctic biogeographical region. Environmental fluctuations due to solar activity and intensification of North Atlantic current during interglaciation time developed oscillations in distribution and quantitative abundance of species and also their disappearance (Golikov, 1990).

The deep cold water movement pattern is largely determined by sea-floor topography. The circulation forces of deep-water currents are driven by differences in density due to temperature (colder) and salinity. Most of the North Atlantic Deep Water originally comes from the Norwegian Sea (in Davies, *et al.* 2001). This cold water flows south over the sills between Iceland and Scotland as well as over sills between Iceland and Greenland and into the eastern and central parts of the North Atlantic, moving along the basin walls defined by the mid-Atlantic Ridge and the continental shelves (Berch, 1995).

Studies on North Atlantic faunal distribution

The North Atlantic Ocean is certainly the most intensively sampled region of all deep-sea environments, even though there is no comprehensive biogeographic analysis of the living species so far (Watling, 2009). Many questions must be left unanswered and much remains to be learned from future research and exploration efforts but particularly from the "pooling" of knowledge.

Moreover the integration of an almost forbiddingly extensive diverse literature demands such a taxing effort that exhaustive coverage of the areas of interest could never be achieved. Biogeographic patterns have been investigated for several deep-sea taxa individually, e.g., protobranchs (Allen and Sanders, 1996), asteroids (Sibuet, 1979; Price *et al*., 1999), tunicates (Monniot, 1979), octocorals (Watling and Auster, 2005), scleractinians (Cairns and Chapman, 2001), hydroids (Henry *et al*.,2008), cumaceans (Watling, 2009) pycnogonids (Raiskii & Turpaeva, 2006) and fish on the continental slopes (Haedrich and Merrett, 1990; Koslow, 1993).

Recently, the biogeographical relationships of several invertebrate taxa found on the Reykjanes Ridge and North-eastern Atlantic seamounts were summarized by Mironov *et al*. (2006) and Mortensen *et al*. (2008). Vinogradova (1979) produced a biogeographic map of abyssal and hadal fauna for the world ocean, but did not offer many details of the macrofauna on which her map was based.

The species diversity of deep-sea fauna (latitudinal and bathymetric gradients) has been a controversial theme throughout the last decades (Grassle, 1989; Grant, 2000; Gage, *et al.* 2000; Gray, 1994 and 2001, Macpherson, 2002).

In the study area that will be covered by the present text, the Porcupine Abyssal Plain, the Rockall Bank and the Hebrides Terrace, are beyond the OSPAR regional delimitations. These areas are located on the Region V, also called the "Wider Atlantic", which is limited by 62º N, south to 36º N east ward to 11º W (Gubbay, *et al.* 2002). A more comprehensive study of the biogeographic limits must be done, especially for offshore areas to assure their management and establishment of MPAs on the OSPAR maritime area. Slopes as the Hebridean and Rockall have been regarded as pristine environments; however these areas have been trawled for deep sea fish during several years and are now actively prospected for oil (Grant, 2000; Gray, 2001). Marked environmental changes within the Atlantic Ocean are translated into significant differences in the composition of fauna assemblages both in a latitudinal range, between western and eastern sides and also between shelf to bathyal and abyssal depths. In the present work, composition and affinities of the actiniarian fauna of the main biogeographical areas of the North Atlantic are discussed.

MATERIAL AND METHODS

Biogeographical areas and data resources

The present study aims, at this stage of knowledge, to compare the actiniarian fauna of various zoogeographical areas of the North Atlantic Ocean. One difficulty found was to establish the most adequate approach, once different authors use diverse terminologies (zones, provinces, regions, domains, realms, biomes, divisions, ecotones, etc). However, according to biogeographic works for benthic invertebrates, the comparison of areas was established on the basis of Ekman's (1967) biogeographical divisions, which has been widely used with slight modifications (Briggs, 1974; Lopez de la Cuadra & Garcia-Gomez, 1992; Carballo *et al*, 1997; Medel & López-González, 1998).

The covered area comprises the North-western Region (North American Province); the Norwegian-Greenland Sea (Arctic Region); all of Europe (Boreal Subregion from the northern boundary to the western entrance of the English Channel); the Atlanto-Mediterranean Subregion (Lusitanian province, from the English Channel to south of the Strait of Gibraltar, including Azores and Madeira), along with the Mediterranean Province and the Northern parts of the North of Africa (Mauritanian Province).

The North Atlantic and Mediterranean actiniarians were analyzed to discriminate possible trends in the bathymetric and latitudinal distribution.

For this study, we used a classification that comprises three regions, two sub-regions and four provinces, detailed below (see also Fig. V):

I. ARCTIC REGION (AR)
II. NORTH-EASTERN REGION (NEA)
    i. BOREAL SUBREGION (BO)
    ii. ATLANTIC-MEDITERRANEAN SUBREGION (ATM)
        1. *Lusitanian Province* (LU)
        2. *Mediterranean Province* (ME)
        3. *Mauritanian Province* (MA)
III. NORTH-WESTERN REGION
        North-American Province (NA)

The data compilation used in the present study is based on a bibliographic revision, including the results obtained in the present study. Species checklists were compiled by combining information obtained from us and from bibliographical sources. An impressive amount of distributional data is already available on the online database *"Hexacorallians of the World"* (http://hercules.kgs.ku.edu/Hexacoral/Anemone2/index.cfm). However, some part (ex. the Lusitanian province) is hidden in a recondite literature and an exhaustive review was necessary in order to elaborate this species/area checklist.

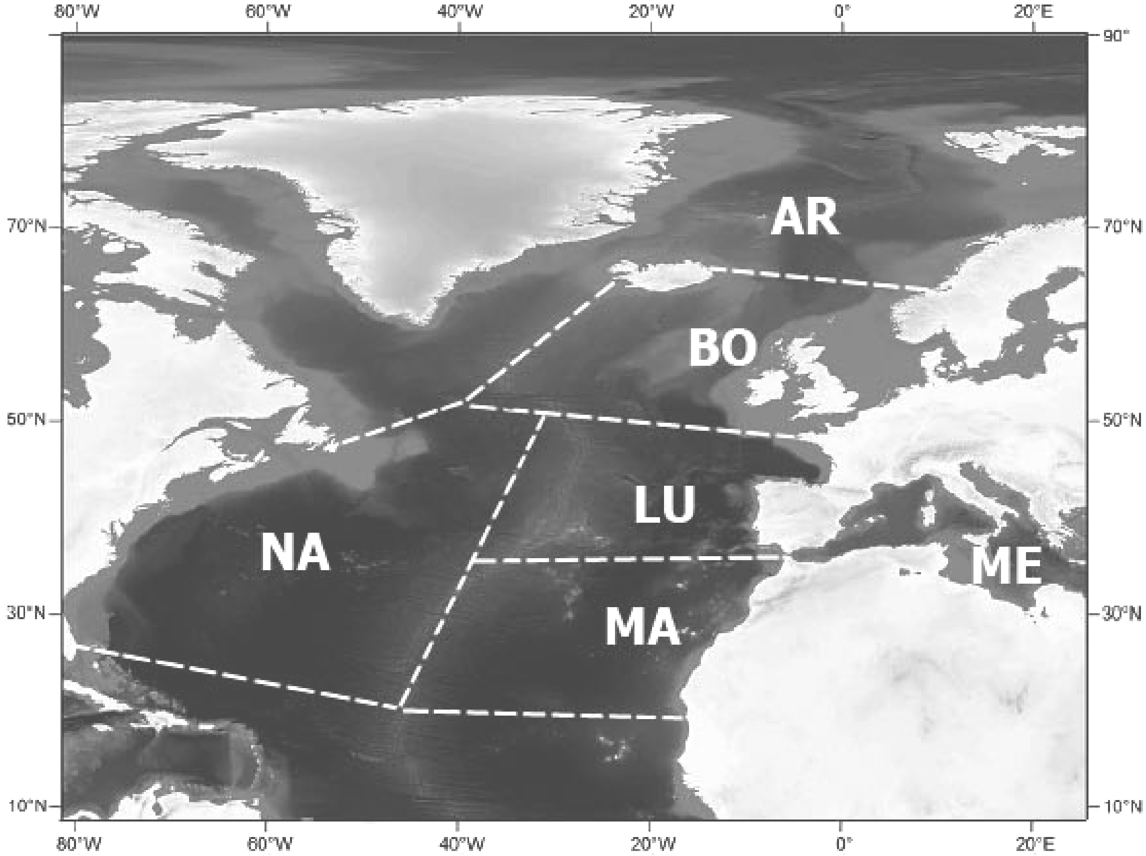

Figure V.– Map of Biogeographical regions, subregions and provinces of the North Atlantic considered in this study: Arctic Region (AR), Boreal Subregion (BO), Lusitanian Province (LU), Mediterranean Province (ME), Mauritanian Province (MA) and North-American Province (NA). White lines represent theoretical limits between regions. Adapted from Medel & López-González (1998) and Watling (2009).

Bathymetric zonation

Our research was conducted by comparing actiniarian fauna from most of the North Hemisphere (Atlantic and Mediterranean) regions among depth zonation. For bathymetric comparisons all regions were divided within the following boundaries: shelf (0 to 200m), bathyal (200 to 3000m) and abyssal (3000 to 6000m).

In studies examining general faunal change from the shelf break at 200m to the abyss, up to seven different faunal zones have been recognised. 3000m has been proposed as the start of the abyssal fauna (Hansen, 1975; Sibuet, 1979; Billett, 1991). If these depth boundaries occur at many locations worldwide it may be considered as evidence that important controlling variables are present at these depths and probably they may occur globally. However, Olabarria (2006) argued that there is no global consistency in such patterns suggesting that processes structuring bathymetric patterns diversity in the slope zones and abyssal benthos are likely to be different, either in magnitude or type, at the same areas and between different areas with similar depth characteristics, affecting different taxa.

We made the option described above, also to enable the comparison between temperate waters (such as the Mediterranean) and very cold waters (such as the Arctic), once more than 200m depth in the latter may be considered deep-sea.

Affinities based on faunal composition

In order to study the zoogeographical affinities between regions and subregions considered in the North Atlantic using the actiniarian fauna here recorded, we assigned a zoogeographic category to each of the sea anemone species listed according to its general geographical distribution. The zoographical categories considered for this study are shown on Table II.

Classification analyses

The species matrix data was transformed into presence/absence data. This transformation was applied in order to investigate faunal change from the large data set.

The Bray-Curtis similarity coefficient was used in order to obtain a hierarchical clustering with group average linking. Non-metric multidimensional scaling was also performed (PRIMER 5.0, Clarke and Warwick, 1994). This routine was also used to see the development of individual taxa on genera and familial ranks, in order to observe their distribution, degree of endemism, dispersion capacity and looking for relationships between bathymetric zones of the regions encompassed by the bibliographic revision, all species were aggregated in their respective genera and families.

Table II. Zoogeographic categories applied in this study.

I. ENDEMICS
I.a. Arctic - **AE**
I.b. Boreal - **BE**
I.c. Lusitanian - **LE**
I.d. Mediterranean - **ME**
I.e. Mauritanian - **MAE**
I.f. North American - **NAE**

II. ATLANTIC NORTHEAST (WHITHOUT MEDITERRANEAN) - AN
II.a. Arctic + Boreal
II.b. Boreal + Lusitanian
II.c. Arctic + Boreal + Lusitanian

III. ATLANTIC NORTHEAST (WITH MEDITERRANEAN) - ANME
III.a. Boreal + Mediterranean
III.b. Mediterranean + Lusitanian
III.c. Lusitanian + Boreal + Mediterranean
III.d. Arctic + Mediterranean + Boreal
III.e. Arctic + Boreal + Mediterranean + Lusitanian

IV. ATLANTIC NORTHEAST (WITH MAURITANIAN) - ANMA
IV.a. Lusitanian + Mauritanian
IV.b. Boreal + Mauritanian
IV.c. Mediterranean + Mauritanian
IV.d. Mediterranean + Mauritanian + Lusitanian
IV.e. Mediterranean + Mauritanian + Boreal
IV.f. Mediterranean + Mauritanian + Boreal + Lusitanian
IV.g. Arctic + Boreal + Lusitanian + Mauritanian
IV.h. Arctic + Boreal + Lusitanian + Mediterranean + Mauritanian

V. AMPHI-ATLANTIC - ANF
V.a. Boreal + North American
V.b. North American + Arctic
V.c. Boreal + North American + Arctic
V.d. Lusitanian + Boreal + North American
V.e. Boreal + Lusitanian + Mauritanian + North American
V.f. Boreal + Mediterranean + North American
V.g. Lusitanian + Boreal + Arctic + North American
V.h. Boreal + Mediterranean + Mauritanian + North American
V.i. Arctic + Boreal + Lusitanian + Mediterranean + North American
V.j. Arctic + Boreal + Lusitanian + Mauritanian + North American

VI. WIDE DISTRIBUTION- WI
VI.a. Arctic + Boreal + Lusitanian + Mediterranean + North Atlantic + Mauritanian
VI.b. Atlantic (North + South)
VI.c. Cosmopolitan

RESULTS

Actiniarian fauna composition in the North Atlantic areas

The complete census in the study area considered for this zoogeographic approach showed a total of 212 sea anemone species, in 89 genera and 32 families. The species checklist is shown on Appendix II.A, and families list at Table 18. The best represented family was Hormathiidae (46 species), followed by Edwardsiidae (32 species) and Actiniidae (32 species) at the same level, and by Actinostolidae (21 species). The best represented genus was *Edwardsia* (23 species), followed by *Amphianthus* and *Sagartiogeton* (10 species each one) and *Phelliactis* (7 species).

Data of affinity groups by bathymetric ranges (in absolute numbers and percentages) obtained was the base for the data matrix of the similarity analysis (see Appendix II.C).

Bathymetric distribution in the North Atlantic areas

Species distribution

The number of actiniarian species by bathymetric zones is shown on Figure 17 (and complemented with Appendix II.C). More than half (53% or 113 spp.) of the sea anemone species are restricted to the continental shelf (until 200m). Only 5% (10 spp.) are restricted to abyssal benthos.

Approximately, 18% (39 spp.) are between the surface till 3000m depth (accumulation of all species shared between the shelf and bathyal), 20% (42 spp.) lives only at bathyal depths (between 200-3000m). *Actinauge richardi* and *A. verrilli*, are the only present at all bathymetric zones.

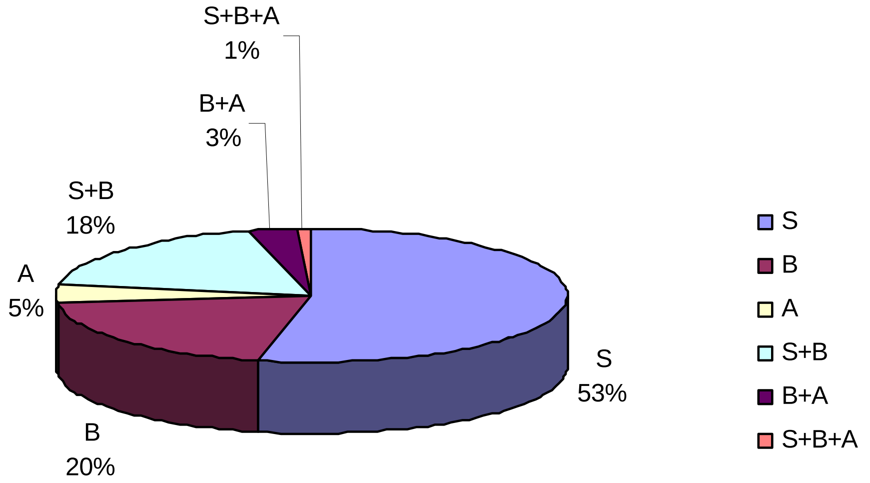

Figure 17. Bathymetric distribution of the total North-Atlantic Actiniarians species (%). Categories: S- Shelf; B- Bathyal; A- Abyssal.

Genera distribution

The best represented genus is *Edwardsia* with a shelf/bathyal distribution. Followed by *Amphianthus* and *Sagartiogeton* which are mainly shelf/bathyal. *Phelliactis,* which is mainly bathyal/abyssal, has also a shelf distribution in the Arctic cold waters (see Appendix II.A).

Families distribution

The best represented family is the Hormathiidae, distributed in all bathymetric zone. The Edwardsiidae has a shelf/bathyal distribution; the Actiniidae has mainly a shelf distribution (the only genera that extend their distribution to bathyal depths are *Bolocera; Epiactis and Bunodactis*) and the Actinostolidae has also a shelf/bathyal distribution (see below on Tab. 18).

Actiniarian composition at the North-eastern deep sea areas studied herein

The Porcupine Abyssal Plain fauna is composed of species that are either endemic or exhibit a very restricted distribution that extends only to nearby locations. Comparatively with other deep-sea areas, the Porcupine Abyssal Plain has a high number of endemic species such as *Daontesia porcupina*, *Segonzactis platypus* and *Iosactis vagabunda*. However its fauna was found to be most similar to the Boreal deep-sea region. For instance, *Actinauge abyssorum*, *Amphianthus bathybium* are shared with adjacent areas of the study and the Iberian area (in the Lusitanian province) and *Parasicyonis biotrans* near the Mid Atlantic Ridge at abyssal areas. Also, the Porcupine abyssal has low diversity, with only seven species recorded. However, these species are highly abundant and small in height (low biomass). *Parasicyonis biotrans* is the unique large species on this area.

The locations in the North of Ireland (in the case of the Hebrides Terrace and Rockall slope) are more diverse (11 species collected) however have more shared species (*Actinauge richardi*, *Phelliactis hertwigi*, *Bolocera tuediae*, *Actinostola abyssorum, Monactis vestita*) with other regions and depths. The faunistic composition is different between biotopes because the actiniarians live in different substrate types. Therefore, the fauna found was rather heterogeneous depending on the substrate or biotope type. *Actinauge richardi* has a Lusitanian/Mediterranean and Mauritanian component and is typical from mud bottoms; *Actinoscyphia aurelia* is Lusitanian and Mauritanian also from soft-bottoms. However, *Carlgrenia desiderata*, *Caracolactis maternalis* and *Antipodactis* *ifremeri* described in this work seem to be from special habitats, such as deep-sea cold water coral reefs present in continental slopes. Others such as: *Phelliactis hertwigi* occupy the Atlantic Northeast until Mauritanian area; *Bolocera tuediae* is amphi- Atlantic; and *Edwardsia tuberculata* has a southern and deeper distribution. The only known localities for *E. tuberculata* are the Norwegian continental shelf, Iceland coast and the Faroe Islands area (BIOFAR station 9018, Fautin, *et al.,* 2005).

Faunistic affinities among geographic areas and bathymetric zones

Species patterns

A preliminary plot of the cluster analysis, using all species and bathymetric zones per area (regions, subregions, and provinces) is represented in Fig. 18 (see also Appendix II.A, for the complete list of species and distribution). It demonstrates a clear bathymetric (shallow and deep waters) separation for the set of areas considered. Three major groups can be distinguished at the dendrogram (Fig. 18). The first group (G-I) is composed by deep-sea cold waters from all areas, which is separated by slightly less than 10% from the other large group (G-II), which contains bathyal (G-IIa) and shelf waters (G-IIb).

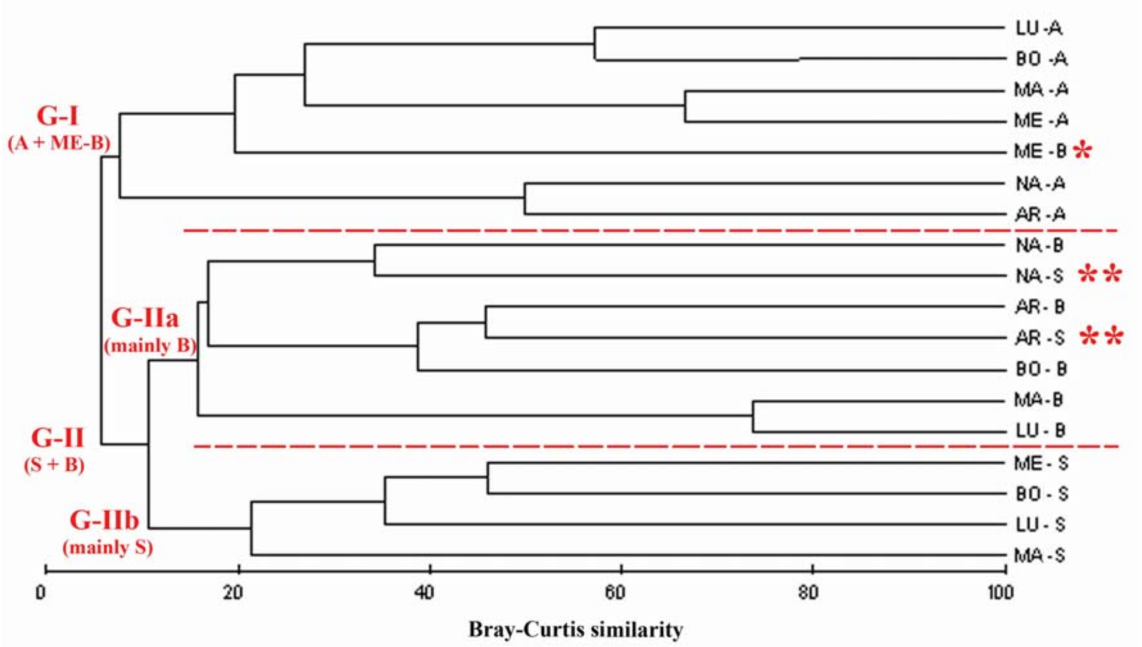

Figure 18.– Hierarchical cluster analysis of presence/absence transformed data of sea anemone species within their bathymetric and geographic distribution, based on a Bray-Curtis similarity coefficient.

In the Group I, the Arctic abyssal waters is closer (nearly 50% similarity) to the North American abyssal region. The other subdivision, the Mediterranean bathyal waters is closer to the Lusitanian-Boreal and Mauritanian-Mediterranean abyssal waters. In the Group IIa, the low presence of amphi-Atlantic species increases the faunistic differences between the western and eastern areas, as it can be observed by the similarity between the North American bathyal and shelf waters (NA-B, NA-S). Instead the Arctic bathyal and shelf waters are closer to the Boreal bathyal waters. The Mauritanian and Lusitanian bathyal waters share more than 70% similarity, probably due to the very scarce studies and therefore limited number of species recorded in those regions. The Group IIb, is composed by the shelf fauna, being the Mediterranean and Boreal closer (45%).

Discussions about similarity indices based on species distribution should be considered as tentative, but, despite the lack of information for the distribution of several species, some trends can be detected. Several species recorded are not relevant for the analysis of such patterns because they seem to be confined to individual areas or sites. The endemism is also high; nearly 55% of endemics were recorded for the studied regions (see Appendix II.C), a total of 116 species (see Appendix II.D). However many of these species were collected few times individually (ex. *Carlgrenia desiderata*, *Kadophellia bathyalis and Caracolactis maternalis*). The other 45% of the species (96 spp.) are recorded from two or more areas.

Many singleton occurrences were found making generalizations difficult. However, according to this approach, several recurrent distributions are frequent and may constitute patterns: 1) The abyssal fauna in the study area is clearly connected to the bathyal Mediterranean (see * in the dendrogram); abyssal faunas from NA and AR are closely positioned; 2) Bathyal fauna from the study areas (except for ME) are connected, and also related with shelf fauna from high latitudes (NA and AR) (see ** in the dendrogram); 3) Shelf fauna from temperate areas (NA and AR are excluded) are connected.

Actinauge richardi is the only species shared by the bathyal Mediterranean and the North Atlantic deep sea . The Arctic shelf/bathyal and Boreal bathyal fauna are connected due the presence of a high number of species common to both areas. Typical deep sea species from cold waters are, for instance: *Actinauge cristata*, *Actinernus nobilis*, *Actinostola abyssorum*, *Daontesia praelonga*, *Hormathia digitata*, *Parasicyonis sarsi* and *Phelliactis hertwigi*. The Boreal/Lusitanian/Mediterranean shelf waters connectivity is evident and represented by a group of species from temperate waters (see Appendix II.C). Just to mention some examples, they are: *Actinothoe sphyrodeta*, *Amphianthus dohrni*, *Anthopleura ballii*, *Aulactinia verrucosa*, *Sagartiogeton laceratus*, *S. undatus* and *Sagartia elegans*.

Genera patterns

The similarity analysis based on the distributions and number of species per genera (Fig. 19) resulted in the separation of two main groups. One group (G-I) is divided into two subgroups, one of them (G-Ia) contains high latitude and North-eastern Atlantic fauna (AR, BO, and LU) from abyssal areas, as well as, bathyal fauna from the Mediterranean region (ME),in one sub-set and the North-western Atlantic (NA) and temperate (ME, MA) abyssal faunal in the other set. The other group (G-Ib) contains the bathyal North-western Atlantic and temperate fauna (MA, LU, NA).

The second main group (G-II) is also divided into two subgroups, the first one (G-IIa) includes bathyal and shelf fauna of high latitudes (AR, BO) and North-western Atlantic (NA) fauna, while the other subgroup (G-IIb) contains shelf temperate fauna (ME, LU, MA).

We do think that the first separation is due to the lower number of species per genera in the southern (including NA) deep-sea benthos probably derived by the scarcity of data at the abyssal bathymetric range resulting from the low sampling effort in these deep-sea zones. However, we can observe that at the genus level the Boreal and Arctic fauna are more related. The high similarity between shallow temperate/warm waters of the southern areas is evidenced. On the contrary the NA shelf genera are closer to the cold northern areas.

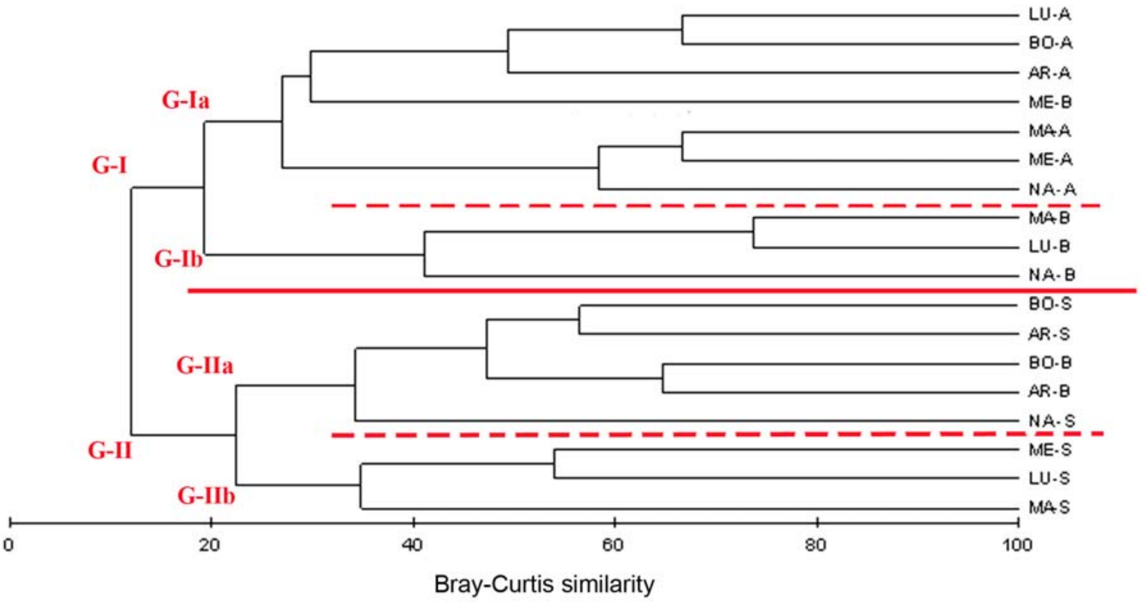

Figure 19.– Hierarchical cluster analysis of non transformed data of sea anemone species per genera within their bathymetric and geographical distribution, based on a Bray-Curtis similarity coefficient.

For a more clear overview of this information, a summary of the genera data in each sub-region or province is provided (numbers of genus on Tab. 17, are detailed in Appendix II.B).

According to the data on Tab. 17, shelves yield a higher number of genera than deeper waters. The Mediterranean shelf is the area with more genera diversity (38gen.), followed by the Boreal shelf (24gen.), the Arctic and the Lusitanian (with 19gen. each) and finally the North American (14gen) and the Mauritanian (with only 9gen.).

The Arctic and Boreal areas have high diversity of genera at depths that can go from shallow waters to 1000m (17 and 14, respectively). At greater depths, it is the Boreal sub-region that contains the higher number of genera (6gen.). The abyssal fauna in each area is represented by a very few number of genera.

Table 17.– Biogeographic distribution of total number of genera per bathymetric zones. Abbr. Geographic: AR, Arctic; BO, Boreal; LU, Lusitanian; ME, Mediterranean; MA, Mauritanian; NA, North American; Bathymetric: S, Shelf; B, Bathyal; A, Abyssal.

		BATHYMETRIC ZONES						
		S	**S + B**	**B**	**B +A**	**A**	**S+B+S**	**TOTAL**
GEOGRAPHIC AREAS	**AR**	**19**	**17**	**6**	**1**	**1**	**3**	**47**
	BO	**24**	**14**	**7**	**6**	**2**	**3**	**56**
	LU	**19**	**2**	**4**	**3**	**2**	**–**	**30**
	ME	**38**	**4**	**1**	**–**	**–**	**1**	**44**
	MA	**9**	**1**	**5**	**–**	**1**	**1**	**17**
	NA	**14**	**4**	**3**	**–**	**–**	**1**	**22**

The dendrogram obtained from the similarity analysis (Fig. 20) illustrates the division between groups of genera, elucidating the main differences between regions and bathymetric zones.

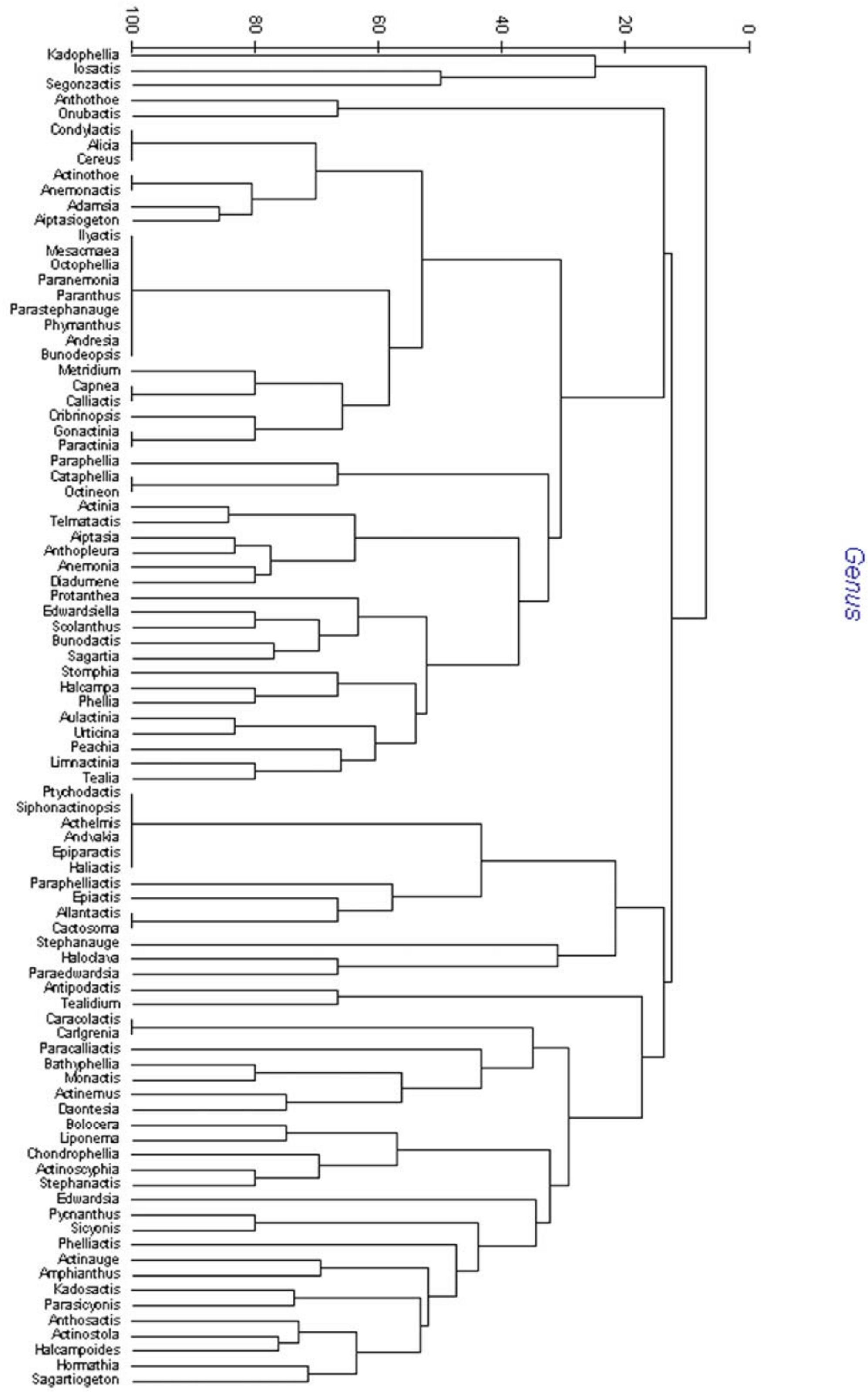

Figure 20.– Hierarchical cluster analysis of non transformed data of actiniarian species per genera within their bathymetric and regional distribution, based on a Bray-Curtis similarity coefficient.

The first group includes species present in the deep-sea and commonly abundant at higher latitudes, mainly cold deep-sea waters from Boreal and Subarctic areas (*Stephanauge*, *Tealidium*, *Actinernus*, *Actinoscyphia*, *Paracalliactis*, *Sicyonis*, *Phelliactis*, *Kadosactis*, *Paraphelliactis*, *Bathyphellia*, *Monactis*, *Carlgrenia*, *Stephanauge* and *Pycnanthus*). At the other side, there is also a cold water group that includes endemic Arctic genera (*Cactosoma*, *Allantactis*, *Haliactis*, *Epiparactis*, *Andvakia*, *Acthelmis*, and *Siphonactinopsis*) mostly from continental shelf benthos.

The other large group is composed by low Boreal, Mediterranean, Mauritanian and Lusitanian genera present in littoral habitats of the continental shelf (see Fig. 20). Several genera, *Kadophellia*, *Iosactis* and *Segonzactis*, form an out-group with low similarity to the other groupsi because these genera are endemisms with a distribution restricted to the Boreal and Mediterranean deep-sea benthos.

The other large group corresponds to genera which contains many genera shared between all bathymetric zones and regions (for instance, *Hormathia*, *Actinostola*, *Amphianthus*, *Actinauge*, *Edwardsia and Sagartiogeton*).

Family patterns

The Hormathiidae is the best represented family in the global evaluation (see Tab. 18), followed by, Actiniidae, Actinostolidae and then Edwardsiidae.

The family Actiniidae is the most abundant at shelf comparatively with slope and deep-sea environments, preferentially occurring on Boreal, Mediterranean and Lusitanian shelves sub-regions. The Edwardsiidae is more diverse at shelf than at slope/deep-sea, especially in Boreal and Arctic areas. Sagartiidae is also abundant especially at Boreal shelf waters while, at great depths, the dominant families are Hormathiidae and Actinostolidae. In the study area, the Kadosactidae, Iosactiidae and Bathyphelliidae are exclusively from deep-sea in Arctic/Boreal regions (see Tab. 18).

Table 18.- Zoogeographic distribution of species within families per bathymetric range.

	ART			BOR			LUS			MED			MAU			NA		
	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A
Actinernidae	1	1	-	-	1	1	-	-	-	-	-	-	-	-	-	-	1	-
Actiniidae	9	5	-	16	3	1	11	1	-	15	-	-	4	1	-	6	2	-
Actinoscyphiidae	1	-	-	-	2	-	-	1	-	-	-	-	-	2	-	-	1	-
Actinostolidae	9	10	3	7	11	1	-	-	-	2	-	-	-	-	-	2	-	1
Aiptasiidae	-	-	-	2	-	-	3	-	-	4	-	-	1	-	-	-	-	-
Aliciidae	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	-	-
Andresiidae	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Andvakiidae	1	-	-	-	-	-	1	-	-	3	-	-	-	-	-	-	-	-
Antipodactidae	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Capneidae	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Bathyphelliidae	-	2	1	-	2	2	-	-	1	-	-	-	-	-	-	-	-	-
Boloceroididae	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Condylanthidae	-	-	-	-	-	1	-	-	-	1	1	-	-	-	-	-	-	-
Diadumenidae	-	-	-	2	-	-	-	-	-	2	-	-	1	-	-	1	-	-
Edwardsiidae	9	5	-	16	4	-	2	-	-	2	-	-	1	-	-	2	-	-
Gonactiniidae	2	1	-	2	1	-	-	-	-	2	1	-	-	-	-	-	-	-
Halcampidae	3	2	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-
Halcampoididae	4	2	-	1	2	-	1	-	-	1	-	-	-	-	-	1	-	-

Table 18.- Cont.	ART			BOR			LUS			MED			MAU			NA		
	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A
Halcuriidae	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Haliactiidae	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Haloclavidae	1	-	-	4	-	-	1	-	-	2	-	-	1	-	-	2	-	-
Hormathiidae	11	13	3	14	22	6	2	5	5	11	3	1	2	6	2	5	6	1
Iosactiidae	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Isophelliidae	-	-	-	1	-	-	3	-	-	4	-	-	-	-	-	-	-	-
Kadosactidae	1	3	-	1	1	2	-	1	1	-	-	-	-	-	-	1	-	-
Limnactiniidae	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Liponematidae	1	1	-	-	1	-	-	1	-	-	-	-	-	1	-	1	-	-
Metridiinae	-	-	-	1	-	-	-	-	-	1	-	-	-	-	-	1	-	-
Octineonidae	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Phymanthidae	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Ptychodactiidae	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sagartiidae	4	5	-	8	2	-	4	-	-	8	1	-	2	-	-	1	1	-

Faunal composition of different areas of the North Atlantic

The graphic representation on histograms (Fig. 21), gives the composition in each sub-region or province, and demonstrates clearly the high percentage of endemic species at Arctic, Boreal and Mediterranean shelves when comparing with groups of shared species and in deeper waters. An overall view of the fauna composition is given in Appendixes II.B and II.C.

In total, the Arctic is the Region with more endemics in total with 47.7% of their fauna; after is the Mediterranean with 36.5%; followed by the Boreal with 31.1%; the North Atlantic with 20.7%; the Mauritanian with 13.0%; and the Lusitanian with 11.6%.

The Mediterranean shelf zone is the area with more percentage of endemic species (20sp. which represents 31.7% of the total Mediterranean species listed). The Mediterranean appears as clearly defined unit. It has a rich and distinctive actiniarian fauna with a high level of endemisms.

Next, the Arctic and the Boreal shelves, with 16 and 17sp., which represents 18% and 14% of their faunas, respectively. The North American, the Mauritanian and the Lusitanian shelves have a very small number of species endemic species (see Appendixes II.B and II.C) they have more shared species with other areas. At bathyal zones, the area with more endemisms is the Arctic (15.9%) followed by the Boreal (10.9%). At abyssal zone, it is the Boreal Sub-region with more endemic species (3.4%). At intermediate zones (S+B, B+A and all depths) there are few endemic species, only the Arctic has 10.2% of endemics that can live since the shallow to bathyal waters.

Regarding Fig. 21.b, the Boreal actiniarian fauna has around 69% of shared species (82sp. in total) to the adjacent locations included in this study. The Boreal sub-region has the highest affinity to Arctic shelf/slope (S+B and B), sharing 18 species, nearly 15% of Boreal species (see data on Appendix II.D and II.E). Just to mention some of the most characteristic species, they are: *Anthosactis janmayeni*, *Daontesia praelonga*, *Kadosactis rosea*, *Parasicyonis sarsi, Amphianthus mopseae* and *Phelliactis robusta*.

The Mediterranean fauna show 63.5% shared species with the other regions. Although has more shared species with North-eastern Atlantic (ANME), 46.0% of species (29sp) from shelves (see Appendix II.C and II.E).

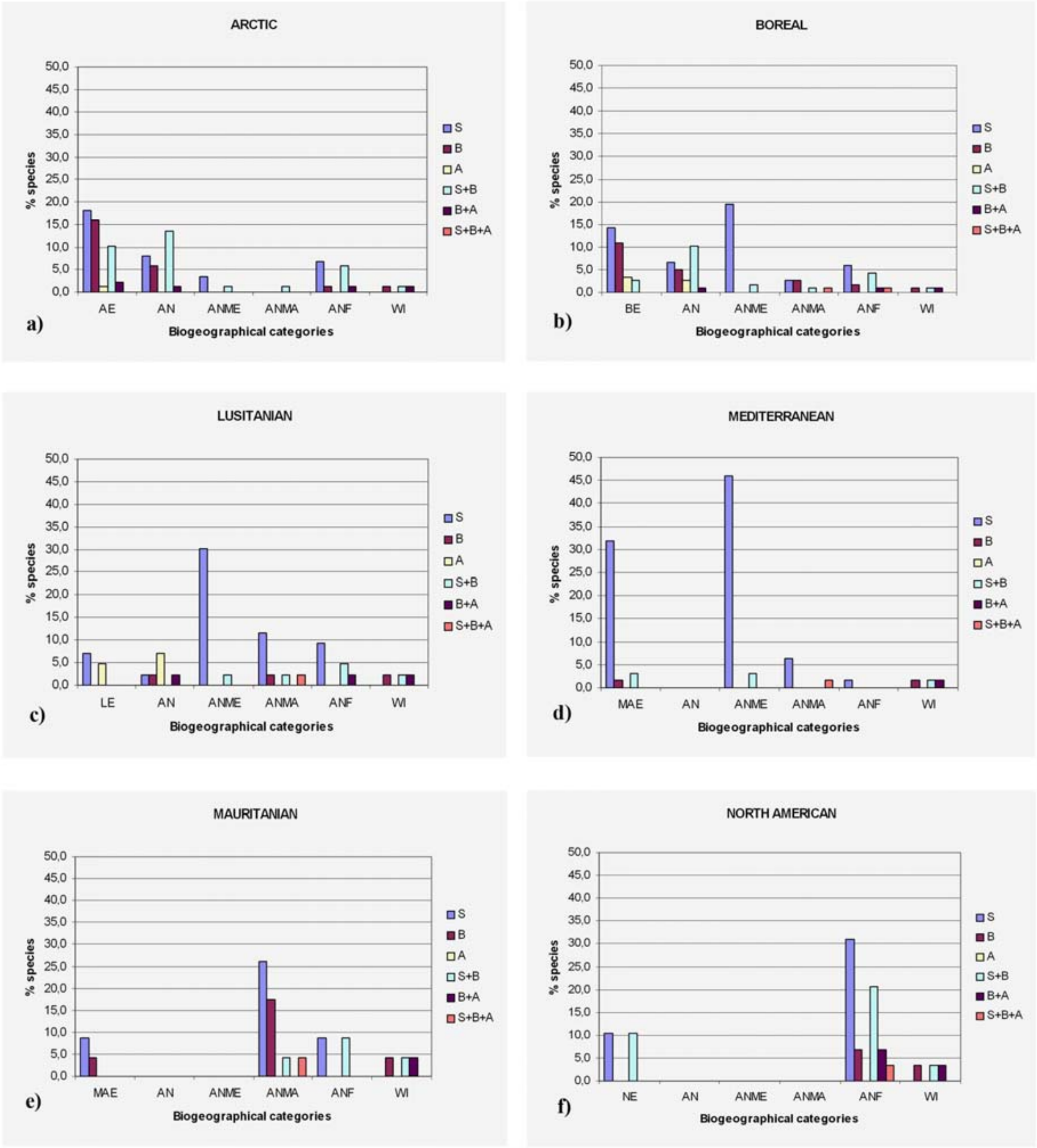

Figure 21.– Histograms of species percentage within biogeographical categories for each area. a) Arctic Region; b) Boreal Sub-region; c) Lusitanian province; d) Mediterranean province; e) Mauritanian province; f) North American province.

There are also close affinities of the ANME with the Lusitanian fauna, showing 13 shared species in shallow waters (representing 30.2% of the Lusitanian total fauna). This result may indicate that these Atlantic-Mediterranean species are presumably of Mediterranean origin. Of the species reported for the Mediterranean only 7.9% also occur in the temperate Mauritanian region, they are: *Anthopleura thallia*, *Anemonactis mazelli*, and *Actinothoe sphyrodeta* in the shelves and *Actinauge richardi* at all depths.

The actiniarian fauna from the Western Atlantic (North American) has a total of 23 shared species, from which 20 are amphi-Atlantic (e.g.: *Actinauge longicornis* and *A. verrilli*, *Amphianthus* *bathybium*, *Aulactinia stella*, *Kadosactis abyssicola*, *Peachia parasitica*; *Sicyonis tuberculata and Stephanauge acanallae*). These species have more affinities with Boreal and Arctic areas (16 and 13sp. respectively) especially at intermediate slope environments (see Appendix II.D).

Widely distributed (category VI) and somewhat doubtful species as *Liponema multicornis*, *Bolocera tuediae*, *Monactis vestita*, *Actinauge verrilli* and *Halcampoides purpurea*.

DISCUSSION

This work constitutes one of the few studies dedicated to the diversity and zoogeographical affinities of the North Atlantic and Mediterranean actiniarian fauna assemblages, with especial emphasis on the deep sea habitats. The IFREMER collections are, from a zoogeographical point of view, of considerable interest as they offer the taxonomists the rare opportunity of simultaneous study of material from different localities at different depths, and enable the update the species list of deep-sea actiniarians at the Boreal region.

This study of the North-eastern Atlantic deep sea fauna focus on the knowledge of the distributional limits of the species of the abyssal plain and deep-sea trenches of Ireland. The affinities of the Ireland fauna with the four biogeographic regions was determined and discussed in a more global context including other nearby regions of the Atlantic.

With four deep-sea boreal endemic species (*Daontesia porcupina*, *Kadosactis commensalis*, *Segonzactis platypus* and *Iosactis vagabunda*) and two Boreal-Lusitanian species (*Actinauge abyssorum* and *Amphianthus bathybium*), the PAP fauna is representative of the abyssal environment and delimitates the southern boundary of the boreal deep-sea fauna in the North of the Iberian abyssal plain. The occurrence of endemisms at great depths, that are not found in shallow waters, permit us to conclude that one of the great barriers in the distribution of this fauna is the depth.

On the other side, the Hebrides Terrace and Rockall stations are representative of the bathyal environment, which encompasses a more heterogeneous patchwork of actiniarian assemblages with very distinct individual distributions. The faunal composition includes some species of the slope bathymetric zone (*Actinoscyphia aurelia*, *Edwardsia tuberculata* and *Carlgrenia desiderata*), species with a temperate-warm component whose distribution reaches the Mauritanian sub-tropical region (*Actinauge richardi* and *Phelliactis hertwigi*), one amphi-Atlantic species (*Bolocera tuediae*) and one wide distributed species (*Monactis vestita*) also recoprded from the Pacific (White, *et al*. 1999).

After the examination of the IFREMER collections and despite the discrepancies in the number of individuals taken into account, there is evidence that some species are very sparsely distributed and others may have a patchy occurrence (*Amphianthus bathybium* and *Actinauge abyssorum*).

According to the data compiled through literature, there are 212 valid actiniarian species. The actiniarian fauna composition varies with depth. In a general overview, for all the areas considered in this study, a higher number of species was recorded in the continental shelf than in the deep-sea (53.3%), some species also overlapped with bathyal (18.4%) and abyssal (0.9%) depths (see Appendix II.C). The species richness of actiniarian fauna restricted to great depths is reduced however its composition is entirely different from shelf fauna at genus and family level. From the abyssal species, 2.8% are extensions of the bathyal fauna, and 4.7% are rare species not found at bathyal depths (see Appendix II.C).

While many individual distributions were established from the species comparisons, the genera composition of biogeographical areas had a contrasting result: a high number of shared genera for all areas. At the generic level, the North Atlantic fauna (all areas considered in this study) has 89 genera. A total of 56 genera are present at the Boreal region.

Some major patterns could be recognized, based on some existing recurrent distributions and by analysing the generic diversity that is an indication of the ecological success of each genus in a particular area. A higher ratio of species per genus was observed at the deep sea than amongst shallow water fauna.

The North Atlantic has a very complicated tectonic history and a great variety of habitats. While the Arctic is a homogeneous biogeographical unit with only partial longitudinal division into areas (ex. Greenland, Scandinavia, Siberia) with distinct faunas, the temperate North Atlantic zone has rather distinct faunas along its western and eastern sides that should be considered separately (G-I, Fig. 22). The Boreal fauna presented an affinity of 25.1% at specific level with the North Eastern Atlantic including the Arctic, which is greater at bathyal and abyssal habitats. Arctic species living on the continental slope may penetrate southwards beyond the latitudinal limit (G-IIa, Fig. 22).

The data suggests that the Boreal shelves has more influence from the Mediterranean Province due to the high number of species distributed in both areas (23sp., 19.3% of the Boreal fauna). However at depths bellow 200m the Boreal fauna has more affinity with the Arctic waters and at the shelf the benthos has more affinity with the Lusitanian and Mediterranean fauna (G-IIb, Fig. 22).

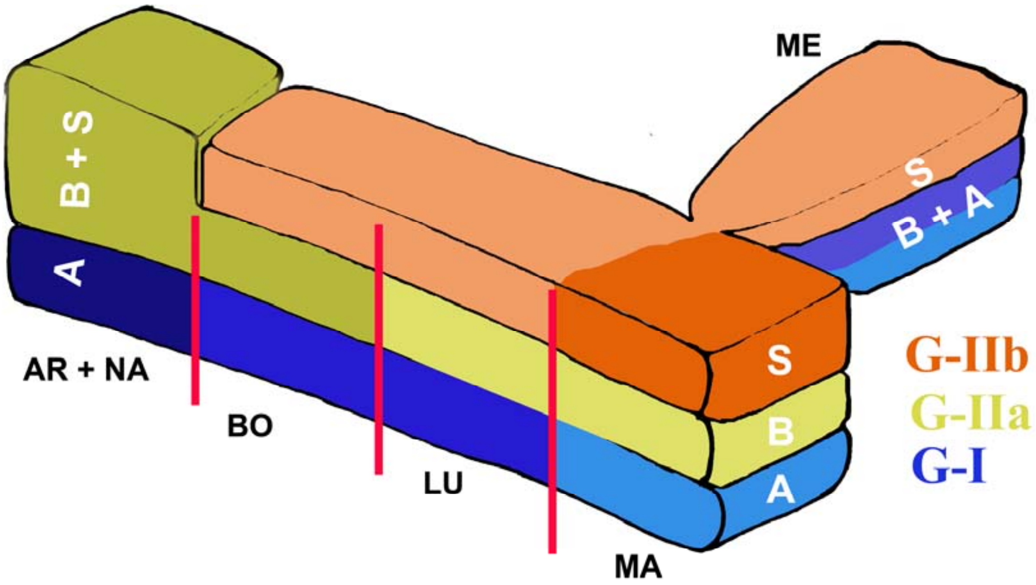

Figure 22.– Representation of the Biogeographic divisions (areas/depth) for the North-Atlantic actiniarian fauna. Abbreviations: AR, Arctic; NA, North American; Bo, Boreal; Lu, Lusitanian, MA, Mauritanian, ME, Mediterranean; G-I, High latitude deep-sea cold water; G-IIa, High latitude shelf and bathyal waters; G-IIb, Temperate shelf waters.

The area with more species shared with other areas, especially with the Arctic and Boreal, is the North American Province (69% of its fauna),. The Boreal area has 16 amphi-Atlantic species, (13.4% of the Boreal fauna), and the Arctic has 13 amphi-Atlantic species (14.8% of the Arctic fauna).

At bathyal environments, the Boreal fauna is influenced by the Arctic and North American waters especially, namely at slopes including shelf cold waters (S+B). We can speculate that the origin of this high latitude fauna might be explained by the Trans-Arctic exchange through the Bering Strait (Gladenkov, *et al.* 2002). For instance, *Actinostola callosa* is one of the species that belongs to these three regions and has also a Pacific distribution. At high latitude areas, data do not support earlier reports (Vinogradova, 1962) of abrupt changes from shelf to depth due to temperature. There is no clear evidence of latitudinal zonation at bathyal depths especially between the Arctic and high latitude North Atlantic. It can be proposed that species had a gradual vertical submergence at lower latitudes.

The analysis of faunal data reveals that three main areas of endemism of the Actiniarian fauna, at genus or species level, can be pointed in the Northern Hemisphere (including Mediterranean): the Arctic is the region with more endemisms, about 19.8% of the total; followed by the Boreal Subregion with 17.5%; and finally the Mediterranean with 10.8%. Such high level of endemic morphological diversity suggests a long period of evolution in isolation.

There is a very high similarity between deep Boreal and Arctic Actiniarian fauna, however, geographical features such as the Greenland-Faroe do not permit exchange at great depths. The abyssal fauna of the Boreal subregion is formed by an endemic group of four species, and others with close affinity with the Lusitanian Province (three species present in both geographic areas). This result confirms the importance of the geological processes that occurred in the Faroes-Greenland district and of the weakening of the North Atlantic current inflow to the Arctic, which originated specific and generic endemisms at the abyssal Arctic and Boreal areas (Golikov, *et al.* 1990). Thus, the diversity pattern with depth is similar at depths shallower than 1000m, but differs considerably deeper 1000m. This agrees with the isopod faunal analysis conducted by Svavarsson, *et al.* (1993).

Besides the Atlantic-Mediterranean waters there are few widely distributed species. Few species show an amphi-Atlantic range and most of these correspond to typically cosmopolitan species.

An explanation for the observed general patterns of actiniarian diversity may be proposed. Obviously, at the present state of knowledge, we can only hypothesize on the different possible historical patterns. In the middle Miocene (16 Ma) a 10ºC cooling of the deep ocean water mass occurred, causing a massive faunal extinction. The development of polar ice caps and the intensification of the deep water mass had its main site of formation in polar oceans (Tyler and Gage, 1992). Hypotheses about the age and origin of the deep-sea fauna have been proposed (Wilson, 1999):

1. The entire deep-sea fauna died out prior to the mid Cenozoic Era, and was replaced by the immigrants from shallow water.

2. Some deep-sea fauna survived from ancient Palaeozoic and Mesozoic Eras, and co-exists with recent immigrants from shallow water.

The submergence argument is defended by many authors who state that fauna was populated through emigration from centres of origin in shallow water at high latitudes, the Antarctic shallow water submergence (Dahl, 1954; Wolff, 1960; Kussakin, 1973; Menzies *et al*. 1973; Wilson, 1999; Mironov, 2006). The Arctic exported species only since the Pleistocene (Gage & Tyler, 1992). The presence of bipolar genera in the study area, can support these theories, for instance: the recently discovered genera *Antipodactis* Rodríguez *et al*., 2009, also *Kadosactis* Danielssen, 1890, *Bolocera* Gosse, 1890; *Actinostola* Verrill, 1883; *Actinoscyphia* Stephenson, 1920; and at family level, the Bathyphelliidae Carlgren 1932.

Recent biogeographic evidence suggests that many abyssal organisms might exist as sink populations from nearby bathyal environments and thus have little potential for evolutionary divergence (Rex *et al.*, 2005). The cold conditions provide an isothermal conduit for migration to the deep-sea.

The similarity between Boreal and South temperate shelf ecosystems is due to environmental features which are principally the temperate-warm waters and the high velocity currents dispersion.

Riemann-Zürneck (1998) stated that deep-sea anemones that live unattached or loosely attached to sediment (*Liponema brevicornis*, *Bolocera tuediae*, *Segonzactis platypus*, *Actinoscyphia aurelia* and *Iosactis vagabunda*) may be passively carried over the sea floor by currents. *Bolocera* is widely distributed; *Segonzactis* also exists in Mediterranean bathyal benthos (*S. hartogi*); *Actinoscyphia aurelia* lives in unstable slope environments of the North Atlantic and was also found in the Northwest of Africa, it stands in the sediment surface with its tiny pedal disc; *Iosactis vagabunda* sometimes leaves its hole, presumably in response to phytodetrital debris, although is still a unique genus of the North Atlantic abyss.

The family Hormathiidae is present in both intertidal and more warm waters but most of its members are from deep bottoms in high latitudes. Carlgren (1946) found that the larvae of Hormathiidae seem to occur usually far from the coast at 1000m and deeper down. Moreover, the Actinostolidae are one of the most succeeded families at high latitudes and great depths (Rodríguez, *et al.* 2008).

Assuming that the larvae are passive dispersers in the ocean currents, many lecitotrophic larvae are dispersed in strong surface currents and can outcome the distance between the continental margin and abyssal plain just as coastal species do (Scheltema, 1989).

The majority of abyssal populations represent deeper range extensions for a subset of bathyal species that have pelagic larval dispersal and abyssal endemism appears to be low. The extraordinarily low densities of many abyssal populations suggests that they could have reduced reproductive viability and are vulnerable to local extinction from inverse density dependence. Some species can partially increase their possibilities of sexual reproduction by an active asexual reproduction (Rex, *et al.* 2005).

A main reason for the difficulties in reaching definitive conclusions about the actiniarian faunal assemblage of the deep-sea has been the still insufficient knowledge on this taxonomic group. More exhaustive collecting is necessary and much more taxonomic work still has to be accomplished before a satisfactory assessment of the entire community and a comprehensive understanding of deep-sea fauna problems can be achieved (Madsen, 1961). The number of species is highly dependent on sampling effort and should not be used for comparisons unless it is demonstrated that the faunas are well characterized. For instance, the Lusitanian (especially Portuguese coast) and Mauritanian need a much higher collecting effort in the future. Besides the Madeira, Canary and Azorean islands (see Ocaña and Hartog, 2002 and Wirtz, *et al*. 2003) published works are very few and there are no updated checklists of sea anemone species, because many localities in these regions are unexplored, especially at greater depths.

A more detailed revision is required in order to assure better insight on the biogeographical patterns and the origin of Boreal fauna. Unfortunately, the grade of knowledge of the actiniarian fauna (and particularly phylogenetic data) is very far from other taxa (e.g.: Isopods). Therefore, the data presented herein, namely the revision and update of knowledge, are considered as a the first step much in need for future detailed studies on the historical biogeographical patterns of the North Atlantic.

CONCLUSIONS

Taxonomy

1. In this contribution 14 actiniarian species from the North Atlantic Irish deep sea were redescribed in detail. This represents approximately 1/4 of the Boreal deep sea (bathyal, abyssal and transition zones included) anemone fauna of the North Atlantic, which includes 14 genera and 11 families. For each of the studied species internal and external anatomy, cnidom diagnosis, geographic and bathymetric distribution and taxonomic discussions were provided.

2. During the development of this work one genus, and two species new to science were detected and described::
   - *Caracolactis* gen. nov., a new genus, with the type species *Caracolactis maternalis* sp. nov.
   - *Antipodactis ifremeri* sp. nov., a new species of the recently created genus *Antipodactis* Rodríguez, López-González & Daly, 2009.

3. Other taxonomical comments and changes were proposed, such as:
   - One new combination: *Parasicyonis biotrans* (Riemann-Zürneck, 1991).
   - Confirmation of *Sicyopus commensalis* as a synonym of *Kadosactis commensalis* (Gravier, 1918).
   - Discussion of some nomenclatural problems in the Hormathidae: namely, the unstable placement of *Actinauge abyssorum* (Gravier, 1918) and *Phelliactis* species according to the characters used and diagnostic key available.
   -

4. New records of species were revealed:
   - *Carlgrenia desiderata* Stephenson, 1918 was reported for thr first time since its original description;
   - *Edwardsia tuberculata* Dueben and Koren, 1847 was cited for the first time in the Irish deep-sea, extending its known distribution both to lower latitudes and deeper habitats.

Biogeography

5. Faunistic composition: The present study compiled a list of 212 valid actiniarian species for the North Atlantic areas here considered (with the Arctic and Mediterranean included, until the Mauritanian province). According to the data analysis, there are three main areas of endemism: the Arctic is the region with more endemisms, about 19.8% of the total; followed by the Boreal Subregion with 17.5%; and finally the Mediterranean with 10.8%. At the generic level, the North Atlantic fauna (all considered areas in this study) has 89 genera. A total of 56 genera are present at the Boreal region. A total of 32 families were recorded for the North Atlantic.

6. Faunistic affinities: the Boreal fauna presented an affinity of 25.1% at specific level with the North Eastern Atlantic including the Arctic, which is greater at bathyal and abyssal habitats; and 21.0% of affinity with the NE Atlantic including the Mediterranean, which is greater at shelf habitats (19.3%). The area with more shared species with the other areas considered, especially with the Arctic and Boreal, is the North American Province (69% of its fauna). The Boreal area has 16 amphi-Atlantic species, which represents 13.4% of the Boreal fauna; and the Arctic has 13 amphi-Atlantic species (14.8%).

7. Data suggests that the Boreal shelves have more influence from the Mediterranean Province – there is a the high number of species distributed in both areas (23sp., 19.3% of the Boreal fauna). This supports a "Tethyan origin" of the Boreal shelves in agreement with the proposal of Golikov, *et al.* (1990) for a Mediterranean-Lusitanian fauna origin of the initial Boreal shores.

8. At bathyal environments, the Boreal fauna is especially influenced by the Arctic and North American waters, namely at slopes including shelf cold waters (S+B). We also speculate that the origin of this high latitude fauna might support the Trans-Arctic exchange through the Bering Strait previously proposed by Gladenkov, *et al.* (2002). At high latitude areas, data do not support earlier reports (Vinogradova, 1962) of abrupt changes from shelf to depth due to temperature. There is no clear evidence of latitudinal zonation at bathyal depths especially between the Arctic and high latitude North Atlantic. It seems that species had a gradual vertical submergence.

9. The abyssal fauna of the Boreal subregion is formed by an endemic group of four species, and three other species share with the Lusitanian Province indicating a close affinity between these geographic areas. This result confirms the importance of the geological processes that occurred in the Faroes-Greenland district and the weakening of the North Atlantic current inflow to the Arctic, which originated specific and generic endemisms at the abyssal Arctic and Boreal areas (Golikov, *et al.* 1990).

10. The question about the origin of the Boreal deep-sea fauna, remains unanswered, however the presence of bipolar genera in the study area, such as the recently discovered genera *Antipodactis* Rodríguez *et al*., 2009, also *Kadosactis* Danielssen, 1890, *Bolocera* Gosse, 1890; *Actinostola* Verrill, 1883; *Actinoscyphia* Stephenson, 1920; and at family level, Bathyphelliidae Carlgren 1932, supports the possibility of the Antarctic centre of origin proposed by Mironov, (2006).

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APPENDIX

Appendix I.A.– Stations list. Abbreviations: PAP, Porcupine Abyssal Plain; HT, Hebrides Terrace; T, Thérèse Mound; R1, Rockall 1; R2, Rockall 2; P, Perseverance Mound; C, Connemara Field.

CRUISE	STATION	COORDENATES	AREA	DEPTH (m)	DATE	METHOD
BENGAL 2	13078 (1)	48º50’N; 16º39’W	PAP	4844	29 Mar 1997	Agassiz Trawl
BENGAL 2	13078 (6)	48º42’N; 16º31’W	PAP	4838	30 Mar 1997	Agassiz Trawl
BENGAL 2	13078 (11)	48º51’N; 16º32’W	PAP	4844	1 Mar 1997	Agassiz Trawl
BENGAL 2	13078 (21)	48º51’N; 16º31’W	PAP	4844	3 Mar 1997	Agassiz Trawl
BENGAL 2	13078 (27)	48º49’N; 16º32’W	PAP	4844	4 Mar 1997	Agassiz Trawl
BENGAL 3	13200 (70)	48º50’N; 16º 33’W	PAP	4845-4848	20 Jul 1997	Agassiz Trawl
BENGAL 3	13200 (84)	48º47’N; 16º40’W	PAP	4840-4843	23 Jul 1997	Agassiz Trawl
BENGAL 3	13200 (93)	48º47’N; 16º30’W	PAP	4844-4849	25 Jul 1997	Agassiz Trawl
BENGAL 3	13200 (94)	48º47’N; 16º32’W	PAP	4847-4851	26 Jul 1997	Agassiz Trawl
BENGAL 5	13368 (47)	48º50’N; 16º 25’W	PAP	4844	17 Mar 1998	Agassiz Trawl
BENGAL 5	13368 (48)	48º45’N; 16º32’W	PAP	4841-4845	17 Mar 1998	Agassiz Trawl
BENGAL 5	13368 (52)	48º46’N; 16º23’W	PAP	4839	19 Mar 1998	Agassiz Trawl
BENGAL 5	13368 (53)	48º49’N; 16º20’W	PAP	4842-4846	20 Mar 1998	Agassiz Trawl
BENGAL 6	13627 (11)	48º54’N; 16º 53’W	PAP	4842	1 Oct 1998	Agassiz Trawl
BENGAL 6	13627 (24)	48º52’N;16º42’W	PAP	4839	5 Oct 1998	Agassiz Trawl
PROSPEC	CPH-01	56º 27’N; 9º18’W	HT	1004	3 Jul 1996	Agassiz Trawl
PROSPEC	CPH-02	56º41’N; 9º12’W	HT	1027	3 Jul 1996	Agassiz Trawl
PROSPEC	CPH-03	56º43’N; 9º10’W	HT	1025	3 Jul 1996	Agassiz Trawl
PROSPEC	CPH-08	55º19’N; 10º09’W	HT	1184	12 Jul 1996	Agassiz Trawl
PROSPEC	CPH-09	55º22’N; 10º04’W	HT	990	12 Jul 1996	Agassiz Trawl
PROSPEC	CPH-10	55º18’N; 10º15’W	HT	1579	12 Jul 1996	Agassiz Trawl
PROSPEC	Arrow 7	56º43.8’N; 9º14’W	HT	1095-1181	5 Jul 1996	Agassiz Trawl
PROSPEC	Arrow 10	56º35.4’N; 10º13.8’W	HT	1727-1845	6 Jul 1996	Agassiz Trawl
PROSPEC	Arrow 14	55º18.4’N; 10º06.8’W	HT	988-1005	10 Jul 1996	Agassiz Trawl
PROSPEC	Arrow 15	55º16.7N; 10º10.7’W	HT	1192-1219	10 Jul 1996	Agassiz Trawl
PROSPEC	Arrow 20	55º29.1’N; 10º02.3’W	HT	1580-1600	13 Jul 1996	Agassiz Trawl
PROSPEC	Arrow 27	56º52.5’N; 10º00.0’W	HT	2000-2012	16 Jul 1996	Agassiz Trawl
CARACOLE	PL 127-05	52º 18’N; 13º 01’W	P	628	Jul-Ago 2001	Usnel corer
CARACOLE	PL 128-06	53º 04’N; 12º 36’W	C	380	Jul-Ago 2001	Slurp gun bottle
CARACOLE	PL 129-07	53º 47’N; 13º 56’W	R1	755	Jul-Ago 2001	ROV big box
CARACOLE	PL 130-08	53º 46’N; 13º 55’W	R1	777	Jul-Ago 2001	CTD top
CARACOLE	PL 132-10	55º 32’N; 15º 40’W	R2	690	Jul-Ago 2001	ROV basket
CARACOLE	KGS 05	51º 25’N; 11º 46’W	T	875	Jul-Ago 2001	Usnel corer
CARACOLE	KGS 08	52º18’N; 13º 02’ W	P	619	Jul-Ago 2001	Usnel corer
CARACOLE	KGS 11	53º 46’N; 13º 56’W	R1	793	Jul-Ago 2001	Usnel corer
CARACOLE	KGS 12	53º 46’N; 13º 56’W	R1	795	Jul-Ago 2001	Usnel corer
CARACOLE	KGS 14	55º 31’N; 15º 39’W	R2	702	Jul-Ago 2001	Usnel corer

Appendix II.A.- Species checklist distributed by regions within bathymetric ranges: Arctic (ART), Boreal (BOR), Lusitanian (LUS), Mediterranean (MED), Mauritanian (MAU), North American (NA), shelf (S), bathyal (B) and abyssal (A), surveyed in literature (cited references numbered).

Species	ART			BOR			LUS			MED			MAU			NA			
	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	REFERENCES
Acthelmis intestinalis (Fabricius, 1780)	+																		**(20)**
Actinauge abyssorum (Gravier, 1918)						+			+										**(5)**
Actinauge cristata (Riemann Zürneck, 1986)	+	+		+	+														**(5)**
Actinauge longicornis Verrill, 1882					+											+			**(3, 21, 38)**
Actinauge richardi (Marion, 1882)	+			+	+	+		+	+	+	+	+	+	+	+				**(1, 8, 21, 22 34, 40, 42)**
Actinauge verrilli (McMurrich, 1893)	+	+	+													+	+	+	**(3, 58, 59)**
Actinernus michaelsarsi Carlgren, 1918						+													**(40)**
Actinernus nobilis Verrill, 1879	+	+			+												+		**(20, 39, 53)**
Actinia cari Delle Chiaje, 1825										+									**(1, 10)**
Actinia equina (Linnaeus, 1758)				+															**(20)**
Actinia fragacea Tugwell, 1856				+															**(2)**
Actinia nigropunctata den Hartog & Ocaña, 2003							+												**(47, 50)**
Actinia prasina Gosse, 1860				+															**(48, 49)**
Actinia sali Monteiro, Solé-Cava & Thorpe, 1997													+						**(48)**
Actinia schmidti Monteiro, Solé-Cava & Thorpe, 1997							+			+									**(48)**
Actinia striata (Rizzi, 1970)										+									**(1, 10)**
Actinia virgata Johnson (1861)							+												**(15)**
Actinoscyphia aurelia (Stephenson, 1920)					+			+						+					**(6)**
Actinoscyphia saginata (Verrill, 1882)					+												+		**(6)**
Actinoscyphia verrilli (Gravier, 1918)														+					**(33)**
Actinostola abyssorum (Danielssen, 1890)	+	+		+	+														**(12, 20)**
Actinostola callosa (Verrill, 1882)	+			+	+											+			**(20, 34, 38, 39)**
Actinostola groenlandica Carlgren, 1899	+																		**(20)**
Actinostola spetsbergensis Carlgren, 1893	+	+																	**(12, 20, 39)**
Actinothoe sphyrodeta (Gosse, 1858)				+			+			+			+						**(1, 8, 9, 43)**
Adamsia palliata (O. F. Müller, 1776)				+			+			+									**(1, 2, 10)**
Aiptasia diaphana (Rapp, 1829)							+			+			+						**(1, 10, 15, 43)**
Aiptasia mutabilis (Gravenhorst, 1831)				+			+			+									**(1, 2, 10, 41)**
Aiptasiogeton hyalinus (Delle Chiaje, 1822)							+			+									**(15, 27)**
Aiptasiogeton pellucidus (Hollard, 1848)				+						+									**(1)**
Alicia mirabilis Johnson, 1861							+			+									**(1, 10, 15, 41, 43)**
Allantactis parasitica Danielssen, 1890	+	+																	**(3, 39, 21)**
Amphianthus bathybium Hertwig, 1882						+			+								+		**(7)**

Appendix II.A.- Cont.

	ART			BOR			LUS			MED			MAU			NA			
	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	REFERENCES
Amphianthus dohrnii (Koch, 1878)				+	+		+			+	+								(1, 10, 43)
Amphianthus ingolfi Carlgren, 1942					+														(3)
Amphianthus islandicus Carlgren, 1942	+	+		+	+														(3)
Amphianthus margaritaceus Danielssen, 1890		+	+																(3, 39)
Amphianthus michaelsarsi Carlgren, 1934					+														(40)
Amphianthus mopseae Danielssen, 1890	+			+															(3)
Amphianthus nitidus Verrill, 1899																+	+		(3, 36)
Amphianthus norvegicus Carlgren, 1942	+			+															(12, 21)
Amphianthus verruculatus Carlgren, 1942		+																	(21)
Andresia parthenopea (Andres, 1883)										+									(1, 10)
Andvakia mirabilis Danielssen, 1890	+																		(20)
Anemonactis mazelii (Jourdan, 1880)				+			+			+			+						(1, 3, 14, 43)
Anemonia melanaster (Verrill, 1910)				+			+						+			+			(15, 16, 41)
Anemonia viridis (Forskal, 1775)				+			+			+									(1, 2, 3, 8, 10, 43)
Anthopleura ballii (Cocks, 1850)				+			+			+									(1, 2, 14, 15, 41, 43)
Anthopleura thallia (Gosse, 1854)				+						+			+						(2, 8, 14, 15)
Anthosactis ingolfi Carlgren, 1921					+														(20)
Anthosactis janmayeni Danielssen, 1890	+	+		+	+											+			(4, 12, 20, 39)
Anthothoe affinis (Johnson, 1861)							+						+						(15, 41)
Antipodactis awii Rodríguez et al., 2009		+																	(60)
Antipodactis ifremeri sp. nov.																			#
Aulactinia stella (Verrill, 1864)	+															+			(20, 52)
Aulactinia verrucosa (Pennant, 1777)				+			+			+									(8, 15, 43, 51)
Bathyphellia margaritacea Danielssen, 1890		+	+		+	+			+										(3, 4, 6)
Bolocera tuediae (Johnston, 1832)	+	+		+	+		+	+					+	+		+	+		(2)
Bunodactis rubripunctata (Grube, 1840)				+						+									(1, 15)
Bunodactis spetsbergensis (Carlgren, 1920)	+	+		+	+														(20)
Bunodeopsis strumosa Andres, 1881										+									(1, 10)
Cactosoma abyssorum Danielssen, 1890	+	+																	(20, 22)
Calliactis parasitica (Couch, 1842)				+						+									(1, 2, 10)
Capnea sanguinea Forbes, 1841				+						+									(1, 2, 3, 8)
Caracolactis maternalis sp. nov.					+														#
Carlgrenia desiderata Stephenson, 1918					+														(3, 34)
Cataphellia brodricii (Gosse, 1859)				+															(8)
Cereus pedunculatus (Pennant, 1777)							+			+									(1, 10, 43)

Appendix II.A.- Cont.

	ART			BOR			LUS			MED			MAU			NA			
	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	REFERENCES
Chondrophellia coronata (Verrill, 1883)		+			+			+						+			+		(21, 42)
Condylactis aurantiaca (Delle Chiaje, 1825)							+			+									(1, 10, 43)
Cribrinopsis crassa (Andres, 1880)										+									(1, 10)
Cribrinopsis similis Carlgren, 1921	+																		(20)
Daontesia porcupina Riemann-Zürneck, 1997						+													(4)
Daontesia praelonga Carlgren, 1928		+			+														(3)
Diadumene cincta Stephenson, 1925				+						+									(1, 2)
Diadumene lineata (Verril, 1869)				+						+			+			+			(1, 2, 3, 8, 15, 17, 24)
Edwardsia allmani M'Intosh, 1866				+															(18)
Edwardsia andresi Danielssen, 1890	+	+		+	+														(18, 20, 22, 39)
Edwardsia arctica Carlgren, 1921	+	+																	(3)
Edwardsia beautempsii Quatrefages, 1842				+			+												(18, 19)
Edwardsia carlgreni Carlgren, 1921				+															(20)
Edwardsia claparedii (Panceri, 1869)				+						+									(1, 8, 18)
Edwardsia coriacea Moseley, 1877							+												(43)
Edwardsia costata Danielssen, 1890		+																	(12, 18)
Edwardsia danica Carlgren, 1921				+	+														(20, 22)
Edwardsia delapiae Carlgren & Stephenson,1928				+															(8, 18)
Edwardsia finmarchica Carlgren, 1921	+																		(20, 18)
Edwardsia fischeri Chevreux et de Guerne, 1889				+															(3, 18)
Edwardsia fusca Danielssen, 1890	+																		(20)
Edwardsia goodsiri M'Intosh, 1866				+															(8, 3, 18)
Edwardsia islandica Carlgren, 1921	+			+															(20)
Edwardsia longicornis Carlgren, 1921	+			+															(18, 20)
Edwardsia maroccana Carlgren, 1931													+						(3, 18)
Edwardsia norvegica Carlgren, 1942		+																	(18, 21)
Edwardsia tecta Haddon, 1889				+															(3, 18)
Edwardsia timida Quatrefages, 1842				+															(18, 19)
Edwardsia tuberculata Düben & Koren 1847				+	+														(20, 18, 22)
Edwardsia vegae Carlgren, 1921	+																		(20)
Edwardsia vitrea (Danielssen, 189)	+	+																	(3, 8, 20)
Edwardsiella carnea (Delphy, 1938)				+															(18, 20)
Edwardsiella janthina (Andres, 1881)										+									(26)

Appendix II.A.- Cont.

	ART			BOR			LUS			MED			MAU			NA			
	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	REFERENCES
Edwardsiella lineata (Verrill in Baird, 1873)																+			(35)
Edwardsiella loveni (Carlgren, 1892)				+	+														(20)
Epiactis arctica (Verrill, 1868)	+	+																	(20)
Epiactis fecunda (Verrill, 1899)	+																		(36)
Epiactis nordmanni Carlgren, 1921		+																	(20)
Epiparactis dubia Carlgren, 1921	+																		(20)
Gonactinia prolifera (Sars, 1835)	+			+						+									(1, 2, 14, 20)
Halcampa arctica Carlgren, 1893	+	+																	(20, 39)
Halcampa duodecimcirrata (Sars, 1851)	+			+												+			(20, 53)
Halcampoides abyssorum Danielssen, 1890	+	+			+														(12, 20, 22)
Halcampoides purpurea (Studer, 1878)	+	+		+	+		+			+						+			(1, 12, 15, 20)
Haliactis arctica Carlgren, 1921	+																		(20)
Haloclava producta (Stimpson, 1856)																+			(20)
Hormathia alba (Andres, 188)										+									(1, 14, 15)
Hormathia coronata (Gosse, 1858)				+						+									(1, 2, 8, 10, 14)
Hormathia digitata (Müller, 1776)	+	+		+	+														(3, 21, 28, 39)
Hormathia marioni Haddon, 1889					+														(3, 25)
Hormathia mediterranea Carlgren, 1935										+	+								(3)
Hormathia nodosa Fabricius, 1780	+	+																	(3, 24, 39)
Ilyactis torquata Andres, 1881										+									(27)
Iosactis vagabunda (Rieman-Zürneck, 1997)						+													(57)
Kadophellia bathyalis Tur, 1991											+								(27)
Kadosactis abyssicola Koren & Danielssen, 1877	+	+		+												+			(3, 13, 21)
Kadosactis commensalis (Gravier, 1918)						+			+										(3)
Kadosactis rosea Danielssen, 1890		+			+														(3, 11, 12, 22, 39)
Kadosactis sptisbergensis (Danielssen 1890)		+																	(3, 21)
Kadosactis sulcata Carlgren, 1934						+		+											(3, 11)
Limnactinia laevis Carlgren, 1921	+			+															(20)
Liponema multicornis (Verrill, 1880)	+	+			+			+						+		+			(12, 20, 22, 37, 39)
Mesacmaea mitchellii (Gosse, 1853)										+									(1, 3, 26)
Metridium senile (Linnaeus, 1761)	+			+						+						+			(2, 3, 8, 39)
Monactis vestita (Gravier, 1918)			+		+	+			+						+				(5, 22)
Octineon suecicum Carlgren, 1940				+															(21)
Octophellia timida (Andres, 1880)										+									(27)

Appendix II.A.- Cont.

	ART			BOR			LUS			MED			MAU			NA			
	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	REFERENCES
Onubactis rocioi López-González *et al*., 1995							+												**(29)**
Paracalliactis azorica Doumenc, 1975									+										**(6)**
Paracalliactis lacazei Dechancé & Dufaure, 1959										+									**(27)**
Paracalliactis michaelsarsi, Carlgren, 1928					+	+													**(3, 6)**
Paracalliactis robusta Tur, 1991										+									**(27)**
Paracalliactis stephensoni Carlgren, 1928					+			+											**(3, 6)**
Paractinia striata (Risso, 1826)	+			+						+									**(1, 10)**
Paraedwardsia arenaria Carlgren in Nordgaard, 1950																+			**(20, 35)**
Paraedwardsia sarsii (Dueben & Koren, 1847)	+																		**(20)**
Paranemonia cinerea (Contarini, 1844)										+									**(1, 10)**
Paranemonia vouliagmeniensis (Doumenc *et. al.,* 1987)										+									**(1)**
Paranthus rugosus (Andres, 188)										+									**(1, 10, 14)**
Paraphellia expansa (Haddon, 1886)				+									+						**(2, 3, 8, 15)**
Parasicyonis biotrans (Riemann-Zürneck, 1991)						+													**(56)**
Parasicyonis groenlandica Carlgren, 1933		+																	**(3, 39)**
Parasicyonis ingolfi Carlgren, 1942		+	+																**(3)**
Parasicyonis sarsii Carlgren, 1921	+	+		+	+														**(3, 20, 22)**
Parastephanauge paxi Dufaure, 1959										+									**(27)**
Peachia boeckii (Danielssen & Koren, 1856)				+															**(20, 30)**
Peachia cylindrica (Reid, 1848)				+			+	+		+									**(1, 2, 8,14, 28, 51)**
Peachia parasitica (Agassiz, 1859)	+															+			**(20, 52)**
Phellia arctica Danielssen, 1890	+																		**(12)**
Phellia gausapata Gosse, 1858	+			+															**(21)**
Phellia murocincta Gosse, 1860				+															**(28)**
Phellia norvegica Danielssen, 1890		+																	**(12)**
Phelliactis carlgreni Doumenc, 1975					+									+					**(6)**
Phelliactis coccinea (Stephenson, 1918)					+														**(3, 34)**
Phelliactis hertwigi Simon, 1892		+		+	+			+						+					**(3, 6, 21, 22)**
Phelliactis incerta Carlgren, 1934					+														**(3, 6)**
Phelliactis michaelsarsi (Carlgren, 1934)					+	+													**(5)**

Appendix II.A.- Cont.

	ART			BOR			LUS			MED			MAU			NA			
	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	REFERENCES
Phelliactis pulchra (Stephenson, 1918)					+														**(3, 6, 34)**
Phelliactis robusta Carlgren, 1928	+	+			+														**(3, 6, 22, 24)**
Phelliactis spinosa Carlgren, 1928		+																	**(3, 21, 24)**
Phymanthus pulcher (Andres, 1883)										+									**(1, 10, 14)**
Protanthea simplex (Carlgren, 1891)	+	+		+	+					+	+								**(1, 2, 3, 10, 20)**
Ptychodactis patula Appellöf, 1893	+																		**(20)**
Pycnanthus densus Carlgren, 1921		+			+														**(20)**
Pycnanthus laevis Carlgren, 1921		+			+														**(20)**
Sagartia elegans (Dalyell, 1848)	+			+						+									**(1, 2, 3, 8, 10, 14, 21)**
Sagartia ornata (Holdsworth, 1855)				+															**(51)**
Sagartia troglodytes (Price in Johnston, 1847)				+						+									**(1, 3, 8, 10, 14, 15, 21, 22)**
Sagartiogeton abyssorum Carlgren, 1942		+																	**(21)**
Sagartiogeton entellae Schmidt, 1972										+									**(1, 10)**
Sagartiogeton flexibilis (Danielssen, 189)		+																	**(3, 21)**
Sagartiogeton ingolfi Carlgren, 1928		+																	**(3, 21)**
Sagartiogeton laceratus (Dalyell, 1848)				+			+			+									**(3, 8, 21, 26)**
Sagartiogeton robustus Carlgren, 1924					+														**(3, 21)**
Sagartiogeton tubicolus (Koren & Danielssen, 1877)		+			+														**(3, 21)**
Sagartiogeton undatus (Müller, 1788)				+						+									**(1, 3, 10)**
Sagartiogeton verrilli Carlgren, 1942																+	+		**(3, 21)**
Sagartiogeton viduatus (Müller, 1776)	+			+															**(3, 21)**
Scolanthus callimorphus (Gosse, 1853)				+						+									**(1, 2, 8, 26)**
Scolanthus ingolfi (Carlgren, 1921)				+	+														**(20, 22)**
Scolanthus nidarosiensis (Carlgren, 1942)	+																		**(21)**
Segonzactis hartogi Vafidis & Chintiroglou, 2002										+	+								**(32)**
Segonzactis platypus Riemann-Zürneck, 1979						+													**(31)**
Sicyonis gossei (Stephenson, 1918)					+														**(3)**
Sicyonis ingolfi Carlgren, 1921		+																	**(3, 6, 20)**
Sicyonis tuberculata Carlgren, 1921		+	+															+	**(6)**
Sicyonis variabilis Carlgren, 1921					+														**(20)**
Siphonactinopsis laevis Carlgren, 1921	+																		**(20)**
Stephanactis impedita Gravier, 1918								+						+					**(33)**
Stephanactis inornata Gravier, 1918					+									+					**(42)**
Stephanauge abyssicola (Moseley, 1877)																+	+		**(55)**

Appendix II.A.- Cont.

	ART			BOR			LUS			MED			MAU			NA			
	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	S	B	A	REFERENCES
Stephanauge acanellae (Verrill, 1883)		+														+	+		**(21, 38)**
Stomphia coccínea *(*Müller, 1776)	+			+	+														**(12, 20, 22)**
Stomphia polaris (Danielssen, 1890)	+																		**(12, 20)**
Tealidium jungerseni Carlgren, 1921		+																	**(20)**
Telmatactis elongata (Delle chiaje, 1825)							+			+									**(27, 43)**
Telmatactis cricoides (Duchassaing, 1850)										+									**(1)**
Telmatactis forskalii (Ehrenberg, 1834)				+			+			+									**(1, 10, 41)**
Telmatactis solidago (Duchassaing & Michelotti, 1864)							+			+									**(1, 44)**
Urticina crassicornis (Müller, 1776)	+			+			+									+			**(20, 43)**
Urticina felina (Linnaeus, 1761)	+			+						+						+			**(2, 12, 20, 62, 63)**
Urticina lofotensis (Danielssen, 1890)	+			+												+			**(12, 20, 54)**

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Appendix II.B.– Bathymetric and geographic distribution of genera. The asterisk denotes genera with unique location in the study area.

	SHELF			SHELF / BATHYAL		BATHYAL	BATHYAL / ABYSSAL	ABYSSAL	ALL DEPTHS
ARCTIC	*Acthelmis** *Andvakia** *Aulactinia* *Cribrinopsis* *Epiparactis** *Gonactinia* *Haliactis**	*Limnactinia* *Monactis* *Paractinia* *Paraedwardsia* *Peachia* *Ptychodactis**	*Sagartia* *Scolanthus* *Siphonactinopsis** *Stomphia* *Tealia* *Urticina*	*Actinernus* *Actinostola* *Allantactis** *Anthosactis* *Bolocera* *Bunodactis* *Cactosoma** *Edwardsia*	*Epiactis* *Halcampa* *Halcampoides* *Hormathia* *Kadosactis* *Liponema* *Phelliactis* *Protanthea* *Sagartiogeton*	*Chondrophellia* *Daontesia* *Paraphelliactis** *Pycnanthus* *Stephanauge* *Tealidium**	*Bathyphellia*	*Antipodactis*	*Actinauge* *Amphianthus* *Parasicyonis*
BOREAL	*Actinia* *Actinothoe* *Adamsia* *Aiptasia* *Aiptasiogeton* *Anemonactis* *Anemonia* *Anthopleura*	*Aulactinia* *Capnea* *Calliactis* *Diadumene* *Gonactinia* *Halcampa* *Limnactinia* *Metridium*	*Octineon** *Paractinia* *Paraphellia* *Peachia* *Sagartia* *Tealia* *Telmatactis* *Urticina*	*Actinostola* *Anthosactis* *Bolocera* *Bunodactis* *Edwardsia* *Edwardsiella* *Halcampoides*	*Hormathia* *Liponema* *Monactis* *Protanthea* *Sagartiogeton* *Scolanthus* *Stomphia*	*Antipodactis** *Actinoscyphia* *Carlgrenia** *Caracolactis** *Chondrophellia* *Pycnanthus* *Stephanactis*	*Actinernus* *Bathyphellia* *Daontesia* *Paracalliactis* *Phelliactis* *Sicyonis*	*Iosactis** *Segonzactis*	*Actinauge* *Amphianthus* *Kadosactis*
LUSITANEAN	*Actinia* *Actinothoe* *Adamsia* *Aiptasia* *Aiptasiogeton* *Alicia*	*Amphianthus* *Anemonactis* *Anemonia* *Anthopleura* *Anthothoe* *Aulactinia*	*Cataphellia* *Cereus* *Condylactis* *Edwardsia* *Halcampoides* *Telmatactis* *Urticina*	*Bolocera* *Sagartiogeton*		*Actinoscyphia* *Chondrophellia* *Kadosactis* *Stephanactis*	*Actinauge* *Paracalliactis* *Phelliactis*	*Amphianthus* *Bathyphellia??*	

Appendix II.B.– Cont.

	SHELF			SHELF / BATHYAL		BATHYAL	BATHYAL / ABYSSAL	ABYSSAL	ALL DEPTHS
MEDITERRANEAN REGION	*Actinia* *Actinothoe* *Adamsia* *Aiptasia* *Aiptasiogeton* *Alicia** *Andresia** *Anemonactis* *Anemonia* *Anthopleura* *Aulactinia* *Capnea* *Bunodactis*	*Bunodeopsis** *Calliactis* *Cereus* *Condylactis* *Cribrinopsis* *Diadumene* *Edwardsia* *Edwardsiella* *Gonactinia* *Halcampoides* *Ilyactis** *Mesacmaea**	*Metridium* *Octophellia** *Paracalliactis* *Paractinia* *Paranemonia** *Paranthus** *Parastephanauge** *Phymanthus* *Sagartia* *Sagartiogeton* *Scolanthus* *Telmatactis* *Urticina*	*Amphianthus* *Hormathia* *Protanthea* *Segonzactis*		*Kadophellia**			*Actinauge*
MAURITANEAN	*Actinia* *Aiptasia* *Anemonactis* *Anemonia* *Anthopleura*	*Anthothoe* *Diadumene* *Edwardsia* *Paraphellia*		*Bolocera*		*Actinoscyphia* *Chondrophellia* *Liponema* *Phelliactis* *Stephanactis*		*Monactis*	*Actinauge*
NORTH AMERICAN	*Actinostola* *Anemonia* *Aulactinia* *Diadumene* *Edwardsiella* *Halcampa* *Halcampoides*	*Haloclava** *Kadosactis* *Liponema* *Metridium* *Paraedwardsia* *Peachia* *Urticina*		*Amphianthus* *Bolocera* *Sagartiogeton* *Stephanauge*		*Actinernus* *Actinoscyphia* *Chondrophellia*			*Actinauge*

Appendix II.C.– Data summary of the bathymetric distribution of groups of species in different biogeographic categories (species numbers and overall percentage).

	Bathymetric distribution (nº)							**Bathymetric distribution (%)**						
	S	**B**	**A**	**S+B**	**B+A**	**S+B+A**	**Total**	**S**	**B**	**A**	**S+B**	**B+A**	**S+B+A**	**Total**
I.a.	16	14	1	9	2	0	42	7,5	6,6	0,5	4,2	0,9	0,0	19,8
I.b.	17	13	4	3	0	0	37	8,0	6,1	1,9	1,4	0,0	0,0	17,5
I.c.	3	0	2	0	0	0	5	1,4	0,0	0,9	0,0	0,0	0,0	2,4
I.d.	20	1	0	2	0	0	23	9,4	0,5	0,0	0,9	0,0	0,0	10,8
I.e.	2	1	0	0	0	0	3	0,9	0,5	0,0	0,0	0,0	0,0	1,4
I.f.	3	0	0	3	0	0	6	1,4	0,0	0,0	1,4	0,0	0,0	2,8
II.a.	7	5	0	12	0	0	24	3,3	2,4	0,0	5,7	0,0	0,0	11,3
II.b.	1	1	3	0	0	0	5	0,5	0,5	1,4	0,0	0,0	0,0	2,4
II.c.	0	0	0	0	1	0	1	0,0	0,0	0,0	0,0	0,5	0,0	0,5
III.a.	13	0	0	0	0	0	13	6,1	0,0	0,0	0,0	0,0	0,0	6,1
III.b.	6	0	0	0	0	0	6	2,8	0,0	0,0	0,0	0,0	0,0	2,8
III.c.	7	0	0	1	0	0	8	3,3	0,0	0,0	0,5	0,0	0,0	3,8
III.d.	3	0	0	1	0	0	4	1,4	0,0	0,0	0,5	0,0	0,0	1,9
IV.a.	2	1	0	0	0	0	3	0,9	0,5	0,0	0,0	0,0	0,0	1,4
IV.b.	0	3	0	0	0	0	3	0,0	1,4	0,0	0,0	0,0	0,0	1,4
IV.d.	1	0	0	0	0	0	1	0,5	0,0	0,0	0,0	0,0	0,0	0,5
IV.e.	1	0	0	0	0	0	1	0,5	0,0	0,0	0,0	0,0	0,0	0,5
IV.f.	2	0	0	0	0	1	3	0,9	0,0	0,0	0,0	0,0	0,5	1,4
IV.g.	0	0	0	1	0	0	1	0,0	0,0	0,0	0,5	0,0	0,0	0,5
V.a.	0	1	0	1	0	1	3	0,0	0,5	0,0	0,5	0,0	0,5	1,4
V.b.	2	0	0	1	1	0	4	0,9	0,0	0,0	0,5	0,5	0,0	1,9
V.c.	2	1	0	2	0	0	5	0,9	0,5	0,0	0,9	0,0	0,0	2,4
V.d.	0	0	0	0	1	0	1	0,0	0,0	0,0	0,0	0,5	0,0	0,5
V.e.	2	0	0	0	0	0	2	0,9	0,0	0,0	0,0	0,0	0,0	0,9
V.f.	1	0	0	0	0	0	1	0,5	0,0	0,0	0,0	0,0	0,0	0,5
V.g.	2	0	0	0	0	0	2	0,9	0,0	0,0	0,0	0,0	0,0	0,9
V.j.	0	0	0	2	0	0	2	0,0	0,0	0,0	0,9	0,0	0,0	0,9
VI.b.	0	1	0	1	0	0	2	0,0	0,5	0,0	0,5	0,0	0,0	0,9
VI.c.	0	0	0	0	1	0	1	0,0	0,0	0,0	0,0	0,5	0,0	0,5
Total	113	42	10	39	6	2	212	53,3	19,8	4,7	18,4	2,8	0,9	100,0

Appendix II.D.– Faunal composition: geographic and bathymetric distribution of groups of species (absolute numbers) in different biogeographic categories per each area (AR; BO; LU; ME; NA).

		Biogeographic categories														
		AE	**BE**	**LE**	**ME**	**MAE**	**NE**	**AN**	**ANME**	**ANMA**	**ANF**	**WI**	**Subtotals (nº sp.)**			
Geographic and bathymetric groups of species	AR(S)	16	0	0	0	0	0	7	3	0	6	0	**32**	**AR Region** **88 spp.**		
	AR(B)	14	0	0	0	0	0	5	0	0	1	1	**21**			
	AR(A)	1	0	0	0	0	0	0	0	0	0	0	**1**			
	AR(S+B)	9	0	0	0	0	0	12	1	1	5	1	**29**			
	AR(B+A)	2	0	0	0	0	0	1	0	0	1	1	**5**			
	AR(S+B+A)	0	0	0	0	0	0	0	0	0	0	0	**0**			
	AR Subtotal	**42**	**0**	**0**	**0**	**0**	**0**	**25**	**4**	**1**	**13**	**3**				
	BO(S)	0	17	0	0	0	0	8	23	3	7	0	**58**	**BO Subregion** **119 spp.**		**NEA Region** **164 spp.**
	BO(B)	0	13	0	0	0	0	6	0	3	2	1	**25**			
	BO(A)	0	4	0	0	0	0	3	0	0	0	0	**7**			
	BO(S+B)	0	3	0	0	0	0	12	2	1	5	1	**24**			
	BO(B+A)	0	0	0	0	0	0	1	0	0	1	1	**3**			
	BO(S+B+A)	0	0	0	0	0	0	0	0	1	1	0	**2**			
	BO Subtotal	**0**	**37**	**0**	**0**	**0**	**0**	**30**	**25**	**8**	**16**	**3**				
	LU(S)	0	0	3	0	0	0	1	13	5	4	0	**26**	**LU Province** **43 spp.**	**ATM Subregion** **127 spp.**	
	LU(B)	0	0	0	0	0	0	1	0	1	0	1	**3**			
	LU(A)	0	0	2	0	0	0	3	0	0	0	0	**5**			
	LU(S+B)	0	0	0	0	0	0	0	1	1	2	1	**5**			
	LU(B+A)	0	0	0	0	0	0	1	0	0	1	1	**3**			
	LU(S+B+A)	0	0	0	0	0	0	0	0	1	0	0	**1**			
	LU Subtotal	**0**	**0**	**5**	**0**	**0**	**0**	**6**	**14**	**8**	**7**	**3**				
	MÊ(S)	0	0	0	20	0	0	0	29	4	1	0	**54**	**ME Province** **62 spp.**		
	ME(B)	0	0	0	1	0	0	0	0	0	0	1	**2**			
	ME(A)	0	0	0	0	0	0	0	0	0	0	0	**0**			
	ME(S+B)	0	0	0	2	0	0	0	2	0	0	1	**5**			
	ME(B+A)	0	0	0	0	0	0	0	0	0	0	0	**0**			
	ME(S+B+A)	0	0	0	0	0	0	0	0	1	0	0	**1**			
	ME Subtotal	**0**	**0**	**0**	**23**	**0**	**0**	**0**	**31**	**5**	**1**	**2**				
	MA(S)	0	0	0	0	2	0	0	0	6	2	0	**10**	**MA Province** **21 spp.**		
	MA(B)	0	0	0	0	1	0	0	0	4	0	1	**6**			
	MA(A)	0	0	0	0	0	0	0	0	0	0	0	**0**			
	MA(S+B)	0	0	0	0	0	0	0	0	1	2	0	**3**			
	MA(B+A)	0	0	0	0	0	0	0	0	0	0	1	**1**			
	MA(S+B+A)	0	0	0	0	0	0	0	0	1	0	0	**1**			
	MA Subtotal	**0**	**0**	**0**	**0**	**3**	**0**	**0**	**0**	**12**	**4**	**2**				
	NA(S)	0	0	0	0	0	3	0	0	0	9	0	**12**	**NA Province** **29 spp.**		
	NA(B)	0	0	0	0	0	0	0	0	0	2	1	**3**			
	NA(A)	0	0	0	0	0	0	0	0	0	0	0	**0**			
	NA(S+B)	0	0	0	0	0	3	0	0	0	6	1	**10**			
	NA(B+A)	0	0	0	0	0	0	0	0	0	2	1	**3**			
	NA(S+B+A)	0	0	0	0	0	0	0	0	0	1	0	**1**			
	NA Subtotal	**0**	**0**	**0**	**0**	**0**	**6**	**0**	**0**	**0**	**20**	**3**				

Appendix II.E.– Faunal composition: Geographic and bathymetric distribution of groups of species (percentage) in different biogeographic categories per each area (AR; BO; LU; ME; NA).

		Biogeographic categories											
		AE	**BE**	**LE**	**ME**	**MAE**	**NE**	**AN**	**ANME**	**ANMA**	**ANF**	**WI**	**Subtotal**
Geographic and bathymetric groups of species	AR(S)	18,2	0	0	0	0	0	8,0	3,4	0	6,8	0	**36,4**
	AR(B)	15,9	0	0	0	0	0	5,7	0	0	1,1	1,1	**23,9**
	AR(A)	1,1	0	0	0	0	0	0	0	0	0	0	**1,1**
	AR(S+B)	10,2	0	0	0	0	0	13,6	1,1	1,1	5,7	1,1	**33,0**
	AR(B+A)	2,3	0	0	0	0	0	1,1	0	0	1,1	1,1	**5,7**
	AR(S+B+A)	0	0	0	0	0	0	0	0	0	0	0	**0**
	AR Subtotal	**47,7**	**0,0**	**0,0**	**0,0**	**0,0**	**0,0**	**28,4**	**4,5**	**1,1**	**14,8**	**3,4**	
	BO(S)	0	14,3	0	0	0	0	6,7	19,3	2,5	5,9	0	**48,7**
	BO(B)	0	10,9	0	0	0	0	5,0	0	2,5	1,7	0,8	**21,0**
	BO(A)	0	3,4	0	0	0	0	2,5	0	0	0	0	**5,9**
	BO(S+B)	0	2,5	0	0	0	0	10,1	1,7	0,8	4,2	0,8	**20,2**
	BO(B+A)	0	0	0	0	0	0	0,8	0	0	0,8	0,8	**2,5**
	BO(S+B+A)	0	0	0	0	0	0	0	0	0,8	0,8	0	**1,7**
	BO Subtotal	**0**	**31,1**	**0**	**0**	**0**	**0**	**25,2**	**21,0**	**6,7**	**13,4**	**2,5**	
	LU(S)	0	0	7,0	0	0	0	2,3	30,2	11,6	9,3	0	**60,5**
	LU(B)	0	0	0	0	0	0	2,3	0	2,3	0	2,3	**7,0**
	LU(A)	0	0	4,7	0	0	0	7,0	0	0	0	0	**11,6**
	LU(S+B)	0	0	0	0	0	0	0	2,3	2,3	4,7	2,3	**11,6**
	LU(B+A)	0	0	0	0	0	0	2,3	0	0	2,3	2,3	**7,0**
	LU(S+B+A)	0	0	0	0	0	0	0	0	2,3	0	0	**2,3**
	LU Subtotal	**0**	**0**	**11,6**	**0**	**0**	**0**	**14,0**	**32,6**	**18,6**	**16,3**	**7,0**	
	MÊ(S)	0	0	0	31,7	0	0	0	46,0	6,3	1,6	0	**85,7**
	ME(B)	0	0	0	1,6	0	0	0	0	0	0	1,6	**3,2**
	ME(A)	0	0	0	0	0	0	0	0	0	0	0	**0**
	ME(S+B)	0	0	0	3,2	0	0	0	3,2	0	0	1,6	**7,9**
	ME(B+A)	0	0	0	0	0	0	0	0	0	0	1,6	**1,6**
	ME(S+B+A)	0	0	0	0	0	0	0	0	1,6	0	0	**1,6**
	ME Subtotal	**0**	**0**	**0**	**36,5**	**0**	**0**	**0**	**49,2**	**7,9**	**1,6**	**4,8**	
	MA(S)	0	0	0	0	8,7	0	0	0	26,1	8,7	0	**43,5**
	MA(B)	0	0	0	0	4,3	0	0	0	17,4	0	4,3	**26,1**
	MA(A)	0	0	0	0	0	0	0	0	0	0	0	**0**
	MA(S+B)	0	0	0	0	0	0	0	0	4,3	8,7	4,3	**17,4**
	MA(B+A)	0	0	0	0	0	0	0	0	0	0	4,3	**4,3**
	MA(S+B+A)	0	0	0	0	0	0	0	0	4,3	0	0	**4,3**
	MA Subtotal	**0**	**0**	**0**	**0**	**13,0**	**0**	**0**	**0**	**52,2**	**17,4**	**13,0**	
	NA(S)	0	0	0	0	0	10,3	0	0	0	31,0	0	**41,4**
	NA(B)	0	0	0	0	0	0	0	0	0	6,9	3,4	**10,3**
	NA(A)	0	0	0	0	0	0	0	0	0	0	0	**0**
	NA(S+B)	0	0	0	0	0	10,3	0	0	0	20,7	3,4	**34,5**
	NA(B+A)	0	0	0	0	0	0	0	0	0	6,9	3,4	**10,3**
	NA(S+B+A)	0	0	0	0	0	0	0	0	0	3,4	0	**3,4**
	NA Total (%)	**0**	**0**	**0**	**0**	**0**	**20,7**	**0**	**0**	**0**	**69,0**	**10,3**	

Abbreviations:

Geographic - AR, Arctic; **BO,** Boreal; **LU,** Lusitanian; **ME,** Mediterranean; **MA,** Mauritanian; **NA,** North American. **Bathymetric - S,** Shelf; **B,** Bathyal; **A,** Abyssal. **Biogeographic - AE,** Arctic Endemics; **BE,** Boreal Endemics; **LE,** Lusitanian Endemics; **ME,** Mediterranean Endemics; **MAE**, Mauritanian Endemics; **NAE**, North American Endemic; **AN**, Atlantic Northeast and Arctic; **ANME**, Atlantic Northeast and Mediterranean; **ANMA**, Atlantic Northeast and Mauritanian; **ANF**, Anfiatlantic; **WI,** Wide distribution; **ATM**, Atlanto-Mediterranean Subregion **NEA**, North Eastern Temperate Region.

Species Synonymies List

Class Anthozoa

Subclass Hexacorallia

Order Actiniaria

Suborder Endocoelantheae Carlgren 1925

Family Actinernidae Stephenson, 1922

Genus *Actinernus*, Verrill, 1879

***Actinernus michaelsarsi* Carlgren, 1918**

***Actinernus nobilis* Verrill, 1879**

Family Halcuriidae Carlgren, 1918

Genus *Carlgrenia* Stephenson, 1918

***Carlgrenia desiderata* Stephenson, 1918**

Suborder Nynantheae Carlgren, 1899

Tribu Boloceroidaria Carlgren, 1924

Genus *Bunodeopsis* Andres, 1881

***Bunodeopsis strumosa* Andres, 1881** [*Tetractis jonica* Goethe, 1897]

Tribu Endomyaria Stephenson, 1921

Family Actiniidae Rafinesque, 1815

Genus *Actinia* Linnaeus, 1758

***Actinia cari* Delle Chiaje, 1825** [*Actinia concentrica* Risso, 1826; *A. cari* de Blainville, 1830; *A. adspersa* Gravenhorst, 1831; *A. graminea* Dana, 1849; *A. lineolata* Dana, 1849; *Paractis lineolata* Milne Edwards, 1857; *A. virgata* Johnson, 1861; *A. equina* Pax, 1907].

***Actinia equina* (Linnaeus, 1758)** [*Priapus equinus* Linnaeus, 1758; *P. ruber* Forsskål, 1775; *Actinia rufa* Müller, 1776; *A. hemispherica* Pennant, 1777; *A. mesembryanthemum* Brandt, 1835; *A. purpurea* Cuvier, 1798; *A. corallina* Risso, 1826; *A. margaritifera* Templeton, 1836; *A. cerasum* Dalyell, 1848; *A. chiococca* Cocks in Johnston, 1847; *A. fragacea* Tugwell, 1856; *A. forskaeli* Milne Edwards, 1857; *A. equini* Cuvier, 1863; *A. equine* Tsurpalo & Kostina, 2003]

***Actinia fragacea* Tugwell, 1856** [*Actinia equine* Nafilyan, 1912]

***Actinia nigropunctata* den Hartog & Ocaña, 2003**

***Actinia prasina* Gosse, 1860** [*Actinia mesembryanthemum* Gosse, 1860; *A. equina* Haddon, 1886; *A. prasina* Haylor, Thorpe & Carter, 1984]

***Actinia sali* Monteiro, Solé-Cava & Thorpe, 1997** [*Actinia equina* Schmidt, 1971]

***Actinia schmidti* Monteiro, Solé-Cava & Thorpe, 1997**

***Actinia striata* (Rizzi, 1970)** [*A. equina* Rizzi, 1907]

***Actinia virgata* Johnson (1861)**

Genus *Anemonia* Risso, 1826

***Anemonia melanaster* (Verrill, 1910)** [*Anemonia sargassensis* Hargitt, 1908; *Anemonia antillensis* Pax, 1924; *Pseudactinia melanaster* Cairns *et. al.,* 1986]

***Anemonia viridis* (Forskal, 1775)** [*Priapus viridis* Forsskål, 1775; *Anemonia sulcata* Andres, 1881]

Genus *Anthopleura* Duchassaing de Fonbressin & Michelotti, 1860

***Anthopleura ballii* (Cocks, 1850)** [*Actinea Balii* Cocks, 1851; *Actinia clavata* Gosse, 1853; *Cereus clavata* Milne Edwards, 1857; *Bunodes balli* Fischer, 1874; *Bunodes listeri* Johnson, 1861; *Aulactinia alfordi* Andres, 1883; *Bunodactis balli* Verrill, 1899; *Bunodactis alfordi* Stephenson, 1922]

***Anthopleura thallia* (Gosse, 1854)** [*Actinia thallia* Gosse, 1854; *Bunodes thallia* Gosse, 1855; *Cereus thalia* Milne Edwards, 1857; *Bunodactis thallia* Verrill, 1899]

Genus *Aulactinia*

***Aulactinia stella* (Verrill, 1864)** [*Bunodes stella* Verrill, 1864; *Bunodes spectabilis* Verrill, 1879; *Bunodactis stella* Verrill, 1899; *Corticifera glareola* Verrill, 1907; *Cribina stella* McMurrich, 1911; *Tealiopsis stella* Verrill, 1922; *Anthopleura stella* Uchida, 1938; *Anthopleura fusco-viridis* Carlgren, 1949]

***Aulactinia verrucosa* (Pennant, 1777)** [*Actinia gemmacea* Ellis and Solander, 1786; *Actinia verrucosa* Bruguiere, 1789; *Actinia pedunculata* Delle Chiaje, 1823; *Actinocereus sessilis de* Blainville, 1830; *Actinia bimaculata* Grube, 1840; *Cribrina gemmacea* Milne Edwards and Haime, 1851; *Bunodes gemmacea* Gosse, 1855; *Cereus gemmaceus* Milne Edwards, 1857; *Cereus bimaculatus* Milne Edwards, 1857; *Bunodes verrucosus* Fischer, 1874; *Bunodes verrucosa* Hertwig, 1882; *Bunodactis verrucosa* Verrill, 1899; *Bunodactis gemmacea* Stephenson, 1922; *Axinella verrucosa* Pax & Mueller, 1953]

Genus *Bolocera* Gosse, 1860

***Bolocera tuediae* (Johnston, 1832)** [*Bolocera longicornis* Carlgren, 1891; *Bolocera kerguelensis* Dunn, 1983]

Genus *Bunodactis* Verrill, 1869

***Bunodactis rubripunctata* (Grube, 1840)** [*Actinia glandulosa* Otto, 1823; *Cribrina glandulosa* Ehrenberg, 1834; *Actinia rubripunctata* Grube, 1840; *Cereus glandulosus* Milne Edwards, 1857; *Bunodes rigidus* Andres, 1881; *Bunodes Duregnei* Fischer, 1889; *Bunodactis rigidus* Carlgren, 1949; *Anthopleura rubripunctata* Schmidt, 1969; *Bunodactis duregnei* Dunn, 1978; *Aulactinia duregnei* Dunn, *et al.,* 1980]

***Bunodactis spetsbergensis* (Carlgren, 1920)** [*Leiotealia spetsbergensis* Kwietniewski, 1898; *Rhodactinia crassicornis* Carlgren, 1902; *Cribrina spetsbergensis* Carlgren, 1921]

Genus *Condylactis* Duchassaing de Fombressin & Michelotti, 1864

***Condylactis aurantiaca* (Delle Chiaje, 1825)** [*Actinia aurantiaca* Delle Chiaje, 1822; *Cereus aurentiacus* Milne Edwards, 1857; *Cereactis aurantiaca* Andres, 1881]

Genus *Cribrinopsis* Carlgren, 1921

***Cribrinopsis crassa* (Andres, 1880)** [*Actinia rhododactylos* Grube, 1840; *Actinia rubripunctata* Grube, 1840; *Cereus digitatus* Milne Edwards, 1857; *Bunodes crassus* Andres, 1881; *Aulactinia crassa* Andres, 1883; *Anthopleura crassa* Carlgren, 1949]

***Cribrinopsis similis* Carlgren, 1921** [*Rhodactinia Dævisii* Agassiz, 1847; *Actinostola abyssorum* Pax, 1915]

Genus *Epiactis* Verrill, 1869

***Epiactis arctica* (Verrill, 1868)** [*Phellia arctica* Verrill, 1868; *Pseudophellia arctica* Verrill, 1899]

***Epiactis fecunda* (Verrill, 1899)** [*Epigonactis fecunda* Verrill, 1899; *Epigonactis regularis* Verrill, 1899]

***Epiactis nordmanni* Carlgren, 1921**

Genus *Onubactis* López-González et al., 1995

***Onubactis rocioi* López-González *et al*., 1995**

Genus *Paractinia*

***Paractinia striata* (Risso, 1826)**

Genus *Paranemonia* Carlgren, 1949

***Paranemonia cinerea* (Contarini, 1844)** [*Anemonia cinérea* Contarini, 1844; *Anthea cinérea* Sars, 1857; *Actinia Contarinii* Heller, 1868; *Anemonia Contarini* Andres, 1883; *Anemonia sulcata* Graeffe, 1884; *Gyrostoma cinerea* Stephenson, 1922]

***Paranemonia vouliagmeniensis* (Doumenc *et. al.,* 1987)**

Genus *Urticina* Ehrenberg, 1834

***Urticina crassicornis* (Müller, 1776)** [*Actinia crassicornis* Müller, 1776; Urticina felina Carlgren, 1921; *Tealia felina* Carlgren, 1934; *Tealia crassicornis* Hand, 1955]

***Urticina felina* (Linnaeus, 1761)** [*Priapus felinus* Linnaeus, 1761; *Actinia felina* Linnaeus, 1767; *Actinia crassicornis* Müller, 1776; *Actinia senilis* Bruguiere, 1789; *Actinia coriacea* Cuvier, 1798; *Actinia holsatica* Müller, 1806; *Actinia papillosa* Ehrenberg, 1834; *Cribrina coriacea* Ehrenberg, 1834; *Cribrina papillosa* Brandt, 1835; *Actinia Gemmacea* Couch, 1844; *Actinia Dævisii* Agassiz, 1847; *Actinea coriacea* Cocks, 1851; *Actinea tuberculata* Cocks, 1851; *Actinea crassicornis* Cocks, 1851; *Actinia obtruncata* Stimpson, 1853; *Bunodes crassicornis* Gosse, 1855; *Cereus coriaceus* Milne Edwards, 1857; *Cereus papillosus* Milne Edwards, 1857; *Tealia crassicornis* Gosse, 1858; *Tealia Greenii* Wright, 1859; *Tealia tuberculata* Gosse, 1860; *Bolocera eques* Gosse, 1860; *Rhodactinia Davisii* Verrill, 1864; *Urticina crassicornis* Verrill, 1869; *Tealia felina* Fischer, 1874; *Madoniactis lofotensis* Danielssen, 1890; *Leiotealia spetsbergensis* Kwietniewski, 1898; *Tealia coriacea* Carlgren, 1902; *Tealia lofotensis* Carlgren, 1902; *Rhodactinia crassicornis* Carlgren, 1902; *Stomphia churchiæ* Elmhirst, 1915; *Urticina davisii* Carlgren, 1916; *Urticina coriacea* Stephenson, 1918; *Urticina columbiana* Verrill, 1922]

***Urticina lofotensis* (Danielssen, 1890)** [*Madoniactis lofotensis* Danielssen, 1890; *Tealia lofotensis* Carlgren, 1902; *Rhodactinia crassicornis* Walton, 1908; *Urticina felina* Carlgren, 1921; *Tealia felina* Stephenson, 1935]

Family Aliciidae Duerden, 1895

Genus *Alicia* Johnson, 1861

***Alicia mirabilis* Johnson, 1861** [*Cladactis mirabilis* Andres, 1883]

Family Andresiidae Stephenson, 1922

Genus *Andresia* Stephenson, 1921

***Andresia parthenopea* (Andres, 1883)** [Actinia diaphana Delle Chiaje, 1841; *Ilyanthus diaphanus* Andres, 1881; *Ilyanthus partenopeus* Andres, 1883; *Andresia parthenopea* Delphy, 1938]

Family Andvakiidae Danielssen, 1890

Genus *Andvakia* Danielssen, 1890

***Andvakia mirabilis* Danielssen, 1890**

Genus *Ilyactis*

***Ilyactis torquata* Andres, 1881**

Family Capneidae Gosse, 1860

Genus *Capnea* Forbes, 1841

***Capnea sanguinea* Forbes, 1841** [*Corynactis heterocera* Thompson, 1853; *Aureliania augusta* Gosse, 1860; *Aureliania heterocera* Gosse, 1860; *Aureliania regalis* Andres, 1883]

Family Condylanthidae Stephenson, 1922

Genus *Segonzactis* Riemann-Zürneck, 1979

***Segonzactis hartogi* Vafidis & Chintiroglou, 2002**

***Segonzactis platypus* Riemann-Zürneck, 1979**

Family Edwardsiidae Andres, 1881

Genus *Edwardsia* de Quatrefages, 1842

***Edwardsia allmani* M'Intosh, 1866** [*Edwardsiella Allmani* Pennington, 1885]

***Edwardsia andresi* Danielssen, 1890** [*Edwardsioides andresi* England, 1987]

***Edwardsia arctica* Carlgren, 1921** [*Edwardsioides arctica* England, 1987]

***Edwardsia beautempsii* Quatrefages, 1842** [*Scolanthus callimorphus* Gosse, 1853; *Edwardsia callimorpha* Gosse, 1855]

***Edwardsia carlgreni* Carlgren, 1921** [*Edwardsia clavata* Carlgren, 1893]

***Edwardsia claparedii* (Panceri, 1869)** [*Halcampa claparedii* Panceri, 1869; *Urophysalus Grubii* Costa, 1869; *Edwardsia timida* Rees & Walton, 1913; *Edwardsia callimorpha* Carlgren & Stephenson, 1928]

***Edwardsia coriacea* Moseley, 1877**

***Edwardsia costata* Danielssen, 1890**

***Edwardsia danica* Carlgren, 1921**

***Edwardsia delapiae* Carlgren & Stephenson, 1928** [*Edwardsia timida* de Quatrefages, 1842; *Edwardsia tecta* Haddon, 1889; *Edwardsia delapiæ* Carlgren & Stephenson, 1928]

***Edwardsia finmarchica* Carlgren, 1921**

***Edwardsia fischeri* Chevreux et de Guerne, 1889** [*nomen dubium* according to (Williams, 1981)]

***Edwardsia fusca* Danielssen, 1890** [*Edwardsioides fusca* England, 1987]

***Edwardsia goodsiri* M'Intosh, 1866** [*nomen dubium* according to Williams, 1981]

***Edwardsia islandica* Carlgren, 1921** [*Edwardsioides islandica* England, 1987]

***Edwardsia longicornis* Carlgren, 1921** [*Edwardsia clavata* Carlgren, 1893]

***Edwardsia maroccana* Carlgren, 1931**

***Edwardsia norvegica* Carlgren, 1942** [*Edwardsioides norvegica* England, 1987]

***Edwardsia tecta* Haddon, 1889** [*nomen dubium* according to Williams (1981)]

Edwardsia timida **Quatrefages, 1842** [*Edwardsia Harassi* de Quatrefages, 1842; *Edwardsiella harassii* Andres, 1883; *Milne-Edwardsia dixonii* Carlgren, 1921; *Edwardsia delapiæ* Carlgren & Stephenson, 1928; *Edwardsia callianthus* Rawlinson, 1935; *Milne Dixoni* Collings, 1938; *Fagesia dixoni* Carlgren, 1949; *Edwardsioides timida* England, 1987]

Edwardsia tuberculata **Düben & Koren 1847** [*Edwardsia clavata* Andres, 1883]

Edwardsia vegae **Carlgren, 1921** [*Edwardsioides vegae* England, 1987]

Edwardsia vitrea (Danielssen, 189) [*Edwardsioides vitrea* Danielssen, 1890]

Genus *Edwardsiella* Andres, 1883

Edwardsiella carnea **(Delphy, 1938)** [*Edwardsia Sarsii* Dueben & Koren, 1847; *Edwardsia carnea* Gosse, 1856; *Halcampa microps* Andres, 1883; *Edwardsia microps* Andres, 1883; *Edwardsiella carnea* Andres, 1883; *Milne-Edwardsia carnea* Carlgren, 1892; *Fagesia carnea* Delphy, 1938; *Favesia carnea* Carlgren, 1940]

Edwardsiella janthina **(Andres, 1881)** [*Edwardsia janthina* Andres, 1881; *Fagesia janthina* Williams, 1981]

Edwardsiella lineata **(Verrill in Baird, 1873)** [*Edwardsia lineata* Verrill in Baird, 1873; *Edwardsia leidyi* Verrill, 1898; *Fagesia lineate* Carlgren, 1949]

Edwardsiella loveni **(Carlgren, 1892)** [*Milne-Edwardsia loveni* Carlgren, 1892; *Favesia loveni* Carlgren, 1940]

Genus *Paraedwardsia* Carlgren in Nordgaard, 1905

Paraedwardsia arenaria **Carlgren in Nordgaard, 1950**

Paraedwardsia sarsii **(Dueben & Koren, 1847)** [*Edwardsia Sarsii* Dueben & Koren, 1847; *Edwardsia carnea* Appellöf, 1891; *Milne-Edwardsia carnea* Grieg, 1913]

Genus *Scolanthus* Gosse, 1853

Scolanthus callimorphus **(Gosse, 1853)** [*Scolanthus callimorphus* Gosse, 1853; *Edwardsia callimorpha* Gosse, 1855; *Halcampa claparedii* Panceri, 1869; *Edwardsia janthina* Andres, 1881; *Edwardsia lucifuga* Fischer, 1888; *Edwardsia beautempsii* Haddon, 1889; *Isoedwardsia mediterranea* Carlgren, 1921; *Isoedwardsia lucifuga* Carlgren, 1949; *Alfredus lucifugus* Schmidt, 1979]

Scolanthus ingolfi **(Carlgren, 1921)** [*Isoedwardsia ingolfi* Carlgren, 1921]

Scolanthus nidarosiensis **(Carlgren, 1942)** [*Isoedwardsia nidarosiensis* Carlgren, 1942]

Family Halcampidae Andres, 1883

Genus *Cactosoma* Danielssen, 1890

Cactosoma abyssorum **Danielssen, 1890** [*Phellia crassa* Danielssen, 1890; *Phelliomorpha crassa* Carlgren, 1902; *Phelliactis crassa* Carlgren, 1949]

Genus *Halcampa* Gosse, 1858

Halcampa arctica **Carlgren, 1893**

Halcampa duodecimcirrata **(Sars, 1851)** [*Edwardsia duodecimcirrata* Sars, 1851; *Edwardsia farinácea* Verrill, 1869; *Edwardsia octodecimcirrata* Verrill, 1879; *Halcampa farinacea* Andres, 1883; *Edwardsia Lütkenii* Andres, 1883; *Halcampa chrysanthellum* Haddon, 1886; *Halcampella duodecimcirrata* McMurrich, 1904]

Family Halcampoididae Appellvf, 1896

Genus *Acthelmis*

***Acthelmis intestinalis* (Fabricius, 1780)** [*Actinia intestinalis* Fabricii, 1780; Actinia truncata Gmelin, 1796; *Actinocereus intestinalis* de Blainville, 1830]

Genus *Halcampoides* Danielssen, 1890

***Halcampoides abyssorum* Danielssen, 1890** [*Halcampa clavus* Hertwig, 1882; *Fenja mirabilis* Danielssen, 1887; *Ægir frigidus* Danielssen, 1887; *Halcampa kerguelensis* Hertwig, 1888; *Halcampa septentrionalis* Pax, 1912; *Halcampoides macrodactyla* Pax, 1922; *Epiactis stephensoni* Pax, 1926]

***Halcampoides purpurea* (Studer, 1878)** [*Halcampa purpurea* Studer, 1879; *Halcampa clavus* Hertwig, 1882; *Ægir frigidus* Danielssen, 1887; *Fenja mirabilis* Danielssen, 1887; *Halcampa kerguelensis* Hertwig, 1888; *Halcampa abyssorum* Danielssen, 1890; *Halcampa septentrionalis* Pax, 1912; *Halcampoides kerguelensis* Stephenson, 1922; *Halcampoides macrodactyla* Pax, 1922]

Genus *Siphonactinopsis* Carlgren, 1921

***Siphonactinopsis laevis* Carlgren, 1921**

Family Haliactiidae Carlgren, 1949

Genus *Haliactis* Carlgren, 1921

***Haliactis arctica* Carlgren, 1921** [*Acthelmis schaudinnii* Carlgren, 1921]

Family Haloclavidae Verrill, 1899

Genus *Anemonactis* Andres, 1881

***Anemonactis mazelli* (Jourdan, 1880)** [*Ilyanthus mazeli* Jourdan, 1880; *Anemonactis magnifica* Andres, 1881; *Eloactis Mazelii* Fischer, 1887; *Halcampella minuta* Wassilieff, 1908; *Haloclava minuta* Carlgren, 1949]

Genus *Haloclava* Verrill, 1899

***Haloclava producta* (Stimpson, 1856)** [*Actinia producta* Stimpson, 1856; *Corynactis albida* Agassiz, 1859; *Halcampa albida* Verrill, 1864; *Halcampa producta* Verrill, 1864; *Halocampa albida* Verrill, 1866; *Halocampa producta* Baird, 1873; *Halcampa Elizabethae* Andres, 1883; *Eloactis producta* McMurrich, 1893; *Haloclava albida* Verrill, 1899]

Genus *Mesacmaea* Andres, 1883

***Mesacmaea mitchellii* (Gosse, 1853)** [*Iluanthos Mitchellii* Gosse, 1853; Ilyanthus stellatus Andres, 1881]

Genus *Peachia* Gosse, 1855

***Peachia boeckii* (Danielssen & Koren, 1856)** [*Siphonactinia Boeckii* Danielssen and Koren, 1856; *Peachia Boeckii* McMurrich, 1893]

***Peachia cylindrica* (Reid, 1848)** [*Actinia cylindrica* Reid, 1848]

***Peachia parasitica* (Agassiz, 1859)** [*Bicidium parasiticum* Agassiz, 1859; *Philomedusa parasítica* Andres, 1883; *Bicidium parasitica* Hargitt, 1912; *Siphonactinia parasitica* Verrill, 1922; *Bicidiopsis tubicola* Verrill, 1922; *Bicidiopsis arctica* Verrill, 1922]

Family Iosactiidae Riemann-Zürneck, 1997

Genus *Iosactis* Riemann-Zürneck, 1997

***Iosactis vagabunda* Riemann-Zürneck, 1997**

Family Limnactiniidae Carlgren, 1921

Genus *Limnactinia* Carlgren, 1921

***Limnactinia laevis* Carlgren, 1921**

Family Liponematidae Hertwig, 1882

Genus *Liponema* Hertwig, 1882

***Liponema multicornis* (Verrill, 1880)** [*Bolocera multicornis* Verrill, 1880; *Urticina multicornis* Verrill, 1882; *Sagartia abyssicola* Danielssen, 1890; *Bolocera brevicornis* McMurrich, 1893; *Bolocera longicornis* Gravier, 1922; *Eubolocera multicornis* Verrill, 1922]

Family Octineonidae Fowler, 1894

Genus *Octineon* Fowler, 1894

***Octineon suecicum* Carlgren, 1940**

Tribu Mesomyaria Stephenson, 1921

Family Actinoscyphiidae Stephenson, 1920

Genus *Actinoscyphia* Stephenson, 1920

***Actinoscyphia aurelia* (Stephenson, 1920)** [*Actinernus aurelia* Stephenson, 1918; *Actinoscyphiopsis aurelia* Carlgren, 1928; *Actinoscyphia saginata* Carlgren, 1934]

***Actinoscyphia saginata* (Verrill, 1882)** [*Actinernus saginatus* Verrill, 1882; *Actinoscyphia aurelia* Carlgren, 1928]

***Actinoscyphia verrilli* (Gravier, 1918)** [*Actinernus Verrilli* Gravier, 1918]

Family Actinostolidae Carlgren, 1932

Genus *Actinostola* Verrill, 1883

***Actinostola abyssorum* (Danielssen, 1890)** [*Bunodes abyssorum* Danielssen, 1890; *Cribrinopsis similis* Carlgren, 1921]

***Actinostola callosa* (Verrill, 1882)** [*Urticina callosa* Verrill, 1882; *Actinostola sibirica* Carlgren, 1901; *Actinostola atrostoma* Stephenson, 1918; *Catadiomene atrostoma* Stephenson, 1920; *Actinostola abyssorum* Carlgren, 1921; *Actinostola groenlandica* Carlgren, 1921; *Actinostola spetsbergensis* Carlgren, 1921]

***Actinostola groenlandica* Carlgren, 1899**

***Actinostola spetsbergensis* Carlgren, 1893** [*Actinostola walteri* Kwietniewski, 1898; *Actinostola sibirica* Carlgren, 1901]

Genus *Anthosactis* Danielssen, 1890

***Anthosactis ingolfi* Carlgren, 1921**

***Anthosactis janmayeni* Danielssen, 1890**

Genus *Antipodactis* Rodríguez et al., 2009

***Antipodactis awii* Rodríguez et al., 2009**

***Antipodactis ifremeri* sp. nov.**

Genus *Epiparactis* Carlgren, 1921

***Epiparactis dubia* Carlgren, 1921**

Genus *Paranthus* Andres, 1883

***Paranthus rugosus* (Andres, 188)** [*Paractis rugosa* Andres, 1881; *Paranthus chromatoderus* Andres, 1883]

Genus *Parasicyonis* Carlgren, 1921

***Parasicyonis biotrans* (Riemann-Zürneck, 1991)** [Sicyonis *biotrans* Riemann-Zürneck, 1991]

***Parasicyonis groenlandica* Carlgren, 1933**

***Parasicyonis ingolfi* Carlgren, 1942** [*Paractinostola ingolfi* Fautin & Barber, 1999]

***Parasicyonis sarsii* Carlgren, 1921**

Genus *Pycnanthus* McMurrich, 1893

***Pycnanthus densus* Carlgren, 1921**

***Pycnanthus laevis* Carlgren, 1921**

Genus *Phymanthus*

***Phymanthus pulcher* (Andres, 1883)** [*Ragactis pulchra* Andres, 1883; *Phymanthus pulcra* Carlgren, 1949]

Genus *Sicyonis* Hertwig, 1882

***Sicyonis gossei* (Stephenson, 1918)** [*Cymbactis gossei* Stephenson, 1918]

***Sicyonis ingolfi* Carlgren, 1921**

***Sicyonis tuberculata* Carlgren, 1921**

***Sicyonis variabilis* Carlgren, 1921**

Genus *Stomphia* Gosse, 1859

***Stomphia coccínea* (Müller, 1776)** [*Actinia coccinea* Müller, 1700; *Actinia carneola* Stimpson, 1853; *Actinia Nitida* Dawson, 1858; *Stomphia Churchiæ* Gosse, 1859; *Rhodactinia Davisii* Verrill, 1864; *Cylista coccinea* Andres, 1883; *Sagartia repens* Danielssen, 1890; *Kylindrosactis elegans* Danielssen, 1890]

***Stomphia polaris* (Danielssen, 1890)** [*Tealiopsis polaris* Danielssen, 1890]

Genus *Tealidium* Hertwig, 1882

***Tealidium jungerseni* Carlgren, 1921**

Family Aiptasiidae Carlgren, 1924

Genus *Aiptasia* Gosse, 1858

***Aiptasia diaphana* (Rapp, 1829)** [*Actinia diaphana* Rapp, 1829; *Cribrina diaphana* Deshayes & Milne Edwards, 1840; *Actinia elongata* Delle Chiaje, 1841; *Adamsia diaphana* Milne Edwards, 1857; *Aiptasia diaphana* Andres, 1883; *Ilyanthus partenopeus* Andres, 1883; *Aiptasiomorpha diaphana* Stephenson, 1920]

***Aiptasia mutabilis* (Gravenhorst, 1831)** [*Actinia mutabilis* Gravenhorst, 1831; *Anthea Couchii* Cocks, 1851; *Entacmæa biserialis* Milne Edwards & Haime, 1851; *Cribrina punctata* Schmarda, 1852; *Aiptasia amacha* Gosse, 1858; *Sagartia Penoti* Jourdan, 1880; *Aiptasia turgida* Andres, 1881; *Aiptasia Couchi* Andres, 1883; *Aiptasiomorpha mutabilis* Carlgren, 1949]

Genus *Aiptasiogeton* Schmidt, 1972

***Aiptasiogeton hyalinus* (Delle Chiaje, 1822)** [*Actinia hyalina* Delle Chiaje, 1822; *Aiptasia lacerata* Andres, 1883; *Aiptasiogeton comatus* Schmidt, 1972; *Aiptasiogeton pellucidus* Manuel, 1981]

***Aiptasiogeton pellucidus* (Hollard, 1848)** [*Actinia pellucida* Risso, 1826; *Sagartia rosea* Gosse, 1860; *Sagartia pellucida* Fischer, 1874; *Paractis comata* Andres, 1881; *Adamsia Fischeri* Andres, 1883; *Aiptasia lacerata* Andres, 1883; *Aiptasiogeton comatus* Schmidt, 1972]

Family Bathyphelliidae Carlgren, 1932

Genus *Bathyphellia* Carlgren, 1932

***Bathyphellia margaritacea* Danielssen, 1890** [*Phellia margaritacea* Danielssen, 1890]

Genus *Daontesia* Carlgren, 1942

***Daontesia porcupina* Riemann-Zürneck, 1997**

***Daontesia praelonga* Carlgren, 1928** [*Sagartiogeton praelongus* Carlgren, 1928]

Family Diadumenidae Stephenson, 1920

Genus *Diadumene* Stephenson, 1920

***Diadumene cincta* Stephenson, 1925** [*Sagartia erythrochila* Fischer, 1874]

***Diadumene lineata* (Verril, 1869)** [*Actinia chrysosplenium* Johnston, 1847; *Sagartia lineata* Verrill, 1869; *Sagartia pustulata* McMurrich, 1887; *Sagartia Luciæ* Verrill, 1898; *Sagartia davisi* Torrey, 1904; *Sagartia luciae* Walton, 1908; *Diadumene luciæ* Carlgren, 1927; *Chrysoela chrysosplenium* Stephenson, 1935; *Aiptasiomorpha luciae* Carlgren, 1949; *Haliplanella luciae* Hand, 1956; *Haliplanella lineata* Manuel, 1981]

Family Hormathiidae Carlgren, 1932

Genus *Actinauge* Verrill, 1883

***Actinauge abyssorum* (Gravier, 1918)** [*Chitonanthus abyssorum* Gravier, 1918]

***Actinauge cristata* (Riemann Zürneck, 1986)** [*Actinauge Verrillii* Carlgren, 1928]

***Actinauge longicornis* Verrill, 1882** [*Urticina longicornis* Verrill, 1882; *Chitonactis longicornis* Verrill, 1883; *Hormathia longicornis* Haddon, 1898]

***Actinauge richardi* (Marion, 1882)** [*Actinea tuberculata* Cocks, 1851; *Tealia tuberculata* Gosse, 1860; *Chitonactis Richardi* Marion, 1882; *Bathyactis Richardi* Durègne, 1886; Chondractinia nodosa Gravier, 1922; *Hormathia Richardi* Delphy, 1939]

***Actinauge verrilli* (McMurrich, 1893)** [*Urticina nodosa* Verrill, 1873; *Actinauge nodosa* Verrill, 1883]

Genus *Adamsia* Forbes, 1840

***Adamsia palliata* (O. F. Müller, 1776)** [*Medusa palliata* Bohadsch, 1761; *Actinia maculata* Bruguiere, 1789; *Actinia carciniopados* Delle Chiaje, 1822; *Actinia picta* Risso, 1826; *Actinia carcinopoda* Delle Chiaje, 1829; *Adamsia maculata* Thompson, 1856; *Actinia palliata* Heller, 1868; *Adamsia carciniopados* Manuel, 1981]

Genus *Allantactis* Danielssen, 1890

***Allantactis parasitica* Danielssen, 1890** [*Calliactis Krøyeri* Danielssen, 1890]

Genus *Amphianthus* Hertwig, 1882

***Amphianthus bathybium* Hertwig, 1882** [*Amphianthus ornatum* Hertwig, 1888; *Amphianthus ornatus* Carlgren, 1949]

***Amphianthus dohrnii* (v. Koch, 1878)** [*Gephyra Dohrnii* Koch, 1878; *Sagartia Dohrnii* Andres, 1883; *Gephyropsis dohrnii* Stephenson, 1925; *Chondranthus denudatus* Migot & Portmann, 1926]

***Amphianthus ingolfi* Carlgren, 1942**

***Amphianthus islandicus* Carlgren, 1942**

***Amphianthus margaritaceus* Danielssen, 1890** [*Korenia margaritacea* Danielssen, 1890]

***Amphianthus michaelsarsi* Carlgren, 1934**

***Amphianthus mopseae* Danielssen, 1890** [*Stelidiactis Mopseæ* Danielssen, 1890; *Stilidiacis mopseae* Carlgren, 1895]

***Amphianthus nitidus* Verrill, 1899** [*Raphactis nitida* Verrill, 1899]

***Amphianthus norvegicus* Carlgren, 1942**

***Amphianthus verruculatus* Carlgren, 1942**

Genus *Calliactis* Verrill, 1869

***Calliactis parasitica* (Couch, 1842)** [*Actinia effoeta* Linnaeus, 1767; *Priapus polypus* Forsskål, 1775; *Actinia Priapus* Gmelin, 1796; *Actinia effeta* Risso, 1826; *Cribrina Polypus* Ehrenberg, 1834; *Cribrina effoeta* Ehrenberg, 1834; *Actinia Rondeleti* Delle Chiaje, 1841; *Actinia parasitica* Gosse, 1855; *Sagartia parasitica* Gosse, 1855; *Adamsia priapus* Milne Edwards, 1857; *Cylista parasitica* Wright, 1859; *Sagartia affinis* Johnson, 1861; *Sagartia effæta* Fischer, 1874; *Calliactis polypus* Klunzinger, 1877; *Calliactis marmorata* Studer, 1879; *Adamsia Rondeletii* Andres, 1883; *Calliactus parasitica* Collings, 1938]

Genus *Cataphellia* Stephenson, 1931

***Cataphellia brodricii* (Gosse, 1859)** [*Phellia Brodricii* Gosse, 1859]

Genus *Caracolactis* gen. nov.

***Caracolactis maternalis* sp. nov.**

Genus *Chondrophellia* Carlgren, 1925

***Chondrophellia coronata* (Verrill, 1883)** [*Actinauge nodosa* Verrill, 1883; *Actinauge fastigata* McMurrich, 1893; *Hormathia elongata* Gravier, 1918]

Genus *Hormathia* Gosse, 1859

***Hormathia alba* (Andres, 188)** [*Phellia nummus* Andres, 1880; *Phelliopsis nummus* Fischer, 1887]

***Hormathia coronata* (Gosse, 1858)** [*Bunodes coronata* Gosse, 1858; *Chitonactis coronata* Fischer, 1874]

***Hormathia digitata* (Müller, 1776)** [*Actinia digitata* Müller, 1776; *Actinia crassicornis* Fabricii, 1780; *Actinia spectabilis* Fabricii, 1780; *Actinia ditata* Gmelin, 1796; *Actinia dilatata* de Blainville, 1830; *Actinea crassicornis* Cocks, 1851; *Cereus digitatus* Milne Edwards, 1857; *Tealia digitata* Gosse, 1858; *Hormathia Margaritæ* Gosse, 1859; *Urticina digitata* Verrill, 1873; *Urticina nodosa* Verrill, 1873; *Hormathia Margaritae* Andres, 1883; *Chondractinia digitata* Haddon, 1889; *Hormathia nodosa* Carlgren, 1942; *Allantactis parasítica* Carlgren, 1942; *Hormathia josefi* Zhiubikas, 1977]

***Hormathia marioni* Haddon, 1889** [*Chitonactis marioni* Haddon, 1889]

***Hormathia mediterranea* Carlgren, 1935**

***Hormathia nodosa* Fabricius, 1780** [*Actinia nodosa* Fabricii, 1780; *Actinoloba nodosa* de Blainville, 1830; *Metridium nodosum* Milne Edwards, 1857; *Tealia digitata* Gosse, 1860; *Chondractinia nodosa* Lütken, 1861; *Urticina nodosa* Verrill, 1873; *Chondrachtinia nodosa* Nordgaard, 1905; *Actinauge rugosa* Verrill, 1922; *Chondractinia tuberculosa* Verrill, 1922; *Actinauge borealis* Verrill, 1922]

Genus *Monactis* (Gravier, 1918)

***Monactis vestita* (Gravier, 1918)** [*Paractis vestita* Gravier, 1918]

Genus *Octophellia* Andres, 1883

***Octophellia timida* (Andres, 1880)** [*Phellia timida* Andres, 1880 (1880)]

Genus *Phellia* Gosse, 1858

***Phellia arctica* Danielssen, 1890**

Phellia gausapata* Gosse, 1858 [Paraphellia gausapata* Verrill, 1868; *Octophellia gausapata* Andres, 1883]

***Phellia murocincta* Gosse, 1860**

***Phellia norvegica* Danielssen, 1890**

Genus *Paracalliactis* Carlgren, 1928

***Paracalliactis azorica* Doumenc, 1975**

***Paracalliactis lacazei* Dechancé & Dufaure, 1959**

***Paracalliactis michaelsarsi*, Carlgren, 1928**

***Paracalliactis robusta* Tur, 1991**

***Paracalliactis stephensoni* Carlgren, 1928**

Genus *Paraphellia* Haddon, 1889

***Paraphellia expansa* (Haddon, 1886)** [*Chitonactis expanda* Haddon, 1886; *Cataphellia brodricii* Carlgren, 1949]

Genus *Parastephanauge*

***Parastephanauge paxi* Dufaure, 1959**

Genus *Phelliactis* Simon, 1892

***Phelliactis carlgreni* Doumenc, 1975**

***Phelliactis coccinea* (Stephenson, 1918)** [*Chondrodactis coccinea* Stephenson, 1918]

***Phelliactis hertwigi* Simon, 1892** [*Chondrodactis duplicate* Stephenson, 1918]

***Phelliactis incerta* Carlgren, 1934**

***Phelliactis michaelsarsi* (Carlgren, 1934)** [*Paraphelliactis michaelsarsi* Carlgren, 1934]

***Phelliactis pulchra* (Stephenson, 1918)** [*Chondrodactis pulchra* Stephenson, 1918]

***Phelliactis robusta* Carlgren, 1928**

***Phelliactis spinosa* (Carlgren, 1928)** [*Paraphelliactis spinosa* Carlgren, 1928]

Genus *Stephanauge* Verrill, 1899

***Stephanauge abyssicola* (Moseley, 1877)** [*Actinia abyssicola* Moseley, 1877; *Raphactis abyssicola* Verrill, 1922]

***Stephanauge acanellae* (Verrill, 1883)** [*Sagartia Acanellæ* Verrill, 1883]

Genus *Stephanactis* Gravier, 1918

***Stephanactis impedita* Gravier, 1918** [*Amphianthus impeditus* Carlgren, 1949]

***Stephanactis inornata* Gravier, 1918** [*Amphianthus inornata* Carlgren, 1949]

Family Isophelliidae Stephenson, 1935

Genus *Telmatactis* Gravier, 1916

***Telmatactis elongata* (Delle chiaje, 1825)**

***Telmatactis cricoides* (Duchassaing, 1850)** [*Entacmæa cricoides* Duchassaing, 1850; *Actinia cricoides* Milne Edwards, 1857; *Dysactis cricoides* Duchassaing de Fonbressin & Michelotti, 1860;

Paractis clavata Duchassaing de Fonbressin & Michelotti, 1860; *Capnea clavata* Duchassaing de Fombressin & Michelotti, 1864; *Capnea cricoides* Duchassaing de Fombressin & Michelotti, 1864; *Phellia Americana* Verrill, 1868; *Phellia cricoides* Andres, 1883; *Phellia Duchassaingi* Andres, 1883; *Euphellia cinclidifera* Pax, 1908; *Telmatactis Valle-Flori* Gravier, 1916; *Telmatactis pseudoroseni* Carlgren, 1949; *Telmatactis rufa* Corrêa, 1964; *Telmatactis cricoides* Cairns *et al.*, 1986]

Telmatactis forskalii **(Ehrenberg, 1834)** [*Actinia Forskålii* Ehrenberg, 1834; Actinia Chamaeleon Grube, 1840; *Actinia elongata* Delle Chiaje, 1841; *Actinia chamaeleon* Wiktor, 1992]

Telmatactis solidago **(Duchassaing & Michelotti, 1864)** [*Capneopsis Solidago* Duchassaing de Fombressin & Michelotti, 1864; *Phellia solidago* Andres, 1883; *Phellia simplex* Verrill, 1901; *Edwardsia horstii* Pax, 1924; *Telmatactis simplex* Carlgren, 1949]

Family Kadosactidae Riemann-Zürneck, 1991

Genus *Kadosactis* Danielssen, 1890

Kadosactis abyssicola **Koren & Danielssen, 1877** [*Phellia abyssicola* Koren & Danielssen, 1877; *Sagartiogeton abyssicola* Carlgren, 1928]

Kadosactis commensalis **(Gravier, 1918)** [*Sicyopus commensalis* Gravier, 1918]

Kadosactis rosea **Danielssen, 1890** [*Phellia bathybia* Danielssen, 1890; *Phellia violacea* Danielssen, 1890; *Hormathia musculosa* Gravier, 1918]

Kadosactis sptisbergensis **(Danielssen 1890)** [*Phellia spitsbergensis* Danielssen, 1890]

Kadosactis sulcata **Carlgren, 1934** [*Kadosactis sulcatus* Carlgren, 1949]

Family Metridiidae Carlgren, 1893

Genus *Metridium* de Blainville, 1824

Metridium senile **(Linnaeus, 1761)** [*Priapus senilis* Linnaeus, 1761; *Actinia senilis* Linnaeus, 1767; *Actinia dianthus* Ellis, 1768; *Actinia rufa* Müller, 1776; *Actinia plumosa* Müller, 1776; *Actinia candida* Müller, 1776; *Actinia pentapetala* Pennant, 1777; *Actinia Dianthus* Ellis and Solander, 1786; *Actinia varians* Müller, 1806; *Metridium Dianthus* Oken, 1815; *Actinia marginata* Le Sueur, 1817; *Metridium plumosa* de Blainville, 1830; *Actinoloba dianthus* de Blainville, 1830; *Actinia pallida* Holdsworth, 1855; *Metridium marginatum* Milne Edwards, 1857; *Actinia pellucida* Alder, 1858; *Thoe pura* Wright, 1859; *Sagartia pura* Gosse, 1860; *Metridium fimbriatum* Verrill, 1865; *Actinoloba marginata* Andres, 1883; *Metridium pallidum* Dons, 1945]

Family Sagartiidae Gosse, 1858

Genus *Actinothoe* Fischer, 1889

Actinothoe sphyrodeta **(Gosse, 1858)** [*Sagartia candida* Gosse, 1855; *Sagartia sphyrodeta* Gosse, 1858; *Thoe sphyrodeta* Wright, 1859]

Genus *Anthothoe* Carlgren, 1938

Anthothoe affinis **(Johnson, 1861)** [*Sagartia affinis* Johnson, 1861]

Genus *Cereus* Oken, 1815

Cereus pedunculatus **(Pennant, 1777)** [*Actinia pedunculata* Pennant, 1777; *Actinia Bellis* Ellis & Solander, 1786; *Hydra Bellis* Gmelin, 1796; *Actinia brevicirrhata* Risso, 1826; *Actinocereus pedunculata* de Blainville, 1830; *Cribrina Bellis* Brandt, 1835; *Actinia Dianthus* Couch, 1844; *Actinia Templetonii* Couch, 1844; *Discosoma brevicirrhata* Milne Edwards, 1857; *Heliactis bellis* Thompson, 1858; *Scyphia bellis* Wright, 1859; *Sagartia troglodytes* Heider, 1877; *Haliactis bellis* Graeffe, 1884]

Genus *Sagartia* Gosse, 1855

Sagartia elegans **(Dalyell, 1848)** [*Actinia elegans* Dalyell, 1848; *Actinia nivea* Gosse, 1853; *Actinia rosea* Gosse, 1853; *Actinia miniata* Gosse, 1853; *Actinia venusta* Gosse, 1854; *Sagartia nivea* Gosse, 1855; *Sagartia rosea* Gosse, 1855; *Bunodes miniata* Gosse, 1855; *Cereus aurora* Milne Edwards, 1857; *Adamsia elegans* Milne Edwards, 1857; *Cereus venusta* Milne Edwards, 1857; *Sagartia miniata* Gosse, 1858; *Sagartia ichthystoma* Gosse, 1858; *Actinia pulcherrima* Andres, 1883;

Heliactis miniata Andres, 1883; *Heliactis venusta* Andres, 1883; *Sagartia rockalliensis* Carlgren, 1924]

***Sagartia ornata* (Holdsworth, 1855)** [*Actinia ornata* Holdsworth, 1855; *Heliactis ornata* Andres, 1883; *Sagartia troglodytes* Stephenson, 1928]

***Sagartia troglodytes* (Price in Johnston, 1847)** [*Actinia troglodytes* Johnston, 1847; *Actinia explorator* Dalyell, 1848; *Actinia aurora* Gosse, 1854; *Actinia ornata* Holdsworth, 1855; *Sagartia Troglodytes* Gosse, 1855; *Cereus aurora* Milne Edwards, 1857; *Phellia murocincta* Gosse, 1858; *Sagartia ornata* Gosse, 1858; *Cylista troglodytes* Wright, 1859; *Heliactis troglodytes* Andres, 1881; *Cylista undata* Andres, 1883; *Scolanthus sphaeroides* Andres, 1883; *Heliactis ornata* Andres, 1883; *Heliactis venusta* Pennington, 1885; *Sagartia undata* Carlgren, 1893]

Genus *Sagartiogeton* Carlgren, 1924

***Sagartiogeton abyssorum* Carlgren, 1942**

***Sagartiogeton entellae* Schmidt, 1972**

***Sagartiogeton flexibilis* (Danielssen, 1890)** [*Phellia flexibilis* Danielssen, 1890]

***Sagartiogeton ingolfi* Carlgren, 1928**

***Sagartiogeton laceratus* (Dalyell, 1848)** [*Actinia hyalina* Delle Chiaje, 1823; *Actinia lacerata* Dalyell, 1848; *Sagartia coccinea* Gosse, 1858; *Phellia picta* Gosse, 1860; *Paractis comata* Andres, 1881; *Cylista coccinea* Andres, 1883; *Aiptasia lacerata* Andres, 1883; *Sagartia lacerata* Fischer, 1887; *Sagartia herdmani* Herdman, 1891; *Actinothoe lacerata* Stephenson, 1935; *Aiptasiogeton lacerates* Schmidt, 1969]

***Sagartiogeton robustus* Carlgren, 1924**

***Sagartiogeton tubicolus* (Koren & Danielssen, 1877)** [*Phellia tubicola* Koren and Danielssen, 1877]

***Sagartiogeton undatus* (Müller, 1788)** [*Actinia undata* Müller, 1778; *Actinea troglodytes* Cocks, 1851; *Sagartia Troglodytes* Gosse, 1855; *Actinia troglodytes* Tugwell, 1856; *Paractis undata* Milne Edwards, 1857; *Cylista troglodytes* Wright, 1859; *Sagartia viduata* Fischer, 1874; *Cylista undata* Andres, 1883; *Actinothoe anguicoma* Stephenson, 1935; *Actinothoë undata* Carlgren, 1940]

***Sagartiogeton verrilli* Carlgren, 1942** [*Sagartia abyssicola* Verrill, 1882; *Sagartiogeton abyssicola* Carlgren, 1928]

***Sagartiogeton viduatus* (Müller, 1776) [**[*Actinia effoeta* Linnaeus, 1767; *Actinia viduata* Müller, 1776; *Actinia anguicoma* Johnston, 1847; *Actinia explorator* Dalyell, 1848; *Actinea viduata* Cocks, 1851; *Sagartia viduata* Gosse, 1855; *Paractis viduata* Milne Edwards, 1857; *Cylista viduata* Wright, 1859; *Heliactis viduata* Andres, 1881; *Actinothoë viduata* Carlgren, 1940]

Genus *Kadophellia* Tur, 1991

***Kadophellia bathyalis* Tur, 1991**

Suborder Protantheae, Carlgren, 1891

Family Gonactiniidae Carlgren, 1893

Genus *Gonactinia* Sars, 1851

***Gonactinia prolifera* (Sars, 1835)** [*Actinia prolifera* Sars, 1835]

Genus *Protanthea* Carlgren, 1891

***Protanthea simplex* (Carlgren, 1891)**

Suborder Ptychodacteae Stephenson, 1922

Family Ptychodactiidae Appellöf, 1893

Genus *Ptychodactis* Appellöf, 1893

***Ptychodactis patula* Appellöf, 1893**