Universidade de Aveiro Departamento de Biologia
2010

Ascensão dos Anjos Alves Ravara

Revisão da Família Nephtyidae (Annelida, Poliqueta), baseada em dados morfológicos e moleculares

A revision of the polychaete family Nephtyidae, based on morphological and molecular data

Universidade de Aveiro Departamento de Biologia
2010

Ascensão dos Anjos Alves Ravara

Revisão da Família Nephtyidae (Annelida, Poliqueta), baseada em dados morfológicos e moleculares

A revision of the polychaete family Nephtyidae, based on morphological and molecular data

Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia, realizada sob a orientação científica da Professora Doutora Maria Marina Ribeiro Pais da Cunha, Professora Auxiliar do Departamento de Biologia da Universidade de Aveiro, e do Professor Doutor Fredrik Pleijel , Professor do Departamento de Ecologia Marinha da Universidade de Gotemburgo, Suécia.

Ascensão Ravara was supported by a PhD grant (SFRH/BD/16563/2004) from Fundação para a Ciência e Tecnologia, co-funded by POPH/FSE.

I would like to dedicate this work to Professor Maria Helena Moreira who always supported my research studies from the very beginning. She provided the basis for all my knowledge on polychaete taxonomy and always supported the various opportunities to improve my training. If we are a reflex of what we learn, the Professor Helena Moreira greatly contributed to who I am. To her my sincere acknowledgments.

o júri / the jury

presidente / president	Professor Doutor Luís Filipe Pinheiro de Castro Professor Catedrático da Universidade de Aveiro
vogais / members	Professor Doutor Guillermo San Martin Professor Catedrático da Universidade Autónoma de Madrid, Espanha
	Professor Doutor Amadeu Mortágua Velho da Maia Soares Professor Catedrático da Universidade de Aveiro
	Professor Doutor Fredrik Pleijel (Co-orientador) Professor Titular da Universidade de Gothenburg, Suécia
	Professora Doutora Maria Helena Moreira Professora Associada Aposentada da Universidade de Aveiro
	Doutor Filipe José Oliveira Costa Professor Auxiliar da Universidade do Minho
	Doutora Maria Marina Ribeiro da Cunha (Orientadora) Professora Auxiliar da Universidade de Aveiro

agradecimentos / acknowledgements

I would like to acknowledge my supervisors Marina Cunha and Fredrik Pleijel for all the guidance and support given during these years. They gave me the opportunity of learning new techniques in different areas and provided me with all that I needed to develop my work. But most of all they made me a much better researcher.

Many people have contributed in one way or another for this work:

- By providing biological material: Fredrik Pleijel, Marina Cunha, Clara Rodrigues, Fernando Gonçalves, Miguel Pardal, Eduardo Lopez, Júlio Parapar, Helena Wiklund, Greg Rouse, Peter Garwood, Victor Quintino, Joana Oliveira, Rui Marques, Alexandra Rizzo, João Gil, and a special thanks to Carlos Miguez for including me in the Portuguese coast campaign. And of course all the museums that lent material: Ricardo Araújo (MMF), Emma Sherlock (NHM), Andy Mackie (NMWZ), Miguel Villena (MNCN), Christina Piotrowski (CASIZ), Angelika Brandt (ZMH), Kennet Lundin (GNM), Elin Sigvaldadöttir (NRM), Danny Eibye-Jacobsen (ZMC), Cheryl Bright (USNM), Adam Baldinger (MCZ) and Koos van Egmond (RMNH).

- By helping me with DNA and phylogenetic analyses: Filipe Costa, Sónia Mendo, Anna Ansebo and specially Helena Wiklund. Per Sundberg gave me the oppurtunity of making a great part of the analyses in the Zoology Department of the Gothenburg University. Edgar Cruz e Silva and Luís Souto from the University of Aveiro allow me to use lab equipment that was essential to my work.

- By helping me with bibliography (providing or translating from german): João Gil (supply), Hermínia Castro and Jörg Frommlet (translation).

And finally thanks to my work colleagues and friends that always had a kind word to comfort me in the difficult moments.

Aos meus pais que sempre me incentivaram e apoiaram, e pela ajuda essencial com os meus filhos nestes últimos cinco anos.

À minha família agradeço a compreensão pelos transtornos causados no decorrer do meu trabalho.

palavras-chave

Poliquetas, Nephtyidae, filogenia, taxonomia

resumo

A família Nephtyidae é uma das mais frequentes em habitats costeiros e marinhos de todo o mundo. São organismos errantes típicos de sedimentos arenosos e lodosos, ocorrendo frequentemente no domínio costeiro até 100 m de profundidade, e mais raramente em profundidades batiais e abissais. As primeiras espécies descritas foram o *Nephtys caeca* (Fabricius, 1780) e o *N. ciliata* (O. F. Müller, 1789), ambas atribuídas inicialmente ao género *Nereis* e posteriormente transferidas para o género *Nephtys* por Savigny, em 1818. A família Nephtyidae foi criada em 1851 por Grube para o género *Nephtys* Cuvier, 1817.

No âmbito desta tese é feito um estudo taxonómico e filogenético da família Nephtyidae. O estudo filogenético inclui dados morfológicos e moleculares de 24 taxa representantes dos cinco géneros da família, Nephtys Cuvier, 1817, *Aglaophamus* Kinberg, 1866, *Micronephthys* (Friedrich, 1939), *Inermonephtys* Fauchald, 1967 e *Dentinephtys* Imajima e Takeda, 1987. A análise evidenciou dois grandes grupos correspondentes aos dois principais géneros, *Aglaophamus* e *Nephtys*. Duas espécies do género *Nephtys* (*N. pulchra* e *N. australiensis*) são transferidas para o género *Aglaophamus*, e consequentemente são propostas novas diagnoses para os géneros. O género *Dentinephtys* é sinonimizado com *Nephtys* e um novo género, *Bipalponephtys*, é descrito para acomodar as espécies *Nephtys cornuta*, *N. danida* e *Micronephthys neotena*. As relações filogenéticas entre os géneros são discutidas.

Do estudo taxonómico resultou a revisão da família Nephtyidae para o Sul da Europa (entre o Canal da Mancha e o Mediterrâneo), com a descrição de uma nova espécie, *Inermonephtys foretmontardoi*. A espécie *Micronephthys maryae* é sinonimizada com *M. stammeri*. Para cada espécie são incluídas notas sobre a sua ecologia bem como a distribuição geográfica e batimétrica. São propostas novas diagnoses para os géneros do Sul da Europa bem como uma chave de identificação taxonómica para as espécies desta região.

Após uma exaustiva revisão bibliográfica da família, e da observação de material museológico relativo a 44 espécies, foi compilada uma lista completa para a família de 128 espécies, distribuídas por cinco géneros (57 *Nephtys*, 53 *Aglaophamus*, sete *Micronephthys*, oito *Inermonephtys* e três *Bipalponephtys*), na qual são incluídas sinonímias e considerações taxonómicas para cada espécie. A espécie *Nephtys serrata* é sinonimizada com *N. serratifolia*. São apresentados as distribuições geográficas e batimétricas das diferentes espécies e notas sobre o seu habitat. São também incluídas tabelas de identificação com as principais características taxonómicas das espécies. O valor diagnóstico dos caracteres morfológicos é discutido. Vários problemas taxonómicos são realçados, indicando a necessidade de revisões adicionais para 23 espécies.

Este trabalho realça a existência de vários problemas taxonómicos e filogenéticos dentro da família Nephtyidae, podendo ser considerado como a base para estudos futuros. Análises filogenéticas adicionais incluindo dados morfológicos e moleculares de um maior número de espécies vão certamente conduzir a uma melhor avaliação do estatuto e relações entre os géneros dentro da família.

keywords Polychaetaes, Nephtyidae, phylogeny, taxonomy

abstract

Nephtyidae is a benthic polychaete family found in almost all marine habitats around the world. They are motile burrowers and typical inhabitants of sandy and muddy sediments that are most often found from the intertidal to about 100 m depth, although they can also occur at bathyal and abyssal depths. The first species being described were *Nephtys caeca* (Fabricius, 1780) and *N. ciliata* (O. F. Müller, 1789) both initially referred to *Nereis* and later transferred to *Nephtys* by Savigny, in 1818. The family Nephtyidae was erected in 1851 by Grube for the genus *Nephtys* Cuvier, 1817.

Within this thesis the family Nephtyidae is studied in both taxonomic and phylogenetic perspectives. A combined morphological-molecular study was done based on 24 nephtyid taxa belonging to the five genera of the family, *Nephtys* Cuvier, 1817, *Aglaophamus* Kinberg, 1866, *Micronephthys* (Friedrich, 1939), *Inermonephtys* Fauchald, 1967 and *Dentinephtys* Imajima and Takeda, 1987. The results revealed two well-supported major clades, corresponding in part to the two main genera of the family, *Aglaophamus* and *Nephtys*. Two species previously assigned to the genus *Nephtys* (*N. pulchra* and *N. australiensis*) were proved to belong to the genus *Aglaophamus* and therefore new diagnoses for the genera are provided. The genus *Dentinephtys* is synonymized with *Nephtys* and a new genus, *Bipalponephtys*, is described to include the species *Nephtys cornuta*, *N. danida* and *Micronephthys neotena*. The phylogenetic relationships between the genera are further discussed.

Within the taxonomic account, a family revision for the southern European fauna (from English channel to the Mediterranean) is provided, with the erection of a new species, *Inermonephtys foretmontardoi*. The species *Micronephthys maryae* is synonymized with *M. stammeri*. Information about geographical and bathymetrical distribution as well as habitat is included for each species. New diagnoses are provided for southern European genera and a key to all species from the region is included.

After revising the available bibliography and some museological material representing 44 species, a complete list of 128 presently accepted species of the family Nephtyidae is compiled, ascribed to five genera (57 *Nephtys*, 53 *Aglaophamus*, seven *Micronephthys*, eight *Inermonephtys* and three *Bipalponephtys*). The list includes synonymies and taxonomic remarks for each species. The species *Nephtys serrata* is synonymized with *N. serratifolia*. The geographical and bathymetrical distribution of the different species is presented as well as ecological notes. Tables with the main diagnostic characters are also included. The diagnostic value of each morphological character is discussed. Several taxonomical problems become apparent from this study, indicating that further revisions are still in need for 23 species.

The taxonomical and phylogenetic issues of the family Nephtyidae raised in this study may be considered a base for future research. Further phylogenetic analyses including morphological and molecular data of more taxa is required and will certainly lead to a better evaluation of the status and relationships of all genera within the family.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Section 1. INTRODUCTION

Systematics is the classification of living organisms into hierarchical series of groups emphasizing their phylogenetic interrelationships, i.e. the evolutionary relationships within and between groups (e.g. Lincoln *et al.*, 1998).

Linnaeus (1758) was a pioneer in traditional systematics, by creating the Nomenclature System where taxa are organized in groups of higher rank according to their morphological similarities. He recognized the class Vermes for soft-bodied worm-like organisms and provided the first descriptions of polychaetes accepted for taxonomic purposes. The Linnean binomial nomenclature was broadly followed by the subsequent natural history authors such as Lamarck (1801; 1815; 1816; 1818), Cuvier (1812; 1817), Savigny (1822), Grube (1850), Ehlers (1864) and Quatrefages (1866), although the major hierarchical groups have changed along time. The group Annelida appeared with Lamarck (1802 (1907)) that introduced the term 'Annélides' and the term Polychaeta was introduced by Grube (1850).

Fauchald and Rouse (1997) present a detailed revision of the taxonomic history of the taxon Polychaeta along with a list of taxonomic classifications given by the different authors between the years 1758 and 1985. The latest of these classifications, given by George and Hartman-Schröder (1985), divide the polychaetes into 22 orders. However, all those classifications are only based on the evaluation of morphological differences between taxa, without having a real concern on their evolutionary relationships.

The interest for the evolutionary relationships of Annelida only arose by the end of the 20th century when comprehensive phylogenetic studies were published by authors such as Nielsen (1995), Eibye-Jacobsen and Nielsen (1996), Rouse and Fauchald (1995; 1997) and Westheide (1997). In these studies the morphological similarities between taxa were addressed within a cladistic framework. The analysis included in Rouse and Fauchald (1997) resulted in a new classification of the polychaetes (Figure 1), which is commonly used at present. In this classification polychaetes are divided in two major groups, Scolecida and Palpata. Palpata is further divided in Aciculata and Canalipalpata. The latter group comprises the order Phyllodocida where the family Nephtyidae is included.

The classification of Annelida is still a matter of discussion and constant improvement as taxa become better known and new data are added to the analyses. The increasing need of further information to better elucidate the phylogenetic relationships lead to the integration of molecular data in the cladistic analyses. However, the existing phylogenetic studies are based on morphologic characters (e. g. Rouse & Fauchald, 1997; Bartolomaeus *et al.*, 2005) or molecular data (e. g. Winnepenninckx *et al.*, 1995; McHugh, 1997; Kojima, 1998; Brown *et al.*, 1999; Bleidorn *et al.*, 2003; Rousset *et al.*, 2007), independently. Comprehensive studies combining morphological and molecular data for the Annelida are scarce, although there are several combined studies at family level (e.g. Rousset *et al.* 2003; Ruta *et al.* 2007). Although the phylogenetic relationships among the Polychaeta remain unsolved and are still debated, some studies have shown that traditional polychaete families are often well supported (Bleidorn *et al.*, 2003). Nevertheless, the phylogeny of many families remains unstudied. A good knowledge of the phylogenetic relationships within each family will surely help to clarify the overall phylogeny of the Annelida.

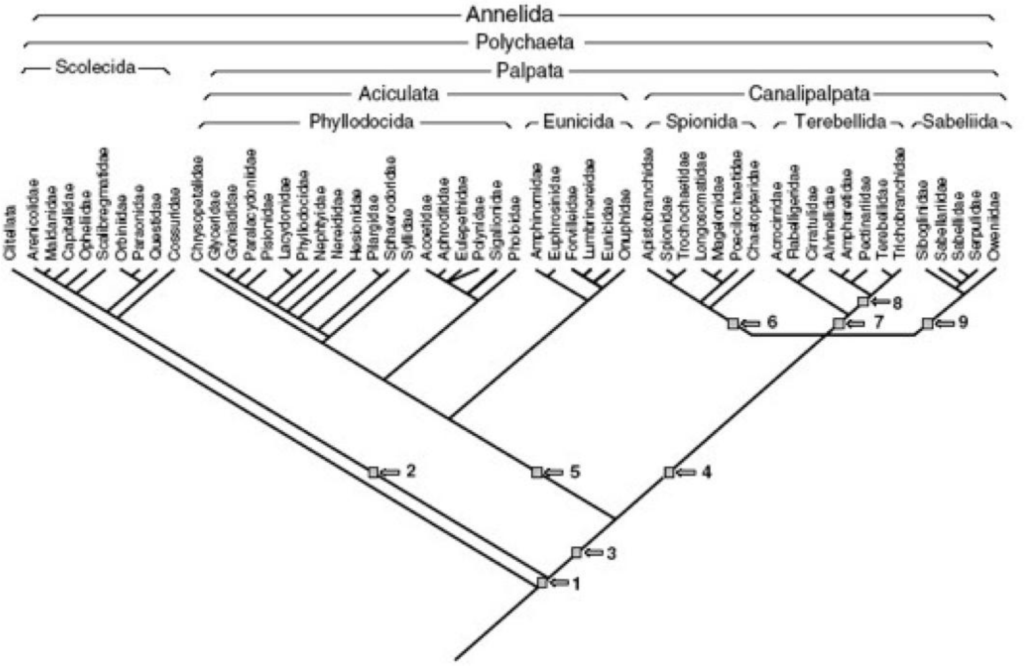


Figure 1. Phylogenetic relationships among the Annelida according to Rouse & Fauchald (1997).

The family Nephtyidae erected as ‘Nephthydea’ by Grube (1850), was placed among other errant groups of polycheates such as ‘Aphroditea’, ‘Amphinomiacea’, ‘Glycerea’, ‘Phyllodocea’, ‘Eunicea’ and ‘Syllidea’. Levinsen (1883) split all these families into several groups and included the Nephtyidae within the ‘Phyllodociformia’, while Hatschek (1893) regrouped the same families as ‘Nereimorpha’. Uschakov (1955) distinguished again a ‘Phyllodocemorpha’ group that included the Nephtyidae, from a

'Nereimorpha' group. After the erection of orders by Dales (1962), based on structural relations of pharynx and nephridia, the Nephtyidae remained within the Phyllodocida group.

Phylogenetic-based studies by Rouse and Fauchald (1997) and Rouse and Pleijel (2001) placed the family within Phyllodocida, close to the families Phyllodocidae, Pisionidae, Paralacydoniidae, Glyceridae and Goniadidae. On the other hand, Pleijel & Dahlgren (1998) placed Nephtyidae as a sister group to Glyceridae and Goniadidae only. More recently, Rousset *et al.* (2007) questioned the monophyletic condition of the Phyllodocida since the taxa within this group appeared scattered over the phylogenetic tree. In this latter analysis the Nephtyidae have a sister relationship with Hesionidae.

The Nephtyidae are currently considered to be a monophyletic group based only on the existence of interramal branchiae (Fauchald & Rouse, 1997). However, the morphological evidence for the monophyly of nephtyids is debatable as this character is present only in part of the group and there are no further obvious apomorphies for the taxa included in the group (Rouse & Pleijel, 2001).

1.1 The history of the family Nephtyidae Grube, 1850

The first nephtyid species described, *Nephtys caeca* (Fabricius, 1780) and *Nephtys ciliata* (O. F. Müller, 1789), were initially ascribed to the genus *Nereis*. The genus *Nephtys* was described by Cuvier (1817), but still placed within the nereid group. Savigny (1820) provided a new diagnosis for the genus that he misspelled as *Nephthys*, and included the species *N. ciliata* but not *N. caeca* for which he suggested the new genus *Aonis*. However, the erection of *Aonis* was based on a misinterpretation of Fabricius (1780) description of *N. caeca* and thus subsequently disregarded (Ehlers 1868).

The family Nephtyidae was later erected by Grube (1850), as Nephtydea Grube, 1850, to include the genus *Nephtys*. Subsequently, Quatrefages (1865) included in this family two new genera, *Portelia*, that he considered to have one pair of antennae (instead of two as in *Nephtys*), and *Diplobranchus* with no antennae. According to Hartman (1950), the erection of these two genera was based on erroneous observations concerning the number of prostomial antennae.

In 1866, Kinberg considered only the genera *Nephtys* and *Portelia* to be valid, and erected two more genera, *Aglaophamus* and *Aglaopheme*, based on morphological differences of the pharyngeal jaws (fusiform in *Aglaophamus*, subconical and laterally depressed with a trilobed base in *Aglaopheme*, and hooked in *Nephtys*; not described for *Portelia*). Ehlers (1868) considered Kinberg's separation invalid and synonymised the genera *Aglaophamus* and *Aglaopheme* with *Nephtys*. *Portelia* was kept to include the species such as *P. rosea*, thought to have a single pair of prostomial antennae and a pair of pygidial processes. Langerhans (1879) suggested the distinction of another genus according to differences in the number of rows of papillae on the pharynx (22 versus 14), but a new genus was not formally erected. Subsequent studies and major revisions such as Michaelsen (1896), McIntosh (1908), Heinen (1911) and Fauvel (1914; 1923) increased the number of described species. Moreover, Fauvel (1923) invalidated the genus *Portelia* by synonymizing *P. rosea* with *N. cirrosa*, and recognized only one genus, *Nephtys*, in the family.

In 1939, Friedrich described the genus *Micronephthys* for specimens with poorly developed parapodial features such as lamellae and branchiae. Later, Hartman (1950) kept the genera *Nephtys* and *Micronephthys* and re-established the genus *Aglaophamus* based on the involute condition of the branchiae. She stated that acicular lobes are more acutely pointed in *Aglaophamus* and that also lyriform chaetae are usually present on this genus while their presence its doubtful in the other genera. Hartman's (1950) suggestions were followed in subsequent works by herself (1959) and Fauchald (1963).

More recently, two new genera were described, *Inermonephtys* Fauchald, 1968 and *Dentinephtys* Imajima & Takeda, 1987, and the two Carboniferous fossil polychaetes *Astreptoscolex anasillosus* Thompson, 1979 and *Didontogaster cordylina* Thompson, 1979 have also been referred to the Nephtyidae (Thompson 1979; Fitzhugh *et al.* 1997).

The number of described species was greatly increased with major revisions on nephtyid taxonomy covering different world areas such as Hartman (1938) for the northeast Pacific, Fauchald (1963; 1968) for Norway and Viet Nam, Paxton (1974), Rainer and Hutchings (1977) and Rainer and Kaly (1988) for Australia, Taylor (1984) for Gulf of México, Rainer (1984, 1989, 1990, 1991) for northern Europe, Imajima and Takeda (1985; 1987) for Japan, Nateewathana and Hilleberg (1986) for Thailand, Hilbig (1997) for California, Jung and Hong (1997) for Chinese Sea, and Dnestrovskaya and Jirkov (2001) for the Artic Ocean. Within these studies, especially the most recent ones, much old museum material have been revised leading to the clarification of many doubts and the erection of new species. But still much material remains misidentified.

1.2 Morphological and biological notes

Nephtyids are widespread polychaetes that are commonly collected in most environments around the world. They inhabit estuarine, coastal and offshore waters covering a broad bathymetric range (Rainer 1991b). However, they are most abundant in shallow water and typically occur in sandy and muddy bottoms (Hilbig 1997; Pleijel 2001), for which reason they are sometimes called as sand worms (Pettibone 1963). Most of the species are stenohaline, but some species such as *Nephtys fluviatilis*, *N. oligobranchia* and *N. polybranchia* tolerate very low salinities and may occur in nearly fresh water (Fauchald 1968; Lana 1986).

Due to their strong muscular body, nephtyids are able to borrow and swim very fast by lateral sinuous movements. The longitudinal musculature of these animals has extra stiffness provided by unique intracellular calcium phosphate granules, and functions like a flexible internal skeleton (Gibbs & Bryan 1984). They are able to borrow swiftly in sandy sediments to a depth of at least 20 cm, but do not construct permanent galleries (Glasby *et al.* 2000).

In most published studies (e.g. Clark 1962; Fauchald & Jumars 1979; Schubert & Reise 1986), nephtyids are considered to be carnivores preying upon other motile invertebrates (which may include smaller conspecifics). They use the strong muscular proboscis, armed with two well-developed jaws to capture their preys. According to Schubert and Reise (1986), nephtyids seem to prey preferentially on adult individuals and hunting occurs within the sediment thus excluding most surface-dwelling fauna and tube-building polychaetes. There are also a few records of subsurface deposit-feeding (Sanders 1960; Clark 1962). According to Clark (1962) the deposit-feeding appears when dense assemblages of specimens occur, and competition forces individuals into fine sediments with higher organic carbon content. Also omnivorous feeding is suggested to occur in certain habitats when population densities become high (Schubert & Reise 1986). Nephtyids are known to be an important item in the diet of other polychaetes (e.g. nereids), crabs, fish and birds (Schubert & Reise 1986).

Nephtyids have separate sexes and gametes are released at the sediment surface (Garwood & Olive 1981; Pleijel 2001). All mature worms in a population breed synchronically (some times within a single day). They are generally iteroparous but do not breed necessarily every year (Olive 1985). The larvae are planktonic and spend up to five weeks in the water column before settling on the bottom sediments where metamorphosis takes place (Noyes 1980). Some species may undergo epitokous stages, with development of modified parapodial lobes and long chaetae (Garwood & Olive 1981). There are some published studies regarding the different development stages of certain nephtyid species. For instance, Olive (1978) described the annual gametogenic cycles for *Nephtys hombergii* and *N. caeca*; Wilson (1936) described the early development of *N. hombergii*, while Rasmussen (1973) described some later stages for the same species; Clark & Clark (1962) described growth and regeneration in the *Nephtys* species. Life span was estimated of up to nine years for *Nephtys assimilis*, based on size models and annual growth rings on the jaws (Kirkegaard 1970; Rainer 1991a), but there are records of older animals. Olive (1985) found nephtyid worms up to 12 years old in a UK population, and Caron *et al.* (1995) reported a specimen of *Nephtys caeca* from Canada with 15 visible jaw rings.

Taxonomically nephtyids are very easily recognized by the presence of an interramal branchia typically attached to the ventral notopodial margin of the parapodia. Also the presence of a single anal cirrus is a unique feature typical of this family. Adult animals vary in size from less than 5 mm up to 30-40 mm for 25-30 up to 250 segments. *In vivo*, these animals are usually pale without pigmentation patterns, although larger animals often have an iridescent cuticle. Dorsal and ventral blood vessels are often conspicuous. The most important characters for species discrimination include the shape of the branchiae and the segments on which they occur, the shape and proportions of parapodial lamellae and the arrangement of papillae on the pharynx.

Commercial usage of nephtyids is only known for intertidal large-bodied species such as *Nephtys hombergii* and *N. caeca*, which are appreciated baits for fishing. The slow growth, infrequent spawning and low recruitment rates make most nephtyid species unsuitable for bait culture. In Europe *Nephtys hombergii* is abundant and easily collected in estuaries and coastal habitats, and is commonly referred to as ”bicha branca” in Portugal and as “catworm” or “silver rag” in Britain (e.g. Olive 1994). *Nephtys cirrosa*, a smaller species frequent in clean sand beaches in Britain and southern Europe, is usually known as “white catworm”.

1.3 Morphology

Nephtyids have an elongated body, widest anteriorly in the phraynx region and posteriorly tapering, typically rectangular in cross-section. Pigmentation patterns are usually absent, although darker brown or green pigment may be present on the prostomium and anterior segments. An iridescent cuticle is common in larger specimens.

One pair of small eyes is usually present subdermally on posterior brain but is only visible in small nephtyid species or in juveniles of larger ones at the level of the anteriormost segments. In some species one or two pairs of eyes may be present on the surface of prostomium.

Pharynx forms an eversible muscular proboscis with a terminal dorsoventral opening surrounded by 10 pairs of bifid papillae separated dorsally and ventrally by a gap or a simple conical papilla (Figure 2A, B). Bifid terminal papillae decrease in size towards middorsal and midventral position. Subterminal region with 14 to 22 rows of simple papillae decreasing in size towards base of proboscis (Figure 2A, B) (papillae are absent in *Inermonephtys*). For some species a single middorsal and a single midventral papilla are also present between the terminal and subterminal papillae (Figure 2A, B). Proximally the proboscis is either smooth or covered with small warts (Figure 2A). One pair of small subterminal jaws is present inside the pharynx (Figure 2C).

The prostomium is generally subpentagonal, anteriorly tapered, and with a V-shaped posterior margin, extending over the first chaetiger (Figure 2A, B). The prostomial proportions vary depending on whether the proboscis is everted or not. A pair of conical antennae is present in the anterior corners of the prostomium and a pair of palps is inserted ventrolaterally near the antennae or further posteriorly on the prostomium (Figure 2B). A pair of nuchal organs is present near the posterior corners of prostomium (Figure 2A, B).

The parapodia are biramous, typically with well-separated rami (Figure 2D). Ciliation is present in patches or continuously along the interramal space (Figure 2D). The noto- and neuropodia are composed of an acicular lobe sustained by one acicula (species of the genus *Inermonephtys* may have more than one acicula per ramus in the anterior and middle parapodia), pre- and postchaetal lamellae, and a ventrally placed cirrus (Figure 2D). In some species a papilliform outgrouth may be present in the acicular lobes of anterior parapodia (Figure 2D), as well as a neuropodial superior lobe (Figure 2E). The parapodia of the first chaetiger are usually anteriorly directed, and their lamellae are less developed than the following ones (Figure 2A). The neuropodial lamellae of the first chaetiger usually form a cylinder around the acicular lobes; the ventral cirri are well-developed and usually longer than the following ones. The following parapodia gradually increase in size attaining their maximal size at midbody. Shape and proportions of acicular lobes and lamellae may exhibit some variation along the body. Except for some *Micronephthys* species, branchiae are present at least in some parapodia along the body. When present, branchiae are typically attached to the ventral margin of the notopodia (below the dorsal cirri) (Figure 2D), have ciliated margins and may be involute, straight or recurved. Chaetae are simple and form dense, fan-shaped fascicles in pre- and postacicular positions. They are usually barred (or chambered) in preacicular position (Figure 2G), and spinulated in postacicular position (Figure 2H). In some species of *Aglaophamus*, *Inermonephtys* and *Micronephthys*, a few lyriform chaetae may be present in postacicular position of both rami (Figure 2I). Neuropodial chaetae of the first chaetiger are usually capillary or indistinctly spinulated and form a single bunch without barred chaetae. Aciculae are thick and usually have curved tips in median and posterior parapodia (in all parapodia in *Aglaophamus*) (Figure 2F).

The anus is terminal, and a single thin, cirriform anal cirrus is typically present.

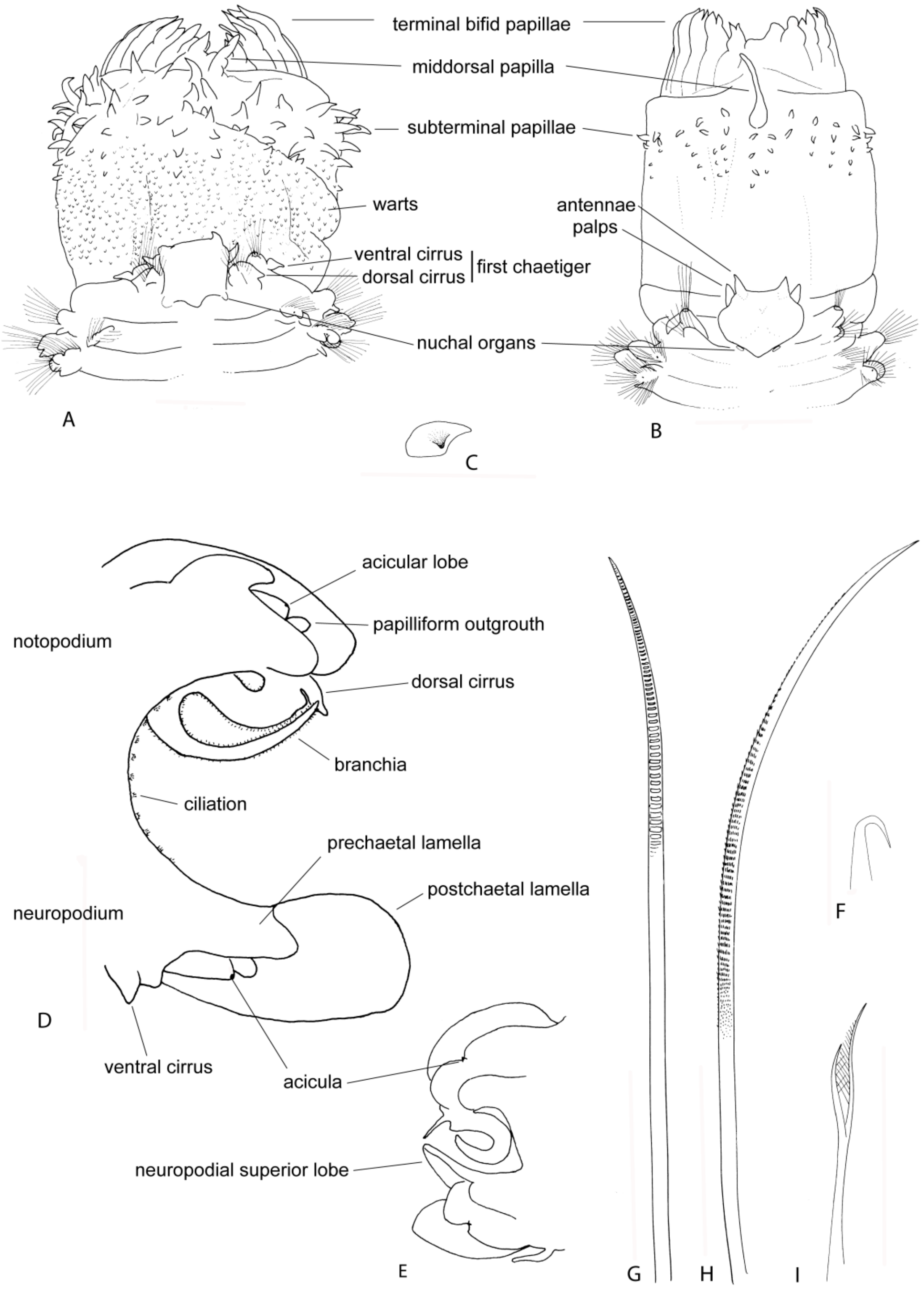


Figure 2. Family Nephtyidae, general morphology. A, B. Prostomium and pharynx. C. Jaw. D, E. Parapodia. F. Acicula. G. Barred preacicular chaeta. H. Spinulated postacicular chaeta. I. Lyriform chaeta.

1.4 Aims and outputs of the study

Nephtyids are among the most dominant animals in benthic monitoring studies, and it is common that a number of species co-occur in the same samples. They constitute important indicator organisms for marine ecologists, and a number of studies have been published on their population dynamics and reproduction. In spite of this general interest, nephtyid taxonomy is poorly known, and to date there are no studies on the phylogeny of the group.

This study aims to provide a systematic revision of the family Nephtyidae in a worldwide perspective, based on morphological and molecular characters. The work includes two main tasks: a morphologic study and a genetic study. The morphologic study was based, whenever possible, on the examination of specimens, including types, and on the literature available. The information was compiled within a database, using DELTA software. The genetic study was based on nephtyid taxa collected in several places around the world and the resulting sequences were submitted to the GenBank database. The two datasets were then integrated for the phylogenetic analyses. The results are presented in two main sections: one with the phylogenetic study (Section 2) and another with the taxonomic study (Section 3). Section 2 includes a study of the phylogenetic relationships within the Nephtyidae based on morphologic and molecular data (Chapter 2.1). Section 3 includes a revision of the South European nephtyid species with a discussion on the geographic and bathymetric distributions (Chapter 3.1), and a comprehensive, updated list of Nephtyidae extant species with synonymies, distribution and taxonomic remarks, along with summary-tables of their diagnostic characters (Chapter 3.2). Final remarks are provided in section 4.

This thesis includes two manuscripts submitted to international peered reviews:

Ravara, A., Cunha, M. R. & Pleijel, F. Phylogenetic relationships within Nephtyidae (Polychaeta, Annelida). *Zoologica Scripta*, in press (early view available online).

Ravara, A., Cunha, M. R. & Pleijel, F. Nephtyidae (Annelida, Polychaeta) from southern Europe. Submitted to *Zootaxa*.

These publications correspond to Chapters 2.1 and 3.1, respectively. Other publications are being prepared based on taxonomical issues raised in Chapter 3.2. All these are, in my opinion, valuable contributions to the systematics of the family Nephtyidae.

References

Bartolomaeus, T., Purschke, G., & Hausen, H. (2005). Polychaete phylogeny based on morphological data - a comparison of current attempts. *Hydrobiologia*, 535/536, 341-356.

Bleidorn, C., Vogt, L., & Bartolomaeus, T. (2003). New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. *Molecular Phylogenetics and Evolution*, 29, 279-288.

Brown, S., Rouse, G. W., Hutchings, P. A., & Colgan, D. (1999). Assessing the usefulness of histone H3, U2 snRNA and 28S rDNA in analyses of polychaete relationships. *Australian Journal of Zoology*, 47, 499-516.

Caron, C., Boucher, L., Desrosiers, G., & Retière, C. (1995). Population dynamics of the polychaete *Nephtys caeca* in an intertidal estuarine environment (Quebec, Canada). *Journal of the Marine Association of the United Kingdom*, 75, 871-884.

Clark, M. E., & Clark, R. B. (1962). Growth and regeneration in Nephtys. .

Clark, R. B. (1962). Observations on the food of *Nephtys*. *Limnology & Oceanography*, 7, 380-385.

Cuvier, G. (1812). Sur une nouveau rapprochment à établir entre les classes qui composant le Règne Animal. *Ann. Mus. Hist.*, 19, 73-84.

Cuvier, G. L. C. F. D. (1817). *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Avec figures, dessinées d'après nature. II. Les reptiles, les poissons, les mollusques et les annélides*. Paris: Deterville.

Dales, R. P. (1962). The polychaete stomodeum and the inter-relationships of the families of polychaeta. *Proc. Zool. Soc. Lond.*, 139, 389-428.

Dnestrovskaya, N., & Jirkov, I. A. (2001). Nephtyidae Grube 1850. In I. A. Jirkov (Ed) *Polychaeta of the Arctic ocean* (pp. 1-632). Moscow: Yanus-K Press.

Ehlers, E. (1864). *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt*. Leipzig: Wilhelm Engelmann.

Ehlers, E. (1868). *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt*. Leipzig: Wilhelm Engelmann.

Eibye-Jacobsen, D., & Nielsen, C. (1996). The rearticulation of annelids. *Zoologica Scripta*, 25, 275-282.

Fabricius, O. (1780). *Animals of Western greenland so far investigated including their specific, common and local names, synonyms used by different authors, description, place, diet, reproduction, habits, behaviour, and capture of all those that could be found, for the most part based on personal observations*. Copenhagen and Leipzig.

Fauchald, K. (1963). Nephtyidae (Polychaeta) from Norwegian waters. *Sarsia*, 13, 1–32.

Fauchald, K. (1968). Nephtyidae (Polychaeta) from the Bay of Nha Trang, South Viet Nam. *Naga Report*, 4, 7–33.

Fauchald, K. (1977). The polychaete worms. Definitions and keys to the orders, families and genera. *Science Series of the Natural History Museum of Los Angeles City*, 28, 1-188.

Fauchald, K., & Jumars, P. A. (1979). The diet of worms: a study of polychaete feeding guilds. *Oceanography and Marine Biology: An Annual Review*, 17, 193-284.

Fauchald, K., & Rouse, G. (1997). Polychaete systematics: past and present. *Zoologica Scripta*, 26, 71-138.

Fauvel, P. (1914). Annélides polychètes non-pelagiques provenant des campagnes de l'Hirondelle et de la Princesse-Alice (1885-1910). *Résultats des campagnes scientifiques accompliés par le Prince Albert I*, 46, 1–432.

Fauvel, P. (1923). Polychètes érrantes. *Faune de France*, 5, 1–488.

Fitzhugh, K., Sroka, S. D., Kruty, S., Henderson, M. D., & Hay, A. A. (1997). 7A. Polychaete worms. In C. W. Shabica & A. A. Hay (Eds) *Richardson's guide to the fossil fauna of Mazon Creek* (pp. 64–88). Chicago: Northeastern Illinois University.

Friedrich, H. (1939). Polychaeten-Studien IV. Zum Polychaeten-Fauna der Barentz-See. *Kieler Meeresforschungen*, 3, 122–132.

Garwood, P. R., & Olive, P. J. W. (1981). The significance of the long chaetal form of Nephtys caeca (Polychaeta: Nephtyidae) and its relationship to N. longosetosa. *Sarsia*, 66, 195–202.

George, J. D. & Hartman-schröder, G. (1985) Polychaetes: British Amphinomida, Spintherida and Eunicida. Keys and notes for the identification of the species. *Synopses of the British Fauna (new series)*, 1-221.

Gibbs, P. E., & Bryan, G. W. (1984). Calcium phosphate granules in muscle cells of *Nephtys* (Annelida, Polychaeta) - a novel skeleton? *Nature*, 310, 494-495.

Glasby, C. J., Hutchings, P. A., Fauchald, K., Paxton, H., Rouse, G. W., Watson Russell, C., *et al.* (2000). Class Polychaeta. In P. L. Beesley, G. J. B. Ross & C. J. Glasby (Eds) *Polychaetes & allies: the southern synthesis* (pp. 1–296). Melbourne: CSIRO Publishing.

Grube, A. E. (1850). Die Familien der Anneliden. *Archiv für Naturgeschichte*, 16, 249–364.

Hartman, O. (1938). Review of the annelid worms of the family Nephtyidae from the Northeast Pacific, with descriptions of five new species. *Proceedings of The United States National Museum*, 85, 143–158.

Hartman, O. (1950). Goniadidae, Glyceridae and Nephtyidae. *Allan Hancock Pacific Expeditions*, 15, 1–181.

Hartman, O. (1959). Catalogue of the polychaetous Annelids of the world. Part I. *Allan Hancock Foundation Publications. Occasional Paper*, 23, 1–353.

Hatschek, B. (1893). System der Anneliden, ein vorläufiger Bericht. *Lotos*, 13, 123-126.

Heinen, A. (1911). Die Nephtyideen und Lycorideen der Nord- und Ostee, einschlieblich der verbindenden Meeresteile. *Wissenschaftliche Meeresuntersuchungen*, 13, 1–87.

Hilbig, B. (1997). Family Nephtyidae Grube, 1850. In J. A. Blake, B. Hilbig & P. H. Scott (Eds) *Taxonomic atlas of the benthic fauna of the Santa Maria basin and the western Santa Barbara channel. 4. The Annelida. Part 1. Oligochaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae)* (pp. 317-349). Santa Barbara, California.

Imajima, M., & Takeda, Y. (1985). Nephtyidae (Polychaeta) from Japan. I. The genera *Inermonephtys*, *Micronephtys* and *Aglaophamus*. *Bulletin of the National Science Museum, Tokyo*, 11, 57–90.

Imajima, M., & Takeda, Y. (1987). Nephtyidae (Polychaeta) from Japan. II. The genera *Dentinephtys* and *Nephtys*. *Bulletin of the National Science Museum, Tokyo*, 13, 41–77.

Jung, R.-H., & Hong, J.-S. (1997). Nephtydae (Annelida: Polychaeta) from the Yellow Sea. *Bulletin of the Marine Science*, 60, 371–384.

Kinberg, J. G. H. (1866). Annulata nova. *Ofversigt af Koniglich Vetenskapsakademiens forhandlingar, Stockholm*, 23, 97–103.

Kirkegaard, J. B. (1970). Age determination of *Nephtys* (Polychaeta: Nephtyidae). *Ophelia*, 7, 277-281.

Kojima, S. (1998). Paraphyletic status of polychaeta suggested by phylogenetic analysis based on the amino acid sequences of elongation factor-1-alpha. *Molecular Phylogenetics and Evolution*, 9, 255-261.

Lamarck, J.-B. (1801). *Systême des Animaux Sans Vertèbres, ou Tableau générales des classes, des orders et des genres de ces animaux; Présantant leurs caractères essentiels et leur distribuition, d'après la considèration de leurs rapports naturelles et de leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Histoire Naturelle, parmi leurs dépouilles conservées; Précédé du discors d'ouverture du cours de Zoologie, donné dans la Muséum National d'Histoire Naturelle l'an 8 de la République*: Chez l'auteur (et) Déterville, Paris.

Lamarck, J.-B. (1802 (1907)). La nouvelle classes des Annélides. *Bull. Mus. Hist. Nat. Paris An X: Disc. d'ouverture, 27 Floréal*.

Lamarck, J.-B. (1815). *Histoire naturelle des Animaux sans Vertèbre, préséntant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs families, lers genres, et la citation des principales espèces qui s'y rapportent; précédée d'une Introduction offrant la détermination des caractères essentiels de l'Animal, sa distinction du Végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la Zoologie*: Verdière, Paris.

Lamarck, J.-B. (1816). *Histoire naturelle des Animaux sans Vertèbre, préséntant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs families, lers genres, et la citation des principales espèces qui s'y rapportent; précédée d'une Introduction offrant la détermination des caractères essentiels de l'Animal, sa distinction du Végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la Zoologie*. Paris: Déterville et Verdière.

Lamarck, J. B. (1818). *Histoire naturelle des animaux sans vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels; enfin, l'exposition des principes fondamentaux de la zoologie*. Paris: Déterville & Verdière.

Lana, P. d. C. (1986). Nephtyidae (Annelida: Polychaeta) do litoral do estado do Paraná (Brasil). *Neritica*, 1, 135-154.

Langerhans, P. (1879). Die wurmfauna von Madeira. *Zeitschrift fur Wissenschaftliche Zoologie*, 32, 513–592.

Levinsen, G. M. R. (1883). Systematisk-geografisk oversigt over de nordiske Annulata, Gephyrea, Chaetognathi og Balanoglossi. Første Halvdel. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 1883, 160–251.

Lincoln, R., Boxhall, G., & Clark, P. (1998). *A dictionary of ecology, evolution and systematics*. Cambridge: Cambridge University Press.

Linnaeus, C. (1758). *Systema Naturae. Per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonyms, locis, 10th ed.* Stockholm: Salvius.

McHugh, D. (1997). Molecular evidence that echiurans and pogonophorans are derived annelids. *Proc. Matl. Acad. Sci. USA*, 94, 8006-8009.

McIntosh, W. C. (1908). A monograph of British annelids. Polychaeta. Nephthyidae to Ariciidae. *Ray Society of London*, 2, 1-232.

Michaelsen, W. (1896). Die Polychaetenfauna der deutschen Meere, einschliesslich der benachbarten und verbindenden Gebiete. *Wissenschaftliche Meeresuntersuchungen*, 2, 1–216.

Müller, O. F. (1789). *Zoologia Danica seu animalium Daniae et Norvegiae rariorum ac minus notorum. Descriptiones et historia*. Havinae.

Nateewathana, A., & Hylleberg, J. (1986). Nephtyid polychaetes from the west coast of Phuket Island, Andaman sea, Thailand, with description of five new species. *Proceedings of the Linnean Society of New South Wales*, 108, 195–215.

Nielsen, C. (1995). *Animal evolution*. Oxford: Oxford Universuty Press.

Noyes, G. S. (1980). The biology of Aglaophamus neotenus (Polychaeta: Nephtyidae), a new species from Maine and Canada. *Biological Bulletin*, 158, 103-117.

Olive, P. J. (1985). *Slow grow white ragworm*. The sea Angling handbook. Winter 85/86. 28-31 pp.

Olive, P. J. W. (1978). Reproduction and annual gametogenetic cycle in *Nephtys hombergii* and *N. caeca* (Polychaeta: Nephtyidae). *Marine Biology*, 46, 83-90.

Olive, P. J. W. (1994). Polychaeta as a world resource: a review of patterns of exploitation as sea angling baits, and potential for aquaculture based production. *Mémoires du Muséum d'Histoire Naturelle, Paris*, 162, 603-610.

Paxton, H. (1974). Contribution to the study of Australian Nephtyidae (Polychaeta). *Records of the Australian Museum*, 29, 197–208.

Pettibone, M. H. (1963). Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. *US National Museum Bulletin*, 227, 1-356.

Pleijel, F., & Dahlgren, T. G. (1998). Position and delineation of Chrysopetalidae and Hesionidae (Annelida, Polychaeta, Phyllodocida). *Cladistics*, 14, 129-150.

Pleijel, F. (2001). 30. Nephtyidae Grube, 1850. In G. W. Rouse & F. Pleijel (Eds) *Polychaetes* (pp. 127–129). Oxford: Oxford University Press.

Quatrefages, M. A. (1865). Note sur la classification des annélides. *Comptes Rendu Hebdomadaires des Séances de l'Academie des Sciences*, 60, 586-600.

Quatrefages, A. d. (1866). *Histoire naturelle des Annelés marins et d'eau douce*. Paris: Librarie Encyclopédique de Roret.

Rainer, S. F. (1991a). Distribution, growth and production of *Nephtys hombergii* and *N. assimilis* Polychaeta: Nephtyidae) in benthic communities of the North Sea. *Bulletin of Marine Science*, 48, 330-345.

Rainer, S. F. (1991b). The genus *Nephtys* (Polychaeta: Phyllodocida) of Northern Europe: a review of species, including the description of *N. pulchra* sp.n. and a key to the Nephtyidae. *Helgoländers Meeresuntersuchungen*, 45, 65–96.

Rainer, S. F., & Hutchings, P. A. (1977). Nephtyidae (Polychaeta: Errantia) from Australia. *Records of the Australian Museum*, 31, 307–347.

Rainer, S. F., & Kaly, U. L. (1988). Nephtyidae (Polychaeta: Phyllodocida) of Australia: new species from the West shelf, and key to Australian species. *Journal of Natural History*, 22, 685–703.

Rasmussen, E. (1973). Systematics and ecology of the Isefjord marine fauna (Denmark). *Ophelia*, 11, 1-507.

Rouse, G., & Fauchald, K. (1995). The articulation of annelids. *Zoologica Scripta*, 24, 269-301.

Rouse, G. W., & Fauchald, K. (1997). Cladistics and polychaetes. *Zoologica Scripta*, 26, 139-204.

Rouse, G. W., & Pleijel, F. (2001). *Polychaetes*. Oxford: Oxford University Press.

Rousset, V., Rouse, G., Féral, J.-P., Desbruyères, D. & Pleijel, F. (2003). Molecular and morphological evidence of Alvinellidae relationships (Terebelliformia, Polychaeta, Annelida). *Zoologica Scripta*, 32, 185-197.

Rousset, V., Pleijel, F., Rouse, G., Erséus, C., & Siddall, M. E. (2007). A molecular phylogeny of annelids. *Cladistics*, 23, 41-63.

Ruta, C., Nygren, A., Rousset, V., Sundberg, P., Tillier, A., Wiklund, H. & Pleijel, F. (2007) Phylogeny of Hesionidae (Aciculata, Polychaeta), assessed from morphology, 18S rDNA, 28S rDNA, 16S rDNA and COI. *Zoologica Scripta*, 36, 99-107.

Sanders, H. L. (1960). Benthic studies in Buzzards Bay III. The structure of the soft-bottom community. *Limnology and Oceanography*, 5, 138-153.

Savigny, J.-C. (1822). Troisième partie. Systèmes de diverses classes d'animaux sans vertèbres. Système des annélides, principalement de celles des côtes de l'Égypte et de la Syrie, offrant les charactères tant distinctifs que naturels des Ordres, Familles et Genres, avec la description des espèces. *Descriptions de l'Egypte, Histoire Naturelle*, 3, 1–128.

Schubert, A., & Reise, K. (1986). Predatory effects of *Nephtys hombergii* on other polychaetes in tidal flat sediments. *Marine Ecology Progress Series*, 34, 117-124.

Taylor, J. L. (1984). Family Nephtyidae Grube, 1850. In J. M. Uebelacker & P. G. Johnson (Eds) *Taxonomic guide to the polychaetes of the Northern Gulf of Mexico* (pp. 35.31–35.20). Alabama: V. Barry A. Vittor and Associates, Mobile.

Thompson, I. (1979). Errant polychaetes (Annelida) from the Pennsylvanian Essex fauna of northern Illinois. *Palaeontographica*, 163, 169–199.

Uschakov, P. V. (1955). Polychaeta of the Far Eastern Seas of the U.S.S.R. *Academiya Nauk SSSR, Keys to the Fauna of the SSSR*, 56, 1–433 (translated from Russian by the Israel Program for Scientific Translations, Jerusalem 1965).

Westheide, W. (1997). The direction of evolution within the Polychaeta. *Journal of Natural History*, 31, 1–15.

Wilson, D. P. (1936). Notes on the early stages of two polychaete *Nephtys hombergi* Lamarck and *Pectinaria koreni* Malmgren. *Journal of the Marine Biological Association of the United Kingdom*, 21, 305–310.

Winnepenninckx, B., Backeljau, T., & De Wachter, R. (1995). Phylogeny of protostome worms derived from 18S rRNA sequences. *Molecular Biology and Evolution*, 12, 641–649.

Section 2. PHYLOGENETIC ACCOUNT

Chapter 2.1. Phylogenetic relationships within Nephtyidae

Abstract

We present the first phylogeny of nephtyids, a common, soft-bottom living polychaete family comprising five genera and over 100 species. Characters used to distinguish nephtyid genera are a matter of controversy and considerable confusion remains as to the generic delineations. The phylogeny is estimated with molecular data from the mitochondrial genes COI and 16S rDNA, the nuclear genes 18S rDNA and 28S rDNA, and morphological data. The results reveal two well-supported major clades, corresponding in part to the two main genera of the family, *Aglaophamus* and *Nephtys*. The species *N. pulchra* and *N. australiensis* are transferred to *Aglaophamus*, and new diagnoses for the genera are provided. *Dentinephtys* is synonymized with *Nephtys*, and *N. cornuta* is sister to the remaining nephtyids and is referred to the new genus *Bipalponephtys*, together with *N. danida* and *Micronephthys neotena*. *Micronephthys* is sister to *Nephtys* and *Inermonephtys* is of uncertain position.

Keywords: Nephtyidae, phylogeny, COI, 16S, 18S, 28S, morphology

Ravara, A, Wiklund, H, Cunha, MR & Pleijel, F (in press) Phylogenetic relationships within Nephtyidae (Polychaeta, Annelida). *Zoologica Scripta*.

2.1.1 Introduction

Nephtyidae is a family of aciculate polychaetes, which occurs worldwide at all depths, but is usually most abundant in shallow waters on sandy and muddy bottoms. The first nephtyid species were described as *Nereis* Linnaeus, 1758, and transferred to the new genus *Nephtys* by Cuvier (1817). The family name Nephtyidae was later introduced by Grube (1850). A large number of species has subsequently been described by authors such as Malmgren (1865), Ehlers (1868; 1887), Malm (1874), Hansen (1878), Théel (1879), Michaelsen (1896), McIntosh (1885; 1900; 1908), Heinen (1911), Hartman (1940; 1965; 1967), Eliason (1951), Hartmann-Schröder (1959; 1960) and Fauchald (1972), among others. The family today contains five genera and over 100 described species (Pleijel 2001). The majority of the species are referred to two genera, *Nephtys* (c. 60 species) and *Aglaophamus* Kinberg, 1866 (c. 50), while the remaining genera (*Micronephthys* Friedrich, 1939, *Inermonephtys* Fauchald, 1968 and *Dentinephtys* Imajima and Takeda, 1987) include only one or few species. The two Carboniferous fossil polychaetes *Astreptoscolex anasillosus* Thompson, 1979 and *Didontogaster cordylina* Thompson, 1979 have also been referred to as nephtyids (Thompson 1979; Fitzhugh *et al.* 1997). A very close similarity between species makes nephtyids easy to recognize as a group yet the genera and species are often difficult to identify. The delineations of the genera within the nephtyid family have been a matter of discussion by several authors (e.g., Fauchald 1968; Rainer & Kaly 1988), and uncertainty still exists about diagnostic characters. Several generic descriptions were provided by Hartman (1950), Fauchald (1968; 1977), Taylor (1984), Nateewathana & Hylleberg (1986), Imajima & Takeda (1985; 1987), Rainer & Kaly (1988), Jirkov (1989) and Hilbig (1997). There are a number of nephtyid taxonomic revisions covering regional geographic areas (Hartman 1938, 1950; Fauchald 1963, 1968; Paxton 1974; Rainer & Hutchings 1977; Rainer 1984; Taylor 1984; Imajima & Takeda 1985; Nateewathana & Hylleberg 1986; Imajima & Takeda 1987; Rainer & Kaly 1988; Rainer 1989, 1990, 1991; Jirkov & Paraketsova 1996; Hilbig 1997; Jung & Hong 1997). However, no studies have previously been published on the phylogenetic relationships within the nephtyids.

Fauchald and Rouse (1997) referred to them as a monophyletic group with the interramal branchiae being the only evidence for the monophyly. More general studies such as Rouse and Fauchald (1997) and Rouse and Pleijel (2001) placed the family within Phyllodocida, close to the families Phyllodocidae, Pisionidae, Paralacydoniidae, Glyceridae and Goniadidae. In the present study, the phylogeny within the family Nephtyidae is assessed for the first time using molecular data from the mitochondrial genes cytochrome oxidase I (COI) and 16S rDNA, the nuclear genes 18S rDNA and 28S rDNA, and morphological data. Twenty-one taxa, referred to the genera *Nephtys*, *Aglaophamus* and *Micronephthys*, were included in the analysis with molecular and morphological data. The two remaining genera in the family, *Dentinephtys* and *Inermonephtys*, plus another member of the genus *Micronephthys*, were included in a second analysis with morphological data only for these three taxa. Five other taxa belonging to Phyllodocidae, Amphinomidae, Nereididae, Glyceridae and *Lacydonia* were included in the analyses as outgroups.

2.1.2 Material and methods

Taxa

The phylogenetic analysis includes morphological and molecular data from twenty-one nephtyids and five outgroup taxa, including one amphinomid (*Paramphinome jeffreysii* McIntosh, 1868), one glycerid (*Glycera alba* (O.F. Müller, 1776)), one lacydoniid (*Lacydonia* sp.), one nereidid (*Nereis pelagica* Linnaeus, 1758) and one phyllodocid (*Notophyllum foliosum* (M. Sars, 1835)) (Table 1). Three other nephtyid taxa (*Dentinephtys glabra* (Hartman, 1950), *Inermonephtys inermis* (Ehlers, 1887), and *Micronephthys oculifera* Mackie, 2000), for which we had morphological data only, were included in a second analysis. The choice of outgroup taxa was based on earlier phylogenetic analyses of polychaete relationships (Rouse & Fauchald 1997; Bleidorn *et al.* 2003; McHugh 2005; Rousset *et al.* 2007; Struck *et al.* 2007). Specimens collected for DNA sequencing were preserved in 95% ethanol and stored in +4°C. Vouchers are deposited at Museu Nacional de História Natural de Lisboa (Museu Bocage) (MNHN MB), Gothenburg Natural History Museum (GNHM) and California Academy of Sciences, Invertebrate Zoology (CASIZ). For some taxa, as for the outgroups, previously published sequences were obtained from GenBank (Table 1).

Table 1. Taxa, collection sites, NCBI GenBank accession numbers and vouchers. "-" – indicates missing data.

Taxon	**Locality**	**COI**	**16S**	**18S**	**28S**	**Voucher** [a]
Nephtyidae						
Aglaophamus circinata [b, d]	-	-	-	DQ790072	DQ790020	-
Aglaophamus elamellata	Setúbal submarine canyon, Portugal	GU179404	GU179361	GU179365	GU179385	hologenophore MNHN MB36000104
Aglaophamus malmgreni [1]	Svalbard, Arctic	GU179405	GU179362	GU179366	-	hologenophore MNHN MB36000138
Aglaophamus malmgreni [1]	off Norway	-	-	-	GU179386	hologenophore MNHN MB36000133
Aglaophamus malmgreni [b]	-	AY996126	AY996070	AY996091	AY996109	--
Aglaophamus rubellus	Bohuslän, Sweden	GU179406	GU179363	GU179367	GU179387	hologenophore MNHN MB36000137
Aglaophamus trissophyllus	Deception Island, Antarctic	-	-	GU179368	GU179388	hologenophore MNHN MB36000154
Aglaophamus pulcher n. comb.	Nazaré submarine canyon, Portugal	GU179413	GU179360	GU179384	GU179403	hologenophore MNHN MB36000129
Aglaophamus australiensis n. comb. [1]	Gulf St. Vincent, Australia	-	GU179347	GU179371	-	hologenophore MNHN MB36000143
Aglaophamus australiensis n. comb. [b, c, 1]	-	-	-	-	AF185166	-
Bipalponephtys cornuta n. gen., n. comb.	San Francisco Bay, California, USA	GU179409	GU179352	GU179375	GU179394	hologenophore CASIZ 168329
Nephtys assimilis	off Cascais, Portugal	-	GU179346	GU179370	GU179390	hologenophore MNHN MB36000105
Nephtys caeca	Bohuslän, Sweden	-	GU179348	GU179372	GU179391	hologenophore MNHN MB36000135
Nephtys caecoides	San Francisco Bay, California, USA	-	GU179349	-	-	hologenophore CASIZ 154226
Nephtys ciliata	Svalbard, Arctic	-	GU179350	GU179373	GU179392	hologenophore MNHN MB36000139
Nephtys cirrosa [1]	Vila Nova Milfontes, Portugal	GU179408	-	-	-	hologenophore MNHN MB36000112
Nephtys cirrosa [1]	Galiza, Spain	-	GU179351	GU179374	GU179393	hologenophore MNHN MB36000106
Nephtys ferruginea	San Francisco Bay, California, USA	-	GU179353	GU179376	GU179395	hologenophore CASIZ 170852
Nephtys hombergii [1]	Ria Aveiro, Portugal	GU179410	-	GU179377	GU179396	hologenophore MNHN MB36000118
Nephtys hombergii [1]	Bohuslän, Sweden	-	GU179354	-	-	hologenophore MNHN MB36000136
Nephtys hombergii [b]	-	-	-	U50970	X80649	-
Nephtys hystricis	Bohuslän Sweden	-	GU179355	GU179378	GU179397	hologenophore MNHN MB36000155
Nephtys incisa	Bohuslän, Sweden	-	GU179356	GU179379	GU179398	hologenophore MNHN MB36000158
Nephtys kersivalensis	Off Northumberland, England	-	-	GU179380	GU179399	hologenophore MNHN MB36000149

Nephtys paradoxa	Trondheimsfjord, Norway	GU179412	GU179358	GU179382	GU179401	hologenophore MNHN MB36000140
Nephtys paradoxa	Gulf of Cadiz	-	GU179357	GU179381	GU179400	hologenophore MNHN MB36000128
Nephtys pente	Bohuslän, Sweden	-	GU179359	GU179383	GU179402	hologenophore GNHM P 13179
Micronephthys stammeri	Tanabe Bay, Japan	GU179407	GU179364	GU179369	GU179389	hologenophore MNHN MB36000144
Dentinephtys glabra [e]	-	-	-	-	-	-
Inermonephtys inermis [d]	-	-	-	-	-	-
Amphinomidae						
Paramphinome jeffreysii [b,g]	-	AY838875	AY838840	AY838856	AY838865	-
Lacidonia						
Lacydonia sp. [b, h]	-	AY996120	AY996061	AY996082	AY996102	-
Phyllodocidae						
Notophyllum foliosum [b, i]	-	AY996117	DQ779627	AY996079	AY996100	-
Nereididae						
Nereis pelagica [b, j]	-	-	AY340470	AY340438	AY340407	-
Glyceridae						
Glycera alba [b, k]	-	-	DQ779615	DQ779651	DQ779689	-

[a] Voucher terminology follows Pleijel *et al.*, 2008; [b] Sequences obtained from NCBI GenBank; [c] As *Nephtys australiensis* in GenBank; Main literature sources for character information: [d] Taylor, 1984; [e] Imajima & Takeda, 1987, Hilbig, 1997; [f] Imajima & Takeda, 1985; [g] George & Hartmann-Schroeder, 1985; [h] Rouse & Pleijel, 2001; [i] Pleijel & Dales, 1991, Kato & Pleijel, 2002; [j] Chambers & Garwood, 1992; [k] O'Connor, 1987; [l] Different genes were obtained from different specimens due to sequencing problems.

DNA Analysis

Extraction of DNA was done either with Chelex® 100, Na+-form (Fluka), or with E.Z.N.A. Tissue DNA Kit (Omega Bio-tek) following the protocol supplied by the manufacturer. 1200-1800 bp of 18S, and *ca* 800 bp of 28S D1-D2 region, 500 bp of 16S, and 600 bp of COI, were amplified using a range of primers (Table 2). PCR mixtures contained ddH2O, 1 µl of each primer (10µM), 2µl template DNA and puReTaq Ready-To-Go PCR Beads (Amersham Biosciences) in a mixture of total 25 µl. The temperature profile was as follows: 96ºC/120s -(94ºC/30s-48ºC/30s-72ºC/60s)*45cycles-72ºC/480s. PCR products were purified with the E.Z.N.A. Cycle-Pure Kit (Omega Bio-tek) or QIAquick PCR Purification Kit (Qiagen). The majority of the sequences were obtained with a BeckmanCoulter CEQ8000. The primers used for sequencing are listed in Table 2. Each sequence mixture contained 1 µl primer (5mM), 4 µl DTCS Quick Start Mix, purified amplification product and ddH2O. The sequence reaction profile was as follows: (96ºC/20s-50ºC/20s-60ºC/240s)*29 cycles.

Part of the sequencing was performed by the Macrogen Sequencing System in Korea, on an ABI 3730XL DNA Analyser (Applied Biosystems).

Table 2. PCR and sequencing primers.

Primer	Sequence 5'-3'	References
TimA	AMCTGGTTGATCCTGCCAG	Norén and Jondelius (1999)
620F	TAAAGYTGYTGCAGTTAAA	Nygren and Sundberg (2003)
584R	ACGCTATTGGAGCTGGAAT	J. Eklöf, pers comm
1100R	GATCGTCTTCGAACCTCTG	Norén and Jondelius (1999)
1324F	GGTGGTGCATGGCCG	Cohen et al. (1998)
1324R	CGGCCATGCACCACC	Cohen et al. (1998)
1806R	CCTTGTTACGACTTTTACTTCCTC	Hovmöller et al. (2002)
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
COI-E	TATACTTCTGGGTGTCCGAAGAATCA	Bely and Wray (2004)
16S arL	CGCCTGTTTATCAAAAACAT	Palumbi et al. (1996)
16S brH	CCGGTCTGAACTCAGATCACGT	Palumbi et al. (1996)
28S C1’	ACCCGCTGAATTTAAGCAT	Lê et al. (1993)
28S D2	TCCGTGTTTCAAGACGG	Lê et al. (1993)

Overlapping sequence fragments were merged into consensus sequences and aligned using Geneious v4.5.4 (Drummond *et al.* 2009) with default settings. Different alignment parameters (Gap open penalty/Gap extension penalty of 12/3, 20/5 and 30/10) were applied to identify ambiguous sequence regions, and those that could not be unambiguously aligned were excluded. Alignments and the morphological matrix are available at TreeBase, http://www.treebase.org (S2519; M4812-M4815). Molecular and morphological data were combined in a single matrix. For some taxa, with missing data for some of the genes, data from two different specimens were combined (see Table 1). PAUP* 4.0b10 (Swofford 2002) was used for the parsimony (PA) analyses, with heuristic searches under default settings except for the addition sequence set to 1,000 repetitions. Clade support was assessed using jackknife with 10,000 replicates, 36% of characters deleted in each replicate and heuristic search as above. Bayesian phylogenetic analyses (BA) were conducted with MrBayes 3.1.2 (Ronquist & Huelsenbeck 2003). The models used for the molecular data in BA were obtained from MrModelTest 2.2 (Nylander 2004), choosing the AIC criterion. The model GTR+I+G was suggested as best fit for 16S, 18S and 28S. For COI, the data was partitioned into codon positions, with SYM+G for position 1, GTR+G for position 2, and HKY+G for position 3. The parameters used for the partitions were unlinked. The morphological data were analyzed under the Mkv model (Lewis, 2001) with a gamma correction for rate heterogeneity. The two analyses, of 29 and 32 taxa, respectively, were run three times with four chains, and 200,000 generations were discarded as burn-in. The analysis of 29 taxa was run for

for 4,000,000 generations, and the analysis of 32 taxa for 15,000,000 generations. Acceptance rates of attempted swaps between the chains fell within a span of 20-60%, which is considered optimal by e.g. Roberts & Rosenthal (2001). The treefiles were tested with AWTY (Are We There Yet) (Nylander *et al.* 2008) to see that the analyses had reached a stationary phase.

Morphological characters and character distributions

The morphological dataset is based mainly on examined specimens. Character observations of non-examined taxa are based on literature information (Table 1). Characters and character states are summarized in Table 3 and explained below. The morphological matrix is presented in Table 4.

Table 3. Summary of the characters.

1	Palp position (0-slightly behind antennae/1-further back)
2	Palp morphology (0-simple/1-bifid)
3	Median antenna (0-absent/1-present)
4	Eyes (0-absent/1-present)
5	Position of eyes (0-on prostomium/ 1-posterior to prostomium)
6	Number of eyes (single pair/1-two pairs)
7	Nuchal organs shape (0-knobs/1-caruncle/2-cirriform/3-ciliated slits/4-epaulettes)
8	Pharynx papillae (0-absent/1-present)
9	Warts on proximal pharynx surface (0-absent/1-present)
10	Middorsal and midventral simple terminal papillae (0-absent/1-present)
11	Terminal ring of papillae (0-absent/1-present)
12	Shape of papillae of terminal ring (0-simple/1-bifid)
13	Rows of subterminal papillae (0-absent/1-present)
14	Extension of rows of subterminal papillae (0-occupying less than half the length of the pharynx/1-occupying more than half the length of the pharynx)
15	Number of rows of subterminal papillae (0-22/1-less than 22)
16	Papillae per row (0-less than 10/1-between 10 and 20/2-more than 20
17	Long middorsal papillae (0-absent/1-present)
18	Jaws (0-absent/1-present)
19	Number of jaws (0-single pair/1-two pairs)
20	Dorsal notopodial branchiae (0-absent/1-present)
21	Ventral notopodial branchiae (0-absent/1-present)
22	Ventral notopodial branchiae direction (0-coiled inwards/1-coiled outwards)
23	Ventral notopodial branchiae start (0-untill chaetiger 5/1-after chaetiger 5)
24	Ventral notopodial branchiae stop (0-before posterior end/1-near posterior end)
25	Branchiae shape (0-cirriform/1-with membranous expansions)
26	Neuropodial superior lobe (0-absent/1-present)
27	Acicular lobes of median parapodia (0-conical/1-rounded to bilobed)
28	Prechaetal lamellae of median parapodia (0-rudimentary or simple/1-bilobed)
29	Notopodial postchaetal lamellae (0-simple/1-bilobed)
30	Notopodial postchaetal lamellae length (0-equal or slightly larger than acicular lobe/1-much larger than acicular lobe)
31	Neuropodial postchaetal lamellae (0-simple/1-bilobed)
32	Neuropodial postchaetal lamellae length (0-equal or slightly larger than acicular lobe/1-much larger than acicular lobe)
33	Chaetae start (0-segment 1/1-further back)
34	Compound chaetae (0-absent/1-present)
35	Lyrate chaetae (0-absent/1-present)
36	Number of pygidial cirri (0-single/1-pair)

Palps (1-2). In nephtyids the palps can be simple or bifid (Hilbig 1997: fig. 13.8b-d; Rouse & Pleijel 2001: fig. 30.2c) and may be inserted anteriorly, slightly behind and very close to the antennae, or ventro-laterally and further back on the prostomium

(Fauchald 1963: fig. 1, 1977: fig. 26A; Ohwada 1985: fig. 1). The outgroup taxa have simple palps. In *Glycera alba* and *Lacydonia* sp. the palps are inserted in a position corresponding to the paired antennae but on the ventral side (Rouse & Pleijel 2001: figs. 24.2, 26.1). In *Nereis pelagica* and *Notophyllum foliosum* the palps are inserted further back than the paired antennae (Hartmann-Schröder 1996: fig. 86A; Kato & Pleijel 2002: fig. 1A).

Median antenna (3). A median, or unpaired, prostomial antenna is absent in nephtyids but present in three outgroups *Paramphinome jeffreysii* (George & Hartmann-Schröder 1985: fig. 6A), *Lacydonia* sp. (Pleijel & Fauchald 1993), and *Notophyllum foliosum* (Pleijel & Dales 1991: fig. 42A; Kato & Pleijel 2002: figs. 1A, 3A).

Eyes (4-6). In nephtyids one or two pairs of subdermal eyes may be present on the prostomium or anterior segments. They are usually placed directly on the brain lobes (Wesenberg-Lund 1949: fig. 24; Rainer & Kaly 1988: figs. 1a, 5a), and are often absent or externally invisible in adult specimens. In the outgroups eyes are absent in *Paramphinome jeffreysii* (F. Pleijel pers. obs.) and *Glycera alba* (Böggemann 2002), present as single pairs in *Lacydonia* sp. (Rouse & Pleijel 2001: fig. 30.2c) and *Notophyllum foliosum* (Pleijel & Dales 1991: fig. 42A; Kato & Pleijel, 2002: fig. 3A), and as two pairs in *Nereis pelagica* (Chambers & Garwood 1992: fig. 45a).

Nuchal organ shape (7). In nephtyids the nuchal organs are present as a pair of ciliated rounded or cirriform knobs on the dorso-posterior corners of the prostomium (Taylor 1984: fig. 35-16; Hilbig, 1997: fig. 13.2a; Rouse & Pleijel 2001: fig. 30.2c). For the outgroup taxa they appear as lateral ciliated knobs on each side of the prostomium in *Glycera alba* (Rouse & Pleijel 2001: fig. 24.2b), as elongated ciliated slits on the dorso-posterior side of prostomium in *Lacydonia* sp. (Rouse & Pleijel 2001: fig. 26.1b), as a pair of epaulettes on the posterior side of the prostomium in *Notophyllum foliosum* (Pleijel & Dales 1991: fig. 42A; Kato & Pleijel 2002: figs. 1A, 3A), and as a caruncle in *Paramphinome jeffreysii* (George & Hartmann-Schröder 1985: fig. 6A).

Pharynx papillae (8). All nephtyid taxa, excluding *Inermonephtys,* have a papillose pharynx (Fauchald 1963: fig. 2; Wilson 2000: fig. 1.79B; Laborda 2004: fig. 145B). Pharynx papillae are also present in *Glycera alba* (O'Connor 1987: fig. 5b; Wilson

2000: fig. 1.73A) and *Notophyllum foliosum* (Pleijel 1993: fig. 3B; Kato & Pleijel 2002: figs. 1B-C, 3C), but absent from the remaining outgroup taxa.

Warts on proximal pharynx surface (9). Apart from papillae there may be warts on the proximal part of the pharynx surface (Imajima & Takeda 1987: fig. 11b). Pharynx warts are absent in the outgroup taxa.

Terminal ring of papillae (10-12). In nephtyids as well as in *Notophyllum foliosum*, the pharynx ends in a ring of papillae (absent in *Inermonephtys*). These papillae are simple in *N. foliosum* (Pleijel pers. obs.), but in nephtyids, except *Inermonephtys*, there are two sets of ten bifid papillae on each side of a dorso-ventral slit (Wilson 2000: fig. 1.79B; Laborda 2004: fig. 145B); a middorsal and/or a midventral simple terminal papillae may also be present (Hilbig 1997: fig. 13.6E).

Rows of subterminal papillae (13-17). In nephtyids the subterminal part of the pharynx is covered with 14-22 longitudinal rows of conical to cirriform papillae (Fauchald 1963: fig. 2; Laborda 2004: fig. 145B). These papillae vary in number in each row and may occupy only the distal part of the pharynx or extend to the base. Occasionally a single middorsal and a single midventral papilla arise between the terminal and subterminal papillae (Fauchald 1963: fig. 2c; Pettibone 1963: fig. 6; Laborda 2004: fig. 145B). The midventral papilla is usually equal in length to the subterminal papillae and therefore difficult to distinguish, but the middorsal papilla may be very long. Only taxa with distinct long middorsal papilla are scored as present for this feature. Subterminal rows of papillae are absent from the outgroup taxa.

Jaws (18-19). One pair of lateral jaws is present in Nephtyidae (Fauchald 1968: fig. 13.4B; Laborda 2004: fig. 145E) and Nereididae (Wilson 2000: fig. 1.80B, C), and two pairs in Glyceridae (Chambers & Garwood 1992: fig. 2a, b; Wilson 2000: fig. 1.73A). Jaws of *Inermonephtys inermis* are spindle-shaped instead of hook-like (Imajima & Takeda 1985: fig. 2d, e), and *Dentinephtys glabra* has an additional pair of plates carrying rows of teeth (Fauchald 1968: fig. 13.4B-C; Imajima & Takeda 1987: fig. 13.4B). These two features are autapomorphic for *I. inermis* and *D. glabra*, respectively, and are not included here. Remaining taxa lack jaws.

Branchiae (20-25). Branchiae are present on the dorsal side of the notopodia in *Paramphinome jeffreysii* (George & Hartmann-Schröder 1985: fig. 6A) and *Glycera alba* (O'Connor 1987: figs. 2, 5e), and absent in the remaining outgroup taxa. In nephtyids branchiae can be absent (*Micronephthys*), or present on the ventral side of the notopodia (Wilson 2000: fig. 1.79C; Laborda 2004: fig. 145a). The branchiae may be cirriform or with membranous expansions (Imajima & Takeda 1987: fig. 5f, g) and coiled inwards (*Aglaophamus*, *Inermonephtys*) or outwards (*Nephtys*, *Dentinephtys*) (Fauchald 1963: fig. 3). They may be absent on the anteriormost and posteriormost segments.

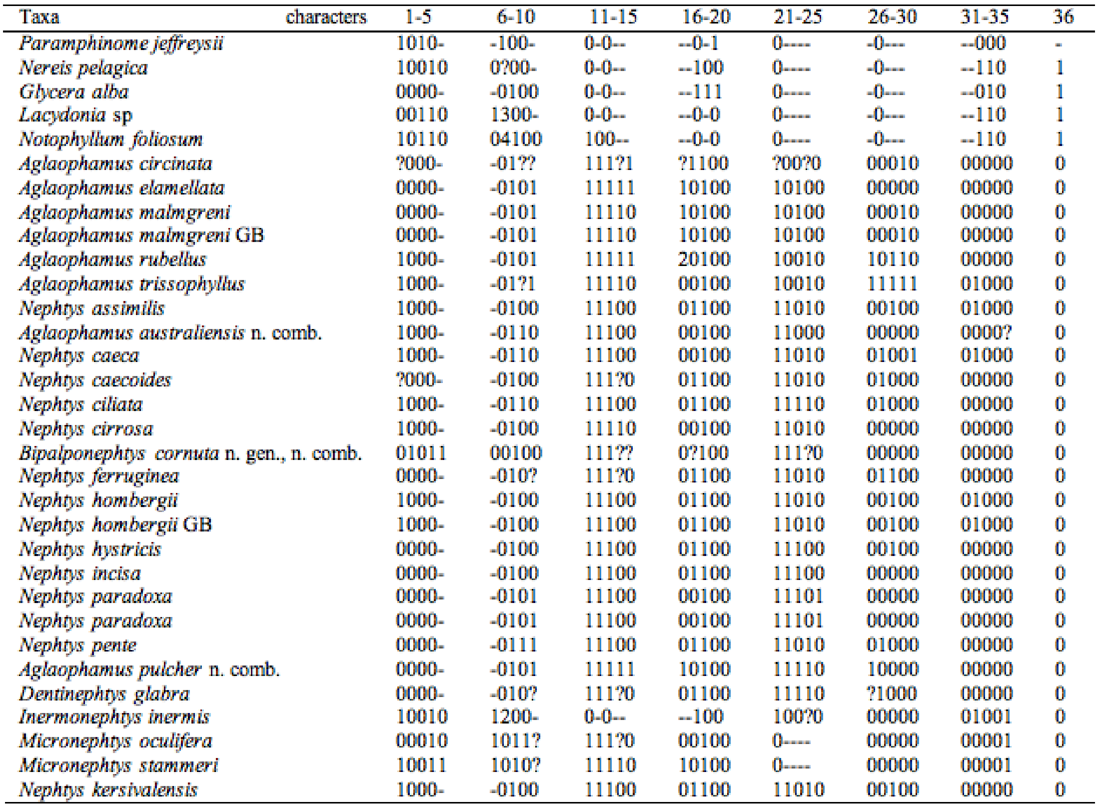
Neuropodial superior lobes (26). In some nephtyid species the parapodia of a certain number of segments have a digitiform lobe inserted on the dorsal side of neuropodium (Fauchald 1968: fig. 13.1; Rainer & Kaly 1988: fig. 6d-f). This character is absent from the outgroup taxa.

Parapodia (27-32). In nephtyids the parapodia are complex with acicular lobes carrying pre- and postchaetal lamellae and dorsal (notopodial) and ventral (neuropodial) cirri (Fauchald 1977: fig. 26B; Rainer 1991: figs. 1-3; Laborda 2004: fig. 145A). Acicular lobes (character 27) may be acutely pointed as in *Aglaophamus* and *Inermonephtys* (Imajima & Takeda 1985: fig. 7h), conical as in *Micronephthys* and some *Nephtys* (Rainer 1991: fig. 1G), or rounded to bilobed as in *Dentinephtys* and other *Nephtys* (Rainer 1991: fig. 1H). Since the difference between acutely pointed and conical states may sometimes be tenuous, only two states were scored (conical/rounded to bilobed). Prechaetal lamellae (character 28) may be rudimentary to well developed and simple or bilobed (Rainer 1991: fig. 1G, H). Postchaetal lamellae (characters 29-32) are usually well developed although very small in *Micronephthys*, equalling or surpassing the length of acicular lobes and can also be simple or bilobed (Rainer 1991: fig. 1). Lamellae may assume slightly different shapes but only the more obvious and unambiguous shapes (simple / bilobed) are scored here. These characters were examined in fully developed parapodia at the middle part of the specimens. With the exception of the conical acicular lobes, the characters relating to parapodial structures were not scored for the outgroups. The different lobes and lamellae in nephtyids differ considerable from other taxa and homology statements are difficult to make.

Chaetae (33-35). In *Lacydonia* sp., *Nereis pelagica* and *Notophyllum foliosum*, chaetae are present from segment 2 or further back, while in the remaining taxa chaetae are present from segment 1. Compound chaetae (Rouse & Pleijel 2001: figs. 20.2d, 32.2e) are present in the neuropodia of *Glycera alba*, *Notophyllum foliosum* and *Lacydonia* sp., and in the noto- and neuropodia of *Nereis pelagica*. In some nephtyids (*Aglaophamus*, *Inermonephtys* and *Micronephthys*) there are lyriform noto- and neurochaetae (Taylor 1984: fig. 35-16c; Wilson 2000: fig. 1.79G; Laborda 2004: fig. 145C).

Number of pygidial cirri (36). Nephtyids are unique within Phyllodocida in possessing a single median pygidial cirrus (Rouse & Pleijel 2001: fig. 30.2f). The other taxa have one pair of cirri (Pleijel & Dales 1991: fig. 42C; Chambers & Garwood 1992: fig. 6a, b), and in *Paramphinome jeffreysii* pygidial cirri are absent.

Table 4. Morphological matrix. “?” denotes missing information and “-“ non applicable condition.



Taxa	characters	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36
Paramphinome jeffreysii		1010-	-100-	0-0--	--0-1	0----	-0---	--000	-
Nereis pelagica		10010	0?00-	0-0--	--100	0----	-0---	--110	1
Glycera alba		0000-	-0100	0-0--	--111	0----	-0---	--010	1
Lacydonia sp		00110	1300-	0-0--	--0-0	0----	-0---	--110	1
Notophyllum foliosum		10110	04100	100--	--0-0	0----	-0---	--110	1
Aglaophamus circinata		?000-	-01??	111?1	?1100	?00?0	00010	00000	0
Aglaophamus elamellata		0000-	-0101	11111	10100	10100	00000	00000	0
Aglaophamus malmgreni		0000-	-0101	11110	10100	10100	00010	00000	0
Aglaophamus malmgreni GB		0000-	-0101	11110	10100	10100	00010	00000	0
Aglaophamus rubellus		1000-	-0101	11111	20100	10010	10110	00000	0
Aglaophamus trissophyllus		1000-	-01?1	11110	00100	10010	11111	01000	0
Nephtys assimilis		1000-	-0100	11100	01100	11010	00100	01000	0
Aglaophamus australiensis n. comb.		1000-	-0110	11100	00100	11000	00000	0000?	0
Nephtys caeca		1000-	-0110	11100	00100	11010	01001	01000	0
Nephtys caecoides		?000-	-0100	111?0	01100	11010	01000	00000	0
Nephtys ciliata		1000-	-0110	11100	01100	11110	01000	00000	0
Nephtys cirrosa		1000-	-0100	11110	00100	11010	00000	00000	0
Bipalponephtys cornuta n. gen., n. comb.		01011	00100	111??	0?100	111?0	00000	00000	0
Nephtys ferruginea		0000-	-010?	111?0	01100	11010	01100	00000	0
Nephtys hombergii		1000-	-0100	11100	01100	11010	00100	01000	0
Nephtys hombergii GB		1000-	-0100	11100	01100	11010	00100	01000	0
Nephtys hystricis		0000-	-0100	11100	01100	11100	00100	00000	0
Nephtys incisa		0000-	-0100	11100	01100	11100	00000	00000	0
Nephtys paradoxa		0000-	-0101	11100	00100	11101	00000	00000	0
Nephtys paradoxa		0000-	-0101	11100	00100	11101	00000	00000	0
Nephtys pente		0000-	-0111	11100	01100	11010	01000	00000	0
Aglaophamus pulcher n. comb.		0000-	-0101	11111	10100	11110	10000	00000	0
Dentinephtys glabra		0000-	-010?	111?0	01100	11110	?1000	00000	0
Inermonephtys inermis		10010	1200-	0-0--	--100	100?0	00000	01001	0
Micronephtys oculifera		00010	1011?	111?0	00100	0----	00000	00001	0
Micronephtys stammeri		10011	1010?	11110	10100	0----	00000	00001	0
Nephtys kersivalensis		1000-	-0100	11100	01100	11010	00100	00000	0

2.1.3 Results

The combined dataset consisted of 3782 morphological and molecular characters with 1194 variable and 658 parsimony-informative. For each data set, 16S consisted of 429 characters with 190 variable and 129 parsimony-informative, 18S of 1877 characters with 395 variable and 125 parsimony-informative, 28S of 743 characters with 250 variable and 131 parsimony-informative, and COI of 696 characters with 322 variable and 247 parsimony-informative. The morphological data set consisted of 36 characters with 30 parsimony-informative characters in the 29-taxon analysis and 31 in the 32-taxon analysis. The two analyses, of 29 and 32 (including three taxa with morphological data only) terminals, yielded similar results with 21 matching clades of totally 25 and 26 clades, respectively (Figure 3, 4). Bayesian and parsimony analyses (BA and PA, respectively) also gave very similar results from both datasets, although the support values from both are generally higher for the 29 terminal data set. The tree from the BA-29 terminal (Figure 3) supports 25 nodes, of which 20 have clade credibilities above 95%. The PA-29 taxa tree supports 21 nodes, the majority of which were recovered by the BA, and 15 of these have support values above 70%. For the 32 terminal dataset the BA tree (Figure 4) supports 26 nodes, of which ten have clade credibilities above 95%, and the PA tree supports 18 nodes, similar to the ones from BA, with six having support values above 70%. The same topologies are obtained in both BA and PA with only some small differences for the taxa *Nephtys pulchra* Rainer, 1991, *N. kersivalensis* McIntosh, 1908, *N. cornuta* Berkeley & Berkeley, 1945 and *Micronephthys stammeri* (Augener, 1932). All analyses retrieve two major groups, one including all the *Aglaophamus* taxa and the other including the majority of the *Nephtys* taxa. Both clades are well supported. *Aglaophamus* includes also, and invariably, the taxa *Nephtys pulchra* and *Nephtys australiensis* Fauchald, 1965. *Nephtys* is always subdivided in two subgroups (A and B). *Dentinephtys glabra* (Hartman 1950) is nested within subgroup B of *Nephtys* (Figure 4). *Nephtys cornuta* is positioned outside both *Aglaophamus* and *Nephtys* and is the sister group to all remaining nephtyids. In the PA this taxon is included in a trichotomy with *Aglaophamus* and *Nephtys*. A similar situation occurs with the *Micronephthys* taxa that come out either as sister group to *Nephtys* (in BA) or to all other nephtyids (in PA). *Inermonephtys inermis* (Ehlers, 1887) (for which we have morphological data only) appears in the BA associated with the outgroup taxon *Nereis pelagica*, with clade credibility of 59%, but in the PA it instead appears as sister to all remaining nephtyids, with a 72% support value.

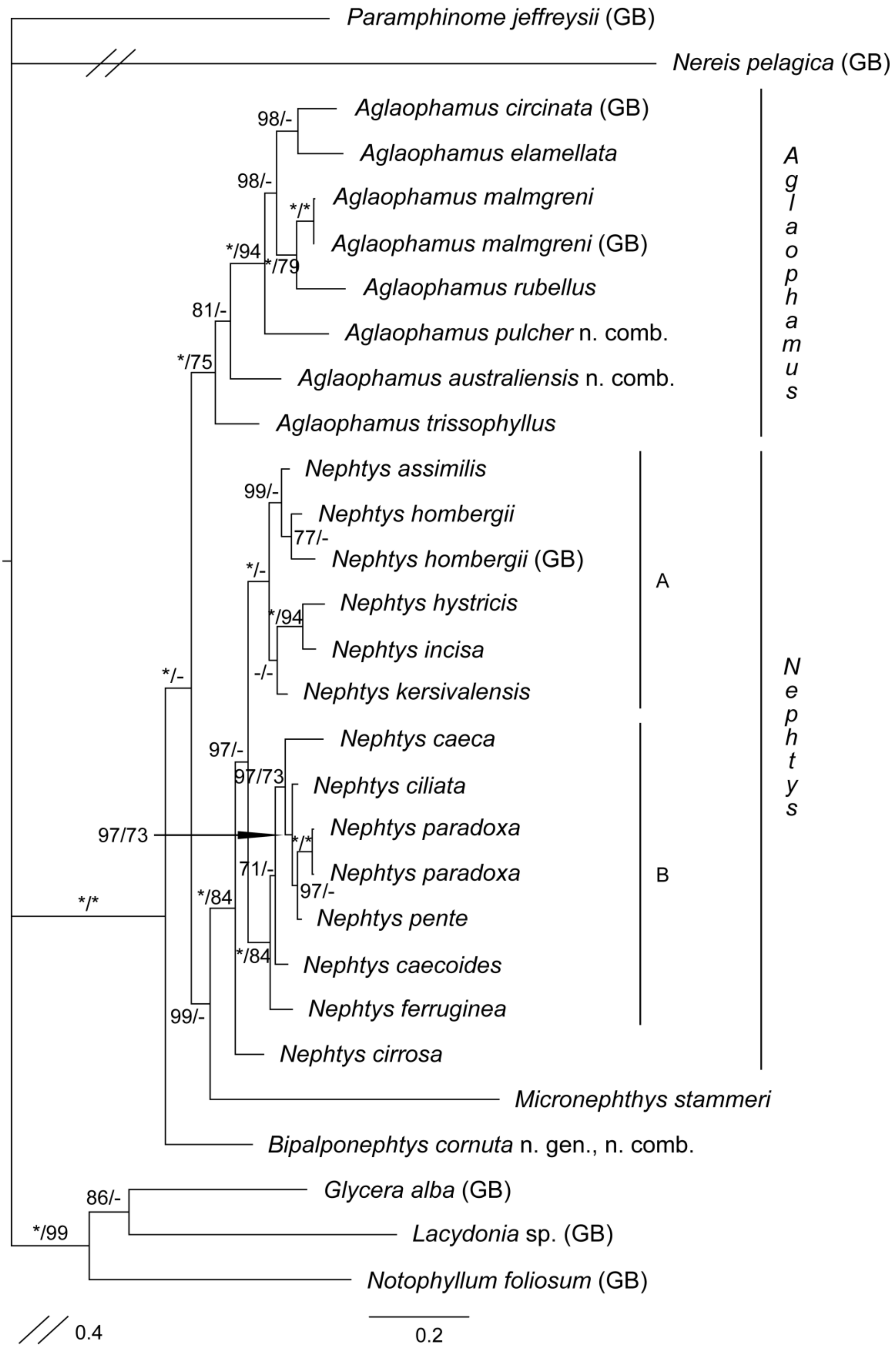


Figure 3. Majority rule consensus tree from the Bayesian analysis (BA) of the combined data with 29 taxa. The first values for each node represent clade credibilities from Bayesian analyses, the second are jackknife support from the parsimony analyses. * indicates support value of 100, - support value below 70. GB indicates sequences obtained from NCBI GenBank.

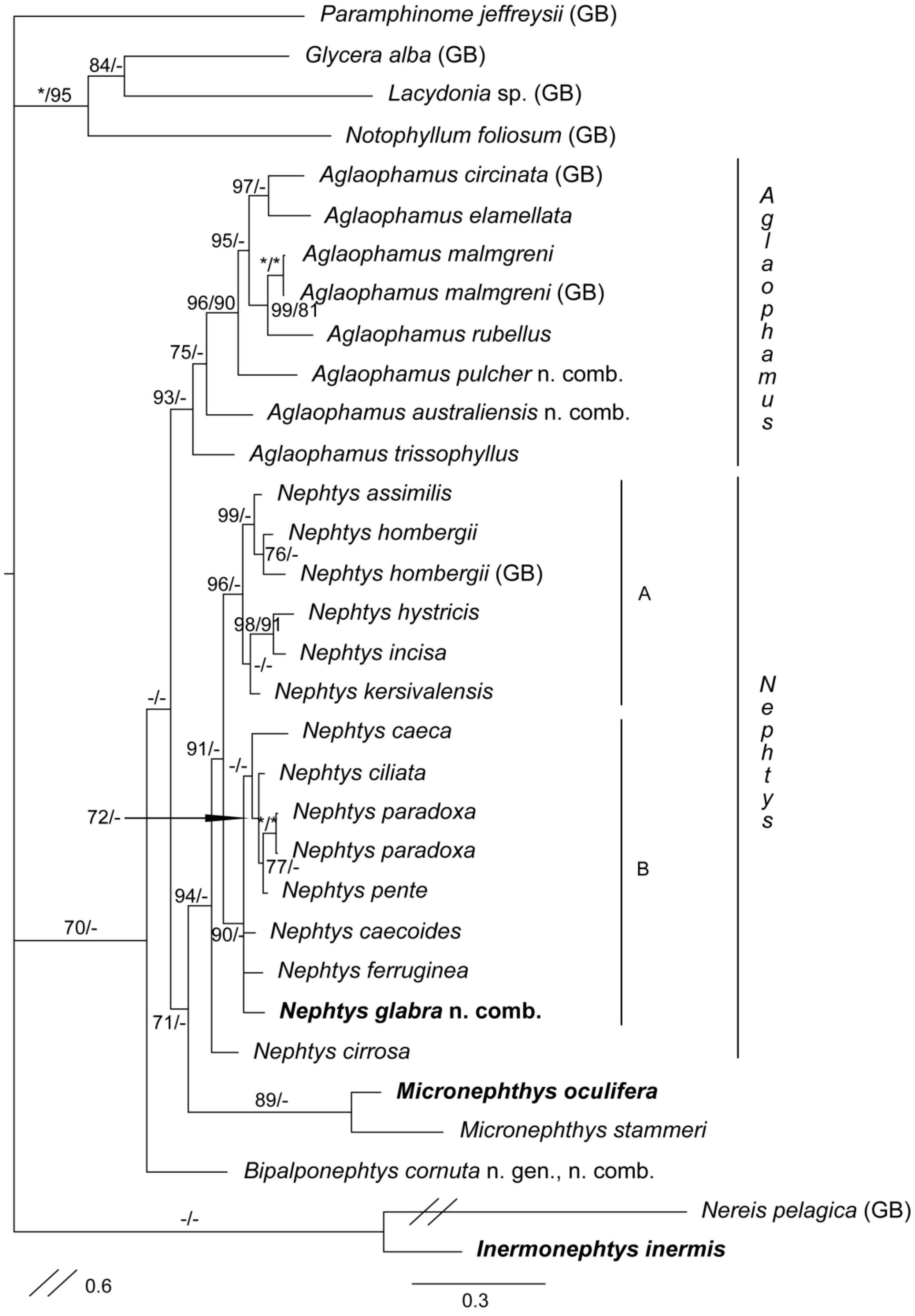


Figure 4 - Majority rule consensus tree from the Bayesian analysis (BA) of the combined data with 32 taxa (including the three taxa *Dentinephtys glabra*, *Inermonephtys inermis*, and *Micronephthys oculifera*, with morphological characters only). The first values for each node represent clade credibilities from Bayesian analyses, the second are Jackknife support from the parsimony analyses. * indicates support value of 100, - support value below 70. GB indicates sequences obtained from NCBI GenBank. Terminals in bold face are taxa with morphological data only.

2.1.4 Discussion

Both analyses (Figure 3, 4) retrieve the two major nephtyid clades *Aglaophamus* and *Nephtys* with high support in the 29 terminal tree and slightly lower in the 32 terminal tree.

Nephtys pulchra and *N. australiensis* are both nested within *Aglaophamus* and are here formally transferred to this genus as *A. pulcher*, new comb., and *A. australiensis*, new comb. The morphological similarity between *N. pulchra* and *Aglaophamus* species was already noted by Rainer (1991) in its original description. However, the recurved branchiae conditioned its inclusion in the genus *Nephtys*. The branchiae in *N. australiensis* are poorly developed but slightly recurved, which was the reason for the previous inclusion in the genus *Nephtys*. Branchiae shape and development, whether involute (*Aglaophamus*, *Inermonephtys*), recurved (*Nephtys*, *Dentinephtys*), absent or poorly developed (*Micronephthys*) have until now been the main morphological character distinguishing the nephtyid genera, although a combination of other characters have also been used. The inclusion of *N. pulchra* and *N. australiensis* in the *Aglaophamus* clade demonstrates the presence of homoplasy in this feature. The only morphological apomorphies found for the genus *Aglaophamus* are the acutely pointed acicular lobes and the finely spinulated postacicular chaetae. Nevertheless, a combination of characters such as the presence or absence of lyrate chaetae, pharynx papillae organization and nuchal organs shape should also be taken into account. Table 5 gives the diagnostic characteristics for the different genera within the Nephtyidae.

Nepthys is divided into two clades (clade A and B in Figure 3, 4). Once again parapodial lobes shape and development and postacicular chaetae spinulation show a well-defined pattern within these clades. Taxa from clade A have conical acicular lobes, well developed and bilobed prechaetal lamellae and finely spinulated chaetae while taxa from clade B have rounded to bilobed acicular lobes, rudimentary or poorly developed prechaetal lamellae and coarsely spinulated chaetae. Further subdivision of these clades emphasize other more particular features of the lamellae.

Unfortunately there were no *Dentinephtys* specimens available for molecular study. However, based on morphology, *Dentinephtys* is nested with clade B in *Nephtys* (Figure 4). This is unsurprising, considering that the only feature mentioned in the original description that distinguishes the monotypic *Dentinephtys* from

Nephtys is the autapomorphy presence of a pair of pharyngeal trepans. Therefore *Dentinephtys* is here formally synonymized with *Nephtys*.

Table 5. Character summary for nephtyid genera.

	Aglaophamus	***Bipalponephtys*, new genus**	***Inermonephthys***	***Micronephtys***	***Nephtys***
Antennae	+	+	-	+	+
Palps	simple	bifid	simple, small	simple	simple
nuchal organs	rounded	rounded	cirriform	rounded	rounded
pharynx papillae	+	+	-	+	+
rows of subterminal papillae	14 - 22 frequently ending in triangle of small papillae proximaly	16/18	--	18 - 22	22
acicular lobes	acutely pointed	conical	conical	conical	conical / rounded / bilobed
preacicular chaetae	barred	anteriorly barred, posterioly smooth	spinulated	barred	barred
spinulation postacicular chaetae	light	light	light	ligth / smooth	light / coarse
lyrate chaetae	- / +	-	+	- / +	-
branchiae	involute / recurved	recurved	involute	poorly developed / absent	recurved

Micronephthys has a well supported sister group relationship to *Nephtys*. However, the genus *Micronephthys* is heterogenous and in need of revision. It can be split into two groups of species, one with branchiae and no lyrate chaetae, and another without branchiae and with lyrate chaetae in median and posterior parapodia. For the group with branchiae, the branchiae are poorly developed and straight, a feature also observed in some smaller species of *Nephtys* and *Aglaophamus,* thus bringing many doubts about the proper placement of some of the branchiate species. The two species included in this study both belong to the abranchiate group with lyrate chaetae, and further analyses including branchiate forms must be carried out in order to further investigate the status of *Micronephthys*.

Inermonephtys is another genus for which we only had morphological information, and this taxon actually forms a clade with *Nereis* and is not part of the ingroup. However, considering the very low support values and limited data we are of the opinion that a position outside nephtyids is likely to be incorrect, although we at present cannot specify any particular position within the nephtyids.

Nephtys cornuta appear as sister group to all remaining nephtyids and we here erect a new generic name for it, *Bipalponephtys* (gender femininum). Morphologically this species presents conical acicular lobes, poorly developed parapodial lamellae and branchiae, bifid palps and preacicular chaetae of posterior chaetigers that are capillary instead of barred (Table 5). The last two characters are unique for this new genus and constitute morphological apomorphies. Up to date there are only two other described species with similar characteristics, *N. danida* Nateewathana & Hylleberg, 1986 from Phuket Island and *M. neotena* (Noyes 1980) from eastern coast of North America. Thus the three species *N. cornuta*, *N. danida* and *M. neotena* are here formally transferred to the new genus as *Bipalponephtys cornuta*, new comb., *B. danida* new comb. and *B. neotena* new comb., with the first being type species of the genus.

Nephtyidae is a problematic group in several ways. Although the family is likely to be monophyletic, the deeper relationships within the group have not been addressed and the delineation of genera has lacked stability. Previous research has mainly focused on delineating species, often in geographically restricted areas. We have here provided a first analysis of the phylogeny within the group, mainly designed to address delineation problems between the genera. We conclude that *Aglaophamus*, *Nephtys* and *Micronephthys* are monophyletic (notwithstanding a few misplaced taxa), but that the position of *Inermonephtys* require further research. Also, the delineation of *Micronephthys* requires reassessment following the inclusion of more species.

Acknowledgments

We thank Eduardo López (Universidad Autónoma de Madrid) for specimens donation, Julio Parapar (Universidade da Coruña) for specimens collection from *Bentart* cruises (projects REN2001-1074/ANT and CGL2004/01856 funded by the Spanish Ministry of Science and Technology), Carlos Miguez for assistance with specimens collection in the Portuguese coast, the HERMES project (EC contract GOCE-CT-2005-511234, funded by the European Commission’s Sixth Framework Program) for the collection of deep-sea specimens from off Portugal, and California Academy of Sciences for specimens loan. We also thank the Zoological Institution and Marine Ecology, Tjärnö, both University of Gothenburg, for providing working facilities. This work is a contribution to the LUSOMARBOL (PTDC/MAR/69892/2006) funded by Fundação para a Ciência e Tecnologia. The first author is supported by a PhD grant (SFRH/BD/16563/2004) from Fundação para a Ciência e a Tecnologia.

References

Bely, A. E., & Wray, G. A. (2004). Molecular phylogeny of naidid worms (Annelida: Clitellata) based on cytochrome oxidase I. *Molecular Phylogenetics and Evolution*, 30, 50-63.

Bleidorn, C., Vogt, L., & Bartolomaeus, T. (2003). New insights into polychaete phylogeny (Annelida) inferred from 18S rDNA sequences. *Molecular Phylogenetics and Evolution*, 29, 279-288.

Böggemann, M. (2002). Revision of the Glyceridae Grube, 1850 (Annelida: Polychaeta). *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft*, 555, 1–249.

Chambers, S. J., & Garwood, P. R. (1992). *Polychaetes from Scottish waters. Part 3. Family Nereidae*. Edinburgh: National Museums of Scotland.

Cohen, B. L., Gawthorp, A. B., & Cavalier- Smith, T. (1998). Molecular phylogeny of brachiopods and phoronids based on nuclear- encoded small subunit ribosomal RNA gene sequences. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 353, 2039–2061.

Cuvier, G. L. C. F. D. (1817). *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Avec figures, dessinées d'après nature. II. Les reptiles, les poissons, les mollusques et les annélides*. Paris: Deterville.

Drummond, A. J., Ashton, B., Cheung, M., Heled, J., Kearse, M., Moir, R., *et al.* (2009). *Geneious v4.5.4, Available from http://www.geneious.com/*.

Ehlers, E. (1868). *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt*. Leipzig: Wilhelm Engelmann.

Ehlers, E. (1887). Reports on the annelids of the dredging expedition of the U.S. coast survey steamer “Blake“. *Memoirs of the Museum of Comparative Zoology of Harvard College*, 15, 1–335.

Eliason, A. (1951). Polychaeta. *Reports of the Swedish Deep-Sea Expedition 1947-1948*, 2, 130–148.

Fauchald, K. (1963). Nephtyidae (Polychaeta) from Norwegian waters. *Sarsia*, 13, 1–32.

Fauchald, K. (1968). Nephtyidae (Polychaeta) from the Bay of Nha Trang, South Viet Nam. *Naga Report*, 4, 7–33.

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

Fauchald, K. (1977). The polychaete worms. Definitions and keys to the orders, families and genera. *Science Series of the Natural History Museum of Los Angeles City*, 28, 1-188.

Fauchald, K., & Rouse, G. (1997). Polychaete systematics: past and present. *Zoologica Scripta*, 26, 71-138.

Fitzhugh, K., Sroka, S. D., Kruty, S., Henderson, M. D., & Hay, A. A. (1997). 7A. Polychaete worms. In C. W. Shabica & A. A. Hay (Eds) *Richardson's guide to the fossil fauna of Mazon Creek* (pp. 64–88). Chicago: Northeastern Illinois University.

Folmer, O., Black, M., Hoeh, W., Lutz, R., & Vrijenhoek, R. (1994). DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, 3, 294-299.

George, J. D., & Hartmann-Schröder, G. (1985). Polychaetes: British Amphinomida, Spintherida and Eunicida. *Synopses of the British Fauna (new series)*, 32, 1–221.

Grube, A. E. (1850). Die Familien der Anneliden. *Archiv für Naturgeschichte*, 16, 249–364.

Hansen, G. A. (1878). Annelider fra den norske nordhavsexpedition i 1876. *Nyt Magazin for Naturvidenskaberne*, 24, 1–17.

Hartman, O. (1938). Review of the annelid worms of the family Nephtyidae from the Northeast Pacific, with descriptions of five new species. *Proceedings of the United States National Museum*, 85, 143–158.

Hartman, O. (1940). Polychaetous annelids. Part II. Chrysopetalidae to Goniadidae. *Allan Hancock Pacific Expeditions*, 7, 173–287.

Hartman, O. (1950). Goniadidae, Glyceridae and Nephtyidae. *Allan Hancock Pacific Expeditions*, 15, 1–181.

Hartman, O. (1965). *Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas*. Los Angeles: University of Southern California Press.

Hartman, O. (1967). Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic seas. *Allan Hancock Monographs in Marine Biology*, 2, 1–387.

Hartmann-Schröder, G. (1959). Zur Ökologie der Polychaeten des Mangrove-Estero-Gebietes von El Salvador. *Beiträge zur Neotropischen Fauna*, 1, 69–183.

Hartmann-Schröder, G. (1960). Zur Polychaeten-fauna von Peru. *Beiträge zur Neotropischen Fauna*, 2, 1–44.

Hartmann-Schröder, G. (1996). Annelida, Borstenwürmer, Polychaeta. Tierwelt Deutschlands, 58, 1–648.

Heinen, A. (1911). Die Nephtyideen und Lycorideen der Nord- und Ostee, einschlieblich der verbindenden Meeresteile. *Wissenschaftliche. Meeresuntersuchungen*, 13, 1–87.

Hilbig, B. (1997). Family Nephtyidae Grube, 1850. In J. A. Blake, B. Hilbig & P. H. Scott (Eds) *Taxonomic atlas of the benthic fauna of the Santa Maria basin and the western Santa Barbara channel. 4. The Annelida. Part 1. Oligochaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae)* (pp. 317-349). Santa Barbara, California.

Hovmöller, R., Pape, T., & Källersjö, M. (2002). The Palaeoptera problem: basal pterygote phylogeny inferred from 18S and 28S rDNA sequences. *Cladistics*, 18, 313-323.

Imajima, M., & Takeda, Y. (1985). Nephtyidae (Polychaeta) from Japan. I. The genera *Inermonephtys*, *Micronephthys* and *Aglaophamus*. *Bulletin of the National Science Museum, Tokyo*, 11, 57–90.

Imajima, M., & Takeda, Y. (1987). Nephtyidae (Polychaeta) from Japan. II. The genera *Dentinephtys* and *Nephtys*. *Bulletin of the National Science Museum, Tokyo*, 13, 41–77.

Jirkov, I. A. (1989). *Bottom fauna of the USSR. Polychaeta*. Moscow: Moscow University Press.

Jirkov, I. A., & Paraketsova, N. (1996). Review of the species of the genus *Micronephthys* (Polychaeta: Nephthyidae) from the White Sea. *Zoologicheskii Zhurnal*, 75, 831–840. [In Russian].

Jung, R.-H., & Hong, J.-S. (1997). Nephtydae (Annelida: Polychaeta) from the Yellow Sea. *Bulletin of the Marine Science*, 60, 371–384.

Kato, T., & Pleijel, F. (2002). A revision of *Notophyllum* Orsted, 1843 (Phyllodocidae, Polychaeta). *Journal of Natural History*, 36, 1135-1178.

Laborda, A. J. (2004). Familia *Nephtyidae* Grube, 1850. In J. M. Viéitez, C. Alós, J. Parapar, C. Besteiro, J. Moreira, J. Nuñez, A. J. Laborda & G. San Martin (Eds) *Annelida, Polychaeta I* (pp. 390–419). Madrid: Museo Nacional de Ciencias Naturales. CSIC.

Lê, H. L. V., Lecointre, G., & Perasso, R. (1993). A 28S rRNA based phylogeny of the gnathostomes: first steps in the analysis of conflict and congruence with morphologically based cladograms. *Molecular Phylogenetics and Evolution*, 14, 1–10.

Lewis, P. O. (2001). A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, 50, 913–925.

Malm, A. W. (1874). Annulater i hafvet utmed Sveriges vestkust och omkring Göteborg. *Göteborgs Kungl. Vetenskaps och Vitterhets Samhälles Handlingar*, 14, 67–105.

Malmgren, A. J. (1865). Nordiska hafs-annulater. Öfversigt af Kongliga Vetenskapsakademiens förhandlingar, 1865, 51–110.

McHugh, D. (2005). Molecular systematics of polychaetes (Annelida). *Hydrobiologia*, 535/536, 309-318.

McIntosh, W. C. (1885). Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873-76. *Report of the Scientific Results of the Voyage of H.M.S. Challenger 1873-76*, 12, 1–554.

McIntosh, W. C. (1908). A monograph of British Annelids. *Ray Society of London*, II. Part I. Polychaeta. Nephthydidae to Syllidae, 1–232.

McIntosh, W. C. (1900). A monograph of the British Annelids. vol.1.Part 2. Polychaeta Amphinomidae to Sigalionidae. *Ray Society of London*, I.

Michaelsen, W. (1896). Die Polychaetenfauna der deutschen Meere, einschliesslich der benachbarten und verbindenden Gebiete. *Wissenschaftliche Meeresuntersuchungen*, 2, 1–216.

Nateewathana, A., & Hylleberg, J. (1986). Nephtyid polychaetes from the west coast of Phuket Island, Andaman sea, Thailand, with description of five new species. *Proceedings of the Linnean Society of New South Wales*, 108, 195–215.

Norén, M., & Jondelius, U. (1999). Phylogeny of the Prolecithophora (Platyhelminthes) inferred from 18S rDNA sequences. *Cladistics*, 15, 103-112.

Nygren, A., & Sundberg, P. (2003). Phylogeny and evolution of reproductive modes in Autolytinae (Syllidae, Annelida). *Molecular Phylogenetics and Evolution*, 29, 235-249.

Nylander, J. (2004). *MrModeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.*

Nylander, J. A. A., Wilgenbusch, J. C., Warren, D. L. & Swofford, D. L. (2008). AWTY (Are We There Yet?): a system for graphical exploration of MCMC convergence in Bayesian phylogenetics. *Bioinformatics*, 24, 581-583.

O'Connor, B. D. S. (1987). The Glyceridae (Polychaeta) of the North Atlantic and Mediterranean, with descriptions of two new species. *Journal of Natural History*, 21, 167-189.

Ohwada, T. (1985). Prostomium morphology as a criterion for the identification of nephtyid polychaetes (Annelida: Phyllodocida), with reference to the taxonomic status of Aglaophamus neotenus. *Publications of the Seto Marine Biological Laboratory*, 30, 55-60.

Palumbi, S. R., Martin, A., Romano, S., & McMillan, W. O. (1996). *The simple fool's guide to PCR* Honolulu: University of Hawaii.

Paxton, H. (1974). Contribution to the study of Australian Nephtyidae (Polychaeta). *Records of the Australian Museum*, 29, 197–208.

Pettibone, M. H. (1963). Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. *US National Museum Bulletin*, 227, 1-356.

Pleijel, F. (1993). Polychaeta. Phyllodocidae. *Marine Invertebrates of Scandinavia*, 8, 1–159.

Pleijel, F. (2001). 30. Nephtyidae Grube, 1850. In G. W. Rouse & F. Pleijel (Eds) *Polychaetes* (pp. 127–129). Oxford: Oxford University Press.

Pleijel, F., & Dales, R. P. (1991). Polychaetes: British Phyllodocoideans, Typhloscolecoideans and Tomopteroideans. Keys and notes for the identification of the species. *Synopses of the British Fauna (New series)*, 45, 1-200.

Pleijel, F., & Fauchald, K. (1993). *Scalispinigera oculata* Hartman, 1967 (Scalibregmatidae: Polychaeta), senior synonym of *Lacydonia antarctica* (Lacydoniidae) Hartman-Schröder & Rosenfeldt, 1988. *Proceedings of the Biological Society of Washington*, 106, 673–677.

Pleijel, F., Jondelius, U., Norlinder, E., Oxelman, B., Schander, C., Sundberg, P., & Thollesson, M. (2008). Phylogenies without roots? A plea for the use of vouchers in molecular phylogenetic studies. *Molecular Phylogenetics and Evolution*, 48, 369–371.

Rainer, S. F. (1984). *Nephtys pente* sp. nov. (Polychaeta: Nephtyidae) and a key to *Nephtys* from Northern Europe. *Journal of the Marine Biology Association of the United Kingdom*, 64, 899–907.

Rainer, S. F. (1989). Redescription of *Nephtys assimilis* and *N. kervalensis* (Polychaeta, Phyllodocida) and a key to *Nephtys* from northern Europe. *Journal of the Marine Biological Association of the United Kingdom*, 69, 875–890.

Rainer, S. F. (1990). The genus *Nephtys* (Polychaeta: Phyllodocida) in northern Europe: redescription of *N. hysticis* and *N. incisa*. *Journal of Natural History*, 24, 361–372.

Rainer, S. F. (1991). The genus *Nephtys* (Polychaeta: Phyllodocia) of northern Europe: a review of species, including the description of *N. pulchra* sp. n. and a key to the Nephtyidae. *Helgoländers Meeresuntersuchungen*, 45, 65–96.

Rainer, S. F., & Hutchings, P. A. (1977). Nephtyidae (Polychaeta: Errantia) from Australia. *Records of the Australian Museum*, 31, 307–347.

Rainer, S. F., & Kaly, U. L. (1988). Nephtyidae (Polychaeta: Phyllodocida) of Australia: new species from the West shelf, and key to Australian species. *Journal of Natural History*, 22, 685–703.

Roberts, G. O., & Rosenthal, J. S. (2001). Optimal scaling for various Metropolis-Hastings algorithms. *Statistical Science*, 16, 351-367.

Ronquist, F., & Huelsenbeck, J. P. (2003). MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*, 19, 1572–1574.

Rouse, G., & Fauchald, K. (1997). Cladistics and polychaetes. *Zoologica Scripta*, 26, 139-204.

Rouse, G. W., & Pleijel, F. (2001). *Polychaetes*. Oxford: Oxford University Press.

Rousset, V., Pleijel, F., Rouse, G., Erséus, C., & Siddall, M. E. (2007). A molecular phylogeny of annelids. *Cladistics*, 23, 41-63.

Struck, T., Schult, N., Kusen, T., Hickman, E., Bleidorn, C., McHugh, D., *et al.* (2007). Annelid phylogeny and the status of Sipuncula and Echiura. *BMC Evolutionary Biology*, 7, 1-57.

Swofford, D. L. (2002). *PAUP*. Phylogenetic Analysis Using Parsimony (* and other methods). Version 4*. Sunderland, Massachusetts: Sinauer Associates.

Taylor, J. L. (1984). Family Nephtyidae Grube, 1850. In J. M. Uebelacker & P. G. Johnson (Eds) *Taxonomic guide to the polychaetes of the Northern Gulf of Mexico* (pp. 35.31–35.20). Alabama: V. Barry A. Vittor and Associates, Mobile.

Théel, H. (1879). Les annélides polychètes des mers de la Nouvelle-Zemble. *Kungliga Svenska Vetenskapsakademiens Handlingar*, 16, 1–75.

Thompson, I. (1979). Errant polychaetes (Annelida) from the Pennsylvanian Essex fauna of northern Illinois. *Palaeontographica*, 163, 169–199.

Wesenberg-Lund, E. (1949). Polychaetes of the Iranian Gulf. *Danish Scientific Investigations in Iran*, 4, 247–400.

Wilson, R. S. (2000). Family Nephtyidae. In P. L. Beesley, G. J. B. Ross & C. J. Glasby (Eds) *Polychaetes & allies: the southern synthesis. Fauna of Australia. Vol. 4a Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula* (pp. 136–137). Melbourne: CSIRO Publishing.

Section 3. MORPHOLOGIC ACCOUNT

Chapter 3.1. Nephtyidae from southern Europe

Abstract

Nineteen nephtyid species belonging to four different genera are known from southern Europe. In this study we review records of South European nephtyids and provide descriptions of all species. Geographical and bathymetrical distibution as well as ecological notes are given. *Inermonephtys foretmontardoi*, new species, is described. *Micronephthys maryae* is newly synonymized with *M. stammeri*. New diagnoses are provided for southern European genera and a key to all species from the region is included.

Key words: *Aglaophamus*, *Inermonephtys*, *Micronephthys*, *Nephtys*, taxonomy, South Europe

Ravara, A, Cunha, MR & Pleijel, F Nephtyidae (Annelida, Polychaeta) from southern Europe. Submitted to *Zootaxa*.

3.1.1 Introduction

Nephtyidae is a common family of polychaetes comprising five genera and over 100 described species (Ravara *et al.* in press). The first species described were *Nephtys ciliata* (O. F. Müller, 1776) and *N. caeca* (Fabricius, 1780), both from the North Atlantic. The majority of northern European nephtyid species were described between 1842 and 1908 by Örsted (1842, 1843), Malmgren (1865), Ehlers (1868), Malm (1874), Théel (1879), Michaelsen (1896) and McIntosh (1900, 1908). Major revisions of the northern European nephtyids include Fauchald (1963), Rainer (1984, 1989, 1990, 1991) and Dnestrovskaya and Jirkov (2001), with descriptions of three more species. Apart from a revision of the Iberian fauna (Laborda 2004), up to date no other major study was made on the Nephtyidae from southern European waters, although many of the species occurring in northern Europe extend their distribution further south, often into the Mediterranean Sea. Nineteen nephtyid species are known from South European waters (from the English Channel to the Mediterranean Sea) of which ten belong to the genus *Nephtys*, five to *Aglaophamus*, three to *Micronephthys*, and one to *Inermonephtys*. In this study we provide diagnoses of the five genera and redescriptions of the nineteen southern European species based on examined specimens, with comprehensive lists of synonyms and remarks on geographical and bathymetric distributions. A new species of *Inermonephtys*, *I. foretmontardoi*, previously misidentified as *I. inermis*, is described from northwestern Spain. *Micronephtys maryae* is newly synonymised with *M. stammeri*. A key for southern European species is also included.

3.1.2 Material and methods

Part of the nephtyid material examined in this study was collected by the first author in intertidal and shallow waters along the Portuguese coast, and specimens from Gulf of Cadiz and Portuguese submarine canyons were collected by the second author. A large number of specimens were collected by the third author in several places around the world. Most specimens were fixed and preserved in 90-95% ethanol and deposited in the invertebrate collection of the Department of Biology of the University of Aveiro (DBUA) and the Museu Nacional de História Natural (Museu Bocage) in

Lisbon (MNHN MB). Additional examined material came from collections of the University of Aveiro (DBUA), the Museu Municipal do Funchal, Madeira (MMF) the Natural History Museum of London (NHM), the National Museum of Wales (NMWZ), the Museo Nacional de Ciencias Naturales, Madrid (MNCN), the California Academy of Sciences, Invertebrate Zoology (CASIZ), Zoologisches Museum, Hamburg (ZMH), Naturhistoriska Museum, Gothenburg (GNHM), Naturhistoriska Riksmuseet, Stockholm (NRM), Zoologisk Museum, Copenhagen (ZMC), the Muséum National d’Histoire Naturelle, Paris (MNHN), the United States National Museum of Natural History (USNM), and the Museum of Comparative Zoology, Harvard University (MCZ).

All drawings were prepared from preserved animals with a camera lucida. Measurements of body width were recorded from the widest part of the body, and include parapodia, but exclude chaetae. Body length excludes anal cirrus. Incomplete animals were excluded from the graphics that comprise body length and number of chaetigers.

3.1.3 Systematics

Nephtyids have an elongated body, widest anteriorly in the phraynx region and posteriorly tapering, typically rectangular in cross-section. Pigmentation patterns are usually absent, although darker brown or green pigment may be present on the prostomium and anterior segments. An iridescent cuticle is common in larger specimens.

One pair of small eyes is usually present subdermally on posterior brain but is only visible in small nephtyid species or in juveniles of larger ones at the level of the anteriormost segments. In some species one or two pairs of eyes may be present on the surface of prostomium.

Pharynx forms an eversible muscular proboscis with a terminal dorsoventral opening surrounded by 10 pairs of bifid papillae separated dorsally and ventrally by a gap or a simple conical papilla. Bifid terminal papillae decrease in size towards middorsal and midventral position. Subterminal region with 14 to 22 rows of simple papillae decreasing in size towards base of proboscis (Figure 7A) (papillae are absent in *Inermonephtys*). For some species a single middorsal and a single midventral papilla are also present between the terminal and subterminal papillae (Figure 24A).

Proximally the proboscis is either smooth or covered with small warts (Figure 16A). One pair of small subterminal jaws is present inside the pharynx.

The prostomium is generally subpentagonal, anteriorly tapered, and with a V-shaped posterior margin, extending over the first chaetiger (Figure 7A). The prostomial proportions vary depending on whether the proboscis is everted or not. A pair of conical antennae is present in the anterior corners of the prostomium and a pair of palps is inserted ventrolaterally near the antennae or further posteriorly on the prostomium (Figure 7A). A pair of nuchal organs is present near the posterior corners of prostomium (Figure 7A).

The parapodia are biramous, typically with well-separated rami. Ciliation is present in patches or continuously along the interramal space. The noto- and neuropodia are composed of an acicular lobe sustained by one acicula (species of the genus *Inermonephtys* may have more than one acicula per ramus in the anterior and middle parapodia), pre- and postchaetal lamellae, and a ventral cirrus. The parapodia of the first chaetiger are usually anteriorly directed, and their lamellae are less developed than the following ones (Figure 18A). The neuropodial lamellae of the first chaetiger usually form a cylinder around the acicular lobes; the ventral cirri are well-developed and usually longer than the following ones. The following parapodia gradually increase in size attaining their maximal size at midbody. Shape and proportions of acicular lobes and lamellae may exhibit some variation along the body. Except for some *Micronephthys* species, branchiae are present at least in some parapodia along the body. When present, branchiae are typically attached to the ventral margin of the notopodia (below the dorsal cirri), have ciliated margins and may be involute, straight or recurved. Chaetae are simple and form dense, fan-shaped fascicles in pre- and postacicular positions. They are usually barred (or chambered) in preacicular position (Figure 7H), and spinulated in postacicular position (Figure 7I). In some species of *Aglaophamus*, *Inermonephtys* and *Micronephthys*, a few lyriform chaetae may be present in postacicular position of both rami (Figure 10H). Neuropodial chaetae of the first chaetiger are usually capillary or indistinctly spinulated and form a single bunch without barred chaetae. Aciculae are thick and usually have curved tips in median and posterior parapodia (in all parapodia in *Aglaophamus*) (Figure 7J).

The anus is terminal, and a single thin, cirriform anal cirrus is typically present.

Key for the Southern European species of Nephtyidae

Parapodial features (acicular lobes and pre- and postchaetal lamellae shape and size), branchiae shape and location, and pharynx structure are the main distinctive characters used in this key. Pharynx dissection is not always necessary unless to confirm some identifications. Parapodial features are based on parapodia from median segments.

1 Prostomium without antennae; nuchal organs digitiform (Fig. 10A); pharynx without papillae; jaws spindle-shaped; branchiae from chaetiger 4…………………………………***Inermonephtys foretmontardoi*** sp. nov. (Fig. 10)

- Prostomium with antennae; nuchal organs rounded; pharynx papillae present; jaws conical, hook-like ……………………………………………………………….2

2 Branchiae absent or present only on a few chaetigers, poorly developed, nearly straight; pre- and postchaetal lamellae rudimentary; body small…***Micronephthys*** ....……………………………………………………………….………..………3

- Branchiae well developed, involute or recurved; at least postchaetal lamellae well developed……………………………………………………………………...5

3 Branchiae present from chaetiger 6-9 to 10-14 …………….……………***M. minuta***

- Branchiae absent……………………………………………………………………..4

4 Modified chaetae present on notopodia of first chaetiger (Fig. 13E); two pairs of coalescent eyes present at third chaetiger level (Fig. 13C) …***M. stammeri*** (Fig. 13)

- Modified chaetae absent; one pair of small subdermal eyes may be visible at level of chaetiger 2-3 …………………………………………***M. sphaerocirrata*** (Fig. 12)

5 Acicular lobes acutely pointed (Fig. 5, 7-9); neuropodial superior lobes may be present (Fig. 8F); pharynx with rows of more than 10 subterminal papillae, proximal papillae sometimes arranged in small groups, middorsal papilla absent, proximal region always smooth; branchiae involute or recurved … ***Aglaophamus***……………………………………………………………6

- Acicular lobes conical (Fig. 25E, G), rounded or bilobed (Figs. 16B-D); neuropodial superior lobes absent; pharynx with rows of less then 10 subterminal papillae (usually up to 5-7), long middorsal papillae present in some species, proximal region smooth or covered with warts; branchiae recurved…***Nephtys***……………..9

6 Prechaetal lamellae more or less distinctly bilobed; postchaetal lamellae longer than acicular lobes; neuropodial superior lobe distinctly present; branchiae involute, from chaetiger 2 …………………….………………………***A. rubellus*** (Fig. 9)

- Prechaetal lamellae simple; postchaetal lamellae shorter or not much longer than acicular lobes; neuropodial superior lobe if present, very small and difficult to observe; branchiae present posteriorly to chaetiger 5…………………………...7

7 Notopodial postchaetal lamellae poorly developed, rounded; pharynx with 20-22 rows of 6-11 subterminal papillae, extending to base of pharynx…***A. elamellatus*** (Fig. 5)

- Notopodial postchaetal lamellae well developed, bilobed at least in middle parapodia……………………………………………………………………...8

8 Branchiae from chaetigers 11-13, involute; pharynx with 22 rows of 2-17 short subterminal papillae, extending over 1/2 length of pharynx …***A. malmgreni*** (Fig. 7)

- Branchiae from chaetigers 5-7, recurved; pharynx with 14 well defined rows of 10-15 subterminal papillae, extending to base of pharynx…………***A. pulcher*** (Fig. 8)

9 Notopodial acicular lobes rounded with prechaetal lamellae rudimentary; neuropodial acicular lobes conical with prechaetal lamellae well developed; branchiae from chaetigers 4 to near end of body; dorsal cirri in posterior chaetigers as long as branchiae (Fig. 19G); pharynx with 22 rows of 4-9 subterminal papillae extending to base of pharynx (Fig. 19A) ………………………***N. cirrosa*** (Fig. 19)

- Noto- and neuropodial acicular lobes and prechaetal lamellae of similar shape and size; dorsal cirri always smaller than branchiae; pharynx subterminal papillae extending over 1/3 or 1/2 length of pharynx…………………………………...10

10 Acicular lobes conical; prechaetal lamellae well developed, rounded or bilobed (Fig. 14D-E); postacicular chaetae finely spinulated; branchiae from chaetigers 4-7……………………………………………………………………….…11

- Acicular lobes rounded to bilobed; prechaetal lamellae rudimentary or poorly developed (Fig. 16B-D); postacicular chaetae coarsely spinulated; branchiae from chaetigers 3-14…………………………………………………………………15

11 Acicular lobes with a papilliform outgrowth (Figs. 14C, 21E-F); postchaetal lamellae of neuropodia extending well beyond acicular lobes (Figs. 14D-E, 21G-H); pharynx middorsal papilla long or short ………………………………….…12

- Acicular lobes without papilliform outgrowth; postchaetal lamellae well or poorly developed; pharynx middorsal papilla at least twice as long as subterminal papillae (Fig. 22A) ..……………………………………………………………………….13

12 Acicular lobes with low papilliform outgrouth (Fig. 14C); branchiae from chaetiger 4; neuropodial postchaetal lamellae broadly rounded with internal vascular structure (Fig. 14D); interramal region of posterior chaetigers with prominent raised ciliary pads (Fig. 14E) ……………………***N. assimilis*** (Fig. 14)

- Acicular lobes with prominent papilliform outgrouth (Fig. 21E-F); branchiae from chaetiger 4 or 5 (rarely 6); neuropodial postchaetal lamellae slender without vascular structure; interramal region of posterior chaetigers with ciliated patches ……………………………………………………………***N. hombergii*** (Fig. 21)

13 Postchaetal lamellae more than twice as long as acicular lobes, which have a rugose area near aciculae (Fig. 25D, F, H); branchia from chaetiger 4 to near posterior end ..……………………………………………***N. kersivalensis*** (Fig. 25)

- Postchaetal lamellae shorter than or no longer than twice the length of acicular lobes, which lack a rugose area; branchia from chaetigers 5-10, absent in posterior chaetigers…………………………………………………………………………..14

14 Postchaetal lamellae up to twice the length of acicular lobes; branchia from chaetigers 5-7, usually 6 ………….…………………………***N. hystricis*** (Fig. 22)

- Postchaetal lamellae shorter than or as long as acicular lobes; Branchiae from chaetigers 9-10…………………………………………………***N. incisa*** (Fig. 24)

15 Postchaetal lamellae more than twice as long as acicular lobes; branchiae start at chaetigers 3-5 (usually chaetiger 3 or 4) to near posterior end ..…………………16

- Postchaetal lamellae equal in size or slightly shorter than acicular lobes; branchiae from chaetigers 7-14, reduced in posterior chaetigers……………………………17

16 Postchaetal lamellae well-developed in notopodia and neuropodia; branchiae from chaetigers 4 (rarely 5); pharynx proximal region with numerous warts…***N. caeca*** (Fig. 16)

- Notopodial postchaetal lamellae of middle and posteror chaetigers much shorter than in neuropodia; branchiae from chaetiger 3; pharynx proximal region smooth…***N. longosetosa*** (Fig. 26)

17 Branchiae cirriform, present from chaetigers 7-11; acicular lobes of anterior and middle chaetigers distinctly bilobed; pharynx proximal region with numerous warts (Fig. 18A) …………………………………………………***N. ciliata*** (Fig. 18)

- Branchiae foliaceous (Fig. 27C), present from chaetigers 9-14; acicular lobes rounded in anterior and middle parapodia, conical in posterior parapodia; pharynx proximal region smooth ……………………………………***N. paradoxa*** (Fig. 27)

Aglaophamus **Kinberg, 1866**

Type species. *Aglaophamus lyratus* Kinberg, 1866, by monotypy.

Diagnosis. The genus *Aglaophamus* is distinguished from other nephtyid genera by the acutely pointed acicular lobes. Parapodial lamellae usually well developed; neuropodial superior lobes often present in anterior parapodia. Branchiae involute or recurved (Ravara *et al.* in press). Lyriform chaetae may be present or absent. All aciculae have curved tips. Antennae present. Pharynx usually with rows of more than 10 close together subterminal papillae of which the proximal ones are sometimes arranged in small groups; middorsal papilla absent; proximal region smooth. Jaws conical, hook-like. Nuchal organs rounded.

? ***Aglaophamus agilis*** **(Langerhans, 1880)**

Nephthys agilis Langerhans, 1880: 304, pl. XVI, fig. 39; Fauvel 1923: 372, fig. 145C-G.
Aglaophamus agilis Friedrich 1964: 135; Guille and Laubier 1966: 266; Campoy 1982: 507; Laborda 2004: 412, fig. 151A.

Type locality. Funchal, Madeira Island, Portugal.

Material examined. Atlantic Ocean. Madeira Island, Câmara de Lobos, 30 m, haul net, Jun 2000, 1 complete spm in poor condition (MMF.36457).

Remarks. The only specimen examined is in very poor condition and the observation of several important features was not possible. No other material was available for examination.

This species was originally described from Madeira Island by Langerhans (1880) who provided a very short and incomplete description. Friedrich (1964) recollected the species in the same locality and gave a more complete description together with a comparison with the other known species of *Aglaophamus*. He stated the isolated occurrence of *A. agilis* in Madeira Island as an endemic condition. However, other authors, such as Fauvel (1923), Guille and Laubier (1966) and Desbruyères *et al.* (1972), report the same species from the Mediterranean Sea, although without any further comments. *Aglaopamus agilis* is very similar to *A. rubellus* and conforms its geographical distribution. According to Friedrich (1964), the two species differ in the development of the prechaetal lamellae which are rudimentary in *A. agilis* and well developed and bilobed in *A. rubellus* (Figure 9D-E), and the shape of the notopodial postchaetal lamellae which are entire in *A. agilis* and bilobed in *A. rubellus*. However, the pair of eyes in the anterior chaetigers of *A. agilis* mentioned by Friedrich (1964) is a feature typical for juvenile stages, which may also explain the rudimentary condition of the prechaetal lamellae. Since the prechaetal lamellae are smaller than the acicular lobes, they may be difficult to examine if not completely developed as it often happens in smaller juvenile specimens. As for the notopodial postchaetal lamellae, Friedrich (1964) also refers to the occasional presence of a small constriction at their lower edge. We think this constriction might be equivalent to the lower very small lobe of the bilobed lamellae in *A. rubellus*. Since all the differences between the two species may be explained by the juvenile condition of the *A. agilis* specimens examined by Friedrich we consider that the taxonomic status of this species is doubtful. In our opinion *A. agilis* may be considered a junior synonym of *A. rubellus*.

Distribution. Atlantic Ocean (Madeira; Mauritania); Mediterranean Sea (NE Spain; S France) (Campoy 1982; Laborda 2004).

Habitat. Fine sand and mud, down to 50 m depth (Laborda 2004).

***Aglaophamus elamellatus* (Eliason, 1951)**

Figures 5, 6

Nephthys elamellata Eliason, 1951: 133, fig. 2; Kirkegaard 1956: 68, fig.7.
Aglaophamus elamellata Kirkegaard 1980: 85; Kirkegaard 1995: 36.

Type locality. Central Atlantic (near Canary and Azores Islands).

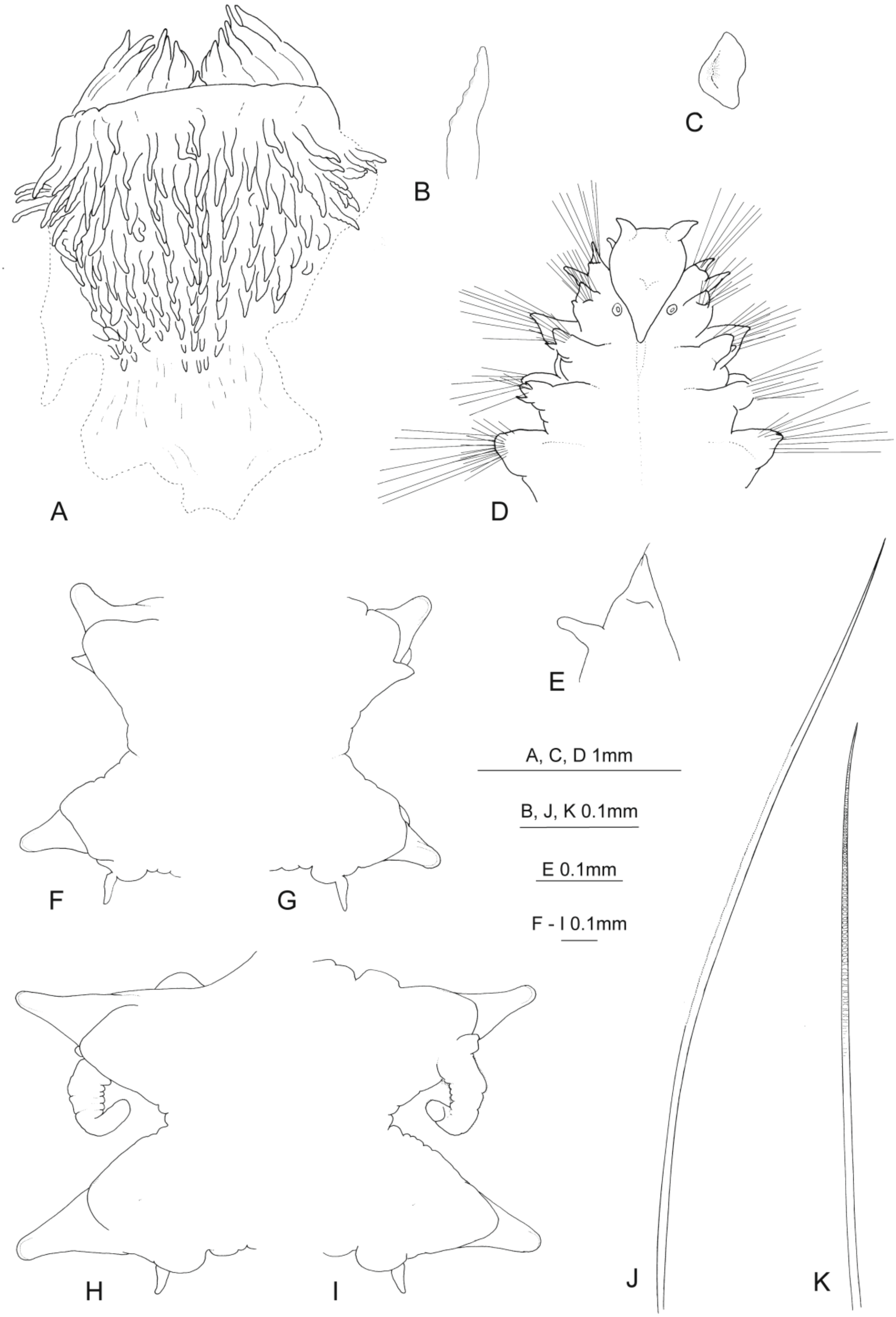


Figure 5. *Aglaophamus elamellatus*. A. Dissected pharynx, dorsal view. B. Detail of pharynx subterminal papillae. C. Jaw. D. Prostomium and anterior chaetigers, dorsal view. E. Left neuropodium of chaetiger 1. F. Right parapodium of chaetiger 10, anterior view. G. Same, posterior view. H. Right parapodium of chaetiger 20, anterior view. I. Same, posterior view. J. Preacicular chaeta from chaetiger 15. K. Postacicular chaetae from chaetiger 15.

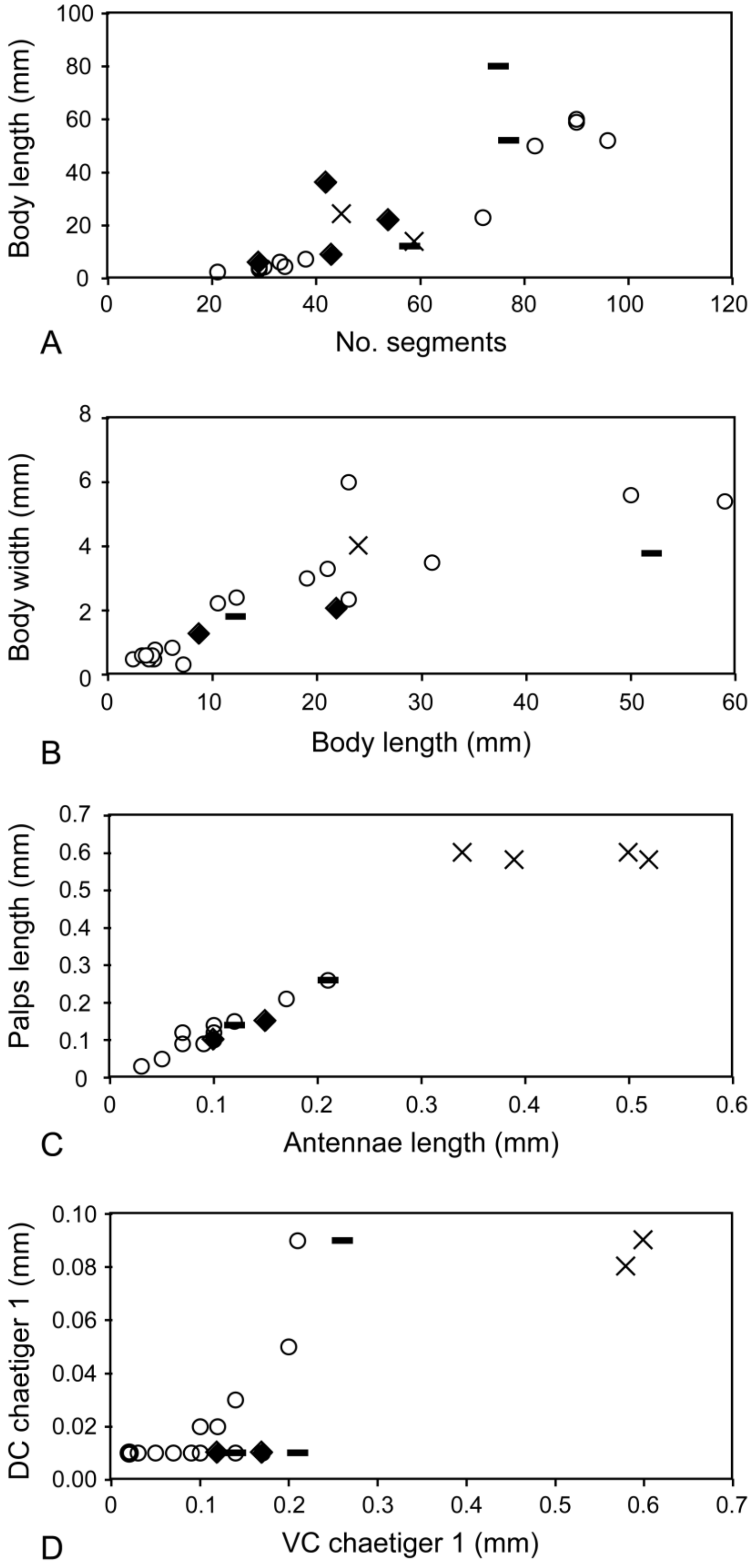


Figure 6. Relationships between: A. Number of segments and body length. B. Body length and body width. C. Antennae and palps length. D. Length of ventral cirri (VC) and dorsal cirri (DC) of chaetiger 1. ◆ *Aglaophamus elamellatus*. - *A. malmgreni*. ○ *A. pulcher*. × *A. rubellus*. Minute dorsal cirri were scored as 0.01. *A. elamellatus*, *A. malmgreni* and *A. pulcher* plots include measurements from the original description (Théel, 1879; Eliason, 1951; Rainer, 1991).

Material examined. Atlantic Ocean. Central Atlantic: 40º33'N, 35º24'W – 40º34'N, 35º52'W, 4540-4600 m, Sep 1948, 1 incomplete spm, syntype (GNHM Polych. 10990). Portugal, Nazaré Canyon: cruise D297, RV *Discovery,* 39º30.62'N, 9º56.19'W, 3461 m, box-corer, 8 Aug 2005, 4 complete spms (DBUA 00837-01); 39º30.02'N, 9º56.17'W, 3465 m, box-corer, 10 Aug 2005, 6 complete and 1 incomplete spm (DBUA 00837-02); 39º30.02'N, 9º56.22'W, 3464 m, box-corer, 11 Aug 2005, 3 complete spms (DBUA 00837-03); 39º35.00'N, 10º19.04'W, 4336 m, box-corer, 11 Aug 2005, 1 complete spm (DBUA 00837-04); cruise CD179, RV *Charles Darwin*, 39º29.99'N, 9º55.97'W, 3517 m, megacorer, 9 May 2006, 1 complete spm (DBUA 00838-01); 39º29.99'N, 9º56.01'W, 3517 m, megacorer, 9 May 2006, 3 complete spm (DBUA 00838-02); 39º30.00'N, 9º55.98'W, 3522 m, megacorer, 11 May 2006, 1 complete spm (DBUA 00838-03); Cascais Canyon: cruise CD179, RV *Charles Darwin*, 38º17.97'N, 9º46.89'W, 3214 m, megacorer, 27 Apr 2006, 1 complete spm (DBUA 00839-01); 38º18.01'N, 9º47.02'W, 3218 m, megacorer, 27 Apr 2006, 2 complete spms (DBUA 00839-02); 38º22.49'N, 9º53.52'W, 4244 m, megacorer, 3 May 2006, 1 complete spm (DBUA 00839-03); Setúbal Canyon: cruise CD179, RV *Charles Darwin*, 38º09.27'N, 9º36.93'W, 3275 m, megacorer, 21 Apr 2006, 3 complete spms (DBUA 00840-01); 38º09.26'N, 9º36.94'W, 3275 m, megacorer, 21 Apr 2006, 3 complete spms (DBUA 00840-02); 38º09.22'N, 9º37.02'W, 3224 m, megacorer, 23 Apr 2006, 2 complete and 1 incomplete spm (DBUA 00840-03); cruise 64PE252, RV *Pelagia*, 38º17.10'N, 9º06.00'W, 970 m, box-corer, 17 Sep 2006, 1 complete spm (DBUA 00841-01); 38º17.10'N, 9º06.00'W, 970 m, box-corer, 17 Sep 2006, 1 incomplete spm (MB36000104).

Description. Examined specimens up to 22 mm long for up to 54 chaetigers. See Figure 6 for length and width measurements. Body small, slightly wider anteriorly, tapering posteriorly. Poor dorsal delineation between segments. Colour in ethanol white, chaetae and aciculae amber. Eyes not visible. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by simple conical dorsal and ventral papilla; middorsal and midventral papillae absent; subdistal region with 20-22 rows of 6-11 lanceolate subterminal papillae with crenulated ventral borders, rows extending to base of pharynx (Figure 5A-B); proximal region without warts. Jaws conical (Figure 5C). Prostomium subpentagonal, anterior margin straight or slightly convex, posterior margin V-shaped, extending over first chaetiger (Figure 5D); antennae and palps conical, subequal in length (Figure 6C), palps inserted ventrolaterally on anterior part of prostomium, directed ventrally (often not visible in dorsal view). Nuchal organs rounded. Parapodia biramous; interramal space “U-shaped” anteriorly and “V-shaped” medially and posteriorly; ciliation not seen. Parapodia of chaetiger 1 slightly longer than subsequent ones, anteriorly directed, parallel to prostomium; noto- and neuropodial acicular lobes acutely pointed; pre- and postchaetal lamellae rudimentary; acicula of neuropodia protruding from acicular lobes (Figure 5E); dorsal cirri rounded, minute (Figure 6D); ventral cirri digitiform, with broad bases and tapered distally. Parapodia of chaetigers 2 and 3 with notopodia smaller than neuropodia. Acicular lobes of following parapodia acutely pointed; pre- and postchaetal lamellae of both rami smaller than acicular lobes (rudimentary on smaller specimens), rounded, becoming rudimentary in posteriormost parapodiae; dorsal cirri short, conical to rounded, with broad base; ventral cirri digitiform (Figure 5F-I). Branchiae involute, lightly ciliated, present from chaetigers 11-13, absent on posterior chaetigers (totally absent on specimens with less than 26 chaetigers); occupy 2/3 of interramal space when fully developed. Chaetae thin and very long (preacicular chaetae almost as long as postacicular ones), of three kinds: barred chaetae in preacicular position (Figure 5J), finely spinulated chaetae in postacicular position (Figure 5K), and capillary chaetae in neuropodia of chaetiger 1. One acicula with curved tip per ramus.

Remarks. The species name is here corrected from *A. elamellata* to *A. elamellatus* according to the gender of the generic name. This species was originally described by Eliason (1951) from the central Atlantic (Azores and Canary Islands), and have only been recollected a few times since from the Atlantic, Indian and Pacific oceans (Kirkegaard, 1956, 1980, 1995). This study extends its distribution to the Nazaré submarine canyon off the western coast of Portugal (NE Atlantic). Although the geographical distribution appears to be excessively wide, according to Kirkegaard (1995) there are no apparent morphological differences between the Atlantic specimens and those from the Indian Ocean and around New Zealand. Nevertheless, specimens from those localities were not examined within the present study and the descriptions given by Kirkegaard (1956, 1980, 1995) are not very detailed. Therefore the Indian and Pacific Oceans references should be considered with caution. In the specimens examined, the occurrence of branchiae varies with the number of chaetigers (Table 6). Thus, although they always start between chaetigers 11 and 14 (most frequently on chaetiger 13), they extend further posteriorly in longer specimens, and are absent in specimens with less than 26 chaetigers. The pharynx is described herein for the first time.

Distribution. Atlantic Ocean (W Portugal, Azores, Canary Islands, off W Africa); Indian Ocean (off E Africa, Sri Lanka); Pacific Ocean (Tasman Sea, Kermadec Trench) (Kirkegaard 1956, 1980, 1995).

Habitat. Mud, 990-7000 m depth (Kirkegaard 1956, 1980, 1995).

Table 6. *Aglaophamus elamellatus*. Branchiae occurrence and development according to the number of chaetigers.

Local	Depth	No. chaetigers	Branchiae start and end	Posterior chaetigerous without branchiae	Observations on branchiae morphology
Central Atlantic (syntype)	4540-4600m	> 42	13/14 - > 42	--	Well developed, involute
Setúbal canyon	3275m	54	11-28	26	well developed, involute
Cascais canyon	3218m	50	13-25	25	well developed, involute
Nazaré canyon	3465m	43	12-21	22	well developed, involute
Setúbal canyon	3224m	33	13-18	15	
Nazaré canyon	3465m	32	13-17	15	small, straight to slightly involute
Nazaré canyon	3461m	31	13-16	15	reduced
Nazaré canyon	3465m	31	13-17	14	small, straight to slightly involute
Nazaré canyon	3461m	30	14-17	13	small, straight to slightly involute
Nazaré canyon	3461m	29	12-16	12	small, straight to slightly involute
Nazaré canyon	4336m	29	13-20	9	well developed, involute
Nazaré canyon	3465m	28	-	--	
Nazaré canyon	3464m	28	-	--	
Setúbal canyon	970m	28	-	--	
Cascais canyon	4244m	27	14-19	8	small, slightly involute
Nazaré canyon	3465m	26	-	--	
Nazaré canyon	3465m	26	-	--	
Setúbal canyon	3275m	26	-	--	
Nazaré canyon	3465m	24	-	--	
Setúbal canyon	3275m	21	-	--	
Nazaré canyon	3517m	21	-	--	
Cascais canyon	3275m	19	-	--	
Nazaré canyon	3465m	18	-	--	
Setúbal canyon	3275m	18	-	--	
Setúbal canyon	3275m	18	-	--	
Setúbal canyon	3224m	18	-	--	
Setúbal canyon	3275m	17	-	--	
Nazaré canyon	3461m	17	-	--	
Cascais canyon	3214m	16	-	--	
Nazaré canyon	3522m	11	-	--	
Nazaré canyon	3517m	10	-	--	
Nazaré canyon	3517m	10	-	--	
Nazaré canyon	3517m	10	-	--	

Aglaophamus malmgreni **(Théel, 1879)**

Figures 6, 7

Nephthys malmgreni Théel, 1879: 26, pl. I, fig. 17, pl. II, fig. 17; Marenzeller 1904: 304-308; Augener 1912: 206; not Treadwell 1914: 192; Fauvel 1923: 371, fig. 145K; Ditlevsen 1937: 19.
Nephthys longisetosa [misspelling of *longosetosa*] Malmgren 1865: 106, pl. XII, fig. 20; Malmgren 1867: 19 (not *Nephtys longosetosa* Örsted, 1843).
Nephthys atlantica Hansen, 1878: 4, pl. III, figs. 1 and 2.
Nephthys grubei McIntosh 1908: 33, pl. LVII, figs. 13 and 14; pl. LXVII, fig. 1; pl. LXXVI, figs. 9 and 9A.
Nephtys malmgreni Uschakov 1955: 217, fig. 69E.
Nephtys (Aglaophamus) malmgreni Berkeley and Berkeley 1956: 235; Day 1967: 343, fig. 15.1N-O.
Aglaophamus malmgreni Pettibone 1956: 557; Fauchald 1963: 17, figs. 1F, 2F and 3G; Pettibone 1963: 191, fig. 48B; Hartmann-Schröder 1971: 224; Jirkov 1989: 73, fig. 15.2 and 15.3; Dnestrovskaya and Jirkov 2001: 187,1 text-fig.
Aglaophamus malmgreni ?Imajima 1970: 116, 120; Campoy 1982: 507; Imajima and Takeda 1985: 68, fig. 6A-N; Laborda 2004: 412, fig. 151B.

Type locality. Off Novaya Zemlya.

Material examined. Arctic Ocean. Svalbard, Billefjord: coll. RV *Jan Mayen*, 78º37.764’N, 16º25.359’E, 38 m, grab, Sep 2003, 1 incomplete spm (DBUA 01043); Wijdefjord: coll. RV *Jan Mayen*, 79º07.623’N, 16º02.743’E, 217 m, grab, Sep 2003, 1 complete spm (DBUA 01043-02) and 1 incomplete spm (MB36000138); Spitsbergen: 1 complete spm (NHM 1865.9.23.11 as *N. longosetosa*).

Atlantic Ocean. Faroe Channel: Knight-Errant Faroe Channel expedition, 60º3’N, 5º51’W, 540 fms, Aug 1880, 1 complete spm (NHM 1921.5.1.832, holotype of *N. grubei*); off Norway: TTR16 cruise, coll. RV *Prof. Logachev*, 64º40.014’N, 5º17.411’E, 735 m, grab, Jun 2006, 1 incomplete spm (MB36000133); Portugal, off Setúbal: Challenger expedition, 1 incomplete spm in poor condition (NHM 1885.12.1.129).

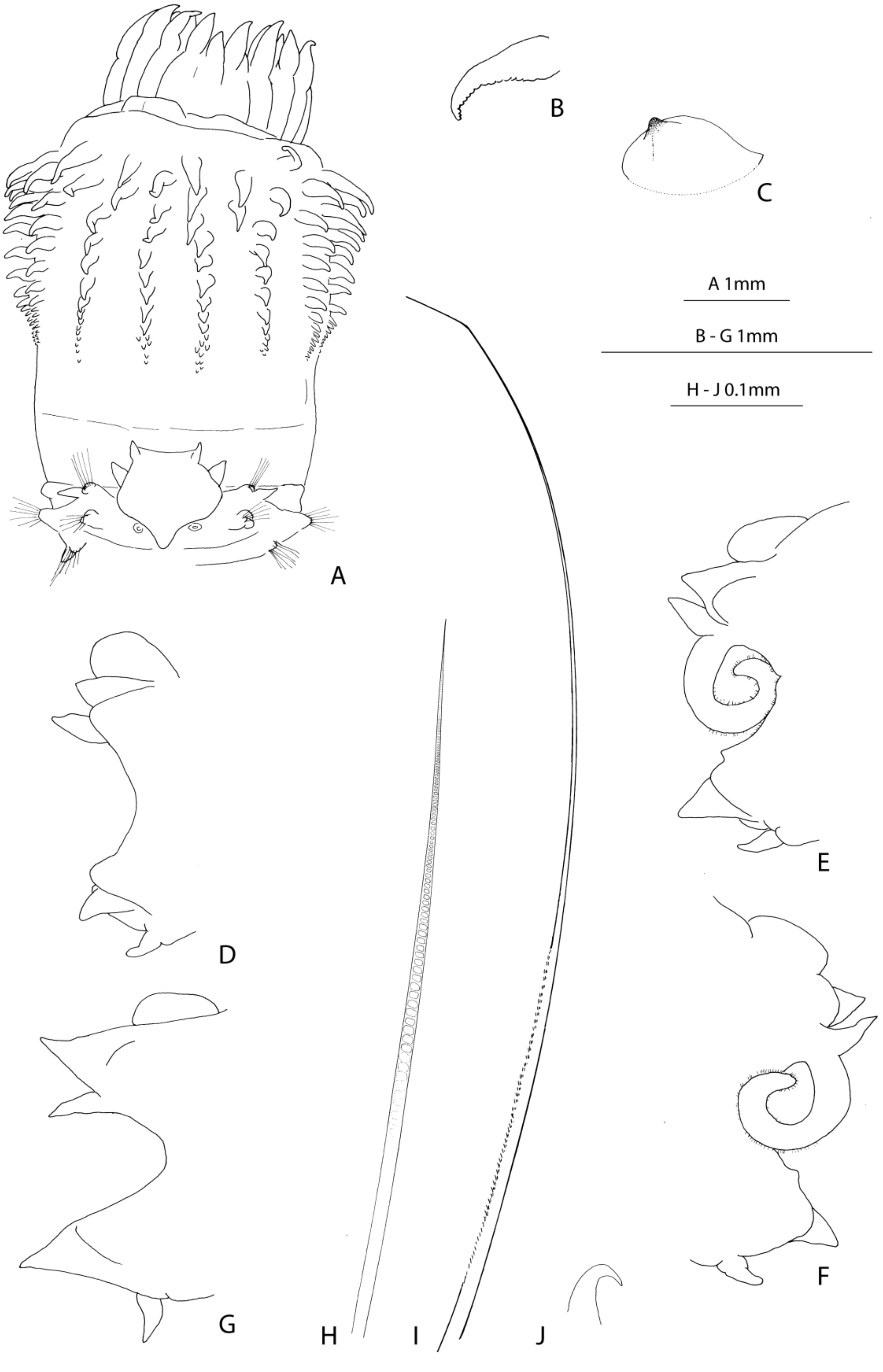


Figure 7. *Aglaophamus malmgreni*. A. Pharynx and prostomium, dorsal view. B. Pharynx subterminal papillae detail. C. Jaw. D. Right parapodium of chaetiger 10, anterior view. E. Right parapodium of chaetiger 20, anterior view. F. Same, posterior view. G. Right parapodium of chaetiger 40, anterior view. H. Preacicular chaeta from chaetiger 20. I. Postacicular chaetae from chaetiger 20. J. Acicula from chaetiger 20.

Description. Examined specimens up to 52 mm long for up to 77 chaetigers. See Figure 6 for length and width measurements. Body slightly wider anteriorly, gradually tapering from middle region to pygidium. Poor dorsal delineation between anterior segments. Colour in ethanol pink with darker areas in first segments and near bases of parapodia; prostomium with two darker areas near the bases of antennae; chaetae and aciculae amber. Eyes not visible. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by simple conical dorsal and ventral papilla; middorsal and midventral papilla absent; subdistal region with 22 rows of 2-18 subterminal papillae, extending over 1/2 length of pharynx, proximal papillae close together and sometimes arranged in pairs, larger papillae ventrally crenulated (Figure 7A-B); proximal region smooth. Jaws conical (Figure 7C). Prostomium subpentagonal, anterior margin slightly concave, tapered, forming membrane between antennae; posterior margin V-shaped, extending over first chaetiger (Figure 7A); antennae and palps conical, palps slightly longer than antennae (Figure 6C), inserted ventrolaterally on anterior part of prostomium. Nuchal organs rounded. Parapodia biramous; interramal space “U-shaped” anterioly and medially, “V-shaped” posteriorly, with small ciliated patches. Parapodia of chaetiger 1 equal in size to subsequent ones, anteriorly directed, parallel to prostomium; notopodial acicular lobes conical, prechaetal lamellae rudimentary, postchaetal lamellae poorly developed, rounded; neuropodium with pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal cirri very small, rounded (Figure 6D); ventral cirri conical to digitiform with broad bases and tapering distally. Acicular lobes of following parapodia acutely pointed; pre- and postchaetal lamellae of both rami well developed but not extending beyond acicular lobes, becoming less developed more posteriorly and rudimentary in posteriormost parapodia; notopodial prechaetal lamellae rounded, postchaetal lamellae of median parapodia bilobed with dorsal part directed dorsally, rounded on other parapodia but always directed dorsally; neuropodial pre- and postchaetal lamellae conical to rounded; dorsal and ventral cirri conical (Figure 7D-G). Branchiae involute, cirriform, lightly ciliated, on chaetigers 11-13 to 36-41, always well developed; occupy all interramal space when fully developed. Chaetae of three kinds: barred chaetae in preacicular position (Figure 7H), spinulated chaetae in postacicular position (Figure 7I), and capillary chaetae in neuropodia of chaetiger 1. One acicula with curved tip per ramus (Figure 7J).

Remarks. *Aglaophamus malmgreni* is herein included in the South European fauna, based on the scarce records from the Mediterranean Sea and the western coasts of Spain and Portugal (Fauvel 1923; Campoy 1982; Laborda 2004). Unfortunately there were no specimens available to confirm these records. The only material examined was a single specimen from Portugal, in very poor condition, from which the identity could not be confirmed. Fauvel (1923) and Campoy (1982) provided descriptions for southern Europe specimens that agree with *A. malmgreni*. On the other hand, Laborda (2004) described notopodial postchaetal lamellae as rounded (only slightly bilobed in anteriormost parapodia) instead of distinctly bilobed in median parapodia. The same feature was described by Imajima and Takeda (1985) for Japanese specimens, although, considering the very different geographical regions, the Japanese specimens are not likely to be conspecific with the southern European ones. The material examined and most literature references suggest a circumpolar distribution for *A. malmgreni*. We thus believe that the South European records require confirmation and must be considered with caution until more specimens from this region become available for further examination.

In the specimens examined the pharynx has 14 rows of 11-18 papillae intercalated with 8 rows of only 2 or 3 papillae, adding to a total of 22 rows of 2-18 papillae. Those shorter rows seem to have been overlooked in previous studies. Pettibone (1956) noticed the presence of “some additional scattered papillae more distally” in the pharynx, but did not consider them as additional rows of papillae. Thus the original description of *A. malmgreni* is herein emended to include 22 rows of 2-18 pharynx papillae instead of 14 rows of 10-18 papillae as stated in previous descriptions.

Distribution. Arctic Ocean (Svalbard, Barents Sea, Kara Sea, Laptev Sea); Atlantic Ocean (Norway, Sweden, North Sea; Greenland, Canada, NE coast of North America); Pacific Ocean (Bering Sea, Sea of Okhotsk, N Japan Sea) (Hartman 1938; Pettibone 1956; Imajima & Takeda 1985; Dnestrovskaya & Jirkov 2001; Laborda 2004). There are further reports of this species from NW Spain, Portugal and the Mediterranean Sea (Fauvel 1923; Pettibone 1956; Campoy 1982; Laborda 2004), but these records require confirmation.

Habitat. Muddy bottoms, 22-3820 m depth (Dnestrovskaya & Jirkov 2001)

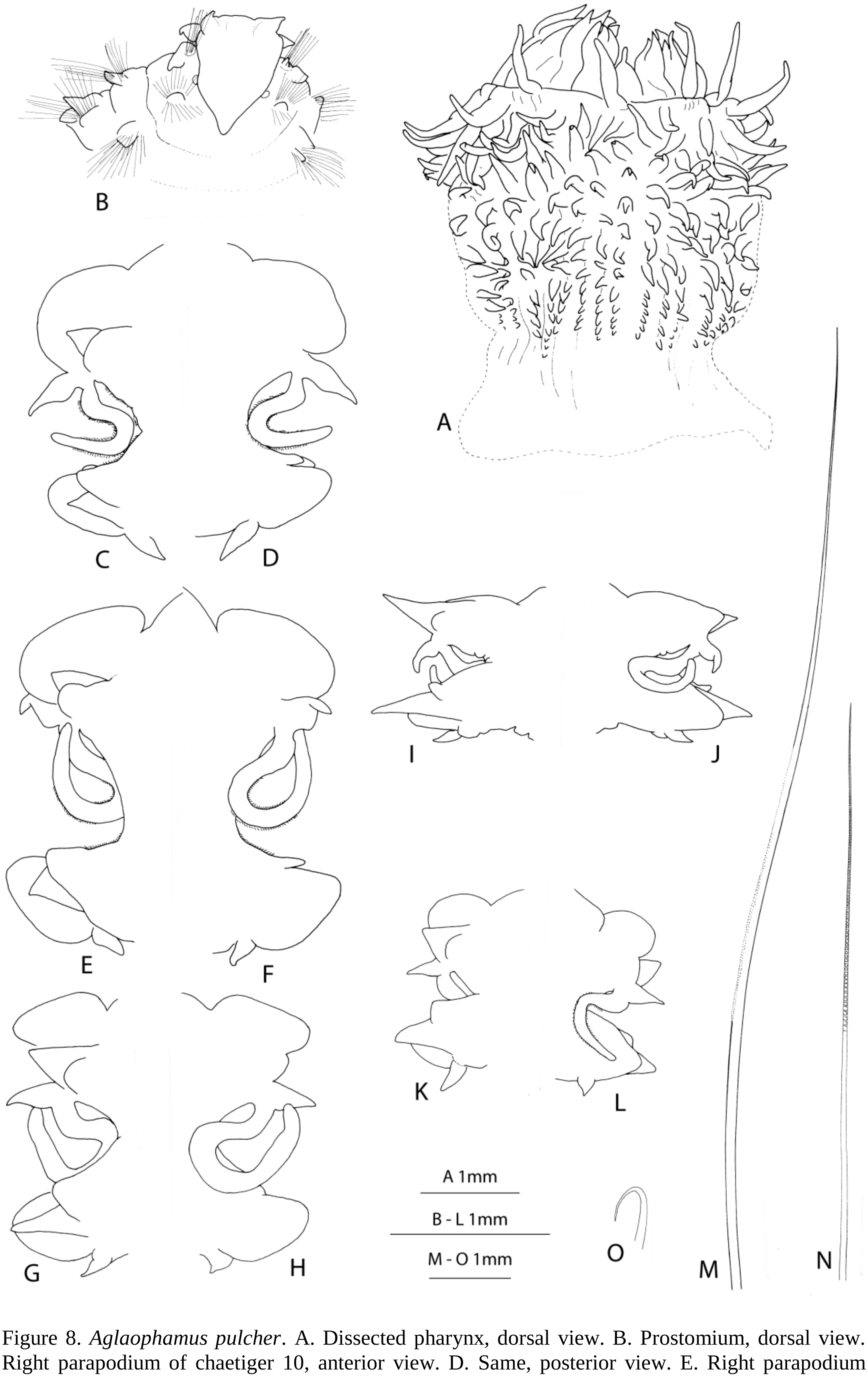


Figure 8. *Aglaophamus pulcher*. A. Dissected pharynx, dorsal view. B. Prostomium, dorsal view. C. Right parapodium of chaetiger 10, anterior view. D. Same, posterior view. E. Right parapodium of chaetiger 20, anterior view. F. Same, posterior view. G. Right parapodium of chaetiger 40, anterior view. H. Same, posterior view. I. Right parapodium of chaetiger 80, anterior view. J. Same, posterior view. K. Right parapodium of chaetiger 30 of a smaller specimen, anterior view. L. Same, posterior view. M. Preacicular chaeta from chaetiger 20. N. Postacicular chaetae from chaetiger 20. O. Acicula from chaetiger 20.

Aglaophamus pulcher **(Rainer, 1991)**

Figures 6, 8

Nephtys pulchra Rainer, 1991: 83, fig. 1A-F; Dnestrovskaya and Jirkov 2001: 210, fig.; Laborda 2004: 410, fig. 150C-D.
Nephthys hystricis McIntosh 1900: 259 (partim); McIntosh 1908: 27 (partim).
Nephtys incisa Fauchald 1963: 15, figs. 1H, 2C, 3B (partim).
Aglaophamus malmgreni Hartmann-Schröder 1974: 205 (partim).
Aglaophamus rubella Hartmann-Schröder 1974: 205 (partim).

Type locality. Norway.

Material examined. Atlantic Ocean. Norway: 1 complete spm, holotype (NHM 1921.5.1.794 as *Nephtys pulchra*). North Sea, Sweden, Skagerrak, Bohuslän: 58º07.726’-58º07.909’N, 10º48.698’-10º48,074’E, 212-250 m, Aug 2006, 1 incomplete spm (MB36000160); 58º19.728’-58º20.116’N, 10º26.550’-10º26,849’E, 333-370 m, Aug 2006, 4 incomplete spms, (DBUA 01136-01). Portugal, Nazaré canyon: 64PE252 cruise, RV *Pelagia*, 39º35.80’N, 9º24.25’W, 897 m, box-corer, 11 Sep 2006, 1 complete spm (DBUA 00867-01) and 1 incomplete spm (MB36000129); 39º35.80’N, 9º24.24’W, 897 m, box-corer, 11 Sep 2006, 2 complete and 1 incomplete spm, (DBUA 00867-02); Cascais Canyon: 64PE252 cruise, RV *Pelagia*, 38º27.89’N, 9º28.51’W, 935 m, box-corer, 18 Sep 2006, 2 complete spms, (DBUA 00868-01) and 1 incomplete spm, (MB36000130); 38º27.86’N, 9º28.49’W, 1014 m, box-corer, 18 Sep 2006, 4 complete and 2 incomplete spms, (DBUA 00868-02); 38º27.90’N, 9º28.50’W, 1020 m, box-corer, 18 Sep 2006, 1 complete spm (DBUA 00868-03); Setúbal Canyon: 64PE252 cruise, RV *Pelagia*, 38º17.10’N, 9º05.98’W, 970 m, box-corer, 17 Sep 2006, 1 incomplete spm (DBUA 00869-01); 38º17.10’N, 9º06.00’W, 970 m, box-corer, 17 Sep 2006, 2 incomplete spms, (DBUA 00869-02); Open slope off Sines: 64PE252 cruise, RV *Pelagia*, 37º49.99’N, 9º28.50’W, 1001 m, box-corer, 16 Sep 2006, 1 complete spm (DBUA 01055-01); 37º49.98’N, 9º28.49’W, 1001 m, box-corer, 16 Sep 2006, 2 complete spms (DBUA 01055-02); Open slope south of Nazaré Canyon: 64PE252 cruise, RV *Pelagia*, 39º10.36’N, 10º15.23’W, 1030 m, box-corer, 6 Sep 2006, 1 incomplete spm (MB36000145). Gulf of Cadiz, Mercator mud volcano: MSM01-03 cruise, RV *M.S. Merian*, 35º17.918’N, 6º38.717’W, 353 m, box-corer, 6 May 2006, 1 incomplete spm (MB36000131); Pen Duick Escarpment: M2007 cruise, RV *Pelagia*, 35º10.29’N, 6º47.28’W, 750 m, box-corer, May 2007, 1 incomplete spm (DBUA 00872-01).

Description. Examined specimens up to 52 mm long for up to 96 chaetigers. See Figure 6 for length and width measurements. Body small, slightly wider anteriorly, gradually taperng posterioly. Poor dorsal delineation between anterior segments, strong on middle and posterior segments. Colour in ethanol cream, some specimens with light brown area dorsally on anterior region; chaetae white, glistening; tip of aciculae dark. Eyes not visible. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by a low, conical dorsal and ventral simple papilla (Figure 8A); middorsal and midventral papillae absent; subdistal region with 14 well defined rows of 10-15 conical and long subterminal papillae, extending to base of pharynx, plus several distal ones that do not necessarily fit within the rows; proximal region otherwise smooth. Jaws conical. Prostomium pentagonal, anterior margin slightly convex, tapered, forming a membrane between antennae, posterior margin V-shaped extending over first chaetiger (Figure 8B); antennae conical, with broad base and cirriform tip; palps conical, similar to antennae but longer and with broader base (Figure 6C), inserted ventrolaterally in anterior region of prostomium. Nuchal organs rounded. Parapodia biramous; interramal space “U-shaped” anteriorly and medially, “V-shaped” posteriorly; moderately ciliated. Parapodia of chaetiger 1 directed anteriorly, parallel to prostomium; notopodial acicular lobes conical, prechaetal lamella poorly developed, rounded, postchaetal lamella well developed but not extending beyond acicular lobes, rounded; neuropodial pre- and postchaetal lamellae forming a cylinder around acutely pointed acicular lobes; dorsal cirri conical, small (Figure 6D); ventral cirri with broad bases and cirriform tips. Acicular lobes of following parapodia acutely pointed; prechaetal lamellae smaller than acicular lobes, rounded in notopodia, conical in neuropodia, becoming poorly developed posteriorly; postchaetal lamellae extending beyond acicular lobes in anterior parapodia, rounded, becoming smaller than acicular lobes in posterior parapodia; dorsal cirri long and conical, with bulbous bases and tapering tips; ventral cirri conical (Figure 8C-L). In some middle parapodia, the notopodial postchaetal lamellae gradually shift to a more dorsal position giving the lamellae a bilobed appearance (Figure 8G-H). This effect is more appearent in smaller specimens (Figure 8K-L). Branchiae recurved, cirriform, long and thin, moderately ciliated; present from chaetigers 5-7 to near posterior end;

occupy all interramal space when fully developed. Neuropodial superior lobe conical and small (difficult to observe), present in anterior and middle parapodia (Figure 8D, F). Chaetae long and thin, of three kinds: barred chaetae in preacicular position (Figure 8M), minutely spinulated chaetae in postacicular position (Figure 8N), and capillary chaetae in neuropodia of chaetiger 1. One acicula with curved tip per ramus (Figure 8O).

Remarks. Nephtys pulchra was erected by Rainer (1991), based on specimens from the Norwegian region that were previously included in four other species: *N. hystricis*, *N. incisa*, *A. malmgreni* and *A. rubella*. Recently, Laborda (2004) included *N. pulchra* in the Iberian Fauna and provided a brief description for specimens reported from the Gulf of Biscay. The present study updates the previous descriptions and extends the species distribution further south, to Portugal and Gulf of Cadiz. *Nephtys pulchra* was formally transferred to *Aglaophamus*, as *A. pulcher*, by Ravara *et al.* (in press) according to the results from a phylogenetic analysis based on morphological and molecular data. The morphological similarity between *N. pulchra* and *Aglaophamus* species was previously noted by Rainer (1991) in that *N. pulchra* has only 14 rows of subterminal papillae on the pharynx and a neuropodial superior lobe on anterior and middle parapodia. However, the recurved branchiae conditioned its inclusion in the genus *Nephtys*. The value of branchiae shape as a generic level distinctive character is discussed below, in discussion section.

The description herein presented includes some minor differences from the original description given by Rainer (1991), such as the number of subterminal papillae per row on the pharynx (10-15 instead of 14-16) the postacicular chaetae, which are in fact minutely spinulated instead of smooth, and the notopodial postchaetal lamellae that have a bilobed appearance in some middle parapodia (Figure 8G-H, K-L). In the smaller specimens examined (with less than 34 chaetigers) branchiae begin further posteriorly (chaetigers 18-20) or are absent, and postchaetal lamellae are poorly developed (Table 7). Variations on the chaetigers where branchiae occur, in smaller specimens, were already observed in *A. elamellatus*, a deep-water species also common in the Portuguese canyons (see above). In this later species, branchiae always start on the same chaetigers but extend further posterior according to the specimen size and are absent in the smallest ones. Despite the clearly larger dorsal cirri in *A. pulcher* than in *A. elamellatus*, the distinction between smaller specimens of these species is not easy and requires the examination of the pharynx papillae (see Table 8 for differences in the number of rows of pharynx papillae).

A comparison between *A. pulcher* and the other *Aglaophamus* species is summarized in Table 8. *A. pulcher* is close to *A. malmgreni* from which it can be distinguished by the branchiae shape and starting chaetiger, the number of subterminal papillae in the pharynx, and the bilobed postchaetal lamellae of notopodia, which occur further posteriorly and only in a few chaetigers of *A. pulcher*. Also the notopodial postchaetal lamellae of posterior chaetigers are dorsally oriented in *A. malmgreni* and directed laterally in *A. pulcher*.

Table 7. *Aglaophamus pulcher*. Branchiae occurrence, neuropodial superior lobes presence and notopodial postchaetal lamellae development according to the number of chaetigers.

Local	No. chaetigers	Branchiae start (right / left)	Posterior chaetigers without branchiae	Neuropodial superior lobe	Notopodial postchaetal lamellae (anterior/middle)
Nazaré Canyon	96	4 / 5	7	+	Rounded/bilobed
Norway	90	5 / 6		+ ?	Rounded/bilobed
Setúbal Canyon	72	5 / 6	4	-	Rounded/bilobed
OS, S Nazaré Canyon	> 71	6 / 8	-	-	Rounded/bilobed
Nazaré Canyon	> 48	6 / 6	-	+	Rounded/bilobed
Sweden	> 47	5 / 6	-	+	Rounded/bilobed
Gulf of Cadiz	> 44	5 / 6	-	+	Rounded/bilobed
Cascais Canyon	> 42	7 / 6	-	-	Rounded/bilobed
Nazaré Canyon	> 38	7 / 7	-	-	Poorly devel
Nazaré Canyon	38	7 / 7	0	-	Poorly devel
Gulf of Cadiz	> 36	5 / 5	-	+ (rudim.)	Rounded/bilobed
Sweden	> 35	5 / 5	-	+	Rounded/bilobed
Nazaré Canyon	34	8 / 8	4	-	Poorly devel
Cascais Canyon	33	18 / 19	7	-	Rudim.
Cascais Canyon	32	19 / 20	10	-	Rudim.
Cascais Canyon	32	19 / 19	8	-	Rudim.
Cascais Canyon	30	-	-	-	Rudim.
OS, off Sines	30	-	-	-	Rudim.
OS, off Sines	29	-	-	-	Rudim.
Cascais Canyon	29	-	-	-	Rudim.
Cascais Canyon	29	-	-	-	Rudim.
OS, off Sines	21	9 / 9	2	-	Rudim.
Cascais Canyon	21	-	-	-	Rudim.

Distribution. Atlantic Ocean (Norway, Oslofjord, Skagerrak, NW Spain, Portugal and Gulf of Cadiz) (Rainer 1991; Laborda 2004; this study).

Habitat. Mud and clay, 200-1000 m depth (Rainer 1991; Laborda 2004).

Table 8. Diagnostic characteristics of south European *Aglaophamus* species.

	A. elamellatus	*A. malmgreni*	*A. pulcher*	*A. rubellus*
Branchiae shape	involute	involute	recurved	involute
Branchiae start	11-13	11-13	5-7	2
Branchiae end	Before end of body	Before end of body	Near end of body	End of body
Neuropodial superior lobes	Absent	Absent	Present	Present
Prechaetal lamellae	Rudimentary	Rounded	Rounded	Bilobed
Notopodial postchaetal lamellae shape	Poorly developed, rounded in all parapodia	Bilobed in middle parapodia	Bilobed in some middle parapodia	Bilobed in anterior and middle parapodia
Pharynx subterminal pap.	20-22 rows of 6-11 pap.	22 rows of 2-17 pap.	14 rows of 10-15 pap.	14 rows of up to 34 pap.
Depth	990 – 7000m	38 - 2300m	200 – 1000m	Inferior intertidal – 1100m

Aglaophamus rubellus (Michaelsen, 1896)

Figures 6, 9

Nephthys rubella Michaelsen, 1896: 19, pl. I, figs. 5-8; Fauvel 1923: 373, fig. 145H-I; not Berkeley and Berkeley 1945: 327.

? *Nephthys squamosa* Fauvel 1936: 41.

Nephtys rubella Eliason 1962: 249.

Nephtys (Aglaophamus) rubella Southward 1956: 264; Foret-Montardo 1969: 818, pl. IV, figs. 1-6.

Aglaophamus rubella Hartman 1950: 127; Fauchald 1963: 20, figs. 1E, 2A and 3H; Guille and Laubier 1966: 266; Hartmann-Schröder 1971: 223, fig. 73C-D; Campoy 1982: 508.

Aglaophamus rubellus Dnestrovskaya and Jirkov 2001: 189, fig.; Laborda 2004: 414, fig. 151C.

Type locality. Norwegian waters.

Material examined. Atlantic Ocean. Norwegian waters: 1 incomplete spm, holotype (MH V-3960). North Sea, Sweden, West Gullmarsfjorden, Bondens Hamn: RV *Oskar von Sydow*, 58º12.69’N, 11º19.00’E, 14-20 m, dredge, Apr 2003, 1 incomplete spm (MB36000137). Scotland, off Shetland Islands: 2 incomplete spms (NHM: 1865.3.9.18 as *N. longisetosa*). Portugal, off Aveiro: cruise Aveiro95, RV *Côte d’Aquitaine,* 40º48.434’N, 8º49.142’W, 34.9 m, grab, 1 Aug 1995, 3 incomplete spms (DBUA 00062); off Cascais: 38º39’–38º42’N, 9º25’–9º30’W, 40 m, Jun 1998, 1 incomplete spm (DBUA 00871) and 1 incomplete spm (MB36000132). Mediterranean Sea. France, Banyuls: RV *Nereis*, 42º29.75’N, 3º8.40’E, 24 m, dredge, Jul 2004, 3 complete spm (DBUA 01048) and 1 incomplete spm (MB36000142).

Description. Examined specimens up to 24 mm long (for 45 chaetigers), and up to 59 chaetigers. See Figure 6 for length and width measurements. Body slightly wider anteriorly, gradually tapering from middle region to pygidium. Poor dorsal delineation between anterior segments. Colour in ethanol salmon with two longitudinal rows of purple spots near bases of parapodia; first two segments darker than following ones; prostomium with lightly pigmented area in middle of anterior region; two dark V-shaped lines near the posterior limit of prostomium; chaetae and aciculae amber. Eyes not visible. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by simple dorsal and ventral papilla; middorsal and midventral papillae absent; subdistal region with 14 rows of up to 34 subterminal papillae, extending over 2/3 length of pharynx, proximal papillae close together and often 2-3 papillae arranged in triangular groups; proximal region smooth. Jaws conical. Prostomium subpentagonal, anterior margin slightly convex, posterior margin V-shaped extending over first chaetiger (Figure 9A); antennae and palps long and conical with cirriform tip; palps slightly longer than antennae (Figure 6C), inserted ventrolaterally on posterior region of prostomium. Nuchal organs rounded. Parapodia biramous; interramal space “U-shaped” anterioly, “V-shaped” medially and posteriorly, with small ciliated patches. Parapodia of chaetiger 1 shorter than subsequent ones, anteriorly directed, parallel to prostomium; notopodial acicular lobes conical, prechaetal lamellae poorly developed, rounded, postchaetal lamellae well developed but not extending beyond acicular lobes, rounded; neuropodium with pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal cirri very small, conical (Figure 6D); ventral cirri cirriform with broad bases, similar in length to palps. Acicular lobes of following parapodia acutely pointed; prechaetal lamellae of both rami well developed but not extending beyond acicular lobes, bilobed with outer lobes shorter than inner; postchaetal lamellae extending beyond acicular lobes, conical in neuropodium, bilobed in notopodium, with dorsal lobes much larger than ventral, directed dorsally; dorsal cirri long, cirriform with broad bases; ventral cirri conical, lamelliform (Figure 9B-G). Posterior parapodia acicular lobes acutely pointed; prechaetal lamellae of both rami poorly developed, slightly bilobed; postchaetal lamellae of both rami not extending beyond acicular lobes, rounded, directed dorsally on notopodium; dorsal cirri cirriform; ventral cirri conical, lamelliform. Branchiae involute, cirriform, lightly ciliated, present from chaetiger 2 to near posterior end of the body; occupy all interramal space when fully developed. Neuropodial superior lobe small and lamelliform, present from chaetiger 5. Chaetae long, of three kinds: barred chaetae in preacicular position (Figure 9H), spinulated chaetae in postacicular position (Figure 9I), and capillary chaetae in the neuropodia of chaetiger 1. One acicula with curved tips per ramus (Figure 9J).

Remarks. Aglaophamus rubellus can be easily distinguished from the other southern European *Aglaophamus* species by the earlier beginning of branchiae (from chaetiger 2), the bilobed prechaetal lamellae and the higher number of pharynx subterminal papillae (Table 8). From the measurements shown in Figure 6, it is also evident the greater length of antennae, palps and first chaetiger ventral cirri of *A. rubellus* in comparision to other species.

Distribution. Atlantic Ocean (from Norway to Portugal); Mediterranean Sea (Sicily, Corsega, Gulf of Génova) (Fauchald 1963; Foret-Montardo 1969; Laborda 2004).

Habitat. Mud and *Amphioxus* sand, from the lower intertidal to 1100 m depth (Foret-Montardo 1969; Laborda 2004). Specimens from the deeper locations were not available for examination and therefore these records should be considered with caution, as this species has been frequently confused with *A. malmgreni*.

***Inermonephtys* Fauchald, 1968**

Type species. *Inermonephtys inermis* (Ehlers, 1887), by original designation.

Diagnosis. The genus *Inermonephtys* is distinguished from the other genera by the lack of antennae and all pharynx papillae, the long eversible cirriform nuchal organs, and the spindle-shaped jaws. Acicular lobes usually conical to acutely pointed; parapodial lamellae well developed; neuropodial superior lobes may be present in anterior parapodia. Branchiae long, thin and involute. Lyriform chaetae present. Anterior parapodia may have more than one acicula. Aciculae of posterior parapodia with curved tips.

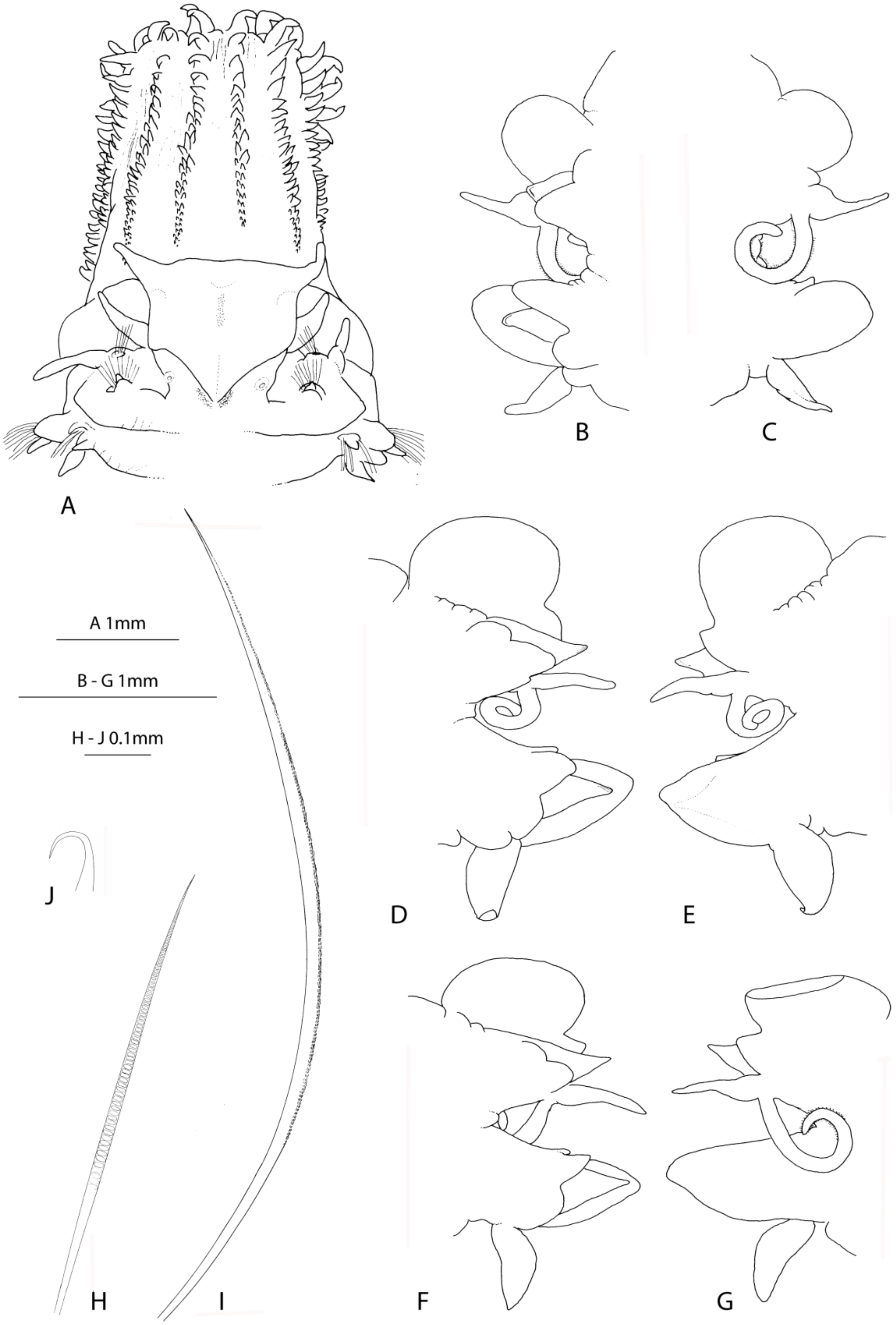


Figure 9. *Aglaophamus rubellus*. A. Pharynx and prostomium, dorsal view. B. Right parapodium of chaetiger 10, anterior view. C. Same, posterior view. D. Right parapodium of chaetiger 29, anterior view. E. Same, posterior view. F. Right parapodium of chaetiger 45, anterior view. G. Same, posterior view. H. Pre-acicular chaeta from chaetiger 29. I. Postacicular chaeta from chaetiger 29. J. Acicula from chaetiger 10.

Inermonephtys foretmontardoi sp. nov.

Figure 10

? Nephthys inermis Fauvel 1923: 375, fig. 147; Augener 1932: 679, fig. 3; Fauvel 1933b: 47-50, fig. 3; Fauvel 1940: 11.

Nephtys (Aglaophamus) inermis Foret-Montardo 1969: 820, pl. V, figs. 1-5 (not Ehlers, 1887).

Inermonephtys inermis ?Campoy 1982: 504; Laborda 2004: 418, fig. 152D.

Etymology. The species is named for Dr. P. Foret-Montardo who provided the first accurate description of this species, although under the name of *Nephtys (Aglaophamus) inermis* (Foret-Montardo 1969).

Type locality. Cape Finisterre (42º44'N, 9º23'W), NW Spain, 81 fms depth.

Material examined. Atlantic Ocean. England, Eddystone, Plymouth: 1 incomplete spm (NHM 1969.301 as *Nephtys longosetosa*). Spain, Cape Finisterre: coll. H. M. S. Porcupine, 42º44'N, 9º23'W, 81 fms, Jul 1870, incomplete spm, holotype (NHM 1921.5.1.861, identified by McIntosh as *Aglaophamus inermis*); 42º44'N, 9º23'W, 81 fms, Jul 1870, 3 incomplete spms, paratypes (NHM 2009.143-144, identified by McIntosh as *Aglaophamus inermis*). Portugal: 1 incomplete spm, 37º14.1'N, 9º05.3'W, 145 m, May 1981; 1 incomplete spm, 37º38.9'N, 8º52.9'W, 113 m, Oct 1981; 1 incomplete spm, 37º38.9'N, 8º53.1'W, 113 m, Oct 1981; 1 incomplete spm, 37º49.9'N, 8º56.8'W, 130 m, Dec 1981 (not deposited). Mediterranean. Adriatic Sea: 1 complete and 1 incomplete spms, collection P. Fauvel, 1948 (MNHN A409).

Description. Holotype 28.8 mm long posteriorly incomplete specimen with 44 chaetigers. Body width including parapodia 3.6 mm, excluding parapodia 2.5 mm. Anterior segments poorly delineated. Colour in ethanol yellowish, without pigmentation; chaetae amber; aciculae brownish with dark tips. Eyes not visible. Pharynx smooth, without papillae. Jaws with spindle-shaped base and straight free margin. Prostomium subpentagonal, 0.58 mm long, 0.51 mm wide, anterior margin straight, posterior margin V-shaped and extending over first chaetiger (Figure 10A); antennae absent; palps ovoid, very small (0.07 mm), inserted ventrolaterally on prostomium (not visible dorsally). Nuchal organs well developed, digitiform.

Parapodia biramous; interramal space "U-shaped", moderately ciliated. Parapodia of chaetiger 1 similar in size to subsequent ones, anteriorly directed, parallel to prostomium; notopodial acicular lobes rounded, prechaetal lamellae rudimentary, postchaetal lamellae extending beyond acicular lobes, rounded; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobe; dorsal and ventral cirri well developed, 0.24 mm long, conical. Anterior parapodial acicular lobes rounded, becoming conical in median parapodia and acutely pointed in posterior parapodia; prechaetal lamellae well developed but not extending beyond acicular lobes, rounded; postchaetal lamellae extending well beyond acicular lobes, rounded in notopodia of anterior chaetigers, becoming slender and leaf-like in median parapodia, slender in neuropodia; dorsal cirri conical in anterior parapodia (0.34 mm), cirriform in median parapodia (0.43 mm); ventral cirri conical, as long as neuropodial postchaetal lamellae (0.29 mm in anterior chaetigers, 0.34 mm in middle chaetigers) (Figure 10B-E). Branchiae involute, thin and long, cirriform, moderately ciliated, with conspicuous conical basal projections; present from chaetiger 4; occupy half of interramal space when fully developed. Chaetae short (exposed length 1.2 mm), of three kinds: finely spinulated chaetae in pre- and postacicular position (Figure 10F-G), lyriform chaetae with subequal rami in postacicular position (Figure 10H) and capillary chaetae in the neuropodia of first chaetiger. Anteriormost parapodia with up to five aciculae in neuropodia and four in notopodia. Number of aciculae decreases gradually towards end of body. Single aciculae of posterior parapodia with curved tips. Smaller specimens have a lower number of aciculae (Table 9).

Table 9. *Inermonephtys foretmontardoi* n. sp. Number of aciculae in notopodium (NO) and neuropodium (NE) from anterior to posterior chaetigers according to specimen size.

Local	No. chaetigers	Body length (mm)	Width (mm) (without/with parapodia)	No. aciculae (from anterior to posterior chaetigers)
Cape Finisterre	>27	13.6	3.5/4.9	NO - 4/3/2/1; NE – 5/4/3/2/1
Cape Finisterre	>44	28.8	2.5/3.6	NO – 3/2/1; NE – 4/3/2/1
Cape Finisterre	>36	19.5	2.6/3.6	NO – 3/2/1; NE – 4/3/2/1
Cape Finisterre	>57	23.2	2.0/2.9	NO – 2/1; NE – 3/2/1
Plymouth	>56	19.2	2.0/2.7	NO – 2/1; NE – 2/1

Remarks. The species *Inermonephtys foretmontardoi* is herein erected based on European specimens previously identified as *I. inermis*. *Inermonephtys inermis* was originally described as *Nephtys (Aglaophamus) inermis* by Ehlers (1887) from specimens found in Florida, and has up to now been considered to have a cosmopolitan distribution in temperate, tropical and subtropical seas (including Atlantic, Pacific and Indian Oceans) (e.g. Hartman 1940, 1950; Fauchald 1968; Day 1973; Taylor 1984; Kirkegaard 1995). We compared specimens previously identified as *I. inermis* from Europe with the holotype of *I. inermis* from Florida (MCZ 1088), and the observed differences justify the erection of a new species (*I. foretmontardoi*). The main difference is the presence of well-developed neuropodial postchaetal lamellae (extending well beyond acicular lobes) in *I. foretmontardoi,* while they are rudimentary in *I. inermis*. Also the prechaetal lamellae of both rami are more developed, although not extending beyond acicular lobes in the former, but rudimentary or poorly developed in the latter. Records of *Inermonephtys inermis* from European waters include specimens from Cape Finisterre and the Adriatic Sea (Fauvel 1923), Alboran Sea (Mediterranean) and S Portugal (Bellan 1959, 1960), and Marseille (Mediterranean) (Foret-Montardo 1969). Campoy (1982) and Laborda (2004) also refer to *Inermonephtys inermis* as a member of the Iberian fauna. In some cases the descriptions and drawings provided by these authors were taken from the original description of *I. inermis* (Ehlers 1887) but morphological differences in European specimens were already noticed by some authors. The brief description provided by Fauvel (1923), in Faune de France, matches the original description of *I. inermis*, although with some doubts regarding the presence of antennae, absence of eyes, and the rudimentary condition of the neuropodial postchaetal lamellae. The drawings were taken from the original description. The detailed description and drawings by Foret-Montardo (1969) as well as the brief description and a parapodium drawing by Laborda (2004) match the characters herein assigned to *I. foretmontardoi*. Although not confirmed from specimens, we assume that all European records of *I. inermis* belong to the new species *I. foretmontardoi*. There are five more species described in the genus *Inermonephtys,* all from the Pacific (Thailand, Viet Nam, Japan and Australia). The new species is distinguished from all these species by the chaetiger were branchiae start and the morphology of the parapodia.

Distribution. Atlantic Ocean (S England, Spain, Portugal); Mediterranean Sea (from Alboran Sea to Aegean Sea, and Adriatic Sea).

Habitat. Muddy and sandy sediments, 0-450 m depth (Foret-Montardo 1969; Laborda 2004).

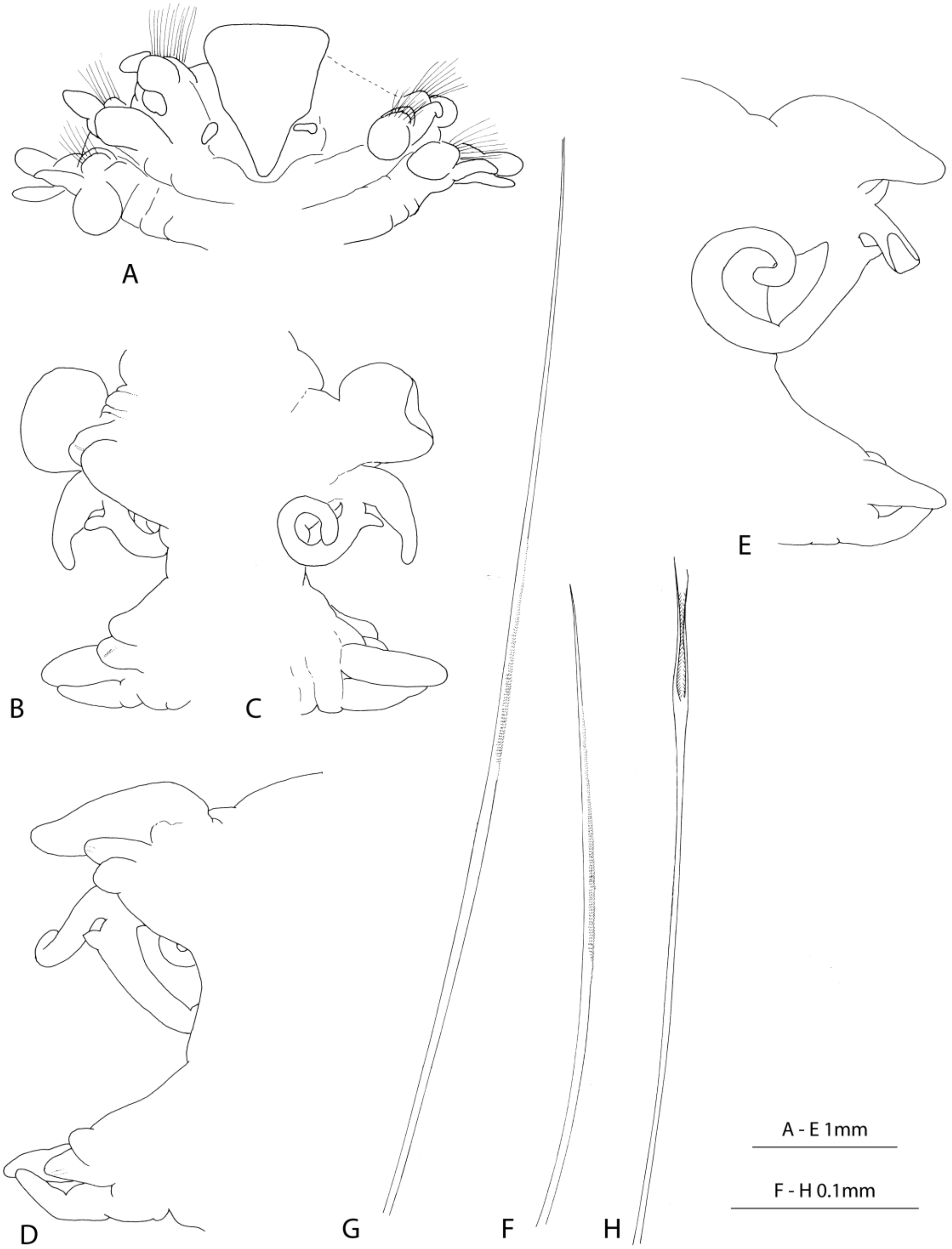


Figure 10. *Inermonephtys foretmontardoi* n. sp. A. Prostomium and anterior chaetigers, dorsal view. B. Right parapodium of chaetiger 10, anterior view. C. Same, posterior view. D. Right parapodium of chaetiger 30, anterior view. E. Same, posterior view. F. Preacicular chaeta from a posterior chaetiger. G. Postacicular chaetae from a posterior chaetiger. H. Lyriform chaetae from a posterior chaetiger.

Micronephthys Friedrich, 1939

Type species. *Micronephthys minuta* (Théel, 1879), by monotypy.

Diagnosis. The genus *Micronephthys* is distinguished from the other genera by their small-sized body with poorly developed parapodial lamellae. Acicular lobes conical; neuropodial superior lobes absent. Branchiae usually absent or if present of restricted number and poorly developed, straight. Lyriform chaetae may be present. Aciculae of median and posterior parapodia with curved tips. Antennae present. Pharynx subterminal papillae present; middorsal papilla absent; proximal region smooth. Jaws conical, hook-like. Nuchal organs rounded.

Micronephthys cf. *minuta* (Théel, 1879)

Figure 11

Nephthys minuta Théel, 1879: 28, pl. II, fig. 18.
Nephtys minuta Annenkova 1937: 164; Annenkova 1938: 162; Gorbunov 1946: 38; Zatsepin 1948: 122, table 30 (partim); Uschakov 1955: 217, fig. 68 (partim).
Micronephtys minuta Augener 1912: 206; Friedrich 1939: 123, fig. 3-4; Hartman 1950: 130; Reish 1965; Curtis 1979; Tzetlin 1980: 25 (partim).
Micronephthys minuta Taylor 1984: 35-5, fig. 35-1 and 2A-E; Jirkov 1989: 74, fig. 15.4 (partim); ?Parapar *et al*. 1993: 375, fig. 7; Jirkov and Paraketsova 1996: 831, fig. 1; not Pettibone 1963: 188, fig. 47B, C; Dnestrovskaya and Jirkov 2001: 192,1 fig.
Micronephtys sp. aff minuta Fournier and Pocklington 1984: 261.

Type locality. Besimennïa Bay and occidental region of Matotchkin, Novaya Zemlya, Barents Sea, 7-34 m depth.

Material examined. Atlantic Ocean. Portugal, off Cascais: 38º39'-38º42'N, 9º25'-9º30'W, 50 m, Jun 1998, 1 incomplete spm in poor condition (DBUA 01137.01).

Description. The only specimen examined was incomplete, with 11 chaetigers. See Figure 11 for length and width measurements. Body small, slightly wider anteriorly, gradually tapered from middle region to pygidium. Colour in ethanol white; chaetae and aciculae amber. One pair of eyes present subdermally at level of chaetiger 3. Pharynx distal region with 9 pairs of terminal, bifid papillae, separated by dorsal and ventral gap; long middorsal papillae present; subdistal region with 18-20 rows of 3-4 small subterminal papillae; proximal region smooth. Prostomium subquadrangular, anterior margin slightly convex, posterior margin poorly defined; antennae and palps long and cirriform, subequal in size. Nuchal organs rounded. Parapodia biramous. Parapodia of chaetiger 1 anteriorly directed, parallel to prostomium; notopodial acicular lobes conical; pre- and postchaetal lamellae rudimentary; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal and ventral cirri very small. Acicular lobes of following parapodia conical; pre- and postchaetal lamellae rudimentar; dorsal and ventral cirri conical. Branchiae straight or slightly involute, strongly ciliated; present from chaetiger 6-9 to 10-14. Chaetae of three kinds: barred chaetae in preacicular position, very finely spinulated chaetae in postacicular position, capillary chaetae in neuropodia of first chaetiger and in outer edges of the postacicular chaetae bundles. One acicula with curved tip per ramus.

Remarks. Only one incomplete specimen of *M. minuta* in poor condition was examined within this study. The type material was not available. Thus the description here presented is also based on the literature (e.g. Théel 1879; Jirkov & Paraketsova 1996) especially in what refers to pharynx and branchiae characters. This species was described for the Barents Sea and seems to be frequent in Arctic and Subarctic regions (Jirkov 1989; Jirkov & Paraketsova 1996). The specimen examined agrees well with the accepted description for *M. minuta*, although it was found further south, off the western coast of Portugal. Parapar *et al.* (1996) recorded two specimens from northwestern of Spain that differ from *M. minuta* in having 12 rows of large subterminal papillae in the pharynx, spherical to oval dorsal and ventral cirri, and branchiae absent. Thus this record must be considered with caution until further material is available for study.

Distribution. Arctic Ocean (Barents Sea, White Sea, N Spitsbergen, Chukchi and Beaufort Seas); Atlantic Ocean (from Canada to Gulf of Mexico); Pacific Ocean (Bering Sea) (Reish 1965; Taylor 1984; Jirkov & Paraketsova 1996; Jirkov 2001). There are further reports of this species from NW Spain (Parapar *et al.* 1993) and Portugal, but these records require confirmation.

Habitat. Coarse to fine-very fine sand with moderate mixtures of silt and clay, mud, and foraminiferan ooze, 10-270 m depth (Taylor 1984; Jirkov & Paraketsova 1996; Dnestrovskaya & Jirkov 2001).

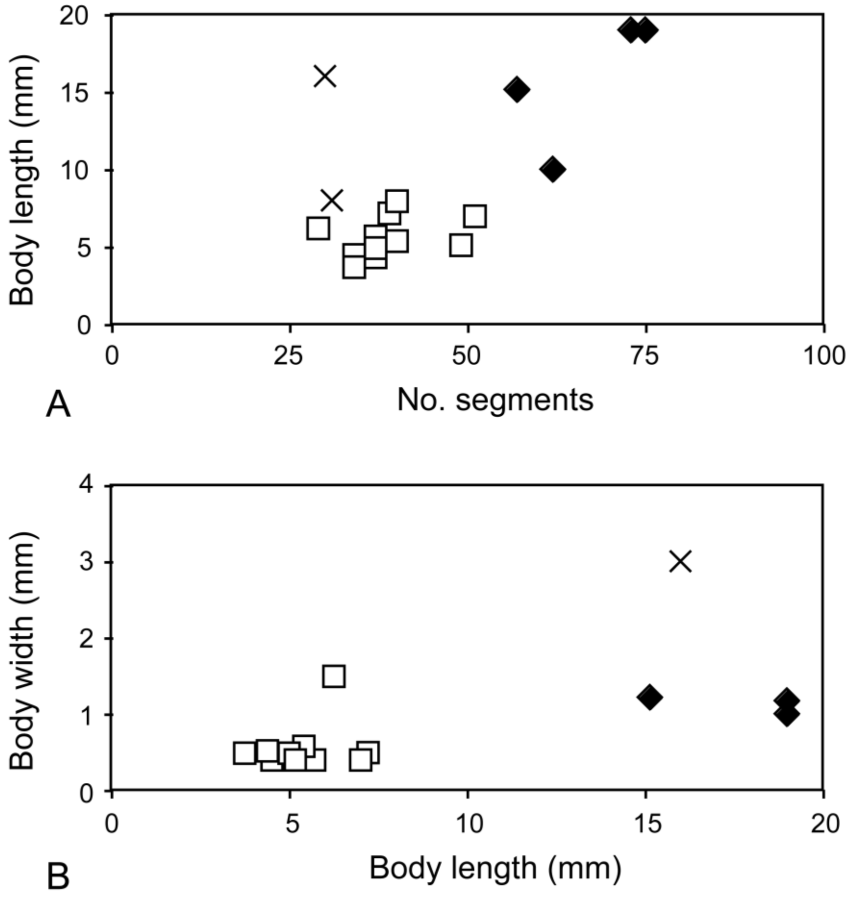


Figure 11. Relationships between: A. Number of segments and body length. B. Body length and body width. × *M. minuta*. ◆ *M. sphaerocirrata*. □ *M. stammeri*. *M. minuta* plot is based on the literature (Théel, 1879; Pettibone, 1963; Jirkov & Paraketsova, 1996). *M. sphaerocirrata* plot includes measurements from Wesenburg-Lund (1949) and Rainer & Hutchings (1977). *M. stammeri* plot includes measurements from Banse (1958), San Martin (1982) (original description of *M. maryae*) and Rainer & Kaly (1988) (for *M. maryae*).

Micronephthys sphaerocirrata (Wesenberg-Lund, 1949)

Figures 11, 12

Nephthys sphaerocirrata Wesenberg-Lund, 1949: 294, figs. 24-26; Day 1953: 431.

Nephthys (Micronephthys) sphaerocirrata Day 1967: 347, fig. 15.3A-D; not Gibbs 1971: 155.

Micronephthys sphaerocirrata Rainer and Hutchings 1977: 320, figs. 12 and 41; not Fauchald 1968: 17, figs. 36-40.

Micronephthys sphaerocirrata ?Imajima 1970; Rullier 1972; Campoy 1982: 506; ?Nateewathana and Hylleberg 1986: 209; Laborda 2004: 415.

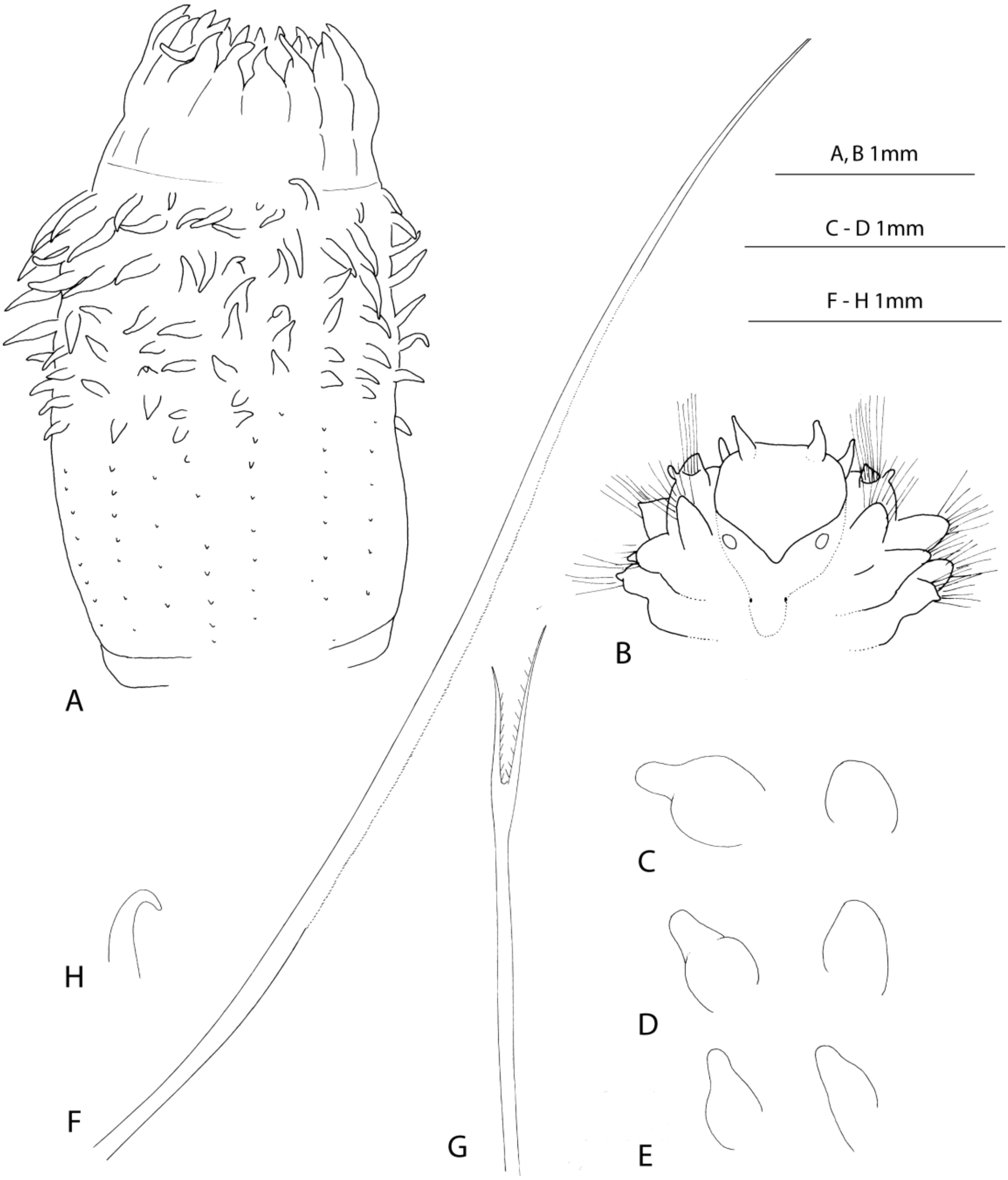


Figure 12. *Micronephthys sphaerocirrata*. A. Pharynx, dorsal view. B. Prostomium and anterior chaetigers, dorsal view. C. Dorsal (left) and ventral (right) cirrus from anterior parapodia. D. Dorsal (left) and ventral (right) cirrus from median parapodia. E. Dorsal (left) and ventral (right) cirrus from posterior parapodia. F. Postacicular chaetae. G. Lyriform chaetae. H. Acicula from posterior chaetiger.

Type locality. Off Kharg, Persian Gulf.

Material examined. Indian Ocean. Persian Gulf, off Kharg: 13 m, Mar 1937, 2 complete and 1 incomplete spms, syntypes (ZMUC-Pol-1473 to 1475). South Africa, Gqutywa Estuary, eastern Cape Province: 33º21.8’S, 27º21.5’E, 1 m, Jun 1998, 2 complete and 1 incomplete spms (NMWZ 1999.071.002); South African Collection from Prof. J. H. Day, 9 complete and 26 incomplete spms (NHM 1961.9.80/119).

Description. Examined specimens up to 19 mm long for up to 73 chaetigers. See Figure 11 for length and width measurements. Body small, slightly wider anteriorly, gradually tapering from median region to pygidium. Colour in ethanol light salmon; chaetae and aciculae amber. One pair of eyes present subdermally at level of chaetiger 2-3. Distal pharynx region with 10 (?) pairs of terminal, bifid papillae, separated by dorsal simple papilla (Figure 12A); middorsal and midventral papillae absent; subdistal region with 22 rows of 7-10 conical subterminal papillae, followed by several minute papillae, extending to base of pharynx; proximal region smooth. Prostomium subpentagonal, anterior margin straight or slightly convex, posterior margin V-shaped and extending over first chaetiger; antennae and palps conical to cirriform; palps slightly shorter than antennae, inserted ventrolaterally and medially on prostomium (Figure 12B). Nuchal organs rounded. Parapodia biramous; interramal space “U-shaped”. Parapodia of chaetiger 1 anteriorly directed, parallel to prostomium; notopodial acicular lobes conical; pre- and postchaetal lamellae rudimentary; neuropodial pre- and postchaetal lamellae forming a cylinder around acutely pointed acicular lobes; dorsal cirri minute; ventral cirri cirriform. Acicular lobes of following parapodia conical; prechaetal lamellae rudimentary; postchaetal lamellae well developed but not extending beyond acicular lobes, rounded, becoming rudimentary posteriorly; dorsal cirri with sphaerical base and conical tip; ventral cirri subsphaerical becoming more elongated in posterior chaetigers (Figure 12C-E). Branchiae absent. Chaetae of four kinds: barred chaetae in preacicular position, finely spinulated chaetae (Figure 12F) and lyriform chaetae with unequal rami (Figure 12G) in postacicular position, capillary chaetae in the neuropodia of first chaetiger. One acicula per ramus, posterior ones with curved tips (Figure 12H).

Remarks. This species was first described by Wesenberg-Lund (1949) from the Persian Gulf with a number of subsequent records from other regions, including Thailand, South Africa, Mediterranean Sea and several localities in the Pacific Ocean

(Japan, Vietnam, NE Australia, Marshall and Solomon Islands and New Caledonia) (e.g. Day 1967; Fauchald 1968; Rainer & Hutchings 1977; Nateewathana & Hylleberg 1986; Laborda 2004). In this study we only include the South African and Australian records as correctly identified. South African specimens were examined and the identification confirmed. As for the NE Australia, Rainer and Hutchings (1977) could find no difference between their specimens and the original description or the specimens they examined from South Africa. On the other hand, we examined specimens identified as *M. sphaerocirrata* from the Marshall (USNM 118681) and Solomon (NHM 1970.396) Islands that were in fact *M. stammeri* and *M. oculifera*, respectively. The Vietnam reference (Fauchald, 1968) was already synonymyzed by Lee and Jae (1983) to the subspecies *M. sphaerocirrata orientalis* described from specimens found in Korea. This subspecies differ from *M. s. sphaerocirrata* by the number of pharynx papillae in each row (12-15 instead of 6-9/8-11) and the prominent preacicular lamellae. Imajima and Takeda (1985) also attributed specimens found in Japan to this subspecies. Nateewathana and Hylleberg (1986) identified Thailand specimens as *M. sphaerocirrata* despite some minor differences in the parapodial lamellae proportions. Thailand specimens differ in having the neuropodial prechaetal lamellae well developed (as long as acicular lobes) and the notopodial postchaetal lamellae larger than acicular lobes. We consider that the identification of these specimens as *M. sphaerocirrata* needs further study and comparison with type material. Specimens from the Mediterranean Sea were not available to us but Laborda (2004) reports a small difference in the number of pharynx papillae in each row (8-16). Until further confirmation we advise that this reference should also be considered with caution.

Distribution. Atlantic Ocean (SW Africa); Indian Ocean (Persian Gulf, South Africa); Pacific Ocean (NE Australia) (Rainer & Hutchings 1977). There are further reports of this species from southern Spain, Thailand and New Caledonia (Nateewathana & Hylleberg 1986; Laborda 2004), but these records require confirmation.

Habitat. Fine and muddy sand, from shallow subtidal to 500 m depth (Rainer & Hutchings 1977; Laborda 2004).

Micronephthys stammeri **(Augener, 1932)**

Figures 11, 13

Nephthys stammeri Augener, 1932: 678, fig. 2.

Nephthys inermis Augener 1932: 663.

Micronephthys stammeri Hartman 1950: 131; Banse 1959: 302, fig. 6.

Micronephthys maryae San Martin, 1982: figs. 1-3; Rainer and Kaly 1988: 696, figs. 5A-E and 6B; Laborda 2004: 416, fig. 152A-C.

Type locality. Adriatic Sea (Timavo-Geviet region).

Material examined. Mediterranean Sea. Adriatic Sea, Croatia, Rovinj: 4 complete and 4 incomplete spms (ZMH-V12889); Istra, off Rovinj: *RV Burin*, 45º05.769'N, 13º37.406'E, 18 m, Sep 2008, 1 complete spm (DBUA 01050). Spain, between Cabo San Antonio and Puerto de Valencia: 1 complete and 1 incomplete spms (MNCN 16.01/2210 as *M. maryae*); Mallorca Island, Santa Ponça: 1 complete spm (MNCN 16.01/278, paratype of *M. maryae*).
Pacific Ocean. Japan, Tanabe Bay: 33º42.772'N, 135º22.248'E, 10 m (?), Nov 2008, 4 complete and 1 incomplete spms (DBUA 01051-01), and 1 incomplete spm (MB36000144); Shirahama, 33º41.481'N, 135º20.181'E, 0.5 m, Nov 2008, 2 complete spms (DBUA 01051-02). Marshall Islands, Parry Island (lagoon side), Enewetak atoll: 11º24'N, 162º23'E, 90 ft, summer 1957, 1 complete spm (USNM 118681 as *M. sphaerocirrata*).

Description. Examined specimens up to 6 mm long for up to 49 chaetigers. See Figure 11 for length and width measurements. Body small, slightly wider anteriorly, tapering posteriorly. Poor dorsal delineation between anterior segments. Colour in ethanol white; chaetae and acicula amber. Two pairs of large coalescent eyes visible at level of chaetiger 3. Pharynx subdistal region with 20-22 rows of about 8 long and conical subterminal papillae decreasing in size towards base of pharynx, followed by several minute (wart-like) papillae, extending over 2/3 length of pharynx (Figure 13A); proximal region smooth. Jaws conical (Figure 13B). Prostomium subpentagonal, anterior margin slightly convex; antennae and palps subequal in length, cirriform with swollen tips; palps inserted ventrolaterally on median region of prostomium (Figure 13C). Nuchal organs rounded. Parapodia biramous. Parapodia of chaetiger 1 similar in size to subsequent ones, anteriorly directed, parallel to prostomium; notopodial acicular lobes conical, pre- and postchaetal lamellae rudimentary; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal cirri small and sphaerical; ventral cirri cirriform with swollen tips, similar in size to palps. Following parapodia with conical acicular lobes; pre- and postchaetal lamellae of both rami rudimentary or poorly developed, rounded; dorsal and ventral cirri subsphaerical (Figure 13D). Branchiae absent. Chaetae of five kinds: barred chaetae, with a peak in center of each bar (slightly thicker than barred chaetae from other chaetigers) in preacicular position of notopodia of chaetiger 1 (Figure 13E); simple barred chaetae in preacicular position of following parapodia; finely spinulated chaetae in postacicular position of all parapodia (Figure 13F); lyriform chaetae with unequal rami and thin and long spines on the internal side, in postacicular position of parapodia from chaetiger 3 (Figure 13G), and capillary chaetae in the neuropodia of chaetiger 1. One acicula with curved tips per ramus (Figure 13H).

Remarks. The original description by Augener (1932) is incomplete and the holotype has been lost. Banse (1959) redescribed the species based on specimens also collected from the Adriatic Sea. Those specimens were examined within this study and Banse's description is here emended and completed with the following: dorsal cirri are present from chaetiger 1 (instead of chaetiger 2); special chaetae are present in the notopodia of first chaetiger; lyriform chaetae are present from the chaetiger 3 (instead of chaetiger 15). There are no records of this species after Banse (1959). In 1982, San Martin described a new species, *M. maryae*, for specimens collected in the Mediterranean Sea. However, he has not examined the type material of *M. stammeri* and based his conclusions on the description given by Banse (1959). Consequently, the differences used by San Martin to distinguish these two species are exactly the characteristics that are here included in the emended description of *M. stammeri*. Therefore we consider *M. maryae* to be a junior synonym of *M. stammeri*. Both the description of *M. maryae* by San Martin (1982) and the description of *M. stammeri* by Banse (1959) refer to the presence of 20-22 rows of subterminal papillae in the pharynx. However, Rainer and Kaly (1988) emended the description of *M. maryae* to include 14 rows of subterminal papillae, instead of 20-22, based on a paratype of *M. maryae* and on specimens from Australia. According to the specimens examined in this study, especially the ones from Adriatic Sea, the pharynx actually has at least 20 rows of papillae. On the paratype of *M. maryae* and on the specimens from Japan the 20 rows of papillae were not possible to assess with certainty, although they seem to have more than 14 rows.

Apart from the differences mentioned above, *M. stammeri* clearly differs from the other two *Micronephthys* species in body size (Figure 11). *Micronephthys sphaerocirrata* is a larger species in length and number of segments. As for *M. minuta* the scarce data do not allow a reliable conclusion althought the specimens appear larger than *M. stammeri* for the same number of segments.

Distribution. Adriatic Sea; Mediterranean Sea (Balearic Islands); Indian Ocean (W Australia); Pacific Ocean (Japan, Marshall Islands) (San Martin 1982; Rainer & Kaly 1988; Laborda 2004).

Habitat. Median sand with gravel, 4-7 m depth (Banse 1959; Laborda 2004).

***Nephtys* Cuvier, 1817 in Audouin & Milne Edwards, 1833**

Type species. *Nephtys hombergii* Savigny, 1822 by subsequent designation (first designation unclear, if not previously so at least by Hartman (1959)).

Diagnosis. The genus *Nephtys* presently includes specimens with conical, rounded or bilobed acicular lobes and well-developed parapodial lamellae. Neuropodial superior lobes absent. Branchiae recurved. Lyrate chaetae absent. Aciculae of median and posterior parapodia with curved tips. Antennae present. Pharynx usually with rows of less than 10 subterminal papillae (usually up to 5-7); long middorsal papilla often present; proximal region smooth or covered with small warts. Jaws conical, hook-like. Nuchal organs rounded.

***Nephtys assimilis* Örsted, 1843**

Figures 14, 15

Nephthys assimilis Örsted, 1843: 33; Malmgren 1865: 105, pl. XII, fig. 19; not Treadwell 1914: 192; not Berkeley 1924: 290; not Hartman 1940: 239, pl. 39, figs. 87-88.

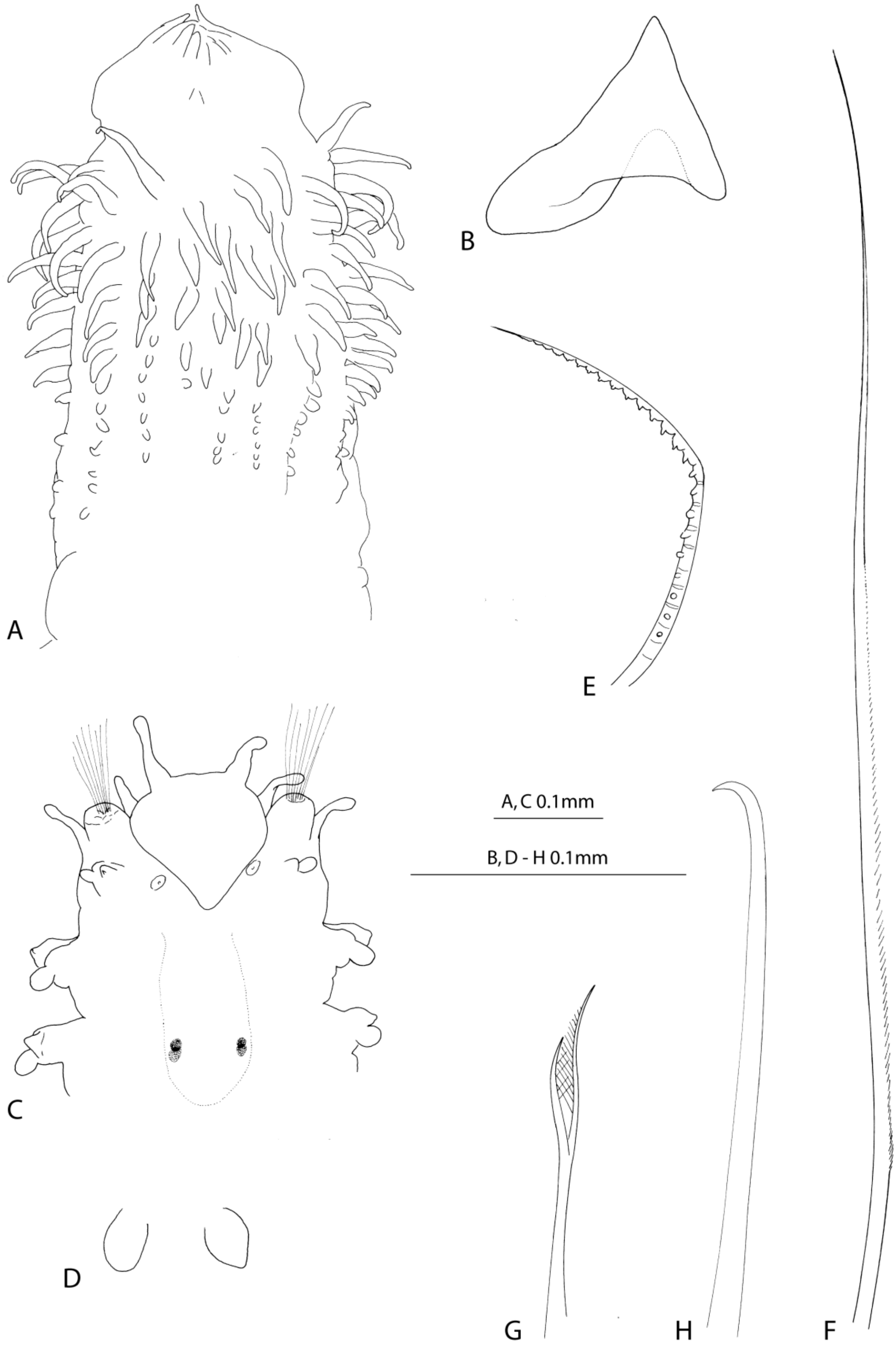


Figure 13. *Micronephthys stammeri*. A. Pharynx. B. Jaw. C. Prostomium and anterior chaetigers, dorsal view. D. Dorsal (left) and ventral (right) cirrus from median parapodia. E. Barred chaetae from notopodia of chaetiger 1. F. Postacicular chaetae of median chaetiger. G. Lyriform chaetae. H. Acicula from median chaetiger.

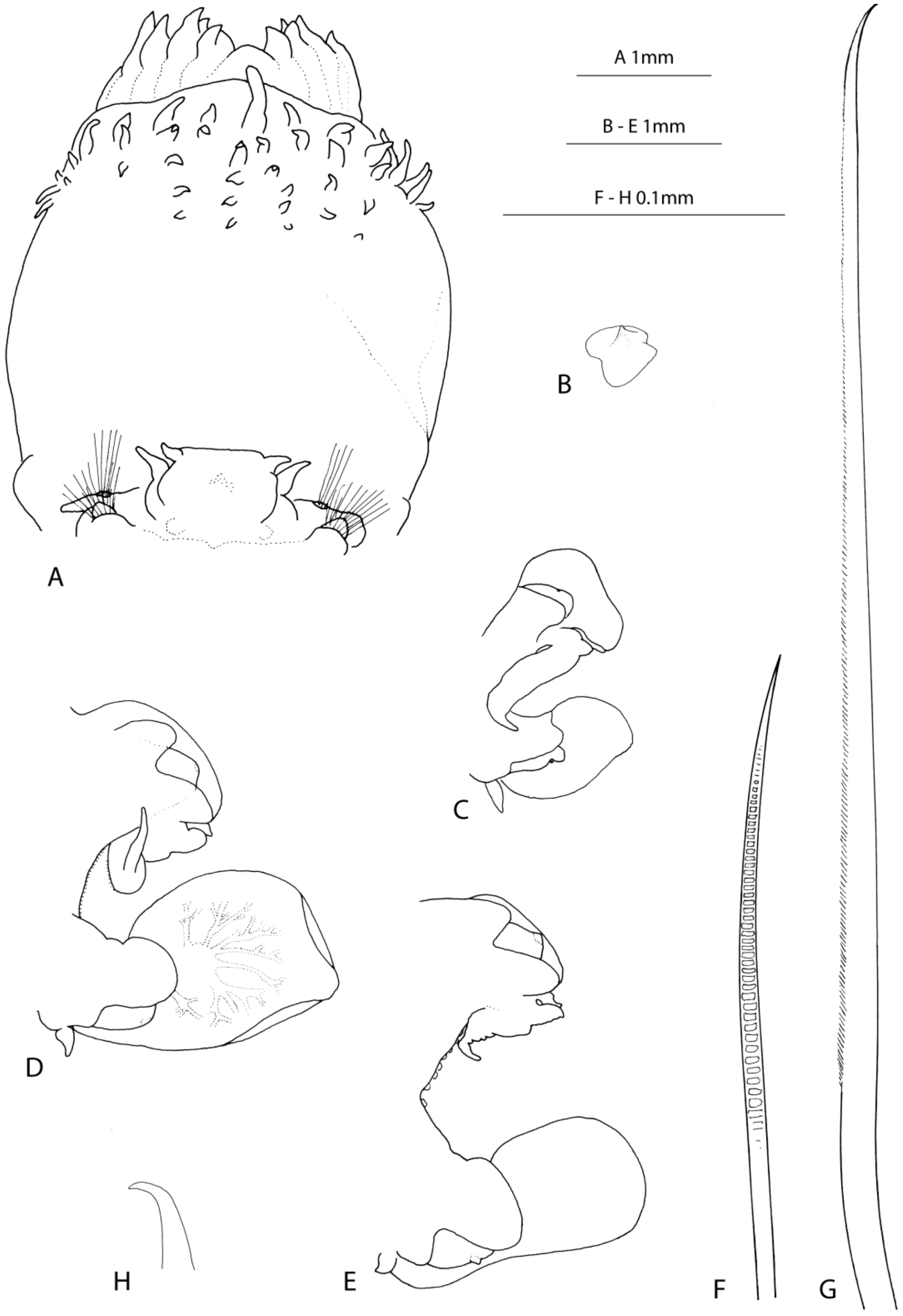


Figure 14. *Nephtys assimilis*. A. Pharynx, prostomium and first chaetiger, dorsal view; B. Jaw. C. Left parapodium of chaetiger 10, anterior view. D. Left parapodium of chaetiger 40, anterior view. E. Left parapodium of chaetiger 80, anterior view. F. Preacicular chaeta from chaetiger 40. G. Postacicular chaeta from chaetiger 40. H. Acicula from chaetiger 40.

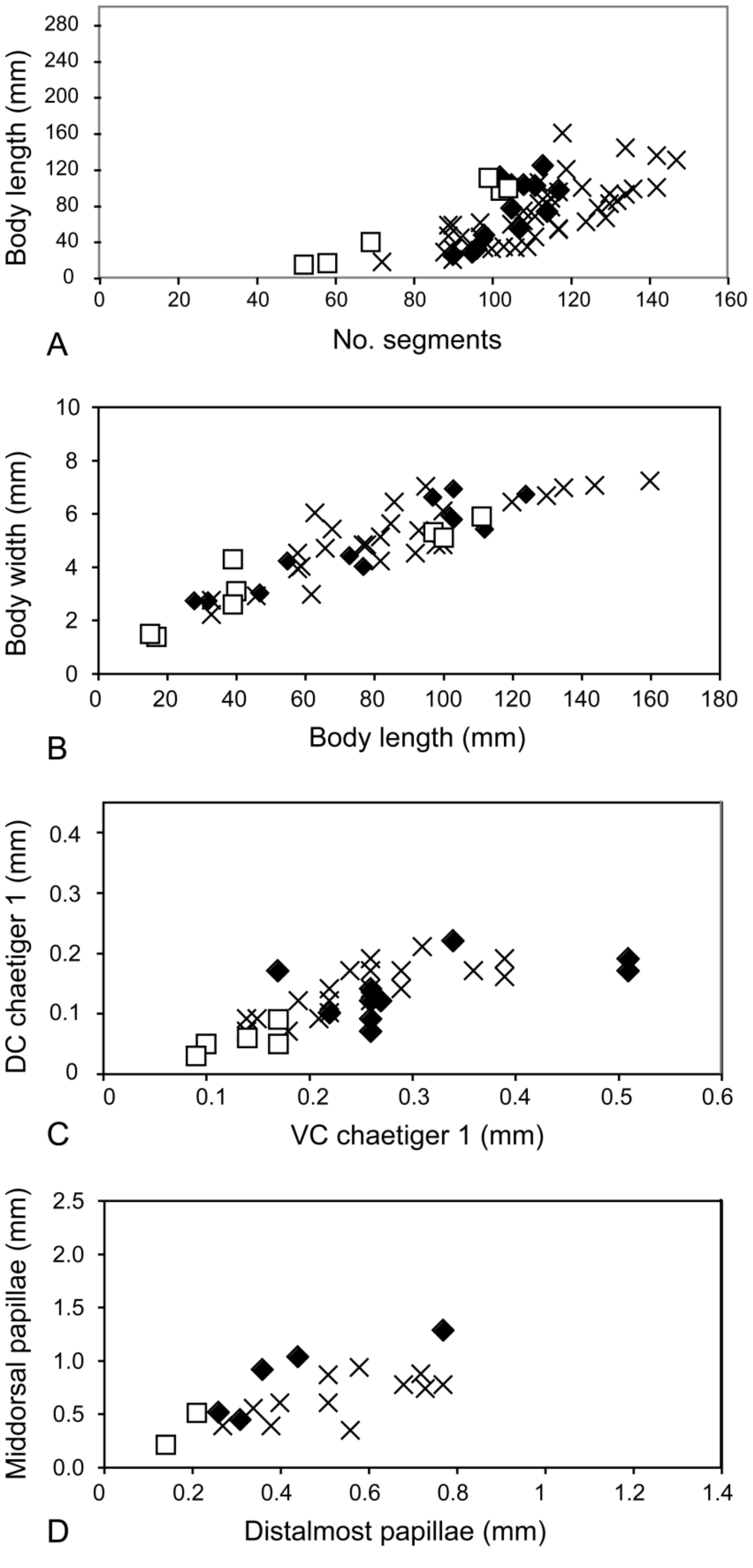


Figure 15. Relationships between: A. Number of segments and body length. B. Body length and body width. C. Length of Ventral cirri (VC) and dorsal cirri (DC) of chaetiger 1. D. Length of pharynx distalmost subterminal papillae and middorsal papilla. ◆ *Nephtys assimilis*. × *N. hombergii*. □ *N. kersivalensis*.

Nephtys assimilis Rainer 1989: 877, fig. 1A-E; Rainer 1991: 66, fig. 2A; Böggemann 1997: 80, fig. 53; Dnestrovskaya and Jirkov 2001: 195,1 fig; Laborda 2004: 396, fig. 146A, B.

? *Nephtys cuvieri* Quatrefages, 1865: 421.

? *Nephthys assimilis* Malm 1874: 78.

Nephtys hombergii Saint-Joseph 1894: 3 (partim); Augener 1912: 197 (partim); Kirkegaard 1969: 47 (partim); Hartmann-Schröder 1971: 215, fig. 70a, b (partim); Hartmann-Schröder 1974: 206 (partim); Hartmann-Schröder 1977: 88 (partim); Hartmann-Schröder 1981: 31(partim); Hartmann-Schröder 1982: 10 (partim) (not Savigny, 1822).

Nephtys scolopendroides Michaelsen 1896: 57 (partim).

Nephtys hombergii var. *vasculosa* McIntosh 1908: 21 (partim).

Nephtys caeca Heinen 1911: 13 (partim).

Nephtys incisa var. *bilobata* Heinen 1911: 25 (partim).

Nephthys breogani Laborda and Vieitez, 1984: 211, figs. 2-6; Laborda 1987: 131.

Type locality. Hellebæk, Öresund, Denmark. (neotype from off Hornbæk Bay, coll. 05.07.1963, stns 225-227, 18 m, designated by Rainer 1989).

Material examined. Atlantic Ocean. Kattegat, Denmark, Hornbæk Bay: Jul 1963, 1 complete spm, neotype (ZMUC-Pol-1470). North Sea, Scotland, Monterose Bay: 1870, 3 complete and 1 incomplete spms (NHM 1921.5.1.810-813 as *N. hombergii* var. *vasculosa*, syntypes). Portugal, off Aveiro: cruise Aveiro94, RV *Côte d'Aquitaine*, 40º41.125'N, 8º46.303'W, 13.6 m, grab, Jul 1994, 3 incomplete spms (DBUA 00060-02); 40º39.631'N, 8º45.705'W, 11.2 m, grab, Jul 1994,1 complete and 1 incomplete spms (DBUA 00060-03); 40º39.600'N, 8º45.714'W, 11.1 m, grab, Jul 1994, 1 complete and 2 incomplete spms (DBUA 00060-04); 40º38.626'N, 8º48.636'W, 21.9 m, grab, Jul 1994, 3 incomplete spms (DBUA 00060-05); 40º38.533'N, 8º48.235'W, 48.2 m, grab, Jul 1994, 1 incomplete spm (DBUA 00060-06); 40º37.683'N, 8º47.575'W, 18.0 m, grab, Jul 1994, 1 incomplete spm, (DBUA 00060-07); 40º37.657'N, 8º50.151'W, 33.1 m, grab, Jul 1994, 2 complete and 1 incomplete spms (DBUA 00060-08); cruise Aveiro95, RV *Côte d'Aquitaine*, 40º43.489'N, 8º45.210'W, 12.7 m, grab, 27 Jul 1995, 1 complete and 5 incomplete spms (DBUA 00060-01); 40º33.468'N, 8º48.232'W, 28.7 m, grab, 28 Jul 1995, 3 incomplete spms (DBUA 00060-09); Figueira da Foz, mouth of Mondego estuary: 40º08’43.352’’N, 08º52’06.218’’W, 8.5 m, 7 Dec 2005, 2 complete and 1 incomplete spms (not deposited); off Cascais: 38º39’-38º42’N, 9º25’-9º30’W, 40 m, Jul 2005, 3 complete and 2 incomplete spms (DBUA 00842-01) and 1 complete spm (MB36000105); Jan 2006, 7 complete and 2 incomplete spms (DBUA 01054-01); Lagos: 37º06.824’N, 08º38.500’W, 8 m, Apr 2006, 1 complete spm (DBUA 01061-01).

Mediterranean Sea. Naples: 1 complete spm (NHM 1919.11.6.31-33 as *N. hombergii*). South Africa: South African Collection of Prof. J. H. Day, Nov 1960, 1 incomplete spm (NHM 1961.9.71/79 as *N. hombergii*); 4 incomplete spm (NHM 1961.19.76/81 as *N. hombergii*).

Description. Examined specimens up to 124 mm long for up to 117 chaetigers. See Figure 15 for length and width measurements. Body slightly wider anteriorly, gradually tapering from median region to pygidium. Colour in ethanol cream; some larger specimens brownish mid-dorsally on anterior segments, with green pigment near prostomium and anteriormost segments; prostomium with brown pigment spot medially in anterior region; chaetae amber in anterior chaetigers, darker in posterior ones; aciculae amber with dark tips, surrounded by red pigment on anterior segments. One pair of eyes visible in smaller specimens at level chaetiger 2. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by dorsal and ventral gap (Figure 14A); middorsal papilla cirriform, long (Figure 15D); midventral papilla if present, small, similar in size and shape to distalmost subterminal papillae; subdistal region with 20-22 rows of 2-5 conical subterminal papillae (papillae of lateral rows slightly longer than dorsal or ventral ones), extending over 1/3 length of pharynx; proximal region smooth. Jaws conical, slightly incised at base (Figure 14B). Prostomium subrectangular, anterior margin slightly convex, posterior margin V-shaped extending over first chaetiger; antennae conical; palps conical with bulbous bases, subequal in length to antennae, inserted ventrolaterally on prostomium. Nuchal organs rounded, conspicuous. Parapodia biramous; interramal space “U-shaped”, with ciliation in raised pads posteriorly. Parapodia of chaetiger 1 slightly smaller than subsequent ones, directed anteriorly, parallel to prostomium; notopodial acicular lobes conical; pre- and postchaetal lamellae well developed but not extending beyond acicular lobe, rounded; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal cirri poorly developed, rounded (Figure 15C); ventral cirri conical, with broad base and tapered distally. Acicular lobes of anterior parapodia rounded, with low papiliform outgrowth on interramal side of aciculae (Figure 14C), becoming more conical and without outgrowths posteriorly; notopodial prechaetal lamellae well developed but not extending beyond acicular lobes, rounded in anterior parapodia, bilobed in following ones, postchaetal lamellae extending beyond acicular lobes (much larger in anterior parapodia), rounded; neuropodial prechaetal lamellae not extending beyond acicular lobes, unequally bilobed, with dorsal lobe much larger than ventral one, postchaetal lamellae extending well beyond acicular lobes, asymmetrically triangular in anterior parapodia, broadly rounded in following ones, directed dorsally, with internal vascular structure starting around chaetiger 13 (absent in posterior parapodia); dorsal cirri cirriform; ventral cirri conical (Figure 14C-E). Branchiae recurved, cirriform, lightly ciliated, with conspicuous conical basal projection; present from chaetiger 4 to near posterior end; occupies half of interramal space when fully developed. Chaetae short, of three kinds: barred chaetae in preacicular position (Figure 14F), finely spinulated chaetae in postacicular position (Figure 14G), and capillary chaetae on neuropodia of chaetiger 1 and near interramal space of noto- and neuropodia of other chaetigers. One acicula per ramus, posterior ones with curved tips (Figure 14H).

Remarks. Nephtys assimilis was originally described by Örsted (1843), but the type material appearently has been lost (Rainer 1989). Consequently, Rainer (1989) designated a neotype from a locality close to the original one. The original description did not mention the vascular structure of the neuropodial postchaetal lamellae or the raised ciliated pads in the interramal region of midbody and posterior chaetigers. Thus Laborda and Viéitez (1984) described *N. breogani* as a new species from NE Spain using these features to separate the two species. Rainer (1989) re-examined *N. breogani* and synonymized it with *N. assimilis*. Specimens of *N. assimilis* have been frequently identified as *N. hombergii* (especially in older studies), due to their close morphological similarity. Both species have bilobed prechaetal lamellae, a papiliform outgrowth on the acicular lobes, very large neuropodial postchaetal lamellae, branchiae starting on chaetiger 4 and a similar pattern in the pharynx papillae. Furthermore, they have overlapping geographical distributions and are often collected simpatrically or even in the same sample. However, in *N. hombergii* the neuropodial postchaetal lamellae are narrower and do not have internal vascularization, the papiliform outgrowth of the acicular lobes are much more developed and the interramal region of midbody chaetigers have low ciliated papillae instead of prominent raised pads. Differences between other morphologicaly close related species with similar geographical distribution are summarized in Table 10. *Nephtys hystricis* and *N. kersivalensis* are smaller species (Figure 15, 23) with similar in size noto- and neuropodium postchaetal lamellae, acicular lobes without outgrowths, interramal space of parapodia without raised papillae, and pharynx middorsal papillae much longer than the other subterminal papillae. Furthermore *N. hystricis* has branchiae from chaetigers 5-7 which are absent in posterior chaetigers. *Nephtys hystricis* usually occurs at higher depths, while *N. kersivalensis* frequently occurs in shallow water together with *N. hombergii* and *N. assimilis*.

Table 10. Diagnostic characteristics for the morphologically close species *N. assimilis*, *N. hombergii*, *N. hystricis* and *N. kersivalensis*.

	N. assimilis	*N. hombergii*	*N. hystricis*	*N. kersivalensis*
No. chaetigers	Up to 117	Up to 142	Up to 74	Up to 90
Branchiae start	4	4 (5)	5-7	4
Branchiae end	End of body	End of body	Before end of body	End of body
Acicular lobes extra features	Low papiliform outgrowth	Prominent papiliform outgrowth	-	Rugose area
Neuropodial postchaetal lamellae	More than twice as long as acicular lobes; with internal vascularization	More than twice as long as acicular lobes	Up to twice as long as acicular lobes	Up to twice as long as acicular lobes
Notopodial postchaetal lamellae	Much shorter than neuropodial postchaetal lamellae	Much shorter than neuropodial postchaetal lamellae	Similar to neuropodial postchaetal lamellae	Similar to neuropodial postchaetal lamellae
Interramal ciliation	In prominent raised pads	In small raised papillae	Continuous	Continuous
Pharynx middorsal papillae	Longer than subterminal pap.	Longer than subterminal pap.	Very long	Very long
Pharynx subterminal pap.	20-22 rows of 2-5 pap.	22 rows of 2-5 pap.	22 rows of 3-6 pap.	22 rows of 3-6 pap.
Depth	Intertidal – 100m	Intertidal – 1000m	100 – 800m	Shallow subtidal – 300m

Distribution. Atlantic Ocean (W Baltic, Oresund, Skagerrak, North Sea, English Channel, NW Spain, Portugal, W Africa; Mexico); Mediterranean Sea (Rainer 1989, 1991; Laborda 2004).

Habitat. Sandy to muddy sediments, most abundant in muddy sand with strong tidal currents, from the intertidal to 100 m depth (Rainer 1989, 1991; Laborda 2004).

***Nephtys caeca* (Fabricius, 1780)**

Figures 16, 17

Nereis caeca Fabricius, 1780: 304.

Aonis caeca Savigny 1822: 45.

Nephtys margaritacea Johnston, 1835: 341, fig.33; Quatrefages 1865: 423.

Nephtys ingens Stimpson, 1854: 33.

Portelia caeca Quatrefages 1865: 433.

Nephtys bononensis Quatrefages, 1865: 425.

Nephtys oerstedi Quatrefages, 1865: 427.

Nephthys caeca Malmgren 1865: 104, pl. XII, fig. 18; Ehlers 1868: 588, fig. 10-34; Saint-Joseph 1894: 16, Pl. I, fig. 14-18; Izuka 1912: 213; Fauvel 1923: 365, fig. 142A-L; Okuda 1938: 123; Okuda and Yamada 1954: 186, fig. 4.

Nephtys nudipes Ehlers, 1868: 635, pl. XXIII, fig. 61.

Nephtys caeca Möbius 1875: 168 (partim); Verrill 1881: 294, 307, 314; Webster and Benedict 1887: 709; Michaelsen 1896: 25; Whiteaves 1901: 82; McIntosh 1908: 8; Heinen 1911: 10, fig. 1; Fauvel 1933a: 39; Berkeley and Berkeley 1948 : 54, figs. 80-81; Hartman 1948: 24-25; Hartman 1950: 95; Uschakov 1955: 217, fig.68; Imajima 1961: 88, fig. 4; Uschakov and Wu 1962: 131; Fauchald 1963: 11, figs. 1D and 3D; Pettibone 1963: 203, fig. 51B; Imajima and Hartman 1964: 156; Hartmann-Schröder 1971: 220, fig. 72A-B; Paik 1973: 124, pl. I, figs. B-D; Hartmann-Schröder 1974: 208; Garwood and Olive 1981: 195, figs. 3, 4A, 5B-C and 9; Campoy 1982: 510; Lee and Jae 1983: 24, fig. 2; Imajima and Takeda 1987: 63, figs. 12A-M and 14; Jirkov 1989: 75, Figs. 15.5 and 15.6; Rainer 1991: 69, fig. 3C; Böggemann 1997: 80, fig. 54; Dnestrovskaya and Jirkov 2001: 196,1 fig; Laborda 2004: 398, fig. 146C.

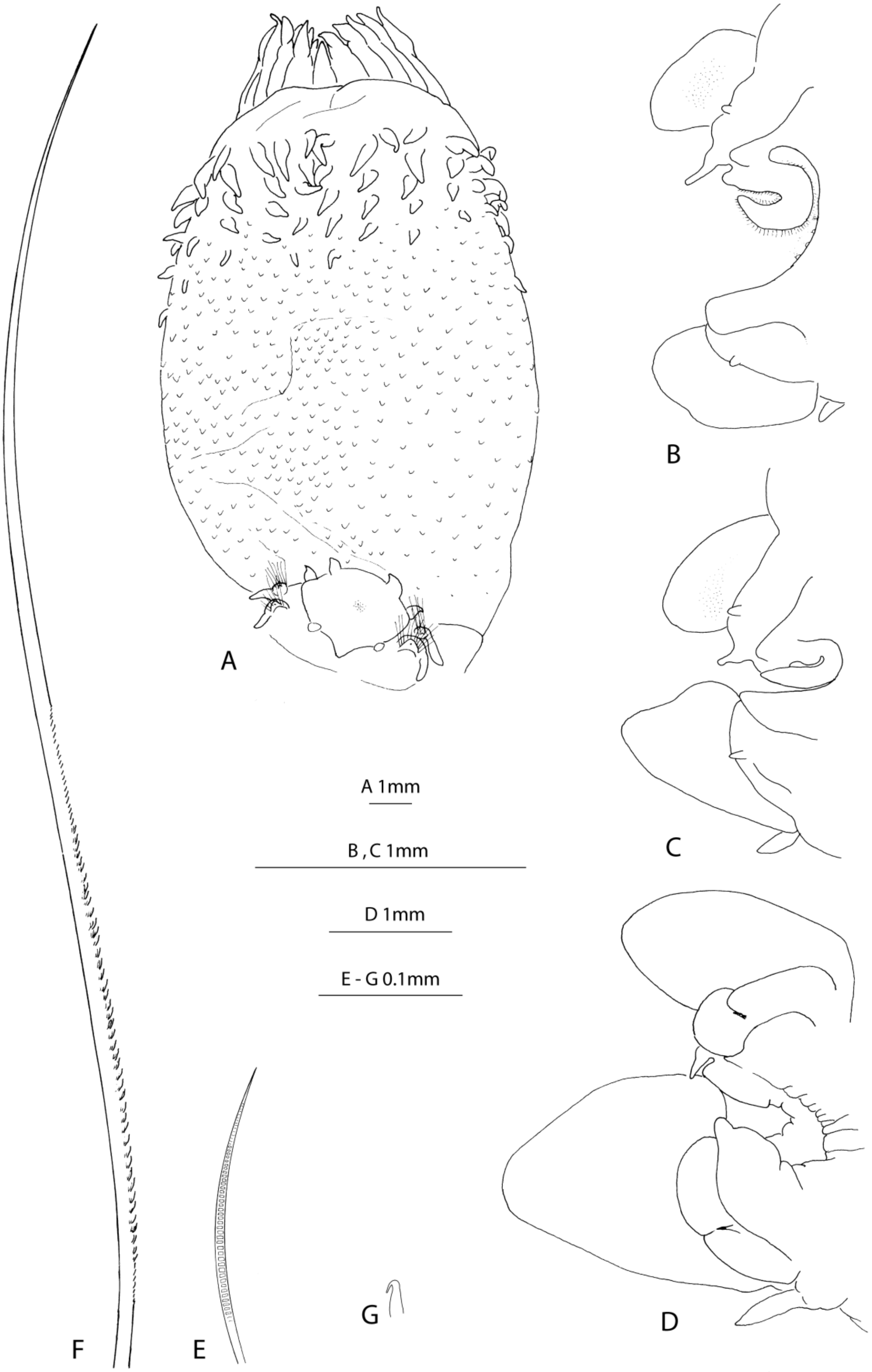


Figure 16. *Nephtys caeca*. A. Pharynx, prostomium and first chaetiger, dorsal view. B. Right parapodium of chaetiger 10, anterior view. C. Right parapodium of chaetiger 20, anterior view. D. Median parapodium of a larger specimen, anterior view. E. Pre-acicular chaeta from chaetiger 20. F. Post-acicular chaeta from chaetiger 20. G. Acicula from chaetiger 20.

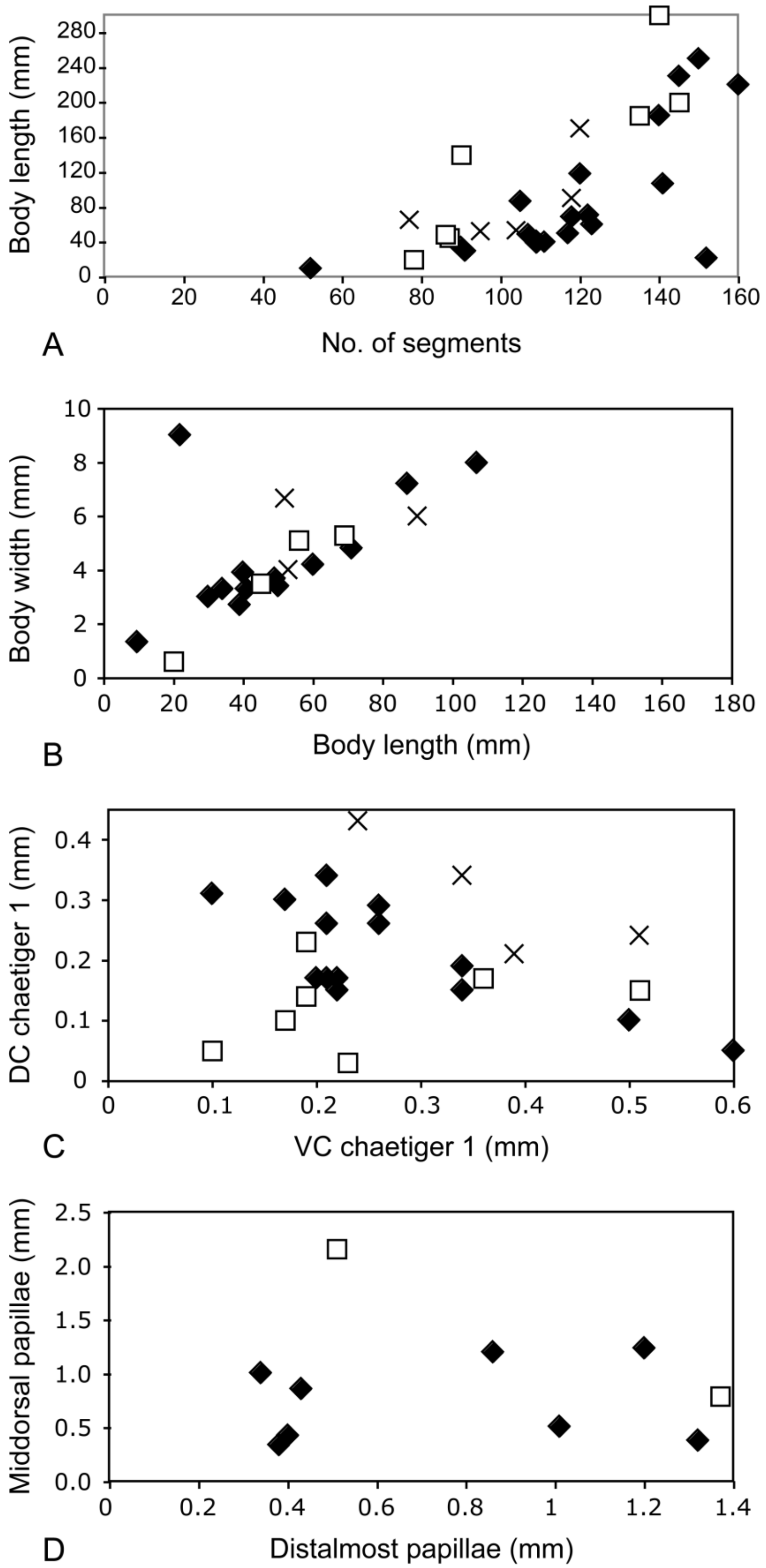


Figure 17. Relationships between: A. Number of segments and body length. B. Body length and body width. C. Length of ventral cirri (VC) and dorsal cirri (DC) of chaetiger 1. D. Length of pharynx distalmost subterminal papillae and middorsal papilla. ◆ *Nephtys caeca*. □ *N. ciliata*. × *N. longosetosa*.

Nephtys coeca [misspelling of *caeca*] Johnson 1901: 401 (partim); Nordgaard 1905: 236; Gorbunov 1946: 38; Thorson 1946: 71, fig. 34; Wesenberg-Lund 1950a: 20; Wesenberg-Lund 1950b: 7; Wesenberg-Lund 1951: 43.

Nephtys caeca var. *ciliata* McIntosh 1908: 13, pl. LXVI, fig. 3; Augener 1912: 191; ?Okuda 1939: 231, fig. 6.

Nephthys johnstoni McIntosh 1908: 34 (partim).

Nephtys hombergii Heinen 1911: 13 (partim).

Nephtys longisetosa Heinen 1911: 26 (partim).

Nephtys hombergii var. *ehlersi* Augener 1940: 137 (partim).

Type locality. Greenland.

Material examined. Arctic Ocean. Greenland: 2 incomplete spms (NHM 1921.5.1.704).

Atlantic Ocean. North Sea, Sweden, Långholmsrännan: Aug 2001, 1 complete and 1 incomplete spms (DBUA 01040-01) and 1 incomplete spm (MB36000135). Scotland, off Shetland Islands: 2 incomplete spms (NHM: 1865.3.9.18 as *N. longisetosa*). England: collected near low water mark, 1 complete spm in poor condition, syntype (NHM 1847.9.15.10); Blyth, Northumberland: intertidal, Nov 2008, 1 complete spm (MB36000152). Coast of Spain/Portugal: 1 complete and 2 incomplete spms in poor condition (NHM 1872.2.3.143).

Mediterranean Sea. Naples: 1 complete spm (NHM 1919.11.6.31-33 as *N. hombergii*).

Pacific Ocean. Canada, Nanaimo River flats, Vancouver Island, Strait of Georgia, British Columbia: Jun 1912, 7 complete and 5 incomplete spms (CASIZ 14253).

Description. Examined specimens up to 141 mm long for up to 152 chaetigers. See Figure 17 for length and width measurements. Body large and stout, slightly wider anteriorly, gradually tapering from median region to pygidium. Poor dorsal delineation between anterior segments. Colour in ethanol brownish cream; prostomium with pigmented area anteriorly; chaetae amber; tip of aciculae red. One pair of eyes visible only in small specimens at posterior limit of chaetiger 3. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by dorsal and ventral small simple papillae; middorsal and midventral papillae when present similar in size to largest subterminal ones (Figure 17D); subdistal region with 22 rows of 4-6 long conical subterminal papillae (papillae of lateral rows slightly larger than dorsal or ventral ones), extending over 1/3 length of harynx (Figure 16A); proximal region covered with very small warts (better seen in compound microscope). Jaws conical, incised at base. Prostomium subpentagonal, anterior margin slightly convex, posterior margin V-shaped and extending over chaetiger 1; antennae and palps conical; palps slightly longer than antennae, inserted ventrolaterally on median region of prostomium (Figure 16A). Nuchal organs rounded. Parapodia biramous; interramal space “U-shaped”, heavily ciliated. Parapodia of chaetiger 1 slightly smaller than subsequent ones, anteriorly directed, parallel to prostomium; notopodial acicular lobes rounded, prechaetal lamellae rudimentary, postchaetal lamellae well developed but not extending beyond acicular lobes, rounded; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal cirri well developed, cirriform (Figure 16C); ventral cirri digitiform, with broad base and tapering distally. Acicular lobes of following parapodia rounded in smaller specimens to distinctly bilobed in larger specimens; prechaetal lamellae poorly developed, rounded, becoming progressively lower toward median segments; postchaetal lamellae extending well beyond acicular lobes, rounded and directed ventrally in notopodium, triangular in neuropodium; dorsal cirri small, lameliform, with enlarged base and acute tip; ventral cirri conical (Figure 16B-D). Branchiae recurved, cirriform, heavily ciliated, with a small rounded papillae-like basal projection; present from chaetiger 4 (rarely from 5) to near posterior end; occupy all interramal space when fully developed. Chaetae of same size or slightly longer than postchaetal lamellae, of three kinds: barred chaetae in preacicular position (Figure 16E), coarsely spinulated chaetae in postacicular position (Figure 16F), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips (Figure 16G).

Remarks. *Nephtys caeca* is a common species in cold-water circumboreal areas, although, occasionally, it can also occur in southern regions. Since it was the first nephtyid species described and it is also very common in northern Europe along with other species, much of the older *Nephtys* material is incorrectly identified as *N. caeca*. There has been also a considerable confusion between this species and the morphologically close species *N. longosetosa*, especially when the “*N. caeca* var. *ciliata*” form is present. This form has unusual long chaetae and is considered to be a pre-reproductive dispersal/migratory phase of the *N. caeca* life cycle (Garwood & Olive 1981). *Nephtys caeca* and *N. longosetosa* are very similar in size (Figure 17) but differ by the chaetiger were branchiae starts (4 in the former, 3 in the later), the presence of a long middorsal papilla in the pharynx of *N. longosetosa* (in *N. caeca*, when present, of same size as other subterminal papillae), the presence of warts in the proximal region of *N. caeca* pharynx (proximal region smooth in *N. longosetosa*), and the different shape and proportions of the various parapodial lamellae. Postchaetal lamellae in *N. caeca* are both much larger than acicular lobes and broadly rounded, while in *N. longosetosa* only the neuropodial postchaetal lamellae extend well beyond the acicular lobes and have a narrower appearance due to a small ventral incision. Garwood and Olive (1981), Fauchald (1963) and Imajima and Takeda (1987) mention that *N. caeca* does not have middorsal nor midventral papillae. On the contrary, Rainer (1991) mentions that a slender middorsal papilla is often present in *N. caeca* and large animals may have a similar midventral papilla. In some of the specimens examined, we observed a median papillae of the same length as the other subterminal papillae but slightly more cirriform, although the presence or absence is sometimes difficult to asses.

Distribution. Arctic Ocean (Greenland); Atlantic Ocean (from the Arctic to the English Channel, including the North Sea, Skagerrak, Kattegat, western and middle Baltic Sea; NW Spain; Portugal); Mediterranean Sea (as far as the Black Sea); Pacific Ocean (Sea of Okhotsk, Japan, Yellow sea, China sea; NE Pacific south to central California - rare) (Hartman 1938; Fauchald 1963; Imajima & Takeda 1987; Rainer 1991; Jung & Hong 1997; Laborda 2004).

Habitat. In a wide variety of sediments (sand, gravel and mud), from the lower intertidal to nearly 1000 m depth (Fauchald 1963; Rainer 1991; Jung & Hong 1997; Laborda 2004).

Nephtys ciliata **(O. F. Müller, 1776)**

Figures 17, 18

Nereis ciliata Müller, 1776: 17; Müller 1789: 14, pl. VXXXIX, figs. 1-4.

Nephtys borealis Örsted, 1843: 32.

Nephthys ciliata Malmgren 1865: 104, pl. XII, fig. 17; Malmgren 1867: 17; Ehlers 1868: 629, pl. XXIII, fig. 36; Kupffer 1873: 150; Möbius 1873: 113; Malm 1874: 76; ?McIntosh 1879: 501; Théel 1879: 24; Moore 1903: 433; Nordgaard 1905: 235;

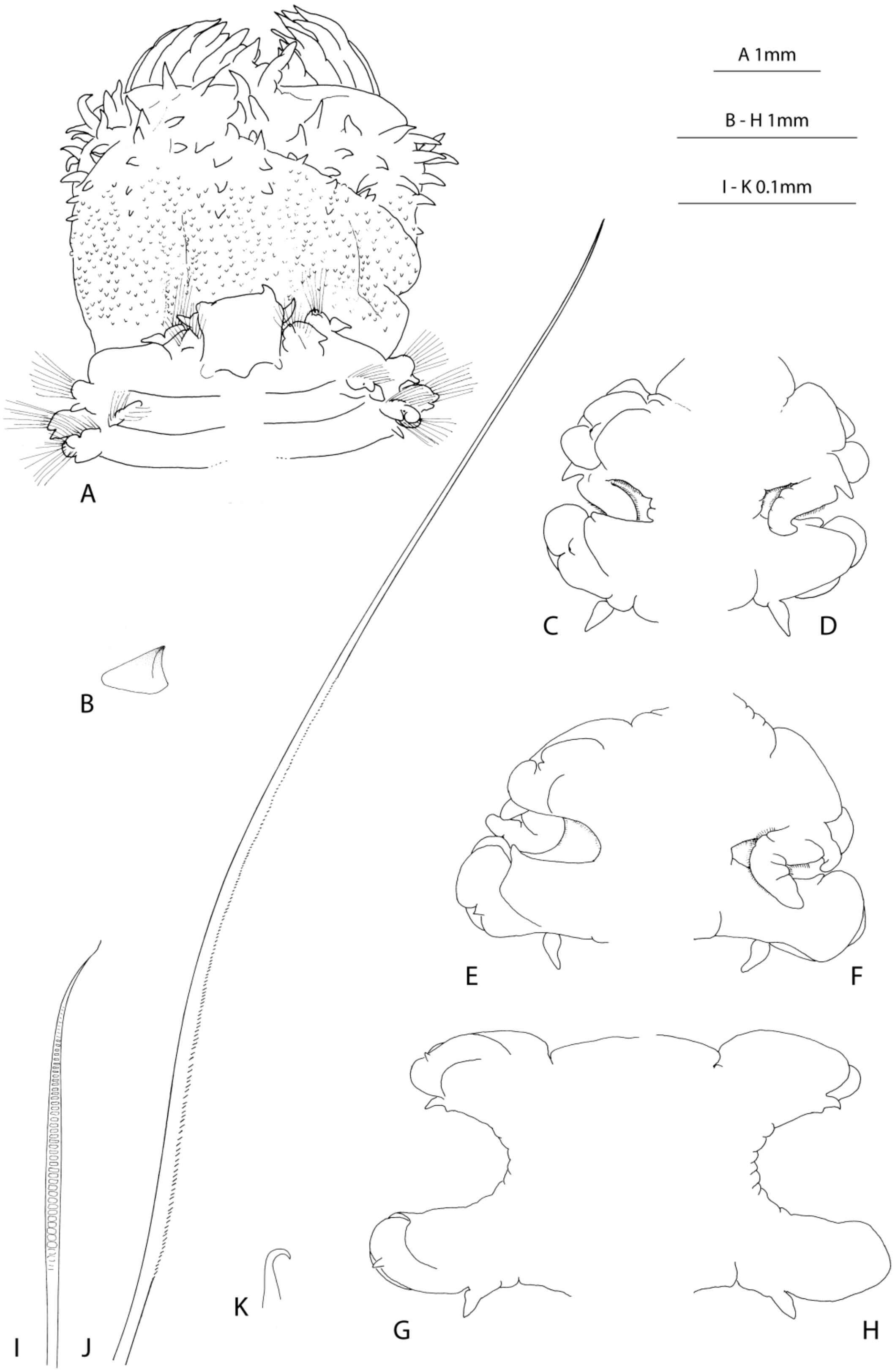


Figure 18. *Nephtys ciliata*. A. Pharynx, prostomium and anteriormost chaetigers, dorsal view. B. Jaw. C. Right parapodium of chaetiger 10, anterior view. D. Same, posterior view. E. Right parapodium of chaetiger 40, anterior view. F. Same, posterior view. G. Right parapodium of chaetiger 70, anterior view. H. Same, posterior view. I. Preacicular chaeta from chaetiger 20. J. Postacicular chaeta from chaetiger 20. K. Acicula from chaetiger 20.

Heinen 1911: 21, fig. 5 (partim); Izuka 1912: 215; Fauvel 1923: 371, fig. 145A-B; Ditlevsen 1937: 20; Takahashi 1938: 204; Pettibone 1954: 270.

Nephthys caeca Möbius 1875: 168 (partim).

Nephtys ciliata Hartman 1944: 339, pl. 47, fig. 10; Hartman 1950: 95; Imajima 1961: 91; Eliason 1962: 249; Fauchald 1963: 5, figs. 1B, 2E and 3A; Pettibone 1963: 202, fig. 51C (partim); Imajima and Hartman 1964: 157; Kirkegaard 1969: 46; Hartmann-Schröder 1971: 218, fig. 71A (partim); not Banse and Hobson 1971: 75 (?= *N. Pente*); Campoy 1982: 511; ?Imajima and Takeda 1987: 67; Jirkov 1989: 77, Figs. 16.4 and 16.5; Rainer 1991: 70, fig. 3A; Dnestrovskaya and Jirkov 2001: 197,1 fig; Laborda 2004: 399, fig. 146D; not McIntosh 1908: 23.

Nephtys hombergii Augener 1912: 202 (partim).

Nephtys ciliata form *longosetosa* not Augener 1940: 137.

Nephtys hombergii var. *ehlersi* Augener 1940: 137 (partim).

Type locality. Norway.

Material examined. Arctic Ocean. Svalbard, S Hinlopenstretet, E Olav V Land: RV *Jan Mayen*, 78º40.623'N, 21º23.796'E, 60 m, Sneli-sledge, Sep 2003, 1 incomplete spm (MB36000139).

Atlantic Ocean. Iceland. Sandgerdi: collected at low tide, Jul 2001, 2 complete and 2 incomplete spms (DBUA 00179-01 to 04); NW Iceland, Langeness Bank: between 80 and 95 fms depth, Otter trawl, Aug 1953, 1 incomplete spm (NHM 1954.1.1.198 as *N. hombergii*). North Sea, Sweden, Skagerrak, Bohuslän: 58º10.856'N-58º11.049'N, 10º53.439'E-10º53,024'E, 162-191 m, Aug 2006, 1 complete spm (MB36000157). Scotland, St. Andrews: 1 incomplete spm (NHM 1921.5.1.855/856 as *N. cirrosa*).

Description. Examined specimens up to 69 mm long for up to 90 chaetigers. See Figure 17 for length and width measurements. Body segments of about the same width, last segments abruptly tapering. Poor dorsal delineation between anterior segments. Colour in ethanol cream; chaetae amber; aciculae of anterior segments with red tips and dark tips in median and posterior segments. Eyes not visible. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by small dorsal and ventral elevation; middorsal papilla long and cirriform (Figure 17D); midventral papilla small, similar in size and shape to distalmost subterminal ones; subdistal region with 22 rows of 4-6 (sometimes 3-7) conical subterminal papillae, extending over 1/2 length of pharynx; proximal region covered with small warts (Figure 18A). Jaws conical (Figure 18B). Prostomium subquadrangular, anterior margin straight, posterior margin V-shaped (Figure 18A); antennae and palps conical, short, subequal in length; palps inserted ventrolaterally on anterior region of prostomium, slightly behind antennae. Nuchal organs rounded. Parapodia biramous; interramal space “U-shaped”, heavily ciliated. Parapodia of chaetiger 1 equal in size to subsequent ones, directed anteriorly, parallel to prostomium; notopodial acicular lobes conical, prechaetal lamellae rudimentary, postchaetal lamellae well developed but not extending beyond acicular lobes, rounded; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal cirri conical; ventral cirri digitiform, with broad base and cirriform tip. Acicular lobes bilobed in anterior and median parapodia, rounded in posterior parapodia; prechaetal lamellae poorly developed, rounded, becoming rudimentary in posterior parapodia; postchaetal lamellae well developed but not extending beyond acicular lobes, rounded, directed dorsaly in neuropodium; dorsal and ventral cirri conical (Figure 18C-H). Branchiae recurved, short and thick, heavily ciliated; present from chaetigers 7-11 to near posterior end; occupy all interramal space when fully developed, rapidly decrease in size posteriorly and become vestigial or absent in last chaetigers. Chaetae of three kinds: barred chaetae in preacicular position (Figure 18I), spinulated chaetae in postacicular position (Figure 18J), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips (difficult to see in all specimens observed; Figure 18L).

Remarks. Nephtys ciliata was recorded only once for the Mediterranean Sea by Desbruyères *et al.* (1972), and that is the reason of being included here. Campoy (1982) and Laborda (2004) also include this species in the Iberian Peninsula fauna based on that same reference. However, specimens from that locality were not examined and there are no other records of this species for areas southern than English Channel. Furthermore, the descriptions given by Campoy (1982) and Laborda (2004) mention a wide range of chaetigers where branchiae first appear, which indicates that they may have dealt with a complex of species. We therefore consider those references as doubtful and believe this species have a more circumpolar distribution. Also the references of Hartman (1950) and Imajima and Takeda (1987) refer to the occurrence of the first branchiae on chaetigers 5-7 rather than 7-10. These references must be considered with caution since they probably also include *N. pente* another circumpolar species.

Distribution. Arctic Ocean; Atlantic Ocean (Greenland, Iceland, Norway, Skagerrak, Kattegat, western and middle Baltic Sea, Denmark, North Sea); Pacific Ocean (Alaska; Bering Sea; Sea of Okhotsk, Japan) (Hartman 1938; Imajima & Takeda 1987; Rainer 1991). There are further reports of this species from the Mediterranean Sea (Spain, as far as the Black Sea) (Campoy 1982; Laborda 2004), but these records require confirmation.

Habitat. Sand and mud, from the intertidal to 960 m depth (Rainer 1991; Laborda 2004).

Nephtys cirrosa **Ehlers, 1868**

Figures 19, 20

? Portelia rosea Quatrefages, 1865: 431, pl. VII, fig. 12-15.
Nephthys cirrosa Ehlers, 1868: 624, pl. XXIII, figs. 6-7, 37, 38; McIntosh 1908: 36; Augener 1912: 199; La Greca 1946: 277; Guille and Laubier 1966: 267; Hartmann-Schröder 1974: 208.
Nephthys johnstoni McIntosh 1908: 34 (partim).
Nephtys ehlersi Heinen, 1911: 34, pl. I, fig. 1 and 2.
Nephthys longisetosa Heinen 1911: 26 (partim).
Nephthys cirrosa Fauvel 1923: 369, fig. 144C-H; Fauvel 1936: 40.
Nephtys cirrosa Gibbs 1969: 320 (juvenile stages); Foret-Montardo 1969: 812, pl. II, fig. 117; Hartmann-Schröder 1971: 214, fig. 69A-E; Hartmann-Schröder 1996: 222, fig. 97; Campoy 1982: 512; Laborda 1987; Rainer 1991: 72, fig. 3F; Dnestrovskaya and Jirkov 2001: 199,1 fig; Laborda 2004: 400, fig. 147A-C.
Nephtys cf. cirrosa Böggemann 1997: 80, fig. 55.

Type locality. England.

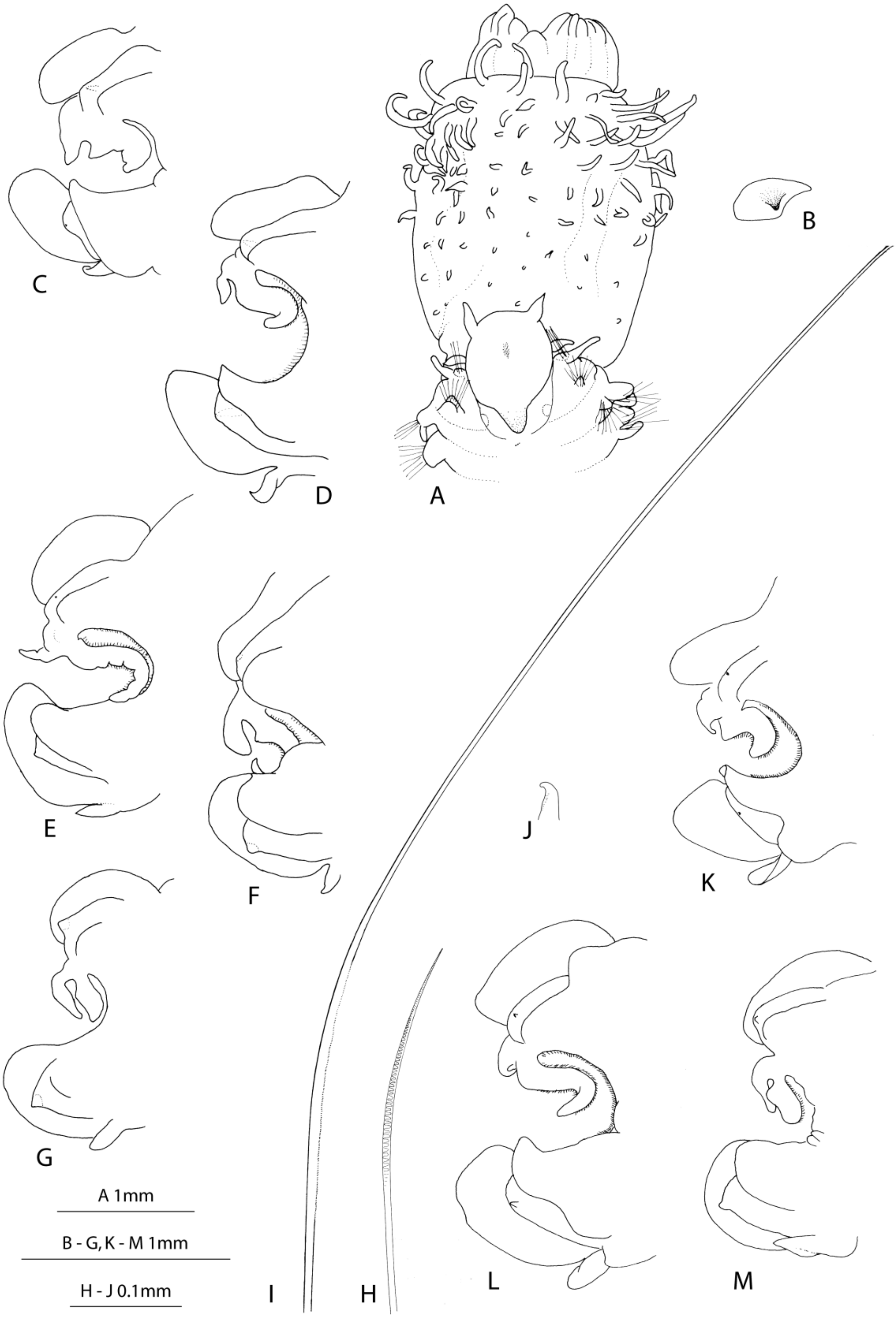


Figure 19. *Nephtys cirrosa* (form A). A. Pharynx, prostomium and anteriormost chaetigers, dorsal view. B. Jaw. C. Right parapodium of chaetiger 10, anterior view. D. Right parapodium of chaetiger 21, anterior view. E. Right parapodium of chaetiger 40, anterior view. F. Right parapodium of chaetiger 80, anterior view. G. Right parapodium of chaetiger 88, anterior view. H. Preacicular chaeta from chaetiger 40. I. Postacicular chaeta from chaetiger 40. J. Acicula from chaetiger 88. Form B. K. Right parapodium of chaetiger 10, anterior view. L. Right parapodium of chaetiger 40, anterior view. M. Right parapodium of chaetiger 90, anterior view.

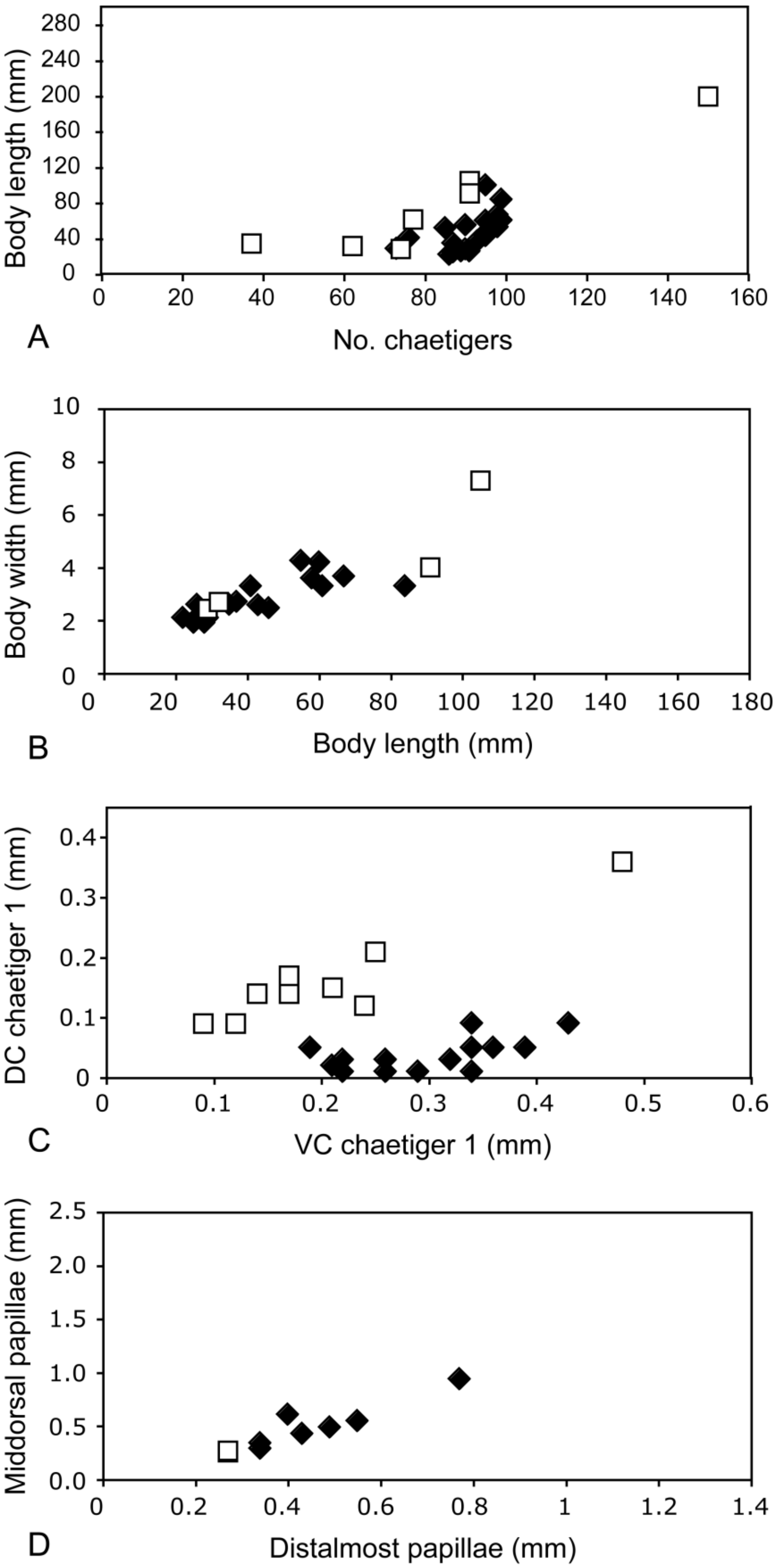


Figure 20. Relationships between: A. Number of segments and body length. B. Body length and body width. C. Length of ventral cirri (VC) and dorsal cirri (DC) of chaetiger 1. D. Length of pharynx distalmost subterminal papillae and middorsal papilla. ◆ *Nephtys cirrosa*. □ *N. paradoxa*. Minute dorsal cirri were scored as 0.01.

Material examined. Atlantic Ocean. North Sea, Scotland, St. Andrews: 2 complete and 1 incomplete spm (NHM 1921.5.1.855/856); Fyfe, “Young Wom Area”: 1 complete spm (NHM 1951.5.2.59 as *N. hombergii*). Irish Sea, Wales, Cemaes Bay: at low tide, Jul 1969, 1 incomplete spm (NHM 1971.160). Spain, Pontevedra, Alanzada beach: 42º27’03.61’’N, 8º52’46.48’’W, intertidal, Mar 2005, 1 complete spm (DBUA 00843-01); Combarro: 42º26’01.47’’N, 8º42’04.77’’W, intertidal, Mar 2005, 2 incomplete spms (DBUA 00843-02); Ensenada O Bao, O Grove: 42º27’24.49’’N, 8º52’16.53’’W, intertidal, Mar 2005, 4 complete spms (DBUA 00843-03), and 1 incomplete spm (MB36000106). Portugal, Vila Praia de Âncora: 41º49.26’N, 8º52.64’W, 12 m, grab, Aug 2001, 1 complete spm (DBUA 00370-01); off Aveiro: cruise AVEIRO94, RV *Côte d’Aquitaine,* 40º39.560’N’, 8º48.327’W, 22.3 m, grab, Jul-Aug 1994, 1 complete and 1 incomplete spms (DBUA 00062-01); 40º39.598’N’, 8º49.561’W, 28.7 m, grab, Jul-Aug 1994, 1 incomplete spm (DBUA 00062-02); 40º38.603’N’, 8º50.038’W, 30.8 m, grab, Jul-Aug 1994, 2 incomplete spms (DBUA 00062-03); cruise AVEIRO95, RV *Côte d’Aquitaine,* 40º48.578’N’, 8º44.192’W, 15.6 m, grab, 1 Aug 1995, 1 complete and 6 incomplete spms (DBUA 00062-04); Ria de Aveiro: subtidal, grab, Mar 1993, 5 complete and 3 incomplete spms (DBUA 00097-01); 1 complete and 7 incomplete spms (DBUA 00097-02); 2 complete spms (DBUA 00097-03); 1 incomplete spm (DBUA 00097-04); Figueira da Foz, Mondego estuary: 40º08’43.352’’N, 08º52’06.218’’W, 8.5 m, Mar 2006 1 incomplete spm, (not deposited); 40º07’57.270’’N, 08º51’07,744’’W, 2.0 m, Nov 2005, 11 incomplete spms (not deposited), and Mar 2006, 2 complete spms (not deposited); 40º07’29.447’’N, 08º50’47.313’’W, 2.5 m, Nov 2005, 13 incomplete spms (not deposited); 5.2 m, Nov 2005, 2 incomplete spms (not deposited); 40º08’33.179’’N, 08º49’38.073’’W, 4.5 m, Nov 2005, 10 incomplete spms (not deposited), and Mar 2006, 4 complete spms (not deposited); 40º08’21,405’’N, 08º48’55.126’’W, 5.2 m, Nov 2005, 5 incomplete spms (not deposited), and Mar 2006, 2 complete spms (not deposited); Sado Estuary: 38º31.075’N, 8º54.056' W, 10 m, Jun 2005, 1 complete spm (DBUA 00844-01); Lisboa, Trafaria: 38º40.31’N, 9º14.20’W, shallow water, Jul 2006, 1 complete spm (MB36000107); Setúbal, Troia Peninsula: 38º26.25’N, 9º06.76’W, shallow water, Jul 2006, 12 complete and 11 incomplete spms (DBUA 00846-01), and 2 incomplete spms (MB36000108 and MB36000109); Sines: 37º58.15’N, 8º52.29’W, shallow water, Jul 2006, 1 complete spm (DBUA 00847-01), and 2 incomplete spms (MB36000110 and MB36000111); Vila Nova de Milfontes: 37º43.30’N, 8º47.25’W, shallow water, Jul 2006, 6 complete and 6 incomplete spms (DBUA 00848-01), and 1 incomplete spm (MB36000112); Ria do Alvôr: 37º07.22’N, 8º37.14’W, shallow water, Jul 2006, 8 complete and 5 incomplete spms (DBUA 00849-01), and 3 incomplete spms (MB36000113, MB36000114 and MB36000115); Portinho de Ferragudo: 37º07.48’N, 8º31.24’W, shallow water, Jul 2006, 4 complete and 5 incomplete spms (DBUA 00850-01), and 2 incomplete spms (MB36000116 and MB36000117).

Description. Examined specimens up to 84 mm long for up to 99 chaetigers. See Figure 20 for length and width measurements. Body slender, slightly wider anteriorly, gradually tapering from median region to pygidium. Poor dorsal delineation between anterior segments. Colour in ethanol yellowish-white; prostomium of some specimens with median pigment spot on anterior region and some orange pigmentation posteriorly; chaetae and aciculae amber. One pair of eyes visible only in small specimens at the level of chaetigers 1-2. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by dorsal and ventral gap; middorsal papilla cirriform, similar in size or longer than distalmost subterminal papillae (Figure 20D); midventral papillae absent. Subdistal region with 22 rows of 4-9 long, cirriform subterminal papillae, extending to base of pharynx (proximal ones may be very small) (Figure 19A); proximal region smooth. Jaws conical (Figure 19B). Prostomium subpentagonal; anterior and lateral margins convex, giving the prostomium a rounded appearence; posterior margin V-shaped extending over first chaetiger; antennae and palps long, conical; palps longer than antennae, inserted ventrolaterally on median region of prostomium. Nuchal organs rounded. Parapodia biramous; interramal space “U-shaped”, heavily ciliated. Parapodia of chaetiger 1 smaller than subsequent ones, directed anteriorly, parallel to prostomium; notopodial acicular lobes conical, pre- and postchaetal lamella well developed but not extending beyond acicular lobes, rounded; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal cirri poorly developed (Figure 20C); ventral cirri cirriform with slightly broad base. Notopodial acicular lobes of following parapodia rounded or slightly bilobed (with acicula in the ventral lobe) in anterior and median parapodia, conical in posterior parapodia; neuropodial acicular lobe conical; notopodial prechaetal lamellae rudimentary and rounded or well developed and bilobed, postchaetal lamellae extending beyond acicular lobes, rounded; neuropodial prechaetal lamellae well developed but not extending beyond acicular lobes, rounded or slightly bilobed, directed dorsaly and surrounding the dorsal part of the acicular lobe, rudimentary in posterior parapodia; postchaetal lamellae extending beyond acicular lobes, rounded; dorsal cirri conical to cirriform, equal in length or longer than branchiae on the last chaetigers; ventral cirri conical, lamelliform (Figure 19C-G, K-M). Branchiae recurved, cirriform, thick in anterior and posterior parapodia, heavily ciliated, with small rounded papillae-like basal projection; present from chaetiger 4 to near posterior end; occupy all interramal space when fully developed; strongly decreases in size posteriorly, reaching the same length as dorsal cirri in posteriormost chaetigers. Chaetae of three kinds: barred chaetae in preacicular position (Figure 19H), very finely spinulated chaetae in postacicular position (Figure 19I), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips (very dificult to see; Figure 19J).

Remarks. Nephtys cirrosa was erected by Ehlers (1968) for specimens having acicular lobes rounded to bilobed and notopodial prechaetal lamellae rudimentary, apart from the other diagnostic features that separates it from other species. Later, Heinen (1911) described *N. ehlersi* from specimens having clearly bilobed notopodial prechaetal lamellae. *Nephtys ehlersi* was synonymized several times with other species such as *N. hombergii* and *N. kersivalensis* and was most recently synonymized with *N. cirrosa* by Rainer (1991), who presents a complete synonymy history for *N. ehlersi*. Rainer (1991) examined the type material of *N. ehlersi* and concluded that it conformed to the descriptions of *N. cirrosa* except for having bilobed prechaetal lamellae and lacking elongated dorsal cirri in posterior chaetigers. However, he also noted that the posterior chaetigers of the type specimen appeared to be in the process of regeneration. Thus the elongated dorsal cirri, typical of *N. cirrosa*, might not be completely developed in that specimen. As for the bilobed prechaetal lamellae, Rainer also found this feature in at least some of the North Sea *N. cirrosa* specimens. Also Foret-Montardo (1969) and Böggemann (1997) found specimens with bilobed prechaetal lamellae in Marseille (Mediterranean Sea) and Germany, respectively. The specimens from Portugal examined in this study also have this type of lamellae. We thus consider the existence of two forms of *N. cirrosa* (A and B). Form A (originally described by Ehlers, 1868) with acicular lobes rounded to bilobed, notopodial prechaetal lamellae rudimentary and pharynx middorsal papilla subequal in size to the other subterminal papillae (Figure 19C-G). Form B has acicular lobes rounded to conical, notopodial prechaetal lamellae well developed and bilobed and pharynx middorsal papilla longer than the other subterminal papillae (Figure 19K-M). Furthermore, form B specimens usually have larger postchaetal lamellae and orange pigmentation in prostomium. In both forms the branchiae of posteriormost chaetigers are of same length as dorsal cirri, a consistent and diagnostic feature for the species *N. cirrosa*. Between these two extremes there are intermediate forms making difficult the distinction between two potentially different species. Although we examined only a few specimens from northern regions, the northernmost specimens (from Scotland, Wales, North Sea and NW Spain) are mostly form A while southernmost specimens (from North Sea, German, Portugal and Marseille) match mostly form B. Further investigation and, possibly, molecular analyses are required to resolve this problem. If future research provides the evidence to consider two distinct species then the name *N. ehlersi* may be reinstated to designate the specimens ascribed presently to form B.

Distribution. Atlantic Ocean (Irish Sea; from North Sea to Côte d'Ivoire); Mediterranean Sea; Black Sea (Foret-Montardo 1969; Rainer 1991; Laborda 2004).

Habitat. Clean to muddy, coarse and fine sands, from shallow waters to 45 m depth. Most common in clean, fine sand in the lower intertidal (Rainer 1991; Laborda 2004).

Nephtys hombergii **Savigny, 1822**

Figures 15, 21

Nephthys hombergii Savigny, 1822: 34; ?Ehlers 1868: 619, figs. 7 and 42 (partim); Théel 1879: 26; Langerhans 1880: 302; Saint-Joseph 1894: 3, pl. I, figs. 1-13 (partim); Charrier 1907: 297-306; McIntosh 1908: 17 (partim); Heinen 1911: 16, figs. 3-4 (partim); Augener 1912: 197, 202 (partim); Fauvel 1923: 367, fig. 143A-D; Fauvel 1936: 40; Ditlevsen 1929: 20; Tebble 1955: 102; Rullier and Amoureux 1970: 124.

Nereis scolopendroides delle Chiaje, 1822 in Audouin and Milne Edwards 1833: 260.
Nephtys neapolitana Grube 1840: 71.
Nephthys macandrewi Baird 1871: 94.
Nephtys scolopendroides Michaelsen 1896: 57 (partim).

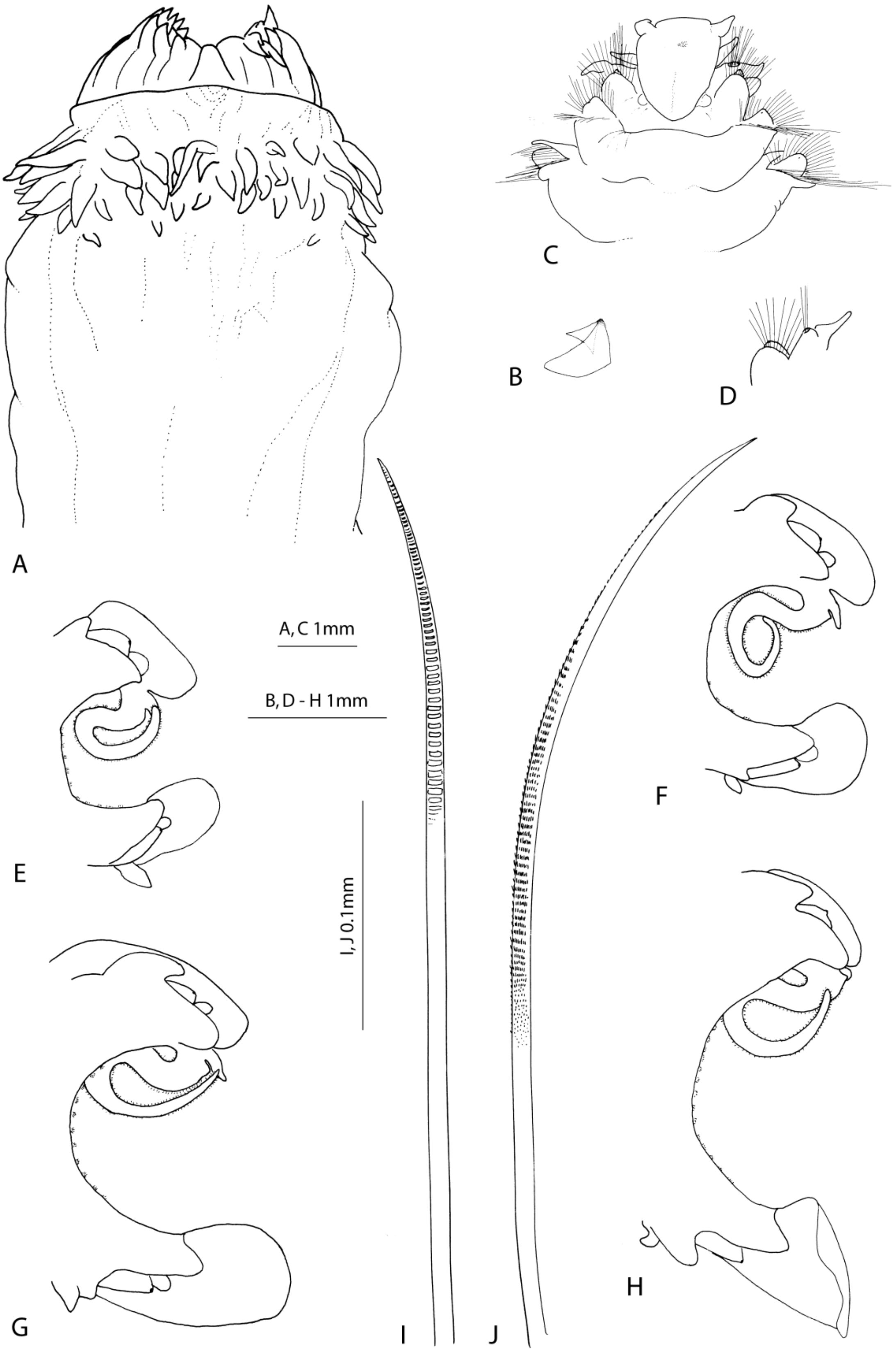


Figure 21. *Nephtys hombergii*. A. Pharynx, dorsal view. B. Jaw. C. Prostomium and anteriormost chaetigers, dorsal view. D. Right parapodium of chaetiger 1, posterior view. E. Left parapodium of chaetiger 10, anterior view. F. Left parapodium of chaetiger 20, anterior view. G. Left parapodium of chaetiger 40, anterior view. H. Left parapodium of chaetiger 80, anterior view. I. Preacicular chaeta from chaetiger 40. J. Postacicular chaeta from chaetiger 40.

Nephthys hombergii var. *kersivalensis* McIntosh 1908: 20 (partim).

Nephthys hombergii var. *vasculosa* McIntosh 1908: 21 (partim).

Nephtys hombergii Hartman 1950: 101, pl. 17, fig. 2; Day 1953: 431; Eliason 1962: 249; Fauchald 1963: 3, figs. 1G, 2D and 3E; Foret-Montardo 1969: 810, pl. I, figs. 1-6; Gibbs 1969: 320 (juvenile stages); Hartmann-Schröder 1971: 215, fig. 70A-B (partim); Hartmann-Schröder 1974: 88 (partim); Clay 1974; not Hartmann-Schröder 1981: 31; Hartmann-Schröder 1982: 10; Campoy 1982: 515; Laborda 1987; Rainer 1991: 73, fig. 2B; Hartmann-Schröder 1996: 224, fig. 98; Böggemann 1997: 80, fig. 56; Dnestrovskaya and Jirkov 2001: 199,1 fig; Laborda 2004: 402, fig. 147D-E.

Nephtys (Nephtys) hombergii Day 1967: 344, fig. 15.2G-I.

not *Nephtys hombergii* var. *kersivalensis* Hartmann-Schröder 1971: 217.

Type locality. Coast of France.

Material examined. Atlantic Ocean. North Sea, Sweden, Koster area, western coast of Sweden: 8 Aug 2001, 1 incomplete spm (MB36000136); Kattegat, Anholt-Lysegrund: Jan 1873, 4 incomplete spms (GNHM Polych. 1232, syntypes of *N. emarginata*). Scotland, St. Andrews, Fyfe, “Young Wom Area”: 1 complete spm (NHM 1951.5.2.59). England, off Northumberland: 48 m, Apr 2008, 2 incomplete spms (DBUA 01056-01), and 1 incomplete spm (MB36000146); Blyth, Northumberland: intertidal, Nov 2008, 1 complete and 1 incomplete spm, (MB36000147 and MB36000148). SW Ireland, off Valentia Island: 1-160 fms, 6 spms (NHM 1921.5.1.796-806, syntypes of *N. kersivalensis*). NW France, Bretagne, Roscoff: low tide, Sep 2001, 1 incomplete spm (DBUA 01039-01), and 1 incomplete spm (MB36000134); Le Guillec Estuary: intertidal, 1 incomplete spm (DBUA 00213-01). Spain, Coruña: 1 complete spm (NHM 1863.9.19.12, holotype of *N. macandrewi*). Portugal, Vila Praia de Âncora: 41º48.83’N, 8º52.24’W, 10 m, Sep 2005, 3 complete spms (DBUA 00851-01); Matosinhos: subtidal, Oct 2005, 3 incomplete spms (DBUA 00852-01, 02); Ria de Aveiro: intertidal, Apr 2005, 34 complete and 14 incomplete spms (DBUA 00853-01), and 1 incomplete spm (MB36000118); Off Aveiro: cruise AVEIRO94, RV *Côte d’Aquitaine*, 40º43.592’N, 8º45.580’W, 14.4 m, grab, Jul-Aug 1994, 2 complete spms (DBUA 00059-02); 40º38.561’N, 9º02.683’W, 79.1 m, grab, Jul-Aug 1994, 2 incomplete spms (DBUA 00059-07); 40º39.617’N, 8º52.265’W, 38.4 m, grab, Jul-Aug 1994, 1 incomplete spm (DBUA 00059-08); 40º38.615’N, 8º45.985’W, 8.7 m, grab, Jul-Aug 1994, 1 complete spm (DBUA 00059-09); 40º38.564’N, 8º47.293’W, 13.8 m, grab, Jul-Aug 1994, 1 incomplete spm (DBUA 00059-010); 40º38.610’N, 8º45.618’W, 21.9 m, grab, Jul-Aug 1994, 2 complete spms (DBUA 00059-011); 40º37.594’N, 8º47.574’W, 17.3 m, grab, Jul-Aug 1994, 1 incomplete spm (DBUA 00059-012); cruise AVEIRO95, RV *Côte d’Aquitaine*, 40º47.620’N, 9º04.853’W, 95.7 m, grab, 3 Aug 1995, 4 incomplete spms (DBUA 00059-01); 40º43.673’N, 9º06.387’W, 98.6 m, grab, 29 Jul 1995, 1 complete spm (DBUA 00059-03); 40º43.486’N, 9º11.955’W, 135.7 m, grab, 29 Jul 1995, 1 incomplete spm (DBUA 00059-04); 40º33.514’N, 9º09.365’W, 96.3 m, grab, 28 Jul 1995, 1 incomplete spm (DBUA 00059-05); 40º33.215’N, 9º14.179’W, 130.1 m, grab, 28 Jul 1995,1 incomplete spm (DBUA 00059-06); Figueira da Foz, Mondego estuary: 40º08’43.352’’N, 08º52’06.218’’W, 8.5 m, Oct 2005, 1 incomplete spms (not deposited), and Mar 2006, 1 complete spm (not deposited) ; 40º08’36.600’’N, 08º51’23.972’’W, 7.5 m, Oct 2005, 2 incomplete spms (not deposited), and Mar 2006, 3 complete and 2 incomplete spms (not deposited); 40º07’57.270’’N, 08º51’07.744’’W, 2.0 m, Mar 2006, 3 complete spm (not deposited); Foz do Arelho: intertidal, Apr 2006, 6 complete and 7 incomplete spm, (DBUA 00854-01), and 2 incomplete spms (MB36000119 and MB36000120); Off Cascais: 38º39’–38º42’N, 9º25’–9º30’W, 40 m, Jul 2005, 1 complete and 5 incomplete spms (DBUA 00855), and 2 incomplete spms (MB36000121 and MB36000161); Jan 2006, 4 complete and 11 incomplete spms (DBUA 01053); Sado Estuary: 38º31.075’N, 8º54.056' W, 10 m, Jun 2005, 1 complete spm (DBUA 00856-01); 38º30.582’N, 8º51.993' W, 11 m, Jun 2005, 1 complete spm (DBUA 00856-02); Vila Nova de Milfontes: 37º43.30’N, 8º47.25’W, shallow water, July 2006, 3 complete and 6 incomplete spms (DBUA 00857-01), and 1 incomplete spm (MB36000122); Portinho de Ferragudo: 37º07.48’N, 8º31.24’W, shallow water, Jul 2006, 10 complete and 1 incomplete spms (DBUA 00858-01 and 02), and 2 incomplete spms (MB36000123 and MB36000124);

Ria Formosa, Ilha da Armona: 37º01.55’N, 7º50.40’W, shallow water, July 2006, 3 complete spms (DBUA 00859-01), and 1 complete spm (MB36000125); Ria Formosa, Faro beach: 37º00.481’N, 7º59.598’W, 0.7 m, Mar 2006, 1 complete spm (DBUA 00860-01), 1 incomplete spm (DBUA 00860-02), and 1 incomplete spm (MB36000126). Madeira Island, Machico: 15-32m, July 1999, 2 complete and 2 incomplete spms (not deposited); 10 m, grab, Jun 1992, 1 complete spm (MMF.25182 as *N. caeca*).

Mediterranean Sea. Naples: 3 complete spms (NHM 1919.11.6.31-33); 2 complete spms (NHM 1890.6.7.8); 3 incomplete spms (NHM 1951.5.1.4); Israel, off Caesarea: 1 complete spm (NHM 1955.10.12.40 as *Aglaophamus inermis*).

Atlantic/Indian Ocean. South Africa, South African Collection of Prof. J. H. Day, Nov 1960, 3 complete and 6 incomplete spms (NHM 1961.9.71/79); 1 incomplete spm (NHM 1961.19.76/81).

Description. Examined specimens up to 160 mm long for up to 147 chaetigers. See Figure 15 for length and width measurements. Body slightly wider anteriorly, gradually tapering from median region to pygidium. Poor dorsal delineation between anterior segments. Colour cream in ethanol or with brownish-reddish pigment dorsaly on anterior and median setigers of larger specimens; prostomium with brown pigment spot in anterior region; chaetae amber in anterior chaetigers, darker in posterior ones; aciculae amber, sometimes with reddish pigment around tip. One pair of eyes visible only in small specimens at level of chaetiger 2. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by small dorsal and ventral elevation; middorsal papilla cirriform, long (Figure 15D); midventral papillae absent (or if present equal in length to distalmost subterminal papillae); subdistal region with 22 rows of 2-5 conical subterminal papillae (papillae of lateral rows slightly longer than dorsal or ventral ones), extending over 1/3 length of pharynx (Figure 21A); proximal region smooth. Jaws conical, deeply incised at base (Figure 21B). Prostomium subrectangular, anterior margin slightly convex, posterior margin V-shaped extending over first chaetiger (not very well deliniated; Figure 21C); antennae and palps conical; palps slightly longer than antennae, inserted ventrolaterally on median region of prostomium. Nuchal organs rounded, conspicuous. Parapodia biramous; interramal space “U-shaped”, with ciliated patches. Parapodia of chaetiger 1 (Figure 21D) smaller than subsequent ones, directed anteriorly, parallel to prostomium; notopodial acicular lobes conical, pre- and postchaetal lamellae well developed but not extending beyond acicular lobes, prechaetal lamellae slightly bilobed, postchaetal lamellae rounded; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal cirri poorly developed, rounded, lamelliform (Figure 15C); ventral cirri conical, with broad base and tapering distally. Acicular lobes of following parapodia conical to rounded, with a distinct papilliform outgrowth on interramal side of aciculae; prechaetal lamellae well developed but not extending much beyond acicular lobes, bilobed (in neuropodium, dorsal lobe much larger than ventral one); postchaetal lamellae extending beyond acicular lobes, truncated in notopodium, rounded and much larger in neuropodium; dorsal cirri digitiform; ventral cirri conical (Figure 21E-H). Branchiae recurved, long and cirriform, moderately ciliated, with papiliform basal projection; present from chaetigers 4 or 5 (rarely 6) to near posterior end; occupy half of interramal space when fully developed. Chaetae of three kinds: distally barred chaetae in preacicular position (Figure 21I), spinulated chaetae in postacicular position (Figure 21J), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips.

Remarks. Nephtys hombergii has a wide latitudinal distribution in the eastern Atlantic (from the Barents Sea to South Africa). We suggest that the northernmost as well as the southernmost records should be considered with caution. We examined one specimen from Iceland identified as *N. hombergii* (NHM 1954.1.1.198) that was in fact *N. ciliata*, and there probably exist other misidentifications. *Nephtys hombergii* was one of the earlier described species and there are many old references that included several other species under this designation. Also the references from deeper locations (below 150 m depth) were not confirmed and should be considered with caution, since this species appears to be typical of shallower waters and is very abundant in coastal and estuarine habitats. Among all the specimens examined (from Sweden to South Africa, and Mediterranean Sea), some morphological differences between the northernmost and the southernmost specimens became apparent. Specimens from northern regions (Sweden to N Portugal) are all very similar with same parapodial morphology, whereas specimens from southern regions (S Portugal, Madeira Island and Mediterranean Sea) present some small variation in parapodial morphology. In these later specimens the neuropodial postchaetal lamellae are broader (more like *N. assimilis* but without vascularization), the notopodial postchaetal lamellae are also broader and some times slightly bilobed, the branchiae are shorter and thicker and for some specimens the papilliform outgrowth of the acicular lobes is larger, giving the acicular lobes an almost bilobed appearance. The specimens from South Africa are even more distinct, with much longer postchaetal lamellae and very reduced papilliform outgrowth on acicular lobes. Apart from this small variation in parapodial morphology all specimens examined are in agreement with the above description and we could find no obvious reasons to separate them into different species. Nevertheless we consider that further investigation, specially using molecular analyses, is required to clarify this subject with particular attention to the South African specimens.

Distribution. Atlantic Ocean (from Barents Sea to South Africa, including outer Baltic, Skagerrak, Kattegat, North Sea and the coast of France, Spain and Portugal); Mediterranean Sea (Rainer 1991; Laborda 2004).

Habitat. Muddy or gravely sand, from the intertidal to continental shelf depths, also cited until 1000 m depth; tolerant to a wide range of salinity and temperature (Rainer 1991; Laborda 2004).

***Nephtys hystricis* McIntosh, 1900**

Figures 22, 23

Nephthys hystricis McIntosh, 1900: 259; Marenzeller 1904: 304-308; McIntosh 1908: 27, pl. LVII, figs.8-9; pl. LXVI, figs. 10; not Fauvel 1914: 200, pl. XVIII, figs. 1 and 2; not Fauvel 1923: 373, fig. 146A-E; Fauvel 1936: 41.
Nephtys hombergii var. *kersivalensis* McIntosh 1908: 20, pl. LXXVII, fig. 4 (partim).
Nephthys malmgreni Heinen 1911: 29, fig. 8 (partim).
Nephthys incisa Heinen 1911: 23 (partim); Fauvel 1914: 198; Fauvel 1923: 369, fig. 144A-B; ?Foret-Montardo 1969: 814, Pl. 3, figs. 8-10 (partim); (not Malmgren 1865).
Nephthys incisa var. *bilobata* Heinen 1911: 25, pl. I, figs. 1 and 2 (partim).
Nephtys incisa Fauchald 1963: 15 (partim); Kirkegaard 1969: 51 (partim); Hartmann-Schröder 1971: 217, fig. 70d, e; Hartmann-Schröder 1974: 207 (partim); ?Campoy 1982: 516.
Nephtys incisa bilobata Campoy 1982: 518.
Nephtys (Nephtys) hystricis not Day 1967: 345.
? *Nephtys hystricis* not Guille and Laubier 1966: 267; not Wolff 1968: 6; Laborda 2004: 402, fig. 147D-E.
Nephtys hystricis not Campoy 1982: 514; Rainer 1990: 362, fig. 1A-E; Rainer 1991: 75, fig. 2C; Dnestrovskaya and Jirkov 2001: 201,1 fig.

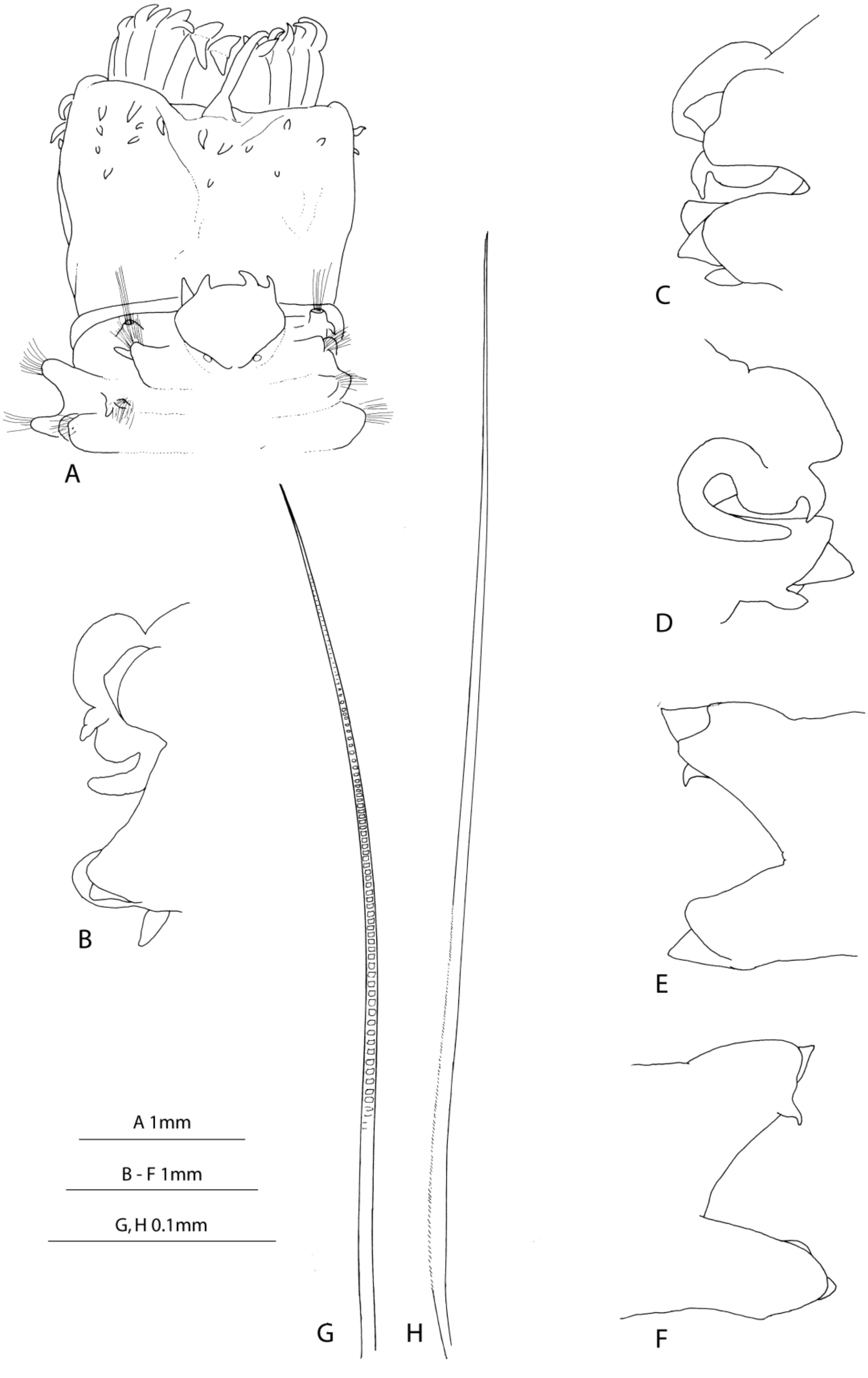


Figure 22. *Nephtys hystricis*. A. Pharynx, prostomium and anteriormost chaetigers, dorsal view. B. Right parapodium of chaetiger 10, anterior view. C. Right parapodium of chaetiger 20, anterior view. D. Same, posterior view. E. Right parapodium of a posterior chaetiger, anterior view. F. Same, posterior view. G. Preacicular chaeta from chaetiger 20. H. Postacicular chaeta from chaetiger 20.

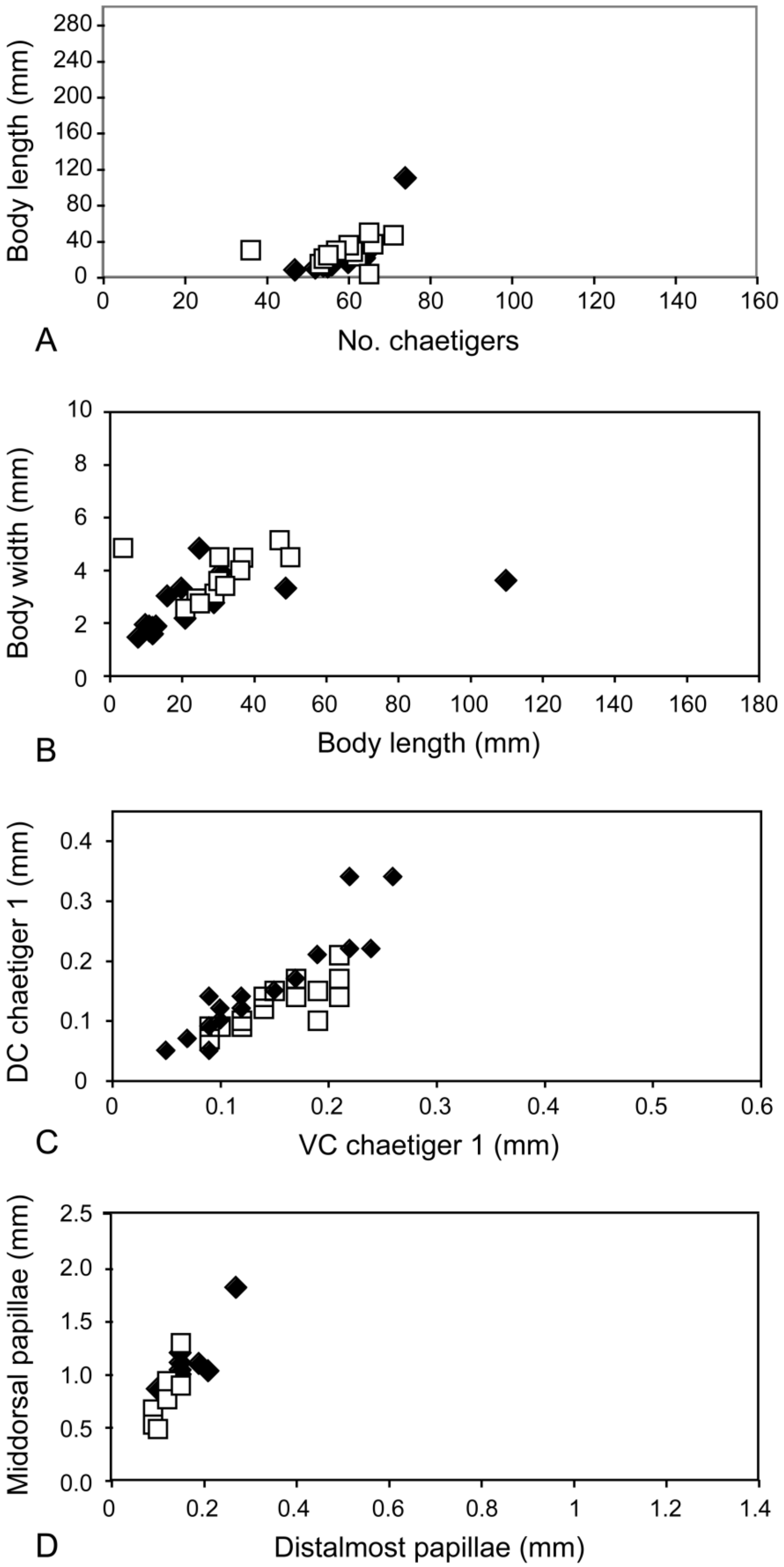


Figure 23. Relationships between: A. Number of segments and body length. B. Body length and body width. C. Length of ventral cirri (VC) and dorsal cirri (DC) of chaetiger 1. D. Length of pharynx distalmost subterminal papillae and middorsal papilla. ◆ *Nephtys hystricis*. □ *N. incisa*.

Type locality. Off Bergen, Norway.

Material examined. Atlantic Ocean. Norway, off Bergen: 1 incomplete spm, lectotype (NHM 1921.5.1.291). North Sea, Sweden, Skagerrak, Bohuslän: 58º17.103'-58º17.455'N, 10º28.948'-10º28,681'E, 335-395 m, Aug 2006, 4 complete and 3 incomplete spms (DBUA 01132-01); 58º07.422'-58º08.068'N, 10º48.549'-10º48,074'E, 206-248 m, Aug 2006, 1 incomplete spm (MB36000155); 58º24.178'-58º23.770'N, 10º31.053'-10º30,702'E, 329-367 m, Aug 2006, 1 incomplete spm (MB36000156). SW Ireland, off Valentia Island: 1-160 fms, 3 spms (NHM 1921.5.1.796-806, syntypes *N. kersivalensis*). Portugal, off Cape Sagres: Porcupine Expedition, 2 incomplete spms (NHM 1921.5.1.769-770); Gulf of Cadiz, near Kidd mud volcano: TTR14 cruise, RV *Prof. Logachev,* 35º24.777'N, 6º43.782'W, 552 m, box-corer, Aug 2004, 1 incomplete spm (DBUA 00861-01); Kidd mud volcano: cruise TTR14, RV *Prof. Logachev,* 35º25.602'N, 6º44.099'W, 526 m, box-corer, Aug 2004, 2 incomplete spms (DBUA 00861-02), and 1 incomplete spm (MB36000127); Pen Duick Escarpment: cruise M2005, RV *Pelagia,* 35º18.029'N, 6º47.437'W, 570 m, box-corer, May 2005, 1 incomplete spm (MB36000162); Mercator mud volcano: cruise MSM01-03, *RV M. S. Merian,* 35º17.918'N, 6º38.717'W, 353 m, box-corer, May 2006, 1 incomplete spm (DBUA 00863-01).

Description. Examined specimens up to 31 mm long for up to 74 chaetigers. See Figure 23 for length and width measurements. Body small, slightly wider anteriorly, gradually tapering posteriorly. Poor dorsal delineation between anterior segments. Colour in ethanol cream; prostomium without pigmentation; chaetae amber; tip of aciculae of median chaetigers black. One pair of eyes visible only in small specimens at level of chaetiger 2. Pharynx distal region with 10 pairs of bifid terminal papillae, separated by dorsal and ventral gaps; middorsal papilla cirriform, very long (Figure 23D); midventral papillae absent; subdistal region with 22 rows of 3-6 very small, conical subterminal papillae, extending over 1/3 length of pharynx (Figure 22A); proximal region smooth. Jaws conical. Prostomium subpentagonal (Figure 22A), anterior margin slightly convex, posterior margin rounded; antennae and palps conical; palps slightly longer than antennae, inserted ventrolaterally on anterior region of prostomium, near antennae. Nuchal organs rounded. Parapodia biramous; interramal space "V-shaped"; ciliation not seen. Parapodia of chaetiger 1 similar in size to subsequent ones, directed anteriorly, parallel to prostomium; notopodial acicular lobes conical; pre- and postchaetal lamellae well developed but not extending beyond acicular lobes, rounded; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal and ventral cirri conical, equal in size (Figure 23C). Acicular lobes of following parapodia conical; prechaetal lamellae well developed but not extending beyond acicular lobes, bilobed in middle parapodia, postchaetal lamellae extending beyond acicular lobes in anterior and middle parapodia, smaller than acicular lobes in posterior parapodia, rounded; dorsal cirri flattened, triangular and ventral cirri conical (Figure 22B-F). Branchiae recurved, cirriform, present from chaetigers 5-7 (usually chaetiger 6), absent in posterior parapodia; occupy all interramal space when fully developed. Chaetae of three kinds: barred chaetae in preacicular position (Figure 22G), finely spinulated chaetae in postacicular position (Figure 22H), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips.

Remarks. Nephtys hystricis was originaly described by McIntosh (1900) for specimens collected in Berehaven, Ireland (during Royal Irish Academy's Expedition), in the Mediterranean Sea (during "Porcupine" Expedition of 1870), and off Bergen, Norway. Rainer (1990) examined all these syntypes and designated the specimens from Bergen as lectotype and paralectotypes.

Nephtys hystricis has often been confused with the morphologically close species *N. incisa* and many of the earlier descriptions include characteristics of both, suggesting that the authors had a mixture of the two species. Examples of this are in Foret-Montardo (1969), Campoy (1982) and Laborda (2004), who provide descriptions for both species although with some mixed characters and figures often corresponding to only one of the species (*N. incisa* in Foret-Montardo (1969) and *N. hystricis* in Laborda (2004)). Rainer (1990) re-examined much of the old material and provided a re-description of the two species. Specimens from both species are small (up to 75 chaetigers) and fragile and can be found simpatrically. The main differences between the two species are the chaetiger where branchiae start (5-7, usually 6, in *N. hystricis*, 9-10 in *N. incisa*) and the shape and size of parapodial lamellae. In *N. hystricis* the prechaetal lamellae of the median parapodia are bilobed and smaller than acicular lobes, and the postchaetal lamellae are larger than acicular lobes and broadly rounded, while in *N. incisa* pre- and postchaetal lamellae are both broadly rounded and of the same length or slightly smaller than the acicular lobes. Also the number and pattern of pharynx papillae is somewhat different in the two species (22 rows of 3-6 subterminal papillae for *N. hystricis* and 20 rows of 1-5 papillae for *N. incisa*). *Nephtys hystricis* generally have less posterior chaetigers without branchiae, when comparing with *N. incisa*. Rainer (1990) mentioned 15-18 posterior chaetigers without branchiae for *N. hystricis* and a relatively constant number of 25 posterior chaetigers in *N. incisa*. In the specimens examined in the present study those values showed larger variation – 11-21 posterior chaetigers without branchiae in *N. hystricis* (only 4 entire specimens examined) and 19-30 for *N. incisa* (9 entire specimens examined). We could also find differences in the preacicular chaetae of the two species; in *N. hystricis* they are barred in all its extension (Figure 22G), while in *N. incisa* they are only distally barred (Figure 24H).

Nephtys kersivalensis is another species that is morphologically similar to *N. hystricis*. However, the two species can be differentiated by the chaetigers where branchiae start and end (from chaetiger 4 to the end of body in the former, from chaetigers 5-7 to before the end of body in the later) and by the presence of a rugose area near the aciculae on the acicular lobes of *N. kersivalensis*. *Nephtys hystricis* usually occurs in deeper water than *N. kersivalensis*.

Laborda (2004) reported this species from the Red Sea and the Indian Ocean. However, these records were not confirmed and should be considered with caution. Only one specimen from off Mozambique (NHM 1934.1.19) of this material was examined and had been incorrectly identified as *N. hystricis*.

Distribution. Atlantic Ocean (from Norway to Gulf of Cadiz); Mediterranean Sea (Rainer 1990, 1991). There are further reports of this species from Red Sea and Indian Ocean (E Africa) (Laborda 2004), but these records require confirmation.

Habitat. Mud and sandy mud, 100-800 m depth (Rainer 1991; Laborda 2004).

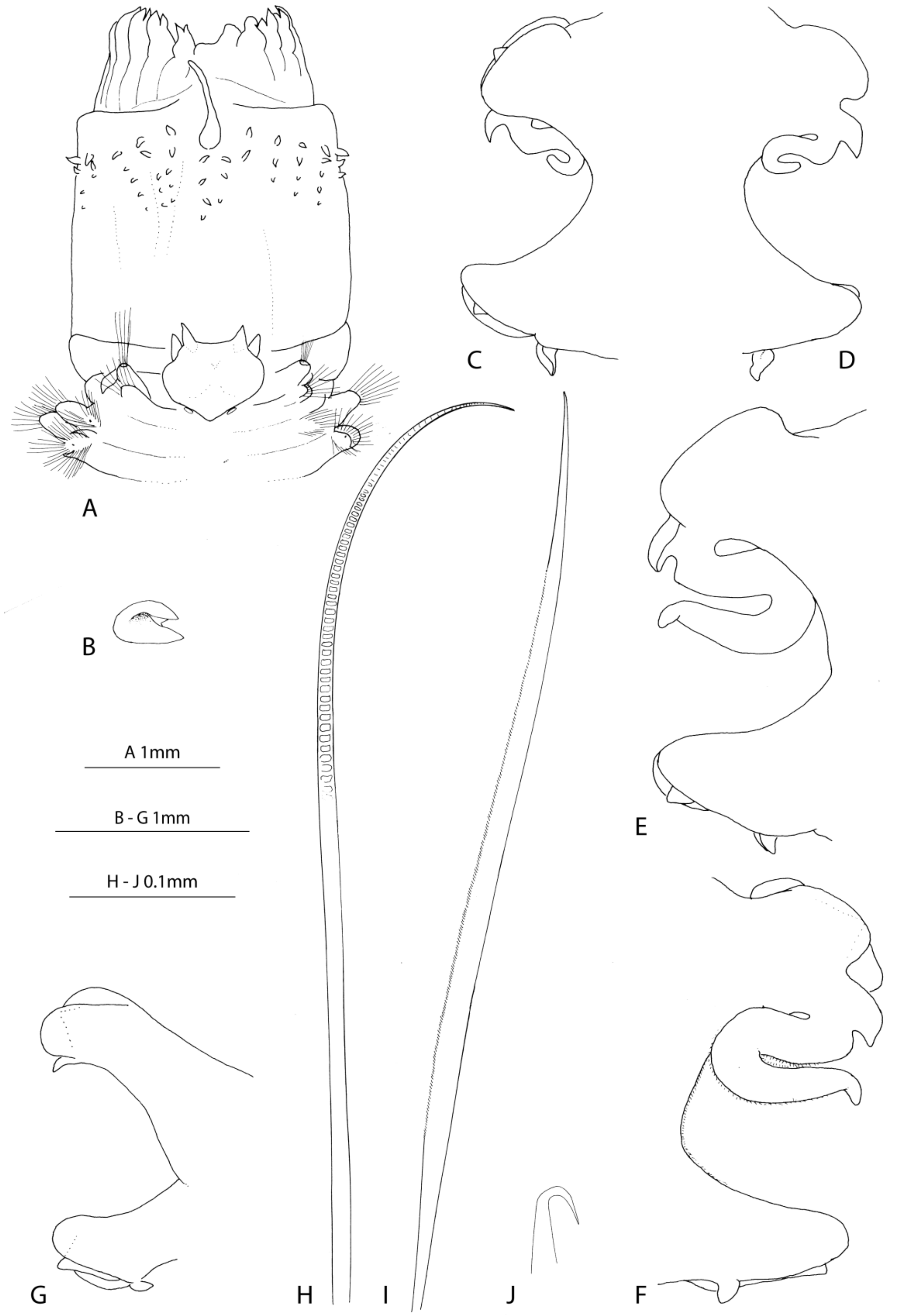


Figure 24. *Nephtys incisa*. A. Pharynx, prostomium and anteriormost chaetigers, dorsal view. B. Jaw. C. Right parapodium of chaetiger 11, anterior view. D. Same, posterior view. E. Right parapodium of chaetiger 20, anterior view. F. Same, posterior view. G. Right parapodium of chaetiger 40, anterior view. H. Preacicular chaeta from chaetiger 20. I. Postacicular chaeta from chaetiger 20. J. Acicula of chaetiger 40.

Nephtys incisa **Malmgren, 1865**

Figures 23, 24

Nephthys incisa Malmgren, 1865: 105, pl. XII, fig. 21; Michaelsen 1896: 58 (partim); Nordgaard 1905: 162; McIntosh 1908: 38; Heinen 1911: 23, fig. 6 (partim); Augener 1912: 203 (partim); not Treadwell 1914: 193; not Fauvel 1914: 198, pl. XVIII, fig. 3; not Fauvel 1923: 369, fig. 144A-B.

Nephthys sp.nr *incisa* McIntosh 1900: 262.

Nephthys hystricis McIntosh 1908: 27, pl. LVII, figs. 8,9; pl. LXVI, figs. 10 and 10A (partim); Fauvel 1914: 200; Fauvel 1923: 373, fig. 146A-E.

Nephtys incisa ?Hartman 1944: 340, pl. XV, fig. 9; ?Hartman, 1950: 108; Eliason 1962: 249; Fauchald 1963: 15, figs. 1H, 2C and 3B (partim); Pettibone 1963: 198, fig. 49A, B, 51A; ?Foret-Montardo 1969: 814, pl. III, figs. 8-10; Kirkegaard 1969: 51 (partim); Hartmann-Schröder 1971: 217, fig. 70D-E; Day 1973: 43; Hartmann-Schröder 1974: 207; Gardiner 1976: 154, fig. 16C, D; Campoy 1982: 516; Hartmann-Schröder 1982: 11; ?Taylor 1984: 35-7, fig. 35-3, 4A-D; Rainer 1990: 366, fig. 2A-E; Rainer 1991: 76, fig. 3G; Böggemann 1997: 80, fig. 57; Dnestrovskaya and Jirkov 2001: 202,1 fig; Laborda 2004: 405, fig. 148C-D; not Wolff 1968: 4; not Taylor 1984: 35-7, figs. 35-3 and 4A-D.

Nephtys (Nephtys) hystricis Day 1967: 345.

Nephtys hystricis Wolff 1968: 6; ?Foret-Montardo 1969: 816, pl. III, figs. 1-4; Campoy 1982: 514.

Aglaophamus malmgreni Hartmann-Schröder 1974: 205 (partim).

Type locality. Väderöarna and Koster, Bohuslän, Sweden, Skagerrak, in 36-146 m depth.

Material examined. Atlantic Ocean. Sweden, Skagerrak, Bohuslän: 58º10.856’-58º11.049’N, 10º53.439’-10º53,024’E, 162-191 m, Aug 2006, 1 incomplete spm (MB36000158); Koster: 127-146 m, 2 complete and 1 incomplete spms, paralectotypes (SMNH-type-2460); Väderöarna: 36-127 m, 5 complete and 2 incomplete spms, paralectotypes (SMNH-type-2461); 109 m, 1 complete spm, paralectotype (SMNH-type-2459); 106,88 m, 1 complete spm, paralectotype (NHM 1865.9.23.8). England, off Northumberland: 90 m, Apr 2008, 1 incomplete spm (MB36000150). Portugal, off Cascais: 38º39’-38º42’N, 9º25’-9º30’W, 40 m, 1997, 1 incomplete spm (DBUA 00065-01); off Cape Sagres: Porcupine expedition, 4 incomplete spms (NHM 1921.5.1.769-770 as *N. hystricis*). NE USA, off Cape Cod: 10-50 fms, 1 complete and 6 incomplete spms (NHM 1890.8.23.21/22); off Vineyard Sound: 10-20 fms, 1 incomplete spm in very poor condition (NHM 1880.9.27.57); Hudson Canyon: RV *Chain*, 39º35.363'N, 72º24.9255'W, 360-380 m, Feb 1973, 1 complete and 4 incomplete spms (MCZ 37133); 39º31'N, 72º18'W, 855 m, Feb 1973, 2 incomplete spms (MCZ 37299); Massachusetts: 41º29.2'N, 70º53.8'W, 15 m, Jan 1966, 41 complete and 6 incomplete spms (4 adults) (MCZ 57201); Florida: 2 complete spms in poor conditions (MCZ 1424).

Mediterranean Sea. France, off Banyuls: RV *Nereis*, 42º29.35'N, 03º11.16'E, 70 m, Apr 2001, dredge, 2 incomplete spms (DBUA 01047-01); 42º29.55'N, 03º09.90'E, 45 m, dredge, Jul 2004, 2 complete and 2 incomplete spms (DBUA 01046-01), and 1 incomplete spm (MB36000141). Israel: Dec 1924, 1 incomplete spm (NHM 1926.11.12.123 as *N. hystricis*). Suez: Suez Canal expedition, 7 incomplete spms (NHM 1955.10.12.35/39 as *N. hystricis*).

Description. Examined specimens up to 50 mm long for up to 71 chaetigers. See Figure 23 for length and width measurements. Body small, slightly wider anteriorly, gradually tapering from middle region to pygidium. Poor dorsal delineation between anterior segments. Colour in ethanol cream; chaetae amber; tip of aciculae dark. Eyes not visible. Pharynx distal region with 10 pairs of very small terminal bifid papillae, separated by dorsal and ventral gap; middorsal papilla cirriform, very long (Figure 23D); midventral papillae absent; subdistal region with 20 rows of 1-5 very small subterminal papillae, extending over 1/3 length of pharynx (Figure 24A); proximal region smooth. Jaws conical (Figure 24B). Prostomium subpentagonal, anterior margin slightly concave, posterior margin rounded (Figure 24A); antennae and palps conical, equal in length; palps inserted ventrolaterally on anterior region of prostomium. Nuchal organs rounded, inconspicuous. Parapodia biramous; interramal space "U-shaped" anteriorly and "V-shaped" posteriorly, heavily ciliated. Parapodia of chaetiger 1 slightly smaller than subsequent ones, directed anteriorly, obliquely to prostomium; notopodial acicular lobes conical, prechaetal lamellae rudimentary, postchaetal lamellae well developed but not extending beyond acicular lobes, rounded; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobes; dorsal cirri rounded, foliaceous; ventral cirri conical, with broad base and tapering distally similar in size to dorsal cirri (Figure 23C). Acicular lobes of following parapodia conical; pre- and postchaetal lamellae of both rami well developed, as long as acicular lobes (or slightly smaller, in posterior parapodia), rounded; dorsal and ventral cirri flattened, triangular (Figure 24C-G). Branchiae recurved, cirriform, heavily ciliated; present from chaetiger 9 or 10, absent in posterior parapodia; occupy half of interramal space when fully developed. Chaetae short, of three kinds: distally barred chaetae in preacicular position (Figure 24H), finely spinulated chaetae in postacicular position (Figure 24I), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips (Figure 24J).

Remarks. Nephtys incisa and *N. hystricis* are morphologically very similar, and are often confused. Rainer (1990) re-examined much of the older material and provided a re-description of these two species. The main differences between them are summarized in the remarks on *N. hystricis*. Both species occur in the same geographical regions although *N. incisa* seems to have a wider distribution in the eastern and western Atlantic. Rainer (1990) advised caution regarding the western Atlantic records, and stated that they likely refer to *N. hystricis*. In this study some material from several localities in the NW Atlantic were examined, and some differences from the typical *N. incisa* or *N. hystricis* specimens were found, indicating that these records are in need of revision.

Distribution. Atlantic Ocean (from Iceland to off NW Africa, including the North Sea, Skagerrak, Kattegat and the coasts of Spain and Portugal); Mediterranean Sea (as far as the Bosphorus) (Rainer 1990, 1991; Laborda 2004). There are further reports of this species from the western Atlantic (Rainer 1990, 1991), but these records require revision.

Habitat. Gravel and mud to soft silts (most common in silty sand and/or mud), from the shallow subtidal to 930 m depth, also reported from depths to 1700 m in the western Atlantic (Rainer 1990, 1991; Laborda 2004).

***Nephtys kersivalensis* McIntosh, 1908**

Figures 15, 25

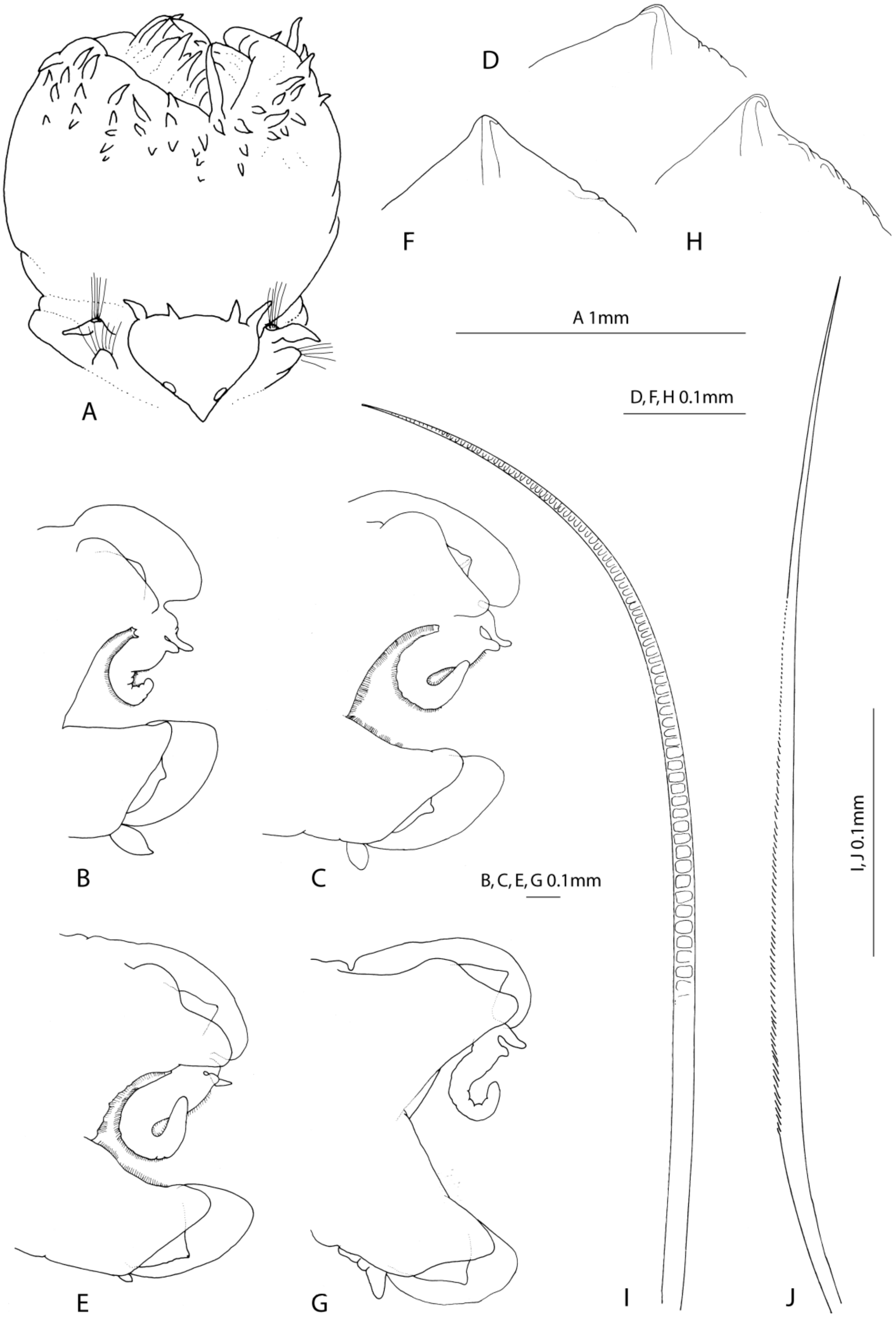


Figure 25. *Nephtys kersivalensis*. A. Pharynx, prostomium and first chaetiger, dorsal view. B. Left parapodium of chaetiger 10, anterior view. C. Left parapodium of chaetiger 20, anterior view. D. Detail of notopodial acicular lobe of chaetiger 20. E. Left parapodium of chaetiger 40, anterior view. F. Detail of neuropodial acicular lobe of chaetiger 40. G. Left parapodium of chaetiger 60, anterior view. H. Detail of neuropodial acicular lobe of chaetiger 60. I. Preacicular chaeta from chaetiger 10. J. Postacicular chaeta from chaetiger 10. K. Acicula of chaetiger 60.

Nephthys hombergii var. *kersivalensis* McIntosh, 1908: 20 (partim).

Nephthys incisa Michaelsen 1896: 59 (partim); Augener 1912: 203; George 1979: 198 (not Malmgren 1865).

Nephtys hombergii forma *ehlersi* Fage and Legendre 1927: 124.

Nephtys incisa Fauchald 1963: 15 (partim).

Nephtys hombergi kersivalensis Fauchald 1963: 5.

Nephtys hombergii var. *kersivalensis* Hartmann-Schröder 1971: 217.

Nephtys kersivalensis Rainer 1989: 882, fig. 2A-F; Rainer 1991: 78, fig. 2D; Dnestrovskaya and Jirkov 2001: 203,1 fig; Laborda 2004: 406, fig. 149A-C.

Type locality. Connemara, Ireland.

Material examined. Atlantic Ocean. SW Ireland, off Valentia Island: 1-160 fms, 19 incomplete spms, syntypes (NHM 1921.5.1.796-806). England, off Northumberland: 48 m, Apr 2008, 1 complete spm (MB36000149). Portugal, Sado Estuary: 38º30.994’N, 8º54.077'W, 11 m, Jun 2005, 2 complete and 1 incomplete spms (DBUA 00864-01 to 03); Lagos, 37º04.948’N, 8º38.500’W, 30 m, Apr 2006, 1 incomplete spm (DBUA 00865-01).

Description. Examined specimens up to 40 mm long for up to 69 chaetigers. See Figure 15 for length and width measurements. Body slightly wider anteriorly, gradually tapering from middle region to pygidium; Poor dorsal delineation between anterior segments. Colour in ethanol cream; prostomium with dark spot in the medioanterior region; chaetae amber; tip of aciculae dark. One pair of eyes visible only in small specimens at posterior limit of chaetiger 2. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by dorsal and ventral gap; middorsal papilla very long and cirriform (Figure 15D), midventral papilla absent; subdistal region with 22 rows of 3-6 small, conical subterminal papillae, extending over 1/3 length of pharynx (Figure 25A); proximal region smooth. Jaws not examined. Prostomium subpentagonal, anterior margin slightly convex, posterior margin V-shaped extending over first chaetiger (Figure 25A); antennae and palps conical to cirriform, equal in length; palps inserted ventrolaterally on mid-anterior region of prostomium. Nuchal organs rounded. Parapodia biramous; interramal space “V-shaped”, moderately ciliated. Parapodia of chaetiger 1 similar in size to subsequent ones, directed anteriorly, parallel to prostomium; notopodial acicular lobes conical;

pre- and postchaetal lamella well developed but not extending beyond acicular lobes; neuropodial pre- and postchaetal lamellae forming a cylinder around acutely pointed acicular lobes; dorsal cirri small (Figure 15C), rounded; ventral cirri conical, with broad base and tapering distally. Acicular lobes of following parapodia conical with rugose area on ventral side, near acicula (Figure 25D, F, H); prechaetal lamellae well developed but not extending beyond acicular lobes, rounded or slightly bilobed anteriorly, clearly bilobed on middle parapodia; postchaetal lamellae extending beyond acicular lobes, rounded; dorsal cirri digitiform; ventral cirri conical (Figure 25B, C, E, G). Branchiae recurved, moderately ciliated, with conspicuous rounded papillae-like basal projection; present from chaetiger 4 to near posterior end (may be reduced in posteriormost chaetigers); occupy 2/3 of interramal space when fully developed. Chaetae short, of three kinds: barred chaetae in preacicular position (Figure 25I), finely spinulated chaetae in postacicular position (Figure 25J), and capillary chaetae in the neuropodia of chaetiger 1. One acicula per ramus, middle and posterior ones with curved tips (Figure 25D, F, H).

Remarks. This species was first described by McIntosh (1908) as *Nephthys hombergii* var. *kersivalensis*. Rainer (1989) raised it to specific level and provided a complete re-description and comparison with other northern European *Nephtys* species. This study extends the geographical distribution of *N. kersivalensis* to the western and southern coasts of Portugal. However, this species seems to be less frequent in Portuguese waters than in northern Europe (Rainer, 1989). Also the Portuguese specimens are usually smaller, with less distinctly bilobed prechaetal lamellae. Differences between *N. kersivalensis* and other morphologically close species are summarized in Table 5. It differs from *N. assimilis* and *N. hombergii* especially in parapodial structures and from *N. hystricis* in the appearance of the branchiae. *Nephtys kersivalensis* is unique in having a rugose area on acicular lobes near aciculae. *Nephtys kersivalensis* and *N. hystricis* are clearly smaller when compared to *N. assimilis* and N. *hombergii* (Figure 15, 23).

Distribution. Atlantic Ocean (Outer Hebrides, lreland, North Sea, Kattegat, W France, W and S Portugal); Mediterranean Sea (SE Spain) (Rainer 1991; Laborda 2004; Malonda 2009; this study).

Habitat. Gravel, silty, muddy and clean sand, from the shallow subtidal to 295 m depth (Rainer 1991; Laborda 2004).

Nephtys longosetosa **Örsted, 1842**

Figures17, 26

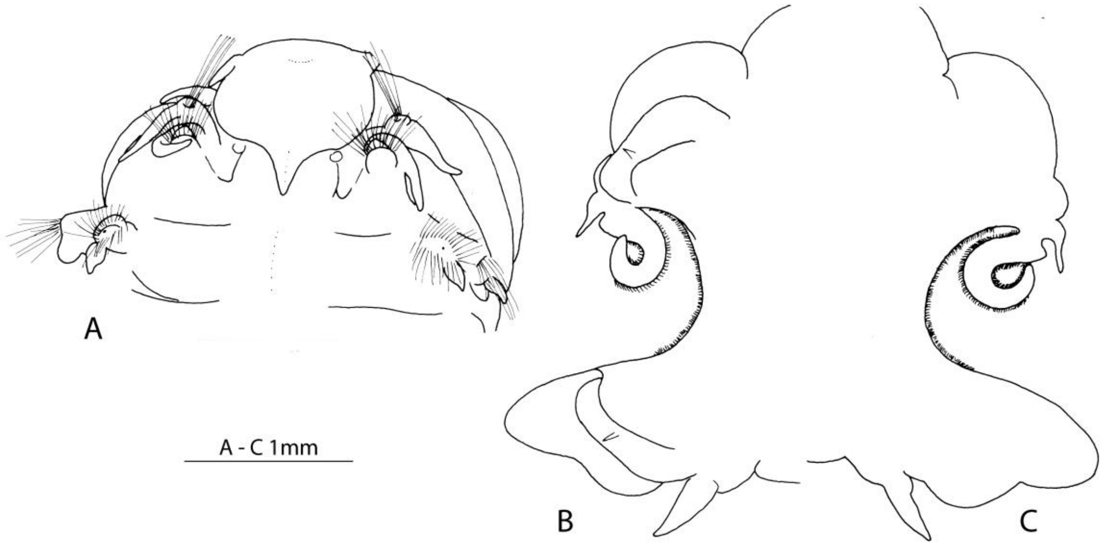


Figure 26. *Nephtys longosetosa*. A. Prostomium and first chaetigers, dorsal view. B. Right parapodium of chaetiger 39, anterior view. C. Same, posterior view.

Nephthys longosetosa Örsted, 1842: 123; Örsted 1843: 195, pl. VI, figs. 75 and 76; Saint-Joseph 1894: 20, pl. I, fig. 19; Fauvel 1923: 367, fig. 143f-h; Ditlevsen 1937: 20; Uschakov 1955: 219, fig. 68C-E; Southward 1956: 264.

Nephthys longisetosa [misspelling of *longosetosa*] Johnston 1865 (partim); not Malmgren 1865: 106, tab. XII, fig. 20; Verrill 1881: 295, 319; Michaelsen 1896: 24; Heinen 1911: 26, fig. 7; Augener 1912: 193; Okuda 1939: 231; not McIntosh 1908: 29, pl. LVII, figs.10-12, pl. LXVI, figs. 11, pl. LXXVII, fig. 8.

Nephthys johnstoni Ehlers, 1874: 293; Ehlers 1875: 38, pl. III, figs. 1-4; McIntosh 1908: 34 (partim).

Nephthys emarginata Malm, 1874: 77, pl. I, fig. 1.

Nephthys ciliata form. *longosetosa* Augener 1940: 137.

Nephthys longosetosa Hartman 1944: 339, pl. XV, fig. 7; Pettibone 1954: 268, fig. 301; Pettibone 1956: 558; Imajima 1961: 87, fig. 3; Fauchald 1963: 8, figs. 1C, 3F; Pettibone 1963 : 204, fig. 47A; Imajima and Hartman 1964: 157; Hartmann-Schröder

1971: 221, fig. 71C, 73A-B; Paik 1973: 125, pl. I, figs. E and F; Garwood and Olive 1981: 195, figs. 1, 2, 4B, 5A and 6; Imajima and Takeda 1987: 60, fig.10A-I, 14; Jirkov 1989:78, Figs. 16.10 and 16.11; Rainer 1991: 80, fig. 3D; Böggemann 1997: 80, fig. 58; Dnestrovskaya and Jirkov 2001: 205,1 fig.
Nephtys longesetosa [misspelling of *longosetosa*] Laborda 2004: 406, fig. 149D.

Type locality. Greenland, Arctic.

Material examined. Arctic Ocean. Greenland: 2 incomplete spms (NHM 1921.5.1.704 as *N. caeca*).
Atlantic Ocean. Kattegat, Anholt: 1 incomplete spm (GNHM Polych. 49, syntype of *N. emarginata*); Anholt-Lysegrund: Jan 1873, 1 complete and 3 incomplete spms (GNHM Polych. 1231, syntypes of *N. emarginata*) and 5 incomplete spms (GNHM Polych. 1232, syntypes of *N. emarginata*). North Sea, Scotland, off Shetland Islands: 1 complete spm (NHM: 1865.3.9.18 as *N. longisetosa*). Belgium, Oostend: 2 complete spms (NHM 1928.4.26.559/560).

Description. Examined specimens up to 90 mm long for up to 118 chaetigers. See Figure 17 for length and width measurements. Body long and slender, of about same wide, slightly tapering posteriorly. Colour in ethanol cream; chaetae whitish; tip of aciculae brown. Eyes not visible. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by dorsal and ventral small elevation; middorsal papilla cirriform, long (Figure 17D); subdistal region with 22 rows of 4-7 long and conical subterminal papillae, extending over 1/2 length of pharynx; proximal region smooth. Jaws conical, brown. Prostomium subpentagonal, anterior margin slightly convex, tapering between antennae, posterior margin V-shaped (Figure 26A); antennae and palps conical, subequal in length; palps inserted ventrolaterally on median region of prostomium. Nuchal organs rounded, somewhat hidden by a fold made by first chaetiger anterior limit. Parapodia biramous; interramal space “U-shaped”, heavily ciliated. Parapodia of chaetiger 1 similar in size to subsequent ones, directed anteriorly, parallel to prostomium; notopodial acicular lobes rounded; pre- and postchaetal lamellae well developed but not extending beyond acicular lobes, rounded; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobe; dorsal and ventral cirri well developed, subequal in length (Figure 17C), conical to cirriform. Acicular lobes of following parapodia rounded or slightly bilobed; prechaetal lamellae poorly developed, rounded; notopodial postchaetal lamellae extending beyond acicular lobes, unequally bilobed, with dorsal lobe much larger than ventral one; neuropodial postchaetal lamellae extending well beyond acicular lobes, with a ventral incision medianly that gives it a typical S-shaped appearence; dorsal cirri slender, with broad base and a cirriform tip; ventral cirri conical somewhat flattened (Figure 26B-C). Branchiae recurved, heavily ciliated, with very small, rounded basal projection; present from chaetiger 3 to near posterior end; occupy 2/3 of interramal space when fully developed. Chaetae very thin and long, of three kinds: barred chaetae in preacicular position, coarsely spinulated chaetae in postacicular position, and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips.

Remarks. Nephtys longosetosa has often been confused with other species, especially with *N. caeca*. Fauchald (1963) summarized the synonymy history for both species and Garwood and Olive (1981) provided a detailed comparison between them. The main differences between these two species were already mentioned in the remarks on *N. caeca*, and consist on start of branchiae, parapodial lamellae proportions and pharynx papillae patterns. All specimens of *N. longosetosa* examined have branchiae starting from chaetiger 3 and neuropodial postchaetal lamellae with a soft ventral incision giving an “S” appearance to the lamellae. Pharynx of *N. longosetosa* differs from *N. caeca* in having a long middorsal papillae and a smooth proximal region. Both *N. caeca* and *N. longosetosa* are cold-water species, with overlapping geographical distributions, occurring more frequently in northern regions. Specimens from NW Spain, Mediterranean Sea and Pacific Ocean were not available for confirmation and therefore these records should be considered with caution. Nevertheless, the Spanish records are the reason why this species is included in this paper. Two examined specimens, from Panama (NHM 1928.9.13.22) and Alaska (CASIZ 22792), labelled as *N. longosetosa* do not belong to this species.

Distribution. Arctic Ocean (Greenland); Atlantic Ocean (Norway, North Sea, Skagerrak, Kattegat, western Baltic, NW Spain); Mediterranean Sea (as far as the Black Sea); Pacific Ocean (Bering Sea; Sea of Okhotsk; Japan; Yellow Sea; China sea; Alaska to California) (Imajima & Takeda 1987; Rainer 1991; Jung & Hong 1997;

Laborda 2004). There are further reports of this species to the strait of Magellan (Imajima & Takeda 1987), but this records require revision.

Habitat. In a wide variety of sediments, most common in well-sorted fine or medium sands, from the lower intertidal to 1000 m depth (Rainer 1991; Jung & Hong 1997; Laborda 2004).

Nephtys paradoxa **Malm, 1874**

Figures 20, 27

Nephthys paradoxa Malm, 1874: 78, pl. I, fig. 2; Levinsen 1887; Augener 1912: 204; Fauvel 1914: 199; Fauvel 1923: 375, fig. 146F-I; Augener 1928: 701; Ditlevsen 1937: 19.
Nephtys pansa [*nomen oblitum*] Ehlers, 1874: 293; Ehlers 1875: 40, pl. III, figs. 1 and 2; Horst 1881; McIntosh 1908.
Nephtys phyllobranchia McIntosh, 1885: 164, pl. XXVI, fig. 10; pl. XXVII, fig. 3; pl. XIVA, figs. 12 and 13; Hartman 1950: 111.
Nephthys hombergii Heinen 1911: 16 (partim).
Nephtys schmitti Hartman, 1938: 152, fig.65; Hilbig 1997: 342, fig. 13.11.
Nephtys paradoxa Hartman 1944: 335, 339, pl. XV, fig. 6; Hartman 1950: 111; Pettibone 1954: 271, fig. 30J-K; Eliason 1962: 249; Fauchald 1963: 13, figs. 1A, 2B and 3C; Pettibone 1963: 200, fig. 47D; Hartman 1965: 92; Hartman 1967: 81; Foret-Montardo 1969: 818; Bellan 1969: 42; Hartmann-Schröder 1971: 214; Amoureux 1972: 66; Fauchald 1972 : 91; Hartmann-Schröder 1974: 207; Paxton 1974: 204; ?Rozbaczylo and Castilla, 1974: 201; Rainer and Hutchings 1977: 338, fig. 43; Hartmann-Schröder 1977: 88; Campoy 1982: 513; Imajima and Takeda 1987: 50, figs. 5A-I and 6; Jirkov, 1989: 78, Figs. 16.6; Rainer 1991: 81, fig. 3E; Kirkegaard 1995: 39; Dnestrovskaya and Jirkov 2001: 206,1 fig; Laborda 2004: 408, fig. 150A-B.
Nephtys (Nephtys) paradoxa Day 1967: 347, fig. 15.2N-O.

Type locality. Sweden.

Material examined. Norway, Trondheimsfjord, Vannviksbukt: RV *Harry Borthen*, 63º32.745’-63º32.160’N, 10º14.910’-10º14.540’E, 200 m, Sneli-sledge, Feb 2003, 1 incomplete spm (MB36000140). Sweden, Skagerrak, Bohuslän: 58º24.024’-

58º24.255’N, 10º38.147’-10º40,005’E, 218-264 m, Aug 2006, 1 complete spm (MB36000159); Koster: 120 fms, Jul 1965, 1 incomplete spm, syntype (GNHM Polych. 55); Kosterfjorden: 120 fms, Jul 1965, 1 incomplete spm, syntype (GNHM Polych. 1208). Gulf of Cadiz, Pen Duick Escarpment: TTR12 cruise, RV *Prof. Logachev,* 35º17.695' N, 6º47.082' W, 560 m, grab, Jul 2002, 1 complete spm (DBUA 00673-01); TTR16 cruise, RV *Prof. Logachev,* 35º17.693’N, 6º47.089’W, 556 m, grab, May 2006, 1 complete spm (MB36000128). American coast, off Delaware: Challenger Expedition, 38º34’N, 72º10’W, 1240 fms, May 1873, 1 incomplete spm (NHM 1885.12.1.128, as *N. phyllobranchia*, holotype); cruise 9504, RV *Albatross IV*, 43º38’N, 68º56’W, 126 m, Sep 1995,1 incomplete spm (MCZ 37222); RV *Eastward*, 33º38’N, 75º51’W, 2300m, Mar 1972, 1 spm in two fragments (MCZ 37209).
Pacific Ocean. Alaska, NE Gulf of Alaska: 58º32.20’N, 139º32.60’W, 261 m, Nov 1979, 1 complete spm (CASIZ BLM 36208, as *N. schmitti*); South Alaska Peninsula: RV *Albatross*, 54º00.00’N, 162º40.30’W, 483 fms, 2 complete spms (USNM 20323).

Description. Examined specimens up to 179 mm long for up to 91 chaetigers. See Figure 20 for length and width measurements. Body stout, slightly wider anteriorly, gradually tapering from middle region to pygidium. Poor dorsal delineation between anterior segments. Colour in ethanol brownish with darker brown pigment on prostomium and anterior segments; some specimens with purple spots on prostomium; chaetae amber; tips of aciculae red. Eyes not visible. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by dorsal and ventral simple, conical papillae (in some specimens the dorsal simple papilla is low and rounded); middorsal papilla slightly larger than subterminal ones (Figure 20D); midventral papillae if present similar in size and shape to subterminal ones; subdistal region with 22 rows of 4-6 (3) conical subterminal papillae, extending over 1/3 length of pharynx (Figure 27A); proximal region without warts but usually wrinkled. Jaws not examined. Prostomium subquadrangular (subpentagonal when pharynx everted), anterior margin straight, posterior margin U-shaped; antennae and palps conical, very short; palps inserted ventrolaterally on anterior region of prostomium, slightly behind antennae. Nuchal organs conspicuous, rounded. Parapodia biramous; interramal space “U-shaped”; moderately ciliated; posterior parapodia with well separated rami. Parapodia of chaetiger 1 equal in size to subsequent ones, directed anteriorly, parallel to prostomium; notopodial acicular lobes conical, prechaetal lamellae rudimentary, postchaetal lamellae well developed but not extending beyond acicular lobes, rounded; neuropodial pre- and postchaetal lamellae forming a cylinder covering acicular lobe; dorsal cirri small, rounded; ventral cirri small, conical, slightly larger than dorsal cirri (Figure 20C). Acicular lobes of following parapodia rounded with a "conical tip" due to acicula, becoming conical in posterior parapodia; pre- and postchaetal lamellae poorly developed (prechaetal lamellae almost rudimentary), surrounding inner part of acicular lobes in each rami; dorsal cirri small, lamelliform and concave dorsally (as an extension of pre- and postchaetal lamellae); ventral cirri conical, small (Figure 27B-E). Branchiae recurved, with membranous expansions externally and internally when fully developed; moderately ciliated; present from chaetiger 9-14 still very rudimentar, well visible from chaetigers 13-15; becomes rudimentary again in posterior chaetigers and vestigial or absent in posteriormost chaetigers (from about chaetiger 60-65); occupy all interramal space when fully developed. Chaetae short, of three kinds: barred chaetae in preacicular position (Figure 27F), spinulated chaetae in postacicular position (Figure 27G), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips (Figure 27H).

Remarks. Fauchald (1963) provided an earlier synonymy history for *N. paradoxa* species. He referred to “*N. phyllocirra* McIntosh” as a possible synonym of *N. paradoxa*, thus accepting the earlier suggestion by Hartman (1950). However, the species that Hartman suggested to be a possible synonym of *N. paradoxa* was *N. phyllobranchia* McIntosh and not *N. phyllocirra*. Furthermore, the authorship of *N. phyllocirra* is Ehlers and not McIntosh as mentioned by Fauchald (1963). Assuming these corrections, Fauchald was in fact referring to *N. phyllobranchia* (and not *N. phyllocirra*) as a synonym of *N. paradoxa*. *Nephtys phyllocirra* was described by Ehlers (1887) for specimens from off southern Florida and differs mainly by having cirriform branchiae from chaetiger 6 until the end of body. Imajima and Takeda (1987) synonymized *N. schmitti* Hartman, 1938 from Alaska to *N. paradoxa*, although with doubts since they have not examined the type material. Later, Hilbig (1997) examined the holotype of *N. schmitti* along with other *N. schmitti* specimens from California, as well as specimens of *N. paradoxa* from Alaska, and concluded that the two species differ by the number of pharynx terminal papillae (20 in *N. schmitti*, 22 in *N. paradoxa*), the shape of subterminal papillae (short in *N. schmitti*, long and slender in *N. paradoxa*), and the occurrence of foliaceous branchiae on segments 12-30 in *N. schmitti* and on segments 20-65 in *N. paradoxa*. We examined specimens of *N. schmitti* from Alaska (including the holotype) and apart from slightly better developed postchaetal lamellae, we found no significant differences between these specimens and the ones of *N. paradoxa* from Europe. The 22 terminal bifid papillae mentioned by Hilbig (1997) are in fact 20 (10 on each side), separated dorsally and ventrally by a simple papilla, and this occurs in both species. Significant differences in length of subterminal papillae in the two species were not found. Both *N. schmitti* and European *N. paradoxa* specimens have foliaceous branchiae between chaetigers 12-42. However, in *N. paradoxa* specimens from eastern coast of USA the branchiae start being foliaceous only in the middle chaetigers (from 25-26 until 40-64). In these specimens the postchaetal lamellae also are slightly longer than acicular lobes, as it happens in *N. schmitti* specimens. Thus the specimens from Alaska ascribed to *N. schmitti* have mixed characters from European and American *N. paradoxa* specimens. Nevertheless, *N. schmitti* is here considered to be a synonym of *N. paradoxa*. The *N. paradoxa* from America should be carefully revised with examination of more specimens. According to the many records from deep-waters of very different geographical regions *N. paradoxa* has a worldwide distribution. However, many of these records require revision.

Distribution. Arctic Ocean; Atlantic Ocean (Greenland; from Iceland to South Africa and from Gulf of St. Lawrence to off Delaware); Mediterranean Sea (NE Spain); Pacific Ocean (Bering Strait, Bering Sea, Sea of Okhotsk, Japan; Australia; off Guatemala; off Peru; off Chile; Magellan Strait) (Fauchald 1972; Rozbaczylo & Castilla 1974; Imajima & Takeda 1987; Kirkegaard 1995; Laborda 2004).

Habitat. Muddy sediments; 50-8000 m depth (Rainer & Hutchings 1977; Laborda 2004).

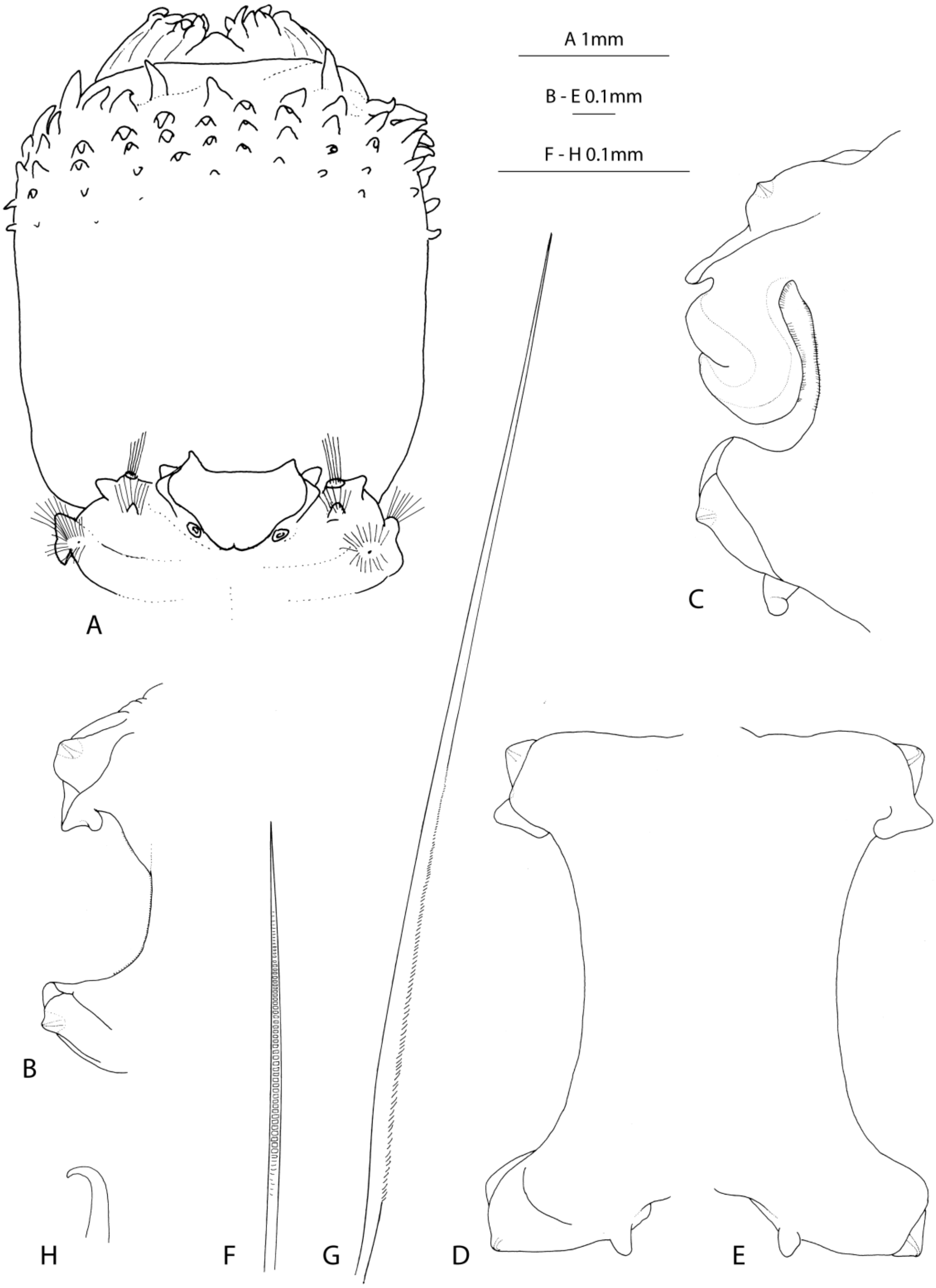


Figure 27. *Nephtys paradoxa*. A. Pharynx, prostomium and first chaetigers, dorsal view. B. Right parapodium of chaetiger 10, anterior view. C. Right parapodium of chaetiger 29, anterior view. D. Right parapodium of chaetiger 50, anterior view. E. Same, posterior view. F. Preacicular chaeta from chaetiger 10. G. Postacicular chaeta from chaetiger 10. H. Acicula of chaetiger 50.

3.1.4 Discussion

Due to the close morphological similarities between species nephtyids are very easily recognised as a group. However, further identification often proves difficult, especially for the smaller forms with poorly developed parapodial structures. The characteristics that traditionally have been used to differentiate genera within the Nephtyidae have been debated by many authors (e.g. Clark 1957; Fauchald 1968; Ohwada 1985; Rainer & Kaly 1988) and there are still doubts as to the boundaries between the genera (Rainer & Kaly 1988). In fact some of the characters used to distinguish the nephtyid genera are poorly defined and may overlap among genera, as stated by Hilbig (1997), thus requiring the examination of a combination of characters in order to establish the proper placement of a species within a genus. Branchiae shape and development (whether involute, recurved, absent or poorly developed) have always been one of the main diagnostic morphological characters for distinguishing the nephtyid genera. However, the phylogenetic analysis carried out by Ravara *et al.* (in press) placed two *Nephtys* species (*N. australiensis* and *N. pulchra*) within the *Aglaophamus* group and suggests the presence of homoplasy for the branchiae shape character thus making it less suitable for generic differentiation. These results will further increase the difficulty in distinguishing nephtyid genera since the branchiae shape was considered to be the only invariable distinctive feature between genera (Hilbig 1997). Therefore, other diagnostic characters for the genera are required. In this study new diagnosis for the nephtyid genera are suggested, as summarized in Table 11. The genera *Bipalponephtys* Ravara *et al.* (in press) is also included in the table although not represented in southern European fauna.

Aglaophamus species can be distinguished from other genera mainly by the acutely pointed acicular lobes, the curved tips of aciculae in all chaetigers and the higher number of subterminal papillae in the pharynx that are often organised in groups at the proximal end of rows.

Inermonephtys species may also have acutely pointed acicular lobes but distinctly differ from *Aglaophamus* and the other genera by the lack of antennae and pharynx papillae, the spindle-shaped jaws and the cirriform nuchal organs.

For *Micronephthys* genus there are at present no diagnostical morphological characters independent on size, as earlier mentioned by Jirkov (1989). The poor development of parapodial lamellae is also characteristic for some *Aglaophamus* species and can be found in the juvenil stages of any species. And the same situation occurs with the poor development or absence of branchiae. As mentioned above for the species *A. elamellatus* and *A. pulcher*, there are species for which the number of chaetigers with branchiae decreases with decreasing body size and are absent in the smallest specimens. Therefore *Micronephthys* species must be examined with caution considering their similarities to the juveniles of other species.

As for the genus *Nephtys*, the most distinctive characteristics are the shape of acicular lobes and arrangement of the pharynx papillae. However, generally a combination of characters should be used before assigning any species to a genus. The monotypic genus *Dentinephtys* was considered to be a júnior synonym of *Nephtys* by Ravara *et al*. (in press).

Bipalponephtys was recently erected by Ravara *et al.* (in press) to accommodate three species previously belonging to the genus *Nephtys*, based on the results of a phylogenetic analysis of the family. This genus includes at present three small-bodied species with poorly developed parapodial lamellae and branchiae, and it differs from all other genera in having bifid palps.

Table 11. Diagnostic characteristics for the genera of Nephtyidae in Europe.

	Aglaophamus	*Bipalponephtys*	*Inermonephtys*	*Micronephthys*	*Nephtys*
Antennae	Present	Present	Absent	Present	Present
Palps	Simple	Bifid	Simple, small	Simple	Simple
Nuchal organs	Rounded	Rounded	Cirriform	Rounded	Rounded
Acicular lobes	Acutely pointed	Conical	Conical / acutely pointed	Conical	Conical / rounded / bilobed
Parapodial lamellae	Usually well developed	Poorly developed	Well developed	Poorly developed	Well developed
Neuropodial superior lobes	Often present	Absent	Present / absent	Absent	Absent
Branchiae	Involute / recurved	Almost straight	Long, thin, involute	Absent / poorly developed	Recurved
Lyrate chaetae	Present / absent	Absent	Present	Present / absent	Absent
Acicular tips	Curved in all parapodia	Curved in median/posterior parapodia	Curved in posterior parapodia	Curved in median/posterior parapodia	Curved in median/posterior parapodia
Pharynx papillae	Present	Present	Absent	Present	Present
Subterminal papillae per row	More than 10, close together; proximal ones often in small groups	Up to 8	--	Up to 10	Less than 10 (usually up to 5-7)
Pharynx middorsal papilla	Absent	Present or absent	--	Absent	Often present
Pharynx proximal region	Smooth	Smooth	--	Smooth	Smooth / with warts
Jaws	Conical	Conical	Spindle-shaped	Conical	Conical

From the nineteen nephtyid species reported up to date from South European waters, only two, have their distributions restricted to this region. *Inermonephtys foretmontardoi* occurs from southern England to the Mediterranean Sea, and *Aglaophamus agilis*, if valid (see remarks of the species), occurs from the Mediterranean Sea to Mauritania. *Nephtys cirrosa* occurs mainly in southern Europe (from the English Channel to the northwestern coast of Africa and the Mediterranean Sea) but has also been recorded further north to the Irish Sea and the North Sea. Two other species, not known from the northern Europe, *M. stammeri* (Mediterranean) and the deep-sea species *A. elamellatus* (Portugal, Azores islands, Canary Islands) have been also reported from the Indian and Pacific Oceans.

Six species *A. pulcher*, *A. rubellus*, *N. assimilis*, *N. hystricis*, *N. incisa* and *N. kersivalensis* have their distributions extending all around Europe and except for *A. pulcher* also into the Mediterranean Sea. *Nephtys hombergii* has a wide distribution in the eastern Atlantic Ocean extending from the Barents Sea to South Africa. Two other species, *N. caeca* and *N. longosetosa*, are typically cold-water species with a circumboreal distribution, thus occurring more frequently in northern European regions.

There are four species reported only once or few times from NW Spain or the Mediterranean Sea with records that require confirmation. Three of these species, *A. malmgreni*, *M. minuta* and *N. cilitata*, have a typical circumpolar distribution while the fourth, *M. sphaerocirrata* is also reported from Indian and South Pacific Oceans.

Nephtys paradoxa has been reported from several different localities in the Atlantic Ocean (from Arctic to South Africa and the northeastern coast of North America), and in the Pacific Ocean (from Bering Strait to Japan, Australia, and western coast of South America). This apparently cosmopolitan species is obviously in need of revision as it might represent a complex of different species.

The described distributions follow the patterns of variation that we observed. However, there are reasons for caution when regarding species with wide distributions, and we have no doubts that future closer analyses including molecular data will change the picture and show them to consist of species complexes.

Acknowledgments

We thank Eduardo López (Universidad Autónoma de Madrid), Miguel Pardal (Universidade de Coimbra), Susana Carvalho, João Cúrdia and Fábio Pereira (IPIMAR, Olhão) and Dulce Subida (Instituto de Ciencias Marinas de Andalucía) for specimens donation, and Carlos Barroso for assistance with specimens collection in the Portuguese coast. Deep-sea specimens from the Portuguese canyons and Gulf of Cadiz were collected within the HERMES project (EC contract GOCE-CT-2005-511234, funded by the European Commission's Sixth Framework Program). Loans of specimens were kindly arranged by Ricardo Araújo (MMF), Emma Sherlock (NHM), Andy Mackie (NMWZ), Miguel Villena (MNCN), Christina Piotrowski (CASIZ), Angelika Brandt (ZMH), Kennet Lundin (GNM), Elin Sigvaldadöttir (NRM), Danny Eibye-Jacobsen (ZMC), Cheryl Bright (USNM) and Adam Baldinger (MCZ). The first author is supported by a PhD grant (SFRH/BD/16563/2004) from Fundação para a Ciência e Tecnologia. Financial support for FP was obtained from VR, dnr 2009-5125.

References

Amoureux, L. (1972) Annélides polychètes recueillies sur les pentes du talus continental, au large de la Galice (Espagne), campagnes 1967 et 1968 de la "Thalassa". *Cahiers de Biologie Marine, 13,* 63–89.

Annenkova, N. (1937) Fauna of Polychaeta from the northern part of the Sea of Japan. [In Russian.]. *Issledovaniya Morei SSSR, 23,* 139–216.

Annenkova, N. (1938) Polychaeta of the North Japan Sea and their horizontal and vertical distribution. *In: Reports of the Japan Sea Hydrobiological Expedition of the Academy of Sciences of the USSR in 1934, pt. 1* pp. 81-230.

Audouin, J. V. & Milne Edwards, H. (1833) Classification des annélides, et description de celles qui habitent les côtes de la France. *Annals de Sciences Naturelles, Paris (Sér. 1), 29,* 195–269.

Augener, H. (1912) Beitrag zur kenntnis verschiedener anneliden und bemerkungen uber die nordischen nephthys-arten und deren epitoke formen. *Archiv fur Naturgeschichte, Berlin, 78A*, 162–212.

Augener, H. (1928) Die Polychäten von Spitzbergen. *Fauna Arctica, 5,* 647–834.

Augener, H. (1932) Die polychaeten und Hirudineen des Timavogebietes in der adriatischen Karstregion. *Zoologisches Jahrbücher Jena (Syst.), 63,* 657–681.

Augener, H. (1940) Beitrag zur Polychaetenfauna der Ostsee. *Kieler Meeresforschungen, 3,* 133–147.

Baird, M. D. (1871) Description of some new species of annelida and gephrea in the collection of the British Museum. *Journal of the Linnean Society of London, 11*, 94–97.

Banse, K. (1959) Polychaeten aus Rovinj (Adria). *Zoologischer Anzeiger, 162,* 296–313.

Bellan, G. (1959) Campagnes de la Calypso: Mer d'Alboran. 2. Annélides Polychètes. *Annales de l'Institut Océanographique, 37*, 315–342.

Bellan, G. (1960) Résultats scientifiques de la Campagne du N. R. P. Faial (1957). 2. Annélides Polychètes. *In: Gabinete de Estudos das Pescas*, Lisboa, pp. 1-31.

Bellan, G. (1969) Annélides polychètes récueillies dans l'archipel de Madére au cours de la campagne scientifique du navire océanographique "Jean Charcot" (Julliet 1966). *Cahiers de Biologie Marine, 10*, 35–57.

Berkeley, E. (1924) Polychaetous annelids from the Nanaimo district. Part 2. Phyllodocidae to Nereidae. *Contributions to Canadian Biology and Fisheries, 2*, 287–293.

Berkeley, E. & Berkeley, C. (1945) Notes on polychaeta from the coast of western Canada. III. Further notes on Syllidae and some observations on other polychaeta Errantia. *Annals and Magazine of Natural History, London, 12*, 316-335.

Berkeley, E. & Berkeley, C. (1948) Canadian Pacific Fauna. 9. Annelida. 9b(1) Polychaeta Errantia. *Fish. Res. Bd. Canada*, 1–100.

Berkeley, E. & Berkeley, C. (1956) On a collection of polychaetous annelids from northern Banks Island, from the south Beaufort Sea, and from northwest Alaska; together with some new records from the east coast of Canada. *Journal of the Fisheries Research Board of Canada, 13*, 233–246.

Böggemann, M. (1997) Polychaeten aus der Deutschen Bucht. *Courier Forschungsinstitut Senckenberg, 202*, 1–315.

Campoy, A. (1982) Fauna de anelidos poliquetos de la Peninsula Iberica. *Publicaciones de Biologia de la Universidad de Navarra. Serie Zoologica, 7,* 1–781.

Charrier, H. (1907) Notes sur *Nephthys hombergii* Aud. et Edu. Arcachon. *Travaux de la Société Scientifique et Station Zoologique d'Arcachon, 10*, 297-306.

Chiaje, S., delle (1822) *Memorie sulla storie e notomia degli animali senza vertebre del regno di Napoli*. Napoli: Stamperia delle Societa Tipografica.

Clark, R. B. (1957) The influence of size on the structure of the brain of *Nephtys*. *Zoologische Jahrbücher (Abteilung für Allgemeine Zoologie und Physiologie der Tiere), 67*, 261–282.

Clay, E. (1974) *Literature survey of the common fauna of estuaries. 6. Nephthys hombergi Lamarck*: I.C.I. Ltd., Brixham Laboratory, Brixham, Devon, Revd Edn.

Curtis, M. A. (1979) A list of benthic polychaetes from Godhavn, West Greenland, with remarks on new records for Greenland. *Astarte, 12*, 1-3.

Day, J. H. (1953) The polychaete fauna of South Africa. Part 2. Errant species from Cape shores and estuaries. *Annals of the Natal Museum, 12*, 397–441.

Day, J. H. (1967) *A monograph on the Polychaeta of southern Africa. Part 1. Errantia*. London: Trustees of the British Museum (Natural History).

Day, J. H. (1973) New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. *NOAA Technical Report NMFS, 375*, 1–140.

Desbruyères, D., Guille, A. & Ramos, J. M. (1972) Bionomie benthique du plateau continental de la côte catalagne espagnole. *Vie et Milieu, 23*, 335-366.

Ditlevsen, H. (1929) Polychaeta. *Zoology of the Faroes, 16*, 1–83.

Ditlevsen, H. (1937) Polychaeta. The Goothaab expedition 1928. *Meddelelser om Grønland, 80*, 1-64.

Dnestrovskaja, N. & Jirkov, I. A. (2001) Nephtyidae Grube 1850. *In: Polychaeta of the Arctic ocean*. Yanus-K Press, Moscow, pp. 1-632.

Ehlers, E. (1868) *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt*. Leipzig: Wilhelm Engelmann.

Ehlers, E. (1874) Annulata nova vel minus cognita in Expeditione “Porcupine” capta. *Annals and Magazine of Natural History, Series 4, 13*, 292–298.

Ehlers, E. (1875) Beiträge zur Kenntnis der Verticalverbreitung der Borstenwürmer in Meere. *Zeitschrift fur Wissenschaftliche Zoologie, 25*, 1–102.

Ehlers, E. (1887) Reports on the annelids of the dredging expedition of the U.S. coast survey steamer “Blake“. *Memoirs of the Museum of Comparative Zoology of Harvard College, 15*, 1–335.

Eliason, A. (1951) Polychaeta. *Reports of the Swedish Deep-Sea Expedition 1947-1948, 2,* 130–148.

Eliason, A. (1962) Die Polychaeten der Skagerak-Expedition 1933. *Zoologiska Bidrag fran Uppsala, 33,* 207–293.

Fabricius, O. (1780) *Fauna Groenlandica, systematica sistens, Animalia Groenlandiae occidentalis hactenus indagata, quoad nomen specificum, triviale, vernaculumque; synonyma auctorum plurium, descriptionem, locum, victum, generationem, mores, usum, capturamque singuli; prout detegendi occasio fuit, maximaque parti secundum proprias observationes. Copenhagen*.

Fage, L. & Legendre, R. (1927) Péches planctoniques à la lumière, effectuées à Banyuls-sur-Mer et à Concarneau. I. Annélides polychètes. *Archives de Zoologie Expérimentale et Génerale, 67,* 23–222.

Fauchald, K. (1963) Nephtyidae (Polychaeta) from Norwegian waters. *Sarsia, 13,* 1–32.

Fauchald, K. (1968) Nephtyidae (Polychaeta) from the Bay of Nha Trang, South Viet Nam. *NAGA Report, 4,* 7–33.

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

Fauvel, P. (1914) Annélides polychètes non-pelagiques provenant des campagnes de l'Hirondelle et de la Princesse-Alice (1885-1910). *Résultats des campagnes scientifiques accompliés par le Prince Albert I, 46,* 1–432.

Fauvel, P. (1923) Polychètes érrantes. *Faune de France, 5,* 1–488.

Fauvel, P. (1933a) Annélides polychètes du Golfe du Pei Tcheu Ly, de la collection du Musée Hoang ho Pai ho. *Publs. Mus. Hoang Pai ho Tien-Tsin, 15,* 1–67.

Fauvel, P. (1933b) Mission Robert Ph. Dolfus en Egypte. Annèlides polychètes. *Mémoires de l'Institute d'Égypte, 21,* 31-83.

Fauvel, P. (1936) Contribution a la faune des annélides polychètes du Maroc. *Mémoires de la Société des Sciences Naturelles du Maroc,* 43: 1-144.

Fauvel, P. (1940) Annèlides polychètes de la Haute Adriatique. *Thalassia, Rovigno, 4,* 1-24.

Foret-Montardo, P. (1969) Étude systématique et écologique des Nephtyidae (Polychètes Errantes) des parages de Marseille. *Tethys, 1,* 807–832.

Fournier, J. A. & Pocklington, P. (1984) The sublittoral polychaete fauna of the Bras d'Or lakes. Nova Scotia, Canada. *In: Proceedings of the First International Polychaete Conference, Publications of the Linnean Society of New South Wales,* pp. 254–278.

Friedrich, H. (1939) Polychaeten-Studien IV. Zum Polychaeten-Fauna der Barentz-See. *Kieler Meeresforschungen, 3,* 122–132.

Friedrich, H. (1964) *Aglaophamus agilis* (Langerhans) 1879 (Polychaeta Errantia, Fam. Nephthyidae) neubeschreibung und synonymie. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven, 3,* 135-138.

Gardiner, S. L. (1976) Errant polychaete annelids from North Carolina. *Journal of the Elisha Mitchell Scientific Society, 91*, 77–220.

Garwood, P. R. & Olive, P. J. W. (1981) The significance of the long chaetal form of *Nephtys caeca* (Polychaeta: Nephtyidae) and its relationship to *N. longosetosa*. *Sarsia, 66,* 195–202.

George, J. D. (1979) The polychaetes of Lewis and Harris with notes on other marine invertebrates. *Proceedings of the Royal Society of Edinburgh, 77B,* 189–216.

Gibbs, P. E. (1969) A quantitative study of the polychaete fauna of certain fine deposits in Plymouth Sound. *Journal of the Marine Association of the United Kingdom, 49,* 311-326.

Gibbs, P. E. (1971) The Polychaete fauna of the Solomon Islands. *Bulletin of the British Museum (Natural History), 21*, 101–211.

Gorbunov, G. (1946) Bottom life of the Novosiberian shoalwaters and the central part of the Arctic Ocean. [In Russian with English summary.]. *Transactions of the Drifting Ice Expedition in the Central Arctic Ocean in the Ice-Breaker "G. Sedov", 1937-1940 3*, 30–138.

Grube, A. E. (1840) *Actinien, Echinodermen und Würmer des Adriatischen- und Mittelmeers nach einigen Sammlungen beschreiben.* Königsberg.

Guille, A. & Laubier, L. (1966) Additions à la faune des annélides polychètes de Banyuls-sur-Mer. *Vie et Milieu, 17,* 259–283.

Hansen, G. A. (1878) Annelider fra den norske nordhavsexpedition i 1876. *Nyt Magazin for Naturvidenskaberne, 24,* 1–17.

Hartman, O. (1938) Review of the annelid worms of the family Nephtyidae from the Northeast Pacific, with descriptions of five new species. *Proceedings of The United States National Museum, 85*, 143–158.

Hartman, O. (1940) Polychaetous annelids. Part II. Chrysopetalidae to Goniadidae. *Allan Hancock Pacific Expeditions, 7*, 173–287.

Hartman, O. (1944) New England Annelida. Part 2. Including the unpublished plates by Verrill with reconstructed captions. *Bulletin of the American Museum of Natural History, 82*, 327–344.

Hartman, O. (1948) The polychaetous annelids of Alaska. *Pacific Science, 2*, 3–59.

Hartman, O. (1950) Goniadidae, Glyceridae and Nephtyidae. *Allan Hancock Pacific Expeditions, 15*, 1–181.

Hartman, O. (1959) Catalogue of the polychaetous Annelids of the world. Part I. *Allan Hancock Foundation Publications. Occasional Paper, 23*, 1–353.

Hartman, O. (1965) Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic areas. *Allan Hancock Foundation Publications. Occasional Paper, 28*, 1–378.

Hartman, O. (1967) Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic seas. *Allan Hancock Monographs in Marine Biology, 2*, 1–387.

Hartmann-Schröder, G. (1971) Annelida, Borstenwürmer, Polychaeta. *Tierwelt Deutschlands, 58*, 1–594.

Hartmann-Schröder, G. (1974) Polychaeten von Expeditionen der “Anton Dohrn“ in Nordsee und Skagerrak. *Veröffentlichungen des Instituts für Meeresforschung in Bremerhaven, 14*, 169–274.

Hartmann-Schröder, G. (1977) Polychaeten aus dem Sublitoral und Bathyal vor der portugiesischen und marokkanischen Küste Auswertung der Fahrt 8 (1967) von F.F., “Meteor”. *Meteor Forschungsergebnisse, Reihe D, 26*, 65–99.

Hartmann-Schröder, G. (1981) Die Polychaeten der Fahrten 11, 19, 21 und 26 (1967-1972) von F.S. “Meteor” in das Gebiet zwischen dem Golf von Biscaya und dem Auftriebsgebiet vor Westafrika. *Meteor Forschungsergebnisse, Reihe D, 33*, 23–36.

Hartmann-Schröder, G. (1982) Die Polychaeten der Fahrt 36 (1975) von F.S. “Meteor” in das Auftriebsgebiet vor Nordwest-Afrika. *Meteor Forschungsergebnisse, Reihe D, 35*, 1–20.

Hartmann-Schröder, G. (1996) Annelida, Borstenwürmer, Polychaeta. 2. neubearbeitete Auflage. *Tierwelt Deutschlands, 58*, 1–648.

Heinen, A. (1911) Die Nephtyideen und Lycorideen der Nord- und Ostee, einschlieblich der verbindenden Meeresteile. *Wissenschaftliche Meeresuntersuchungen, 13*, 1–87.

Hilbig, B. (1997) Family Nephtyidae Grube, 1850. *In:* J. A. Blake, B. Hilbig & P. H. Scott (Eds), *Taxonomic atlas of the benthic fauna of the Santa Maria basin and the western Santa Barbara channel. 4. The Annelida. Part 1. Oligochaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae),* Santa Barbara, California, pp. 317-349.

Horst, R. (1881) Die anneliden gesammelt wahrend der Fahrten des "Willem Barentz" in den Jahren 1878 und 1879. *Archives Neerlandaises de Zoologie, 1*.

Imajima, M. (1961) Polychaetous annelids collected off the west coast of Kamchatka. I. Notes on species found in the collections of 1957-58. *Publications of the Seto Marine Biological Laboratory, 9*, 81–102.

Imajima, M. (1970) Errant polychaetous annelids collected from the areas around the Tsushima Islands. *Memoirs of the National Science Museum of Tokyo, 3,* 113–122.

Imajima, M. & Hartman, O. (1964) The polychaetous annelids of Japan. Part 1. *Allan Hancock Foundation Publications. Occasional Paper, 26,* 1–166.

Imajima, M. & Takeda, Y. (1985) Nephtyidae (Polychaeta) from Japan. I. The genera *Inermonephtys*, *Micronephthys* and *Aglaophamus*. *Bulletin of the National Science Museum, Tokyo, 11,* 57–90.

Imajima, M. & Takeda, Y. (1987) Nephtyidae (Polychaeta) from Japan. II. The genera *Dentinephtys* and *Nephtys*. *Bulletin of the National Science Museum, Tokyo, 13,* 41–77.

Izuka, A. (1912) The Errantiate Polychaeta of Japan. *Journal of the College of Science, Imperial University of Tokyo, 30,* 1–262.

Jirkov, I. A. (1989) *Bottom fauna of the USSR. Polychaeta*. Moscow: Moscow University Press.

Jirkov, I. A. & Paraketsova, N. (1996) Review of the species of the genus *Micronephthys* (Polychaeta: Nephthyidae) from the White Sea. *Zoologicheskii Zhurnal, 75,* 831–840. [In Russian].

Johnson, H. P. (1901) The polychaeta of the Puget Sound region. *Proceedings of the Boston Society of Natural History, 29,* 381–437.

Johnston, G. (1835) Illustrations in British Zoology. *Nephtys* Cuvier. *Natural History Magazine, 8,* 341–343.

Johnston, G. (1865) *A catalogue of the British non-parasitical worms in the collection of the British Museum*. London: British Museum.

Jung, R.-H. & Hong, J.-S. (1997) Nephtydae (Annelida: Polychaeta) from the Yellow Sea. *Bulletin of the Marine Science, 60,* 371–384.

Kirkegaard, J. B. (1956) Benthic Polychaeta from depths exceeding 6000 meters. *Galathea Report, 2,* 63–78.

Kirkegaard, J. B. (1969) A quantitative investigation of the central North Sea polychaeta. *Spolia Zoologica Musei Hauniensis, 29,* 1–285.

Kirkegaard, J. B. (1980) Abyssal benthic polychaetes from the Northeast Atlantic Ocean, Southwest of the British Isles. *Steenstrupia, 6,* 81–98.

Kirkegaard, J. B. (1995) Bathyal and abyssal polychaetes (errant species). *Galathea Report, 17,* 7–56.

Kupffer, K. (1873) Die auf der Fahrt nach Arendal gefangenen Thiere. Die Expedition zurphysikalisch-chemischen und biologischen Untersuchung der Ostsee im Sommer 1871 auf S.M. Avisodampfer Pommerania. *Wissenschaftliche Meeresuntersuchungen der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere, 1,* 150–152.

La Greca, M. (1946) Studii sui policheti del Golfo di Napoli. *Pubblicazioni della Stazione Zoologica di Napoli, 20,* 270–280.

Laborda, A. J. (1987) Estudio con el SEM (Scanning Electron Mycroscopy) de tres especies del genero *Nephtys*. *Cahiers de Biologie Marine, 28,* 131–146.

Laborda, A. J. (2004) Familia *Nephtyidae* Grube, 1850. *In:* J. M. Viéitez, C. Alós, J. Parapar, C. Besteiro, J. Moreira, J. Nuñez, A. J. Laborda & G. San Martin (Eds), *Annelida, Polychaeta I.* Museo Nacional de Ciencias Naturales. CSIC, Madrid, pp. 390–419.

Laborda, A. J. & Viéitez, J. M. (1984) Anélidos poliquetos intermareales endémicos de Galicia (con la descripción de una nueva especie del género Nephthys). *Cuadernos Marisqueros publication Técnico, 7,* 207–221.

Langerhans, P. (1880) Die wurmfauna von Madeira. II. *Zeitschrift fur Wissenschaftliche Zoologie, 33,* 271–316.

Lee, J.-H. & Jae, J.-G. (1983) Polychaetous annelids from the Yellow Sea. I. Family Nephtyidae. *Bulletin of the Korea Ocean Research and Development Institute, 5*, 19–27.

Levinsen, G. M. R. (1887) Kara-Havets Ledorme (Annulata). *In:* C. F. Lütken (Ed), *Djimphna-Togtets Zoologiske-botaniske Udbytte*. J. Hagerup, Köbenhaven, pp. 288–303.

Malm, A. W. (1874) Annulater i hafvet utmed Sveriges vestkust och omkring Göteborg. *Göteborgs Kungl. Vetenskaps och Vitterhets Samhälles Handlingar, 14*, 67–105.

Malmgren, A. J. (1865) Nordiska hafs-annulater. *Öfversigt af K. Vetenskapsakademiens förhandlingar*, 51–110.

Malmgren, A. J. (1867) Annulata polychaeta Spetsbergiæ, Grönlandiæ, Islandiæ et Scandinaviæ hactenus cognita. *Öfversigt af K. Vetenskapsakademiens förhandlingar, 24*, 127–235.

Malonda, I. (2009) Estudio de la taxocenosis de poliquetos como parte de la evaluacion de la calidad ambiental en el puerto de Cartagena (Murcia, España - Study on the polychaete taxocene as part of the environmental quality assesment in Cartagena Harvour (Murcia, España) Universidad Autónoma de Madrid, Madrid. 320 pp.

Marenzeller, E. (1904) Berichte der Commission für Oceanographische Forschungen. Achte Reihe. Forschungen im Østlichen mittelmeere. Zoologische Ergebnisse XIII. Polychäten des Grundes, gesammelt 1893, 1894. *Denkschriften der Akademie der Wissenschaften, 74*, 295–323.

Marenzeller, E. (1904) Zoologische ergebnisse XIII. Polychäten des grundes-expedit. *S. M. Schiff "Pola" in das Östliche Mittelmeer. Denk. Ak. Wien, 74*, 295-323.

McIntosh, W. C. (1879) On the annelida obtained during the cruise of H. M. S. "Valorous" to Davis Strait in 1875. *Transactions of the Linnean Society of London, 1*, 499–511.

McIntosh, W. C. (1885) Report on the Annelida Polychaeta collected by H.M.S. Challenger during the years 1873-76. *Report of the Scientific Results of the Voyage of H.M.S. Challenger 1873-76, 12*, 1–554.

McIntosh, W. C. (1900) Notes from the Gatty Marine Laboratory, St. Andrews. *Annals and Magazine of Natural History (Ser. 7), 5*, 254-268.

McIntosh, W. C. (1908) A monograph of British Annelids. *Ray Society of London, II. Part I. Polychaeta. Nephthydidae to Syllidae*, 1–232.

Michaelsen, W. (1896) Die Polychaetenfauna der deutschen Meere, einschliesslich der benachbarten und verbindenden Gebiete. *Wissenschaftliche Meeresuntersuchungen, 2*, 1–216.

Möbius, K. (1873) Die wirbellosen Thiere der Ostsee *Wissenschaftliche Meeresuntersuchungen der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere, 1*.

Möbius, K. (1875) Vermes. *Jahresbericht der kommission zur wissenschaftlichen Untersuchung der Deutschen Meere in Kiel für die Jahre 1872, 1873, 2-3*, 153–172.

Moore, P. (1903) Polychaeta from the coastal slope of Japan and from Kamchatka and Bering sea. *Proceedings of the Academy of Natural Sciences, Philadelphia, 55*, 401–490.

Müller, O. F. (1776) *Zoologicae Danicae Prodromus, seu Animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium*. Havniae [Copenhagen]: Hallageriis.

Müller, O. F. (1789) *Zoologia Danica seu animalium Daniae et Norvegiae rariorum ac minus notorum. Descriptiones et historia* (Vol. 3). Havinae.

Nateewathana, A. & Hylleberg, J. (1986) Nephtyid polychaetes from the west coast of Phuket Island, Andaman sea, Thailand, with description of five new species. *Proceedings of the Linnean Society of New South Wales, 108*, 195–215.

Nordgaard, O. (1905) Hydrographical and biological investigations in Norwegian Fiords. *(published by Bergen Mus. as a separate Vol.) Vermes*, 157-164, 235, 241-245.

Ohwada, T. (1985) Prostomium morphology as a criterion for the identification of nephtyid polychaetes (Annelida: Phyllodocida), with reference to the taxonomic status of *Aglaophamus neotenus*. *Publications of the Seto Marine Biological Laboratory, 30,* 55-60.

Okuda, S. (1938) Polychaete annelids from the Ise Sea. *Zoological Magazine, Tokyo, 50,* 122-131.

Okuda, S. (1939) Annelida polychaeta in Onagawa Bay and its vicinity. II: Polychaeta errantia with some addenda of polychaeta sedentaria. *Science Reports of the Tohoku Imperial University, 14,* 219–244.

Okuda, S. & Yamada, M. (1954) Polychaetous annelids from Matsushima Bay. *Journal of the Faculty of Science, Hokkaido University, Ser. 6, 12*, 175–199.

Örsted, A. S. (1842) Udtag af en beskrivelse af Grønlands annulata dorsibranchiata. *Naturhistorisk Tidsskrift, 4*, 109–127.

Örsted, A. S. (1843) *Annulatorum Danicorum Conspectus. Fasc. 1. Maricolæ, Hafniea*. Copenhagen.

Paik, E.-I. (1973) Some benthic polychaetous annelids from the Yellow Sea. *Bull. Korean Fish. Soc., 6*, 123–131.

Parapar, J., San Martin, G., Urgorri, V. & Besteiro, C. (1993) Anélidos poliquetos mesopsámmicos sublitorales de la costa de Ceuta (España). *Cahiers de Biologie Marine*, *34*, 363–381.

Paxton, H. (1974) Contribution to the study of Australian Nephtyidae (Polychaeta). *Records of the Australian Museum, 29*, 197–208.

Pettibone, M. H. (1954) Marine polychaete worms from Point Barrow, Alaska, with aditional records from the North Atlantic and North Pacific. *Proceedings of the Unites States National Museum, 103*, 203–356.

Pettibone, M. H. (1956) Marine polychaete worms from Labrador. *Proceedings of The United States National Museum, 105*, 531–584.

Pettibone, M. H. (1963) Marine polychaete worms of the New England region. *Bulletin of the United States National Museum, 227*, 1–356.

Quatrefages, A. d. (1865) *Histoire naturelle des Annelés marins et d'eau douce. Annélides et Géphyriens. Tome premier*. Paris: Librairie Encyclopédique de Roret.

Rainer, S. F. (1984) *Nephtys pente* sp. nov. (Polychaeta: Nephtyidae) and a key to *Nephtys* from Northern Europe. *Journal of the Marine Biology Association of the United Kingdom*, 64, 899–907.

Rainer, S. F. (1989) Redescription of *Nephtys assimilis* and *N. kersivalensis* (Polychaeta: Phyllodocida) and a key to *Nephtys* from Northern Europe. *Journal of the Marine Biology Association of the United Kingdom, 69*, 875–889.

Rainer, S. F. (1990) The genus *Nephtys* (Polychaeta: Phyllodocida) in northern Europe: redescription of *N. hysticis* and *N. incisa*. *Journal of Natural History, 24*, 361–372.

Rainer, S. F. (1991) The genus *Nephtys* (Polychaeta: Phyllodocida) of northern Europe: a review of species, including the description of *N. pulchra* sp.n. and a key to the Nephtyidae. *Helgoländers Meeresuntersuchungen, 45*, 65–96.

Rainer, S. F. & Hutchings, P. A. (1977) Nephtyidae (Polychaeta: Errantia) from Australia. *Records of the Australian Museum, 31*, 307–347.

Rainer, S. F. & Kaly, U. L. (1988) Nephtyidae (Polychaeta: Phyllodocida) of Australia: new species from the West shelf, and key to Australian species. *Journal of Natural History, 22*, 685–703.

Ravara, A., Wiklund, H., Cunha, M. R. & Pleijel, F. (in press) Phylogenetic relationships within Nephtyidae (Polychaeta, Annelida). *Zoologica Scripta*.

Reish, D. J. (1965) Benthic polychaetous annelids from Bering, Chukchi, and Beaufort Seas. .

Rozbaczylo, N. & Castilla, J. C. (1974) La familia Nephtyidae en Chile (Annelida, Polychaeta). *Studies on the Neotropical Fauna, 9*, 179-206.

Rullier, F. (1972) Annélides polychètes de Nouvelle-Calédonie. *6*, 1–169.

Rullier, F. & Amoureux, L. (1970) Nouvelle contribution à l'étude de la faune des annélides polychètes du Maroc. *Bulletin de la Société des Sciences Naturelles et Physiques du Maroc, 49*, 109–142.

Saint-Joseph, A. (1894) Les Annélides polychètes des côtes de Dinard. Troisième partie. *Annales des Sciences Naturelles (Zoologie), Série 7, 17*, 1–395.

San Martín, G. (1982) Una nueva especie de Nephthyidae (Poliquetos: Errantes) del Mediterraneo: *Micronephthys maryae* n. sp. *Cahiers de Biologie Marine, 23*, 427–434.

Savigny, J.-C. (1822) Troisième partie. Systèmes de diverses classes d'animaux sans vertèbres. Système des annélides, principalement de celles des côtes de l'Égypte et de la Syrie, offrant les charactères tant distinctifs que naturels des Ordres, Familles et Genres, avec la description des espèces. *Descriptions de l'Egypte, Histoire Naturelle, 3*, 1–128.

Southward, E. C. (1956) On some polychaeta of the Isle of Man. *Annals and Magazine of Natural History, 9*, 257-279.

Stimpson, W. (1854) Synopsis of the marine invertebrata of Grand Manan: or the region about the mouth of the Bay of Fundy, New Brunswick. *Smithsonian Contributions to the Knowledge, 6*, 1-67.

Takahashi, K. (1938) Polychaetous Annelid of Izu Peninsula. I. Polychaeta, collected by the 'Misago' during the Zoological Survey around the Izu Peninsula. *Science Reports, Tokyo Bunrika Daigaku, 3,* 193–220, plate 120.

Taylor, J. L. (1984) Family Nephtyidae Grube, 1850. *In:* J. M. Uebelacker & P. G. Johnson (Eds), *Taxonomic guide to the polychaetes of the Northern Gulf of Mexico*. V. Barry A. Vittor and Associates, Mobile, Alabama, pp. 35.31–35.20.

Tebble, N. (1955) The Polychaete fauna of the Gold Coast. *Bulletin of the British Museum (Natural History), 3*, 59–148.

Théel, H. (1879) Les annélides polychètes des mers de la Nouvelle-Zemble. *Kungliga Svenska Vetenskapsakademiens Handlingar, 16*, 1–75.

Thorson, G. (1946) Reproduction and larval development of Danish marine bottom invertebrates with special reference to the planktonic larvae in the Sound (Øresund). *Meddelelser fra Kommissionen for Danmarks Fiskeri- Og Havundersøgelser, Serie: Plankton, 4*, 1–523.

Treadwell, A. L. (1914) Polychaetous annelids of the Pacific coast in the collections of the zoological museum of the University of California. *University of California Publications in Zoology, 13*, 175–234.

Tzetlin, A. B. (1980) *Practical determinations of the polychaete worms from the White Sea.* Moscow: Moscow University Press.

Uschakov, P. & Wu, B.-L. (1962) Polychaete worms of the Yellow Sea II. Fam. Chrysopetalidae, Glyceridae and Nephtyidae (Polychaeta, Errantia). *Studia Marina Sinica, 1*, 1–32.

Uschakov, P. V. (1955) Polychaeta of the Far Eastern Seas of the U.S.S.R. *Academiya Nauk SSSR, Keys to the Fauna of the SSSR, 56*, 1–433 (translated from Russian by the Israel Program for Scientific Translations, Jerusalem 1965).

Verrill, A. E. (1881) New England Annelida. Part I. Historical sketch, with annotated lists of the species hitherto recorded. *Transactions of the Connecticut Academy of Arts and Sciences, 4,* 285–324.

Webster, H. E. & Benedict, J. E. (1887) The Annelida Chaetopoda from Eastport, Maine. *Report of the United States Commissioner of Fisheries, 1885*, 707–755.

Wesenberg-Lund, E. (1949) Polychaetes of the Iranian Gulf. *Danish Scientific Investigations in Iran, 4*, 247–400.

Wesenberg-Lund, E. (1950) Polychaeta. *The Danish Ingilf-Expedition, 4*, 1–80.

Wesenberg-Lund, E. (1950) The polychaeta of west Greenland. *Meddelelser om Gronland, 151*, 1–171.

Wesenberg-Lund, E. (1951) Polychaeta. *The Zoology of Iceland, 2*, 1–182.

Whiteaves, J. F. (1901) Catalogue of the marine invertebrata of eastern Canada. *Report on geological Survey of Canada*, 1–272.

Wolff, W. J. (1968) De famile Nephtyidae (Polychaeta). *Tabellenserie van de Strandwerk-Gemeenschap, 22*, 1–7.

Zatsepin, V. I. (1948) *Polychaete worms. Determination of fauna and flora of Northern Sea in USSR.*: Superior School of Moscow.

Chapter 3.2. Taxonomy of the family Nephtyidae

3.2.1 Introduction

The five genera, *Aglaophamus*, *Dentinephtys*, *Inermonephtys*, *Micronephthys* and *Nephtys*, in the family Nephtyidae include, according to Rizzo and Amaral (2007), 186 nominal species from which 30% are synonyms or *nomina nuda*. Following a phylogenetic analysis of the family Nephtyidae, Ravara *et al.* (in press, see section 2 – chapter 2.1) erected a new genus, *Bipalponephtys*, to include two species previously assigned to the genus *Nephtys* and one to the genus *Micronephthys*, synonymised the genus *Dentinephtys* with *Nephtys*, and transferred two other *Nephtys* species to the genus *Aglaophamus*. Subsequently, Ravara *et al.* (submitted, see section 3 – chapter 3.1), in their review of the southern European Nephtyidae, described a new species of *Inermonephtys*, *I. foretmontardoi*, and synonymised *Micronephthys maryae* with *M. stammeri*. In this chapter a revised species list of the Nephtyidae is included, where the species *N. serratus* is synonymised with *N. serratifolia*. The family Nephtyidae is therefore considered to have five genera and 128 species. The majority of the species fall into two main genera, *Nephtys* (57 species) and *Aglaophamus* (53 species). The remaining eighteen species belong to the three other genera of the family (*Inermonephtys* – eight species, *Micronephthys* - seven species, *Bipalponephtys* – three species).

In this chapter I review available taxonomical information and point out some discrepancies and eventual taxonomical problems within the Nephtyidae. Therefore, I provide an annotated species list including comprehensive synonymy, and information on species habitat, and geographical and bathymetric distributions. Whenever possible the type or other museological material was examined for each species. Where necessary, terminations of adjectival epithets have been changed to conform the gender of the generic name. A list of invalid taxonomical names is also included.

Diagnostic tables including all species are given at the end of the chapter, as well as graphics and maps illustrating depth and geographical distribution, respectively. For practical purposes, the species were grouped according to comprehensive geographical areas; i) N and S America; ii) Europe and Africa; iii) Indopacific region; iv) polar or wide distribution. These four groups have no biogeographical meaning. Plates with figures of the species parapodia are also presented. A table with information on deposit of type material is included in Annex I, and a list of major revisions for the family Nephtyidae is included in Annex II.

3.2.2 Material and methods

Part of the material examined in this study was collected along the Portuguese coast and from several places around the world. Most specimens were fixed and preserved in 90-95% ethanol and deposited in the Biological Research Collection of the Department of Biology of the University of Aveiro (DBUA) and the Museu Nacional de História Natural (Museu Bocage) in Lisbon (MNHN MB). Additional examined material came from collections of the University of Aveiro (DBUA), the Museu Municipal do Funchal, Madeira (MMF) the Natural History Museum of London (NHM), the National Museum of Wales (NMWZ) the Museo Nacional de Ciencias Naturales, Madrid (MNCN), the California Academy of Sciences, Invertebrate Zoology (CASIZ), Zoologisches Museum, Hamburg (ZMH), Naturistoriska Museum, Gothenburg (GNHM), Naturhistoriska Riksmuseet, Stockholm (NRM), Zoologisk Museum, Copenhagen (ZMC), the Museu de Zoologia da Universidade Estadual de Campinas "Adão José Cardoso" (ZUEC), the United States National Museum of Natural History (USNM), and the Museum of Comparative Zoology, Harvard University (MCZ).

Drawings were prepared from preserved animals with a camera lucida or redrawn from the literature.

3.2.3 Distinctive characters

A list of distinctive characters is here included and their diagnostic value discussed.

Pigmentation. Nephtyids are usually unpigmented although some species may have a typical dorsal pigmentation pattern along the body (e.g. *Nephtys ferruginea*, *N. picta*) or on the prostomium (e.g. *N. caecoides*, *N. californiensis*, *N. ferruginea*). Thus, when present, pigmentation may help to distinguish these species from unpigmented ones. The absence of pigmentation, however, is not decisive for the species identification since younger specimens may have not yet developed pigmentation and furthermore, pigmentation may fade with time in preserved specimens.

Pharynx. Except for the genus *Inermonephtys* in which pharynx papillae are absent, nephtyids pharynx have 10 pairs of terminal bifid papillae separated dorsally and ventrally by a gap or a simple conical papilla, and 14 to 22 rows of simple papillae decreasing in size towards the base of proboscis. For some species a single middorsal and a single midventral papilla are also present between the terminal and subterminal papillae. Proximally the proboscis is either smooth or covered with small warts. According to Lovell (1997), the inner and outer parts of the terminal bifid papillae originate separately and not jointly on the distal rim of the proboscis. Thus this author considers the term paired preferred over the term bifid. However, since the terminal papillae are often counted as pairs of papillae, and the term bifid has been commonly used in the literature, the term bifid is maintained and used herein to avoid confusion. The number of pairs of terminal papillae may be less than 10 for smaller nephtyid forms, nevertheless its diagnostic value may be considered as less important than the number of subterminal papillae. The number of rows of subterminal papillae and the number of papillae per row, as well as the presence or absence of a single middorsal papilla and warts in the proximal part of the pharynx, are important diagnostic characters at species level. The number of rows and number of papillae in each row are important for species differentiation. Most *Aglaophamus* species have 14 or 22 rows, often with up to more than ten papillae per row. An additional set of small papillae, organized in triangular groups, is often present in the proximal end of each row. *Bipalponephtys* and *Micronephthys* species have 16-22 and 18-22 rows, respectively, with up to ten papillae per row. *Nephtys* species have 20 or 22 rows of less than ten papillae, with a few exceptions (e.g. *N. mesobranchia*). Whether these rows occupy all or only a small distal part or the pharynx may also be a helpful character, although it is obviously directly related to the number of papillae per row. The presence of warts on the proximal part of the pharynx is sometimes of difficult observation under a stereomicroscope, however it is a valuable diagnostic character. Because the pharynx in nephtyids is rarely completely everted, all these features are difficult to examine and to be used in species identification. As a result of this difficulty, there are still several species for which the pharynx is not yet described.

Jaws. Jaws are located within the pharynx and can only be examined by dissection, thus being frequently overlooked. According to Fauchald (1968), jaw shape seems to be a good generic and specific diagnostic character. This author described the differences between the jaws of the genera *Nephtys*, *Aglaophamus*, *Micronephthys* and *Inermonephtys*. *Nephtys* jaws have a roughly triangular base with a spur on posterior edge and a recurved tip. *Aglaophamus* jaws have the same general shape but differ by having an inner supportive ridge. *Micronephthys* jaws have a more elongated base with a poorly developed spur, and also have an inner supportive ridge. *Inermonephtys* jaws have a spindle-shaped base and a straight free edge and practically lack spur. The recurved tip is absent. These differences were not investigated in this study, because the majority of the specimens examined belong to museum collections and dissection was not authorized. Apart from jaws, specimens of *Nephtys glabra* (previously included in the genus *Dentinephtys*, Ravara *et al.* in press) also have a pair of trepans with eight teeth each. This feature may have been overlooked in other species.

Prostomium. The prostomium shape and proportions can only be observed when pharynx is not everted, and is usually pentagonal, with a nearly straight anterior margin and a U or V-shaped posterior margin. Prostomium morphology may vary somewhat between the species but has poor diagnostic value.

Antennae and palps. Antennae and palps may be subequal in shape and length or more frequently palps are larger than antennae. Their relative position in the prostomium varies between species and may be used as a distinctive character (Ohwada 1985a). Antennae are located on the anterior corners of the prostomium, while palps may be placed posteriorly close to the antennae or further back on the ventro-lateral sides of the prostomium. *Inermonephtys* species lack antennae and their palps are small and hardly visible.

Nuchal organs. These organs are located near the posterior corners of the prostomium and are rounded on *Aglaophamus, Bipalponephtys*, *Micronephthys* and *Nephtys* species, and cirriform on *Inermonephtys* species. In one *Inermonephtys* species (*I. palpata*) the nuchal organ is formed by three cirriform processes.

Eyes. One pair of small eyes is usually present dorsally on the posterior part of the brain of nephtyids (Clark 1956) and is only visible through the dorsal cuticle of the anterior chaetiger in small nephtyid species or in juveniles of large ones (Mackie 2000). Nevertheless, there are several species with one or two pairs of eyes visible on the prostomium. For these species the presence of prostomial eyes may be considered as a diagnostic character although with caution because it sometimes varies between specimens of a same species.

Chaetiger 1. The parapodia of chaetiger 1 may be similar in size to the subsequent ones but are usually less developed and directed forward. The notopodia of chaetiger 1 are morphologically similar to the following ones, while the neuropodia are distinct by having a conical to acutely pointed acicular lobe surrounded by the neuropodial pre- and postchaetal lamellae that form a cylinder. Dorsal cirri are usually present on this chaetiger although they may be very small. Ventral cirri are well developed, conical to cirriform, and usually larger than on the following chaetigers. The shape and size of ventral cirri is sometimes helpful for species distinction.

Parapodia. Parapodia have well-separated rami, and the cilia present on the interramal space may form a continuous row or be gathered in tuffs or ciliated pads. Both rami have one acicular lobe sustained by one acicula with curved tips (more than one acicula are present in *Inermonephtys* species) and pre- and postchaetal lamellae. The aciculae were initially described as straight in *Nephtys* species and with curved tips in *Aglaophamus*, *Inermonephtys* and *Micronephthys* species (Fauchald 1968). However, from my personal observations I conclude that all nephtyids have aciculae with curved tips although sometimes this character is difficult to observe (especially on *Nephtys* species). This is thus an invalid diagnostic character. Some *Nephtys* species have a chitinous plaque covering the tip of aciculae, although this is not always easy to observe and has poor distinctive interest. Acicular lobes may be acutely pointed, conical, rounded or bilobed and are an important distinctive character between species and also between genera. With some exceptions (e.g. *A. foliosus*, *A. trissophyllus*), the majority of the accepted *Aglaophamus* species as well as *Inermonephtys* species have acutely pointed acicular lobes. *Nephtys* species may have conical, rounded or bilobed acicular lobes. *Micronephthys* and *Bipalponephtys* species have conical acicular lobes. Some *Nephtys* species have outgrowths (near acicula) (e.g. *N. assimilis*, *N. hombergii*, *N. gravieri*) on the outer parts of acicular lobes (dorsally in notopodia, ventrally in neuropodia). This feature has restricted distinctive value for this particular species. The shape and proportions of the pre- and postchaetal lamellae also are important diagnostic characters at specific level, although a degree of variation is present along the body. Comparisons must be made between parapodia from the same body region (usually median, but anterior and posterior are also useful). For *Nephtys* species there is frequently a correlation between the shape of the acicular lobe and the shape and length of prechaetal lamellae. When acicular lobes are conical the prechaetal lamellae are usually well developed and frequently bilobed, while when acicular lobes are rounded to bilobed the prechaetal lamellae are usually rudimentary or poorly developed. *Micronephthys* species have rudimentary or poorly developed pre- and postchaetal lamellae, a feature that characterizes the genus. Dorsal and ventral cirri are present at the ventral side of noto- and neuropodia, respectively. Ventral cirri have poor distinctive value, while dorsal cirri may have different shapes (conical to cirriform, lamelliform) and sizes and thus contribute to species distinction.

Branchiae. Branchiae shape (whether involute – *Aglaophamus* and *Inermonephtys*, recurved – *Nephtys*, poorly developed or absent – *Micronephthys*) has been used as the main distinctive character between genera, although some difficulties were present regarding several species. For species with small branchiae or juvenile forms it is sometimes doubtful to establish their condition (whether involute or recurved). Furthermore, small branchiae are also present in some *Micronephthys* species. The results in Ravara *et al.* (Ravara *et al.* in press) proved that branchiae shape cannot be considered as the main distinctive character between genera, since there are species with recurved branchiae now included in the genus *Aglaophamus*, based on molecular data. However, it still can be used in combination with other characters. The chaetiger where branchiae start and end is also an important character to distinguish species, although some small variation may occur in some species. For *Micronephthys* species, when present, branchiae occur only on a few median chaetigers. However, caution is advised as there are small *Aglaophamus* species (e.g. *A. elamellatus*, *A. pulcher*) for which the number of chaetigers with branchiae varies with the body length and, in the smallest specimens, they may even be absent (Ravara, *et al.* submitted). For many species branchiae have a small basal accessory cirrus dorsally. The presence and shape of this accessory cirrus may have some additional value to distinguish species. There are two *Nephtys* species (*N. paradoxa*, *N. tulearensis*) on which branchiae have a foliaceous appearance owing to the presence of dorsal and ventral membranous expansions.

Chaetae. Nephtyids have four main types of chaetae: capillary chaetae in the neuropodia of the first chaetiger, barred (or chambered) chaetae in preacicular position of the remaining parapodia and spinulose and lyriform chaetae in postacicular position. Lyriform chaetae are only present on *Inermonephtys* species, some species of *Aglaophamus* and *Micronephthys*, and one species of *Nephtys* (*N. oligobranchia*), while the other types of chaetae are present in almost all nephtyid species, although with some small morphological differences. Preacicular chaetae may be barred on all extension or only distally. Spinulose chaetae may vary between lightly to coarsely spinulated and there are a few species for which spinulose chaetae have a few coarser spines (e.g. *N. cryptomma, N. fluviatilis*) or a spur at the base (e.g. *N. acrochaeta*, *N. serratifolia*). With a few exceptions*, Aglaophamus, Bipalponephtys*, *Inermonephtys* and *Micronephthys* species usually have very lightly spinulated postacicular chaetae, while *Nephtys* species may roughly be subdivided into two groups. The species with conical acicular lobes usually have lightly spinulated chaetae, while the ones with rounded to bilobed acicular lobes usually have more coarsely spinulated chaetae. These observations were made mainly on European species, and further confirmation is required for species from other locations. On small nephtyid species preacicular barred chaetae are often replaced by smooth or lightly spinulose chaetae on posterior chaetigers (e.g. *A. australiensis*, *A. gippslandicus*, *N. fluviatilis*, *N. gravieri*, *N. mesobranchia*, *N. palatii*, *N. semiverrucosa*, *N. sukumoensis*, *Bipalponephtys* species and some *Micronephthys* species). On *Inermonephtys* barred chaetae may be absent (*I. foretmontardoi*, *I. inermis*, *I. tetrophthalmus*), present on anterior and median chaetigers (*I. brasiliensis*, *I. gallardi*, *I. patongi*), or also spinulated (*I. japonica*, *I. palpata*). On *Micronephthys stammeri* the barred chaetae of the first chaetiger are slightly modified by the development of a peak on the middle region of each bar. The presence or absence of lyriform or special chaetae are important diagnostic characters at specific and generic level, while the different appearance of barred and spinulose chaetae may be useful at species level but somehow subjective frequently overlooked. According to Rainer and Hutchings (1977), the distribution and number of the various types of chaetae along the body is also useful in distinguishing closely related species, although some size-related variation within species may occur.

3.2.4 List of species

Genus *Aglaophamus* Kinberg, 1866

Aglaopheme Kinberg, 1866 (type species: *A. juvenalis* Kinberg, 1866).

Type species. *Aglaophamus lyratus* Kinberg, 1866, by monotypy.

? *Aglaophamus agilis* (Langerhans, 1880)
(see chapter 3.1, pg. 55)

***Aglaophamus amakusaensis* Imajima & Takeda, 1985**
Figures 28A, 34A, 35; Table 14

Aglaophamus amakusaensis Imajima and Takeda, 1985: 81, fig. 12A-N.

Type locality. Off Tomioka, Amakusa, Kyushu, S Japan, W Pacific Ocean, 8 m depth.

Remarks. *Aglaophamus amakusaensis* is morphologically close to *A. dicirroides* from Bay of Nha Trang in Viet Nam, from which it differs mostly by the shape of lyriform chaetae. *Aglaophamus amakusaensis* has both limbs of lyriform chaetae well developed, while lyriform chaetae of *A. dicirroides* have one long and one very short, spur like limb (Imajima & Takeda 1985) (Figure 28).

Distribution. Pacific Ocean (S Japan) (Imajima & Takeda 1985).

Habitat. 8-75 m depth.

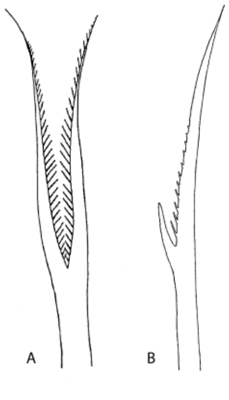


Figure 28. Lyriform chaetae. A. *Aglaophamus amakusaensis* (Imajima & Takeda 1985); B. *A. dicirroides* (Fauchald 1968).

Aglaophamus australiensis **(Fauchald, 1965)**

Figures 34B, 35; Table 14

Nephtys australiensis Fauchald, 1965: 334, figs. 1 and 2; Paxton 1974: 202, fig. 7 (partim); Hutchings 1974: 180; Hutchings and Recher 1974: 105; Weate 1975: 108; Rainer and Hutchings 1977: 322, figs. 13-16 and 42.
Nephtys gravieri Augener 1927: 116; Rullier 1965: 182 (not Augener, 1913).
Aglaophamus australiensis Ravara *et al.* in press.

Type locality. Port Vincent, Yorke Peninsula, S Australia, Southern Ocean.

Material examined. Southern Ocean, Australia: Edithburg Jetty, Torke Peninsula, Cowbowie field station, Gulf of St. Vincent, 35º05.172'S, 137º44.825'E, 3-5 m, 12 Feb 2005, 1 incomplete spm (MB36000143).

Remarks. *Aglaophamus australiensis* was originally described as belonging to the genus *Nephtys,* according to the shape of the branchiae that is often slightly recurved. However, the phylogenetic study presented in chapter 2.1 (Ravara *et al* submitted) indicates that this species should be assigned to *Aglaophamus*. In fact this species present acutely pointed acicular lobes, especially the neuropodial ones; this is one of the most typical characteristics of *Aglaophamus* species. The validity of branchia shape as a generic level distinctive character is already discussed in chapter 3.1.

Aglaophamus australiensis has been often misidentified as *Nephtys gravieri*, a morphologically similar species described also from Australia (Fremantle, W Australia). The two species differ by the shape of dorsal cirri (slightly foliaceous in the former, cirriform in the latter) and branchiae (shorter and stouter in *N. graveri*), the chaetiger where branchiae start to appear (chaetiger 4 in *A. australiensis*, 3 in *N. gravieri*), the presence of well-developed supra- and subacicular lobes on the noto- and neuropodia of *N. gravieri*, and the presence of a middorsal subterminal papillae on the pharynx of *A. australiensis* (Fauchald 1965; Rainer & Hutchings 1977). Both species have barred preacicular chaetae on anterior chaetigers, which are replaced by spinulose and spinose chaetae in posterior chaetigers. Similar characteristic is also present in *A. gippslandicus* and smaller species of *Nephtys* and *Micronephthys*.

Distribution. Pacific and Southern Oceans (SE Australia) (Rainer & Hutchings 1977).

Habitat. Common in coastal lagoons, estuarine or sheltered bay conditions, in muddy sand, often in *Zostera* or *Posidonia* beds (Rainer & Hutchings 1977).

***Aglaophamus circinatus* (Verrill, 1874)**

Figures 30A, 31; Table 12

Nepthys circinata Verrill, *in* Smith *et al*. 1874: 38.

Aglaophamus circinata Pettibone 1963: 192, fig. 48A; Gardiner 1976: 157, fig. 17C; Taylor 1984: 35-17, figs. 35-13 and 14A-B.

Nepthys (*Aglaophamus*) *circinata* Day 1973: 43, fig. 5P-Q.

Nephtys macroura Hartman 1942: 113, fig. 9H; Hartman 1944a: 339, pl. 47, fig. 11 (not Schmarda, 1861).

Type locality. St. Georges Bank, Maine, USA, West Atlantic Ocean, in 85 fms depth. (holotype: USNM 15882)

Remarks. *Aglaophamus circinatus* was synonymised with *A. macroura* from the Indopacific region by Hartman (1942, 1950). Pettibone (1963) re-established *A. circinatus* and enunciated the differences between the two species. According to Pettibone (1963) *A. circinatus* can be distinguished from *A. macroura* by its conical acicular lobes, rather than bilobed in anterior and middle segments, the presence of branchiae to near posterior end (in *A. macroura* branchiae are small or absent on posterior segments), and the different shape of neuropodial postchaetal lamellae and dorsal cirri (Figure 30A, 34L).

Distribution. Atlantic Ocean (East coast of North America from Gulf of St. Lawrence to off Long Island Sound, Gulf of Mexico) (Pettibone 1963; Taylor 1984).

Habitat. Coarse to fine-very fine sand, and clayey to silty sand, 14-786 m depth (Pettibone 1963; Taylor 1984).

***Aglaophamus dibranchis* (Grube, 1877)**

Figures 36A, 37; Table 15

Nephthys dibranchis Grube, 1877: 536; McIntosh 1885: 161, pl. 26, figs. 8 and 9, pl. 27, fig. 5; Ehlers 1905: 14; Augener 1922: 17, fig. 5; Augener 1927: 116; Fauvel

1932: 117 (partim); Hartman 1938b: 146 (partim); Hartman 1940: 237 (partim); Wesenberg-Lund 1949: 292.

Aglaophamus dibranchis Hartman 1950: 121; Fauchald 1965: 336; Paxton 1974: 199; Rainer and Hutchings 1977: 309.

Nephtys (Aglaophamus) dibranchis Day 1967: 341, fig.15.1A-H.

Type locality. New Guinea, Arafura Sea, Indo-Pacific region.

Remarks. The descriptions of *A. dibranchis* in Fauvel (1932) and Hartman (1938, 1940) refer in part to *A. verrilli*. Hartman (1950) re-described *A. dibranchis* and erected a new species, *A. dicirris*. Later, *A. dicirris* was synonymised with *A. verrilli* by Knox (1960). Differences between *A. dibranchis* and *A. verrilli* are summarised in Table 15.

Distribution. Pacific Ocean (New Guinea, New Zealand, Australia); Indian Ocean (Red Sea; Gulf of Aden; Gulf of Iran; Gulf of Oman; India; South Africa; Australia) (Wesenberg-Lund 1949; Hartman 1950; Day 1967; Rainer & Hutchings 1977).

Habitat. No information in literature.

***Aglaophamus dicirroides* Fauchald, 1968**

Figures 28B, 34C, 35; Table 14

Aglaophamus dicirroides Fauchald, 1968: 10, figs. 3, 4 and 9-11.

Type locality. Bay of Nha Trang, Viet Nam, W Pacific Ocean, 35 m depth.

Remarks. *Aglaophamus dicirroides* is morphologically close to *A. amakusaensis* from southern Japan, from which it differs mostly by the shape of lyriform chaetae. *Aglaophamus amakusaensis* has both limbs of lyriform chaetae well developed, while lyriform chaetae of *A. dicirroides* have one long and one very short, spur like limb (Imajima & Takeda 1985) (Figure 28).

Distribution. Pacific Ocean (Viet Nam) (Fauchald 1968).

Habitat. Coarse shelly sand, 35 m depth (Fauchald 1968).

Aglaophamus digitatus **Hartman, 1967**

Figures 36B, 37; Table 15

Aglaophamus digitatus Hartman, 1967: 71, pl. 20, fig. A-C.

Type locality. Off South Sandwish Islands, Antarctic Ocean.

Distribution. Antarctic Ocean (South Sandwish Islands) (Hartman 1967).

Habitat. 2452-2531 m depth (Hartman 1967).

Aglaophamus elamellatus **(Eliason, 1951)**

(see chapter 3.1, pg. 56)

Aglaophamus erectanoides **Hartmann-Schröder, 1965**

Figures 30B, 31; Table 12

Aglaophamus erectanoides Hartmann-Schröder, 1965: 136, figs. 104 and 105.
Nephtys (Aglaophamus) erectanoides Rozbaczylo and Castilla 1974: 182, fig. 1A-C.

Type locality. Chile, E Pacific Ocean.

Remarks. According to Hartmann-Schröder (1965) this species is very similar to *A. erectans* from which it can be distinguished by the smaller dorsal cirri and neuropodial superior lobes. The notopodial postchaetal lamellae are also more developed in *A. erectans*. The two species occupy different geographical areas in the eastern Pacific Ocean (Figure 30B, C).

Distribution. Pacific Ocean (Chile) (Rozbaczylo & Castilla 1974).

Habitat. Mud and fine sand, 220-264 m depth (Hartmann-Schröder 1965; Rozbaczylo & Castilla 1974).

Aglaophamus erectans Hartman, 1950

Figures 30C, 31; Table 12

Aglaophamus erectans Hartman, 1950: 125, pl. 19, figs. 1-10; Hartman 1963; Hartman 1968; Hilbig 1997: 322, fig. 13.1; Hernández-Alcántara and Solís-Weiss 1991; Hernández-Alcántara and Solís-Weiss 1999.
Nephthys malmgreni Treadwell 1914: 192 (partim) (not Théel, 1879).

Type locality. SW Santa Catalina Island, E Pacific Ocean, 81 m depth.

Distribution. Pacific Ocean (California to Mexico) (Hartman 1950; Hilbig 1997).

Habitat. Mud and silt, 37-440 m (Hartman 1950; Hilbig 1997).

***Aglaophamus eugeniae* Fauchald, 1972**

Figures 30D, 31; Table 12

Aglaophamus eugeniae Fauchald, 1972: 82, pl. 14, figs. A-E.

Type locality. Natividad Island light, Mexico, E Pacific Ocean.

Remarks. *Aglaophamus eugeniae* is morphologically very similar to *A. paucilamellatus* from the same locality and depth range. Both species have branchiae starting on chaetiger 8-9, poorly developed parapodial lamellae, absence of neuropodial superior lobes and lyriform chaetae, and 14 rows of pharynx subterminal papillae, although the number of subterminal papillae in each row is slightly different (8-10 in *A. paucilamellatus* and 10-12 in *A. eugeniae*). According to Fauchald (1972) the two species differ only in the shape of prostomium (circular in *A. eugeniae*, quadrangular in *A. paucilamellatus*), and the absence of dorsal cirri in the first chaetiger of *A. eugeniae*, which are present and well developed in *A. paucilamellatus*.

Distribution. Pacific Ocean (Mexico) (Fauchald 1972).

Habitat. Green mud, 459-2439 m depth (Fauchald 1972).

***Aglaophamus foliocirratus* Rainer & Kaly, 1988**

Figures 34D, 35; Table 14

Aglaophamus foliocirrata Rainer and Kaly, 1988: 686, figs. 1A-F and 6A.

Type locality. W Australia, E Indian Ocean.

Remarks. This species is morphologically close to *A. macroura* from which it differs by the presence of prostomial eyes, the number of rows of pharynx papillae (14 instead of 22), and the slightly different shape of parapodial lamellae and cirri (Figure 35D, L).

Distribution. Indian Ocean (Australia) (Rainer & Kaly 1988).

Habitat. 55-80 m depth (Rainer & Kaly 1988).

***Aglaophamus foliosus* Hartman, 1967**

Figures 36D, 37; Table 15

Aglaophamus foliosus Hartman, 1967: 72, pl. 21, fig. A and B.
Nephtys (Aglaophamus) foliosus Rozbaczylo and Castilla 1974: 184.

Type locality. South Sandwish Islands, Antarctic Ocean.

Remarks. According to Hartman (1967) this species is mainly characterized by its large and distally acute notopodial cirri, the development of an inferior lobe in the neuropodial prechaetal lamellae (conferring an unequally bilobed appearance to the lamellae), and the branchiae starting from the chaetiger 4. The large dorsal cirri as well as the unequally bilobed appearance of the prechaetal lamellae are also shared by *A. trissophyllus*, which also has a similar geographical distribution. However, judging by the description and figure in Hartman (1967, p. 72, fig. 21), *A. foliosus* differs from *A. trissophyllus* by the more posterior beginning of branchiae (from chaetiger 4 instead of 2), the 14 rows of 10-14 subterminal papillae in the pharynx which do not subdivide to form small triangular groups proximally, the lack of neuropodial superior lobes, and the shape of the notopodial postchaetal lamellae (Table 15, Figure 37D, H). Nevertheless, this species should be considered with caution until further examination of the type material.

Distribution. Antarctic Ocean (? Falkland Islands, South Sandwich Islands; Cape Horn) (Hartman 1967).

Habitat. (?567)1482-2013 m depth (Hartman 1967).

Aglaophamus fossae **Fauchald, 1972**

Figures 30E-F, 31; Table 12

Aglaophamus fossae Fauchald, 1972: 84, pl. 14, fig. F, pl. 15, figs. A-I.

Type locality. Las Animas Island, Gulf of California, E Pacific Ocean, 1071 m depth.

Distribution. Pacific Ocean (Mexico) (Fauchald 1972).

Habitat. 864-1395 m depth (Fauchald 1972).

Aglaophamus gippslandicus **Rainer & Hutchings, 1977**

Figures 34E, 35; Table 14

Aglaophamus gippslandicus Rainer and Hutchings, 1977: 309, figs. 1-3 and 41.
? *Aglaophamus gippslandicus bisectus* Imajima and Takeda 1985: 70, fig. 7A-I.
? *Aglophamus* cf. *gippslandicus* Jung and Hong 1997: 373, fig. 2A-G.

Type locality. New South Wales and Victoria, Australia, Tasman Sea, SW Pacific Ocean, 95 m depth.

Remarks. *Aglaophamus gippslandicus* is morphologically close to *A. hedlandensis*, from western Australia, from which it differs by the number and arrangement of pharynx papillae. *Aglaophamus hedlandensis* has 14 rows of 3-4 subterminal papillae, a middorsal single papilla and warts in proximal region, while *A. gippslandicus* has 14 rows of 12-15 subterminal papillae, no middorsal papillae and no warts (Table 14).

Imajima and Takeda (1985) erected the subspecies *A. gippslandicus bisectus* for specimens from Japan. According to these authors the referred subspecies is distinguished by the shape of neuropodial postchaetal lamellae, which are triangular and hidden behind the acicular lobe in *A. gippslandicus bisectus* and are rounded in the other specimens of *A. gippslandicus*. Later Jung and Hong (1997) recorded two specimens from Korea matching the original description of *A. gippslandicus* (including the rounded neuropodial postchaetal lamellae) except for the dorsal cirri of the first chaetiger, present in Korean specimens but stated by Rainer and Hutchings

(1977) as absent in the holotype. This character is also absent in the specimens from Japan (Imajima and Takeda 1985). In spite of the different localities in the W Pacific Ocean (N and S hemisphere), the differences between the specimens found in Japan and Korea and the ones from Australia seem to be of little relevance and might result from intraspecific variation. Although none of the specimens were examined within this study, I consider that there are no sufficient grounds to establish a subspecies for *A. gippslandicus*.

Distribution. Pacific Ocean (Australia, cf. Korea, cf. Japan) (Rainer & Hutchings 1977; Imajima & Takeda 1985; Jung & Hong 1997).

Habitat. Sand, 70-95 m depth for Australian and Korean specimens (Rainer & Hutchings 1977; Jung & Hong 1997), and 20-704 m depth for Japanese specimens (Imajima & Takeda 1985).

***Aglaophamus groenlandiae* Hartman, 1967**

Figures 30G, 31; Table 12

Aglaophamus groenlandiae Hartman, 1967: 73, pl. 22, fig. A and B; Hartman and Fauchald 1971: 60; Kirkegaard 1980: 85.

Type locality. S Greenland (58º15’N, 48º36’-37’W), W Atlantic Ocean.

Remarks. *Aglaophamus groenlandiae* resembles *A. elamellatus* in having rudimentary or poorly developed parapodial lamellae, and branchiae starting on chaetigers 11-13. They differ mostly by the shape of the notopodial cirri, which are triangular in *A. groenlandiae* and oval in *A. elamellatus*, and by the unusually long chaetae present in the anterior chaetigers of *A. elamellatus* (Hartman & Fauchald 1971; Kirkegaard 1980). According to Hartman (1967), the notopodial postchaetal lamellae of *A. groenlandiae* are entire. However, the drawing by this author shows a lamella with bilobed appearance, similar to the one of *A. malmgreni*. In *A. malmgreni* the branchiae also start on chaetigers 11-13, however, the postchaetal lamellae are more developed, the dorsal cirri are much larger and the number of pharynx subterminal papillae is different (11 rows of up to 9 in *A. groenlandiae* (Hartman & Fauchald 1971), 22 rows of 2-18 in *A. malmgreni*). *Aglaophamus groenlandiae* and *A.*

elamellatus are deep-water species, while *A. malmgreni* usually occurs at shallower depths. *Aglaophamus malmgreni* has mainly a circumpolar distribution, *A. groenlandiae* occurs in temperate waters of the North Atlantic Ocean, and *A. elamellatus* occurs in temperate and tropical areas of the Atlantic, Indian and Pacific oceans.

Distribution. Atlantic Ocean (off S Greenland, Bermuda rise; E Atlantic) (Hartman 1967; Hartman & Fauchald 1971; Kirkegaard 1980).

Habitat. 1102- 4265 m depth (Hartman & Fauchald 1971; Kirkegaard 1980).

***Aglaophamus hedlandensis* Rainer & Kaly, 1988**

Figures 34F-G, 35; Table 14

Aglaophamus hedlandensis Rainer and Kaly, 1988: 688, figs. 2A-E and 6C.

Type locality. W Australia, E Indian Ocean.

Remarks. *Aglaophamus hedlandensis* is morphologically close to *A. gippslandicus* from which it differs by the number and arrangement of pharynx papillae (see remarks on *A. gippslandicus* and Table 14).

Distribution. Indian Ocean (Australia) (Rainer & Kaly 1988).

Habitat. 40-80 m depth (Rainer & Kaly 1988).

***Aglaophamus heteroserratus* Hartmann-Schröder, 1965**

Figures 30H, 31; Table 12

Aglaophamus heteroserrata Hartmann-Schröder, 1965: 137, figs. 106-109.
Nephtys (Aglaophamus) heteroserrata Rozbaczylo and Castilla 1974: 184, fig. 1D-F.

Type locality. Chile, E Pacific Ocean.

Remarks. According to Hartmann-Schröder (1965), this species differs from other *Aglaophamus* species by the coarsely serrated postacicular chaetae.

Distribution. Pacific Ocean (Chile) (Rozbaczylo & Castilla 1974).

Habitat. 26-264 m depth (Rozbaczylo & Castilla 1974).

Aglaophamus igalis **Hartman, 1965**

Figures 30I, 31; Table 12

Aglaophamus igalis Hartman, 1965: 89, pl. 13, fig. A.

Type locality. Off New England (39º58.23’N, 70º40.18’W), W Atlantic Ocean, 300 m depth.

Remarks. According to Hartman (1965), *A. igalis* is very similar to *A. circinatus* also present in the same geographical region and at the same depths. The two species differ by the shape of notopodial postchaetal lamellae and neuropodial prechaetal lamellae, which are entire in *A. igalis* and bilobed in *A. circinatus*. Nevertheless, Hartman (1965) is inconsistent when she refers to the entire neuropodial prechaetal lamellae of *A. igalis* as a difference from *A. circinatus* and then describes them as medially incised and depicted them with a very slight incision in the figure presented.

Distribution. Atlantic Ocean (off New England) (Hartman 1965).

Habitat. 200-300 m depth (Hartman 1965).

Aglaophamus japonicus **Imajima & Takeda, 1985**

Figures 34H, 35; Table 14

Aglaophamus japonicus Imajima and Takeda, 1985: 73, fig. 8A-L.

Type locality. Off Nii-jima, Japan, W Pacific Ocean, 30-65 m depth.

Distribution. Japan (Imajima & Takeda, 1985).

Habitat. 23-125 m depth (Imajima & Takeda 1985).

Aglaophamus jeffreysii **(McIntosh, 1885)**

Figures 34I, 35; Table 14

Nephthys jeffreysii McIntosh, 1885: 162.
Nephtys jeffreysii McIntosh 1901: 220, pl. 1, fig. 1.
Aglaophamus jeffreysii Imajima and Hartman 1964: 155; Imajima and Takeda 1985: 86, fig. 13A-J and 14A-K.

Type locality. Near Kyushu, Japan (33º56’N, 130º27’E), W Pacific Ocean, 30 fms depth.

Material examined. Pacific Ocean, Japan: North of Kyushu, 33º56’N, 130º27’E, 54.8 m, 1876, 1 incomplete spm, holotype (NHM 1921.5.1.860).

Remarks. *Aglaophamus jeffreysii* resembles *A. verrilli* and *A. victoriae* from Australian coasts. This species differs from the latter two mainly by the lack of warts in the pharynx. Furthermore, *A. jeffreysii* differs from *A. victoriae* in having only one pair of prostomial eyes instead of two, and from *A. verrilli* by the branchiae and neuropodial superior lobes starting on chaetiger 3 rather than on chaetiger 7-8.

Distribution. Pacific Ocean (Japan) (Imajima & Takeda 1985).

Habitat. 10-100 m depth (Imajima & Takeda 1985).

***Aglaophamus juvenalis* (Kinberg, 1866)**

Figures 30J, 31; Table 12

Aglaopheme juvenalis Kinberg, 1866: 240.
Aglaophamus juvenalis Hartman 1948: 51; Fauchald 1976: 16, fig. 1A-C; Lana 1986: 143, figs. 16 and 17; Rizzo and Amaral 2007: 255, fig. 1.

Type locality. Rio de Janeiro, Brazil, W Atlantic Ocean.

Remarks. *Aglaophamus juvenalis* original description was reviewed and broadened by Hartman (1949) and later by Fauchald (1976).

Distribution. Atlantic Ocean (Brazil) (Lana 1986; Rizzo & Amaral 2007).

Habitat. Silty fine sand, 2-71 m depth (Fauchald 1976; Lana 1986; Rizzo & Amaral 2007).

Aglaophamus lobatus Imajima & Takeda, 1985

Figures 34J, 35Table 14

Aglaophamus lobatus Imajima and Takeda, 1985: 75, fig. 9A-M.

Type locality. Sagami Bay, Japan, W Pacific Ocean.

Distribution. Pacific Ocean (Japan) (Imajima & Takeda 1985).

Habitat. 11-270 m depth (Imajima & Takeda 1985).

Aglaophamus longicephalus Hartman, 1974

Figures 32C, 33; Table 13

Aglaophamus longicephalus Hartman, 1974: 218, fig. 6A-C.

Type locality. Arabian Sea, Indian Ocean.

Distribution. Indian Ocean (Arabian Sea) (Hartman 1974).

Habitat. 92-95 m depth (Hartman 1974).

Aglaophamus lutreus (Baird, 1871)

Figures 29A, 37; Table 15

Nephtys lutrea Baird, 1871: 95.
Aglaophamus lutreus Hartman 1950: 129; Wesenberg-Lund 1962: 99.
Nephtys (Aglaophamus) lutrea Rozbaczylo and Castilla 1974: 185.
? *Nephthys virginis* Ehlers 1897: 19-23, pl. 1, figs. 9-12 (not Kinberg, 1866).

Type locality. Otter Island, Patagonia, SW Atlantic Ocean.

Material examined. Atlantic Ocean, coast of Patagonia, Argentina, Otter Island: Dec 1868, 1 incomplete spm in poor condition, holotype (NHM 1869.6.16.7).

Remarks. The original description of this species is very short and incomplete, with no illustrations. Hartman (1950) examined the holotype, which was already in poor condition, and added some details to the description regarding parapodial features. However neither Baird (1871) nor Hartman (1950) include a description of the pharynx. The same specimen was examined in this study and the observations of the everted pharynx allowed the following description: distal pharynx region with 10 pairs of terminal bifid papillae, separated by a simple conical dorsal papilla and a ventral gap or small elevation; middorsal and midventral papillae are present; subdistal region with 22 rows of 2-8 short subterminal papillae ending proximally in a group of many (more than 30) small papillae arranged in triangle (Figure 29A); the rows of papillae extend over 1/3 of the pharynx's length; proximal region is smooth. These characteristics correspond to the pharynx description of *A. trissophllus*. However, in *A. lutreus*, the parapodia seem to have a somewhat different appearance. Since no other specimens were examined and given the poor condition of the holotype, the status of this species remains doubtful.

Distribution. Atlantic and Pacific Oceans (southern South America) (Hartman 1950).

Habitat. No information in literature.

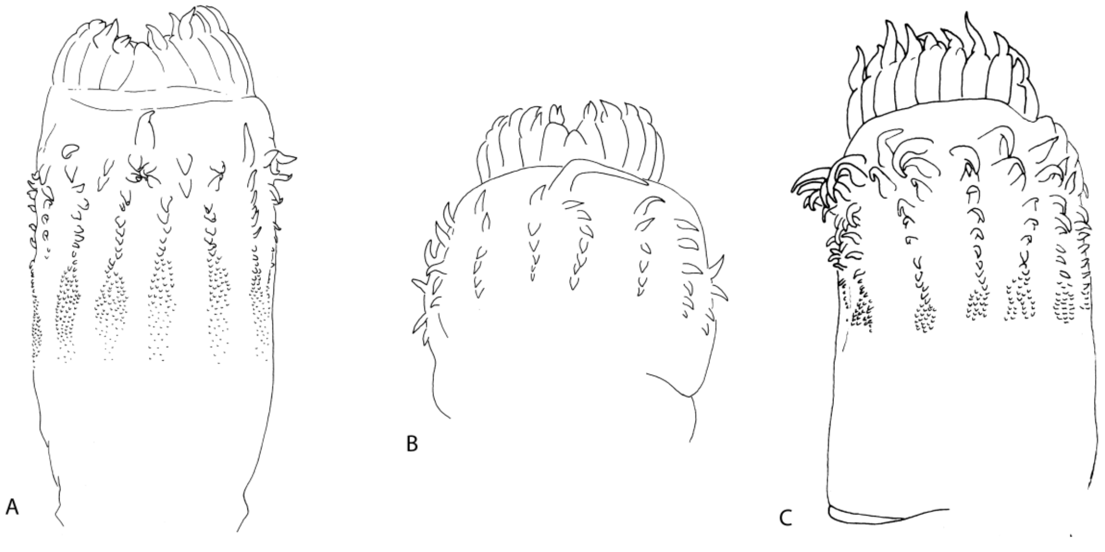


Figure 29. Pharynx. A. *Aglaophamus lutreus*, dorsal view; B. *A. munamaorii*, dorsal view; C. *A. trissophyllus*, lateral view.

cf. *Aglaophamus lyratus* Kinberg, 1866

Figures 34K, 35; Table 14

Aglaophamus lyratus Kinberg, 1866: 240; Hartman 1948: 50, pl. 7, fig. 1.
Nephthys digitifera Augener, 1933: 210, fig. 2.

Type locality. Bangka Strait, Indopacific region.

Remarks. The description of *Aglaophamus lyratus* was based on a single damaged specimen without the anterior part of the body. Later Hartman (1948) re-described the species based on the same incomplete specimen and, in the same work, considered *N. digitifera* as a junior synonym of *A. lyratus*. The original description of *N. digitifera* by Augener (1933) is based on a single incomplete specimen without the posterior part of the body. The prostomium and pharynx were not described for either of these species and the information on the chaetiger where branchiae start is only provided for *N. digitifera*. However, according to Hartman (1948) the description of the parapodia seem to agree as both species have rounded acicular lobes ending with a digitate process, similar parapodial lamellae, and lyriform chaetae. The diagnostic characters given in Table 15 are based on the descriptions of Hartman (1948) for *A. lyratus* and Augener (1933) for *N. digitifera*. Later Fauchald (1968) erected the species *Inermonephtys gallardi* based on four specimens from Viet Nam. These specimens have no antennae or pharynx papillae, and have cirriform nuchal organs, which characterize the genus *Inermonephtys*. Nevertheless, the parapodia are very similar to those of *A. lyratus* and the branchiae are present from chaetiger 15 (in *N. digitifera* branchiae start on chaetiger 18). Since the holotype of *A. lyratus* is incomplete anteriorly a possible synonymy of *I. gallardi* with *A. lyratus* would have to be based on the observation of the prostomium and pharynx of the *N. digitifera* holotype.

Distribution. Indopacific region (Hartman 1948).

Habitat. 47.5 m depth (Augener 1933).

Aglaophamus lyrochaetus (Fauvel, 1902)

Figures 32D, 33; Table 13

Nephthys lyrochaeta Fauvel, 1902: 72, fig. 9-13; Augener 1918: 160, pl. 2, fig. 12, pl. 3, fig. 59; Monro 1930: 113, fig. 40A-B; Wesenberg-Lund 1949: 293.
Aglaophamus lyrochaetus Tebble 1955: 102.
Nephtys (Aglaophamus) lyrochaeta Day 1967: 341, fig. 15.1I.
? *Aglaophamus lyrochaetus* Hernández-Alcántara and Solís-Weiss 1991; Hernández-Alcántara and Solís-Weiss 1999.

Type locality. Estuary of the R. Casamance Senegal, W Africa, E Atlantic Ocean.

Remarks. *Aglaophamus lyrochaetus* was described by Fauvel (1902) from W Africa as having one pair of eyes in the posterior region of prostomium and short dorsal cirri on parapodia. This author makes no reference to the presence of a neuropodial superior lobe. Later Fauvel (1927) mentions the presence of a small lobe in the dorsal part of neuropodia, which was confirmed by Monro (1930). According to Augener (1918) and Monro (1930) the parapodial dorsal cirri are very long, instead of short as stated and illustrated by Fauvel (1902). Wesenberg-Lund (1949) reported this species from several localities in the Iranian Gulf and also mentions the presence of long dorsal cirri and a cirriform neuropodial superior lobe. This author further states that, in the specimens he observed, the branchiae usually started on chaetiger 5 but could also start from chaetigers 3 or 6. There is a possibility that the specimens from the Iranian Gulf may refer to more than one species (also considering the different localities). Day (1967), in contradiction with the original description, states that eyes are absent in *A. lyrochaetus*. As far as I know, this species was not reported since Day (1967) as its possible occurrence in the Gulf of California (Hernández-Alcántara & Solís-Weiss 1991, 1999) requires confirmation. For all this reasons, *A. lyrochaetus* is obviously in need of revision.

Distribution. Atlantic Ocean (Morocco, W Africa); Indian Ocean (Gulf of Iran; Gulf of Oman) (Wesenberg-Lund 1949; Day 1967). Reports from the Gulf of California (Hernández-Alcántara and Solís-Weiss 1991, 1999) require further confirmation.

Habitat. Estuary, 3.5-11 m depth (Tebble 1955).

***Aglaophamus macroura* (Schmarda, 1861)**

Figures 34L, 35; Table 14

Nephthys macroura Schmarda, 1861: 91, figs. A, K, a and b.
Nephthys macroura ? Monro 1936: 140; Støp-Bowitz 1949: 19.
Aglaophamus macroura ? Hartman 1948: 10; Wesenberg-Lund 1962: 95, figs. 40-43.
Aglaophamus macroura Hartman 1964: 103, pl. 32, fig. 1 (partim); Hartman 1967: 74, pl. 23, fig. A-D.

Type locality. Auckland, New Zealand, SW Pacific Ocean, littoral sands.

Remarks. *Aglaophamus macroura* was originally described as having the proximal surface of the pharynx finely tuberculated (Schmarda 1861). However, following descriptions (e.g. Hartman 1967) stated the pharynx as smooth. Schmarda (1861) also remarked the presence of lyriform chaetae, but according to Hartman (1967) the original drawing of the lyriform chaeta probably corresponds to a broken limbate chaeta.

Aglaophamus macroura was recorded for the first time from New Zealand in shallow water. However, it has been referred to occur in several different areas of the Antarctic region, Chile, and subantartic islands around southern South America, at similar and higher depths (Hartman 1950; Rozbaczylo & Castilla 1974). Hartman (1967) provided an emended description of this species and remarked that the specimens of *A. macroura* reported from Antarctic areas probably refer to other species, such as *A. trissophyllus*, for specimens from shallow waters, and *A. posterobranchus*, for specimens from abyssal depths. In fact, the descriptions from Hartman (1950) and Rozbaczylo & Castilla (1974), for specimens collected in these areas, agree well with *A. trissophyllus*. Thus the geographical distribution of *A. macroura* is here limited to the New Zealand area, from where this species was originally described.

Distribution. Pacific Ocean (New Zealand) (Hartman 1967).

Habitat. Intertidal (Hartman 1967).

Aglaophamus malmgreni (Théel, 1879)

(see chapter 3.1, pg. 62)

Aglaophamus minusculus Hartman, 1965

Figures 31K, 32; Table 12

Aglaophamus minusculus Hartman, 1965: 90, pl. 13, figs. B-D; Hartman and Fauchald 1971: 61; Ohwada 1985b: 605, fig. 1A-E.

Type locality. Off New England (40º01.8’N, 70º42’W), W Atlantic Ocean, 200 m depth.

Remarks. *Aglaophamus minusculus* was originally described by Hartman (1965) based on a single specimen from off New England. Later Ohwada (1985b) re-examined the holotype along with other specimens collected from Florida at similar depths and, in order to correct some previous discrepancies, provided a re-description of the species including the description of the pharynx.

Distribution. Atlantic Ocean (New England, Florida) (Ohwada 1985b).

Habitat. 97-200 m depth (Ohwada 1985b).

Aglaophamus munamaorii Gibbs, 1971

Figures 29B, 34M, 35; Table 14

Nephtys (Aglaophamus) munamaorii Gibbs, 1971: 154, fig. 9A-B.

Type locality. Solomon Islands, W Pacific Ocean.

Material examined. Pacific Ocean, Solomon Islands, Marovo Lagoon, New Georgia: Royal Society Solomon Islands Expedition 1965, 22 m, 5 complete and 3 incomplete spms, paratypes (NHM 1970.38).

Remarks. Gibbs (1971) described *A. munamaorii* for the Solomon Islands and provided drawings of median and posterior parapodia. In the present study the paratypes were re-examined and the pharynx was illustrated (Figure 29B).

Distribution. Pacific Ocean (Solomon Islands) (Gibbs 1971).

Habitat. Mud and silty sand, 2-22 m depth (Gibbs 1971).

***Aglaophamus orientalis* Fauchald, 1968**

Figures 34N, 35; Table 14

Aglaophamus orientalis Fauchald, 1968: 11, figs. 12-15.

Type locality. Bay of Nha Trang, Viet Nam, W Pacific Ocean, 24 m depth.

Distribution. Pacific Ocean (Viet Nam) (Fauchald 1968).

Habitat. Coarse sand, 24 m depth (Fauchald 1968).

***Aglaophamus paramalmgreni* Hartmann-Schröder & Rosenfeldt, 1992**

Figures 36F, 37; Table 15

Aglaophamus paramalmgreni Hartmann-Schröder and Rosenfeldt, 1992: 105, figs. 37-40.

Type locality. Antarctic Ocean (64º7.63’S, 65º23.8’W), 546 m depth.

Remarks. *Aglaophamus paramalmgreni* is very similar to *A. posterobranchus* that is also a deep-water Antarctic species. Both species have involute branchiae starting on chaetigers 9-16, dorsal cirri small and triangular, prechaetal lamellae poorly developed and postchaetal lamellae rounded not extending beyond acicular lobes. However, according to the original illustrations, the notopodial postchaetal lamellae of *A. posterobranchus* seem to be larger than the ones of *A. paramalmgreni* (Hartman 1967, p. 325, fig. 25B; Hartmann-Schröder & Rosenfeldt 1992, p. 119, figs. 39, 40). According to Hartmann-Schröder and Rosenfeldt (1992) the two species differ by the shape of the prostomium and the number of rows of papillae in the pharynx (14 on *A. paramalmgreni*, 21-22 on *A. posterobranchus*). Material from *A. paramalmgreni* was not available for examination and thus these differences could not be confirmed. I advise the revision of this species with examination of more specimens. The two species also resemble *A. groenlandiae* and *A. malmgreni*, which occur in the North

Atlantic and Arctic Oceans. However, apart from the very different localities, *A. groenlandiae* has 11 rows of subterminal papillae in the pharynx and apparently poorly developed and bilobed notopodial postchaetal lamellae, as illustrated by Hartman (1967) (see remarks of *A. groenlandiae*), and *A. malmgreni* has 22 rows of subterminal papillae in the pharynx, well developed and bilobed notopodial postchaetal lamellae, and larger dorsal cirri.

Distribution. Antarctic Ocean (Hartmann-Schröder & Rosenfeldt 1992).

Habitat. Soft silt with detritus, 645 m depth (Hartmann-Schröder & Rosenfeldt 1992).

Aglaophamus paucilamellatus **Fauchald, 1972**

Figures 30L, 31; Table 12

Aglaophamus paucilamellata Fauchald, 1972: 86, pl. 16, figs. A-F; Hilbig 1997: 324, fig. 13.2.

Type locality. Natividad Island light (27º54,25’N, 115º40’W), Mexico, E Pacific Ocean.

Remarks. *Aglaophamus paucilamellatus* is morphologically very similar to *A. eugeniae*. Both species have the same geographical distribution and depth range. Similarities and differences between this two species were already mentioned above (see remarks of *A. eugeniae*).

Distribution. Central California to W Mexico (Hilbig 1997).

Habitat. Mixed sediments, 220-2439 m depth (Fauchald 1972; Hilbig 1997).

Aglaophamus peruanus **(Hartman, 1940)**

Figures 30M, 31; Table 12

Nephtys macroura peruana Hartman, 1940: 236, pl. 39, figs. 89 and 90; pl. 40, fig. 96 and 97.
Aglaophamus peruana Hartman 1950: 120; Hartman 1967: 78; Rozbaczlo *et al*. 2005: 85, fig. 7l-7P.

Nephtys (Aglaophamus) peruana Rozbaczylo & Castilla 1974: 189.
Aglaophamus macroura Hartmann-Schröder 1965: 134; (not Schmarda 1861).

Type locality. Peru, E Pacific Ocean, 10-40 fms depth.

Remarks. *Aglaophamus peruanus* was originally described as a subspecies of *A. macroura* based on the presence of a distal digitate process on the parapodial acicular lobes (Hartman 1940). Subsequently, Hartman (1950) raised it to the specific rank based on differences such as the shape of prostomium, the chaetiger where branchiae start (chaetiger 3), the shape of notopodial postchaetal lobes (entire instead of bilobed), and the larger distal prolongation of the acicular lobes in *A. peruana*. Hartmann-Schröder (1965) found those differences not consistent enough to consider the two species as distinct thus synonymizing them. However, the same differences were confirmed by Hartman (1967) and Rozbaczylo and Castilla (1974) for specimens from Chile, and the species considered again as distinct. Note that the species *A. macroura* reported by Rozbaczylo and Castilla (1974) correspond in fact to *A. trissophyllus*. The two species, *A. peruana* and *A. trissophyllus*, have slightly different geographical and bathymetric distribution (Figure 31, 37). *Aglaophamus peruana* has a shelf distribution in the western coast of South America, while *A. trissophyllus* extends to deeper water of Antarctic and Subantarctic regions.

Distribution. Pacific Ocean (Peru; Chile) (Hartman 1940; Hartmann-Schröder 1965; Rozbaczylo & Castilla 1974)

Habitat. 12-209 m depth (Hartman 1950; Rozbaczylo & Castilla 1974)

***Aglaophamus phuketensis* Nateewathana & Hylleberg, 1986**

Figures 34O, 35; Table 14

Aglaophamus phuketensis Nateewathana and Hylleberg, 1986: 196, figs. 1A-F and 2.

Type locality. Airport Bay, Phuket Island, Thailand, E Indian Ocean, 20 m depth.

Distribution. Indian Ocean (Thailand) (Nateewathana & Hylleberg 1986).

Habitat. Very coarse sand to silty clay, 10-30 m depth (Nateewathana & Hylleberg 1986).

Aglaophamus polypharus **(Schmarda, 1861)**

Figures 30N, 31; Table 12

Nephthys polyphara Schmarda, 1861: 89, figs. a-b and A, pl. 30, fig. 237.
Aglaophamus polyphara Wesenberg-Lund 1962: 99; Hartmann-Schröder 1965: 131, figs. 100 and 101.
Nephtys (Aglaophamus) polyphara Rozbaczylo and Castilla 1974: 191, fig. 3B-D.
Nephthys lobophora Hartman, 1940: 234, pl. 40, figs. 91-94.
Aglaophamus lobophora Hartman 1950: 129.

Type locality. Viña del Mar, Chile, E Pacific Ocean.

Remarks. This species was originally described for specimens from Chile, and later recorded also from Peru by Hartman (1940) that described it as *N. lobophora* new species. Later, these two species were synonymised by Hartmann-Schröder (1965) and confirmed by Rozbaczylo and Castilla (1974), although without examining the type material of *A. polypharus* that seems to be lost.

Distribution. Pacific Ocean (Peru, Chile) (Rozbaczylo & Castilla 1974).

Habitat. Middle to fine sand, intertidal to 55 m depth (Hartmann-Schröder 1965; Rozbaczylo & Castilla 1974).

Aglaophamus posterobranchus **Hartman, 1967**

Figures 36G, 37; Table 15

Aglaophamus posterobranchus Hartman, 1967: 78, pl. 25; Hartman 1978: 150.
Nephtys (Aglaophamus) posterobranchus Rozbaczylo and Castilla 1974: 192.

Type locality. South Shetland Islands, Antarctic Ocean.

Remarks. See remarks of *A. paramalmgreni*.

Distribution. Pacific Ocean (Off Chile); Atlantic Ocean (South Georgia); Antarctic Ocean (Drake Passage, Bransfield Strait, South Shetland Islands, South Orkney Islands) (Hartman 1967).

Habitat. 1180-4758 m depth (Hartman 1967).

Aglaophamus profundus **Rainer & Hutchings, 1977**

Figures 34P, 37; Table 14

Aglaophamus profundus Rainer and Hutchings, 1977: 313, figs. 4-6 and 41; Kirkegaard 1995: 37.
Nephthys macrura Benham, 1915: 203, fig. 57; Benham 1916: 130; Augener 1927: 116.
Aglaophamus macroura Fauchald 1965: 336; (not Schmarda 1861).
Aglaophamus verrilli Paxton 1974: 199, fig. 1.

Type locality. S Australia, Tasman Sea, SW Pacific Ocean, 2195 m depth.

Remarks. *Aglaophamus profundus* was originally described by Benham (1915) as *A. macrura* based on a single specimen from NE Tasmania at 2195 m depth. This specimen was later examined by Paxton (1974) that assigned it to *A. verrilli* and then by Rainer and Hutchings (1977) that assigned it to the new species *A. profundus*. *Aglaophamus profundus* was recently recorded by Kirkegaard (1995) in the Great Australian Bight at 795 and 1360 m depth.

Distribution. Indian Ocean (Great Australian Bight); Pacific Ocean (NE Tasmania) (Kirkegaard 1995).

Habitat. 795-2195 m depth (Kirkegaard 1995).

Aglaophamus pulcher **(Rainer, 1991)**

(see chapter 3.1, pg. 67)

Aglaophamus rubellus **(Michaelsen, 1896)**

(see chapter 3.1, pg. 71)

***Aglaophamus rubellus anops* Hartman, 1950**

Aglaophamus rubella anops Hartman, 1950: 127.

Type locality. Mittelnacht Island, eastern end of Vancouver Island, Canada.

Remarks. This subspecies is here considered separately from *A. rubellus* because of the relevance of morphology and distribution differences. The subspecies *A. rubella anops* has a smaller body size, the branchiae start on chaetiger 4 instead of 2, and the number of pharynx subterminal papillae in each row is 15-20 instead of 30-40. Hartman (1950) does not present any figure but according to the description the parapodia morphology seems to agree with *A. rubellus*. However, and unless the specimen described is a juvenile, the differences mentioned above together with a distinct geographical distribution are enough in my opinion to distinguish this subspecies as a different species. The description of *A. rubella anops* does not agree with any other described species occurring in the same geographical region. Nevertheless, the erection of new species requires the thorough examination of the holotype and further material.

Distribution. Pacific Ocean (Alaska, Canada) (Hartman 1950).

Habitat. 36.7-548.6 m depth (Hartman 1950).

***Aglaophamus sinensis* (Fauvel, 1932)**

Figures 34Q, 35; Table 14

Nephthys sinensis Fauvel, 1932: 536, fig. 1A-K; Fauvel 1933: 40, fig. 5; Monro 1934: 363, fig. 2; Treadwell 1936: 276.
Aglaophamus sinensis Hartman 1950: 117; Fauchald 1968: 12, figs. 16-18; Imajima 1970: 116 and 118; Lee and Jae 1983: 22, fig. 2, pl. 1G-K; Imajima and Takeda 1985: 65, fig. 4A-I, 5A-D; Jung and Hong 1997: 382.
Nephthys (Aglaophamus) sinensis Uschakov and Wu 1962: 11, 26-27, pl. 4, figs. A and B; Uschakov and Wu 1979: 57, fig. 18A-C.

Type locality. Che-Foo, Yellow Sea, China, W Pacific Ocean.

Remarks. *Aglaophamus sinensis* was first described from China by Fauvel (1932) and has been recorded from several localities from the Yellow Sea (Korea and Japan) to Viet Nam. These records denote some variability of the parapodial morphology, especially in preacicular lamellae shape. According to Imajima and Takeda (1985) the incongruences in the descriptions by different authors can be explained by the variation of the parapodial morphology along the body of *A. sinensis*. The specimens from Viet Nam, described by Fauchald (1968), differ by having a higher number of subterminal papillae in the pharynx (22 rows of 20-30 pap. instead of 14 rows of 15-20 pap.), an entire notopodial postacicular lamellae and a large digitiform lobe ventrally to the acicula in notopodia. These specimens need further revision as they may refer to another species.

Distribution. Pacific Ocean (Korea, Japan, China, cf. Viet Nam) (Lee & Jae 1983; Imajima & Takeda 1985; Jung & Hong 1997).

Habitat. Sand and mud, 7-170 m depth (Lee & Jae 1983; Imajima & Takeda 1985; Jung & Hong 1997).

***Aglaophamus surrufus* Fauchald, 1972**

Figures 30O, 31; Table 12

Aglaophamus surrufa Fauchald, 1972: 87, pl. 16, figs. H-I, pl. 17, figs. A-C.

Type locality. Maria Magdalena Island (21º19.30’N, 106º42’W), Mexico, E Pacific Ocean.

Distribution. Pacific Ocean (Mexico) (Fauchald 1972).

Habitat. 2178-3137 m depth (Fauchald 1972).

***Aglaophamus tabogensis* (Monro, 1933)**

Figures 30P, 31; Table 12

Nephthys tabogensis Monro, 1933: 53, fig. 23 (partim).
Aglaophamus tabogensis Hartman 1950: 125; Fauchald 1977: 33.

Type locality. Panama, E Pacific Ocean.

Material examined. Pacific Ocean, Panama: Scientific Research Association South Pacific Expedition 1924-1926, between Taboga and Taboguilla, 11-22 m, 9 Apr – 31 Oct 1924, 16 incomplete spms, syntypes (NHM 1932.12.24.125/126).

Remarks. According to Hartman (1950) the type material described by Monro (1933) included two species, *A. tabogensis* and *Nephtys monroi* new species. *Aglaophamus tabogensis* is morphologically very similar to *A. juvenalis* from Brazil. Both species are only known from their type locality or adjacent areas, and have similar habitats. According to Fauchald (1976) the two species differ by the shape of acicular lobes in the anterior parapodia (rounded in *A. tabogensis*, pointed in *A. juvenalis*), and the chaetiger where branchiae start (8 in *A. tabogensis*, 4 in *A. juvenalis*). However, in the syntypes of *A. tabogensis* examined in this study the branchiae were detected from chaetiger 4 and the parapodia appear very similar to the drawings of *A. juvenalis* in Fauchald (1976, p. 17, Fig. 1a-c) and Lana (1986, p. 153, Fig. 16, 17) (Figure 30P). The only difference observed was the number of pharynx papillae, 2-3 per row, while *A. juvenalis* have 16 rows of 4-6 papillae. The pharynx of *A. tabogensis* was examined by dissection in only one specimen, thus some degree of uncertainty is associated to those observations. Therefore the status of this species must be considered with caution until further evaluation is carried out.

Distribution. Pacific Ocean (Panama) (Hartman 1950).

Habitat. Mud, 11-22 m depth (Hartman 1950).

***Aglaophamus tepens* Fauchald, 1968**

Figures 34R, 35; Table 14

Aglaophamus tepens Fauchald, 1968: 13, figs. 19, 20, 27 and 28.

Type locality. Bay of Nha Trang, Viet Nam, W Pacific Ocean, 12 m depth.

Distribution. Pacific Ocean (Viet Nam) (Fauchald 1968).

Habitat. Mud, 12 m depth (Fauchald 1968).

Aglaophamus toloensis Ohwada, 1992

Figures 34S, 35; Table 14

Aglaophamus toloensis Ohwada, 1992: 150, figs. 2 and 3.

Type locality. Tolo Channel, Hong Kong, China, W Pacific Ocean.

Distribution. Pacific Ocean (Hong Kong, Jakarta Bay) (Ohwada 1992).

Habitat. From silty mud to median sand, 6-23 m depth (Ohwada 1992).

Aglaophamus trissophyllus (Grube, 1877)

Figures 29C, 36H, 37; Table 15

Nephthys trissophyllus Grube, 1877: 533, pl. 26, figs. 1-5, pl. 27, figs. 1 and 4, pl. 30, fig. 8, pl. 14A, figs. 9-11; McIntosh 1885: 159, pl. 30, fig. 8, pl. 14A, figs. 9-11; Rioja 1944: 124, figs. 29-31; Rioja 1946: 45, pl. 3, figs. 29-31; Hartman 1978: 150.
Aglaophamus trissophyllus Knox and Cameron 1998: 58, fig. 120.
Nephthys macroura Fauvel 1916: 436, pl. 8, figs. 1-3; Fauvel 1941: 283.
Aglaophamus macroura Hartman 1950: 118 (partim); Hartman 1964: 103, pl. 32, fig. 1 (partim).
Nephtys (Aglaophamus) macroura Day 1967: 343, fig. 15.1J-M; Rozbaczylo and Castilla 1974: 185, fig. 2A-E, 3A.
Aglaophamus virginis Hartman 1953: 30-31, fig. 7A-B (partim).
Aglaophamus ornatus Hartman, 1967: 76-78, pl. 24; Bellan 1974: 789; Hartmann-Schröder and Rosenfeldt 1988: 47; 1990: 101.
Nephtys (Aglaophamus) ornatus Rozbaczylo and Castilla 1974: 188.

Type locality. Kerguelen Islands, Antarctic Ocean.

Material examined. Antarctic Ocean, South Shetland Islands: Bentart 1995, Livingston Island, 80 m, 18 Jan 1995, 7 spms in poor condition (MNCN 16.01/3202 as *A. ornatus*); Decepción Island, 330 m, 31 Jan 1995, 2 complete and 4 incomplete spms (MNCN 16.01/3199 as *A. ornatus*); Bentart 2006, RV Hespérides, Decepción Island, 62º58.858’-62º59.016’S, 60º36.127’-60º35.610’W, 106.1-112.6 m, Agassiz grab, 8 Jan 2006, 1 complete (DBUA 01131-02); 62º58.858’-62º59.016’S, 60º36.127’-60º35.610’W, 106.1-112.6 m, Agassiz grab, 8 Jan 2006, 1 incomplete spms (MB36000147); 14 Jan 2006, 1 incomplete spm (DBUA 01131-01).

Remarks. Specimens of *A. trissophyllus* have been often misidentified as other subantarctic species such as *A. macroura* from New Zealand or *A. virginis* from Strait of Magellan. The main difference between *A. trissophyllus* and those other species is the shape of the notopodial postchaetal lamellae which are unequally bilobed with both lobes rounded in *A. trissophyllus* (Figure 35H) while in the other two species the inner part of the lamellae is splited in two erect lobes (Figure 34L, 36J). Branchiae start in chaetiger 2 in *A. trissophyllus* and *A. virginis*, and in chaetigers 3-4 in *A. macroura*. Hartman (1967) erected the species *A. ornatus* for specimens from Bransfield Strait that were later ascribed to *A. trissophyllus* (Knox & Cameron 1998).

The pharynx of *A. trissophyllus* has been described as having 14 rows of 8-10 subterminal papillae ending proximally in a triangular group of smaller papillae. The specimens examined within this study have that same number of rows and papillae intercalated with eight shorter rows of only two papillae, present always in the same pattern (two long rows middorsaly followed to the right by one shorter row, three long, one short, one long, one short, one long and one short; same pattern in the left side). Thus the pharynx has in fact 22 rows of 2-10 subterminal papillae, from which the longer rows are followed proximally by a triangular group of smaller papillae (Figure 29C).

Distribution. Antarctic Ocean (Antarctic and Subantarctic areas extending to off the coasts of the southern main land masses) (Knox & Cameron 1998).

Habitat. 25-1400 m depth (Hartman 1978).

Aglaophamus uruguayi Hartman, 1953

Figures 30S, 31; Table 12

Aglaophamus uruguayi Hartman, 1953: 32, fig. 8A-D; Lana 1986: 144, figs. 18 and 19.

Type locality. Off Rio Grande do Sul (33ºS, 51º10’W), Brazil, W Atlantic Ocean, 80 m depth.

Remarks. This species was originally described by Hartman (1953) for specimens apparently collected from off Uruguay. However, the coordinates of the type locality correspond to the shelf off Rio Grande do Sul in Brazil (Lana 1986).

Distribution. Atlantic Ocean (SE Brazil) (Lana 1986).

Habitat. Mud and sandy mud, 60-95 m depth (Lana 1986).

Aglaophamus urupani **Nateewathana & Hylleberg, 1986**

Figures 34T, 35; Table 14

Aglaophamus urupani Nateewathana and Hylleberg, 1986: 198, figs. 3A-F, 4 and 5.

Type locality. Patong Bay, Phuket Island, Thailand, E Indian Ocean, 30 m depth.

Remarks. *Aglaophamus urupani* is morphologically very similar to *A. vietnamensis*. According to Nateewathana and Hylleberg (1986), the two species differ by the absence of prostomial eyes and the poor development of postchaetal lamellae in *A. vietnamensis* (Figure 34V). Also the dorsal cirri are absent in *A. vietnamensis* (Fauchald 1968) and present in *A. urupani* (Nateewathana & Hylleberg 1986).

Distribution. Indian Ocean (Thailand); Pacific Ocean (Hong Kong) (Nateewathana & Hylleberg 1986, Ohwada 1992).

Habitat. Silty clay to fine sand, 10-30 m depth (Nateewathana & Hylleberg 1986).

Aglaophamus verrilli **(McIntosh, 1885)**

Figures 36I, 37; Table 15

Nephthys verrilli McIntosh, 1885: 163, pl. 26, figs. 6 and 7, pl. 32A, fig. 8; Treadwell, *in* Cowles 1930: 341; Knox 1960: 115.
Aglaophamus verrilli Pettibone 1963: 190, fig. 48C-D; Day 1973: 42; Gardiner 1976: 155, figs. 16K and 17A-B; Rainer and Hutchings 1977: 316, figs. 7-11 and 41; Taylor 1984: 35-15, fig. 35-11 and 12A-C; Imajima and Takeda 1985: 80, fig. 11A-P;

Hernández-Alcántara and Solís-Weiss 1991; ? Kirkegaard 1995: 37; Hilbig 1997: 325, figs. 13.3; Hernández-Alcántara and Solís-Weiss 1999. .

Not *Aglaophamus cf. verrilli* Nateewathana and Hylleberg 1986: 202, figs. 6A-F and 7.

? *Aglaophamus dibranchis* Monro 1933; Treadwell 1937; Hernández-Alcántara and Solís-Weiss 1991.

Nephthys dibranchis Hartman 1938b: 146 (partim); Hartman 1940: 237 (partim); Rullier 1965: 182; Sterpherson *et al*. 1970: 470; Sterpherson *et al.* 1974: 113.

Aglaophamus dicirris Hartman, 1950: 122, pl. 18, figs. 1-8.

cf. *Aglaophamus dicirris* Hartman 1968; Reish 1968; Kudenov 1975: 79; Fauchald 1977: 33; Laverde-Castillo 1986; Sallazar-Vallejo *et al.* 1990; Dean 1996a, b.

Type locality. Queen Charlotte Sound (41º4'S, 174º19'E), New Zealand, W Pacific Ocean, 18 m depth.

Material examined. Pacific Ocean, Queen Charlotte Sound, New Zealand, Cook Strait: Challenger Expedition, near Long Island, 18.3 m, 27 Jun 1874,1 incomplete spm, syntype (NHM 1885.12.1.12).

Remarks. *Aglaophamus verrilli* was originally described for specimens from New Zealand. Posteriorly, Hartman (1950) described a very similar species, *A. dicirris*, from Panama. Knox (1960) synonymised the two species without comment, and Rainer and Hutchings (1977) confirmed this synonymy examining the lectotype of *A. verrilli* and the holotype of *A. dicirris*. *Aglaophamus verrilli* has thus been frequently recorded from these areas, the eastern and western North America, and the Indopacific region. Specimens of *A. dicirris* were not examined in the present study, however, according to the literature, and except for the chaetiger where the neuropodial superior lobes start, the two species (*A. dicirris* and *A. verrilli*) appear to have very similar morphological characteristics. In the specimens of *A. verrilli* from Indopacific region the neuropodial superior lobes start more anteriorly, in the chaetiger 7-8, along with branchiae (Rainer & Hutchings 1977; Imajima & Takeda 1985; specimen examined), while in the specimens from North America (either referred as *A. dicirris* or *A. verrilli*) the neuropodial superior lobes do not start before chaetiger 14 (Hartman 1950; Kudenov 1975; Hilbig 1997). In these latter specimens the branchiae are referred to start on chaetigers 5-8 by the majority of the authors, probably following the previous references. However, in the original description of *A. dicirris*, Hartman (1950) pointed out for the existence of two groups of individuals, one with branchiae starting on chaetiger 5, rarely on 6 (including the holotype), and another with branchiae starting on chaetiger 7-8. Whether this later group have neuropodial superior lobes starting on chaetiger 7-8 is impossible to infer from the description and should be investigated. *Aglaophamus verrilli* may thus include at present two different species and further revision is in need.

Aglaophamus verrilli seems to occur more frequently in shallow water. However, Kirkegaard (1995) recorded it from a depth of 610 m, near New Zealand. He also remarked the differences between this species and *A. profundus,* a morphologically similar species from deep-water (795-2195 m) around Australia.

Distribution. Atlantic Ocean (from Maryland to Gulf of Mexico); Indian Ocean (India); Pacific Ocean (from S California to Panama; Japan, Australia, New Zealand) (Hilbig 1997).

Habitat. Silty sand and mud, intertidal to 200 m depth (Hilbig 1997).

***Aglaophamus victoriae* Rainer & Kally, 1988**

Figures 34U, 35; Table 14

Aglaophamus victoriae Rainer and Kaly, 1988: 691, figs. 3A-F and 6F.

Type locality. W Australia, E Indian Ocean.

Remarks. This species is morphologically very close to *A. verrilli* from which can be distinguished by more anterior start of branchiae and neuropodial superior lobe (3 and 4, respectively, rather than 5-8 and 7-8 in *A. verrilli*), and the presence of two pairs of prostomial eyes rather than one.

Distribution. Indian Ocean (Australia) (Rainer & Kaly 1988).

Habitat. 40-80 m depth (Rainer & Kaly 1988).

***Aglaophamus vietnamensis* Fauchald, 1968**

Figures 34V, 35; Table 14

Aglaophamus vietnamensis Fauchald, 1968: 13, figs. 21, 26, 29 and 30.

Type locality. Bay of Nha Trang, Viet Nam, W Pacific Ocean, 24 m depth.

Distribution. Pacific Ocean (Viet Nam) (Fauchald 1968).

Habitat. Mud, 24 m depth (Fauchald 1968).

Aglaophamus virginis (Kinberg, 1866)

Figures 36J, 37; Table 15

Nephthys virginis Kinberg, 1866: 239.
Aglaophamus virginis Hartman 1953: 30, fig. 7A-B (partim); Fauchald 1965: 336; Hartman 1967: 79, pl. 26, fig. A and B (partim?).
Nephtys (Aglaophamus) virginis Rozbaczylo and Castilla 1974: 193.
? *Nephthys praeticosa* Kinberg, 1866: 239.

Type locality. Off Cape Virgin, Strait of Magellan, 32 fms depth.

Remarks. This species is very similar to *A. macroura*, described from shallow waters of New Zealand, in having the inner part of the notopodial postchaetal lamellae splited in two erect lobes, the upper one slightly smaller than the lower. The two species differ mainly by the shape of the notopodial acicular lobes (conical in *A. virginis* and bilobed in *A. macroura*). Considering the different geographical distribution, these species are here considered as different. However, specimens from both species should be carefully examined and compared.

Distribution. Strait of Magellan, Tierra del Fuego (Hartman, 1967).

Habitat. 82-124 m depth (Hartman 1967).

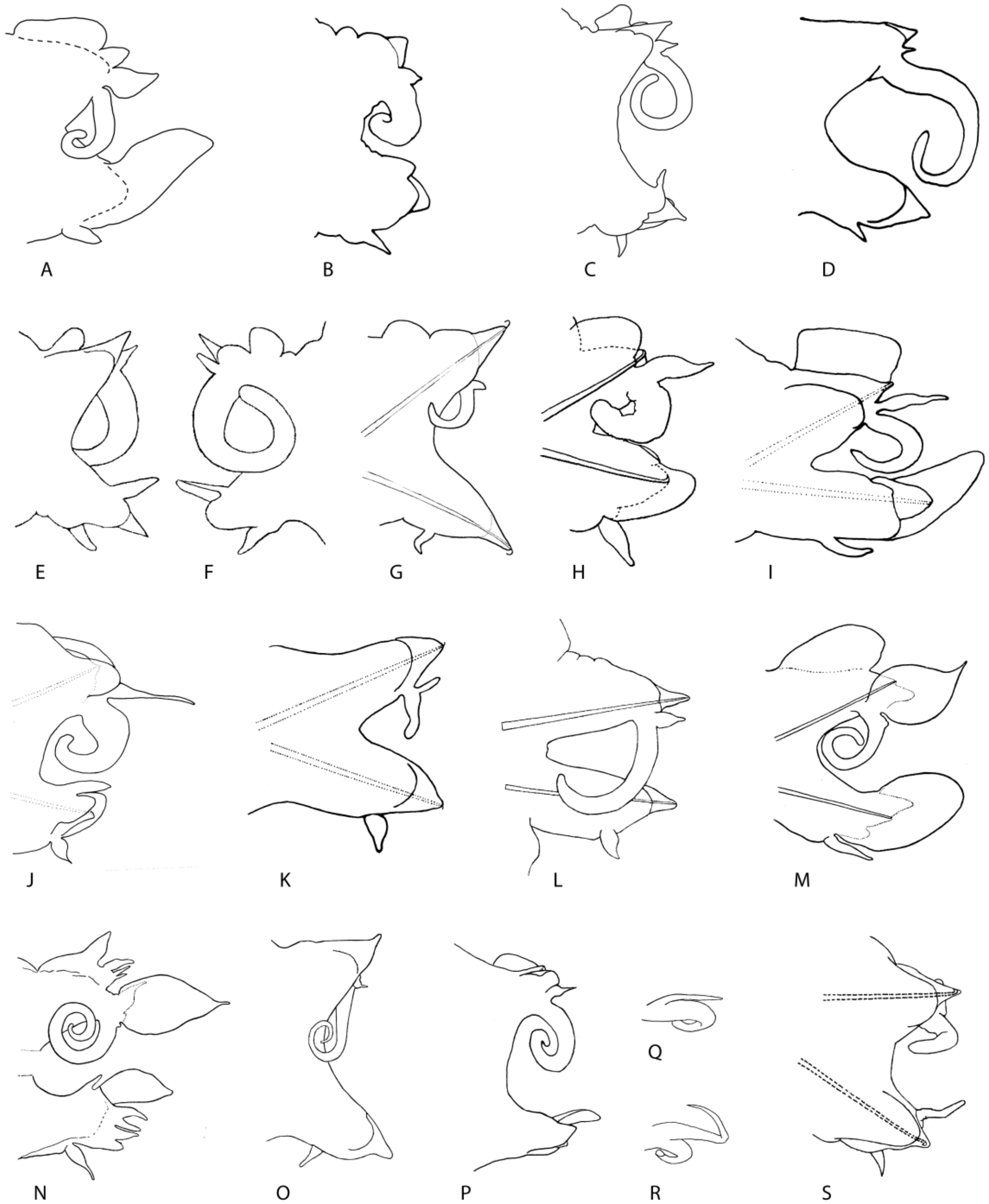


Figure 30. Parapodia of *Aglaophamus*. Species from N and S America. A. *A. circinatus*, median chaetiger, PV (Pettibone 1963); B. *A. erectanoides*, median chaetiger, PV (Hartmann-Schröder 1965); C. *A. erectans*, chaetiger 27, AV (Hartman 1950); D. *A. eugeniae*, chaetiger 18, AV (Fauchald 1972); E. *A. fossae*, chaetiger 28, AV (Fauchald 1972); F. *A. fossae*, chaetiger 28, PV (Fauchald 1972); G. *A. groenlandiae*, posterior chaetiger, posterior PV (Hartman 1967); H. *A. heteroserratus*, chaetiger 18, PV (Hartmann-Schröder 1965); I. *A. igalis*, chaetiger 32, AV (Hartman 1965); J. *A. juvenalis*, chaetiger 25, AV (Fauchald 1976); K. *A. minusculus*, chaetiger 16, AV (Hartman 1965); L. *A. paucilamellatus*, median chaetiger, AV (Hilbig 1997); M. *A. peruanus*, chaetiger 38, PV (Hartman 1940); N. *A. polypharus*, chaetiger 45, AV (Hartman 1940 as *N. lobophora*); O. *A. surrufus*, chaetiger 20, AV (Fauchald 1972); P. *A. tabogensis*, chaetiger 14, AV; Q. *A. tabogensis*, dorsal cirrus and branchiae from chaetiger 21; R. *A. tabogensis*, dorsal cirrus and branchiae from chaetiger 25; S. *A. uruguayi*, parapodium of chaetiger 20, AV (Lana 1986). AV – anterior view; PV – posterior view

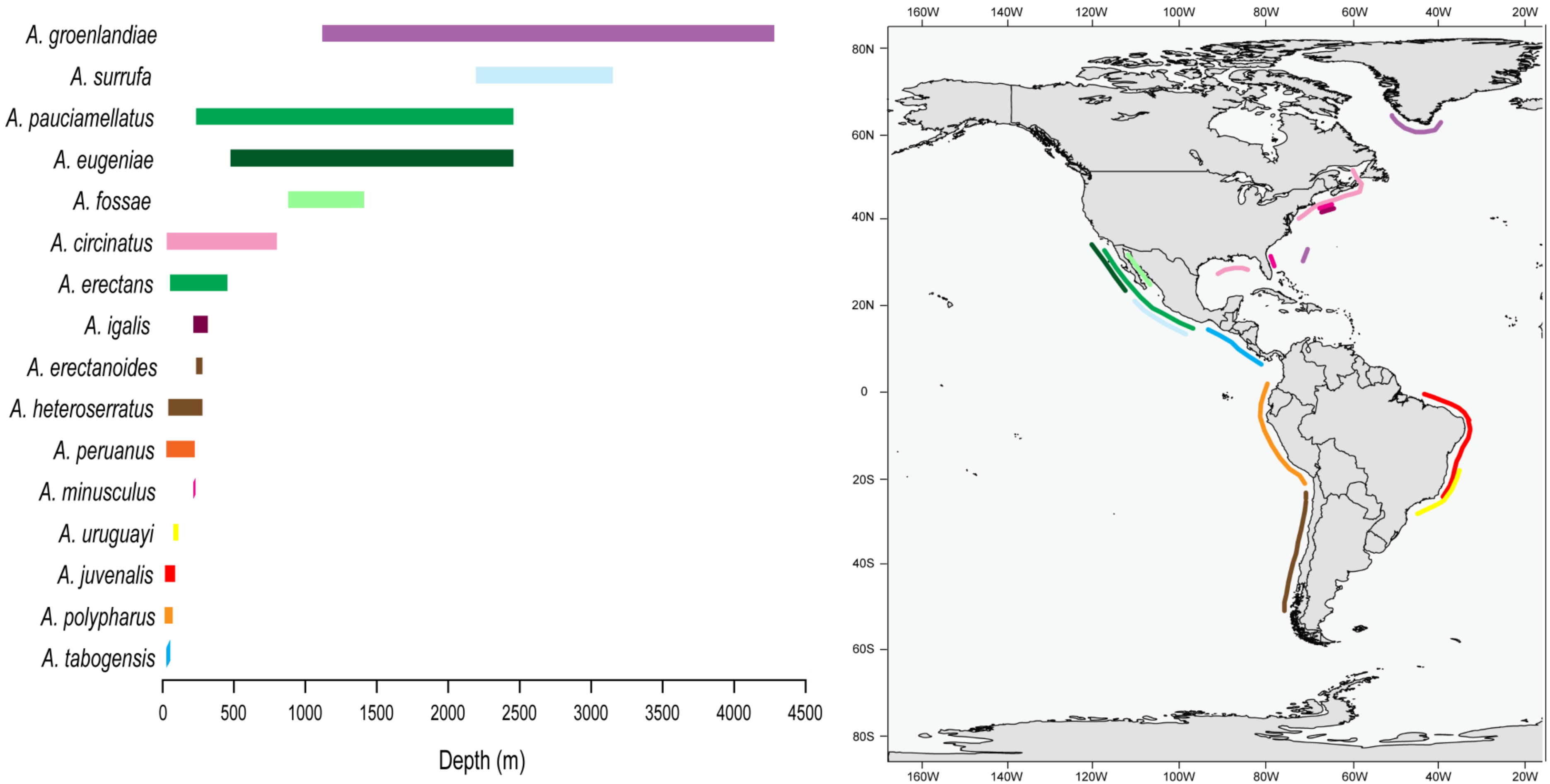


Figure 31. Bathymetrical and geographical distribution of the *Aglaophamus*. Species from N and S America. The position of the lines is the map is approximate and does not reflect the bathymetric range.

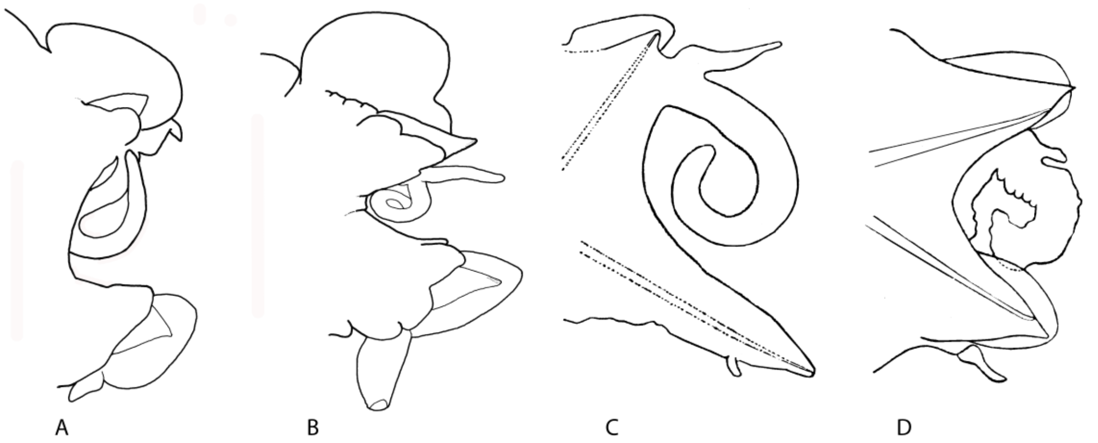


Figure 32. Parapodia of *Aglaophamus*. Species from Europe and Africa. A. *A. pulcher*, chaetiger 20, AV; B. *A. rubellus*, chaetiger 29, AV (Hartman 1967); C. *A. longicephalus*, chaetiger 20, AV (Hartman 1974); D. *A. lyrochaetus*, chaetiger 40, AV (Fauvel 1902). AV – anterior view.

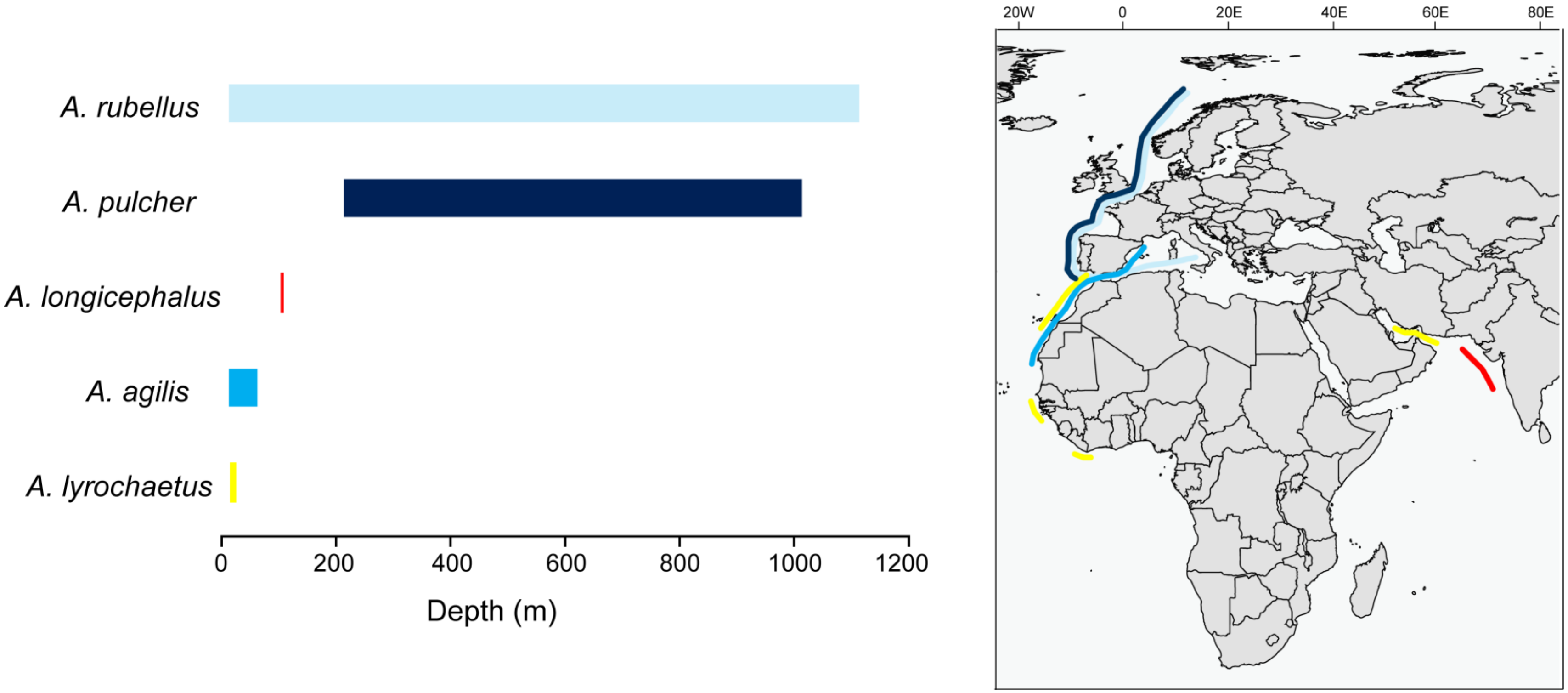


Figure 33. Bathymetrical and geographical distribution of the *Aglaophamus*. Species from Europe and Africa. The position of the lines is the map is approximate and does not reflect the bathymetric range.

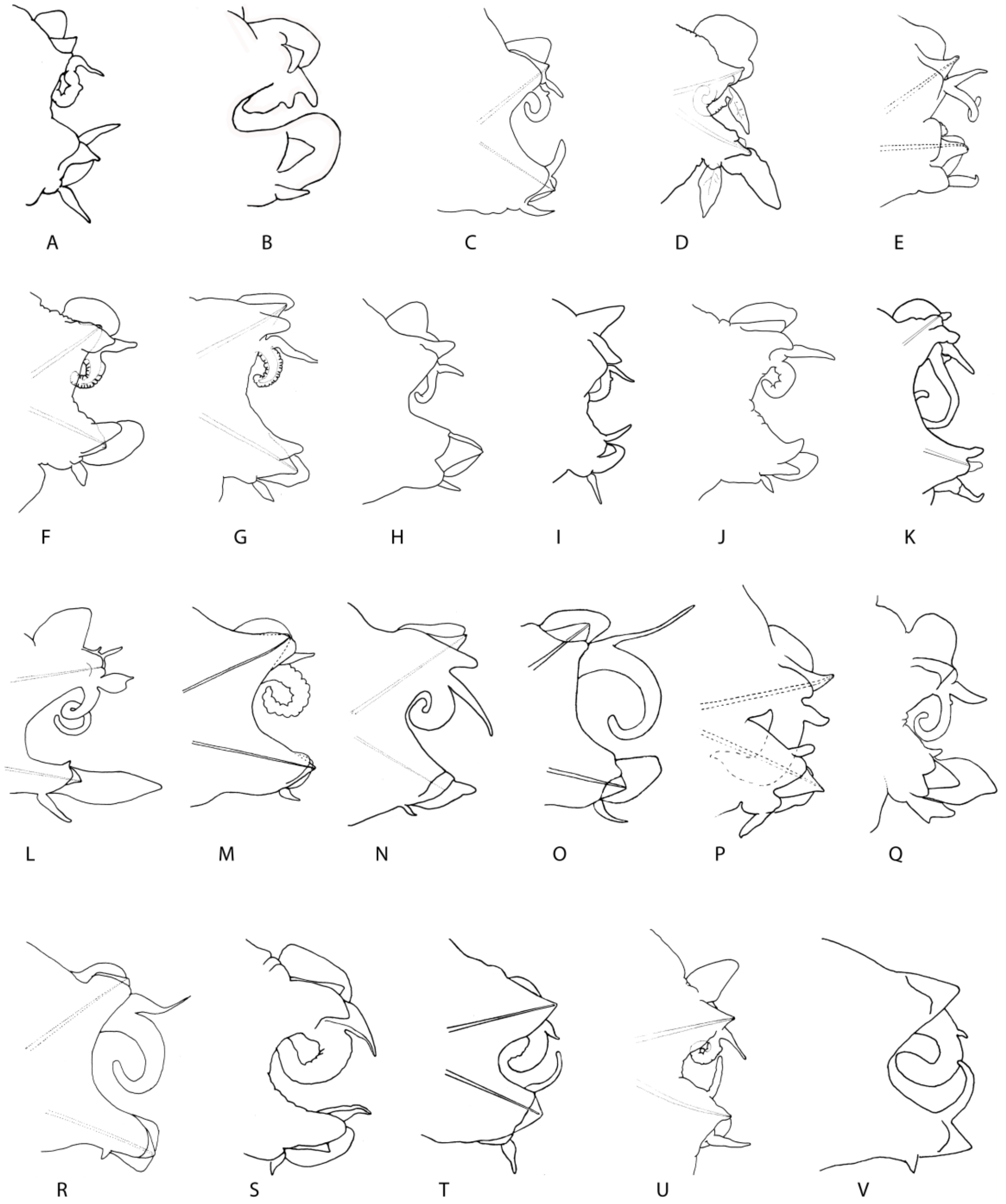


Figure 34. Parapodia of *Aglaophamus*. Species from Indopacific. A. *A. amakusaensis*, chaetiger 33, AV (Imajima & Takeda 1985); B. *A. australiensis*, chaetiger 20, AV; C. *A. dicirroides*, chaetiger 25, AV (Fauchald 1968); D. *A. foliocirratus*, chaetiger 40, AV (Rainer & Kaly 1988); E. *A. gippslandicus*, chaetiger 20, AV (Rainer & Hutchings 1977); F. *A. hedlandensis*, chaetiger 10, AV (Rainer & Kaly 1988); G. *A. hedlandensis*, chaetiger 40, AV (Rainer & Kaly 1988); H. *A. japonicus*, chaetiger 27, AV (Imajima & Takeda 1985); I. *A. jeffreysii*, chaetiger 45, AV (Imajima & Takeda 1985); J. *A. lobatus*, chaetiger 25, AV (Imajima & Takeda 1985); K. *A. lyratus*, median chaetiger, AV (Augener 1933 as *N. digitifera*); L. *A. macroura*, median chaetiger, AV (Hartman 1967); M. *A. munamaorii*, chaetiger 19, AV (Gibbs 1971); N. *A. orientalis*, chaetiger 25, AV (Imajima & Takeda 1985); O. *A. phuketensis*, chaetiger 25, AV (Nateewathana & Hylleberg 1986); P. *A. profundus*, chaetiger 27, AV (Rainer & Hutchings 1977); Q. *A. sinensis*, chaetiger 35, AV (Imajima & Takeda 1985); R. *A. tepens*, chaetiger 25, AV (Fauchald 1968); S. *A. toloensis*, chaetiger 20, AV (Ohwada 1992); T. *A. urupani*, chaetiger 25, AV (Nateewathana & Hylleberg 1986); U. *A. victoriae*, chaetiger 40, AV (Rainer & Kaly 1988) V. *A. vietnamensis*, chaetiger 25, AV (Fauchald 1968). AV – anterior view.

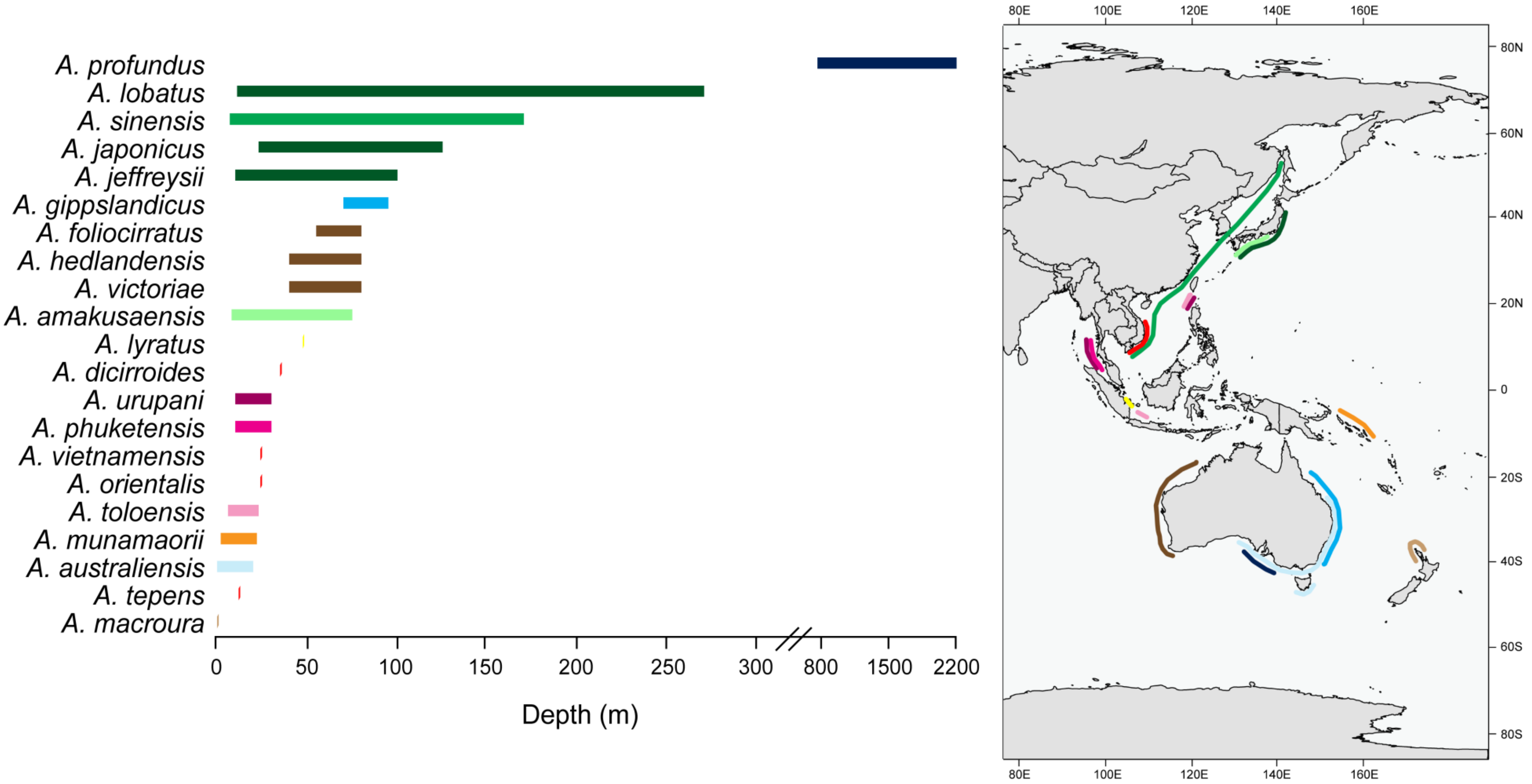


Figure 35. Bathymetrical and geographical distribution of the *Aglaophamus*. Species from Indopacific region. The position of the lines is the map is approximate and does not reflect the bathymetric range.

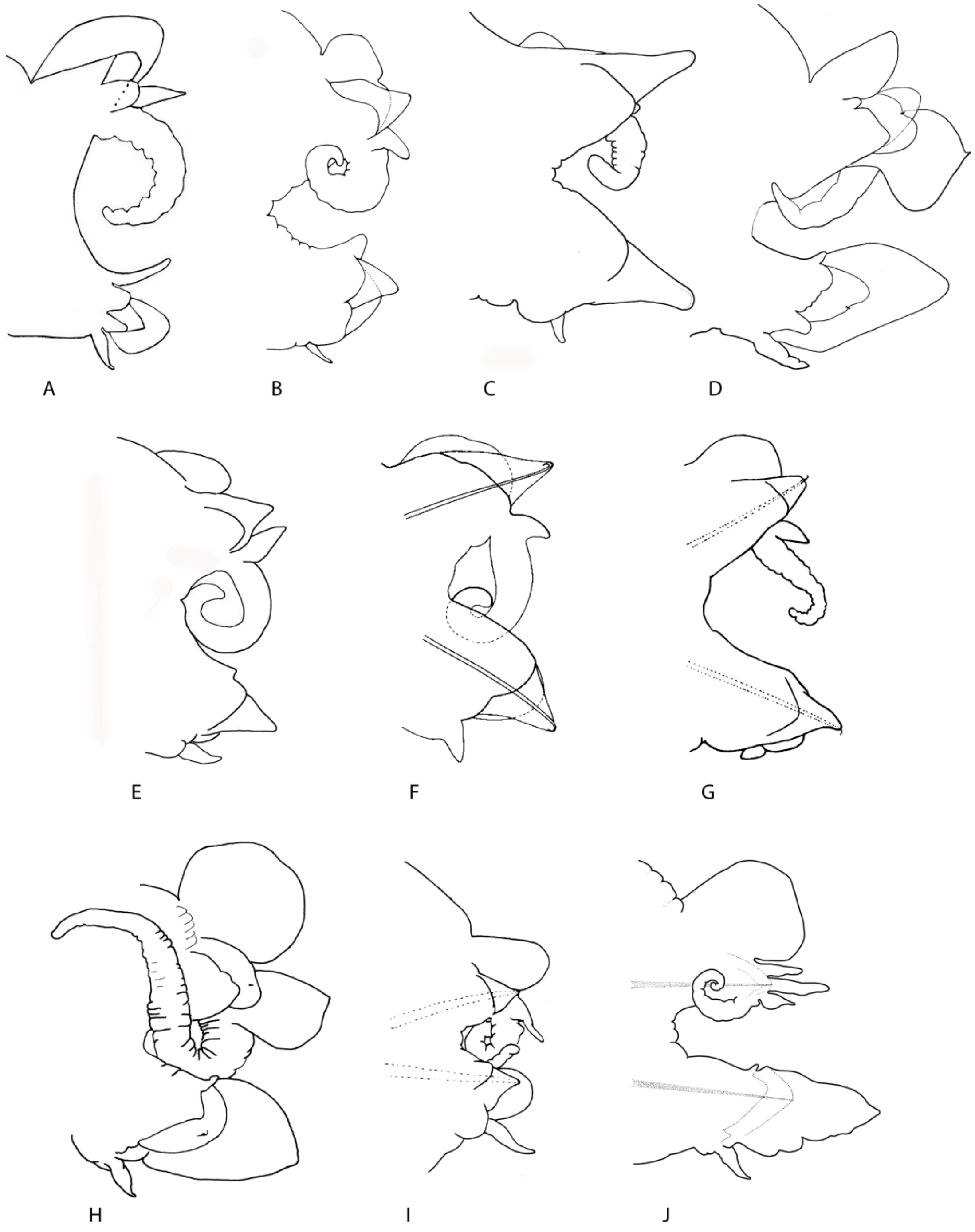


Figure 36 Parapodia of *Aglaophamus*. Polar and widespread species. A. *A. dibranchis*, median chaetiger, AV (Day 1967); B. *A. digitatus*, median chaetiger, AV (Hartman 1967); C. *A. elamellatus*, chaetiger 20, AV; D. *A. foliosus*, chaetiger 36, AV; E. *A. malmgreni*, chaetiger 20, AV; F. *A. paramalmgreni*, chaetiger 21, AV (Hartmann-Schröder & Rosenfeldt 1992); G. *A. posterobranchus*, chaetiger 26, AV (Hartman 1967); H. *A. trissophyllus*, chaetiger 32, AV; I. *A. verrilli*, chaetiger 20, AV (Rainer & Hutchings, 1977); J. *A. virginis*, chaetiger 20, PV (Hartman 1967). AV – anterior view; PV – posterior view.

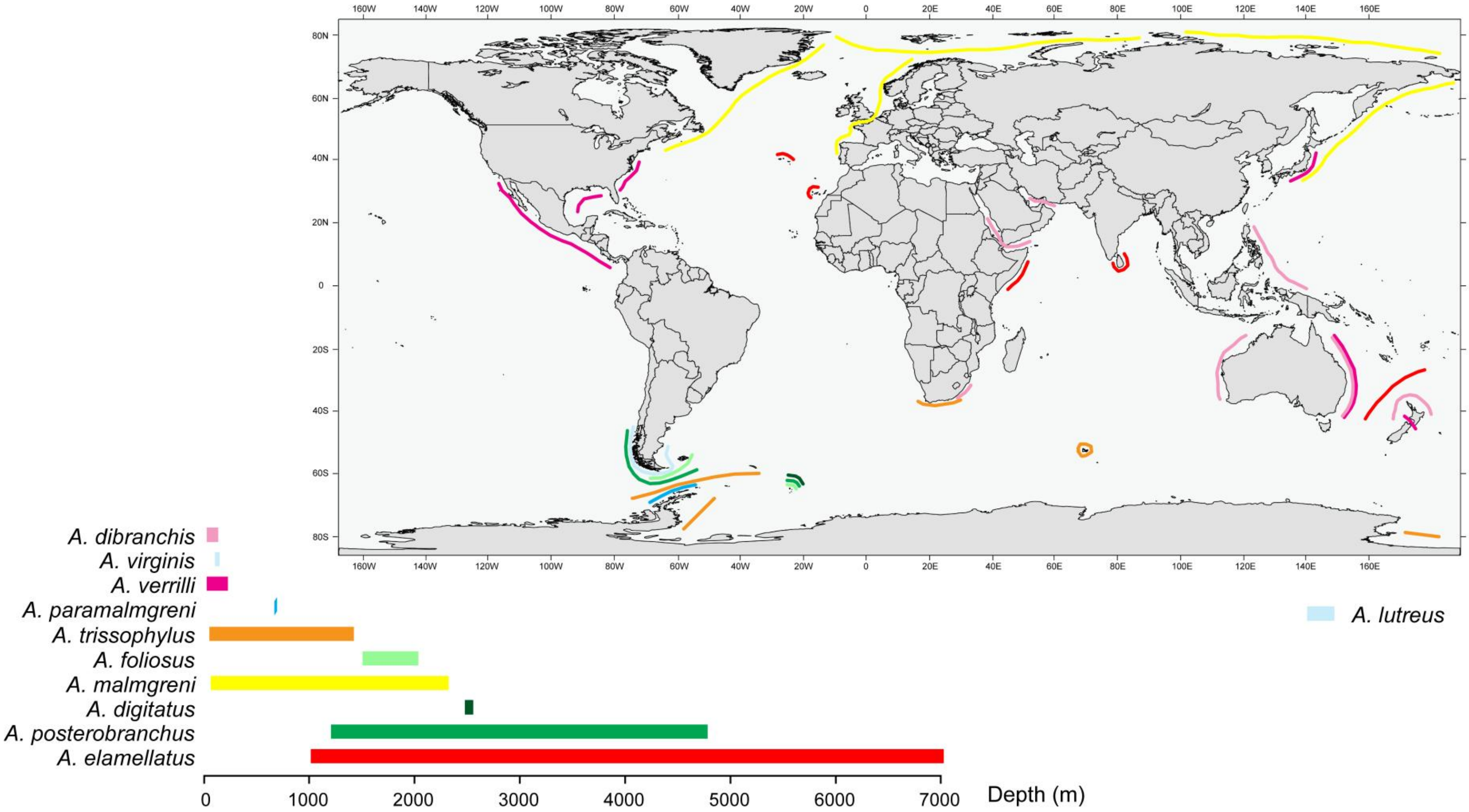


Figure 37. Bathymetrical and geographical distribution of *Aglaophamus*. Polar and widespread species. The position of the lines is the map is approximate and does not reflect the bathymetric range. There is no information available in literature on the bathymetric distribution of *A. lutreus*.

Table 12. Diagnostic characters of *Aglaophamus*. Species from N and S America. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; NO – notopodia(l); NE – neuropodia(l); PreCh – preacicular chaetae; PosCh – postacicular chaetae; PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri. Pharynx subterminal papillae (| , # rows (# pap.), Δ): **|** - middorsal papilla present, number of rows (number of papillae per row), Δ - proximal papillae arranged in triangular groups.

Species	Prostomial eyes	Branchiae present		NE superior lobes	Parapodial lamellae			Lyriform chaeta	Pharynx		Notes
		from Ch	until		PreL	NO PosL	NE PosL		Subterminal papillae	Proximal region	
A. circinatus	Absent	2	Near end of body	Absent	NO – rudimentary; NE – bilobed, < AcL	Bilobed, > AcL	Elongated, > AcL	Absent	14 (around 8), Δ	Smooth ?	DC foliaceous, longer than wide
A. erectanoides	Absent	8-10	last 15	Present (median Ch)	Rudimentary	Rudimentary	Rudimentary	Absent ?	?	?	DC very small
A. erectans	Absent	9-11	End of body	Present (16-17)	Poorly developed	Bilobed (upper lobe directed dorsally), < AcL	Rounded, < AcL	Absent	14 (10-13)	Smooth	--
A. eugeniae	Absent	8-9	?	Absent	Rounded, < AcL	Rounded, < AcL	Rounded, < AcL	Absent	14 (10-12)	Smooth	--
A. fossae	Absent	11-13	End of body	Present (foliose)	Rounded, < AcL	Bilobed, < AcL	Rounded, < AcL	Absent	14 (16-19)	Smooth	--
A. groenlandiae	Absent	11-13	Before end of body	Absent	Rudimentary	Poorly developed, bilobed (?)	Poorly developed, rounded	Absent	11 (up to 9)	Smooth	--
A. heteroserratus	Absent	4	last 8	Absent ?	?	Rounded/unequally bilobed, > AcL	Rounded, > AcL	Absent	20 (7-8)	Smooth ?	PosCh coarsely serrated
A. igalis	Absent	2	Near end of body	Absent	Rounded/slightly bilobed (?)	Rounded, directed dorsally, > AcL	Elongated, > AcL	Present	16 (several)	Smooth	--
A. juvenalis	Absent	4	last 15	Present	Rounded, ≥ AcL	Rounded, ≥ AcL	Rounded, ≥ AcL	Present	Long | , 16 (4-6)	Smooth	DC very long
A. minusculus	Absent	7-9	last 7?	Absent	Rudimentary	Poorly developed	Poorly developed	Present	22 (?)	Smooth	Br short, almost straight (12-17 pairs)
A. paucilamellatus	Absent	8-9	last 3/4	Absent	Rounded, < AcL	Rounded, < AcL	Rounded, < AcL	Absent	14 (8-10)	Smooth	--
A. peruanus	Absent	3	?	Absent	Poorly developed	Rounded, directed dorsaly, ≤ AcL	Elongated, > AcL	Absent	22 (2-8), Δ	Smooth	AcL with a distal digitate process
A. polypharus	Absent	2-3	End of body	?	Elongated in NE, > >AcL, > > PosL	Splited in 4 lobes, > AcL	Splited in 4 lobes, > AcL	?	22? (up to 5)	Smooth	DC foliaceous, elongated
A. surrufus	Absent	12	End of body	Absent	Poorly developed	Poorly developed	Poorly developed	Absent	Long | , 14 (14-16)	Smooth	NO base with thick superior ring

A. tabogensis	Absent	4	at least last 15	Present	Rounded, ≈ AcL	Rounded, ≈ AcL	Rounded, ≈ AcL	Present	| , ? (2-3)	Smooth	DC very long
A. uruguayi	Absent	4	last 14/15	Present	Poorly developed	Poorly developed	Poorly developed	Present	Long | , 20 (6-9)	Smooth	NE sup. lobes ≥ Br

Table 13. Diagnostic characters of *Aglaophamus*. Species from Europe and Africa. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; NO – notopodia(l); NE – neuropodia(l); PreCh – preacicular chaetae; PosCh – postacicular chaetae; PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri. Pharynx subterminal papillae (| , # rows (# pap.), Δ): **|** - middorsal papilla present, number of rows (number of papillae per row), Δ - proximal papillae arranged in triangular groups.

Species	Prostomial eyes	Branchiae present		NE superior lobes	Parapodial lamellae			Lyriform chaeta	Pharynx		Notes
		from Ch	until		PreL	NO PosL	NE PosL		Subterminal papillae	Proximal region	
A. pulcher	Absent	5-7	Near end of body	Present	Rounded, < AcL	Bilobed in some median parapodia, > AcL	Rounded, ≥ AcL	Absent	14 (10-15)	Smooth	Br recurved
A. rubellus	Absent	2	End of body	Present	Bilobed, < AcL	Bilobed in anterior and median parapodia, ≥ AcL	Elongated/rounded, > AcL	Absent	14 (up to 34), Δ	Smooth	--
A. agilis	Absent	2	End of body	Present, small	Rudimentary	Rounded, directed dorsally, > AcL	Elongated/rounded, > AcL	Absent	14 (about 8), Δ?	Smooth	--
A. lyrochaetus	Absent	4-5	End of body	Present ? (small)	Poorly developed	Rounded, ≥ AcL	Rounded, ≥ AcL	Present	Long | , 14 (4-6)	Smooth ?	--
A. longicephalus	1 pair	3	?	Absent	Rudimentary	Rounded, ≥ AcL	Poorly developed	Present	Long | , 14 (4-6)	Smooth	Prostomium much longer than wide

Table 14. Diagnostic characters of *Aglaophamus*. Species from Indopacific region. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); Ant – anterior(ly); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; NO – notopodia(l); NE – neuropodia(l); PreCh – preacicular chaetae; PosCh – postacicular chaetae; PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri. Pharynx subterminal papillae (| , # rows (# pap.), Δ): | - middorsal papilla present, number of rows (number of papillae per row), Δ - proximal papillae arranged in triangular groups.

Species	Prostomial eyes	Branchiae present		NE superior lobes	Parapodial lamellae			Lyriform chaeta	Pharynx		Notes
		from Ch	until		PreL	NO PosL	NE PosL		Subterminal papillae	Proximal region	
A. amakusaensis	1 pair	3	Near end of body	Present (from 4)	Rounded, < AcL	Rounded, ≥ AcL	Triangular, ≥ AcL	Present	22 (4-6)	With warts	
A. australiensis	Absent	4	last 20-30	Absent	Rounded, < AcL	Rounded, > AcL	Rounded, > AcL	Absent	| , 22 (6-9)	With warts	Spinulose PreCh present
A. dicirroides	1 pair	3	End of body	Present (large)	Rounded, < AcL	Triangular, > AcL	Rounded, ≈ AcL	Present	22 (6-8)	With warts	NO AcL with subacicular outgrouth
A. foliocirratus	1 pair	2	?	Absent	Poorly developed	Bilobed, > AcL	Elongated, >> AcL	Absent	14 (12-23)	Smooth	DC and VC leaf-like
A. gippslandicus	Absent	3	?	Absent	NO - rounded, < AcL; NE - bilobed, < AcL	Rounded/slightly bilobed, < AcL	Rounded, ≤ AcL	Absent	14 (12-15)	Smooth	Spinulose PreCh present
A. hedlandensis	Absent	3	?	Absent	Conical, ≈ AcL	Rounded; > AcL	Rounded, > AcL	Absent	| , 14 (3-4)	With warts	--
A. japonicus	Absent	2	?	Absent	Rounded, < AcL	Bilobed, < AcL	Rounded, ≤ AcL	Absent	| , 14 (15-17)	Smooth	NE > NO
A. jeffreysii	1 pair	3	?	Present (from 3)	Rounded, < AcL	Triangular, ≥ AcL	Rounded, ≥ AcL	Present	22 (4-7)	Smooth	--
A. lobatus	Absent	3	?	Absent	Elongated, ≥ AcL	Elongated, > AcL	Elongated, > AcL	Present	Short | , 14 (4-5)	With warts	--
A. lyratus	Absent?	18	?	Present	NO - elongated, ≥ AcL; NE - rudimentary	Rounded, ≥ AcL	Poorly developed	Present	?	?	DC and VC large
A. macroura	Absent	3-4?	Before end of body	Present	Poorly developed, rounded	Dorsal part foliaceous, ventral part splited into two erect lobes, > AcL	Elongated, >> AcL	Absent	14 (8-10), Δ	Smooth	DC foliaceous; NO AcL bilobed
A. munamairii	Absent	3	last 10-15	Absent	Rounded, ≤ AcL	Rounded, ≤ AcL	Rounded, ≤ AcL	Present	Long | , 14 (4-7)	Smooth	--
A. orientalis	Absent	3	?	Absent	NO–triangular, ≈ AcL; NE–poorly developed	Triangular, ≈ AcL	Elongated, > AcL	Absent	Long | , 14 (6-8)	With warts	NE AcL rounded; NO AcL acutely pointed; DC very long
A. phuketensis	Absent	3	End of body	Absent	Conical, < AcL	Rounded, > AcL	Rounded, > AcL	Present	Long | , 14 (3-6)	Smooth	DC long and slender
A. profundus	Absent	7	?	Present	Rounded, < AcL	Rounded, < AcL	Rounded, < AcL	Absent	20-22 (?)	Smooth ?	--

A. sinensis	Absent	2	End of body	Present	NO–rounded/slightly bilobed, < AcL; NE – bilobed, < AcL	Unequally bilobed, ≥ AcL	Elongated, >> AcL	Absent	14 (15-20), Δ	Smooth	DC foliaceous/cirriform
A. tepens	Absent	3	last 43	Absent	Rounded, ≤ AcL	Rounded, ≤ AcL	Rounded, ≤ AcL	Present	Long | , 14 (5-6)	Smooth	DC very long and tapered distally
A. toloensis	Absent	5-6	last 17-29	Present (ant. Ch)	Rounded, ≥ AcL	Rounded, > AcL	Rounded, > AcL	Present	Very long | , 14 (4-6)	Smooth	--
A. urupani	1 pair	7-12	last 13	Present (from 15)	Rudimentary / poorly developed	Rounded, < AcL	Rounded, < AcL	Present	Short | , 14 (6-8)	Smooth	Br as small knobs on Ch 2-11
A. victoriae	2 pairs	3	?	Present (from 4)	Rounded, < AcL	Triangular, > AcL	Rounded, ≥ AcL	Present	22 (4-6)	With warts	--
A. vietnamensis	Absent	8	last 10	Present (12-50)	Poorly developed	Poorly developed	Poorly developed	Present	Short | , 14 (7-8)	Smooth	DC absent; Br with accessory cirrus

Table 15. Diagnostic characters of *Aglaophamus*. Polar and widespread species. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; NO – notopodia(l); NE – neuropodia(l); Prech – preacicular chaetae; Posch – postacicular chaetae; PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri. Pharynx subterminal papillae (| , # rows (# pap.), Δ): **|** - middorsal papilla present, number of rows (number of papillae per row), Δ - proximal papillae arranged in triangular groups.

Species	Prostomial eyes	Branchiae present		NE superior lobes	Parapodial lamellae			Lyriform chaeta	Pharynx		Notes
		from Ch	until		PreL	NO PosL	NE PosL		Subterminal papillae	Proximal region	
A. dibranchis	1 pair	4	?	Present	Rounded, < AcL	Rounded, > AcL	Rounded, > AcL	Present	| , 14 (4-5), Δ	Smooth	--
A. digitatus	Absent	7	?	Present	Rounded, < AcL	Equally bilobed, < AcL	Rounded, < AcL	Present	14 (10-16)	Smooth	Antennae minute
A. elamellatus	Absent	11-13	Before end of body	Absent	Rudimentary	Poorly developed, rounded	Poorly developed, rounded	Absent	20-22 (6-11)	Smooth	Very long chaetae
A. foliosus	Absent	4	?	Absent	Bilobed, < AcL	Bilobed, > AcL	Elongated, >> AcL	?	| , 14 (10-14)	Smooth	DC large and foliaceous
A. lutreus	Absent	4-5	?	Present, large	Rounded, < AcL ?	Rounded, > AcL ?	Rounded, > AcL ?	Absent	22 (2-8), Δ	Smooth	--
A. malmgreni	Absent	11-13	Before end of body	Absent	Rounded, < AcL	Bilobed, ≤ AcL	Rounded, < AcL	Absent	22 (2-17), Δ	Smooth	--
A. paramalmgreni	Absent	12	Before end of body	Absent	Poorly developed	Rounded, < AcL	Rounded, < AcL	Absent	14 (7-8)	Smooth ?	--
A. posterobranchus	Absent	9-15	?	Absent	Poorly developed	Rounded, ≤ AcL	Rounded, < AcL	Absent	21-22 rows	Smooth ?	--
A. trissophyllus	Absent	2	last 6	Present	Rounded	Bilobed (outer lobe larger than inner), > AcL	Elongated, >> AcL	Absent	22 (2-10), Δ	Smooth	Anterior AcL bilobed
A. verrilli	Absent	5-8	Near end of body	Present (7-8/14)	Bilobed, < AcL	Rounded, > AcL	Rounded, > AcL	Present	22 (3-9)	With warts	--
A. virginis	Absent	2	End of body ?	Present	Poorly developed, rounded	With a large foliaceous outer part and an inner part splited into two erect lobes, > AcL	Elongated, >> AcL	Absent	?	Smooth	DC foliaceous with cirriform tip

Genus *Bipalponephtys* Ravara *et al.* (in press)

Type species. *Bipalponephtys cornuta* (Berkeley & Berkeley, 1945), by original designation.

Bipalponephtys cornuta **(Berkeley & Berkeley, 1945)**

Figures 38A, 39; Table 16

Nephthys cornuta Berkeley and Berkeley, 1945: 328, figs. 2-4.
Nephtys cornuta Hartman 1950: 106; Fauchald 1972: 90; Hilbig 1997: 336, fig. 13.8; Lovell 1997: 356, fig. 4A.
Nephtys parva Clark and Jones, 1955: 146, fig. 1A-F; Hartman 1968.
Nephtys signifera Hilbig, 1992: 719, fig. 5 (partim).
Nephtys cornuta franciscana Clark and Jones, 1955: 146, fig. 2; Jones 1961; Hartman 1968: 581, fig. 1, 2; Banse 1972: 216.
Bipalponephtys cornuta Ravara *et al.* in press.

Type locality. Friday Harbor, Washington, NE Pacific Ocean.

Material examined. Arctic Ocean, Alaska: 71º51’N, 160º20’W, 31 Jul 1960, 1 complete spm (USNM 31169, identified as *M. minuta*).
Pacific Ocean, San Francisco Bay, California: 37º90’N, 122º39’W, 2.40 m, 27 Mar 2002, 1 incomplete spm (CASIZ 168329).

Remarks. The genus *Bipalponephtys* was erected by Ravara *et al.* (in press) to accommodate the taxa *Nephtys cornuta*, following the results of a phylogenetic analysis that included 24 different taxa from the five genera of the family Nephtyidae. The results revealed a sister relationship between the taxa *Nephtys cornuta* and all the remaining nephtyids included in the analysis. According to Ravara *et al.* (in press), the bifid condition of the palps together with the absence of barred chaetae on posterior chaetigers is the main diagnostic features of this new genus.

Clark & Jones (1955) differentiated the subspecies *N. cornuta franciscana* from *N. cornuta* based on small morphological differences that were later considered by Ellis & Ronaldson (1988) to be inconsistent or overlapping in the two forms. The holotype of *N. parva* was re-examined by Lovell (1997) and found to be *N. cornuta*.

Although the original description and figures of *N. parva* differ from *N. cornuta*, Lovell (1997) did not found specimens matching that description and thus *N parva* was synonymised with *N. cornuta*. Lovell (1997) also examined paratype material of *N. signifera* from which he separated two *N. cornuta* specimens.

Several authors have reported some differences in the pharynx morphology of *Nephtys cornuta*. Banse (1972) reported 18 terminal bifid papillae and 22 rows of 4-5 subterminal papillae for specimens of *N. cornuta franciscana* from eastern Pacific. Hilbig (1997) reported 14 terminal bifid papillae and 16 rows of about 5 subterminal papillae for specimens from California. Lovell (1997) re-examined the holotypes of *N. cornuta* and *N. cornuta franciscana* and re-described the pharynx as having 18 terminal bifid papillae and 20 rows of 4-5 subterminal papillae. Neither the original descriptions of *N. cornuta* or *N. cornuta franciscana* report to the pharynx morphology. The pharynx of the specimens examined within this study was not observed. Thus the description presented in Table 16 is the one given by Lovell (1997).

Distribution. Pacific Ocean (Alaska to S California) (Hilbig 1997; Lovell 1997).

Habitat. Silty or muddy bottoms, subtidal to 440 m depth (Hilbig 1997) (subtidal to 1600 m, according to Lovell 1997).

Bipalponephtys danida **(Nateewathana & Hylleberg, 1986)**

Figures 38B, 39; Table 16

Nephtys danida Nateewathana and Hylleberg, 1986: 209, figs. 11A-H and 13.
Bipalponephtys danida Ravara *et al.* in press.

Type locality. Bang Tao Bay, Phuket Island, Thailand, E Indian Ocean, 10 m depth.

Remarks. *Bipalponephtys danida* was originally described as belonging to the genus *Nephtys* and transferred to the genus *Bipalponephtys* by Ravara *et al.* (in press), along with the species *N. cornuta* and *M. neotena* due to the presence of bifid palps and absence of barred chaetae on posterior chaetigers.

Distribution. Indian Ocean (Thailand) (Nateewathana & Hylleberg 1986).

Habitat. Very fine sand, 10 m depth (Nateewathana & Hylleberg 1986).

***Bipalponephtys neotena* (Noyes, 1980)**

Figures 38C, 39; Table 16

Aglaophamus neotenus Noyes, 1980: 106, figs. 1-3.
Nephtys neotena Ohwada 1985a: 58.
Micronephthys neotenus Jirkov and Paraketsova 1996: 833, fig. 2.
Micronephthys neotena Dnestrovskaya and Jirkov 2001: 193.
Nephtys minuta Zatsepin 1948: 122, table XXX (partim); Uschakov 1955: 217, fig. 68 (partim); (not Théel 1879).
Micronephthys minuta Tzetlin 1980: 25 (partim).
Micronephthys minuta Jirkov 1989: 74, fig. 15.4 (partim).
Bipalponephtys neotena Ravara *et al.* in press.

Type locality. Maine and eastern Canada, W Atlantic Ocean.

Remarks. *Bipalponephtys neotena* was first described by Noyes (1980) as belonging to the genus *Aglaophamus* due to the slightly involute condition of the branchiae and the curved tips of the aciculae. Later Ohwada (1985a) re-examined the paratypes of *A. neotenus* and recorded the presence of slightly recurved branchiae in the middle chaetigers. He also denoted some prostomium similarities between this species and a group of *Nephtys* species, thus transferring *Aglaophamus neotenus* to *Nephtys neotena*. The species was later synonymised with *N. cornuta* (here referred to as *Bipalponephtys cornuta*) by Hilbig (1997), due to the presence of bifid palps in some of the specimens (10% of all specimens according to Noyes (1980)), although some difference in appearance was denoted between specimens from California (type locality of *B. cornuta*) and Maine (type locality of *N. neotena*) suggesting that the two populations represented two ends of the variability range. Lovell (1997) questioned this synonymy but did not add any comments stating that further investigation was in need. Jirkov & Paraketsova (1996) reported the presence of *N. neotena* in the White Sea and considered it as belonging to the genus *Micronephthys* due to its close similarity with the species *M. minuta* (type species of the genus *Micronephthys*). These authors compared those two species (*M. neotena* and *M. minuta*), both occurring in the White Sea and adjacent areas, and stated that despite the morphological similarities the two species occupy different ecological niches in terms of depth and water temperature and have different spawning time. However, they did not mention the presence of bifid palps in *M. neotena* and made no reference to the specimens reported from Maine (*N. neotena*) and eastern Canada (*B. cornuta*). Later, Dnestrovskaya and Jirkov (2001) re-described *M. neotena* specimens from the White and Barents Seas as having bifid palps, remarked its similarities to *B. cornuta*, and suggested the latter likely to also belong to the genus *Micronephthys*. According to these authors the two species clearly differ in the shape of prostomium, the number of terminal bifid papillae on the pharynx (14 in *B. cornuta*, 16-18 in *M. neotena*), the number of rows of subterminal papillae on the pharynx (16 rows in *B. cornuta*, 20 distally and 14-16 medially in *M. neotena*), the presence of barred chaetae on the anterior and middle chaetigers (present at least on the middle chaetigers in *B. cornuta*), and slight differences in the shape of branchiae. However, some of these differences are incorrectly stated. The original description of *B. cornuta* does not include the pharynx morphology. Hilbig (1997) reported the pharynx as having 14 terminal bifid papillae and 16 rows of subterminal papillae, but Lovell (1997) re-examined the holotype of *B. cornuta* and re-described the pharynx as having 18 terminal bifid papillae and 20 rows of 4-5 subterminal papillae, as described for *M. neotena*. Still the number of papillae per row is slightly different in the two species (2-6 in *M. neotena*, 4-8 in *B. cornuta*). Also the branchiae are absent on posterior chaetigers of *M. neotena* and present until the end of the body in *B. cornuta*. Furthermore the distribution of the two species is different. *Micronephthys neotena* occurs in the Arctic and North Atlantic Oceans and *B. cornuta* occurs in the eastern North Pacific Ocean. For these reasons the two species are here kept as separate. Recently, Ravara *et al.* (in press) transferred the species *M. neotena* to the genus *Bipalponephtys*, along with the species *N. cornuta* and *N. danida*, considering the presence of bifid palps together with the poorly developed parapodial lamellae and absence of barred chaetae on the posterior chaetigers.

Distribution. Atlantic Ocean (Canada to Maine; White Sea; Barents Sea) (Noyes 1980; Jirkov & Paraketsova 1996; Dnestrovskaya & Jirkov 2001).

Habitat. Silty and muddy sand with high organic matter content, in polyhaline environment, 3-318 m depth (Noyes 1980; Jirkov & Paraketsova 1996; Dnestrovskaya & Jirkov 2001).

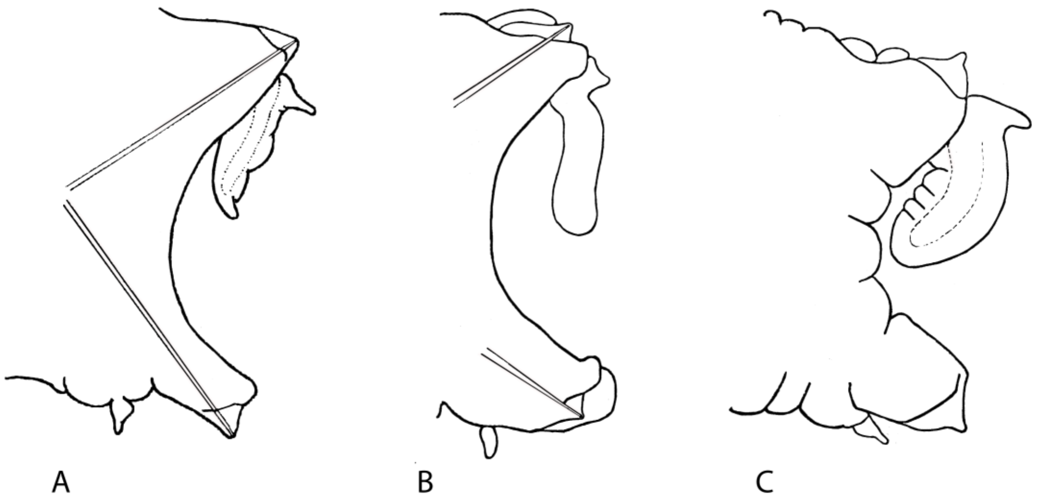


Figure 38. Parapodia of *Bipalponephtys*. A. *B. cornuta*, chaetiger 5, AV (Hilbig 1997); B. *B. danida*, chaetiger 40, AV (Nateewatnana & Hylleberg 1986); C. *B. neotena*, chaetiger 10, AV (Noyes 1980). AV – anterior view.

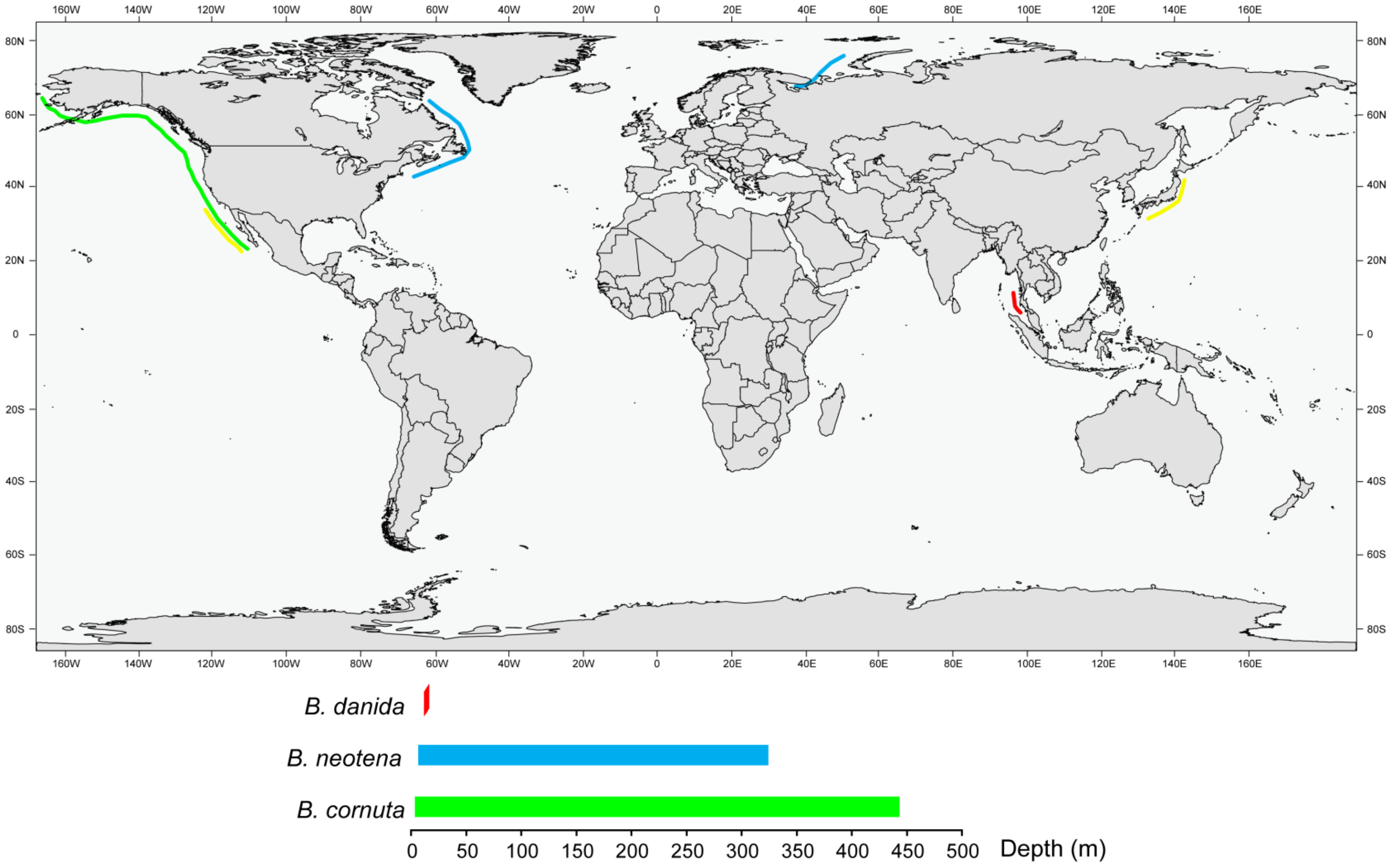


Figure 39. Bathymetrical and geographical distribution of the *Bipalponephtys*. The position of the lines is the map is approximate and does not reflect the bathymetric range.

Table 16. Diagnostic characters of *Bipalponephtys*. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; NO – notopodia(l); NE – neuropodia(l); PreCh – preacicular chaetae; PosCh – postacicular chaetae; PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri. Pharynx subterminal papillae (| , # rows (# pap.), Δ): **|** - middorsal papilla present, number of rows (number of papillae per row), Δ - proximal papillae arranged in triangular groups.

Species	Branchiae		AcL	Parapodial lamellae			Pharynx		Notes
	From Ch	Until		PreL	NO PosL	NE PosL	Subterminal papillae	Proximal region	
B. cornuta	5	Near end of body	Conical	Poorly developed	Poorly developed	Poorly developed	Long | , 20 (4-8)	Smooth	18 terminal bifid pap.
B. danida	5	End of body	Conical	Rounded, ≤ AcL	Rounded, ≤ AcL	Rounded, ≥ AcL	18/16? (6-8)	Smooth	--
B. neotena	5-7	Ch 12-21	Conical	Rudimentary	Rudimentary	Rudimentary	Long | , 20-22 distally/14-16 on middle part (1/2-6)	Smooth	18 terminal bifid pap.; Br. Present on 7-15 Ch (from 5-7 to 12-21); 1 pair of eyes on Ch 3

Genus *Inermonephtys* Fauchald, 1968

Type species. *Inermonephtys (Aglaophamus) inermis* Ehlers, 1887, by original designation.

Inermonephtys brasiliensis Martin, Gil and Lana, 2009

Figures 40A, 41; Table 17

Inermonephtys brasiliensis Martin, Gil and Lana, 2009: 166, figs. 1-4.
Inermonephtys palpata Lana 1986: 141, figs. 11-15 (not Paxton, 1974).

Type locality. Continental shelf off São Paulo and Paraná states (25º26'S, 47º55'W), SE Brazil, W Atlantic Ocean, 25 m depth.

Remarks. The type material of *I. brasiliensis* was previously reported by Lana (1986) from the Brazilian coast as belonging to the species *I. palpata*. Later Martin *et al.* (2009) re-examined the referred material along with the holotype of *I. palpata* from eastern Australia, and erected *I. brasiliensis* to accommodate the Brazilian specimens. *Inermonephtys brasiliensis* differs from *I. palpata* and the remaining *Inermonephtys* species mainly by having two types of lyriform chaetae (with short and long rami, Martin *et al.* 2009:169, Fig. 3C) and branchiae starting from chaetiger 3. *Inermonphtys inermis* also has branchiae starting on chaetiger 3 but only one type of lyriform chaetae is present. Other minor differences in parapodia and palps morphology can also be found (Table 17).

Distribution. Atlantic Ocean (Brazil) (Martin *et al.* 2009).

Habitat. Fine and silty sands, 25-88 m depth (Martin *et al.* 2009).

Inermonephtys foretmontardoi Ravara, Pleijel & Cunha, submitted

(see chapter 3.1, pg. 75)

Inermonephtys gallardi Fauchald, 1968

Figures 40C, 41; Table 17

Inermonephtys gallardi Fauchald, 1968: 15, pl. 1, figs. 5-6, pl. 3, figs. 22-25.

Inermonephtys cf. gallardi Nateewathana and Hylleberg 1986: 205, figs. 8A-F and 10.

Type locality. Bay of Nha Trang, Viet Nam, W Pacific Ocean, 12 m depth.

Remarks. Fauchald (1968) erected the species *Inermonephtys gallardi* based on four specimens from Viet Nam. Previously, Kinberg (1866) described the species *Aglaophamus lyratus* based on a single specimen without anterior end from Bangka Strait. Although the prostomium and pharynx morphology is impossible to compare, the parapodia of *I. gallardi* are very similar to those of *A. lyratus* and the branchiae are first present from chaetiger 15 in *I. gallardi* and 18 in *A. lyratus*. The two species may thus be synonymous. However, further observations including prostomium and pharynx morphology are needed (see remarks of *A. lyratus*).

Distribution. Viet Nam, cf. Thailand (Fauchald 1968; Nateewathana & Hylleberg 1986).

Habitat. Very fine sand, 10-30 m depth (Fauchald 1968).

***Inermonephtys inermis* (Ehlers, 1887)**

Figures 40D, 41; Table 17

Nephtys (Aglaophamus) inermis Ehlers, 1887: 125, pl. 38, figs. 1-6.
Nephtys inermis Hartman 1938a: 9; Hartman 1940: 234, pl. 39, figs. 84-86, pl. 40, fig. 95.
Aglaophamus inermis Hartman 1950: 129; Rioja 1964.
Inermonephtys inermis Fauchald 1968: 16, figs. 5-6 and 31-35; Perkins and Savage 1975; Taylor 1984: 35-19, fig. 35-15 and 16A-C; Kirkegaard 1995: 37.
? *Inermonephtys inermis* Imajima 1970; Uschakov and Wu 1979; Lee and Jae 1983: 22, pl. 2A-D.

Type locality. Off Aligator reef (24º48.5’N, 80º34.45’W), Florida, USA, W Atlantic Ocean, 97 m depth.

Material examined. Atlantic Ocean, USA, Florida: off Aligator Reef, 24º48.5’N, 80º34.45’W, 97 m, 8 May 1869, 1 complete spm, holotype (MCZ 1088).

Remarks. *Inermonephtys inermis* was originally described as *Nephtys (Aglaophamus) inermis* by Ehlers (1887) from specimens found in Florida. Up to now it has been considered to have a cosmopolitan distribution in temperate, tropical and subtropical seas (including Atlantic, Pacific and Indian Oceans) (e.g. Hartman 1940, 1950; Fauchald 1968; Day 1973; Taylor 1984; Kirkegaard 1995). Ravara *et al.* (submitted) reviewed the South European nephtyids and proposed the erection of a new species to accommodate the European specimens previously identified as *I. inermis*. These specimens differ from the holotype of *I. inermis* by the presence of well-developed neuropodial postchaetal lamellae (extending well beyond acicular lobes) and prechaetal lamellae of both rami (although not extending beyond acicular lobes), which are rudimentary or poorly developed in *I. inermis*. The records of *I. inermis* for the W Pacific Ocean (Imajima 1970; Uschakov & Wu 1979; Lee & Jae 1983) probably refer to other species, although some specimens have branchiae starting on chaetiger 4 (Lee & Jae 1983), which is a characteristic of *I. inermis*.

Distribution. Atlantic Ocean (North Carolina, Florida, Bahia Honda); Indian Ocean (Maldives); Pacific Ocean (California, Panama; Viet Nam) (Hartman 1940; Taylor 1984; Kirkegaard 1995). There are further reports of this species from Morocco to Angola (W Africa, E Atlantic Ocean) (Kirkegaard 1995), but these records require confirmation since a new species (*I. foretmontardoi*) was erected for specimens from N Europe (E Atlantic Ocean). Also the reports from W Pacific Ocean (Imajima 1970; Uschakov & Wu 1979; Lee & Jae 1983) require confirmation.

Habitat. Sandy bottoms, 0-131 m depth (Hartman 1950; Taylor 1984). There are further reports of this species up to 450 m depth (Kirkegaard 1995), which require confirmation.

***Inermonephtys japonica* Imajima & Takeda, 1985**

Figures 40E, 41; Table 17

Inermonephtys japonica Imajima and Takeda, 1985: 59, fig. 2A-Q; Imajima 2003.

Type locality. Sagami Bay, Japan, W Pacific Ocean, 84 m depth.

Remarks. *Inermonephtys japonica* is morphologically very similar to *I. palpata* from eastern Australia. According to Imajima & Takeda (1985) the two species can be distinguished by the nuchal organs (single process in *I. japonica,* three processes in *I. palpata*) and by the accessory cirrus of branchiae (present in all branchiae in *I. japonica* and in branchiae from chaetiger 10 in *I. palpata*).

Distribution. Japan (Imajima & Takeda 1985).

Habitat. 6-180 m depth (Imajima & Takeda 1985).

Inermonephtys palpata **Paxton, 1974**

Figures 40F, 41; Table 17

Inermonephtys palpata Paxton, 1974: 200, figs. 2-6; Rainer and Hutchings 1977: 320; Martin *et al*. 2009: 171, figs. 5 and 6.

Type locality. Bowen (20º03’S, 148º15’E), Queensland, Australia, SW Pacific Ocean.

Remarks. The original description of the species *I. palpata* was based on a single specimen and there are no further records of this species. Martin *et al.* (2009) provided a re-description of this species adding some new characteristics that differentiate it from the other *Inermonephtys* and in particular from *I. brasiliensis*. There are two peculiar characteristics only present in the species *Inermonephtys palpata*. The nuchal organs are divided into three cirriform processes (instead of being only one), and the dorsal and ventral cirri of anterior chaetigers (2-10 and 2-11, respectively) have slender bifid tips. Another unusual characteristic is the spinulation of the preacicular barred chaetae. These chaetae are also present in the species *I. japonica*. However, this species differs from *I. palpata* in having single cirriform processes as nuchal organs and accessory cirrus present in all branchiae (instead of starting only in branchiae from chaetiger 10).

Distribution. Pacific Ocean (Australia) (Rainer & Hutchings 1977).

Habitat. Sand flats, intertidal (Rainer & Hutchings 1977).

Inermonephtys patongi **Nateewathana & Hylleberg, 1986**

Figures 40G, 41; Table 17

Inermonephtys patongi Nateewathana and Hylleberg, 1986: 206, figs. 9A-J and 10.

Type locality. Kamala Bay, Phuket Island, Thailand, E Indian Ocean.

Distribution. Indian Ocean (Thailand) (Nateewathana & Hylleberg 1986).

Habitat. Very fine sand to medium sand, 10-20 m depth (Nateewathana & Hylleberg 1986).

Inermonephtys tetrophthalmus **Rainer & Kally, 1988**

Figures 40H, 41; Table 17

Inermonephtys tetrophthalmus Rainer and Kaly, 1988: 693, figs. 4A-F and 7A.

Type locality. W Australia, E Indian Ocean.

Distribution. Indian Ocean (Australia) (Rainer & Kaly 1988).

Habitat. 40-80 m depth (Rainer & Kaly 1988).

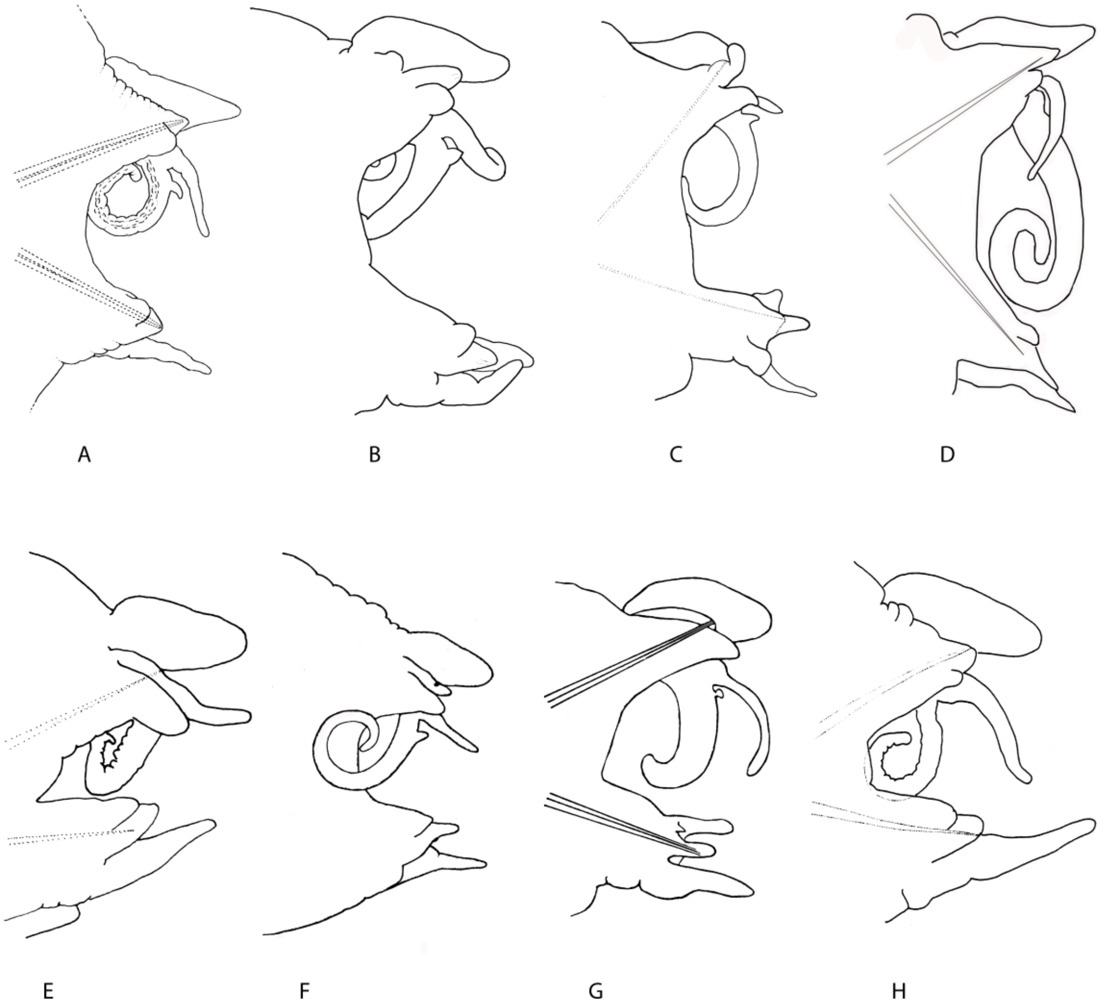


Figure 40. Parapodia of *Inermonephtys*. A. *I. brasiliensis*, median chaetiger, AV (Martin *et al*. 2009); B. *I. foretmontardoi*, chaetiger 30, AV; C. *I. gallardi*, chaetiger 25, AV (Fauchald 1968); D. *I. inermis*, chaetiger 45, AV (Ehlers 1887); E. *I. japonica*, chaetiger 25, AV (Imajima & Takeda 1985); F. *I. palpata*, chaetiger 25, AV (Paxton 1974); G. *I. patongi*, chaetiger 25, AV (Nateewathana & Hylleberg 1986); H. *I. tetrophthalmus*, chaetiger 40, AV (Rainer & Kaly 1988). AV – anterior view.

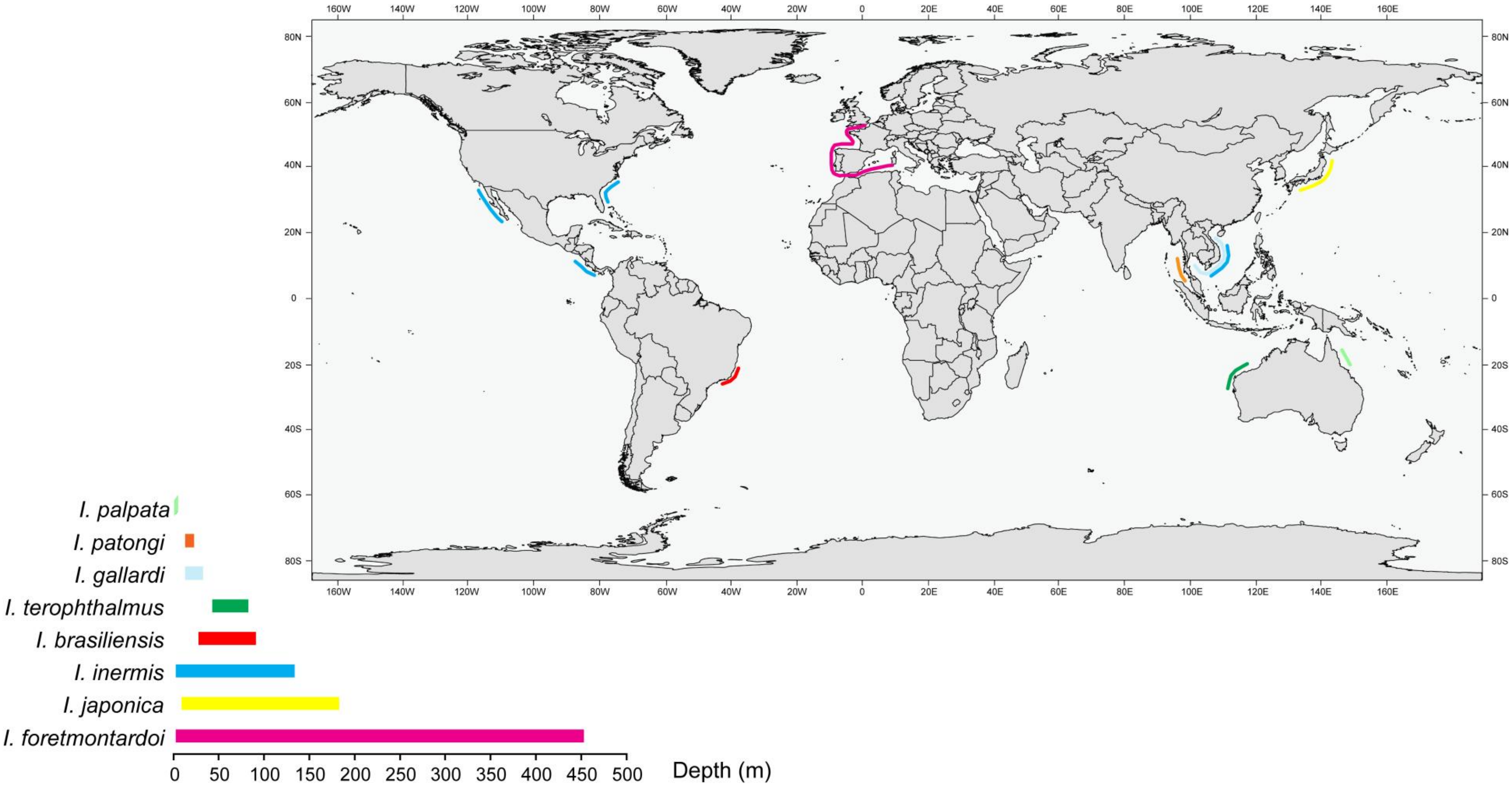


Figure 41. Bathymetrical and geographical distribution of the *Inermonephtys*. The position of the lines is the map is approximate and does not reflect the bathymetric range.

Table 17. Diagnostic characters of *Inermonephtys*. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); AC – branchiae accessory cirrus; Ant – anterior(ly); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; Med – median region; NO – notopodia(l); NE – neuropodia(l); PreCh – preacicular chaetae; PosCh – postacicular chaetae; PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri.

Species	Palps	Branchiae		AcL	Parapodial lamellae			Preacicular chaetae	No. of aciculae	Notes
		From Ch	until		PreL	NO PosL	NE PosL			
I. brasiliensis	Large with small digitate process	3 (AC from 5)	?	Conical	Rounded, < AcL	Elongated, > AcL	Rounded, < AcL	Barred	2	2 kinds of lyriform chaetae present
I. foretmontardoi	Small, cirriform	4 (AC from ?)	?	Conical, pointed	Rounded, < AcL	Ant - rounded; med - elongated, > AcL	Elongated, > AcL	Spinulated	Up to 5	-
I. gallardi	Small, cirriform	15 (AC from 15)	End of body	Conical with distal erect lobe	Conical, ≤ AcL	Rounded, ≤ AcL	Rounded, < AcL	Barred	2	-
I. inermis	Small, cirriform	3-4 (AC from 3-4)	End of body	Conical, pointed	Poorly developed	Elongated, > AcL	Rudimentary	Spinulated	Up to 3	-
I. japonica	Large with small distal pap.	2 (AC from 2)	?	Conical with distal erect lobe	Conical, ≥ AcL	Ellipsoid, rounded, > AcL	Rounded, < AcL	Barred with spinulation	2	-
I. palpata	Large with small digitate process	2 (AC from 10)	last 6	With distal erect lobes	Elongated, ≥ AcL	Elongated, > AcL, inflated in anterior Ch	Rounded, < AcL	Barred with spinulation	2	Nuchal organs as 3 cirriform processes; ant DC and VC with bifid tips
I. patongi	Tiny	6-7 (AC from 6-7)	End of body	Digitiform	Conical, > AcL	Elongated, > AcL	Rudimentary	Barred	2	2 pairs of prostomial eyes
I. tetrophthalmus	Small, cirriform	2 (AC in ant. Ch only)	End of body	Conical	Rounded, < AcL	Ellipsoid, rounded, > AcL	Rounded, < AcL	Spinulated	Up to 4	2 pairs of prostomial eyes

Micronephthys **Friedrich, 1939**

Type species. *Micronephthys minuta* (Théel, 1879), by monotypy.

Micronephthys abranchiata **(Ehlers, 1913)**

Figure 43; Table 18

Nephthys abranchiata Ehlers, 1913: 452, pl. 28, figs. 7-11.
Nephtys abranchiata Hartman 1964: 105.

Type locality. Wilhelm II coast, Antarctic, 385 m depth.

Distribution. Antarctic Ocean (Ehlers 1913).

Habitat. 385 m depth (Ehlers 1913).

Micronephthys ambrizettana **(Augener, 1918)**

Figures 42A, 43; Table 18

Nephthys ambrizettana Augener, 1918: 166, pl. 2, fig. 13, pl. 3, figs. 60 and 61.
Nephtys (Micronephthys) ambrizettana Day 1967: 349.

Type locality. Ambrizette, Angola, W Africa, E Atlantic Ocean.

Remarks. *Micronephthys ambrizettana* is known only from the type locality and a complete description including pharynx characteristics is lacking.

Distribution. Atlantic Ocean (Angola) (Day 1967).

Habitat. No information in literature.

Micronephthys hartmannschroederae **Jirkov & Dnestrovskaya in Jirkov 2001**

Figures 42B, 43; Table 18

Micronephthys hartmannschroederae Dnestrovskaya and Jirkov, 2001: 190.

Type locality. Kieler Bucht, N Germany, Baltic Sea.

Remarks. *Micronephthys hartmannschroederae* was recently described by Dnestrovskaya and Jirkov (2001) for the Baltic Sea. It differs from the other *Micronephthys* species by the presence of two kinds of postacicular chaetae (spinulose and serrated) and the higher number of chaetigers with branchiae. This species is known only from the type locality but, according to Dnestrovskaya and Jirkov (2001), is probably widely distributed in the North Sea and boreal Atlantic.

Distribution. Baltic Sea (Dnestrovskaya & Jirkov 2001).

Habitat. No information in literature.

***Micronephthys minuta* (Théel, 1879)**

(see chapter 3.1, pg. 79)

***Micronephthys oculifera* Mackie, 2000**

Figures 42C and D, 43; Table 18

Micronephthys oculifera Mackie, 2000: 518, figs. 1-4.
Nephthys (Micronephthys) sphaerocirrata Gibbs 1971: 155.

Type locality. Hoi Ha Wan, Hong Kong, China, E Atlantic Ocean.

Material examined. Pacific Ocean, China, Hong Kong: Wong Chuk Kok Tsui (Bluff Head), near northern entrance to Tolo Channel, 12 m, 16 Apr 1986, 3 complete and 2 incomplete spms, paratypes (NMWZ 1986.079.0161). Solomon Islands, New Georgia: Marovo Lagoon, 15 m depth, 1 incomplete spm (NHM 1970.396 as *M. sphaerocirrata*).

Remarks. *Micronephthys oculifera* clearly differ from other *Micronephthys* species by the presence of two pairs of large eyes in the prostomium and the warts in the proximal region of the pharynx. Only two species of *Micronephthys* are reported from W Pacific Ocean, *M. oculifera* and *M. sphaerocirrata*, the latter with a southern distribution (E Australia) (Figure 43).

Distribution. Pacific Ocean (China; Solomon Islands) (Gibbs 1971; Mackie 2000).

Habitat. Sandy sediments, 2-15 m depth (Gibbs 1971; Mackie 2000).

Micronephthys sphaerocirrata **(Wesenberg-Lund, 1949)**

(see chapter 3.1, pg. 81)

Micronephthys sphaerocirrata orientalis **Lee and Jae, 1983**

Micronephthys sphaerocirrata Fauchald 1968: 17, figs. 36-40.
Micronephthys sphaerocirrata orientalis Lee and Jae, 1983: 20, fig. 2, pl. 1A-F; Imajima and Takeda 1985: 63, fig. 3A-H.

Type locality. W South Korea, Yellow Sea, W Pacific Ocean.

Remarks. This subspecies is here considered separately from *M. sphaerocirrata* because of the different morphology and geographical distribution. The subspecies *M. s. orientalis* has 12-15 pharynx papillae per row instead of 6-9/8-11, and well developed preacicular lamellae (equal in length to the acicular lobes) rather than rudimentary. *Micronephthys sphaerocirrata orientalis* occur in the northern part of the Pacific Ocean (from Japan to Viet Nam), while the other specimens of *M. sphaerocirrata* occur in the southern part (Australia) and have a wider distribution including South Atlantic and Indian Oceans. All specimens have similar body sizes (considering the ratio between the number of segments and body length).

Distribution. Pacific Ocean (Japan, Korea, Viet Nam) (Lee & Jae 1983; Imajima & Takeda 1985).

Habitat. Silty sand, 6-150 m depth (Lee & Jae 1983; Imajima & Takeda 1985).

Micronephthys stammeri **(Augener, 1932)**

(see chapter 3.1, pg. 85)

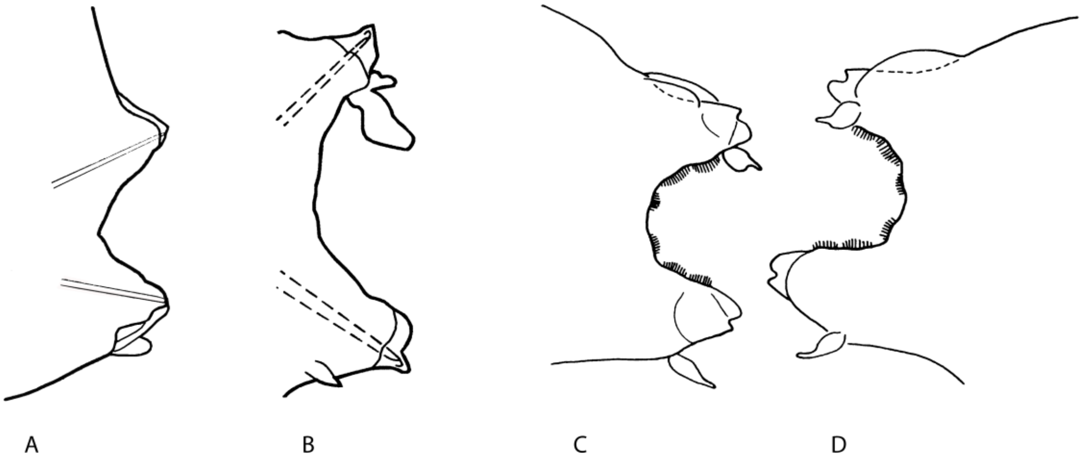


Figure 42. Parapodia of *Micronephthys*. A. *M. ambrizettana*, chaetiger 15, AV (Augener 1818); B. *M. hartmannschroderae*, chaetiger 10, AV (Jirkov & Dnestrovskaya 2001); C. *M. oculifera*, chaetiger 21, AV (Mackie 1998); D. *M. oculifera*, chaetiger 21, PV (Mackie 1998). AV – anterior view; PV – posterior view.

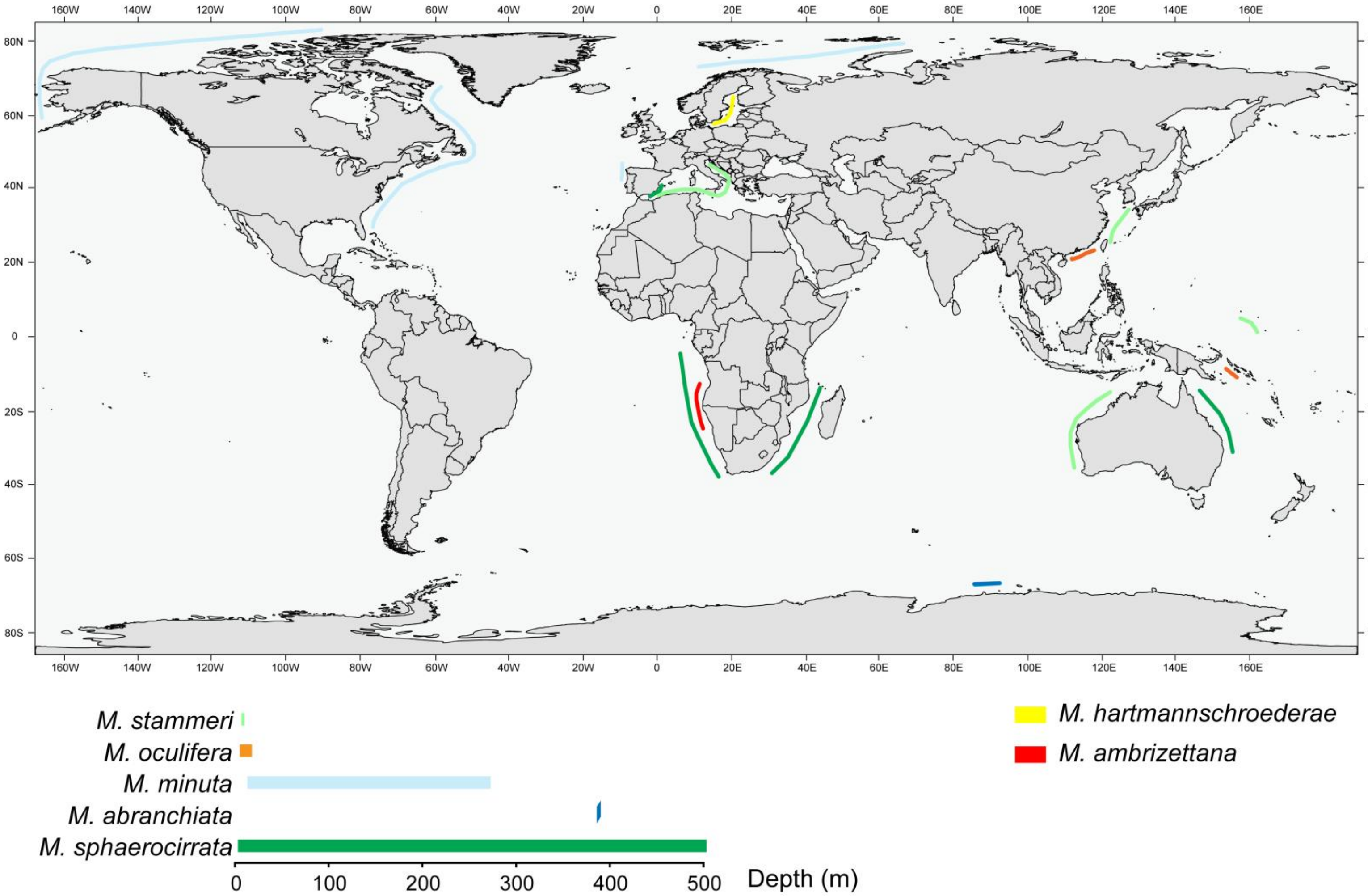


Figure 43. Bathymetrical and geographical distribution of the *Micronephthys*. The position of the lines is the map is approximate and does not reflect the bathymetric range. There is no information available in literature on the bathymetric distribution of *M. ambrizettana* and *M. hartmannschroederae*.

Table 18. Diagnostic characters of *Micronephthys*. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; NO – notopodia(l); NE – neuropodia(l); PreCh – preacicular chaetae; PosCh – postacicular chaetae; PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri. Pharynx subterminal papillae (| , # rows (# pap.), Δ): | - middorsal papilla present, number of rows (number of papillae per row), Δ - proximal papillae arranged in triangular groups.

Species	Eyes	Parapodial lamellae		DC	Lyriform chaeta	Pharynx	Notes
		PreL	PosL			Subterminal papillae	
M. abranchiata	Not visible	Poorly developed	Poorly developed	Absent ?	?	20 (4-5)	--
M. ambrizettana	? Behind prostomium	Rudimentary	Rounded, < AcL	Absent	Absent ?	?	VC small
M. hartmannschroederae	Absent ?	Rudimentary	Rudimentary	Conical	Absent	20 (2-5/6)	Br. present on 14-15 Ch (from 5-6 to 19); 2 kinds of PosCh
M. minuta	1 pair on Ch 3	Rudimentary	Rudimentary	Conical	Absent	Long | , 18-20 (3-6)	Br present on 3-9 Ch (from 6-9 to 10-14)
M. oculifera	2 pairs on prostomium, big	Poorly developed	Rounded, < AcL	Subsphaerical with cirriform tip	Present from Ch 3-4	22 (6-10)	Pharynx proximal region with warts
M. sphaerocirrata	1 pair on Ch 2-3	Rudimentary	Rounded, < AcL	Subsphaerical	Present from Ch 3	22 (8-11)	--
M. stammeri	2 pairs on Ch 3, big	Rudimentary	Rudimentary	Subsphaerical	Present from Ch 3	20-22 (about 8)	Special chaetae present on Ch 1

Nephtys Cuvier, 1817 in Audouin & Milne Edwards, 1833

Aonis Savigny, 1822 (erected for *Nereis caeca* Fabricius, 1780).
Nephthys Savigny, 1822 (misspelling of *Nephtys*).
Diplobranchus Quatrefages, 1865 (erected for *Nereis ciliata* Müller, 1776**)**.
Portelia Quatrefages, 1865 (type species: *P. rosea* Quatrefages, 1865).
Dentinephtys Imajima and Takeda, 1987 (type species: *D. glabra* Imajima and Takeda, 1987).

Type species. *Nephtys hombergii* Savigny, 1822 by subsequent designation (first designation unclear, if not previously so at least by Hartman (1959)).

Nephtys acrochaeta Hartman, 1950

Figures 45A, 46; Table 19

Nephtys acrochaeta Hartman, 1950: 114, pl. 16, figs. 1-6; Hartman 1953: 33, fig. 9A-F; Fauchald 1976: 18, fig. 1D-E; Lana 1986: 138, figs. 1-3; Rizzo and Amaral 2007: 257, fig. 2.

Type locality. Off Rio Grande do Sul (39º00'S, 51°10'W), Brazil, W Atlantic Ocean, 80 m depth.

Material examined. Atlantic Ocean, Brazil: 23°45.28'S, 45°13.43'W, 20 m, 22 Apr 2001, 1 incomplete spm (ZUEC BPO-AR803).

Remarks. This species was originally described by Hartman (1950) for specimens apparently collected from off Uruguay. However, the coordinates of the type locality correspond to the shelf off Rio Grande do Sul in Brazil (Lana 1986).

Hartman (1950) described the pharynx has having about 21 longitudinal rows of 2-3 subterminal papillae distally which are replaced medially by 14 rows of 7-9 subterminal papillae. Rizzo and Amaral (2007) examined a partially everted pharynx and described 14 rows of at least six subterminal papillae. It seems that these later authors only examined the median part of the pharynx and thus overlooked the shorter distalmost rows of papillae. Taking in account that nephtyids usually have a paired number of rows of papillae the pharynx of this species is here considered to have 20 or 22 rows of 2-9 subterminal papillae.

Nephtys acrochaeta resembles *N. serratifolia* in the morphology of the parapodia, including the dorsal prolongations at the base of parapodia, and spinulose postacicular chaetae with a spur at the base. However, the chaetiger where branchiae start is 9-10 in *N. acrochaeta* and 3-4 in *N. serratifolia*. Specimens of *N. serratifolia* were not examined in this study. Hartmann-Schröder (1965) suggested *N. acrochaeta* to be a synonym of *N. serratifolia* but did not formally synonymised the two species.

The acutely pointed acicular lobes together with the subterminal papillae arrangement in the pharynx place this species close to the *Aglaophamus* species. The position of this species in the nephtyid family should be reviewed in future studies.

Distribution. Atlantic Ocean (Brazil) (Fauchald 1976; Lana 1986; Rizzo & Amaral 2007).

Habitat. Mud with organic enrichment, fine to very fine sand and sandy mud with shells, 4-88 m depth (Fauchald 1976; Lana 1986; Rizzo & Amaral 2007).

Nephtys assignis **Hartman, 1950**

Figures 51A, 52; Table 21

Nephtys assignis Hartman, 1950: 112, pl. 14, figs. 1-6; Hartman 1968; Banse and Hobson 1968: 17; Banse 1972: 215, fig. 10A-C; Banse and Hobson 1974; Hilbig 1997: 330, fig. 13.5.
Nephtys discors Pettibone 1954: 270 (partim); Imajima 1961: 89, fig. 6A-D; cf. Imajima and Takeda 1987: 70, fig. 15A-I (not Ehlers, 1868).

Type locality. Santa Catalina Channel, California, E Pacific Ocean, 84-95 fms depth.

Remarks. *Nephtys assignis* is very close to *N. rickettsi*. The two species also have similar geographical and bathymetric distributions (Figure 46, 52). These species appear to differ only by the presence of a neuropodial supracicular lobe on the anterior parapodia of *N. rickettsi*, which was not mentioned for *N. assignis* specimens. According to Banse (1972) the geographical distribution of *N. discors* in the NE Pacific Ocean given by Pettibone (1954) refers to *N. assignis* and *N. rickettsi*. That author reports the presence of both species in the NE Pacific Ocean without comment about their distinction. Banse (1972) examined the specimen of *N. discors* from

Okhotsk Sea (Imajima, 1961) and synonymised it with *N. assignis* without further comments. The Japanese specimen ascribed to *N. discors* by Imajima and Takeda (1987) appears to belong to the same species as the one from Okhotsk Sea and therefore is herein also ascribed to *N. assignis*. The distinctive characteristics between this two species need further elucidation.

Distribution. Pacific Ocean (Washington to California, Mexico, Guatemala; Okhotsk Sea) (Hartman 1950; Hilbig 1997; Banse 1972). *N. discors* (Imajima & Takeda 1987) is here synonymised with *N. assignis* pending on further confirmation, thus extending the distribution to Japan.

Habitat. Sand and Mud, 4-200 m depth (Hartman 1950; Hilbig 1997).

***Nephtys assimilis* Örsted, 1843**

(see chapter 3.1, pg. 87)

***Nephtys bilobatus* Kudenov, 1975**

Figures 45B, 46; Table 19

Nephtys bilobatus Kudenov, 1975: 80, figs. 31-35.

Type locality. Bahía Cholla, Puerto Peñasco, Gulf of California, Mexico, W Pacific Ocean.

Remarks. According to Kudenov (1975), *N. bilobatus* differ from all other *Nephtys* species by having two neuropodial superior lobes on chaetigers 4-30, and by the preacicular chaetae of the first four segments that are unusually longer than the postacicular ones. This species is only known from the original description.

Distribution. Pacific Ocean (Mexico) (Kudenov 1975).

Habitat. Sand, intertidal (Kudenov 1975).

***Nephtys brachycephala* Moore, 1903**

Figures 51B, 52; Table 21

Nephthys brachycephala Moore, 1903: 431; Izuka 1912: 217; Uschakov 1955: 216, fig. 69F and G; Imajima and Hartman 1964: 156; Berkeley 1966: 842; Imajima and Takeda 1987: 52.

Type locality. Sagami Bay, Japan, West Pacific Ocean, 320-347 m depth.

Remarks. *Nephtys brachycephala* was originally described from Sagami Bay and was only recorded a few times afterwards from Japan (Imajima & Hartman 1964), Okhotsk Sea (Ushakov 1955) and British Columbia (Berkeley 1966). This species can be easily distinguished from the other *Nephtys* by the shape of the branchiae (Figure 51B).

Distribution. Pacific Ocean (Okhotsk Sea, Japan; British Columbia) (Moore 1903; Uschakov 1955; Berkeley 1966; Imajima & Takeda 1987).

Habitat. 146-347 m depth (Moore 1903; Berkeley 1966; Imajima & Takeda 1987).

Nephtys brevibranchis **Hartmann-Schröder, 1959**

Figures 45C, 46; Table 19

Nephtys brevibranchis Hartmann-Schröder, 1959: 145, figs. 118-121; Molina-Lara and Vargas-Zamora 1995.

Type locality. Punta San Juan (Estero Jiquilisco), El Salvador, E Pacific Ocean.

Distribution. Pacific Ocean (El Salvador) (Hartmann-Schröder 1959; Molina-Lara & Vargas-Zamora 1995).

Habitat. Sand and muddy sand (Hartmann-Schröder 1959).

Nephtys bruuni **Kirkegaard, 1995**

Figures 49A, 50; Table 22

Nephtys bruuni Kirkegaard, 1995: 38, fig. 22.

Type locality. W New Zealand (42°10’S, 170°10’E), 610 m depth.

Distribution. Pacific Ocean (off W New Zealand) (Kirkegaard 1995).

Habitat. 610 m depth (Kirkegaard 1995).

Nephtys bucera **Ehlers, 1868**

Figures 45D, 44; Table 19

Nephthys bucera Ehlers, 1868: 617, pl. 23, fig. 8; Verrill and Smith 1874: 122 and 289, pl. 12, fig. 58; Verrill 1881: 296 and 300; Webster and Benedict 1884: 702; Andrews 1891: 280; Sumner *et al.* 1913: 619 (partim); Hartman 1938a: 9, pl. 1, fig. 1; Hartman 1944a: 339, not pl. 15, figs. 3 and 4 (= *N. picta*); Hartman 1950: 105; Hartman 1951: 49; Pettibone 1963: 196, figs. 49D, 50A, B and 51D; Perkins and Savage 1975.
Nephtys picta McIntosh 1900: 266, pl. 7, figs. 3-5 and 8, pl. 8, figs. 9-11; Whiteaves 1901: 83; Treadwell 1948: 23, fig. 10B and C (not Ehlers, 1868).

Type locality. Isle of Shoals, New Hampshire?, W Atlantic Ocean.

Remarks. *Nephtys bucera* and the close related species *N. picta* were first described by Ehlers (1868) from NE coast of North America. McIntosh (1900) synonymised *N. bucera* with *N. picta* although recognising some small differences in parapodial morphology. Hartman (1950) compared the holotype of *N. bucera* with specimens of *N. picta* from North Carolina and considered them again as separate species. Apart for being morphologically very similar, the two species have the same geographical and bathymetric distribution, although they seem to prefer different sediment conditions. *Nephtys picta* inhabits a variety of sediments from gravely sand to muddy sand, while *N. bucera* seems to prefer clean sand. The two species can be distinguished by the characteristic pigmentation of *N. picta*, the length of chaetae (long on *N. bucera*, shorter in *N. picta*), and the presence of a basal expansion on the dorsal cirri of *N. bucera*. Also the chaetiger where branchiae start and the number of subterminal papillae per row in the pharynx differ slightly in the two species. On *N. picta* the branchiae start on chaetigers 3-4 and the pharynx has up to 5-6 papillae per row. On *N. bucera* the branchiae start on chaetigers 4-8 and the pharynx has 6-8 papillae per row (Table 19).

Distribution. Atlantic Ocean (Gulf of St Lawrence to North Carolina, Gulf of Mexico) (Hartman 1950; Pettibone 1963).

Habitat. Mainly in clean sand, low water to 179.2 m depth (Pettibone 1963; Taylor 1984).

***Nephtys caeca* (Fabricius, 1780)**

(see chapter 3.1, pg. 95)

***Nephtys caecoides* Hartman, 1938**

Figures 45E, 46; Table 19

Nephtys caecoides Hartman, 1938b: 148, fig. 63; Hartman 1940: 240; Hartman 1944c: 250; Berkeley and Berkeley 1945: 326; Hartman 1950: 101; Hernández-Alcántara and Solís-Weiss 1991; Hilbig 1997: 332, fig. 13.6; Lovell 1997: 352, fig. 2; Hernández-Alcántara and Solís-Weiss 1999.
Nephtys coeca Johnson 1901: 401 (partim); Treadwell 1914: 192 (partim).
Nephthys caeca Moore 1909: 243 (partim); Moore 1911: 243 (partim) (not Fabricius, 1780: 304).
? *Nephthys caeca* Treadwell 1914: 192 (partim); Hilton 1919: 27.
Nephthys malmgreni Treadwell 1914: 192 (partim) (not Théel, 1879).
Nephthys assimilis Treadwell 1914: 192 (partim); Berkeley 1924: 290 (not Malmgren, 1865).

Type locality. Tomales Bay, California, USA, E Pacific Ocean.

Material examined. Pacific Ocean, USA, California: San Francisco Bay, 37º75’N, 122º25’W, intertidal, 31 Mar 2001, 1 fragmented spm (CASIZ 154226).

Remarks. *Nephtys caecoides* is morphologically very similar to *N. californiensis*, differing only by the shape and proportions of some structures like nuchal organs, postchaetal lamellae and dorsal and ventral cirri, by the prostomial pigmentation patterns, the chaetiger were branchiae start (4 in *N. caecoides*, 3 in *N. californiensis*), and the presence of a middorsal subterminal papilla on the pharynx of *N. caecoides* (absent on *N. californiensis*). Also *N. caecoides* is considerably smaller than *N.*

californiensis. The two species co-occur in the same geographical area and depths, though they seem to occupy distinct habitats. *N. californiensis* occurs on exposed beaches with sandy sediment, whereas *N. caecoides* occurs in sheltered muddy areas (Hartman 1938b; Clark and Haderlie 1962).

According to Hartman (1938), *N. caecoides* replaces the polar species *N. caeca* in more temperate waters of eastern Pacific. The two species differ mainly on the size of postchaetal lamellae (much larger in *N. caeca*) and the presence of warts on the proximal part of pharynx in *N. caeca*. *Nephtys caecoides* is notably smaller than *N. caeca* (Hartman 1938b).

Distribution. Pacific Ocean (S Canada to Mexico) (Hilbig 1997; Lovell 1997).

Habitat. Sand, muddy sand and mud, intertidal to 110 m depth (Hilbig 1997; Lovell 1997).

***Nephtys californiensis* Hartman, 1938**

Figures 45F, 46; Table 19

Nephtys californiensis Hartman, 1938b: 150, fig. 64; Hartman 1940: 240; Hartman 1944c: 251; Berkeley and Berkeley 1948: 53, figs. 78 and 79; Hartman 1950: 103; Hartman 1968: 579; Banse and Hobson 1974: 75, fig. 19G-H; Hernández-Alcántara and Solís-Weiss 1991; Bastida-Zavala 1993; Hilbig 1997: 334, fig. 13.7; Lovell 1997: 354, fig. 3; Hernández-Alcántara and Solís-Weiss 1999.
? *Nephtys californiensis* Uschakov and Wu 1962: 8-9, fig. 3A-D; Uschakov and Wu 1979: 53, fig. 17A-D; Imajima and Takeda 1987: 68, figs. 13A-N and 14; Jung and Hong 1997: 379, figs. 6 and 7; Rizzo and Amaral 2007: 259, fig. 3.
Nephthys caeca Moore 1909: 243 (partim).
? *Nephthys caeca ciliata* Berkeley 1935: 770.
? *Nephthys caeca* var. *ciliata* Okuda 1939: 231, fig. 6.
? *Nephthys assimilis* Treadwell 1914: 193 (partim).
? *Nephtys simoni* Lana 1986: 141, figs. 8 and 9 (not Perkins, 1980).

Type locality. Dillon beach, California, USA, E Pacific Ocean.

Material examined. Atlantic Ocean, Brazil: Praia da Fazenda, 23º22.062’S, 44º50.170’W, intertidal, 21 May 2001, 1 complete spm (ZUEC BPO-AR792); 23º22.011’S, 44º50.197’W, intertidal, 9 May 2001, 1 complete spm (ZUEC BPO-AR807); 23º22.010’S, 44º50.197’W, intertidal, 13 Nov 2001, 1 complete spm (ZUEC BPO-AR837).
Pacific Ocean, USA, California, San Francisco Bay: Standard Oil Spill Survey 1971, 37º39.30’N, 122º22.18’W, 7 Jul 1972, 1 complete spm (CASIZ 141778).

Remarks. *Nephtys californiensis* was originally described by Hartman (1938) from California, and is commonly found in clean sands within this region and adjacent areas. Imajima and Takeda (1987) and Jung and Hong (1997) reported this species from Japan, Korea and China and synonymised *Nephthys caeca* var. *ciliata* Okuda, 1939 from Onagawa Bay (Japan) with it. Even though the geographical locations are very different, these authors did not comment further on these specimens. According to the descriptions of Imajima and Takeda (1987) and Jung and Hong (1997), the specimens from Japan and Yellow Sea are in fact very similar to *N. californiensis* from California. However, the former are smaller in size, have smaller branchiae and show differences in the shape of acicular lobes. The acicular lobes in *N. californiensis* are bilobed throughout the body, while in the specimens from Japan and Yellow Sea only the median parapodia acicular lobes (from about chaetiger 20-25 to 60) are bilobed. Considering these differences and the geographical distance, the records from Japan and Yellow Sea should be regarded with caution until further investigation is carried out.

Nephtys californiensis was also recorded from Brazil by Rizzo and Amaral (2007). Some of those Brazilian specimens were examined within this study and I could confirm that branchiae start on chaetiger 4 instead of 3 (as mentioned by the authors). Lana (1986) ascribed some Brazilian specimens to *N. simoni* and these were doubtfully synonymised with *N. californiensis* by Rizzo and Amaral (2007). According to Lana (1986) in those specimens the branchiae start on chaetiger 3. Hartman (1950) remarked some variability in this character for *N. californiensis* specimens from California. However, Hilbig (1997) stated that the specimens reported by Hartman (1950) with branchiae starting on chaetiger 4 are probably *N. caecoides*. The Brazilian specimens identified as *N. magellanica* by Fauchald (1976) were examined in this study and also seem to be similar to the specimens reported by Rizzo

& Amaral (2007). They have branchiae starting on chaetiger 3 and a long middorsal papillae in the pharynx, which is absent in *N. californiensis*. Nevertheless, the description given by Fauchald (1976) is very short and does not allow taking any conclusion. Records of *N. californiensis* from Brazil should thus be considered with caution until further investigation.

Distribution. Atlantic Ocean (Gulf of Mexico); Pacific Ocean (British Columbia to Mexico) (Banse & Hobson 1974; Hilbig 1997; Imajima & Takeda 1987). There are further reports of this species from Brazil (Rizzo & Amaral 2007), Korea, Japan and China (Okuda 1939; Uschakov & Wu 1962, 1979; Imajima & Takeda 1987; Jung & Hong 1997), but these records require confirmation.

Habitat. Exposed beaches in clean sand or silty sand, intertidal to 55 m depth (Hartman 1938b; Hartman 1940). In the Yellow Sea the species is reported from muddy sand at 5-74 m depth (Imajima & Takeda 1987; Jung & Hong 1997) and in Brazil from sandy beaches at intertidal to 45 m depth (Rizzo & Amaral 2007). There are further reports of this species until depths of 330 m (Hilbig 1997; Lovell 1997), but these records require confirmation.

***Nephtys capensis* Day, 1953**

Figures 47B, 48; Table 20

Nephtys capensis Day, 1953: 431, fig. 5G-M; Hartmann-Schröder 1974.
Nephtys (Nephtys) capensis Day 1967: 344, fig. 15.2A-F.
? *Nephtys capensis* Hernández-Alcántara and Solís-Weiss 1999.

Type locality. Woodstock beach, Table Bay, South Africa, SE Atlantic Ocean.

Material examined. Atlantic Ocean, South Africa, Cape Peninsula: 1 complete and 1 incomplete spms, paratypes (NHM 1961.16.29-30).

Remarks. The paratypes of *N. capensis* were examined within this study and the number of the pharynx subterminal papillae per row is here emended to 3-7 (instead of six). This species dimly resembles *N. hombergii* in the large neuropodial postchaetal lamellae. However the two species differ in the shape of prechaetal lamellae (bilobed in *N. hombergii*, rudimentary on notopodiae of *N. capensis*), the number of subterminal papillae on the pharynx (2-5 in *N. hombergii*, 3-7 in *N. capensis*), and the presence of two kinds of postacicular chaetae in *N. capensis*.

Distribution. Atlantic Ocean (South Africa) (Day 1953). There is one report of this species for the Gulf of California (Hernández-Alcántara and Solís-Weiss 1999) but this record is doubtful and requires confirmation.

Habitat. Estuaries and lagoons (Day 1953).

***Nephtys chemulpoensis* Jung & Hong, 1997**

Figures 49B, 50; Table 22

Nephtys chemulpoensis Jung and Hong, 1997: 377, figs. 4A-H and 5A-D.

Type locality. Chokchon station, Tongchun-Dong, Inchon, Korea, Yellow Sea, W Pacific Ocean.

Distribution. Pacific Ocean (Yellow Sea, Korea) (Jung & Hong 1997).

Habitat. Mud and sand with high mud content, intertidal (fairly abundant at the upper intertidal) (Jung & Hong 1997).

***Nephtys ciliata* (Müller, 1776)**

(see chapter 3.1, pg. 100)

***Nephtys cirrosa* Ehlers, 1868**

(see chapter 3.1, pg. 104)

***Nephtys cryptomma* Harper, 1986**

Figures 45G, 46; Table 19

Nephtys cryptomma Harper, 1986: 1, figs. 1-4.

Type locality. Freeport (28º44’N, 95º15’W), Texas, Gulf of Mexico, W Atlantic Ocean, 21 m depth.

Remarks. *Nephtys cryptomma* shows some similarities with *N. simoni* reported from the same geographical areas. According to Harper (1986) some specimens previously identified as *N. simoni* may belong to *N. cryptomma*. *Nephtys cryptomma* differs from *N. simoni* in having conical acicular lobes rather then slightly bilobed, larger prechaetal lamellae, and broadly rounded postchaetal lamellae extending well beyond acicular lobes on anterior parapodia but gradually reducing in size from mid-body to the posterior end. In *N. simoni*, postchaetal lamellae are more elongated rather than oval-shaped, and much larger than acicular lobes on anterior and middle parapodia (Figure 45Y).

Distribution. Atlantic Ocean (Virginia to Gulf of Mexico) (Harper 1986).

Habitat. Sand and muddy sand, 16-36 m depth (Harper 1986).

***Nephtys discors* Ehlers, 1868**

Figures 45H, 46; Table 19

Nephthys discors Ehlers, 1868: 626, pl. 23, fig. 39 and 40; Webster and Benedict 1887: 709; Hartman 1938a: 9, pl. 1, figs. 2 and 3; Hartman 1950: 96; Pettibone 1954: 270, fig. 30M (partim); not Imajima 1961: 89, fig. 6A-D; Pettibone 1963: 203, fig. 51E-F (partim); Banse 1972: 217, fig. 10F; not Imajima and Takeda 1987: 70, fig. 15A-I.

Type locality. Eastport, Maine, E coast of USA, NW Atlantic Ocean.

Remarks. *Nephtys discors* was originally described from Maine and has been reported from the type locality and adjacent areas in the western Atlantic Ocean by several authors (Webster & Benedict 1887; Hartman 1950; Pettibone 1963). Pettibone (1954, 1963) extended the distribution of this species to the northwestern coast of America in the Pacific Ocean. According to Banse (1972), the distribution of *N. discors* in the Pacific Ocean given by Pettibone (1954, 1963) refers to the species *N. rickettsi*. Later Imajima (1961) and Imajima and Takeda (1987) reported *N. discors* from Okhotsk Sea and Japan, respectively. Furthermore, Imajima and Takeda (1987) synonimized *N. rickettsi* with *N. discors*. However, those authors refer to the pharynx as being proximally smooth which is not true for *N. discors*. Furthermore, the authors present a figure of a posterior parapodium with well-developed branchia, while in *N. discors* the branchiae are rudimentary in the posterior half of the body. Therefore, the records by Imajima (1961) and Imajima and Takeda (1987) probably refer to *N. rickettsi* or *N. assignis* as already mentioned by Banse (1972). *Nephtys discors* distribution is thus restricted to the NW Atlantic Ocean.

Distribution. Atlantic Ocean (Gulf of St. Lawrence to Maine) (Hartman 1950; Banse 1972).

Habitat. Mud (?), low water (11 m depth) (Pettibone 1963).

Nephtys ectopa **Chamberlin, 1919**

Figures 45I, 46; Table 19

Nephthys ectopa Chamberlin, 1919: 94, pl. 15, figs. 1-7; Treadwell 1923: 6.

Type locality. Off Aguja Point (5° 46' S, 81° 31.9' W), Peru, E Pacific Ocean, 1865 m depth.

Remarks. *Nephtys ectopa* was originally described from Peru by Chamberlin (1919), who provided a very incomplete description, without mentioning the chaetigers where branchiae appear. Treadwell (1923) reported its occurrence in S California, at 868.7 m depth, although with doubts due to the poor preservation of the specimen, and without providing further comments or details. The holotype of this species should thus be re-examined for a complete description.

Distribution. Pacific Ocean (Peru) (Chamberlin 1919).

Habitat. Dark brown mud, 1865 m depth (Chamberlin 1919).

Nephtys ferruginea **Hartman, 1940**

Figures 45J, 46; Table 19

Nephtys caecoides ferruginea Hartman, 1940: 241, pl. 42, figs. 110-114; pl. 43, fig. 115.

Nephtys ferruginea Berkeley and Berkeley 1945: 327; Hartman 1950: 102; Hartman 1963; Hartmann-Schröder 1965: 140; Hartman 1967: 81, pl. 27; Hartman 1968; Fauchald 1972: 91; Banse and Hobson 1974: 75, fig. 19k-l; Hilbig 1997: 339, fig. 13.9; Lovell 1997: 356, fig. 4B, 5 and 6.
Nephtys (Nephtys) ferruginea Rozbaczylo and Castilla 1974: 193, figs. 4A and 5A.
Nephtys malmgreni Treadwell 1914: 192 (partim).
Nephtys californiensis Hartman 1950: 103 (partim).
Nephtys signifera Hilbig 1992: 719, fig. 5A (partim); Hilbig 1997: 344, fig. 13.12A, C and D.

Type locality. Independencia Bay, Peru, E Pacific Ocean.

Material examined. Pacific Ocean, San Francisco Bay, California: RV *Long Fin*, 5.20 m, 8 Jul 2002, 1 fragmented spm (CASIZ 170852); RV *Cordell*, 37º 86’N, 122º42’W, 5 m, 7 Mar 2003, 1 complete spm (CASIZ 164727).

Remarks. *Nephtys ferruginea* was first described as *Nephtys caecoides ferruginea* by Hartman (1940). Later Berkeley & Berkeley (1945) elevated it from subspecific to specific rank without providing any additional information. Specimens from Ballast point identified as *A. malmgreni* by Treadwell (1914) were re-examined by Hartman (1950) and referred to this species. Lovell (1997) re-examined the type material of *N. signifera* and found juveniles of *N. ferruginea* (holotype and most of paratypes), *N. cornuta* (2 paratypes) and *Aglaophamus* indet. (1 paratype), thus synonymizing *N. signifera* with *N. ferruginea*. He also reported the presence of *N. ferruginea* specimens among the material of *N. californiensis* examined by Hartman (1950).

Nephtys ferruginea is very easily recognised by its typical pigmentation pattern on the dorsum (longitudinal bars of rust-colour pigment along the sides of the segments). However, pigment tends to fade in alcohol and smaller specimens are sometimes entirely unpigmentated (Hilbig 1997). In such cases, the specimens may be mistaken by *N. californiensis* that also occurs in the same geographical area. *Nephtys ferruginea* differs from *N. californiensis* by the presence of middorsal subterminal papilla, the slightly smaller size of the postchaetal lamellae and the shape of acicular lobes, which are distinctly bilobed in anterior parapodia becoming conical in posterior ones (instead of being bilobed throughout all body as in *N. californiensis*).

Distribution. Pacific Ocean (British Columbia to Chile) (Rozbaczylo & Castilla 1974; Lovell 1997). There are further reports of this species from Shag Rocks (S Atlantic Ocean) (Hartman 1967), but these records require confirmation.

Habitat. Sand, mud, silt and clay, 16-500 m depth (Hartmann-Schröder 1965; Lovell 1997). There are further reports of this species from deep-water off Mexico (Fauchald 1972) and from 3403-3484 m depth in Shag Rocks (Hartman 1967), but these records require confirmation.

Nephtys fluviatilis **Monro, 1937**

Figures 45K, 46; Table 19

Nephthys fluviatilis Monro, 1937: 246, fig. 2A-C; Orensanz and Estivariz 1971: 101, figs. 23-31; Orensanz and Gianuca 1974: 10; Lana 1986: 140, figs. 6 and 7.

Type locality. Arroyo de Pando, Canelones, Uruguay, W Atlantic Ocean.

Material examined. Atlantic Ocean, Uruguay: Arroyo de Pando, Canelones, 1 incomplete spm, holotype (NHM 1937.4.22.3).

Distribution. Atlantic Ocean (Brazil to Argentina) (Lana 1986).

Habitat. Mud, shallow waters (intertidal to 5 m depth) with very low salinity (Lana 1986).

Nephtys furcifera **Hartmann-Schröder, 1959**

Figures 45L, 46; Table 19

Nephtys furcifera Hartmann-Schröder, 1959: 142, figs. 111-117; Molina-Lara and Vargas-Zamora 1995.

Type locality. Estero Naranca (Gulf of Fonseca), El Salvador, E Pacific Ocean.

Remarks. Hartmann-Schröder (1959) described *N. furcifera* as having lyriform chaetae in postacicular position, although securing the possibility of those being artefacts created by other broken chaetae since they were not homogeneously distributed along the body. Nevertheless, the author presents a drawing of a lyriform chaetae with equal rami that seems unlikely to be resultant from any other chaetae break. The presence of lyriform chaetae would exclude this species from the genus *Nephtys* as it is presently defined. The genera including species with lyriform chaetae are *Aglaophamus*, *Inermonephtys* and *Micronephthys*. The well-developed parapodial lamellae and branchiae of *N. furcifera* exclude it from *Micronephthys* and information about the presence or absence of pharynx papillae is lacking not allowing verification of the possible inclusion in *Inermonephtys*. Therefore this species needs further revision in order to verify the present or absence of lyriform chaetae and pharynx papillae.

Distribution. Pacific Ocean (El Salvador) (Hartmann-Schröder 1959; Molina-Lara & Vargas-Zamora 1995).

Habitat. Mud, sublitoral (Hartmann-Schröder 1959).

Nephtys glabra **(Hartman, 1950)**

Figures 51E, 52; Table 21

Nephtys glabra Hartman, 1950: 109, pl. 13, figs. 1-9; Hartman 1968: 585; Ravara *et al.* in press.
Dentinephtys glabra Imajima and Takeda 1987: 43, figs. 2A-M and 3A-B; Hilbig 1997: 328, fig. 13.4.
Nephthys malmgreni Treadwell 1914: 192 (partim); (not Théel 1879).

Type locality. Off Anacapa Island light, California, E Pacific Ocean, 48-51 fms depth.

Distribution. Pacific Ocean (Central and S California; Japan) (Hilbig 1997).

Habitat. Sand and silty sand, 68-196 m depth (Hartman 1950; Hilbig 1997).

Nephtys gravieri **Augener, 1913**

Figures 49C, 50; Table 22

Nephthys gravieri Augener, 1913: 123, pl. 2, fig. 5, text-fig. 6A-C; Fauvel 1932a: 118; Fauvel 1953: 226, figs. 114A-C (partim); Fauchald 1965: 336; Paxton 1974: 203; Rainer and Hutchings 1977: 324, figs. 17-22 and 42.

Nephtys mirocirris Fauchald, 1965: 335, figs. 3 and 4.

Nephtys australiensis Paxton 1974: 202 (partim).

Type locality. Fremantle, W Australia, E Indian Ocean.

Remarks. *Nephtys gravieri* was originally described from Fremantle (W Australia) by Augener (1913) who gave a brief description without mentioning the chaetiger where branchiae start nor the presence of warts in proximal region of pharynx. The presence of supra- and subacicular lobes in noto- and neuropodia is also not mentioned but this feature is evident in the illustration of the parapodium (Augener 1913: fig. 6c). Fauchald (1965) could not examine the type material of *N. gravieri* and described a new species, *N. mirocirris*, from Yorke Peninsula (S Australia) with similar characteristics but differing in having warts on the pharynx and what he mentioned as deeply incised acicular lobes with aciculae emerging from the inner lobe. In agreement with Rainer and Hutchings (1977), the later feature is here referred to as conical acicular lobes with a supracicular lobe in the notopodia and a subacicular lobe in the neuropodia. Those characters were incorrectly presumed as absent in *N. gravieri* by Fauchald (1965). The two species were synonymised by Paxton (1974) and by Rainer and Hutchings (1977) who compared the holotype of *N. mirocirris* with a syntype of *N. gravieri*.

Nephtys gravieri is very close and often mistaken by *Aglaophamus australiensis*. Both species have short and almost straight branchiae, similar parapodial lamellae shape and proportions, barred chaetae in anterior chaetigers being replaced by spinulose chaetae posteriorly, similar number of subterminal papillae on the pharynx, and warts on pharynx proximal region. However, they differ by the presence of a middorsal subterminal papilla on the pharynx of *A. australiensis*, and the chaetiger where branchiae start (4 in *A. australiensis*, 3 in *N. gravieri*). There are also some minor differences in the shape of dorsal cirri (slightly foliaceous in *A. australiensis*, cirriform in *N. gravieri*), branchiae (shorter and stouter in *N. graveri*), and supra- and subacicular lobes (much larger in *N.gravieri*) (Fauchald 1965; Rainer & Hutchings 1977). As in *A. australiensis*, the generic position of *N. gravieri* may need revision preferentially with integration of molecular data.

Distribution. Indian Ocean (Bay of Bengal, India; Australia) (Paxton 1974; Rainer & Hutchings 1977).

Habitat. Sand and muddy sand, shallow estuarine and coastal waters (Rainer & Hutchings 1977).

***Nephtys hombergii* Savigny, 1822**

(see chapter 3.1, pg. 110)

***Nephtys hudsonica* Chamberlin, 1920**

Figures 45M, 46; Table 19

Nephthys hudsonica Chamberlin, 1920: 10, pl. 2, figs. 4-6.

Type locality. Richmond Gulf, Hudson Bay, Canada, W Atlantic Ocean.

Remarks. *Nephtys hudsonica* is only known from its original description by Chamberlin (1920), which lacks information on the number of subterminal papillae per row in the pharynx and the chaetiger where branchiae start. According to Chamberlin (1920), *N. hudsonica* differs from the closely related *N. ciliata* by the shape of the prostomium and the insertion of palps closely behind antennae rather then further posteriorly on the prostomium. Nevertheless, the lack of information on the chaetiger where branchiae start and pharynx papillae, two of the most important distinctive characters among the nephtyids, hinders further comparisons. The species thus need further revision.

Distribution. Atlantic Ocean (Hudson Bay) (Chamberlin 1920).

Habitat. 27.4-46.7 m depth (Chamberlin 1920).

***Nephtys hystricis* McIntosh, 1900**

(see chapter 3.1, pg. 116)

***Nephtys impressa* Baird, 1871**

Figures 45N, 46; Table 19

Nephtys impressa Baird, 1871: 94; Hartman 1950: 97, pl. 17, figs. 3 and 4; Hartmann-Schröder 1962: 106, figs. 100 and 101; Wesenberg-Lund 1962: 95.

Nephtys (Nephtys) impressa Rozbaczylo and Castilla 1974: 195, figs. 4B and 5B-D.
Nephtys monilibranchiata Rozbaczylo and Castilla, 1974: 199, fig. 6A-F.

Type locality. Lota, Chile, E Pacific Ocean.

Material examined. Pacific Ocean, Chile: Lota, 1868, 1 complete spm, holotype (NHM 1869.6.16.6).

Remarks. There are some discrepancies in the description of *N. impressa* pharynx by different authors. In the original description, Baird (1871) only mentions the number of terminal papillae and does not describe the subterminal papillae arrangement. Hartman (1950) re-described the holotype as having 7-9 longitudinal rows of subterminal papillae in the pharynx but then states that the species is characterized by having subterminal papillae in only 4 or 5 rows. Rozbaczylo and Castilla (1974) counted 22-24 rows of 6-7 subterminal papillae in their specimens and 5-8 papillae per row in the holotype. The holotype was also examined within this study and 22 rows of 6-9 subterminal papillae were found.

Rozbaczylo and Castilla (1974) described a new species, *N. monilibranchiata*, with the same geographical distribution and occurring at similar depths (lower intertidal) as *N. impressa*. This new species is morphologically similar to *N. impressa* differing only by the shape of branchiae (larger, thinner and apparently without cilia in *N. monilibranchiata*, stated as moniliform by the authors), the shape of dorsal cirri (larger and thinner in *N. monilibranchiata*), and the shape of prostomium (subcircular on *N. monilibranchiata* against pentagonal on *N. impressa*). These differences are here considered as intraspecific variability and therefore not valid to distinguish a new species. All other characteristics, with relevance in distinguishing between species (branchiae occurrence, parapodial lobes and lamellae shape, pharynx papillae arrangement), appear to be similar in *N. monilibranchiata* and *N. impressa*. Although, further studies are advised, there are sufficient grounds to synonymise *N. monilibranchiata* to *N. impressa*.

Distribution. Pacific Ocean (Chile) (Rozbaczylo & Castilla 1974).

Habitat. Intertidal (Rozbaczylo & Castilla 1974).

Nephtys incisa **Malmgren, 1865**

(see chapter 3.1, pg. 123)

Nephtys inornata **Rainer & Hutchings, 1977**

Figures 49D, 50; Table 22

Nephtys inornata Rainer and Hutchings, 1977: 327, figs. 23-28 and 43.
Nephtys australiensis Fauchald 1965: 334, figs. 1 and 2 (partim).

Type locality. Gunnamatta Bay, Port Hacking, E Australia, Tasman Sea, W Pacific Ocean, 4.5 m depth.

Remarks. *Nephtys inornata* is a small nephtyid species with 46-51 chaetigers (Rainer & Hutchings 1977). Eyes are visible in adult specimens at the level of chaetiger 1-4, and branchiae are short and strait but present in almost all chaetigers. Parapodial lamellae are well developed and slightly surpassing the acicular lobes in the postacicular position. Barred chaetae are only present on anterior chaetigers (until chaetiger 14-15) and then replaced by spinulose chaetae, a feature also observed in some *Micronephthys* species and in smaller species of *Aglaophamus* and *Nephtys* like *A. australiensis*, *A. gippslandicus*, *N. fluviatilis*, *N. gravieri*, *N. mesobranchia*, *N. palatii*, *N. semiverrucosa* and *N. sukumoensis*. The small size of this species makes it resemble *Micronephthys*. However, despite some common features, *N. inornata* does not match *Micronephthys* diagnosis.

Distribution. Pacific Ocean (Australia) (Rainer & Hutchings 1977).

Habitat. Sand, muddy sand and firm mud, intertidal to 25 m depth (Rainer & Hutchings 1977).

Nephtys kersivalensis **McIntosh, 1908**

(see chapter 3.1, pg. 125)

Nephtys longipes **Stimpson, 1855**

Figures 49E, 50; Table 22

Nephthys longipes Stimpson, 1855: 392.

Nephtys longipes Paxton 1974: 204; Rainer and Hutchings 1977: 332, figs. 29 and 43; Hutchings and Murray 1984: 44; Hartmann-Schröder 1990: 64.

Nephtys picta Knox and Cameron 1971: 28, figs. 15 and 16 (not Ehlers, 1868).

Nephtys vikingensis Paxton, 1974: 204, figs. 8-13.

Nephtys sp. Hutchings 1974: 181.

Original locality. Botany Bay, New South Wales, Australia, W Pacific Ocean.

Neotype locality. Batmans Bay (35º62'S, 150º11'E), New South Wales, Australia, W Pacific Ocean.

Remarks. *Nephtys longipes* was originally described by Stimpson (1855) from Botany Bay in New South Wales (E Australia) and was later considered as indeterminable due to its insufficient description (Augener 1922; Hartman 1950; Paxton 1974). Paxton (1974) described *N. vikingensis* as a new species from Batmans Bay, a close locality in New South Wales. Although the holotype of *N. longipes* is missing, Rainer and Hutchings (1977) re-examined the holotype of *N. vikingensis* and considered that sufficient information is given by Stimpson's description for *N. vikingensis* to be synonymised with *N. longipes,* thus designating the holotype of *N. vikingensis* as neotype of *N. longipes*. According to Paxton (1974) and Rainer and Hutchings (1977), *N. longipes* distinctly differs from other species by the triangular projection on the anterior margin of prostomium (between antennae) and the long chaetae.

Distribution. Pacific Ocean (Australia) (Rainer & Hutchings 1977).

Habitat. Clean sand, intertidal to shallow subtidal (Rainer & Hutchings 1977).

***Nephtys longosetosa* Örsted, 1842**

(see chapter 3.1, pg. 129)

***Nephtys magellanica* Augener, 1912**

Figures 45O, 46; Table 19

Nephthys magellanica Augener, 1913 (1912): 208, pl. 6, figs. 27 and 28; Wesenberg-Lund 1962: 94; Hartman 1964: 105, pl. 32, figs. 3 and 4; Perkins 1980: 34, fig. 14.

? *Nephthys magellanica* Hartman 1938b: 146, fig. 62; Perkins and Savage 1975; Fauchald 1976: 18, fig. 1F-G; Laverde-Castillo and Ródriguez-Gómez 1987.

Nephtys (Nephtys) magellanica Rozbaczylo and Castilla 1974: 198.

Nephtys cirrosa Ehlers 1901: 67 (not Ehlers, 1868: 624).

Nephtys longisetosa Ehlers 1901: 67 (not Örsted, 1843: 195).

? *Nephtys simoni* Taylor 1984: 35-9, fig. 35-5 and 6A-C.

Type locality. Strait of Magellan, E Pacific Ocean.

Remarks. *Nephtys magellanica* was originally described and reported from Strait of Magellan and Chile regions (Augener 1912, Wesenburg-Lund 1964, Hartman 1964, Rozbaczylo & Castilla 1974). Hartman (1938, 1940, 1944a, 1950, 1968) extended the species distribution to California, Venezuela and Colombia. Fauchald (1976) reported its occurrence in Brazil. Later, Perkins (1980) erected a new species, *N. simoni*, for specimens from Florida, North Carolina and California, and included in this species the specimens recorded by Hartman (1938, 1940, 1944a, 1950, 1968). According to Perkins (1980), *N. magellanica* differs from *N. simoni* by having a very robust prostomium, with a short, broad dorsoposterior projection (instead of long, narrow projection), palps equal in size to ventral cirri of first chaetiger (in *N. simoni* ventral cirri are half as large as palps), and branchiae are long covering 2/3 of the length between rami (in *N. simoni* branchiae only cover 1/3 of the length between rami). Hilbig (1997) confirmed the synonymy for Hartman (1950) and excluded Hartman (1938). According to Hilbig (1997) the specimens from Gulf of Mexico described by Taylor (1984) as *N. simoni* may belong to *N. magellanica*. However, this requires confirmation. The synonymy list of *N. magellanica* and its geographical distribution are here adjusted according to these remarks. Nevertheless, a more thorough revision of this species together with *N. simoni* is in need, preferentially by the integration of molecular information, since the two species are only distinguishable by a few subjective characters. The specimens reported by Fauchald (1976) from Brazil seem to have distinctly bilobed acicular lobes and might belong to another species. The description given by Fauchald is very brief and do not allow an informed decision.

Distribution. Pacific Ocean (Chile, Strait of Magellan) (Rozbaczylo & Castilla 1974). There is a possibility of this species occur in Gulf of Mexico (Hilbig 1997) and Brazil (Fauchald 1976) but it requires confirmation.

Habitat. Lower intertidal to 155.4 m depth (Rozbaczylo & Castilla 1974).

Nephtys mesobranchia **Rainer & Hutchings, 1977**

Figures 49F, 50; Table 22

Nephtys mesobranchia Rainer and Hutchings, 1977: 334, figs. 30-35 and 43.

Type locality. Gladstone, Queensland, E Australia, W Pacific Ocean, 5 m depth.

Remarks. Judging by the size of the holotype (23 mm long for 49 chaetigers), *Nephtys mesobranchia* is a small nephtyid species. The eyes are visible in all specimens (including an ovigerous one) at the level of chaetiger 2 or 3 (specimens with 43 to 49 chaetigers) (Rainer & Hutchings 1977). Branchiae are short, nearly straight, and restricted to the anterior half of the body (present in 15-17 chaetigers). Parapodial lamellae are well developed but not surpassing the acicular lobes. All these characteristics match the diagnosis of the genus *Micronephthys* as it is presently accepted. Furthermore, Rainer and Hutchings (1977) described the presence of a radially-arranged line of about four pairs of narrow cuticular ridges within pharynx, distal to jaws and close to terminal papillae. These structures may be equivalent to the paired lateral pharyngeal trepans described by Imajima and Takeda (1987) as diagnostic of the genus *Dentinephtys*. The position of this species thus requires further attention.

Distribution. Pacific Ocean (Australia) (Rainer & Hutchings 1977).

Habitat. Mud and sandy mud to coarse river gravel with coarse sand, it appears to tolerate some degree of salinity reduction (salinity average 24.5-30.4‰), 3-5 m depth (Rainer & Hutchings 1977).

Nephtys monroi **Hartman, 1950**

Figures 45P and Q, 46; Table 19

Nephtys monroi Hartman, 1950: 107, pl. 17, fig. 1; Hartman 1959; Laverde-Castillo 1986.

Nephthys tabogensis Monro 1933: 53, fig. 23H (partim).

Type locality. Taboga Island, Panama, E Pacific Ocean.

Material examined. Pacific Ocean, Panama, Taboga Island: Scientific Research Association South Pacific Expedition 1924-1926, 6-12 fms, 9 Apr – 31 Oct 1924, 1 incomplete spm, holotype (NHM 1932.12.24.127).

Remarks. *Nephtys monroi* was erected by Hartman (1950) from a single specimen found among the type material of *Aglaophamus tabogensis*, from Panama, deposited in Natural History Museum of London. The holotype of *N. monroi* was examined within this study and the following observations are added to the description: the neuropodial superior lobes are present from chaetiger 15 and not chaetiger 18 as mentioned by Hartman (1950); the postchaetal lamellae of both rami become distally crenulated on the posterior parapodia (Figure 45Q). The specimen was not dissected, thus the pharynx remains undescribed.

Distribution. Pacific Ocean (Taboga Island) (Hartman 1950).

Habitat. Mud, 11-22 m depth (Hartman 1950).

Nephtys multicirrata **Hartmann-Schröder, 1960**

Figures 45R, 46; Table 19

Nephtys multicirrata Hartmann-Schröder, 1960: 17, figs. 35-37.

Type locality. Between Pimentel and Eten, N Peru, E Pacific Ocean.

Distribution. Pacific Ocean (Peru) (Hartmann-Schröder 1960).

Habitat. Sandy beach (Hartmann-Schröder 1960).

Nephtys neopolybranchia **Imajima & Takeda, 1987**

Figures 49G, 50; Table 22

Nephtys neopolybranchia Imajima and Takeda, 1987: 57, fig. 9A-K; Jung and Hong 1997: 375, fig. 3A-K.

Type locality. Usujiri Bay, Hokkaido, Japan, W Pacific Ocean, 5-25 m depth.

Distribution. Pacific Ocean (Korea, Japan) (Imajima & Takeda 1987; Jung & Hong 1997).

Habitat. Sand and muddy sand, 5-64 m depth (Imajima & Takeda 1987; Jung & Hong 1997).

***Nephtys oculata* Hartmann-Schröder,1959**

Figures 45S, 46; Table 19

Nephtys oculata Hartmann-Schröder, 1959: 147, figs. 122-128; Hartmann-Schröder 1962: 128; Rozbaczylo and Castilla 1974: 201; Molina-Lara and Vargas-Zamora 1995.
Nephtys cf. *oculata* Hartmann-Schröder 1965: 141.

Type locality. La Herradura (Estero Jaltepeque), El Salvador, W Pacific Ocean.

Distribution. Pacific Ocean (El Salvador, Peru, Chile) (Rozbaczylo & Castilla 1974; Molina-Lara & Vargas-Zamora 1995).

Habitat. Mud, intertidal to 58m depth (Hartmann-Schröder 1959; Rozbaczylo & Castilla 1974).

***Nephtys oligobranchia* Southern, 1921**

Figures 49H, 50; Table 22

Nephthys oligobranchia Southern, 1921: 610, pl. 24, fig. 12A-C; Fauvel 1932b: 119; Okuda 1943: 100, figs. 1-3; Uschakov and Wu 1962: 25, pl. 3, fig. I; Fauchald 1968: 18, figs. 41-44; Uschakov and Wu 1979: 55, fig. 17I; Lee and Jae 1983: 23, text-fig. 2, pl. 2, figs. E-H; Imajima and Takeda 1987: 47, figs. 4A-L and 6; Jung and Hong 1997: 382.

Type locality. India, Indian Ocean.

Remarks. *Nephtys oligobranchia* and *N. polybranchia* have similar geographical and bathymetrical distributions. The two species are known as euryhaline, occur in the same types of sediment and are frequently found together. They can be distinguished by the presence of a long middorsal papilla on the pharynx of *N. oligobranchia* (absent in *N. polybranchia*), the chaetiger where branchiae start (7-8 in *N. oligobranchia*, 4-5 in *N. polybranchia*), and better development of lamellae in *N. polybranchia* (Figure 49J). Fauchald (1968) described Viet Nam specimens of *N. oligobranchia* has having lyrate chaetae. However, this feature was not observed on the specimens from Korea (Lee & Jae 1983) or Japan (Imajima & Takeda 1987) and Ohwada (1983) referred to the possibility of juvenile specimens of *Aglaophamus* being erroneously identified as *N. oligobranchia*.

Nephtys oligobranchia is usually reported from shallow waters although Imajima & Takeda (1987) recorded this species until 468 m depth.

Distribution. Indian Ocean (India); Pacific Ocean (Korea, Japan, China, Viet Nam) (Fauchald 1968, Jung & Hong 1997).

Habitat. Sandy silt, 0-468 m depth, euryhaline (Lee & Jae 1983; Imajima & Takeda 1987; Jung & Hong 1997).

***Nephtys palatii* Gravier, 1904**

Figures 47H, 48; Table 20

Nephthys palatii Gravier, 1904: 472; Gravier 1906: 129, figs. 286-289, pl. 1, figs. 163 and 164; Fauvel 1919a: 424, pl. 16, figs. 40 and 41.

Type locality. Djibouti, Gulf of Aden, N Indian Ocean.

Distribution. Red Sea (bay of Djibouti) (Gravier 1904; Fauvel 1919a).

Habitat. Muddy sand (Fauvel 1919a).

***Nephtys panamensis* Monro, 1928**

Figures 45T, 46; Table 19

Nepthys panamensis Monro, 1928: 81, figs. 3 and 4; Hartman 1940: 239: pl. 41, fig. 105; pl. 42, figs. 106-109; Hartman 1950: 101; Reish 1968; Perkins and Savage 1975;

Salazar-Vallejo *et al.* 1990; Hernández-Alcántara and Solís-Weiss 1991; Dean 1996; Hernández-Alcántara and Solís-Weiss 1999.

Type locality. Rey Island, Pearls Islands, Panama, E Pacific Ocean, 15 fms depth.

Material examined. Pacific Ocean, Gulf of Panama, Pearl Islands: Challenger Expedition 1914-1916, Rey Island, 15 fms, 1 incomplete spm, syntype (NHM 1928.9.13.51).

Remarks. Monro (1928) described *N. panamensis* as having 22 rows of 3-4 subterminal papillae in the pharynx. However, in the syntype examined within this study 22 rows of 1-5 papillae were observed. The other characteristics match the original description.

Distribution. Pacific Ocean (Gulf of California, Mexico, Costa Rica, Pearls Islands - Panama) (Monro 1928; Hartman 1940, 1950).

Habitat. Sand and shells (Monro 1928), intertidal to 91.5 m depth (Hartman 1940, 1950).

Nephtys paradoxa **Malm, 1874**

(see chapter 3.1, pg. 132)

Nephtys pente **Rainer, 1984**

Figures 44B, 47I, 48; Table 20

Nephtys pente Rainer, 1984: 30; Rainer 1991: 82, fig. 3B; Dnestrovskaya and Jirkov 2001: 208,1 text-fig.
Nephthys caeca Möbius 1875: 168 (partim).
Nephthys ciliata Marenzeller 1889: 127 (partim); Michaelsen 1897: 58 (partim); McIntosh 1908: 23; Heinen 1911: 21 (partim); Augener 1913: 193 (partim).
Nephthys incisa Heinen 1911: 23 (partim).
Nephtys ciliata Pettibone 1963: 202, fig. 51C (partim); Kirkegaard 1969: 46; Hartmann-Schröder 1971: 218, fig. 71A (partim); ?Imajima and Takeda 1987: 67.
Nephtys zatsepini Jirkov, 1986: 39.

Type locality. Süderfahrt, Kiel Bay, N Germany, Baltic Sea, 21 m depth.

Material examined. Atlantic Ocean, Iceland: Hvalfjordur, Saurbar, subtidal, coll. by SCUBA diving, 22 July 2001, 1 complete spm (DBUA 00178-01); Sweden, Bohuslän: 1 complete specimen (GNHM P 13179); Baltic Sea, Süderfahrt, Kiel Bay: 54º33'N, 10º48'E, 21 m, van Veen grab, 10 Jun 1981, 1 complete spm, paratype (NHM 1983.101); North Sea, England: Amethyst Gasfield, East of Humber estuary, 53º35'N, 0º45'E, 20-65 m, 22-24 Jul 1992, 1 incomplete spm (NMWZ 1999.062.0012).

Pacific Ocean, Alaska: Boca de Quadra fjord, main channel, intertidal, Mar 1981, 1 incomplete spm (CASIZ 159398, as *N. ciliata*).

Remarks. *Nephtys pente* is very similar to *N. ciliata*, they have a similar geographical distribution in the North Atlantic Ocean, and appear to occur in similar habitats. Previous reports of *N. ciliata* often include *N. pente*. Together with the description of *N. pente*, Rainer (1984) also provided a narrower definition of *N. ciliata*, thus excluding the *N. pente* forms. *Nephtys pente* differs from *N. ciliata* by having branchiae starting from chaetiger 5 (rarely 6) rather then 7-11, which gradually decrease in size to the end of body (Figure 44B). In *N. ciliata* branchiae are reduced on the posterior part of the body (Figure 44A), and the lamellae are less developed especially the postacicular ones.

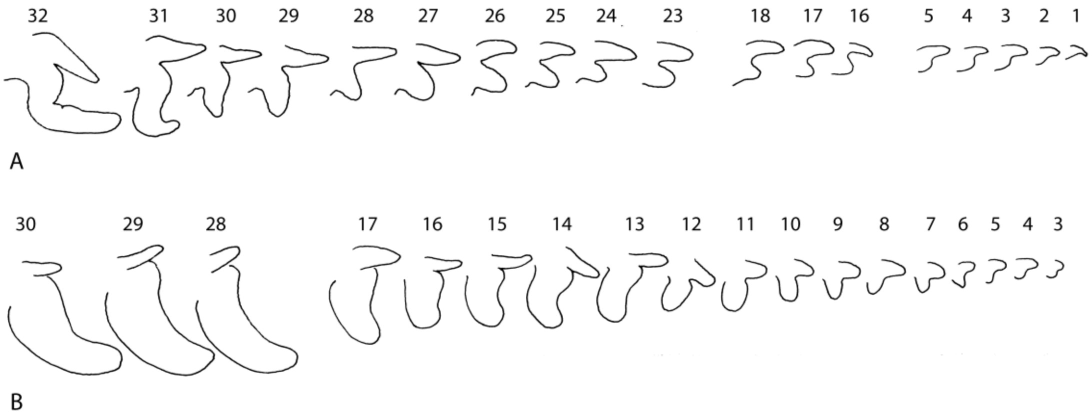


Figure 44. Branchiae from posterior chaetigers. A. *Nephtys ciliata*; B. *N. pente*. Numbers refer to the chaetiger number counting from posterior to anterior part of the body.

Distribution. Atlantic Ocean (Arctic to North Sea) (Rainer 1991).

Habitat. Silty sand, shallow 14-450 m depth (Rainer 1991; Dnestrovskaya & Jirkov 2001).

Nephtys phasuki **Nateewathana & Hylleberg, 1986**

Figures 49I, 50; Table 22

Nephtys phasuki Nateewathana and Hylleberg, 1986: 212, figs. 12A-H and 13.

Type locality. Patong Bay, Phuket Island, Thailand, E Indian Ocean, 20 m depth.

Remarks. *Nephtys phasuki* is known only from its original description. According to Nateewathana & Hylleberg (1986) *N. phasuki* resembles *N. inornata* from eastern Australia in having the pharynx proximal region smooth, branchiae starting on chaetiger 5 and barred chaetae absent from chaetiger 16 on (absent from chaetiger 17 on in *N. phasuki*). The two species differ in minor characters such as the length of ventral cirri of first chaetiger (much longer than dorsal cirri in *N. phasuki*, slightly longer than dorsal cirri in *N. inornata*), the shape of dorsal cirri (cirriform with broad base in *N. phasuki*, pear-shaped in *N. inornata*), and the point of insertion of ventral cirri (near the junction of pre- and postchaetal lamellae in *N. inornata*, more basal in *N. phasuki*) (Figure 49D, I). Both species occur in shallow waters, although in different geographical areas and different sediment types. *Nephtys phasuki* occurs in medium to coarse sands near Thailand, whereas *N. inornata* occurs in sand and mud near eastern Australia. In my opinion the morphological and distribution differences are not sufficient to separate these two species. However, specimens of *N. phasuki* and *N. inornata* could not be examined within this study and thus the present status of the species is kept until further investigation.

Distribution. Indian Ocean (Thailand) (Nateewathana & Hylleberg 1986).

Habitat. Medium and coarse sand, 10-20 m depth (Nateewathana & Hylleberg 1986).

Nephtys phyllocirra **Ehlers, 1887**

Figures 45U, 46; Table 19

Nephtys phyllocirra Ehlers, 1887: 131-134, pl. 38, figs. 7-11; Augener 1906: 154; Augener 1918: 164; Treadwell 1928: 466; Augener 1933: 209; Hartman 1938a: 9; Hartman 1950: 108; Perkins and Savage 1975; Laverde-Castillo and Ródriguez-Gómez 1987.

Type locality. Off S Florida, SE USA, W Atlantic Ocean, 320-339 fms depth.

Remarks. There are only a few descriptions of this species, including the original one from Ehlers (1887), and none of them provides complete information about all characteristics of the species. Figures are only given by Ehlers (1887) in the original description.

Distribution. Atlantic Ocean (off Delaware, off S Florida, off the West Indies, off Colombia) (Hartman 1950).

Habitat. 80.5-1097 m depth (Hartman 1950). Also reported from 6 m depth (Augener 1933).

***Nephtys picta* Ehlers, 1868**

Figures 45V, 46; Table 19

Nephthys picta Ehlers, 1868: 632, pl. 23, figs. 9 and 35; Verrill and Smith 1874: 54, 289, pl. 12, fig. 57; Webster 1879: 214; Verrill 1881: 296, 300 and 317; Webster 1886: 131; Andrews 1891: 281.
? *Nephtys picta* Hartman 1938a: 9; Hernández-Alcántara and Solís-Weiss 1991.
Nephtys picta Hartman 1944a: 339, pl. 15, figs. 3 and 4, (as *N. bucera*, not fig. 8 = *N. ciliata* ?); Hartman 1945: 22; Hartman 1950: 103; Hartman 1951: 49, pl. 10, fig. 4; Pettibone 1963: 195, figs. 49C and 50C-F; Day 1973: 43; Perkins and Savage 1975; Gardiner 1976: 155, fig. 16I-J; Taylor 1984: 35-11, fig. 35-9, 10A-D.

Type locality. Nahant, Massachusetts, USA, W Atlantic Ocean.

Remarks. *Nephtys picta* is morphologically very similar to *N. bucera*. The two species were described by Ehlers (1868) and synonymised as *N. picta* by McIntosh (1900). Hartman (1950) and several other authors considered them as distinct species. The differences between the two species were already mentioned above (see remarks on

N. bucera and Table 19). Both species have similar geographical and bathymetric distribution (Figure 46), although with slightly different habitat preferences. *Nephtys picta* inhabits a variety of sediments from gravely sand to muddy sand, while *N. bucera* seems to prefer clean sand.

Distribution. Atlantic Ocean (Canada to Florida, Gulf of Mexico) (Hartman 1950; Pettibone 1963; Taylor 1984). There are further reports of this species for the northeastern Pacific Ocean (Hartman 1938a; Hernández-Alcántara and Solís-Weiss 1991) but these reports require confirmation.

Habitat. Coarse to fine-very fine sand, silty fine sand, muddy sand, intertidal to 200 m depth (Taylor 1984).

Nephtys polybranchia **Southern, 1921**

Figures 49J, 50; Table 22

Nephthys polybranchia Southern, 1921: 607, pl. 24, text-fig. 11A-B, pl. 24, fig. 11A-G; Fauvel 1932b: 118-119; Okuda 1940: 14, fig. 7.
Nephtys polybranchia Uschakov and Wu 1962: 24, pl. 3, figs. E-H; not Imajima and Hartman 1964: 158; Silva 1965: 546; Imajima 1967: 424; Fauchald 1968: 19, figs. 45-48; Uschakov and Wu 1979: 54, fig. 17E-H; Lee and Jae 1983: 23; Imajima and Takeda 1987: 54, figs. 7A-J and 8; Jung and Hong 1997: 382.

Type locality. Chilka Lake, E India, N Indian Ocean.

Material examined. Pacific Ocean, Japan: Nebama beach, Otsuchi Bay, Honshu, 2 m, 15 Apr 1983, 4 complete spms (NMWZ 1989.083.0003).

Remarks. *Nephtys polybranchia* and *N. oligobranchia* have similar geographical and bathymetrical distributions (Figure 50). Both species are known as euryhaline, occur in similar sediment type and are frequently found together. Differences between these species were already discussed above (see remarks on *N. oligobranchia*).

Nephtys polybranchia is usually reported from shallow waters although Imajima & Takeda (1987) recorded this species down to 330 m depth.

Distribution. Indian Ocean (E India); Pacific Ocean (Korea, Japan, China, Ryukyu Islands, Viet Nam; Gulf of Siam) (Fauchald 1968, Imajima & Takeda 1987, Jung & Hong 1997).

Habitat. Silty sand, 0-330 m depth, euryhaline (Lee & Jae 1983; Imajima & Takeda 1987; Jung & Hong 1997).

Nephtys punctata **Hartman, 1938**

Figures 51H, 52; Table 21

Nephtys punctata Hartman, 1938b: 155, fig. 67; Hartman 1940: 239; Berkeley and Berkeley 1942: 193; Hartman 1950: 96; Imajima 1961: 89, fig. 5; Hartman 1968: 591, figs. 1-4; Imajima and Takeda 1987: 61, fig. 11A-M, 14; Hilbig 1997: 340, fig. 13.10.

Type locality. South of Alaska Peninsula, NE Pacific Ocean, 483 fms depth.

Material examined. Pacific Ocean, USA: Shilshole Bay, King County, Puget Sound, Washington, 47º 41.90’N, 122º27.20’W, 17 May 1989, 2 complete and 2 incomplete spms (CASIZ 173694).

Remarks. *Nephtys punctata* was first described from southern Alaska and California. Later Imajima (1961) and Imajima and Takeda (1987) reported this species in Okhotsk Sea and Japan, respectively. The Japanese and eastern Pacific specimens belong to the same species despite the smaller body size of the Japanese specimens. In the specimens from Okhotsk Sea the branchiae start on chaetiger 7 (rather than 8-9).

Distribution. Pacific Ocean (Alaska to California; Okhotsk Sea, Japan) (Hartman 1938b, 1950; Imajima & Takeda 1987; Hilbig 1997).

Habitat. Silty sand (Hilbig 1997), 56.7-883.3 m depth (Hartman 1938b).

Nephtys rickettsi **Hartman, 1938**

Figures 45W, 46; Table 19

Nephtys rickettsi Hartman, 1938b: 153, fig. 66; Hartman 1950: 97; Banse 1972: 217, fig. 10D-E; Dnestrovskaya and Jirkov 2001: 211,1 text-fig.

Nephtys discors Pettibone 1954: 270, fig. 30M (partim); Pettibone 1963: 203 (partim).

Type locality. Cache Bay, Alaska, NE Pacific Ocean.

Material examined. Pacific Ocean, USA: Shilshole Bay, King County, Puget Sound, Washington, 47º 41.90’N, 122º27.20’W, 204 m, 24 Nov 1981, 1 complete spm (CASIZ 173695).

Remarks. *Nephtys rickettsi* is morphologically very similar to *N. discors* from the Atlantic coast of North America. The two species differ by the presence of warts on the proximal part of the pharynx in *N. discors* (absent in *N. rickettsi*) and, according to Banse (1972), the presence of a neuropodial supracicular lobe on the anterior parapodia of *N. rickettsi* (Figure 45W) (absent in *N. discors*). According to Hartman (1938b) the branchiae in *N. rickettsi* are absent from the last 15-17 chaetigers. However, in the specimen examined in the present study, the branchiae although small are present until the end of the body.

Distribution. Pacific Ocean (Alaska to S California) (Hartman 1950).

Habitat. 58.5-490.1 m depth (Hartman 1950).

***Nephtys semiverrucosa* Rainer & Hutchings, 1977**

Figures 49K, 50; Table 22

Nephtys semiverrucosa Rainer and Hutchings, 1977: 338, figs. 36-40 and 43.

Type locality. Fannie Bay, Darwin, N Australia, Timor Sea, Indopacific region.

Remarks. *Nephtys semiverrucosa* is morphologically similar and has a close geographical distribution to the species *A. australiensis* and *N. gravieri* from which it can be distinguished by the pharynx morphology. *Nephtys semiverrucosa* lacks a middorsal subdistal papilla and has a basal ring of warts on the pharynx, whereas *A. australiensis* has a middorsal papilla and has the proximal region completely covered with warts. *N. gravieri* also lacks a middorsal papilla but has the proximal region completely covered with warts.

Distribution. Indopacific region (Australia) (Rainer & Hutchings 1977).

Habitat. Sand, intertidal (Rainer & Hutchings 1977).

Nephtys serrata **Imajima & Takeda, 1987**

Figures 49L and M, 50; Table 22

Nephtys serrata Imajima and Takeda, 1987: 74, fig.16A-Z.

Type locality. Off Honbekkai, Nemuro Peninsula, Japan, W Pacific Ocean, 3 m depth.

Material examined. Pacific Ocean, Japan: Nebarna beach, Otsuchi Bay, Honshu, 7 m, 18 May 1983, 3 incomplete spms (NMWZ 1989.083.0001).

Remarks. *Nephtys serrata* is a large sized species that can be easily distinguished from other species by the shape of dorsal cirri which varies considerably along the body, from simple conical cirrus on the anterior- and posteriormost chaetigers to broad cirrus with 2-5 irregular tips distally, conferring a serrated appearance (Figure 49M).

Distribution. Pacific Ocean (Japan) (Imajima & Takeda 1987).

Habitat. Sandy mud, 3-7 m depth (Imajima & Takeda 1987).

Nephtys serratifolia **Ehlers, 1897**

Figures 45X, 46; Table 19

Nephthys serratifolia Ehlers, 1897: 24-25, pl. 1, fig. 13; Ehlers 1901: 68; Monro 1930: 114, fig. 41A-B; Monro 1936: 139-140; Wesenberg-Lund 1962: 89, figs. 35-39; Hartman 1964: 106, pl. 32, fig. 7; Hartmann-Schröder 1965: 141, figs. 110-113.
Nephthys serratus Hartman, 1953: 33, fig. 10A-G; Hartman 1964: 106, pl. 32, figs. 5 and 6; Hartman 1967: 82.
Nephtys (Nephtys) serratifolia Rozbaczylo & Castilla 1974: 202, fig. 7A-C.

Type locality. Off southern Argentina (49º53’ S, 64º43’ W), South Atlantic Ocean, in 62 fms depth.

Remarks. *Nephtys serratifolia* was originally described by Ehlers (1897) from southern Argentina. The author did not mention the chaetiger where branchiae start nor the presence of postacicular chaetae with basal spur. Later, Hartman (1953) described the species *N. serratus* based on one specimen from Port William, Falkland Islands, at 40 m depth, mentioning that this species differs from *N. serratifolia* by the presence of branchiae from chaetiger 4 and the presence of a basal spur on postacicular chaetae. This author erroneously assumed that the branchiae of *N. serratifolia* start to appear at chaetiger 13, since it was the parapodium described by Ehlers (1897) as the better developed. Later, Hartmann-Schröder (1965) and Rozbaczylo and Castilla (1974) reported specimens of *N. serratifolia* from Chile with branchiae starting on chaetiger 3, neuropodial postacicular lamellae of median and posterior parapodia with two to three lobes and postacicular chaetae with a basal spur. These authors do not include any reference of *N. serratus*. On the other hand, Hartman (1967) recorded specimens of *N. serratus* from Falkland Islands with branchiae starting on chaetiger three and neuropodial postacicular lamellae of posterior parapodia unequally divided. Furthermore, this author states that the species *N. serratifolia* differ from *N. serratus* by having the postacicular lamellae serrated into about five lobes. However, in the parapodium illustration shown by Hartman (1953) for *N. serratus* the neuropodial postchaetal lamellae have four lobes. The depths reported by all these authors for the two species are similar. Considering all this, and although none of these species were examined within this study, *N. serratus* is here synonymised with *N. serratifolia*, and the geographical and bathymetrical distribution adjusted accordingly.

Nephtys serratifolia resembles *N. acrochaeta* from Brazil, in having dorsal prolongations at the base of parapodia, spinulose postacicular chaetae with a spur at the base, and by having similar parapodia morphology. However, the chaetiger where branchiae start is 3-4 in *N. serratifolia* and 9-10 in *N. acrochaeta*. Hartmann-Schröder (1965) suggested *N. acrochaeta* to be a synonym of *N. serratifolia* but did not formally synonymised the two species.

Distribution. Atlantic Ocean (Argentina, Falkland Islands); Pacific Ocean (Chile); Strait of Magellan (Hartman 1967 as *N. serratus*; Rozbaczylo & Castilla 1974).

Habitat. Fine sand, 20-485 m (Hartman 1953, 1967 as *N. serratus*; Hartmann-Schröder 1965; Rozbaczylo & Castilla 1974).

Nephtys simoni **Perkins, 1980**

Figures 45Y, 46; Table 19

Nephtys simoni Perkins, 1980: 37, fig. 15 and 16; Hernández-Alcántara and Solís-Weiss 1991; Hilbig 1997: 346, fig. 13.13.
Nephtys assimilis Treadwell 1914 (partim).
Nephthys incisa Treadwell 1914: 193 (not Malmgren, 1865).
Nephthys malmgreni Treadwell 1914: 192 (partim).
Nephtys magellanica Hartman 1940: 238, pl. 41, fig. 100-103; Hartman 1944b: 18; Hartman 1950: 100; Hartman 1968: 587, figs. 1-3 (not Augener, 1912).
Nephtys bucera Day 1973: 43 (partim) (not Ehlers, 1868).

Type locality. Hutchinson Island (27º21.6'N, 80º13.2'W), Florida, W Atlantic Ocean, 11 m depth.

Remarks. *Nephtys simoni* was originally described for specimens from Florida, North Carolina and California. According to Perkins (1980) the records of *N. magellanica* from California, Peru, Venezuela and Colombia given by Hartman (1938, 1940, 1944a, 1950, 1968) probably correspond to the species *N. simoni*. The two species, *N. magellanica* and *N. simoni*, are very similar and the main differences, according to Perkins (1980), were already discussed above (see remarks on *N. magellanica*). Hilbig (1997) re-examined one of the *N. magellanica* specimens from Hartman (1950) and confirmed its synonymy with *N. simoni*, but excluded Hartman (1938). Also according to Hilbig (1997), the specimens from Gulf of Mexico described by Taylor (1984) as *N. simoni* may belong to *N. magellanica*. Lana (1986) reported the occurrence of *N. simoni* in Brazil. This author does not describe the shape of the acicular lobes or the prechaetal lamellae but the illustration of the prechaetal lamellae shows that they are very well developed, surpassing the acicular lobes. According to Perkins (1980), the prechaetal lamellae in *N. simoni* specimens are shorter than acicular lobes. Later, Rizzo & Amaral (2007) synonymised this Brazilian record with *N. californiensis* based on other specimens they examined from Brazil. The synonymy list of *N. simoni* is here adjusted according to the remarks on this species and *N. magellanica*. However, a more careful revision of both species is required.

Distribution. Atlantic Ocean (North Carolina, Florida, Colombia, Venezuela); Pacific Ocean (California) (Perkins 1980; Hilbig 1997). There are further reports of this species from Brazil (Lana 1986), but these records require confirmation.

Habitat. Coarse to very fine or silty sands often containing fragments of shell and coral, 7-189 m depth (Perkins 1980; Hilbig, 1997).

Nephtys singularis **Hartman, 1950**

Figures 45Z, 46; Table 19

Nephtys singularis Hartman, 1950: 98, pl. 15, figs. 1-6; Fauchald 1973: 22; Kudenov 1975: 80, fig. 30; Fauchald 1977: 34.

Type locality. Off San José Point, Guatemala, E Pacific Ocean, 7-11 fms depth.

Distribution. Pacific Ocean (Gulf of California, Mexico, Guatemala, Panama) (Hartman 1950; Kudenov 1975).

Habitat. Fine sand, 12.8-27.4 m depth (Hartman 1950).

Nephtys squamosa **Ehlers, 1887**

Figures 45AA, 46; Table 19

Nephtys squamosa Ehlers, 1887: 128, pl. 37, fig. 7-10; not Augener 1918: 159, pl. 3, fig. 67; Monro 1933; not Fauvel 1936: 41; Hartman 1940: 237, pl. 41, figs. 98 and 99; Hartman 1944b: 18; Hartman 1950: 110; Pettibone 1963: 194, fig. 47E; Hartman 1968; Nonato and Luna 1970: 71, figs. 27-31; Fauchald 1972: 92, pl. 16, fig. G; Perkins and Savage 1975; Fauchald and Reimer 1975; Fauchald 1976: 18; Fauchald 1977: 34; Taylor 1984: 35-11, figs. 35-7 and 8A-E; Lana 1986: 139, figs. 4 and 5; Ibarzábal 1986; Laverde-Castillo 1986; Laverde-Castillo and Ródriguez-Gómez 1987; Gobin 1990; Hernández-Alcántara and Solís-Weiss 1991; cf. Kirkegaard 1995: 39; Rizzo and Amaral 2007: 261, fig. 4.
Nephtys assimilis Hartman 1940: 239, pl. 39, figs. 87 and 88 (not Örsted, 1843).
Nephtys picta Day 1973: 43; Gardiner 1976: 154, fig. 16A-B (not Ehlers, 1868).

Type locality. Panama, E Pacific Ocean.

Material examined. Atlantic Ocean, Brazil: 23º22.03’S, 44º52.39’W, 10 m, 25 Aug 2001, 1 incomplete spm (ZUEC BPO-AR844).

Distribution. Atlantic Ocean (Massachusetts to Florida, Gulf of Mexico, Gulf of Paria Brazil); Pacific Ocean (S California to Ecuador) (Hartman 1940, 1950; Pettibone 1963; Fauchald 1972; Taylor 1984; Lana 1986; Gobin 1990; Rizzo & Amaral 2007). There are further reports of this species from SW Africa (537 m depth), Bali Sea (1160 m depth) and Makassar Strait (1560 m depth) (Kirkegaard 1995) but these records require confirmation. Records from Morocco (Fauvel 1936) refer to other species.

Habitat. Sand, fine sand and mud (Pettibone 1963; Lana 1986; Rizzo & Amaral 2007), 10-219.5 m depth (Hartman 1940, 1950; Pettibone 1963; Fauchald 1972; Taylor 1984; Lana 1986; Rizzo & Amaral 2007).

***Nephtys sukumoensis* Kitamori, 1960**

Figures 49N, 50; Table 22

Nephtys sukumoensis Kitamori, 1960: 1083, fig. 2.

Type locality. Sukumo Bay, Japan, W Pacific Ocean, from stomach of a fish (*Poecilopsetta plinthus*).

Remarks. The original description of *N. sukumoensis* was based on a single specimen taken from the stomach contents of a fish caught in Sukumo Bay. According to Kitamori (1960) rudimentary branchiae start to appear at chaetiger 2 as a small lobe, and are well developed, thick and foliaceous from chaetiger 5. However, on the parapodium drawing of chaetiger 2 (Kitamori 1960: 1084, Fig. 2B) there is a dorsal cirrus but there is no evidence on the presence of branchia. Furthermore, judging from the drawing of parapodium 25 (Kitamori 1960: 1084, Fig. 2C), the branchiae may be thick but not foliaceous. The only character that seems to distinguish this species from the other *Nephtys* is the presence of two pairs of eyes on the posterior part of prostomium. Nevertheless, this species should be revised with the re-examination of the holotype and the comparison with the morphologically similar species from adjacent localities.

Distribution. No information in literature.

Habitat. No information in literature.

Nephtys tulearensis Fauvel, 1919

Figures 47J, 48; Table 20

Nephtys tulearensis Fauvel, 1919a: 422, pl. 16, figs. 31-39; Fauvel 1919b: 33, fig. 1. Wesenberg-Lund 1949: 292.
Nephtys (Nephtys) tulearensis Day 1967: 345, fig. 15.2J-M.

Type locality. Tulear, Madagascar, W Indian Ocean.

Material examined. Indian Ocean, Madagascar: Mozambique Channel, Tulear, 1 complete spm, syntype (NHM 1928.4.26.29).

Remarks. Apart from its smaller size, *N. tulearensis* dimly resembles the European species *N. assimilis*, by the presence of large and vascularized neuropodial postchaetal lamellae. Also the chaetigers where branchiae start and end, and the number and arrangement of pharynx subterminal papillae are similar in both species. However, branchiae shape is very different. In *N. tulearensis* the branchiae of middle and posterior parapodia have a well-developed dorsal membranous expansion (Figure 46J), which is absent in *N. assimilis*. In the original and subsequent descriptions of *N. tulearensis* nothing was mentioned regarding the pharynx proximal region. In the syntype examined within this study the pharynx proximal region is covered with very small warts (only visible under compound microscope). This characteristic is another difference from *N. assimilis* that has a smooth pharynx proximally.

Distribution. Indian Ocean (Gulf of Iran; Madagascar; Mozambique to S Cape) (Fauvel 1919a; Wesenburg-Lund 1949; Day 1967).

Habitat. No information in literature.

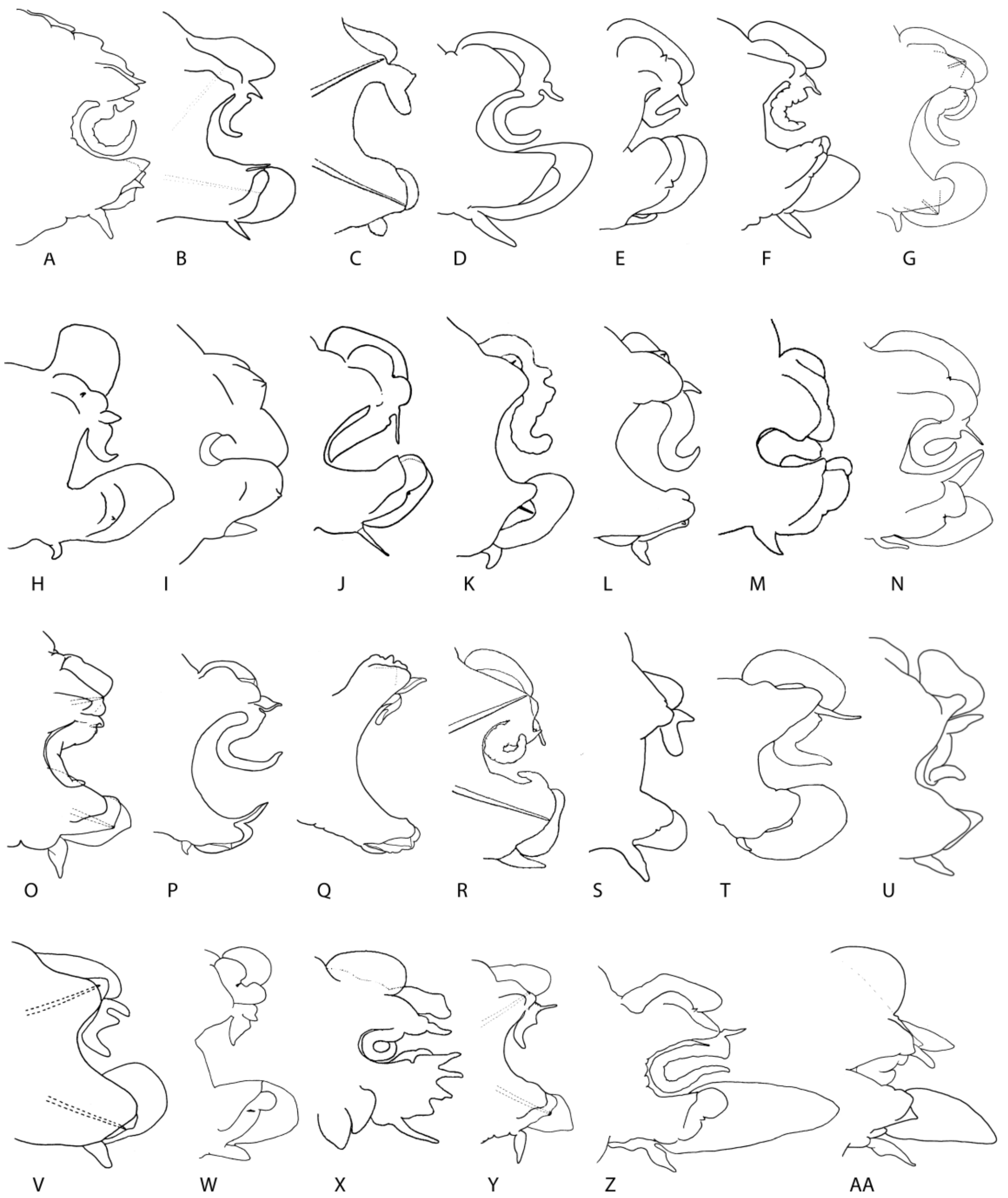


Figure 45. Parapodia of *Nephtys*. Species from N and S America. A. *N. acrochaeta*, chaetiger 36, AV (Hartman 1950); B. *N. bilobatus*, chaetiger 20, AV (Kudenov 1975); C. *N. brevibranchis*, chaetiger 32, AV (Hartmann-Schröder 1959); D. *N. bucera*, median chaetiger, AV (Pettibone 1963); E. *N. caecoides*, chaetiger 41, AV; F. *N. californiensis*, chaetiger 20, AV; G. *N. cryptomma*, chaetiger 50, AV (Harper 1986); H. *N. discors*, median chaetiger, AV (Pettibone 1963); I. *N. ectopa*, chaetiger 38, AV (Chamberlin 1919); J. *N. ferruginea*, chaetiger 20, AV (Hartman 1940); K. *N. fluviatilis*, anterior chaetiger, AV (Monro 1937); L. *N. furcifera*, chaetiger 10, AV (Hartmann-Schröder 1959); M. *N. hudsonica*, chaetiger 33, AV (Chamberlin 1920); N. *N. impressa*, chaetiger 21, AV (Hartman 1950); O. *N. magellanica*, chaetiger 30, AV (Perkins 1980); P. *N. monroi*, chaetiger 24, AV; Q. *N. monroi*, posterior chaetiger, AV; R. *N. multicirrata*, chaetiger 45, AV (Hartmann-Schröder 1960); S. *N. oculata*, chaetiger 15, AV (Hartman 1940); T. *N. panamensis*, chaetiger 25, AV (Hartman 1940); U. *N. phyllocirra*, chaetiger 50, AV (Ehlers 1887); V. *N. picta*, median chaetiger, AV (Taylor 1984); W. *N. rickettsi*, chaetiger 10, AV (Banse 1972); X. *N. serratifolia*, median chaetiger, AV (Ehlers 1897); Y. *N. simoni*, chaetiger 23, AV (Perkins 1980); Z. *N. singularis*, chaetiger 30, AV (Hartman 1950); AA. *N. squamosa*, chaetiger 30, AV. AV – anterior view.

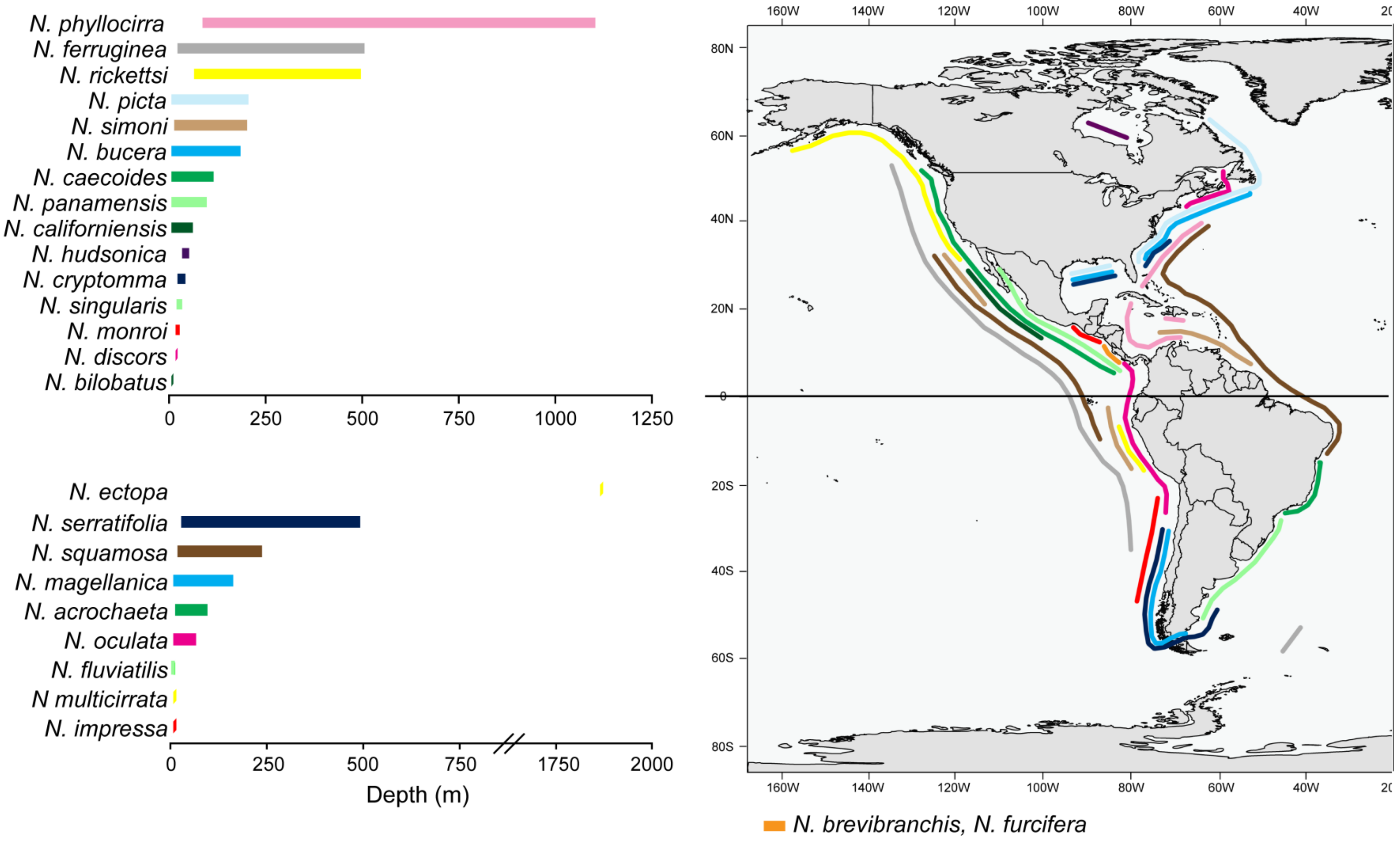


Figure 46. Bathymetrical and geographical distribution of the *Nephtys*. Species from N and S America. The position of the lines is the map is approximate and does not reflect the bathymetric range. There is no information available in literature on the bathymetric distribution of *N. brevibranchis* and *N. furcifera*.

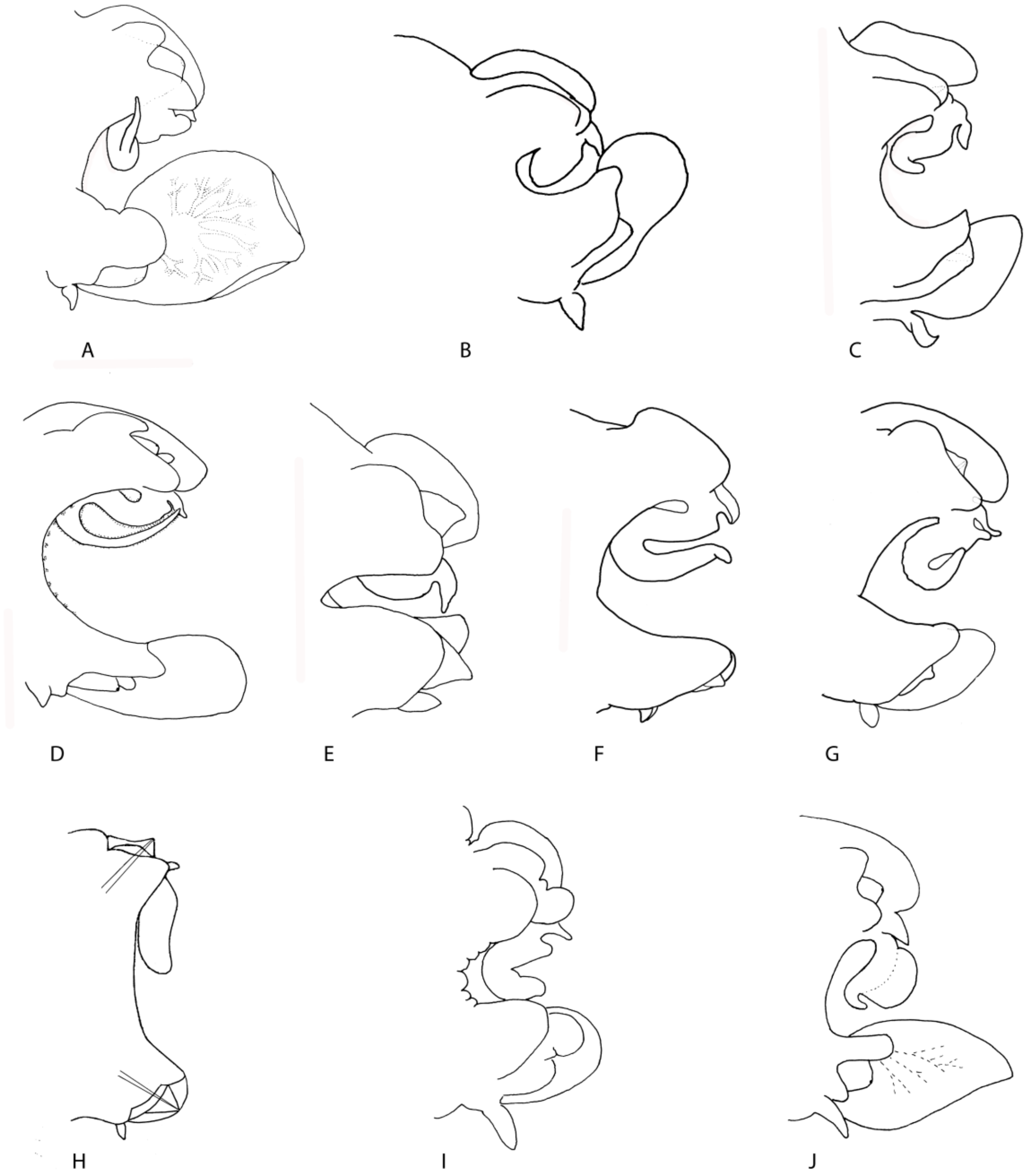


Figure 47. Parapodia of *Nephtys*. Species from Europe and Africa. A. *N. assimilis*, chaetiger 40, AV; B. *N. capensis*, chaetiger 37, AV; C. *N. cirrosa*, chaetiger 21, AV; D. *N. hombergii*, chaetiger 20, AV; E. *N. hystricis*, chaetiger 20, AV; F. *N. incisa*, chaetiger 20, AV; G. *N. kersivalensis*, chaetiger 20, AV; H. *N. palatii*, chaetiger 40, AV (Gravier 1906); I. *N. pente*, chaetiger 30, AV; J. *N. tulearensis*, chaetiger 50, AV (Fauvel 1919). AV – anterior view.

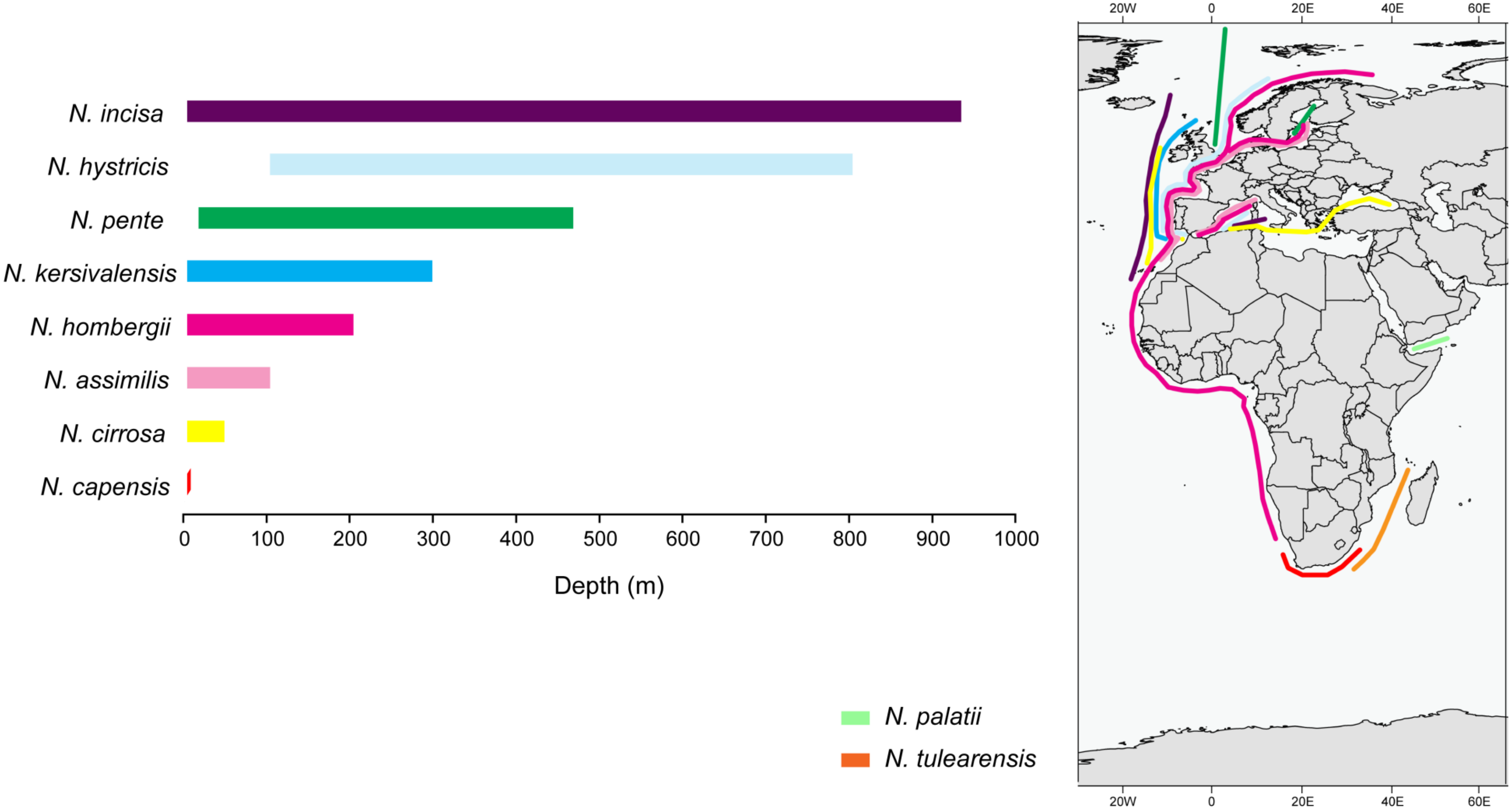


Figure 48. Bathymetrical and geographical distribution of the *Nephtys*. Species from Europe and Africa. The position of the lines is the map is approximate and does not reflect the bathymetric range. There is no information available in literature on the bathymetric distribution of *N. palatii* and *N. tulearensis*.

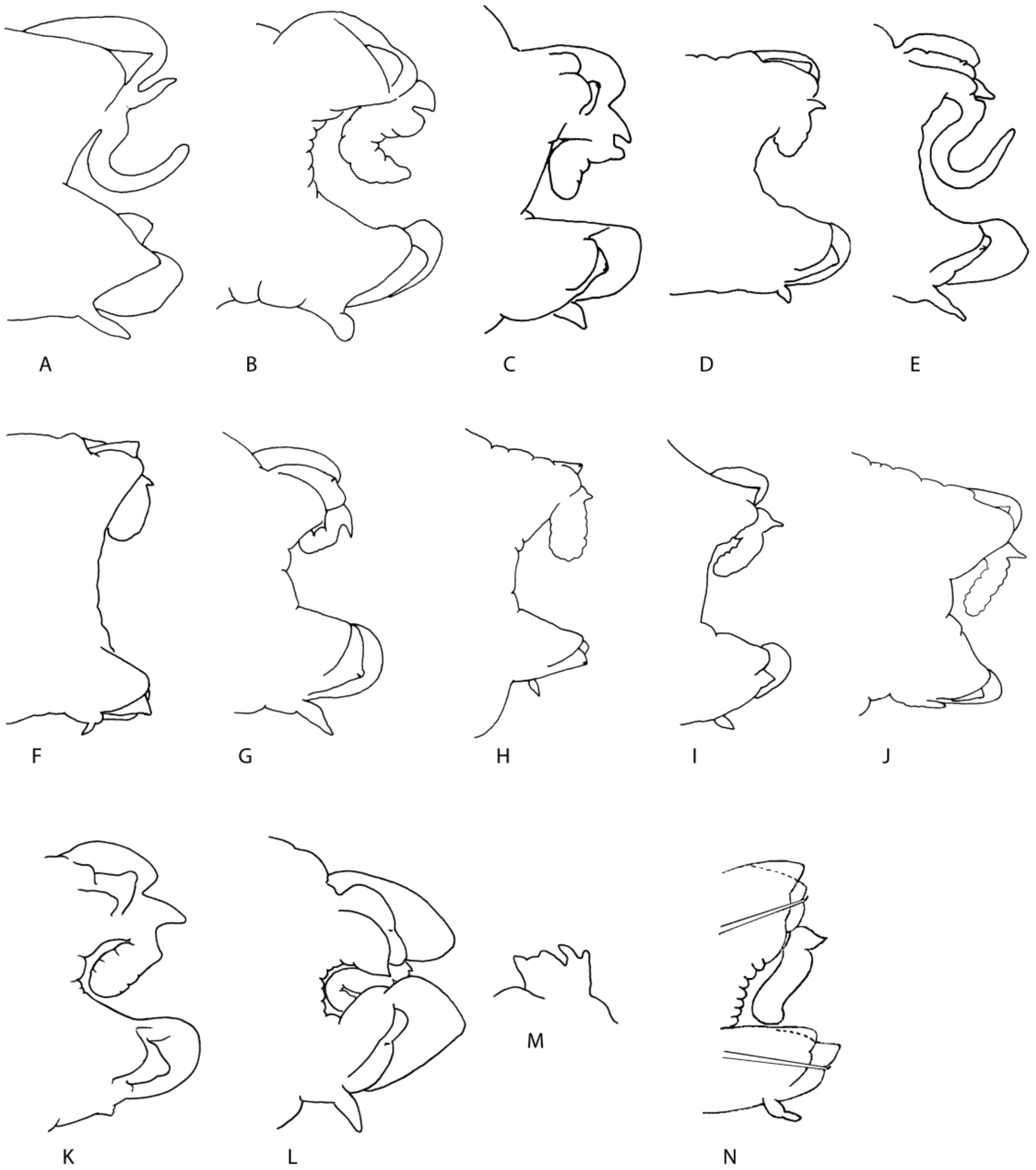


Figure 49. Parapodia of *Nephtys*. Species from Indopacific region. A. *N. bruuni*, median chaetiger, AV (Kirkegaard 1995); B. *N. chemulpoensis*, chaetiger 27, AV (Jung & Hong 1997); C. *N. gravieri*, chaetiger 21, AV (Rainer & Hutchings 1977); D. *N. inornata*, chaetiger 20, AV (Rainer & Hutchings 1977); E. *N. longipes*, chaetiger 27, AV (Rainer & Hutchings 1977); F. *N. mesobranchia*, chaetiger 20, AV (Rainer & Hutchings 1977); G. *N. neopolybranchia*, chaetiger 26, AV (Imajima & Takeda 1987); H. *N. oligobranchia*, chaetiger 13, AV (Imajima & Takeda 1987); I. *N. phasuki*, chaetiger 14, AV (Nateewathana & Hylleberg 1986); J. *N. polybranchia*, chaetiger 27, AV (Imajima & Takeda 1987); K. *N. semiverrucosa*, chaetiger 22, AV (Rainer & Hutchings 1977); L. *N. serrata*, chaetiger 25, AV (Imajima & Takeda 1987); M. *N. serrata*, dorsal cirrus of chaetiger 26 (Imajima & Takeda 1987); N. *N. sukumoensis*, parapodium of chaetiger 25, AV (Kitamori 1960). AV – anterior view.

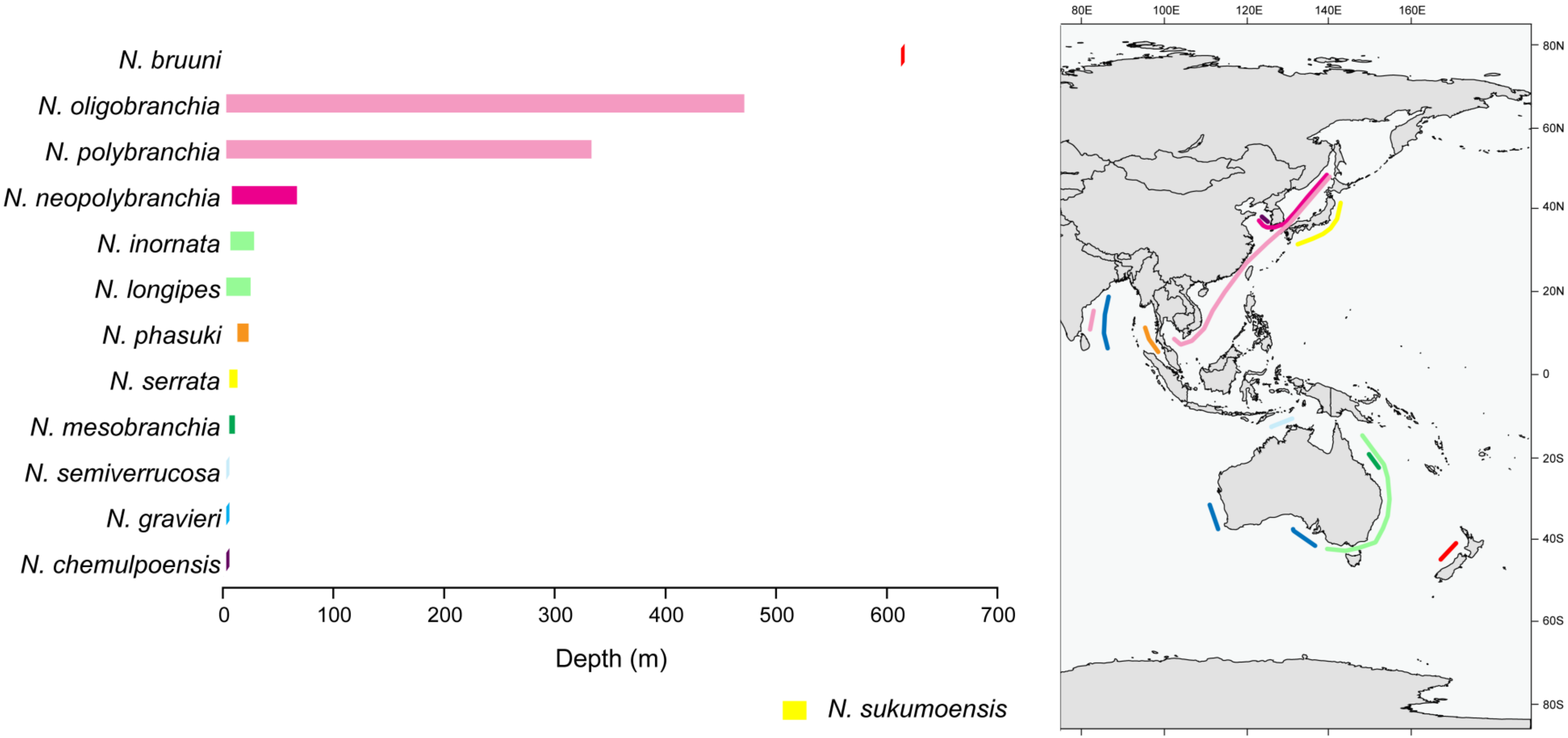


Figure 50. Bathymetrical and geographical distribution of the *Nephtys*. Species from Indopacific region. The position of the lines is the map is approximate and does not reflect the bathymetric range. There is no information available in literature on the bathymetric distribution of *N. sukumoensis*.

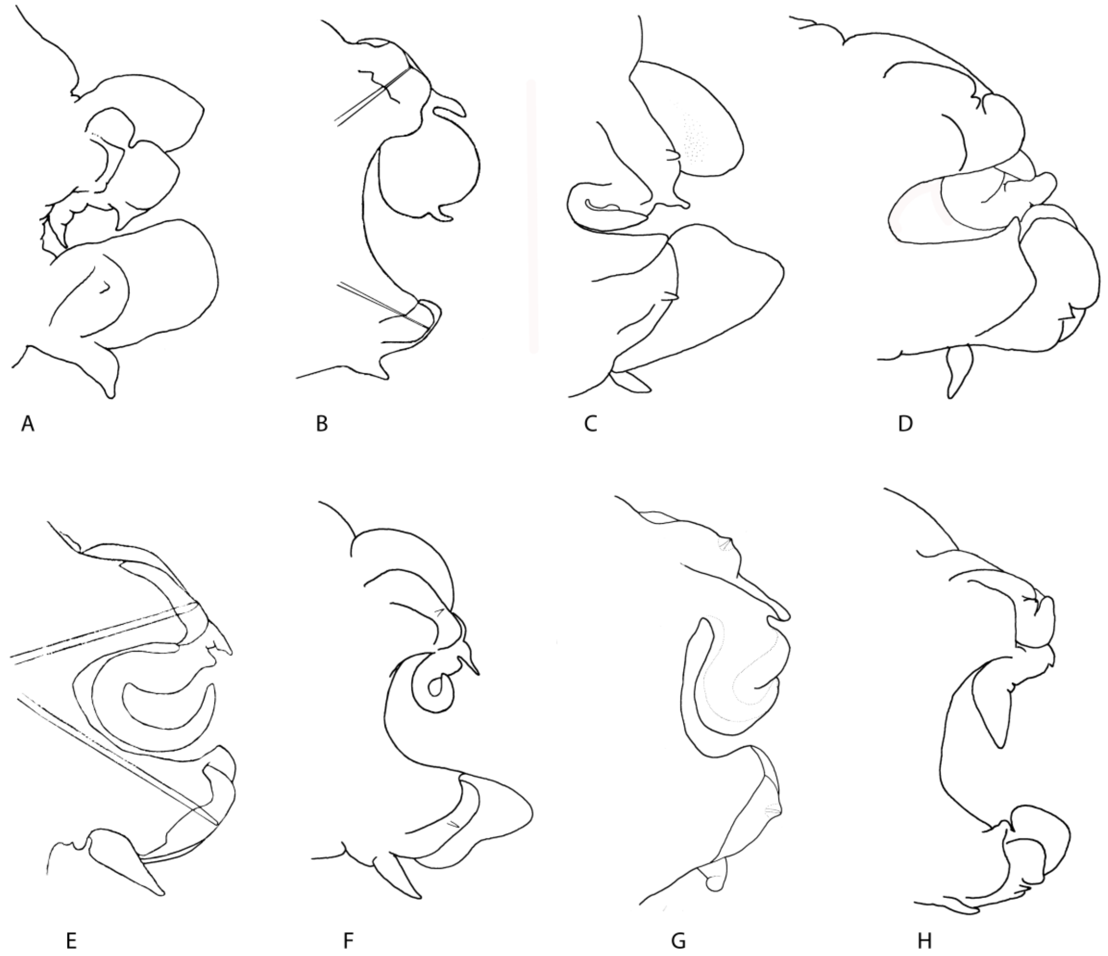


Figure 51. Parapodia of *Nephtys*. Polar and widespread species. A. *N. assignis*, chaetiger 48, AV (Hartman 1950); B. *N. brachycephala*, chaetiger 20, AV (Uschakov 1955); C. *N. caeca*, chaetiger 20, AV; D. *N. ciliata*, chaetiger 40, AV; E. *N. glabra*, chaetiger 63, AV (Hartman 1950); F. *N. longosetosa*, chaetiger 39, AV; G. *N. paradoxa*, chaetiger 29, AV; H. *N. punctata*, chaetiger 38, AV. AV – anterior view.

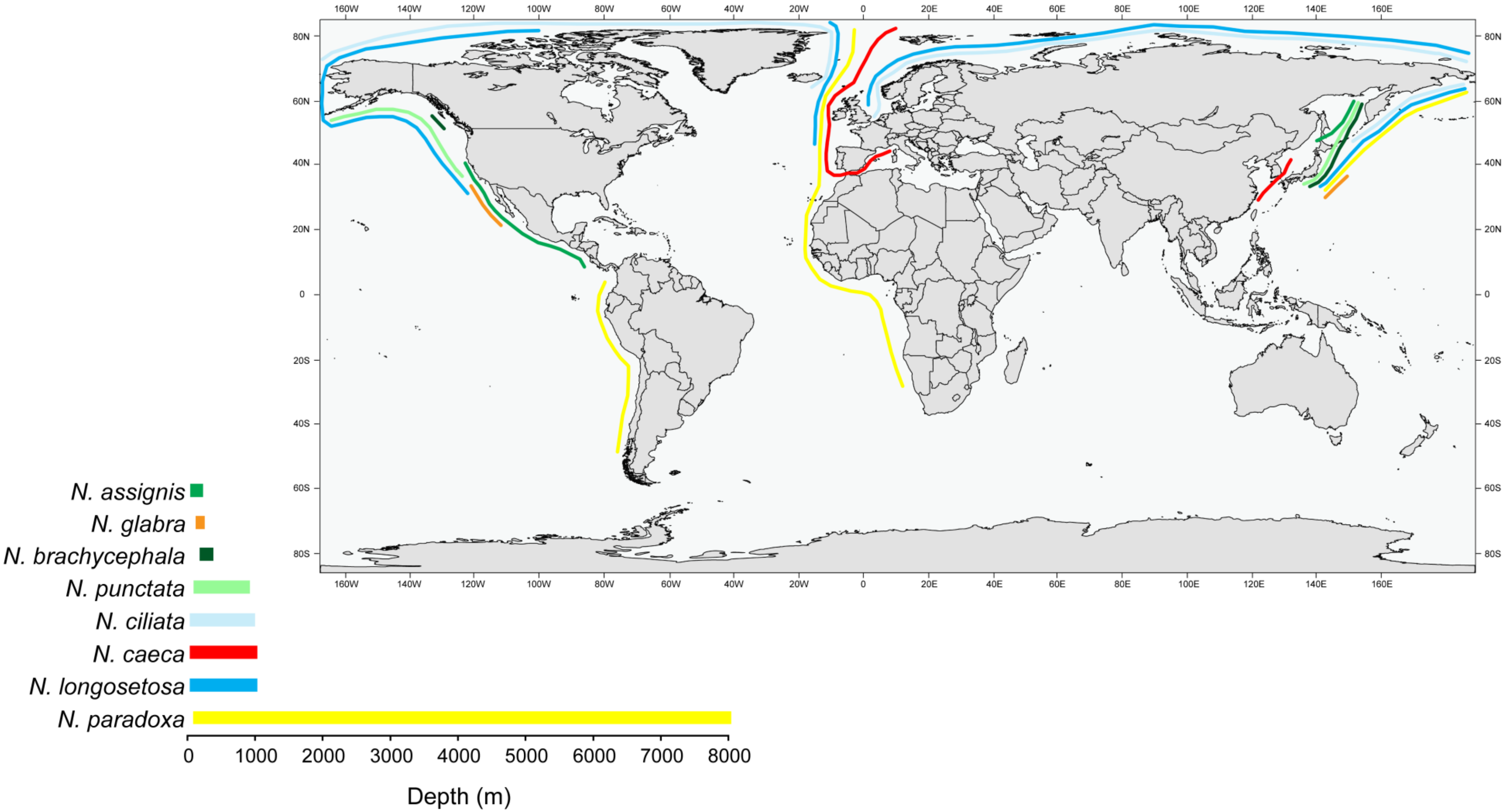


Figure 52. Bathymetrical and geographical distribution of *Nephtys*. Polar and widespread species. The position of the lines is the map is approximate and does not reflect the bathymetric range.

Table 19. Diagnostic characters of *Nephtys*. Species from N and S America. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); Ant – anterior(ly); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; NO – notopodia(l); NE – neuropodia(l); PreCh – preacicular chaetae; PosCh – postacicular chaetae; Post – posterior(ly); PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri. Pharynx subterminal papillae (| , # rows (# pap.)): | - middorsal papilla present, number of rows (number of papillae per row).

Species	Branchiae		AcL	Parapodial lamellae			DC	NE superior lobes	Pharynx		Notes
	From Ch	Until		PreL	NO PosL	NE PosL			Subterminal papillae	Proximal region	
N. acrochaeta	9-10	End of body	Acutely pointed	Rounded, < AcL	Bilobed to distally serrated, ≤ AcL	Rounded to slightly serrated, ≤ AcL	Small, conical (long, cirriform posteriorly)	Absent	20/22 (2-9)	Smooth	With dorsal scale-like expantions; antennae very small; PosCh with a basal spur
N. bilobatus	4	End of body	Slightly bilobed	Rudimentary	Rounded, > AcL	Rounded, > AcL	Conical	2 lobes (Ch. 4-30)	| , 22 (5-6)	Smooth	PreCh > PostCh on first 4 Ch
N. brevibranchis	1	?	Conical	Poorly developed	Rounded, > AcL	Rounded, > AcL	Short, botton-like	Absent	11? (6-8)	Smooth	3 pairs of prostomial eyes; Br short, straight
N. bucera	4-8	last 5	Slightly bilobed	Rounded, < AcL	Rounded, > AcL	Rounded, > AcL	Cirriform with dorsal basal expansion	Absent	| , 22 (6-8)	Smooth	PosCh long
N. caecoides	4	Near end of body	Bilobed	Poorly developed	Rounded, > AcL	Rounded, > AcL	Cirriform	Absent	| , 22 (3-6)	Smooth	"Spread-eagle" pigmentation pattern on prostomium
N. californiensis	3	End of Body	Bilobed	Rudimentary	Rounded, > AcL	Rounded, > AcL	Cirriform, slender	Absent	22 (5-8)	Smooth	"Spread-eagle" pigmentation pattern on prostomium
N. cryptomma	3	last 3	Conical	Rounded, < AcL	Rounded, > AcL	Rounded, > AcL	Digitiform, long	Absent	Long | , 22 (2-6)	Smooth	Some middle PosCh with few large basal teeth in addition to fine spines
N. discors	6	Near end of body	NO – bilobed; NE – slightly bilobed/rounded	Rudimentary	Rounded >> AcL	Rounded >> AcL	Triangular, pointed	Absent	22 (4-6)	With warts	Br rudimentary in posterior half of body
N. ectopa	?	?	Conical/rounded (?)	Rudimentary	Rounded, < AcL (?)	?	?	Absent ?	21 (5)	Smooth	
N. ferruginea	3	End of body	Ant – bilobed; Post - conical	Rudimentary	Rounded, ≥ AcL	Rounded, ≥ AcL	Cirriform, slender	Absent	| , 22 (3-6)	Smooth	"Spread-eagle" pigmentation pattern on prostomium; longitudial rows of pigmentation on dorsum; Br short, heavily ciliated
N. fluviatilis	4-5	36-42	Conical	Rudimentary	Rounded, > AcL	Rounded, > AcL	Small, papiliform	Absent	Long | , 20-21 (numerous)	Smooth	1 pair of prostomial eyes; antennae << palps; PosCh denticulated basally

N. furcifera	7	last 24	Conical	Rounded, < AcL	Rounded, ≤ AcL	Rounded, ≤ AcL	Small, conical	Absent	?	?	Lyriform chaetae present ?
N. hudsonica	?	?	Bilobed	Rounded, < AcL	Rounded, < AcL	Rounded, < AcL	Conical to cirriform	Absent ?	Long | , 22 (?)	Smooth ?	
N. impressa	4	End of body	Bilobed	Rounded, < AcL	Rounded, ≥ AcL	Rounded, ≥ AcL	Cirriform	lamelliform (Ch 4-80)	| , 22 (6-9)	Smooth	
N. magellanica	3	End of body	Indistinctly bilobed	Rounded, < AcL / Rudimentary	Rounded, > AcL	Rounded with slightly pointed tip, > AcL	Cirriform, slender	Absent	| , 20-22 (4-9)	Smooth	Br occupying 2/3 of the interramal space; PosCh coarsely spinulated
N. monroi	8	Near end of body?	Conical	Slightly bilobed /rounded, ≤ AcL	Rounded, ≥ AcL	Rounded, ≥ AcL	Short, broad with acute tip	lamelliform (15-60)	?	?	
N. multicirrata	3	End of body	Rounded/slightly bilobed	Rudimentary ?	Rounded, > AcL	Rounded, > AcL	Cirriform	Papiliform (all Ch)	22 (7-8)	Smooth	
N. oculata	2	End of body	Rounded/slightly bilobed	Poorly developed ?	Rounded, > AcL	Rounded, > AcL	Short, conical	Large (ant. Ch)	22 (4-6)	Smooth	1 pair of big eyes in ch 3; PosCh 3-5 times length PreCh
N. panamensis	3	?	Conical	Slightly bilobed, ≥ AcL	Rounded, > AcL	Rounded, >> AcL	Cirriform	Absent	Long | , 22 (1-5)	Smooth	Dark bands of pigmentation dorsally; PosCh coarsely spinulated
N. phyllocirra	6	?	Conical	Poorly developed ?	Rounded > AcL	Elongated > AcL	Conical	Absent ?	22 (?)	?	PosCh long, coarsely spinulated
N. picta	3-4	last 4-5	Bilobed	Rounded, ≤ AcL	Rounded, > AcL	Rounded, > AcL	Cirriform	Absent	Long | , 22 (3-5 / 5-6)	Smooth	Anterior dorsum with pigment bars; jaws amber colored; PosCh short and coarsely serrated at the base
N. rickettsi	6 (rudim.)	End of Body	NO – Bilobed; NE – rounded	Rudimentary	Rounded, > AcL	Roughly triangular, > AcL	Short, globular with conical tip	Absent	22 (4-5)	With wrinkles	NE AcL with outgrouth near acicula
N. serratifolia	3-4	?	?	?	Elongated, > AcL	With up to 5 lobes, > AcL	Conical to cirriform with broad base	Present ?	15 (6-7)	Smooth?	With dorsal scale-like expantions; palps > ant; Posch with a basal spur
N. simoni	3	End of body	Indistinctly bilobed	Rounded, < AcL/ Rudimentary	Rounded, >> AcL	Triangular, >> AcL	Cirriform, slender	Absent	| , 22 (4-8)	Smooth	Br occupying 1/3 of the interramal space; PosCh coarsely spinulated
N. singularis	4	Near end of body	Bilobed	Poorly developed	Rounded, > AcL	Elongated, >> AcL	Cirriform	Present (Ch 4-12/18)	22 (7-8)	Smooth	PosCh lightly spinulated
N. squamosa	3-4	Near end of body	Conical	NO-rounded, < AcL; NE-Triangular, ≥ AcL	Elongated, > AcL	Elongated, >> AcL	Long, cirriform	Present	| , 22 (5-6)	Smooth	With dorsal and ventral scale-like expantions (from about Ch. 10)

Table 20. Diagnostic characters of *Nephtys*. Species from Europe and Africa. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; NO – notopodia(l); NE – neuropodia(l); PreCh – preacicular chaetae; PosCh – postacicular chaetae; PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri. Pharynx subterminal papillae (| , # rows (# pap.)): | - middorsal papilla present, number of rows (number of papillae per row).

Species	Branchiae		AcL	Parapodial lamellae			DC	NE superior lobes	Pharynx		Notes
	From Ch	Until		PreL	NO PosL	NE PosL			Subterminal papillae	Proximal region	
N. assimilis	4	End of body	Conical with outgrouth	Bilobed, ≤ AcL	Rounded, > AcL	Rounded, >> AcL, vascularized	Short, conical	Absent	| , 20-22 (2-5)	Smooth	Interramal space with ciliated pads
N. capensis	4	End of body	Broadly conical	NO – rudimentary; NE – elongated, ≤ AcL	Rounded, > AcL	Rounded, >> AcL, vascularized	Conical	Absent	| , 22 (3-7)	Smooth ?	Br with dorsal membrane; PosCh of two types – long and very finely spinulated, and short and coarsely serrated.
N. cirrosa	4	Near end	Rounded to conical	Rounded, < AcL	Rounded, > AcL	Rounded, > AcL	Cirriform, as long as Br in post. Ch	Absent	22 (4-9)	Smooth	--
N. hombergii	4-5	End of body	Conical with outgrouth	Bilobed, ≤ AcL	Rounded, > AcL	Rounded, >> AcL	Short, conical	Absent	| , 22 (2-5)	Smooth	--
N. hystricis	5-7	Before end	Conical	Slightly bilobed, < AcL	Rounded, > AcL	Rounded, > AcL	Conical	Absent	Long | , 22 (3-6)	Smooth	--
N. incisa	9-10	Before end	Conical	Rounded, ≈ AcL	Rounded, ≈ AcL	Rounded, ≈ AcL	Short, lamelliform	Absent	Long | , 20 (1-5)	Smooth	--
N. kersivalensis	4	End of body	Conical with rugose area near aciculae	Rounded/slightly bilobed, ≤ AcL	Rounded, > AcL	Rounded, > AcL	Short, cirriform	Absent	Long | , 22 (3-6)	Smooth	--
N. palatii	4	Last 20	Conical	Rounded/bilobed, ≤ AcL	Rounded, < AcL	Rounded, ≈ AcL	Very short, conical	Absent	Long | , 22 (5-6)	Smooth	Barred PreCh present on anterior parapodia only
N. pente	5 (rarely 6)	Near end of body	Bilobed	Poorly developed	Rounded, ≥ AcL	Rounded, ≥ AcL	Short, conical	Absent	| , 22 (3-5)	With warts	PosCh finely spinulated
N. tulearensis	4	End of body	Conical	Bilobed, ≥ AcL	Rounded, > AcL	Broadly triangular, >> AcL	Short, triangular	Absent	Long | , 22 (3-5)	With minute warts	Br from middle and posterior body with dorsal membranose expansion; PosCh short and very finely spinulayed.

Table 21. Diagnostic characters of *Nephtys*. Polar and widespread species. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; NO – notopodia(l); NE – neuropodia(l); PreCh – preacicular chaetae; PosCh – postacicular chaetae; PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri. Pharynx subterminal papillae (| , # rows (# pap.)): | - middorsal papilla present, number of rows (number of papillae per row).

Species	Branchiae		AcL	Parapodial lamellae			DC	NE superior lobes	Pharynx		Notes
	From Ch	Until		PreL	NO PosL	NE PosL			Subterminal papillae	Proximal region	
N. assignis	6 (minute until 12-20)	Near end of body	NO – bilobed; NE - rounded	Poorly developed	Rounded/elongated, > AcL	Rounded, >> AcL	Short, conical with a large base	Absent	22 (4-5)	Smooth	PosCh coarsely spinulated; blood vessel on Br with several loops
N. brachycephala	5	Before end of boby	Bilobed	Rudimentary	Rounded, ≤ AcL	Rounded, ≤ AcL	Short	Absent	22 (?)	?	Br very enlarged at the base with a cirriform tip
N. caeca	4-5	Near end of body	Rounded to bilobed	Rudimentary	Rounded, >> AcL	Rounded, >> AcL	Small, conical	Absent	22 (4-6)	With warts	--
N. ciliata	7-11	Near end of body	Bilobed	Rudimentary	Rounded, ≤ AcL	Rounded, ≤ AcL	Small, conical	Absent	| , 22 (4-6)	With warts	--
N. glabra	6/7	Near end of body	Rounded	Rounded, < AcL	Rounded, ≥ AcL	Rounded, ≥ AcL	Small, conical	Absent	Long | , 22 (1-3)	Smooth	Pharynx with trepan of 8-9 teeth
N. longosetosa	3	Near end of body	Rounded/slightly bilobed	Rudimentary	Unequaly bilobed, > AcL	"S-shaped", > AcL	Cirriform	Absent	Long | ,22 (2-7)	Smooth	--
N. paradoxa	9-14	Before	Rounded with conical	Poorly developed	Poorly developed	Poorly developed	Lamelliform, Short	Absent	| , 22 (4-6)	Wrinkled	Br foliaceous
N. punctata	8-9	~last 20	Bilobed ant.	Poorly developed	Rounded, ≥ AcL	Rounded, > AcL	Conical with cirriform tip	Absent	Long | ,22 (4-5)	With warts	--

Table 22. Diagnostic characters of *Nephtys*. Species from Indopacific region. Unless other way stated the observations on parapodial lamellae refer to fully developed parapodia on median chaetigers. AcL – acicular lobe(s); Ant – anterior(ly); Br – branchia(e); Ch – chaetiger(s); DC – dorsal cirri; Median – median; NO – notopodia(l); NE – neuropodia(l); PreCh – preacicular chaetae; PosCh – postacicular chaetae; PreL – prechaetal lamellae; PosL – postchaetal lamellae; VC – ventral cirri. Pharynx subterminal papillae (| , # rows (# pap.)): **|** - middorsal papilla present, number of rows (number of papillae per row).

Species	Branchiae		AcL	Parapodial lamellae			DC	NE superior lobes	Pharynx		Notes
	From Ch	Until		PreL	NO PosL	NE PosL			Subterminal papillae	Proximal region	
N. bruuni	7	?	Conical	NO-rudimentary; NE-triangular, ≤ AcL	Rounded, > AcL	Rounded, > AcL	Long, cirriform	Absent	?	?	PosCh lightly spinulated
N. chemulpoensis	9	End of body ?	Rounded/slightly bilobed	Rounded, < AcL	Slightly bilobed, ≥ AcL	Rounded, ≥ AcL	Rounded	Absent	| , 22 (1-4)	Smooth	--
N. gravieri	3	End of boby	Conical with outgrouth	Rounded, < AcL	Rounded, > AcL	Rounded, > AcL	Digitiform	Absent	22 (6-10)	With warts	Br short, almost straight; barred PreCh present on ant Ch only (8-17)
N. inornata	5	End of body ?	Conical	Rounded, ≤ AcL	Rounded, > AcL	Rounded, > AcL	Short, conical	Absent	20 (4-7)	Smooth	1 pair of eyes on Ch 1-4 (adults); jaws with secondary tooth; barred PreCh present on ant Ch only (14-15)
N. longipes	3	last 8-10	Rounded with outgrouth on NO	Rounded, < AcL	Rounded, ≥ AcL	Rounded, > AcL	Short, digitiform	Absent	22 (5-7)	With warts	Prostomium with a triangular pre-antennal lobe; Ch 1 greatly prolonged
N. mesobranchia	7(8)	last 22-28	Conical	Rounded, < AcL	Rounded, < AcL	Rounded, ≤ AcL	Short, conical	Absent	| , 18 (10-12)	Smooth	1 pair of eyes on Ch 2/3 (adults); Br short, straight; interramal space with ciliated pads
N. neopolybranchia	3	End of body	Rounded	Rounded, ≤ AcL	Rounded/elongated , >> AcL	Rounded, > AcL	Short, conical	Absent	22 (5-7)	With warts	Nuchal organs not visible
N. oligobranchia	4-6 (rudim. until 7-8)	last 20-27	Conical	Rounded, < AcL	Rounded, < AcL	Rounded, < AcL	Very short, digitiform	Absent	Long | , 22 (6-9)	Smooth	--
N. phasuki	5	?	Conical	Rounded, < AcL	Rounded, > AcL	Rounded, > AcL	Cirriform with broad base	Absent	?	Smooth	Barred PreCh present on ant and med Ch only (16)
N. polybranchia	4-5	End of body	Conical	Rounded, ≤ AcL	Rounded, ≥ AcL	Rounded, ≥ AcL	Short, conical	Absent	22 (6-10)	With warts	--
N. semiverrucosa	4	Near end	Conical with	NO – Rounded;	Rounded, > AcL	Rounded, > AcL	Short, conical	Absent	22 (4-7)	With basal	Prostomium with a small

			outgrouth on NO	NE - bilobed						ring of warts	triangular expansion ant; barred PreCh present on ant and med Ch only (28)
N. serrata	4-5	Near end	Bilobed	Rounded, < AcL	Elongated, >> AcL	Broadly triangular, >> AcL	Broad base, serrated distaly	Absent	22 (3-4)	With warts	--
N. sukumoensis	2? (rudim. until 5)	last 5	Bilobed	Bilobed ?, < AcL	?, < AcL	?; < AcL	Conical	Absent	20 (4-7)	?	2 pairs of eyes in prostomium; barred PreCh present on ant Ch only (8)

List of invalid names

Aglaopheme Kinberg, 1866 – see *Aglaophamus*

Aonis Savigny, 1822 – see *Nephtys*

Dentinephtys Imajima and Takeda, 1987 – see *Nephtys*

Diplobranchus Quatrefages, 1865 – see *Nephtys*

Nephthys Savigny, 1822 – see *Nephtys*

Portelia Quatrefages, 1865 – see *Nephtys*

Aglaophamus bathamae Knox, 1960 - *nomen nudum*

Aglaophamus dicirris Hartman, 1945 – see *A. verrilli*

Aglaophamus lobophora (Hartman, 1940) – see *A. polypharus*

Aglaophamus mirasetis (Hoagland, 1920) - questionable *A. dibranchis* (Hartman 1950)

Aglaophamus ornatus Hartman, 1967 – *A. trissophyllus*

Aglaophamus spiribranchis (Ehlers, 1918) - indeterminable (Hartman 1950)

Micronephthys maryae San Martin, 1982 - see *M. stammeri*

Nephtys atlantica Hansen, 1878- see *Aglaophamus malmgreni*

Nephtys bononensis Quatrefages, 1865 - see *N. caeca*

Nephtys borealis Örsted, 1843 - see *N. ciliata*

Nephtys canadensis McIntosh, 1900 - questionable (Hartman 1950)

Nephtys breogani Laborda & Vieitez, 1984 – see *N. assimilis*

Nephtys cuvieri Quatrefages, 1865 - see *N. assimilis*

Nephtys digitifera Augener 1933 – see *Aglaophamus lyratus*

Nephtys dussumieri Quatrefages, 1865 - indeterminable (Hartman 1950)

Nephtys edwardsii delle Chiaje, 1828 – indeterminable (Hartman 1950)

Nephtys ehlersi Heinen, 1911 – see *N. cirrosa*

Nephthys emarginata Malm, 1874 - see *N. longosetosa*

Nephtys glossophylla Schmarda, 1861 - indeterminable (Hartman 1950)

Nephtys grubei McIntosh, 1908 – see *Aglaophamus Malmgreni*

Nephtys hirsuta Dalyell, 1853 - questionably *N. caeca* (Hartman 1950)

Nephtys imbricata Grube, 1856 - incompletely known (Hartman 1950)

Nephtys ingens Stimpson, 1853 - see *N. caeca*

Nephthys Johnstoni Ehlers, 1874 - see N. longosetosa

Nephthys laciniosa Grube, 1881 - indeterminable (Hartman 1950)

Nephtys lacinosa - misspelling of N. laciniosa

Nephtys lactea Malmgren, 1868 - indeterminable (Hartman 1950)

Nephthys langerhansi Czerniavsky, 1882 – *N. hombergii* (Hartman 1959)

Nephtys lawrencii McIntosh, 1900 - questionable (Hartman 1950)

Nephtys maeotica Czerniawsky, 1882 - see *N. hombergii* (Hartman 1950)

Nephthys margaritacea Johnston, 1835 - see *N. caeca*

Nephthys macandrewi Baird, 1873 - see *N. hombergii*

Nephtys macrura Benham, 1915 - see *Aglaophamus profundus*

Nephtys mirocirris Fauchald, 1965 - see *N. gravieri*

Nephtys modesta Grube, 1878 - incompletely known (Hartman 1950)

Nephtys monilibranchiata Rozbaczylo and Castilla, 1974 – see *N. impressa*

Nephthys neopolitana Grube, 1840 - see *N. hombergii*

Nephtys nudipes Ehlers, 1868 - see *N. caeca*

Nephtys oerstedii Quatrefages, 1865 – see *N. caeca*

Nephtys pansa Ehlers, 1875 – see *N. paradoxa*

Nephtys parva Clarck & Jones, 1955 – see *N. cornuta*

Nephthys phyllobranchia McIntosh, 1885 - see *N. paradoxa*

Nephtys praeticosa Kinberg, 1886 – see *A. virginis*

Nephthys scolopendroides delle Chiaje, 1828 - see *N. assimilis* (partim); *N. hombergii* (partim)

Nephtys schmitti Hartman, 1938 – see *N. Paradoxa*

Nephtys signifera Hilbig, 1992 – see *N. ferruginea* (Lovell 1997)

Nephtys spendida Blainville, 1825 – indeterminable (Hartman 1959)

Nephtys vikingensis Paxton, 1974 – see *N. longipes*

Nephtys zatsepini Jirkov, 1986 - see *N. pente*

Portelia rosea Quatrefages, 1866 - see *Nephtys cirrosa*

Portelia quatrefagesi Kinberg, 1866 - incompletely known (Hartman 1965)

3.2.5 Discussion

Nephtyids are known as a family since 1850. However, the taxonomical relationships between the species were not always clear. The morphological features used to define individual species went through some alterations as new species were described. At present, the species distinction is based mostly on branchiae shape and placement along the body, parapodial features (acicular lobes shape, dorsal and ventral cirri and lamellae shape and proportions), and pharynx papillae number and arrangement. Secondary characteristics are used to confirm identity and distinguish morphologically closer species. Among these, the antennae and palps shape and placement, length proportions of dorsal and ventral cirri of the first chaetiger, and presence or absence of lyriform chaetae are often used. There are also atypical characteristics for some species such as the presence of prostomial eyes, spinulose preacicular chaetae on posterior chaetigers, modified chaetae, dorsal expansions near base of parapodia, and pigmentation patterns. Some characteristics show a clear geographical pattern, such as the foliaceous dorsal cirri of some subantarctic species, the presence of warts in the proximal region of the pharynx of many *Aglaophamus* species from the Indopacific region as well as spinulated preacicular chaetae on posterior chaetigers of several *Nephtys* species from the same region, and the “spread-eagle” pigmentation pattern on the prostomium of several *Nephtys* species from northeastern Pacific Ocean. The latter, form a group of morphologically very close species, difficult to distinguish, and with similar geographical and bathymetric distributions, although eventually different habitats. The same happens with other groups of species from other local geographical areas. Therefore the identification and description of a species must always include a set of several different characters, along with distribution and habitat preferences, whenever possible. This is not always the case, especially for the older references. Thus many doubts remain upon many records and even recently described species. A significant part of the nephtyid species presently accepted is known only from its original description, often based on a single specimen. And many others are only reported in old references, often with poor information. Furthermore, the given geographical distribution of some species (e.g. *Aglaophamus dibranchis*, *A. elamellatus*, *A. verrilli*, *Inermonephtys inermis*, *Micronephthys minuta*, *M. sphaerocirrata*, *M. stammeri*, *N. hombergii*, *N. paradoxa*) appears to be exceptionally wide, leading to hypothesize that each one of this species may in fact represent a species-group. This denotes the need of further revision within the nephtyid family. In the past 50 years several local revisions on nephtyid taxonomy covering different world areas have been made (see Annex II). However, there are still many areas not covered (particularly in Indian Ocean), and species that need reassessment. Within those studies, especially the most recent ones, much of the old museological material has been revised leading to the elucidation of many doubts and the erection of new species. Some material was also revised within this study. But still much material remains misidentified.

References

Andrews, E. A. (1891). Report upon the Annelida Polychaeta of Beaufort, North Carolina. *Proceedings of The United States National Museum*, 14, 277–302 & pl. XII–XVIII.

Augener, H. (1906). Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and the Caribbean Sea, and on the east coast of the United States, l877 to l880, by the U.S. Coast Survey Steamer Blake, Lieut. Commander C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N. commanding. 42. Westindische Polychaeten. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 43, 91–196.

Augener, H. (1913). Polychaeta I, Errantia. *Die Fauna Südwest-Australiens*, 4, 65–304.

Augener, H. (1913 (1912)). Beitrag zur kenntnis verschiedener anneliden und bemerkungen uber die nordischen nephthys-arten und deren epitoke formen. *Archiv fur Naturgeschichte, Berlin*, 78A, 162–212.

Augener, H. (1918). Polychaeta. *Beiträge zur Kenntnis der Meeresfauna Westafrikas*, 2, 67–625.

Augener, H. (1922). Australische polychaeten des Hamburger Zoologischen Museums. *Arch. Naturgesch. Berlin*, 88, 1-37.

Augener, H. (1927). Polychaeten von Südost- und Süd-Australien. Papers from Dr Th. Mortensen's Pacific Expedition 1914-16. *Vidensk. Meddr dansk naturh. Foren.*, 83, 71-275.

Augener, H. (1933). Polychaeten aus den Zoologischen Museum von Leiden und Amesterdam I. *Zoologische Mededelingen*, 15, 177-260.

Baird, M. D. (1871). Description of some new species of annelida and gephrea in the collection of the British Museum. *Journal of the Linnean Society of London*, 11, 94–97.

Banse, K. (1972). On some species of Phyllodocidae, Syllidae, Nephtyidae, Goniadidae, Apistobranchidae, and Spionidae (Polychaeta) from Northeast Pacific Ocean. *Pacific Science*, 26, 191-222.

Banse, K., & Hobson, K. (1974). Benthic errantiate polychaetes from British Columbia and Washington. *Bulletin of the Fisheries Research Board of Canada*, 185, 1–111.

Banse, K., & Nichols, F. H. (1968). Two new species and three new records of benthic polychaetes from Puget Sound (Washington). *Proceedings of the Biological Society of Washington*, 81, 223–230.

Bastida-Zavala, J. R. (1993). Taxonomía y composición biogeográfica de los poliquetos (Annelida: Polychaeta) de la Bahía de La Paz, B.C.S., México. *Revista de Investigación Científica*, 4, 11-39.

Bellan, G. (1974). Polychètes (Serpulidae exclues) des Terres Australes et Antarctiques Françaises. 2. Récoltes L. C. Hureau et P. M. Arnaud aux Isles Kerguelen. *Tethys (Suppl.)*, 6, 779-798.

Benham, W. B. (1915). *Report on the Polychaeta obtained by the F.I.S. 'Endeavour' on the coasts of New South Wales, Victoria, Tasmania and South Australia, Part 1*. Sydney: H.C. Dannevig.

Benham, W. B. (1916). Report on the Polychaeta obtained by the F.I.S. Endeavour on the coasts of New South Wales, Victoria, Tasmania and South Australia. Part II. *Fisheries. Zoological (and Biological) results of the Fishing Experiments carried out by F.I.S. "Endeavour", 1909-1914*, 4, 127–162.

Berkeley, C. (1966). Records of some species of Polychaeta new to British Columbia and of extensions in distribution of some others. *Can. J. Zool.*, 44, 839-849.

Berkeley, E. (1924). Polychaetous annelids from the Nanaimo district. Part 2. Phyllodocidae to Nereidae. *Contributions to Canadian Biology and Fisheries*, 2, 287–293.

Berkeley, E., & Berkeley, C. (1935). Some notes on the polychaetous annelids at Elkhorn Slough, Monterey Bay, California. *American Midland Naturalist*, 16, 766–775.

Berkeley, E., & Berkeley, C. (1942). North Pacific polychaeta, chiefly from the west coast of Vancouver Island, Alaska and Bering Sea. *Canad. Jour. Research*, 20, 183-208.

Berkeley, E., & Berkeley, C. (1945). Notes on polychaeta from the coast of western Canada. III. Further notes on Syllidae and some observations on other polychaeta Errantia. *Annals and Magazine of Natural History, London*, 12, 316-335.

Berkeley, E., & Berkeley, C. (1948). Canadian Pacific Fauna. 9. Annelida. 9b(1) Polychaeta Errantia. *Fish. Res. Bd. Canada*, 1–100.

Chamberlin, R. V. (1919). The annelida polychaeta (In: Reps. Sci. Res. Expeds. U. S. Fish. Steamer "Albatross", 1891, 1899-1900 and 1904-1905). *Memoirs of the Museum of Comparative Zoology at Harvard College*, 48, 1-514.

Chamberlin, R. V. (1920). Annelids, parasitic worms, protozoans, etc. Part B. Polychaeta. *Report of the Canadian Arctic Expedition 1913-1918*, 9, 1–41.

Clark, R. B. (1956). The eyes and photonegative behaviour of Nephtys (Annelida, Polychaeta). *Journal of experimental biology*, 33, 461–477.

Clark, R. B. (1957). The influence of size on the structure of the brain of *Nephtys*. *Zoologische Jahrbücher (Abteilung für Allgemeine Zoologie und Physiologie der Tiere)*, 67, 261–282.

Clark, R. B., & Jones, M. L. (1955). Two new Nephthys (Annelida, Polychaeta) from San Francisco Bay. *Journal of the Washington Academy of Sciences*, 45, 143-146.

Day, J. H. (1953). The polychaete fauna of South Africa. Part 2. Errant species from Cape shores and estuaries. *Annals of the Natal Museum*, 12, 397–441.

Day, J. H. (1967). *A monograph on the Polychaeta of southern Africa. Part 1. Errantia*. London: Trustees of the British Museum (Natural History).

Day, J. H. (1973). New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. *NOAA Technical Report NMFS*, 375, 1–140.

De Silva, P. H. D. H. (1965). New species and records of polychaeta from Ceylon. *Proc. Zool. Soc. Lond.*, 144, 537-563.

Dean, H. K. (1996). Polychaete worms (Annelida) collected in Golfo Dulce, during the *Victor Hensen* Costa Rica expedition (1993/1994). *Revista de Biologia Tropical, suplemento 3*, 44, 82-86.

Ehlers, E. (1868). *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt*. Leipzig: Wilhelm Engelmann.

Ehlers, E. (1887a). Report on the annelids of the dredging expedition of the U. S. coast survey steamer Blake. *Memoirs of the Museum of Comparative Zoology at Harvard College*, 15, 1-335.

Ehlers, E. (1887b). Reports on the annelids of the dredging expedition of the U.S. coast survey steamer “Blake“. *Memoirs of the Museum of Comparative Zoology of Harvard College*, 15, 1–335.

Ehlers, E. (1897). *Hamburger Magelhaenischen Sammelreise. Polychaeten.* Hamburg: Friedrichsen and Co.

Ehlers, E. (1901). Die Polychaeten des magellanischen und chilenischen Strandes. Ein faunistischer Versuch. *Festschrift zur Feier des Hundertfünfzigjährigen bestehens der königlischen Gesellschaft der Wissenschaft zu Göttingen*, 1–232.

Ehlers, E. (1905). Neuseeländische Anneliden. *Abhandlungen der Königlichen Gesellschaft der Wissenschaften zu Göttingen*, 3, 1–80.

Ehlers, E. (1913). Die polychaeten-sammlungen der deutschen Suedpolar-expedition 1901-1903. *Deutsche Suedpolarexpedition*, 13, 197-598.

Fabricius, O. (1780). *Fauna Groenlandica, systematica sistens, Animalia Groenlandiae occidentalis hactenus indagata, quoad nomen specificum, triviale, vernaculumque; synonyma auctorum plurium, descriptionem, locum, victum, generationem, mores, usum, capturamque singuli; prout detegendi occasio fuit, maximaque parti secundum proprias observationes. Copenhagen*.

Fauchald, K. (1965). Some Nephtyidae (Polychaeta) from Australian waters. *Records of the Australian Museum*, 26, 333-340.

Fauchald, K. (1968). Nephtyidae (Polychaeta) from the Bay of Nha Trang, South Viet Nam. *Naga Report*, 4, 7–33.

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

Fauchald, K. (1973). Polychaetes from Central American sandy beaches. *Bulletin of the Southern California Academy of Sciences*, 72, 19–31.

Fauchald, K. (1976). Some Nephtyidae (Polychaeta) from Ubatuba, Brasil. *Bulletin Southern California Academy of Sciences*, 75, 16-19.

Fauchald, K. (1977). *Polychaetes from intertidal areas in Panama, with a review of previous shallow-water records*. Washington: Smithsonian Institution Press.

Fauchald, K., & Reimer, A. A. (1975). Clave de poliquetos panameños con la inclusion de una clave para todas las familias del mundo. *Boletin Inst. Oceanogr. Univ. Oriente*, 14, 71-94.

Fauvel, P. (1902). Annélides polychètes de la Casamance repportées par M. Aug. Chevalier. *Bulletin de la Société Linnéenne de Normandie*, 5, 59-105.

Fauvel, P. (1916). Annélides polychètes des Iles Falkland recuellies par M. Rupert Vallentin Esq. (1902-1910). *Archives de Zoologie Expérimentale et Génerale*, 55, 417–482.

Fauvel, P. (1919a). Annélides polychètes de Madagascar, de Djibouti et du Golfe Persique. *Archives de Zoologie Expérimentale et Génerale*, 58, 315-473.

Fauvel, P. (1919b). Annélides polychètes nouvelles de l'Afrique Orientale. Deuxieme note. *Bulletin du Muséum d'Histoire Naturelle, Paris*, 25, 33-39.

Fauvel, P. (1927). Contribution a l'étude de faune du Cameroun. Polychaeta. *Faun. Colon. Franc.*, 1, 523-533.

Fauvel, P. (1932a). Annelida polychaeta of the Indian Museum, Calcuta. *Memoirs of the Indian Museum*, 12, 1-262.

Fauvel, P. (1932b). Polychètes nouvelles de Che-Foo (Chine). *Bulletin du Muséum d'Histoire Naturelle, Paris*, 24, 536-538.

Fauvel, P. (1933). Annélides polychètes du Golfe du Pei Tcheu Ly, de la collection du Musée Hoang ho Pai ho. *Publs. Mus. Hoang Pai ho Tien-Tsin*, 15, 1–67.

Fauvel, P. (1936). Contribution à la faune des annélides polychètes du Maroc. *Mémoires de la Société des Sciences Naturelles du Maroc*, 43, 1-144.

Fauvel, P. (1941). Annèlides polychètes de la mission du Cap Horn (1882-1883). *Bull. Mus. Hist. Nat. Paris*, 13, 272-298.

Fauvel, P. (1953). *The Fauna of India including Pakistan, Ceylon, Burma and Malaya. Annelida Polychaeta*. Allahabad: The Indian Press.

Gardiner, S. L. (1976). Errant polychaete annelids from North Carolina. *Journal of the Elisha Mitchell Scientific Society*, 91, 77–220.

Gibbs, P. E. (1971). The Polychaete fauna of the Solomon Islands. *Bulletin of the British Museum (Natural History)*, 21, 101–211.

Gobin, J. (1990). A checklist of marine polychaetous annelids (Polychaeta) for the Gulf of Paria, Trinidad, West Indies. *Caribb. Mar. Stud.*, 1, 37-47.

Grube, A.-E. (1877). Anneliden - Ausbeut S. M. S. Gazelle. *Monatsbericht der Koniglich Preussischer Akademie der Wissenschaften zu Berlin*, 1877, 509-554.

Harper, J. D. E. (1986). Nephtys cryptomma, new species (Polychaeta: Nephtyidae) from the northern Gulf of Mexico. *Proceedings of the Biological Society of Washington*, 99, 1-7.

Hartman, O. (1938a). Annotated list of the types of polychaetous annelids in the Museum of Comparative Zoology. *Bull. Mus. Comp. Zool. Harvard*, 85, 1-31.

Hartman, O. (1938b). Review of the annelid worms of the family Nephtyidae from the Northeast Pacific, with descriptions of five new species. *Proceedings of The United States National Museum*, 85, 143–158.

Hartman, O. (1940). Polychaetous annelids. Part II. Chrysopetalidae to Goniadidae. *Allan Hancock Pacific Expeditions*, 7, 173–287.

Hartman, O. (1942). A review of the types of polychaetous annelids at the Peabody Museum of Natural History, Yale University. *Bulletin of the Bingham Oceanographic Collection*, 8, 1–98.

Hartman, O. (1944a). New England Annelida. Part 2. Including the unpublished plates by Verrill with reconstructed captions. *Bulletin of the American Museum of Natural History*, 82, 327–344.

Hartman, O. (1944b). Polychaetous annelids. *Allan Hancock Atlantic Expedition*, 3, 1-33.

Hartman, O. (1944c). Polychaetous annelids, including the description of two new genera and nine new species. *Hancock Pacific Expeditons*, 10, 239-310.

Hartman, O. (1945). The marine annelids of North Carolina. *Duke University Marine Station Bulletin*, 2, 1–54.

Hartman, O. (1948). The marine annelids erected by Kinberg, with notes on some other types in the Swedish State Museum. *Arkiv for Zoologi*, 42A, 1-137.

Hartman, O. (1949). The marine annelids erected by Kinberg, with notes on some other types in the Swedish State Museum. *Arkiv for Zoologi*, 42A, 1-137.

Hartman, O. (1950). Goniadidae, Glyceridae and Nephtyidae. *Allan Hancock Pacific Expeditions*, 15, 1–181.

Hartman, O. (1951). The littoral marine annelids of the Gulf of Mexico. *Publications of the Institute of Marine Science Univ. Texas*, 2, 7-124.

Hartman, O. (1953). Non-pelagic polychaeta of the Swedish Antarctic Expedition 1901-1903. *Further Zoological Results of the Swedish Antarctic Expedition 1901-1903*, 4, 1–83.

Hartman, O. (1959). Catalogue of the polychaetous Annelids of the world. Part I. *Allan Hancock Foundation Publications. Occasional Paper*, 23, 1–353.

Hartman, O. (1963). Submarine canyons of southern California. Part III. Systematics: Polychaetes. *Allan Hancock Pac. Exped.*, 27, 1–93.

Hartman, O. (1964). Polychaeta Errantia of the Antarctica. *Antarctic Research Series*, 3, 1–131.

Hartman, O. (1965). Deep-water benthic polychaetous annelids off New England to Bermuda and other North Atlantic Areas. *Allan Hancock Foundation Publications. Occasional Paper*, 28, 1-378.

Hartman, O. (1967). Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic seas. *Allan Hancock Monographs in Marine Biology*, 2, 1–387.

Hartman, O. (1968). *Atlas of the errantiate polychaetous annelids of California*. Los Angeles: Allan Hancock Foundation, University of Southern California Press.

Hartman, O. (1974). Polychaetous annelids of the Indian Ocean including an account of species collected by members of the International Indian Ocean Expeditions, 1964-1964, and a catalogue and bibliography of the species from India. Part I. *Journal of the Marine Biological Association of India*, 16, 191–252.

Hartman, O. (1978). Polychaeta from the Weddell Sea Quadrant, Antarctica. *Antarctic Research Series*, 26, 124–233.

Hartman, O., & Fauchald, K. (1971). Deep-water benthic polychaetes off New England to Bermuda and other North Atlantic areas. *Allan Hancock Monographs in Marine Biology*, 6, 1-327.

Hartmann- Schörder, G., & Rosenfeldt, P. (1990). The polychaetes collected from expedition 68-1 of the Walter-Hertwig Research Vessel to Elephant Island, Antarctica in 1985. 1. Aphroditidae to Cirratulidae. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 87, 89-115.

Hartmann-Schröder, G. (1959). Zur Ökologie der Polychaeten des Mangrove-Estero-Gebietes von El Salvador. *Beiträge zur Neotropischen Fauna*, 1, 69–183.

Hartmann-Schröder, G. (1960). Zur Polychaeten-fauna von Peru. *Beiträge zur Neotropischen Fauna*, 2, 1–44.

Hartmann-Schröder, G. (1962). Zweiter Beitrag zur Polychaetenfauna von Peru. *Kieler Meeresforschungen*, 18, 109–147.

Hartmann-Schröder, G. (1965). Zur Kenntnis des Sublitorals der chilenischen Küste unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 2. Die Polychaeten des sublitorals. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 62, 59–305.

Hartmann-Schröder, G. (1971). Annelida, Borstenwürmer, Polychaeta. *Tierwelt Deutschlands*, 58, 1–594.

Hartmann-Schröder, G. (1974). Zur Kenntniss des Eulitorals der afrikanischen Westküste zwischen Angola und Kap der Goten Hoffnung und der afrikanische Ostküste von Südafrika und Mocambique unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil II. Die Polychaeten der Untersuchungsgebietes. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 68, 95–228.

Hartmann-Schröder, G. (1990). Zur Kenntnis des Eulitorals der australischen Küsten unter besonderer Berücksichtigung der Polychaeten und Ostracoden. Teil 15. Die Polychaeten der subtropisch-tropischen und tropischen Ostküste Australiens zwischen Lake Macquarie (New South Wales) im Süden und

Gladstone (Queensland) im Norden. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 87, 41–87.

Hartmann-Schröder, G., & Rosenfeldt, P. (1988). Die Polychaeten der “Polarstern”-Reise ANT III/2 in die Antarktis 1984. Teil 1: Euphrosinidae bis Chaetopteridae. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 85, 25–72.

Hartmann-Schröder, G., & Rosenfeldt, P. (1992). Die Polychaeten der “Polarstern”-Reise ANT V/1 in die Antarktis 1986. Teil 1: Euphrosinidae bis Iphitimidae. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 89, 85–124.

Heinen, A. (1911). Die Nephtyideen und Lycorideen der Nord- und Ostee, einschlieblich der verbindenden Meeresteile. *Wissenschaftliche Meeresuntersuchungen*, 13, 1–87.

Hernández-Alcántara, P., & Solìs Weiss, V. (1991). New records of errantiate polychaetous annelids from the Gulf of California. *Bulletin of Marine Science*, 48, 251–260.

Hernández-Alcántara, P., & Solis-Weiss, V. (1999). Systematics and distribution of the polychaetes (Annelida: Polychaeta) from the sublittoral zone in the Gulf of California. *Oceanides*, 13, 25–38.

Hilbig, B. (1992). New polychaetous annelids of the families Nereididae, Hesionidae, and Nephtyidae from the Santa Maria Basin, California, with a redescription of Glycera nana Johnson, 1901. *Proceedings of the Biological Society of Washington*, 105, 709-722.

Hilbig, B. (1997). Family Nephtyidae Grube, 1850. In J. A. Blake, B. Hilbig & P. H. Scott (Eds) *Taxonomic atlas of the benthic fauna of the Santa Maria basin and the western Santa Barbara channel. 4. The Annelida. Part 1. Oligochaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae)* (pp. 317-349). Santa Barbara, California.

Hilton, W. A. (1919). Annelids from Laguna Beach. *Journ. Ent. and Zool., Pomona Colege*, 11, 27.

Hutchings, P. (1974). Polychaeta of Wallis Lake, New South Wales. *Proceedings of the Linnean Society of New South Wales*, 98, 175-195.

Hutchings, P. A., & Recher, H. F. (1974). The fauna of Careel Bay with comments on the ecology of mangrove and seagrass communities. *Australian Zoologist*, 18, 99-128.

Ibarzabal, D. R. (1986). Lista de especies de poliquetos bentonicos Cubanos. *Reporte de Investigacion del Instituto de Oceanología*, 45, 1–17.

Imajima, M. (1961). Polychaetous annelids collected off the west coast of Kamchatka. I. Notes on species found in the collections of 1957-58. *Publications of the Seto Marine Biological Laboratory*, 9, 81–102.

Imajima, M. (1967). Errant polychaetous annelids from Tsukumo Bay and vicinity of Noto Peninsula, Japan. *Bull. Natn. Sci. Mus., Tokyo*, 10, 403–441.

Imajima, M. (1970). Errant polychaetous annelids collected from the areas around the Tsushima Islands. *Memoirs of the National Science Museum of Tokyo*, 3, 113–122.

Imajima, M. (2003). Polychaetous annelids from Sagami Bay and Sagami Sea collected by the Emperor Showa of Japan and deposited at the Showa Memorial Institute, National Science Museum, Tokyo (II), orders included within Phyllodocida, Amphinomida, Spintherida and Eunicida. *National Science Museum Monographs*, 23, 1-221.

Imajima, M., & Hartman, O. (1964). The polychaetous annelids of Japan. Part 1. *Allan Hancock Foundation Publications. Occasional Paper*, 26, 1–166.

Imajima, M., & Takeda, Y. (1985). Nephtyidae (Polychaeta) from Japan. I. The genera *Inermonephtys*, *Micronephthys* and *Aglaophamus*. *Bulletin of the National Science Museum, Tokyo*, 11, 57–90.

Imajima, M., & Takeda, Y. (1987). Nephtyidae (Polychaeta) from Japan. II. The genera *Dentinephtys* and *Nephtys*. *Bulletin of the National Science Museum, Tokyo*, 13, 41–77.

Izuka, A. (1912). The Errantiate Polychaeta of Japan. *Journal of the College of Science, Imperial University of Tokyo*, 30, 1–262.

Jirkov, I. A. (1986). Nephtys zatsepini sp. nov. (Polychaeta, Nephtyidae) from Barents Sea. *Biologicheskie Nauki*, 1, 39-42.

Jirkov, I. A. (1989). *Bottom fauna of the USSR. Polychaeta*. Moscow: Moscow University Press.

Johnson, H. P. (1901). The polychaeta of the Puget Sound region. *Proceedings of the Boston Society of Natural History*, 29, 381–437.

Jones, M. L. (1961). A quantitative evaluation of the benthic fauna off Point Richmond, California. *University of California Publications in Zoology*, 67, 219–320.

Jung, R.-H., & Hong, J.-S. (1997). Nephtydae (Annelida: Polychaeta) from the Yellow Sea. *Bulletin of the Marine Science*, 60, 371–384.

Kinberg, J. G. H. (1866). Annulata nova. *Ofversigt af Koniglich Vetenskapsakademiens forhandlingar, Stockholm*, 22, 239-258.

Kirkegaard, J. B. (1969). A quantitative investigation of the central North Sea polychaeta. *Spolia Zoologica Musei Hauniensis*, 29, 1–285.

Kirkegaard, J. B. (1980). Abyssal benthic polychaetes from the northeast Atlantic Ocean, Southwest of the British Isles. *Steenstrupia*, 6, 81–98.

Kirkegaard, J. B. (1995). Bathyal and abyssal polychaetes (errant species). *Galathea Report*, 17, 7–56.

Kitamori, R. (1960). Two new species of cirratulid and nephthyidae (Annelida: Polychaeta). *Bulletin of the Japanese Society of Scientific Fisheries*, 26, 1082-1085.

Knox, G. A., & Cameron, D. B. (1971). Port Phillip Survey Pt. 2. 4. Polychaeta. *Memoirs of the National Museum of Victoria*, 32, 21–41.

Knox, G. A., & Cameron, D. B. (1998). The marine fauna of the Ross Sea. *NIWA Biodiversity Memoirs*, 108, 1–125.

Kudenov, J. D. (1975). Errant polychaetes from the Gulf of California, Mexico. *Journal of Natural History*, 9, 65-91.

Lana, P. d. C. (1986). Nephtyidae (Annelida: Polychaeta) do litoral do estado do Paraná (Brasil). *Neritica*, 1, 135-154.

Laverde-Castillo, J. J. A. (1986). Lista anotada de los poliquetos (Annelida) registrados para el Pacífico Colombiano, con notas preliminares sobre su zoogeografía. *Actualidades Biológicas*, 15, 123-130.

Laverde-Castillo, J. J. A., & Rodríguez-Gómez, H. (1987). Lista de poliquetos registrados para el Caribe Colombiano, incluyendo comentarios sobre su zoogeografía. *An. Inst. Invest. Mar. Punta Betin*, 17, 95-112.

Lee, J.-H., & Jae, J.-G. (1983). Polychaetous annelids from the Yellow Sea. I. Family Nephtyidae. *Bulletin of the Korea Ocean Research and Development Institute*, 5, 19–27.

Lovell, L. L. (1997). A review of six species of Nephtys (Cuvier, 1817) (Nephtyidae: Polychaeta) described from the eastern pacific. *Bulletin of Marine Science*, 60, 350-363.

Mackie, A. S. Y. (2000). Micronephthys oculifera (Polychaeta: Nephtyidae), a remarkable new species from Hong Kong, China. *Bulletin of Marine Science*, 67, 517-527.

Malmgren, A. J. (1865). Nordiska hafs-annulater. *Öfversigt af K. Vetenskapsakademiens förhandlingar*, 51–110.

Marenzeller, E. (1889). Spitzbergische anneliden. Beiträge zur Fauna Spitzbergens. *Archiv für Naturgeschichte*, 55, 127-132.

Martin, D., Gil, J., & Lana, P. C. (2009). *Inermonephtys brasiliensis* sp. nov. (Polychaeta: Nephtyidae) from SE Brazil, with a redescription of *I. palpata* Paxton, 1974. *Zoosymposia*, 2, 165-177.

McIntosh, W. C. (1901). Notes from the Gatty Marine Laboratory, St. Andrews. 5. On certain Hesionidae from the Porcupine Expeditions. *Annals and Magazine of Natural History*, 8, 227–233.

McIntosh, W. C. (1908). A monograph of British annelids. Polychaeta. Nephthyidae to Ariciidae. *Ray Society of London*, 2, 1-232.

Michaelsen, W. (1897). Die Polychaeten-Fauna der deutschen Meere einschliessich der benachbarten und verbindenden Gebiete. *Wissenschaftliche Meeresuntersuchungen der Kommission zur wissenschaftlichen Untersuchung der deutschen Meere*, 2, 1–216.

Möbius, K. (1875). Vermes. *Jahresbericht der kommission zur wissenschaftlichen Untersuchung der Deutschen Meere in Kiel für die Jahre 1872, 1873*, 2-3, 153–172.

Molina-Lara, O. A., & Vargas-Zamora, J. A. (1995). Poliquetos (Annelida: Polychaeta) del estero de Jaltepeque, El Salvador: una comparación 1959-1991. *Revista de Biologia Tropical*, 43, 195-205.

Monro, C. A. A. (1928). Papers from Dr. Th. Mortensen's Pacific Expedition, 1914-16. On the polychaeta collected by Dr. Th. Mortensen off the coast of Panama. Vidensk. *Meddr. Dansk. Naturh. Foren.*, 85, 75-103.

Monro, C. A. A. (1933). The Polychaeta Errantia collected by Dr. C. Crossland at Colón, in the Panama region, and the Galapagos Islands during the expedition of the S.Y. 'St. George'. *Proceedings of the Zoological Society of London*, 1933, 1–96.

Monro, C. A. A. (1934). On a collection of polychaeta from coast of China. *Ibid., sér. 10*, 13, 353-380.

Monro, C. A. A. (1937). On some freshwater polychaetes from Uruguay. *Ann. Mag. Nat. Hist. London,* 10, 241-250.

Monro, C. C. A. (1930). Polychaete worms. *"Discovery" Reports, Cambridge,* 2, 1–222.

Monro, C. C. A. (1936). Polychaete worms II. *Discovery Reports, Cambridge*, 12, 59-193.

Moore, J. P. (1909). Polychaetous annelids from Monterey Bay and San Diego, California. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 61, 235-295.

Moore, J. P. (1911). The polychaetous annelids dredged by the U. S. S. *Albatross* off the coast of southern California in 1904. 3. Euphrosynidae to Goniadidae. *Proc. Acad. nat. Sci. Philad.*, 63, 234-318.

Moore, P. (1903). Polychaeta from the coastal slope of Japan and from Kamchatka and Bering sea. *Proceedings of the Academy of Natural Sciences, Philadelphia*, 55, 401–490.

Nateewathana, A., & Hylleberg, J. (1986). Nephtyid polychaetes from the west coast of Phuket Island, Andaman sea, Thailand, with description of five new species. *Proceedings of the Linnean Society of New South Wales*, 108, 195–215.

Nonato, E. F., & Luna, J. A. C. (1970). Anelidos poliquetas do nordeste do Brasil. I—Poliquetas bentonicos da costa de Alagoas e Sergipe. *Boletim do Instituto oceanográfico*, 19, 43–56.

Noyes, G. S. (1980). The biology of Aglaophamus neotenus (Polychaeta: Nephtyidae), a new species from Maine and Canada. *Biological Bulletin*, 158, 103-117.

Ohwada, T. (1985a). Prostomium morphology as a criterion for the identification of nephtyid polychaetes (Annelida: Phyllodocida), with reference to the taxonomic status of Aglaophamus neotenus. *Publications of the Seto Marine Biological Laboratory*, 30, 55-60.

Ohwada, T. (1985b). Redescription of the nephtyid polychaete Aglaophamus minusculus Hartman, 1965. *Proceedings of the Biological Society of Washington*, 98, 604-610.

Ohwada, T. (1992). A new species of *Aglaophamus* (Polychaeta: Nephtyidae) from Hong Kong. In B. Morton (Ed) *The marine flora and fauna of Hong Kong and southern China III. Proceedings of the Fourth International Marine Biological Woekshop: The Marine Flora and Fauna of Hong Kong and Southern China, Hong Kong, 11-29 April 1989* (pp. 149-155). Hong Kong: Hong Kong University Press.

Okuda, S. (1939). Annelida polychaeta in Onagawa Bay and its vicinity. II: Polychaeta errantia with some addenda of polychaeta sedentaria. *Science Reports of the Tohoku Imperial University*, 14, 219–244.

Okuda, S. (1940). Polychaetous anelids of the Ryukyu Islands. *Bull. Biogeogr. soc. Japan, Tokyo*, 10, 1-24.

Okuda, S. (1943). Occurrence of a freshwater polychaete in central China. *J. Shanghai Sci. Inst. (N. S.)*, 2, 99-103.

Orensanz, J. M., & Estivariz, M. C. (1971). Los anélidos poliquetos de aguas salobres de la provincia de Buenos Aires. *Revista Mus. La Plata (Zool.)*, 11, 95-114.

Orensanz, J. M., & Gianuca, N. M. (1974). Contribução ao conhecimento dos anelídeos poliquetas do Rio Grande do Sul. I. Lista sistemática preliminar e descrição de três novas espécies. *Comun. Mus. Ci. PUC-RS*, 4, 1-37.

Örsted, A. S. (1843). *Annulatorum Danicorum Conspectus. Fasc. 1. Maricolæ, Hafniea*. Copenhagen.

Paxton, H. (1974). Contribution to the study of Australian Nephtyidae (Polychaeta). *Records of the Australian Museum*, 29, 197–208.

Perkins, T. H. (1980). Review of the species previously referred to *Ceratonereis mirabilis*, and descriptions of new species of *Ceratonereis*, *Nephtys*, and *Goniada* (Polychaeta). *Proceedings of the Biological Society of Washington*, 93, 1–49.

Perkins, T. H., & Savage, T. (1975). A bibliography and checklist of polychaetous annelids of Florida, the Gulf of Mexico, and the Caribbean Region. *Florida Marine Research Publications*, 14, 1–62.

Pettibone, M. H. (1954). Marine polychaete worms from Point Barrow, Alaska, with aditional records from the North Atlantic and North Pacific. *Proceedings of the Unites States National Museum*, 103, 203–356.

Pettibone, M. H. (1963). Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. *US National Museum Bulletin*, 227, 1-356.

Rainer, S. F. (1991). The genus *Nephtys* (Polychaeta: Phyllodocia) of northern Europe: a review of species, including the description of *N. pulchra* sp. n. and a key to the Nephtyidae. *Helgoländers Meeresuntersuchungen*, 45, 65–96.

Rainer, S. F., & Hutchings, P. A. (1977). Nephtyidae (Polychaeta: Errantia) from Australia. *Records of the Australian Museum*, 31, 307–347.

Rainer, S. F., & Kaly, U. L. (1988). Nephtyidae (Polychaeta: Phyllodocida) of Australia: new species from the West shelf, and key to Australian species. *Journal of Natural History*, 22, 685–703.

Ravara, A., Cunha, M. R., & Pleijel, F. (submitted). Nephtyidae (Annelida, Polychaeta) from southern Europe. *Zootaxa*.

Ravara, A., Wiklund, H., Cunha, M. R. d., & Pleijel, F. (in press). Phylogenetic relationships within Nephtyidae (Polychaeta, Annelida). *Zoologica Scripta*.

Reish, D. J. (1968). A biological survey of Bahia de Los Angeles, Gulf of California, Mexico. II. Benthic polychaetous annelids. *Transactions of the San Diego Society of Natural History*, 15, 67–106.

Rioja, E. (1944). Estudios anelidologicos. X. Estudio de algunos poliquetos del Museo Argentino de Ciencias Naturales. *An. Inst. biol. Mexico*, 15, 115-138.

Rioja, E. (1946). Estudio de algunos poliquetos del Museo Argentino de Ciencias Naturales. *An. Mus. Argent. B. Aires*, 42, 39-58. Pls. i-iv.

Rioja, E. (1964 (1963)). Estudios anelidológicos, 26. Algunos anélidos poliquetos de las costas del Pacífico de México. *Anales del Instituto de Biologia, Universidad Nacional Autónoma de México*, 33, 131-229.

Rizzo, A. E., & Amaral, A. C. Z. (2007). Nephtyidae (Annelida: Polychaeta) from São Paulo State, Brazil, including a new record for the Brazilian coast. *Biota Neotropica*, 7, 253-263.

Rozbaczylo, N., & Castilla, J. C. (1974). La familia Nephtyidae en Chile (Annelida, Polychaeta). *Studies on the Neotropical Fauna*, 9, 179-206.

Rozbaczylo, N., Moreno, R. A., & Díaz-Díaz, O. (2005). Poliquetos bentónicos submareales de fondos blandos de la región de Aysén, Chile: Clado Phyllodocida (Annelida, Polychaeta). *Invest. Mar.*, 33.

Rullier, F. (1965). Contribution à la faune des annélides polychètes de l'Australie. *Pap. Dep. Zool. Univ. Qd*, 11, 163-201.

Sallazar-Vallejo, S. I., León-González, J. A., & Chávez-Comparan, J. C. (1990). Poliquetos (Annelida: Polychaeta) de la Bahía de Manzanillo, con una clave ilustrada para las especies de Colima, México. *Revista de Biologia Tropical*, 38, 211-229.

Schmarda, L. K. (1861). *Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erdr 1853 bis 1857. Turbellarien, Rotatorien und Anneliden*. Leipzig: Wilhelm Engelmann.

Smith, S. I., Harger, O., & Verrill, A. E. (1874). Report on the dredgings in the region of St. George's Banks in 1872. *Trans. Connecticut Acad. Arts Sci.*, 3, 1-57.

Southern, R. (1921). Polychaeta of the Chilka Lake, and also of fresh and brackish waters in other parts of India. *Mem. Ind. Mus. Calcutta*, 5, 563-659.

Stephenson, W., Williams, W. T., & Cook, S. D. (1974). The benthic fauna of soft bottoms, southern Moreton Bay. *Mem. Qd Mus.*, 17, 73-123.

Stimpson, W. (1855). Description of some new marine invertebrates. *Proc. Acad. nat. Sci. Philad.*, 7, 385-395.

Støp-Bowitz, C. (1949). Polychètes pelagiques des expéditions norvègiennes antarctiques dé la "Norvegia" 1927-1928, 1928-1929 et 1930-1931. *Scient. Res. Norw. Antarct. Exped. 1927-28, Oslo*, 31, 1-25.

Sumner, F. B., Osburn, R. C., & Cole, L. J. (1913). Annulata *in* A biological survey of the waters of the Woods Hole and vicinity. *Bull. U. S. Bur. Fish.*, 31, 615-636.

Taylor, J. L. (1984). Family Nephtyidae Grube, 1850. In J. M. Uebelacker & P. G. Johnson (Eds) *Taxonomic guide to the polychaetes of the Northern Gulf of Mexico* (pp. 35.31–35.20). Alabama: V. Barry A. Vittor and Associates, Mobile.

Tebble, N. (1955). The Polychaete fauna of the Gold Coast. *Bulletin of the British Museum (Natural History)*, 3, 59–148.

Théel, H. J. (1879). Les annélides polychètes des mers de la Nouvelle-Zemble. *Kungliga Svenska Vetenskapsakademiens Handlingar*, 16, 1-75.

Treadwell, A. L. (1914). Polychaetous annelids of the Pacific coast in the collections of the zoological museum of the University of California. *University of California Publications in Zoology*, 13, 175–234.

Treadwell, A. L. (1923). Polychaetous annelids from lower California with descriptions of new species. *American Museum Novitates*, 74, 1-11.

Treadwell, A. L. (1928). Polychaetous annelids from the Arcturus oceanographic expedition. *Zoologica*, 8, 449–489.

Treadwell, A. L. (1936). Polychaetous annelids from Amoy, China. .

Treadwell, A. L. (1937). The Templeton Crocker Expedition. Polychaetous annelids from the west coast of lower California, the Gulf of California and Clarion Island. *Zoologica*, 22, 139–160.

Treadwell, A. L. (1948). Annelida, Polychaeta *in* Canadian Atlantic Fauna Toronto. *Fish. Res. Bd. Canada*, 9, 1-69.

Tzetlin, A. B. (1980). *Practical determinations of the polychaete worms from the White Sea.* Moscow: Moscow University Press.

Uschakov, P., & Wu, B.-L. (1962). Polychaete worms of the Yellow Sea II. Fam. Chrysopetalidae, Glyceridae and Nephtyidae (Polychaeta, Errantia). *Studia Marina Sinica*, 1, 1–32.

Uschakov, P., & Wu, B.-L. (1979). Polychaeta errantia of the Yellow Sea. *Stud. Mar. Fauna*, 3, 1-137.

Uschakov, P. V. (1955). Polychaeta of the Far Eastern Seas of the U.S.S.R. *Academiya Nauk SSSR, Keys to the Fauna of the SSSR*, 56, 1–433 (translated from Russian by the Israel Program for Scientific Translations, Jerusalem 1965).

Verrill, A. E. (1873). Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region. *Report of the United States Commissioner of Fisheries*, 1871/72, 295–852.

Verrill, A. E. (1874). *Report upon the invertebrate animals of Vineyard Sound and the adjacent waters, with an account of the physical characters of the region*. Washington.

Verrill, A. E. (1881). New England Annelida. Part I. Historical sketch, with annotated lists of the species hitherto recorded. *Transactions of the Connecticut Academy of Arts and Sciences*, 4, 285–324.

Weate, P. (1975). A study of the wetlands of the Myall River. *Operculum*, 4, 105-113.

Webster, H. E. (1879). Annelida chaetopoda of the Virginian coast. *Transactions Albany Institute New York*, 9, 202–269.

Webster, H. E. (1886). The annelida chaetopoda of New Jersey. *Rep. New York State Mus.*, 39, 128-159 (reprint of no. 132, 1880, with plates included).

Webster, H. E., & Benedict, J. E. (1884). The Annelida Chaetopoda from Provincetown and Wellfleet, Mass. *Report of the United States Commissioner of Fisheries*, 1884, 699–747.

Webster, H. E., & Benedict, J. E. (1887). The Annelida Chaetopoda from Eastport, Maine. *Report of the United States Commissioner of Fisheries*, 1885, 707–755.

Wesenberg-Lund, E. (1949). Polychaetes of the Iranian Gulf. *Danish Scientific Investigations in Iran*, 4, 247–400.

Wesenberg-Lund, E. (1962). Reports of the Lund University Chile Expedition 1948-49. 43. Polychaeta Errantia. *Acta Universitatis lundensis, ser. N. F., Avd. 2*, 57, 1-137.

Whiteaves, J. F. (1901). Catalogue of the marine invertebrata of eastern Canada. *Report on geological Survey of Canada*, 1–272.

Zatsepin, V. I. (1948). *Polychaete worms. Determination of fauna and flora of Northern Sea in USSR.*: Superior School of Moscow.

Section 4. Final remarks

The hight homogeneity within the family Nephtyidae represented an obvious difficulty in distinguishing the genera and species and considerable confusion was prevalent in the early descriptions. Valuable revisions such as Ehlers (1868), Michaelsen (1896), Heinen (1911) and Fauvel (1914; 1923) formed a basis for subsequent studies. By 1923 all the genera previously described, including *Nephtys* and *Aglaophamus*, were synonymised and only the genus *Nephtys* was accepted. In 1939, Friedrich described the genus *Micronephthys* and after the revisions of Hartman (1950; 1959) and Fauchald (1963) three different genera (*Nephtys*, *Aglaophamus* and *Micronephthys*) and 79 species were recognized. Still some other authors such as Day (1967; 1973) and Rozbaczyllo and Castilla (1974) considered the family as monogeneric and the remaining genera as subgenera of the single genus *Nephtys*. Later, Fauchald (1977) recognized four genera and 103 species (50 *Nephtys*, 45 *Aglaophamus*, five *Micronephthys* and three *Inermonephtys*). After this, one more genus, *Dentinephtys*, was erected by Imajima and Takeda (1987). Although many taxonomical problems have been solved along time, many doubts remain as to the boundaries between genera and the correct allocation of many species.

Only recently the phylogenetic analyses have been used to assess taxonomical problems within the polychaete group. Phylogenetic studies of the family Nephtyidae have not been carried out up to now. Therefore, I here include the first phylogenetic analysis of the Nephtyidae with the main purpose of addressing problems of delineation between the genera. The importance of including as much information available as possible in the analyses is obvious, and combinations of different types of data have been used in several studies (e.g. Gelder & Siddall 2001; Rousset *et al.* 2003; Wiklund *et al.* 2005; Ruta *et al.* 2007). I included in the analysis morphological and molecular data from the genes COI, 16S, 18S and 28S, which have been commonly used with good results in other studies (e.g. Bleidorn *et al.* 2005; Wiklund *et al.* 2005; Ruta *et al*. 2007). Three main taxonomical changes resulted from this study: i) The species *Nephtys pulchra* and *N. australiensis* are transferred to the genus *Aglaophamus*; ii) the genus *Dentinephtys* is synonymised with *Nephtys*, and iii) a new genus, *Bipalponephtys*, is erected with the inclusion of the species *Nephtys cornuta*, *N. danida* and *Micronephthys neotena* (Ravara *et al.* in press).

The earlier delineations of the genera (e.g. Hartman 1950) were based mainly on the branchiae shape (involute - *Aglaophamus*, recurved - *Nephtys*, or absent -

Micronephthys). Subsequent authors (e.g. Fauchald 1968; Taylor 1984; Imajima & Takeda 1985, 1987; Hilbig 1997) added some other characters to the generic description, such as number of rows of pharynx papillae, shape of tips of parapodial aciculae, shape of acicular lobes and lamellae, and presence or absence of lyriform chaetae, but still the branchiae shape remained the main distinctive character. All other characters were considered to vary within genera and some were common to more than one genus. The phylogenetic analysis included in this work relocated two species previously assigned to the genus *Nephtys* into the genus *Aglaophamus* revealing homoplasy for the branchiae shape character. Therefore, branchiae shape becomes another variable and thus less reliable distinctive character for genera differentiation. Alternative characters, such as the morphology of the acicular lobes and the postacicular chaetae, are suggested but there are no exclusive characteristics for each genus with the exception of the genera *Inermonephtys* (absence of antennae and pharynx papillae, cirriform nuchal organs) and *Bipalponephtys* (bifid palps). It is therefore crucial that a combination of characters is used in order to properly assign a species to a genus. However, there are some species for which the location is still doubtful.

Furthermore, there are some indications that the present genera may need to be subdivided. In the phylogenetic analysis included in this study, the *Nephtys* group is clearly subdivided into two well-supported subgroups of species with different parapodial characteristics. Species of group A have conical acicular lobes, well developed preacicular lamellae and lightly spinulated postacicular chaetae, while species of group B have rounded or bilobed acicular lobes, poorly developed preacicular lamellae and coarsely spinulated chaetae. Also the genus *Aglaophamus* includes a mix of species with different characteristics. This genus was characterised by Hartman (1948; 1950) as having involute branchiae, lyriform chaetae and acutely pointed acicular lobes. However, it presently includes two species with recurved branchiae, three species with rounded acicular lobes, and several species without lyriform chaetae. Although the species with recurved branchiae were showed within this study to belong to *Aglaophamus*, no species with lyriform chaetae were included in the phylogenetic analysis and thus further reassessment of this genus is required in future studies. Furthermore, there are three Antarctic species of *Aglaophamus* that have rounded acicular lobes. One of these species, *A. trissophyllus*, was included in the phylogenetic analysis and remained within the *Aglaophamus* group. Nevertheless, further research with all these species would also be useful. Finally, regarding *Micronephthys*, branchiae are present in some species and absent in others. Mackie (2000) already suggested the possibility that these species form distinct groups. Based on my knowledge, I would further speculate that the branchiate forms currently ascribed to *Micronephtys* may instead belong to the genus *Nephtys*. Unfortunately only two species (without branchiae) were included in my phylogenetic analysis. Thus, once more, further studies are required of this genus.

Apart from the problems with genera distinction, some doubts also remaine upon the validity of many species and their geographical distribution. During the last years several local revisions (mainly from northeastern Pacific Ocean, northern Europe and Indopacific region) were made resulting in a substantial increase of the number of species. In Europe 22 nephtyid species are known, belonging to the five genera of the family. From these, eight species occur only or mainly in colder waters of northern Europe with circumpolar or circumboreal distribution, another eight are frequent all around Europe (from Norway to the Mediterranean), and six are restricted or mainly distributed in southern Europe (from the English Channel to the Mediterranean Sea). The genus *Bipalponephtys* is not represented in southern Europe, while *Inermonephtys* is not represented in northern Europe. Several revisions have been made of the northern Europe, mainly by Rainer (1984; 1989; 1990; 1991). However, except for the revision included in Fauna Ibérica by Laborda (2004), there are no other studies on the southern European species. Therefore I included here a revision of the Nephtyidae from this region with the description of a new species, *Inermonephtys foretmontardoi*, and a discussion of the geographical distribution of the southern European species (Ravara *et al.* submitted). In this study, the species *Micronephthys maryae* is also synonymised with *M. stammeri*.

After Fauchald's (1977) comprehensive revision of the Polychaeta, many other nephtyid species were described and for a certain period of time, there was some uncertainty regarding the accurate number of species in this family. Authors such as Rouse and Pleijel (2001) refer to the family as having five genera and well over 100 species. Recently, Rizzo and Amaral (2007) reported 186 nominal species stating that about 30% are synonyms or *nomina nuda*, but without specifying any further. In the present work, I felt the need to revise the family in order to somehow estimate the current number of species and the eventual taxonomical problems associated with their identification. After revising the available literature and some museological material representing 44 species, 128 accepted species were counted, ascribed to five genera (57 *Nephtys*, 53 *Aglaophamus*, seven *Micronephthys*, eight *Inermonephtys* and three *Bipalponephtys*), although the status and position of several species still need further reassessment. Many of these species are known only from their original descriptions or old references, often with insufficient information. And others again have been recorded from very different geographical regions and with widespread distributions. This denotes the need of further local works and comprehensive revisions. Apart from Europe, North America and the Indopacific (in particular Australia) region, for which nephtyid species are relatively well known, there exists a number of studies of particular areas but still many geographical regions remain unexplored or poorly known.

Although my main conclusions reflect the need of further research, I believe the present work contributes to a more clear insight of the Nephtyidae taxonomy, especially for the southern European fauna, and further explains the relationships between the genera. It reveals problems to be solved, points to potential directions, and I believe it sets the grounds for future research and the better knowledge on the phylogenetic relations within the Nephtyidae and consequently within the Polychaeta.

References

Bleidorn, C., Vogt, L. & Bartolomaeus, T. (2005). Molecular phylogeny of lugworms (Annelida, Arenicolidae) inferred from three genes. *Molecular Phylogenetics and Evolution*, 34, 673-679.

Day, J. H. (1967). *A monograph on the Polychaeta of southern Africa. Part 1. Errantia*. London: Trustees of the British Museum (Natural History).

Day, J. H. (1973). New Polychaeta from Beaufort, with a key to all species recorded from North Carolina. *NOAA Technical Report NMFS*, 375, 1–140.

Ehlers, E. (1868). *Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen dargestellt*. Leipzig: Wilhelm Engelmann.

Fauchald, K. (1963). Nephtyidae (Polychaeta) from Norwegian waters. *Sarsia*, 13, 1–32.

Fauchald, K. (1968). Nephtyidae (Polychaeta) from the Bay of Nha Trang, South Viet Nam. *Naga Report*, 4, 7–33.

Fauchald, K. (1977). The polychaete worms. Definitions and keys to the orders, families and genera. *Science Series of the Natural History Museum of Los Angeles City*, 28, 1-188.

Fauvel, P. (1914). Annélides polychètes non-pelagiques provenant des campagnes de l'Hirondelle et de la Princesse-Alice (1885-1910). *Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert ler Prince Souverain de Monaco*, 46, 1–432.

Fauvel, P. (1923). Polychètes érrantes. *Faune de France*, 5, 1–488.

Friedrich, H. (1939). Polychaeten-Studien IV. Zum Polychaeten-Fauna der Barentz-See. *Kieler Meeresforschungen*, 3, 122–132.

Gelder, S. R. & Siddall, M. (2001). Phylogenetic assessment of the Branchiobdellidae (Annelida, Clitellata) using 18S rDNA, mitochondrial cytochrome c oxidase subunit I and morphological characters. *Zoologica Scripta*, 30, 215-222.

Hartman, O. (1948). The marine annelids erected by Kinberg, with notes on some other types in the Swedish State Museum. *Arkiv for Zoologi*, 42A, 1-137.

Hartman, O. (1950). Goniadidae, Glyceridae and Nephtyidae. *Allan Hancock Pacific Expeditions*, 15, 1–181.

Hartman, O. (1959). Catalogue of the polychaetous Annelids of the world. Part I. *Allan Hancock Foundation Publications. Occasional Paper*, 23, 1–353.

Heinen, A. (1911). Die Nephtyideen und Lycorideen der Nord- und Ostee, einschlieblich der verbindenden Meeresteile. *Wissenschaftliche Meeresuntersuchungen*, 13, 1–87.

Hilbig, B. (1997). Family Nephtyidae Grube, 1850. In J. A. Blake, B. Hilbig & P. H. Scott (Eds) *Taxonomic atlas of the benthic fauna of the Santa Maria basin and the western Santa Barbara channel. 4. The Annelida. Part 1. Oligochaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae)* (pp. 317-349). Santa Barbara, California.

Imajima, M., & Takeda, Y. (1985). Nephtyidae (Polychaeta) from Japan. I. The genera *Inermonephtys*, *Micronephtys* and *Aglaophamus*. *Bulletin of the National Science Museum, Tokyo*, 11, 57–90.

Imajima, M., & Takeda, Y. (1987). Nephtyidae (Polychaeta) from Japan. II. The genera *Dentinephtys* and *Nephtys*. *Bulletin of the National Science Museum, Tokyo*, 13, 41–77.

Laborda, A. J. (2004) Familia *Nephtyidae* Grube, 1850. *In:* J. M. Viéitez, C. Alós, J. Parapar, C. Besteiro, J. Moreira, J. Nuñez, A. J. Laborda & G. San Martin (Eds), *Annelida, Polychaeta I*. Museo Nacional de Ciencias Naturales. CSIC, Madrid, pp. 390–419.

Mackie, A. S. Y. (2000). Micronephthys oculifera (Polychaeta: Nephtyidae), a remarkable new species from Hong Kong, China. *Bulletin of Marine Science*, 67, 517-527.

Michaelsen, W. (1896). Die Polychaetenfauna der deutschen Meere, einschliesslich der benachbarten und verbindenden Gebiete. *Wissenschaftliche Meeresuntersuchungen*, 2, 1–216.

Rainer, S. F. (1984) *Nephtys pente* sp. nov. (Polychaeta: Nephtyidae) and a key to *Nephtys* from Northern Europe. *Journal of the Marine Biology Association of the United Kingdom*, 64, 899–907.

Rainer, S. F. (1989) Redescription of *Nephtys assimilis* and *N. kersivalensis* (Polychaeta: Phyllodocida) and a key to *Nephtys* from Northern Europe. *Journal of the Marine Biology Association of the United Kingdom, 69*, 875–889.

Rainer, S. F. (1990) The genus *Nephtys* (Polychaeta: Phyllodocida) in northern Europe: redescription of *N. hysticis* and *N. incisa*. *Journal of Natural History, 24*, 361–372.

Rainer, S. F. (1991) The genus *Nephtys* (Polychaeta: Phyllodocida) of northern Europe: a review of species, including the description of *N. pulchra* sp.n. and a key to the Nephtyidae. *Helgoländers Meeresuntersuchungen, 45*, 65–96.

Ravara, A., Cunha, M. R., & Pleijel, F. (submitted). Nephtyidae (Annelida, Polychaeta) from southern Europe. *Zootaxa*.

Ravara, A., Wiklund, H., Cunha, M. R. d., & Pleijel, F. (in press). Phylogenetic relationships within Nephtyidae (Polychaeta, Annelida). *Zoologica Scripta*.

Rizzo, A. E., & Amaral, A. C. Z. (2007). Nephtyidae (Annelida: Polychaeta) from São Paulo State, Brazil, including a new record for the Brazilian coast. *Biota Neotropica*, 7, 253-263.

Rouse, G. W., & Pleijel, F. (2001). *Polychaetes*. Oxford: Oxford University Press.

Rousset, V., Rouse, G., Féral, J.-P., Desbruyères, D. & Pleijel, F. (2003). Molecular and morphological evidence of Alvinellidae relationships (Terebelliformia, Polychaeta, Annelida). *Zoologica Scripta*, 32, 185-197.

Rozbaczylo, N., & Castilla, J. C. (1974). La familia Nephtyidae en Chile (Annelida, Polychaeta). *Studies on the Neotropical Fauna*, 9, 179-206.

Ruta, C., Nygren, A., Rousset, V., Sundberg, P., Tillier, A., Wiklund, H. & Pleijel, F. (2007) Phylogeny of Hesionidae (Aciculata, Polychaeta), assessed from morphology, 18S rDNA, 28S rDNA, 16S rDNA and COI. *Zoologica Scripta*, 36, 99-107.

Taylor, J. L. (1984). Family Nephtyidae Grube, 1850. In J. M. Uebelacker & P. G. Johnson (Eds) *Taxonomic guide to the polychaetes of the Northern Gulf of Mexico* (pp. 35.31–35.20). Alabama: V. Barry A. Vittor and Associates, Mobile.

Wiklund, H., Nygren, A., Pleijel, F. & Sundberg, P. (2005). Phylogeny of Aphroditiformia (Polychaetae) based on molecular and morphological data. *Molecular Phylogenetics and Evolution*, 37, 494-502.

ANNEXES

Annex I. Place of deposit of type material and holotype references.

Species	Place of deposit	Reference
Agçlaophamus agilis	Natural Museum of Wien ?	?
Aglaophamus amakusaensis	NSMT	NSMT-Pol. H 192
Aglaophamus australiensis	AM	AMS W3783
Aglaophamus circinata	USNM	USNM 15882
Aglaophamus dibranchis	?	?
Aglaophamus dicirris	AHF	AHF Poly 0786
Aglaophamus dicirroides	LACM	?
Aglaophamus digitatus	LACM ?	?
Aglaophamus elamellatus	GNHM (syntype)	?
Aglaophamus erectans	LACM	?
Aglaophamus erectanoides	ZMH	?
Aglaophamus eugeniae	LACM	?
Aglaophamus foliocirratus	AM	AM W200657
Aglaophamus foliosus	USNM	USNM 55519
Aglaophamus fossae	LACM	?
Aglaophamus gippslandicus	AM	AM W4911
Aglaophamus gippslandicus bisectus	NSMT	NSMT-Pol. H. 186
Nephtys glossophylla	NHM	NHM 1859.10.28.25
Aglaophamus groenlandiae	USNM	USNM 55520
Aglaophamus hedlandensis	AM	AM W200663
Aglaophamus heteroserratus	ZMH	?
Aglaophamus igalis	LACM	?
Aglaophamus japonicus	NSMT	NSMT-Pol. H 188
Aglaophamus jeffreysii	NHM	NHM 1921.5.1.860
Aglaophamus juvenalis	?	?
Aglaophamus lobatus	NSMT	NSMT-Pol. H 190
Aglaophamus longicephlus	?	?
Aglaophamus lutreus	NHM	NHM 1869.6.16.7
Aglaophamus lyratus	SMNH	?
Aglaophamus lyrochaetus	MNHN	POLY TYPE 727 (as *N. lyrochaeta*)
Aglaophamus macroura	SMNH	?
Aglaophamus malmgreni	?	?
Aglaophamus minusculus	LACM	AHF-Poly 0784
Aglaophamus munamaorii	NHM	NHM 1970.34
Aglaophamus orientalis	LACM	?
Aglaophamus ornatus	USNM	?
Aglaophamus paramalmgreni	?	?
Aglaophamus paucilamellatus	LACM	?
Aglaophamus peruanus	?	?
Aglaophamus phuketensis	PMBC; AM; NHM; USNM; ZMUC	PMBC 3159
Aglaophamus polypharus	?	?
Aglaophamus posterobranchus	USNM	?
Aglaophamus profundus	AM	AM E5113
Aglaophamus pulcher	NHM	NHM 1921.5.1.794 (as *N. pulchra*)
Aglaophamus quatrefagesi	?	?
Aglaophamus rubellus	ZMH	V-3960
Aglaophamus rubellus anops	LACM (holotype and paratypes)	?
Aglaophamus sinensis	MNHN	POLY TYPE 185, 186
Aglaophamus surrufa	LACM	?
Aglaophamus tabogensis	NHM (syntypes)	NHM 1932.12.24.125/126 (syntypes)

Aglaophamus tepens	LACM	?
Aglaophamus toloensis	USNM; NHM; AM; NSMT	USNM 123357
Aglaophamus trissophyllus	Seckenberg Museum (syntypes)	?
Aglaophamus uruguayi	SMNH	?
Aglaophamus urupani	PMBC; AM; NHM; USNM; ZMUC	PMBC 3102
Aglaophamus verrilli	NHM	NHM 1885.12.1.127 (syntype/lectotype)
Aglaophamus victoriae	AM	AM W200638
Aglaophamus vietnamensis	LACM	?
Aglaophamus virginis	?	?
Bipalponephtys cornuta	USNM	USNM 32873 (as *N. cornuta*)
Nephtys cornuta franciscana	USNM	USNM 26466
Nephtys parva	USNM	USNM 26464
Bipalponephtys danida	PMBC; AM; NHM; USNM; ZMUC	PMBC 3163
Dentinephtys glabra	LACM	LACM 0793
Inermonephtys brasiliensis	MCBM	MCBM-BPO-24
Inermonephtys foretmontardoi	NHM	NHM 1921.5.1.861
Inermonephtys gallardi	LACM	?
Inermonephtys inermis	MCZ	MCZ 1088
Inermonephtys japonica	NSMT	NSMT-Pol. H 184
Inermonephtys palpata	AMS	AMS W1710
Inermonephtys patongi	PMBC; NHM; ZMC	PMBC 3170
Inermonephtys tetrophthalmus	AM; AHF; NHM; USNM	AM W200651
Micronephthys abranchiata	?	?
Micronephthys ambrizettana	?	?
Micronephthys hartmannschroederae	ZMH	ZMH P-18917 / 18918 ?
Micronephtys neotena	USNM	USNM 47165, 1970 (as *A. neotenus*)
Micronephthys minuta	?	?
Micronephthys oculifera	NMW; SMNH; SWIMS; NHM	NMW.Z.1986.079.156
Micronephthys sphaerocirrata	?	?
Micronephthys stammeri	?	?
Nephtys acrochaeta	SMNH; LACM	SMNH
Nephtys assignis	LACM-AHF	AHF Poly 0458
Nephtys assimilis	ZMC	
Nephtys bilobatus	AHF	AHF 1105
Nephtys brachycephala	USNM	USNM 15722 (dry)
Nephtys brevibranchis	ZMH	?
Nephtys bruuni	ZMUC	ZMUC-POL-00042; 00158 (paratype)
Nephtys bucera	MCZ	MCZ 209
Nephtys caeca	?	?
Nephtys caecoides	USNM	USNM 20319
Nephtys capensis	NHM (paratype)	?
Nephtys californiensis	USNM	USNM 20320
Nephtys chemulpoensis	USNM	USNM 172569
Nephtys ciliata	?	?
Nephtys cirrosa	MCZ	MCZ 1242
Nephtys cryptomma	USNM, TAMU; AMML	USNM 67778
Nephtys digitifera	RMNH	RMNH 1397
Nephtys discors	MCZ	MCZ 700
Nephtys ectopa	?	?
Nephtys ferruginea	LACM	LACM-AHF 0798
Nephtys fluviatilis	NHM	NHM 1937.4.22.3
Nephtys furcifera	ZMH	?
Nephtys gravieri	ZMH	V-7896 (syntype)

Nephtys hombergii	?	?
Nephtys hudsonica	Victoria Memorial Museum, Ottawa; MCZ (paratype)	No. 51
Nephtys hystricis	?	?
Nephtys impressa	NHM	NHM 1869.6.16.6
Nephtys incisa	?	?
Nephtys inornata	AM, USNM, NHM, AHF	AM W8706
Nephtys kersivalensis	BMNH	BMNH ZK 1921.5.1.807
Nephthys lactea	SMNH	?
Nephtys longipes	AM	AM W5251 (neotype)
Nephtys longosetosa	?	?
Nephtys magellanica	ZMH	?
Nephtys mesobranchia	AM	AM W8653
Nephtys mirocirris	AM; AHF	AM W3782
Nephtys monilibranchiata	MNHN - Santiago	MNHN nº 80005
Nephtys monroi	LACM; NHM	NHM 1932.12.24.127
Nephtys multicirrata	ZMH	?
Nephtys neopolybranchia	NSMT	NSMT-Pol. H 237
Nephtys oculata	ZMH	?
Nephtys oligobranchia	?	?
Nephtys palatii	MNHN-Paris	POLY TYPE 481, 482
Nephtys panamensis	NHM	NHM 1928.9.13.51 (syntype)
Nephtys paradoxa	?	?
Nephtys pente	ZI; ZMK; NHM; AHF; USNM; AM	ZI-P-17567
Nephtys phasuki	PMBC	PMBC no. 3172
Nephtys phyllocirra	MCZ	MCZ 62
Nephtys picta	MCZ	MCZ 830 (syntype)
Nephtys polybranchia	?	?
Nephtys punctata	USNM	USNM 20321
Nephtys rickettsi	USNM; AHF (paratypes)	USNM 20322
Nephtys semiverrucosa	AM	AM W5865
Nephtys serratifolia	?	?
Nephtys serrata	NSMT	NSMT-Pol. H 239
Nephtys serratus	SMNH	?
Nephtys signifera	USNM; SBMNH; LACM	USNM 148706
Nephtys simoni	USNM; FSBC	USNM 58725
Nephtys singularis	LACM	?
Nephtys squamosa	?	?
Nephtys sukumoensis	?	?
Nephtys tulearensis	MNHN; NHM (syntype)	POLY TYPE 651, 234-236
Nephtys vikingensis	AM, NHM, AHF	AM W5251

Museum abbreviations

AHF - Allan Hancock Foundation
AM(S) – Australian Museum, Sydney
AMML - Texas A&M Marine Laboratory reference Collection, Galveston
GNHM - Naturistoriska Museum, Gothenburg
FSBC – Invertebrate Reference Collection of the Florida Department of Natural Resources Marine Research Laboratory
LACM – Los Angeles County Museum of Natural History
MCBM – Museu do Centro de Biologia Marinha, Universidade Federal do Paraná
MCZ – Museum of Comparative Zoology, Harvard University
MNHN – Musée National d'Histoire Naturelle, Paris
NHM – Natural Histury Museum, London

NMW – National Museum of Wales, Cardiff
NSMT – National Science Museum, Tokyo
PMBC – Reference Collection of Phuket Marine Biological Center
RMNH – Nationaal Natuurhistorisch Museum (Naturalis)
SBMNH – Santa Barbara Museum of Natural History
SMNH - Swedish Museum of Natural History, Stockholm
SWIMS – Swire Institute of Marine Science, University of Hong Kong
TAMU – Texas A&M University, Department of Oceanography reference collection, Colledge Station
USNM - United States National Museum of Natural History, Smithsonian Institution, Washington, DC
ZI – Zoologisches Institut, Hamburg
ZMH - Zoologisches Museum of Hamburg
ZMK – Zoologisches Museum, Kiel
ZMUC - Zoological Museum, Copenhagen

Annex II. List of major revisions for the family Nephtyidae.

Reference	Taxa	Geographical area
Day 1953, 1967	Nephtyidae	South Africa
Dnestrovskaya & Jirkov & 2001	Nephtyidae	Arctic ocean
Fauchald 1963	Nephtyidae	Norway
Fauchald 1965	Nephtyidae	Australia
Fauchald 1968	Nephtyidae	Viet Nam
Fauchald 1972	Nephtyidae	Western Mexico
Fauchald 1976	Nephtyidae	Ubatuba, Brasil
Fauvel 1923	Nephtyidae	France
Foret-Montardo 1969	Nephtyidae	Marseille, France
Hartman 1938	Nephtyidae	Northeast Pacific
Hartman 1940	Nephtyidae	Northeast Pacific
Hartman 1950	Nephtyidae	Northeast Pacific
Hartman 1967	Nephtyidae	Antarctic
Heinen 1911	Nephtyidae	North Europe
Hilbig 1997	Nephtyidae	California, USA
Imajima & Takeda 1985	*Inermonephtys*, *Micronephthys*, *Aglaophamus*	Japan
Imajima & Takeda 1987	*Dentinephtys*, *Nephtys*	Japan
Jirkov & Paraketsova 1996	*Micronephthys*	White Sea
Jung & Hong 1997	Nephtyidae	Yellow Sea
Laborda 2004	Nephtyidae	Iberian peninsula
Lana 1986	Nephtyidae	Brazil
Lee & Jae 1983	Nephtyidae	Yellow Sea
Lovell 1997	*Nephtys*	Eastern Pacific
Nateewathana & Hylleberg 1986	Nephtyidae	Thailand
Paxton 1974	Nephtyidae	Australia
Pettibone 1963	Nephtyidae	New England
Rainer 1990	*Nephtys*	Northern Europe
Rainer 1991	*Nephtys*	Northern Europe
Rainer & Hutchings 1977	Nephtyidae	Australia
Rainer & Kaly 1988	Nephtyidae	Australia
Ravara *et al.* submitted	Nephtyidae	Southern Europe
Rizzo & Amaral 2007	Nephtyidae	São Paulo, Brasil
Rozbaczylo & Castilla 1974	Nephtyidae	Chile
Taylor 1984	Nephtyidae	Gulf of Mexico
Uschakov & Wu 1962	Nephtyidae	Yellow Sea

Complete references

Day, J. H. (1953) The polychaete fauna of South Africa. Part 2. Errant species from Cape shores and estuaries. *Annals of the Natal Museum, 12*, 397–441.

Day, J. H. (1967) *A monograph on the Polychaeta of southern Africa. Part 1. Errantia*. London: Trustees of the British Museum (Natural History).

Dnestrovskaja, N. & Jirkov, I. A. (2001) Nephtyidae Grube 1850. *In: Polychaeta of the Arctic ocean*. Yanus-K Press, Moscow, pp. 1-632.

Fauchald, K. (1963) Nephtyidae (Polychaeta) from Norwegian waters. *Sarsia, 13*, 1–32.

Fauchald, K. (1965) Some Nephtyidae (Polychaeta) from Australian waters. *Records of the Australian Museum, 26*, 333-340.

Fauchald, K. (1968) Nephtyidae (Polychaeta) from the Bay of Nha Trang, South Viet Nam. *NAGA Report, 4*, 7–33.

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

Fauchald, K. (1976) Some Nephtyidae (Polychaeta) from Ubatuba, Brasil. *Bulletin Southern California Academy of Sciences, 75*, 16-19.

Fauvel, P. (1923) Polychètes érrantes. *Faune de France, 5,* 1–488.

Foret-Montardo, P. (1969) Étude systématique et écologique des Nephtyidae (Polychètes Errantes) des parages de Marseille. *Tethys, 1*, 807–832.

Hartman, O. (1938) Review of the annelid worms of the family Nephtyidae from the Northeast Pacific, with descriptions of five new species. *Proceedings of The United States National Museum, 85*, 143–158.

Hartman, O. (1940) Polychaetous annelids. Part II. Chrysopetalidae to Goniadidae. *Allan Hancock Pacific Expeditions, 7,* 173–287.

Hartman, O. (1950) Goniadidae, Glyceridae and Nephtyidae. *Allan Hancock Pacific Expeditions, 15,* 1–181.

Hartman, O. (1967) Polychaetous annelids collected by the USNS Eltanin and Staten Island cruises, chiefly from Antarctic seas. *Allan Hancock Monographs in Marine Biology, 2,* 1–387.

Heinen, A. (1911) Die Nephtyideen und Lycorideen der Nord- und Ostee, einschlieblich der verbindenden Meeresteile. *Wissenschaftliche Meeresuntersuchungen, 13*, 1–87.

Hilbig, B. (1997) Family Nephtyidae Grube, 1850. *In:* J. A. Blake, B. Hilbig & P. H. Scott (Eds), *Taxonomic atlas of the benthic fauna of the Santa Maria basin and the western Santa Barbara channel. 4. The Annelida. Part 1. Oligochaeta: Phyllodocida (Phyllodocidae to Paralacydoniidae)*, Santa Barbara, California, pp. 317-349.

Imajima, M. & Takeda, Y. (1985) Nephtyidae (Polychaeta) from Japan. I. The genera *Inermonephtys*, *Micronephthys* and *Aglaophamus*. *Bulletin of the National Science Museum, Tokyo, 11,* 57–90.

Imajima, M. & Takeda, Y. (1987) Nephtyidae (Polychaeta) from Japan. II. The genera *Dentinephtys* and *Nephtys*. *Bulletin of the National Science Museum, Tokyo, 13*, 41–77.

Jirkov, I. A. & Paraketsova, N. (1996) Review of the species of the genus *Micronephthys* (Polychaeta: Nephthyidae) from the White Sea. *Zoologicheskii Zhurnal, 75,* 831–840. [In Russian].

Jung, R.-H. & Hong, J.-S. (1997) Nephtydae (Annelida: Polychaeta) from the Yellow Sea. *Bulletin of the Marine Science, 60*, 371–384.

Laborda, A. J. (2004) Familia *Nephtyidae* Grube, 1850. *In:* J. M. Viéitez, C. Alós, J. Parapar, C. Besteiro, J. Moreira, J. Nuñez, A. J. Laborda & G. San Martin (Eds), *Annelida, Polychaeta I*. Museo Nacional de Ciencias Naturales. CSIC, Madrid, pp. 390–419.

Lana, P. d. C. (1986) Nephtyidae (Annelida: Polychaeta) do litoral do estado do Paraná (Brasil). *Neritica, 1*, 135-154.

Lee, J.-H. & Jae, J.-G. (1983) Polychaetous annelids from the Yellow Sea. I. Family Nephtyidae. *Bulletin of the Korea Ocean Research and Development Institute, 5*, 19–27.

Lovell, L. L. (1997) A review of six species of Nephtys (Cuvier, 1817) (Nephtyidae: Polychaeta) described from the eastern pacific. *Bulletin of Marine Science, 60,* 350-363.

Nateewathana, A. & Hylleberg, J. (1986) Nephtyid polychaetes from the west coast of Phuket Island, Andaman sea, Thailand, with description of five new species. *Proceedings of the Linnean Society of New South Wales, 108,* 195–215.

Paxton, H. (1974) Contribution to the study of Australian Nephtyidae (Polychaeta). *Records of the Australian Museum, 29,* 197–208.

Pettibone, M. H. (1963) Marine polychaete worms of the New England region. I. Aphroditidae through Trochochaetidae. *US National Museum Bulletin, 227,* 1-356.

Rainer, S. F. (1990) The genus *Nephtys* (Polychaeta: Phyllodocida) in northern Europe: redescription of *N. hysticis* and *N. incisa*. *Journal of Natural History, 24,* 361–372.

Rainer, S. F. (1991) The genus *Nephtys* (Polychaeta: Phyllodocida) of northern Europe: a review of species, including the description of *N. pulchra* sp.n. and a key to the Nephtyidae. *Helgoländers Meeresuntersuchungen, 45*, 65–96.

Rainer, S. F. & Hutchings, P. A. (1977) Nephtyidae (Polychaeta: Errantia) from Australia. *Records of the Australian Museum, 31*, 307–347.

Rainer, S. F. & Kaly, U. L. (1988) Nephtyidae (Polychaeta: Phyllodocida) of Australia: new species from the West shelf, and key to Australian species. *Journal of Natural History, 22*, 685–703.

Ravara, A., Cunha, M. R. & Pleijel, F. (in prep.) Nephtyidae (Annelida, Polychaeta) from southern Europe. *to submit to Zootaxa*.

Rizzo, A. E. & Amaral, A. C. Z. (2007) Nephtyidae (Annelida: Polychaeta) from São Paulo State, Brazil, including a new record for the Brazilian coast. *Biota Neotropica, 7,* 253-263.

Rozbaczylo, N. & Castilla, J. C. (1974) La familia Nephtyidae en Chile (Annelida, Polychaeta). *Studies on the Neotropical Fauna, 9,* 179-206.

Taylor, J. L. (1984) Family Nephtyidae Grube, 1850. *In:* J. M. Uebelacker & P. G. Johnson (Eds), *Taxonomic guide to the polychaetes of the Northern Gulf of Mexico*. V. Barry A. Vittor and Associates, Mobile, Alabama, pp. 35.31–35.20.

Uschakov, P. & Wu, B.-L. (1962) Polychaete worms of the Yellow Sea II. Fam. Chrysopetalidae, Glyceridae and Nephtyidae (Polychaeta, Errantia). *Studia Marina Sinica, 1,* 1–32.

ANNEX III

Aglaophamus: *A. australiensis, A. elamellata, A. lutreus, A. malmgreni, A. munamaorii, A. pulcher, A. rubellus, A. tabogensis, A. trissophyllus, A. verrilli.*

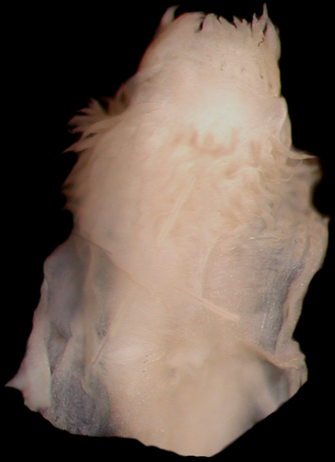
Bipalponephtys: *B. cornuta.*

Inermonephtys: *I. foretmontardoi.*

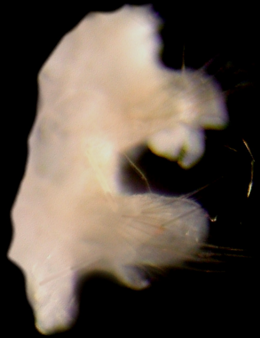
Micronephthys: *M. oculifera, M. sphaerocirrata, M. stammeri.*

Nephtys: *N. acrochaeta, N. assignis, N. assimilis, N. caeca, N. caecoides, N. californiensis, N. capensis, N. ciliata, N. cirrosa, N. ferruginea, N. fluviatilis, N. glossophylla, N. hombergii, N. hystricis, N. impressa, N. incisa, N. kersivalensis, N. longosetosa, N. monroi, N. panamensis, N. paradoxa, N. pente, N. punctata, N. polybranchia, N. rickettsi, N. schmitti, N. serrata, N. squamosa, N. tulearensis.*

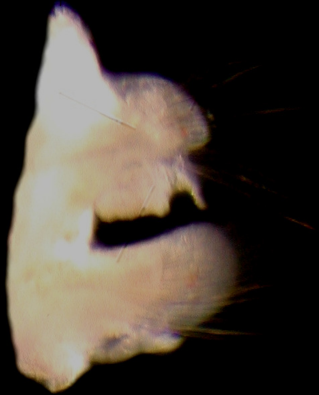
Aglaophamus australiensis



10th

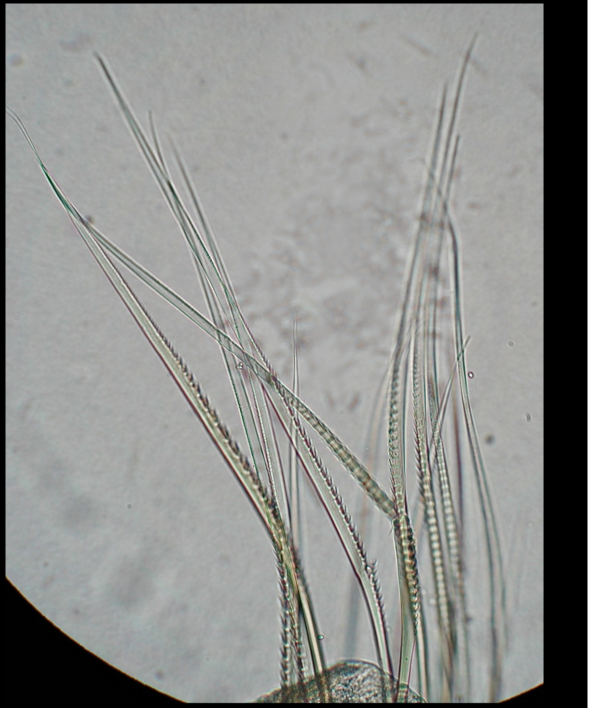


20th

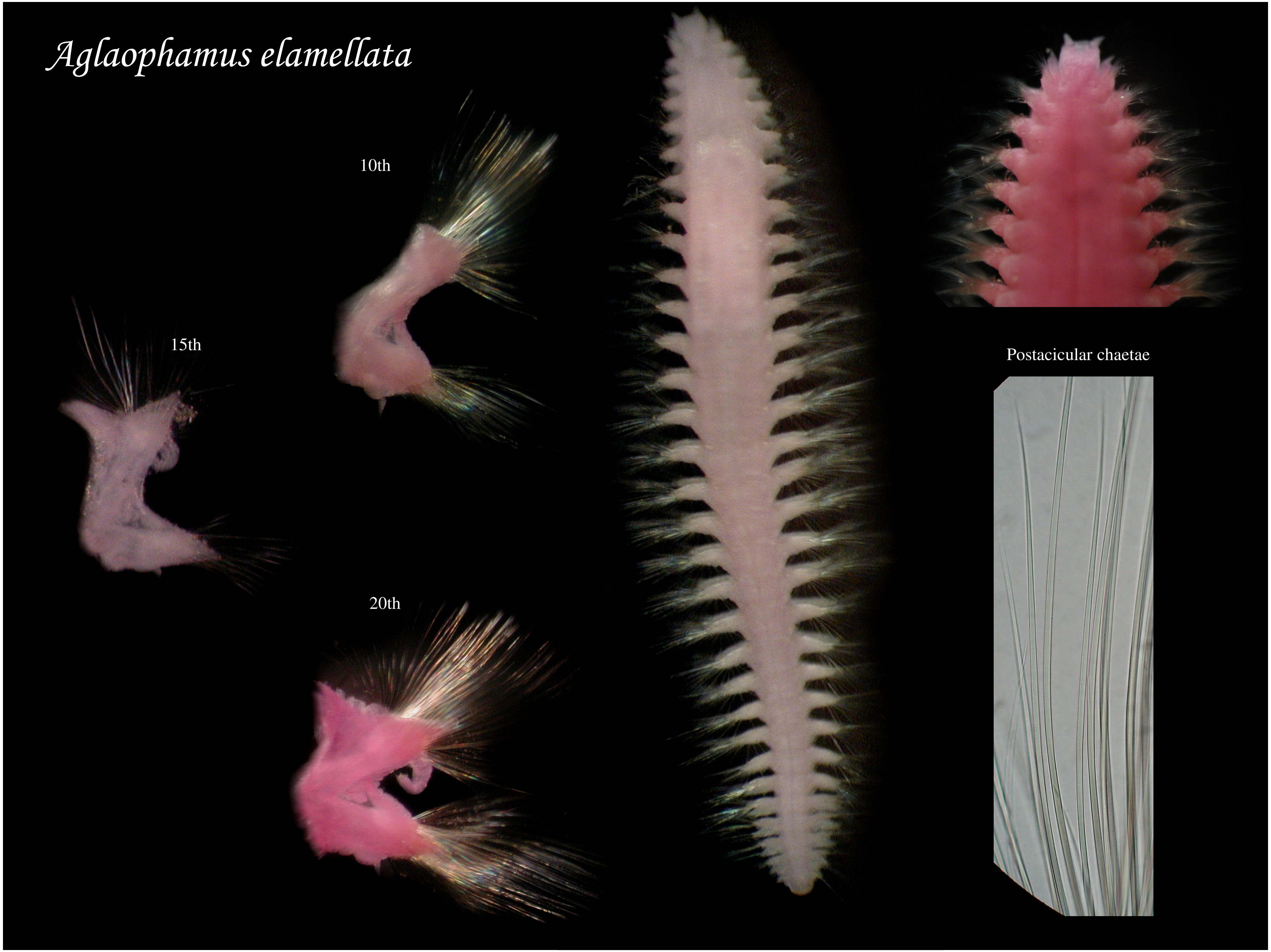


40th

Postacicular chaetae

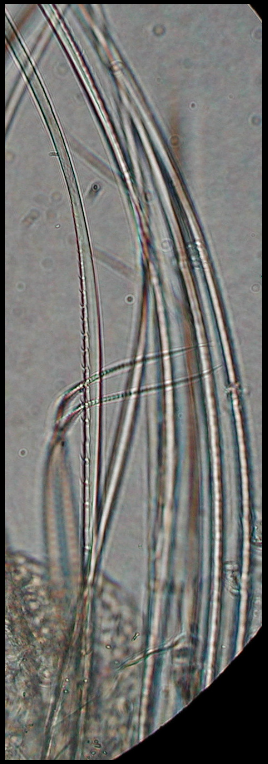


Aglaophamus elamellata

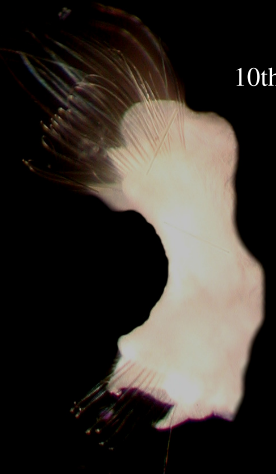


Aglaophamus lutreus

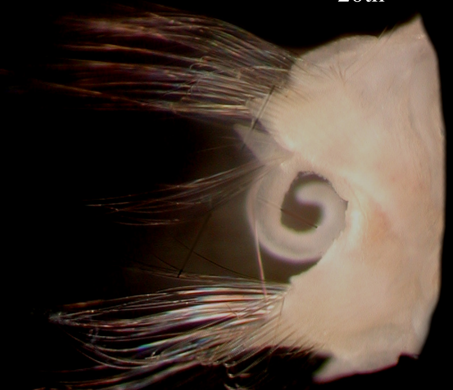
Postacicular chaetae



Aglaophamus malmgreni (Arctic)

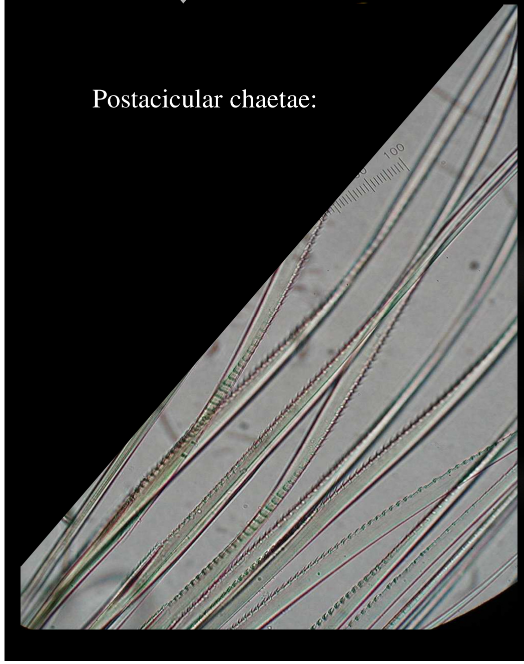


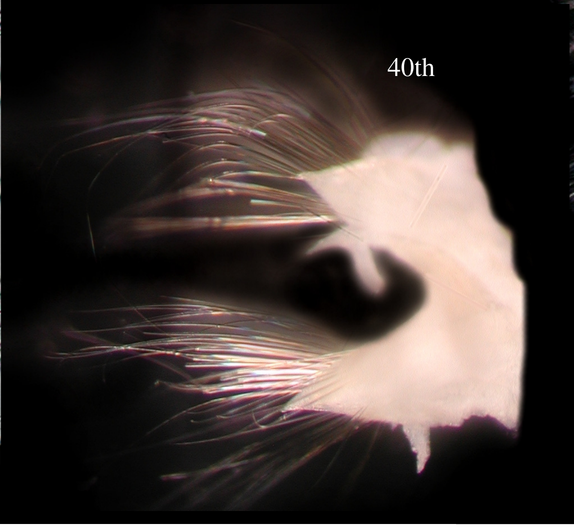
10th



20th

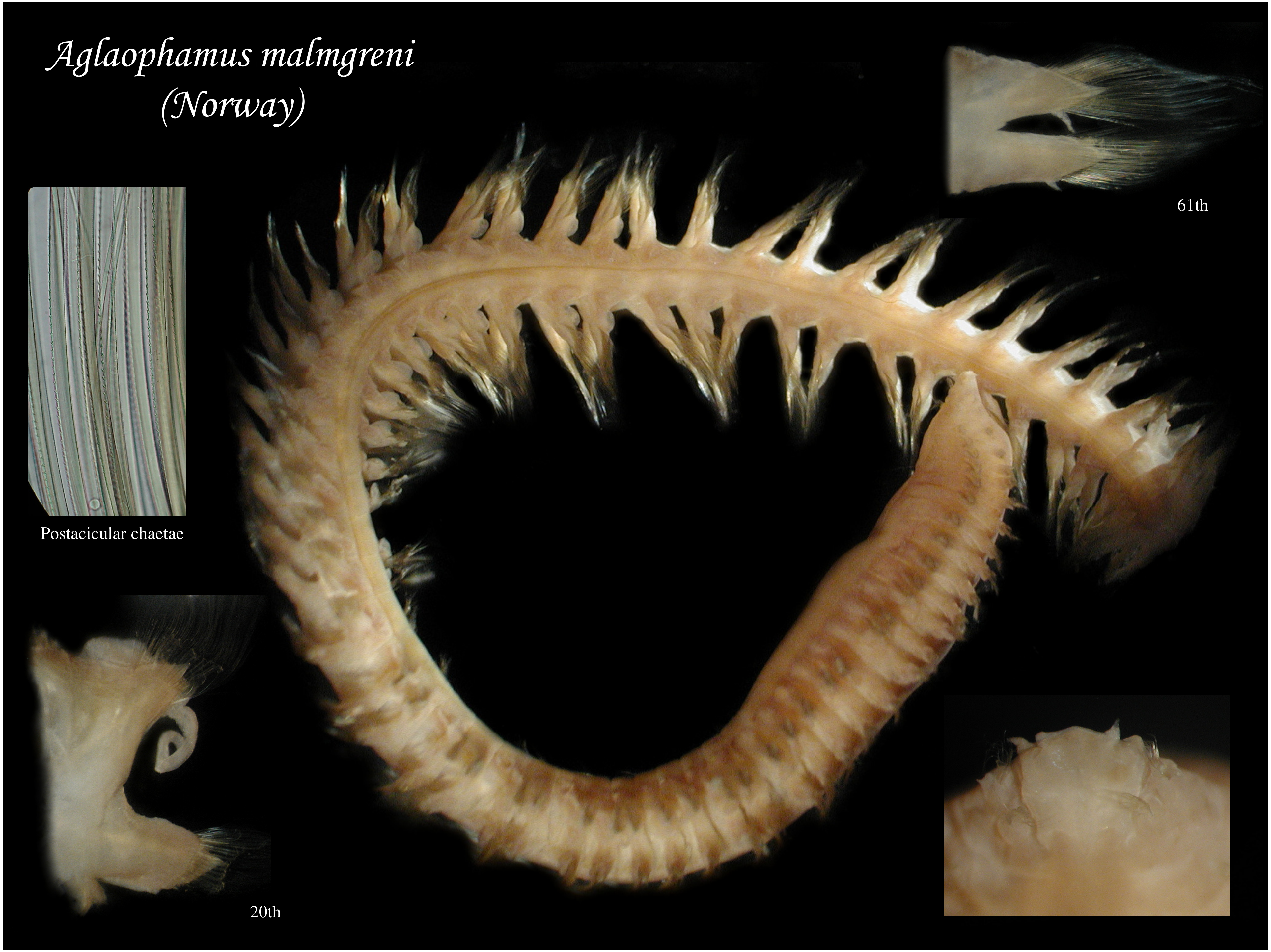
Postacicular chaetae:



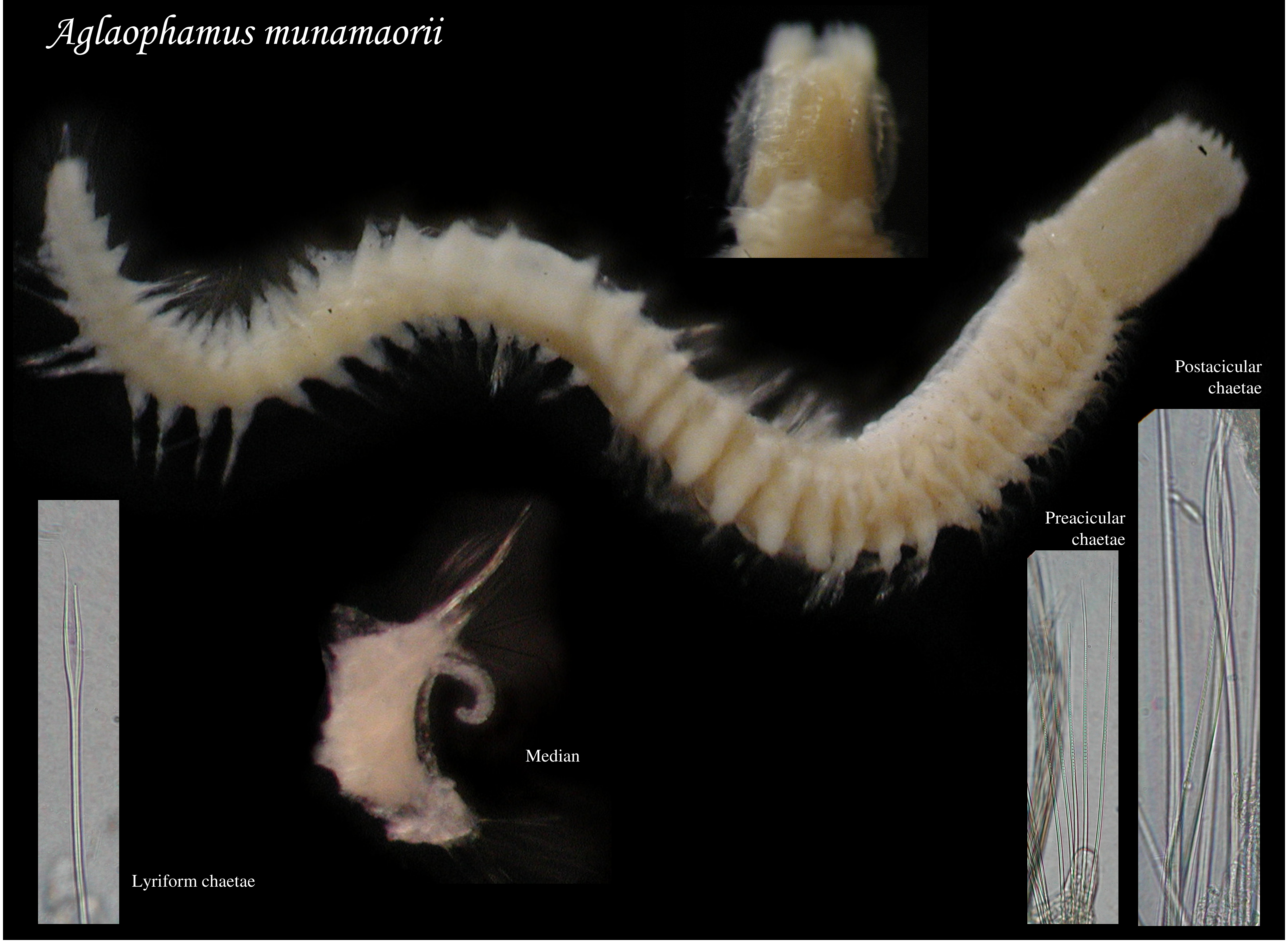


40th

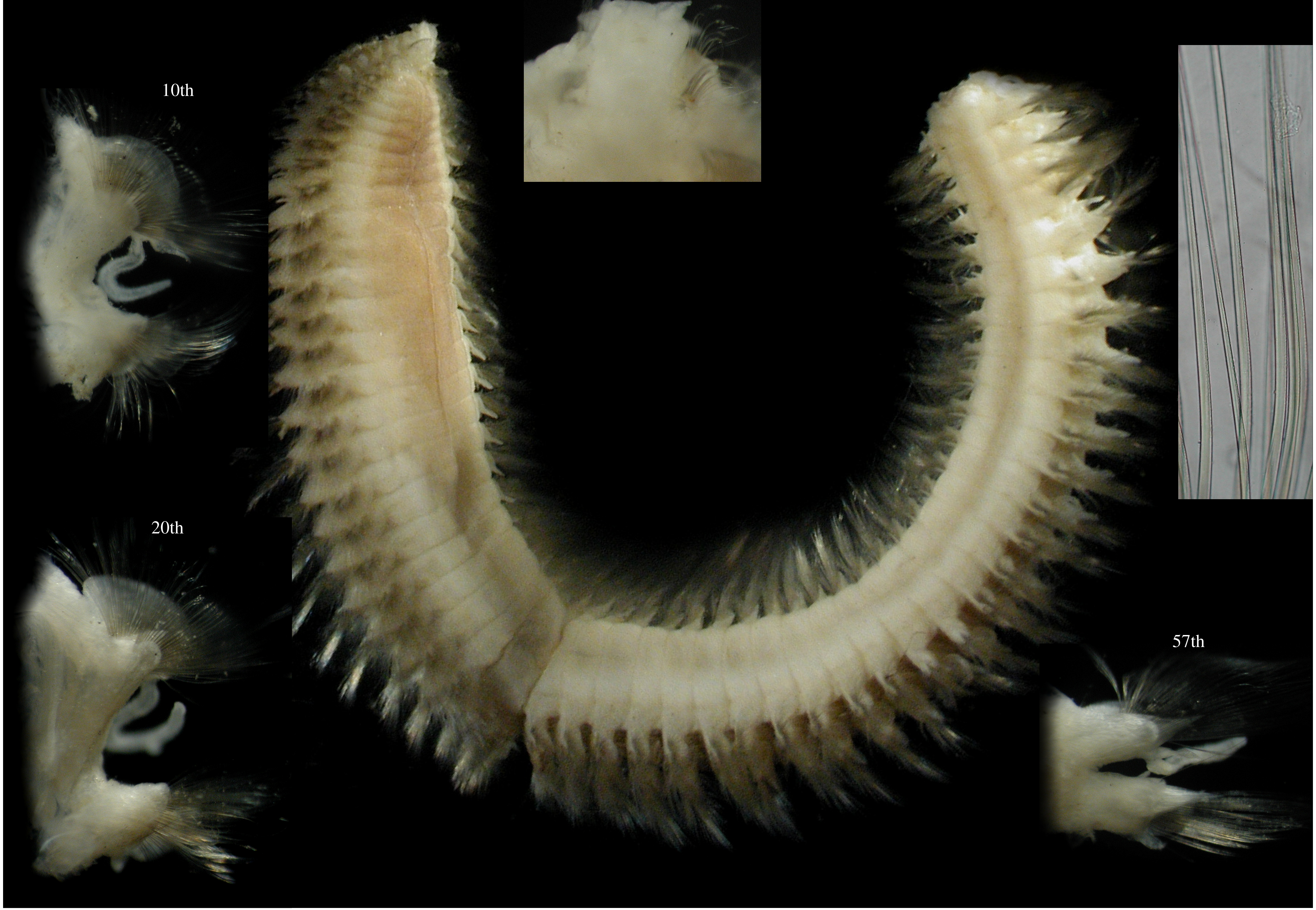
Aglaophamus malmgreni
(Norway)



Aglaophamus munamaorii

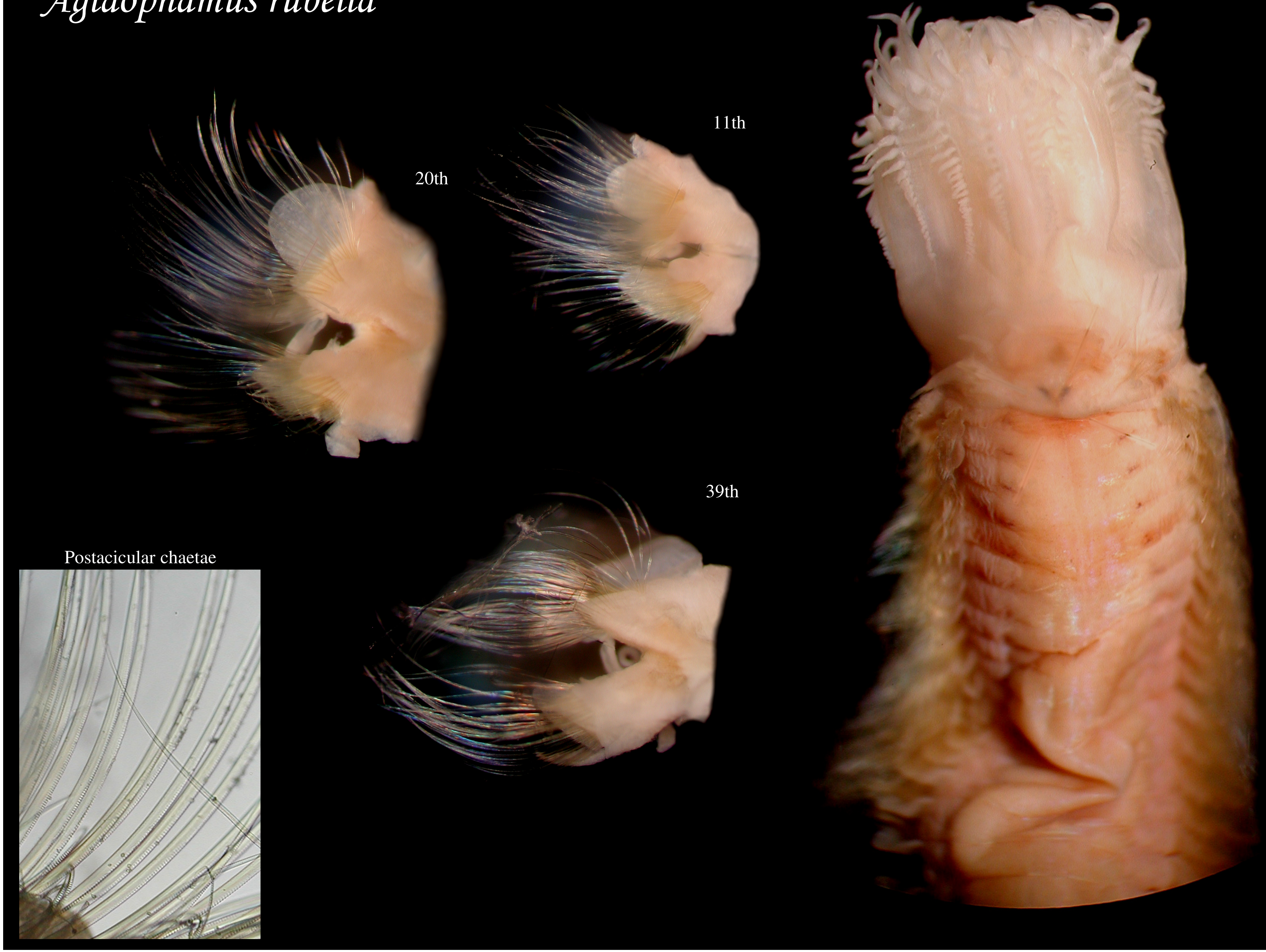


Aglaophamus pulcher



Aglaophamus pulcher (Sweden)

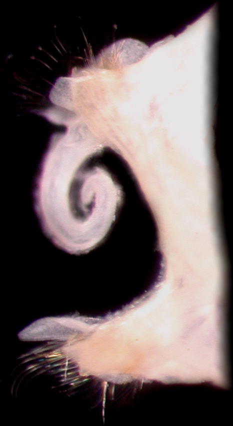
Aglaophamus rubella



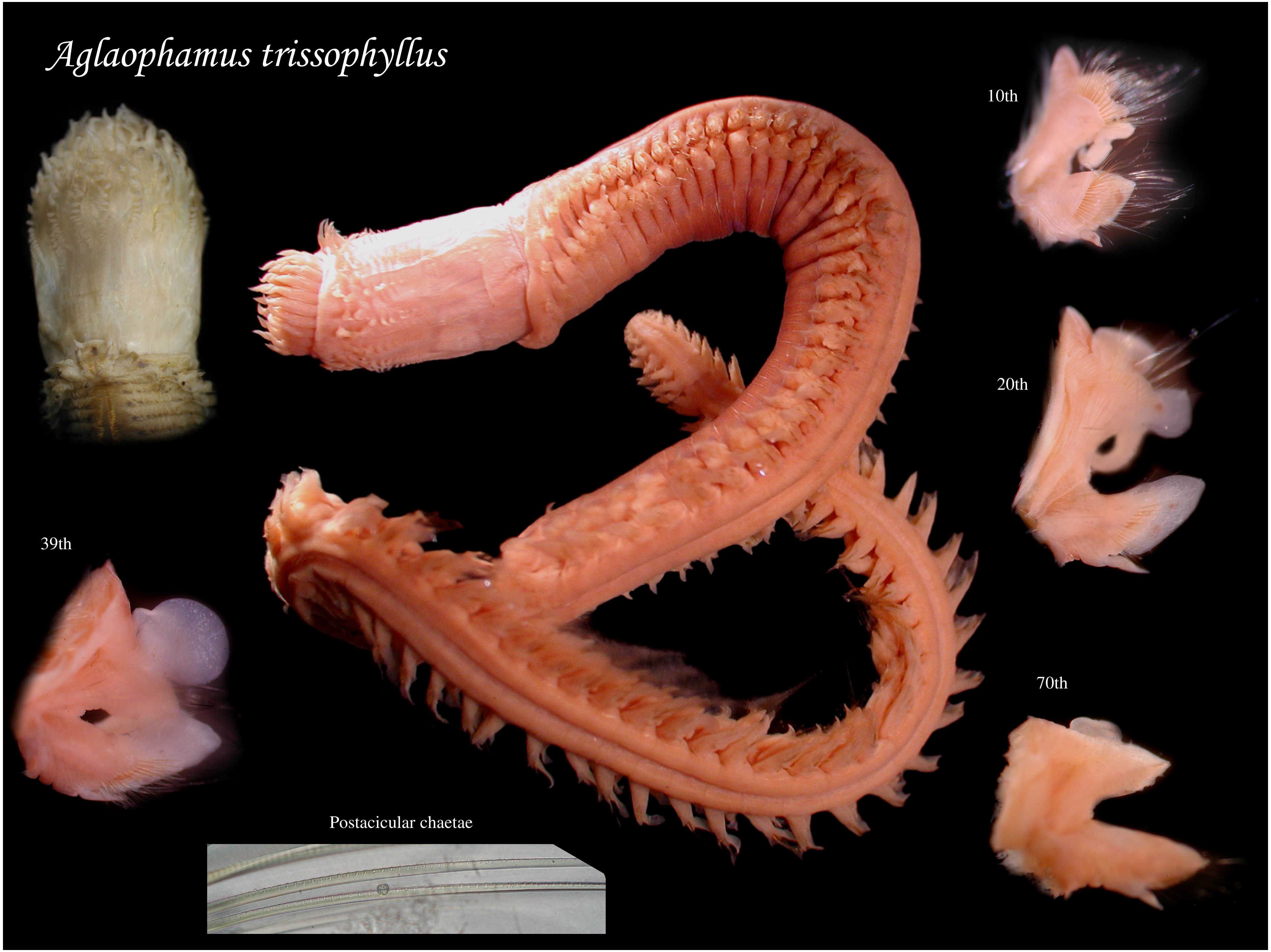
Aglaophamus tabogensis

Lyriform chaetae

14th

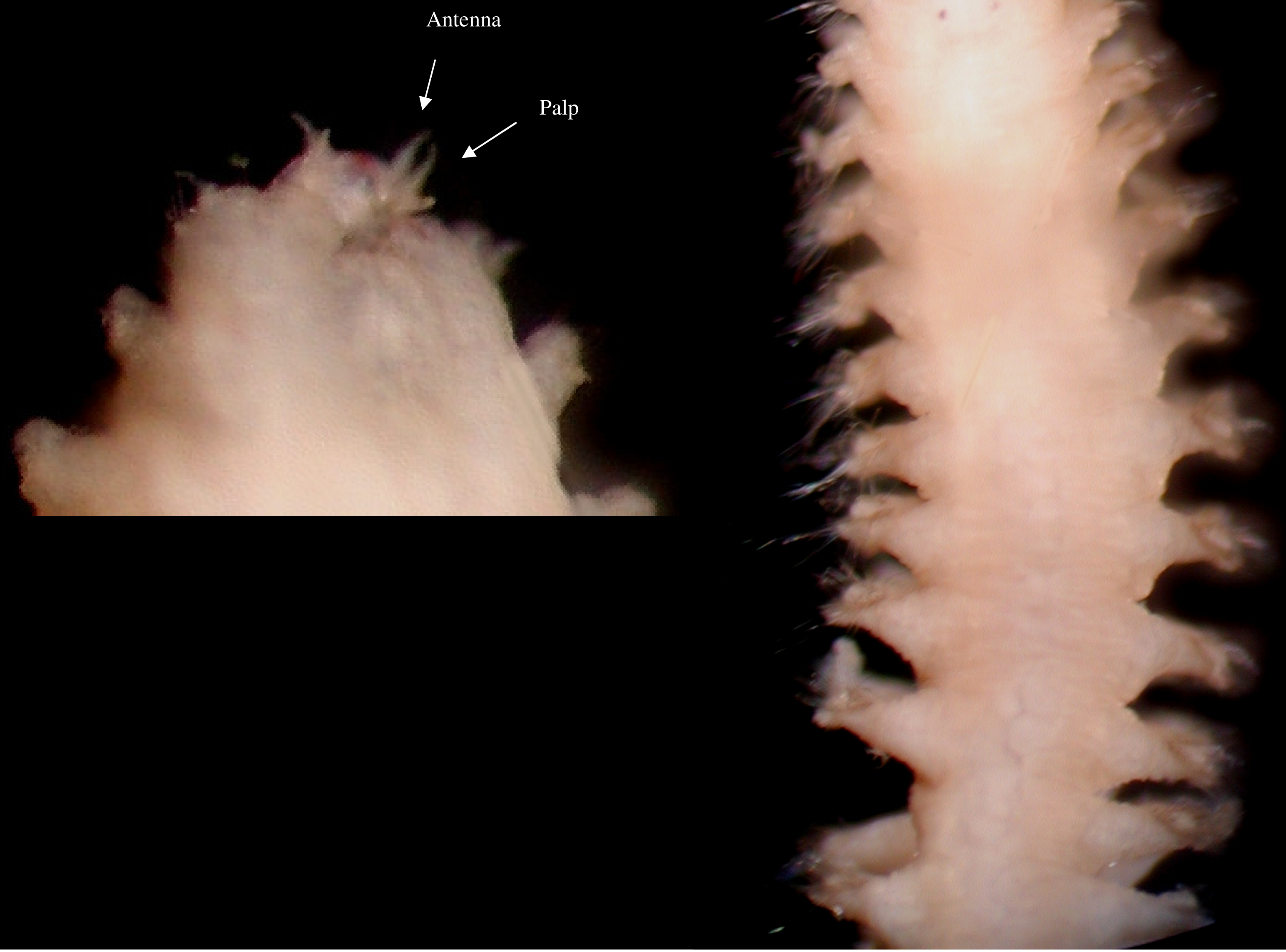


Aglaophamus trissophyllus



Aglaophamus verrilli

Bipalponephtys cornuta



Inermonephtys foretmontardoi

Micronephthys oculifera

Pre- and postacicular chaetae

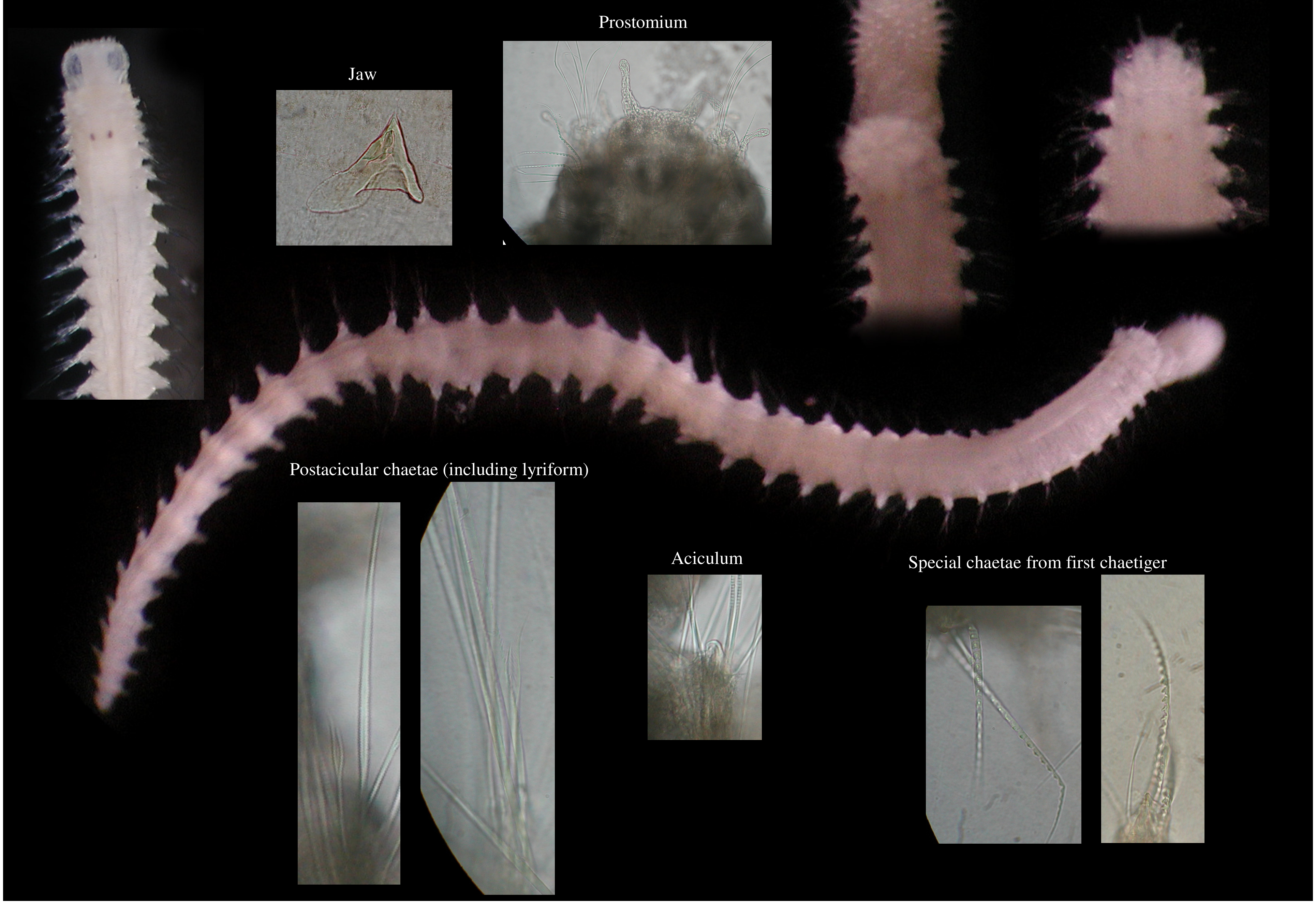
Lyriform chaetae

Micronephthys sphaerocirrata

Postacicular chaetae

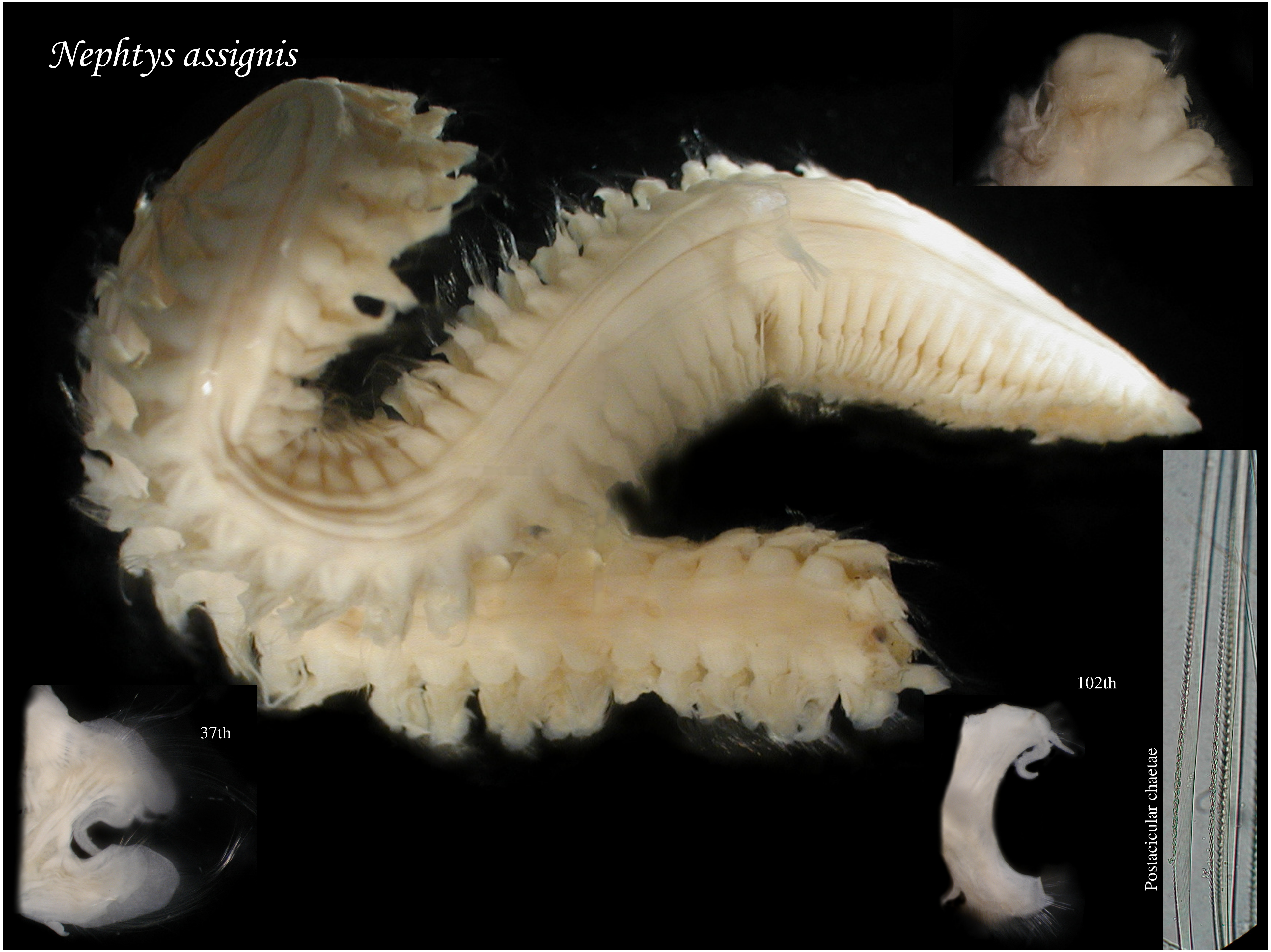
Aciculum

Micronephthys stammeri



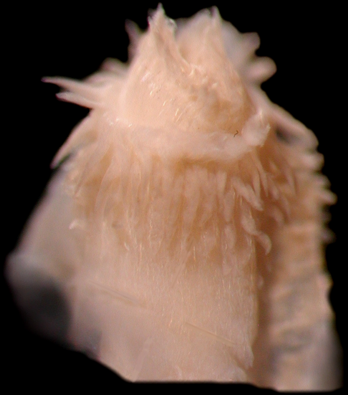
Nephtys acrochaeta

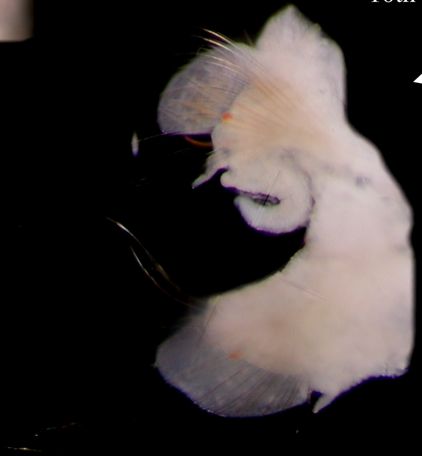
Nephtys assignis

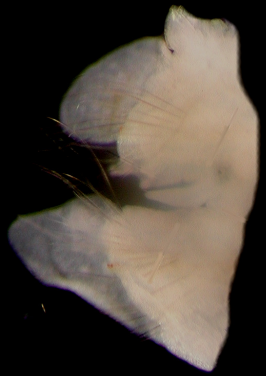


Nephtys assimilis

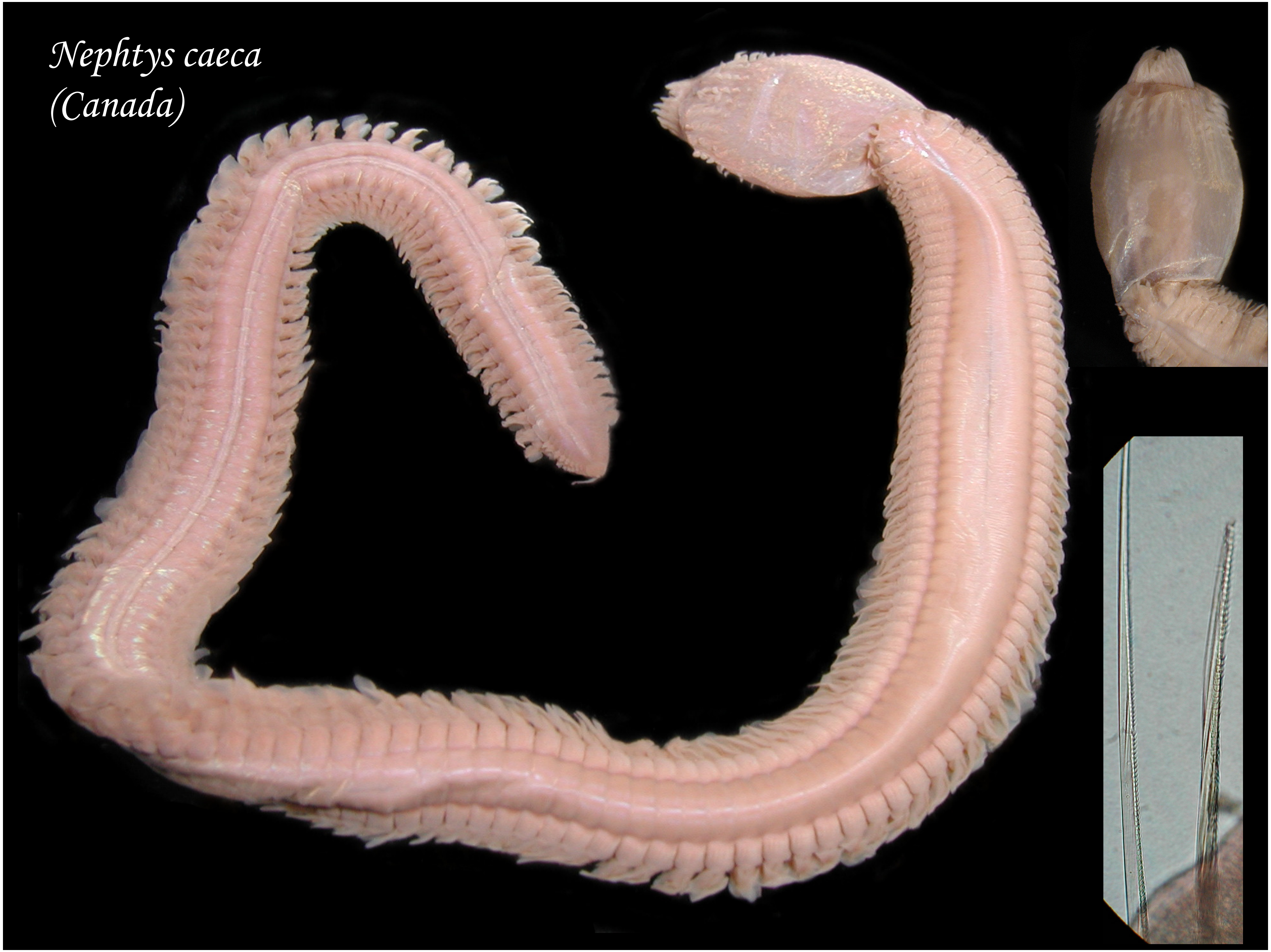
Nephtys caeca








Postacicular chaetae



Nephtys caeca
(Canada)

Nephtys caecoides

Postacicular chaetae

41th

Nephtys californiensis

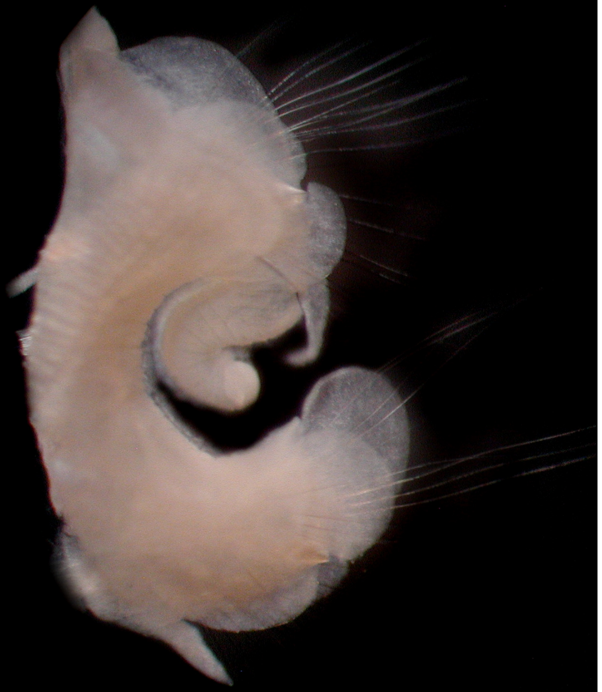
Nephtys californiensis (Brasil)

Nephtys capensis

Nephtys ciliata

Nephtys ciliata
(Iceland)

39th

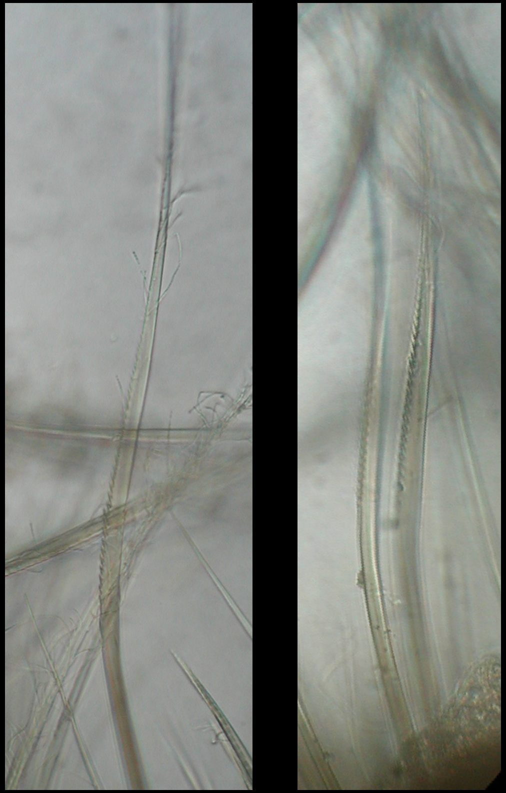


Nephtys cirrosa

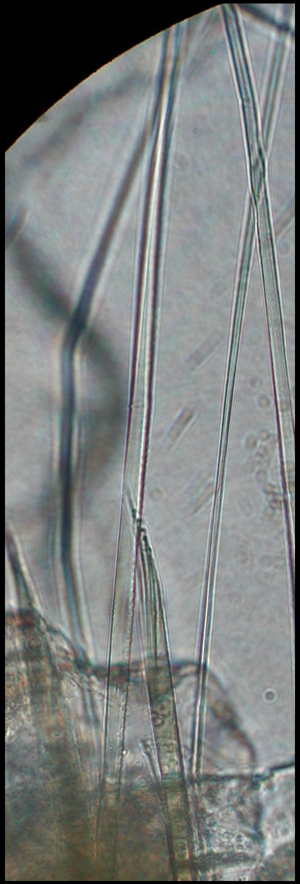
Nephtys ferruginea

Nephtys fluviatilis

Postacicular chaetae

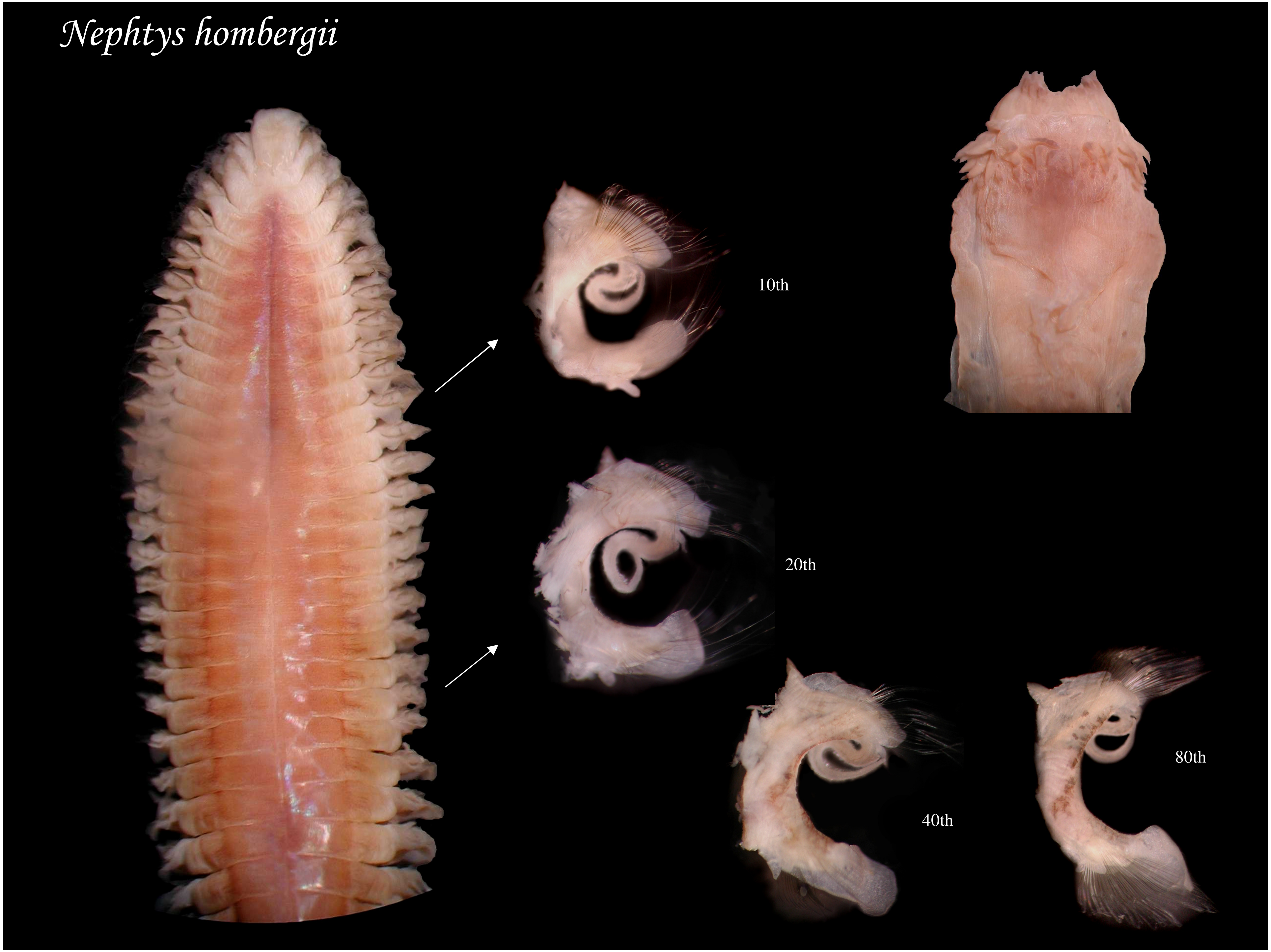


Nephtys glossophylla



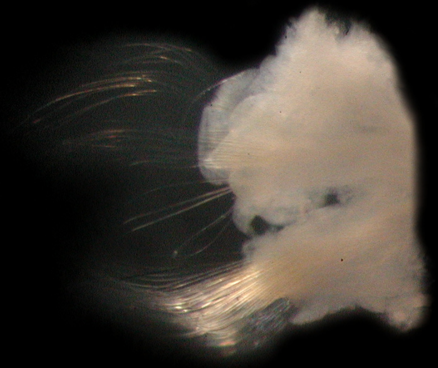
32th

Nephtys hombergii



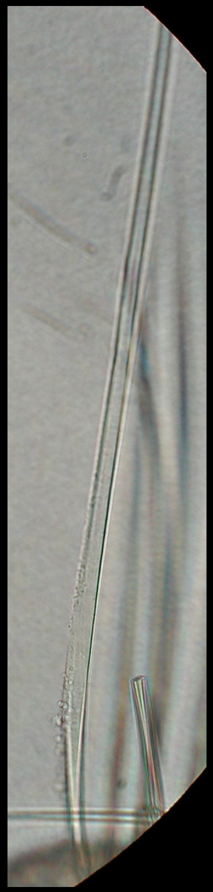
Nephtys hystricis

10th

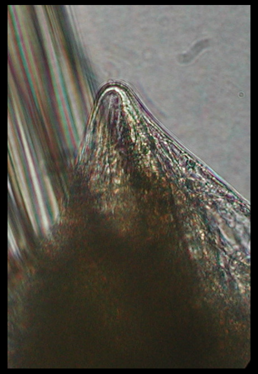


20th

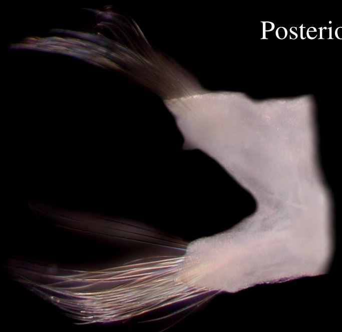
Postacicular chaetae



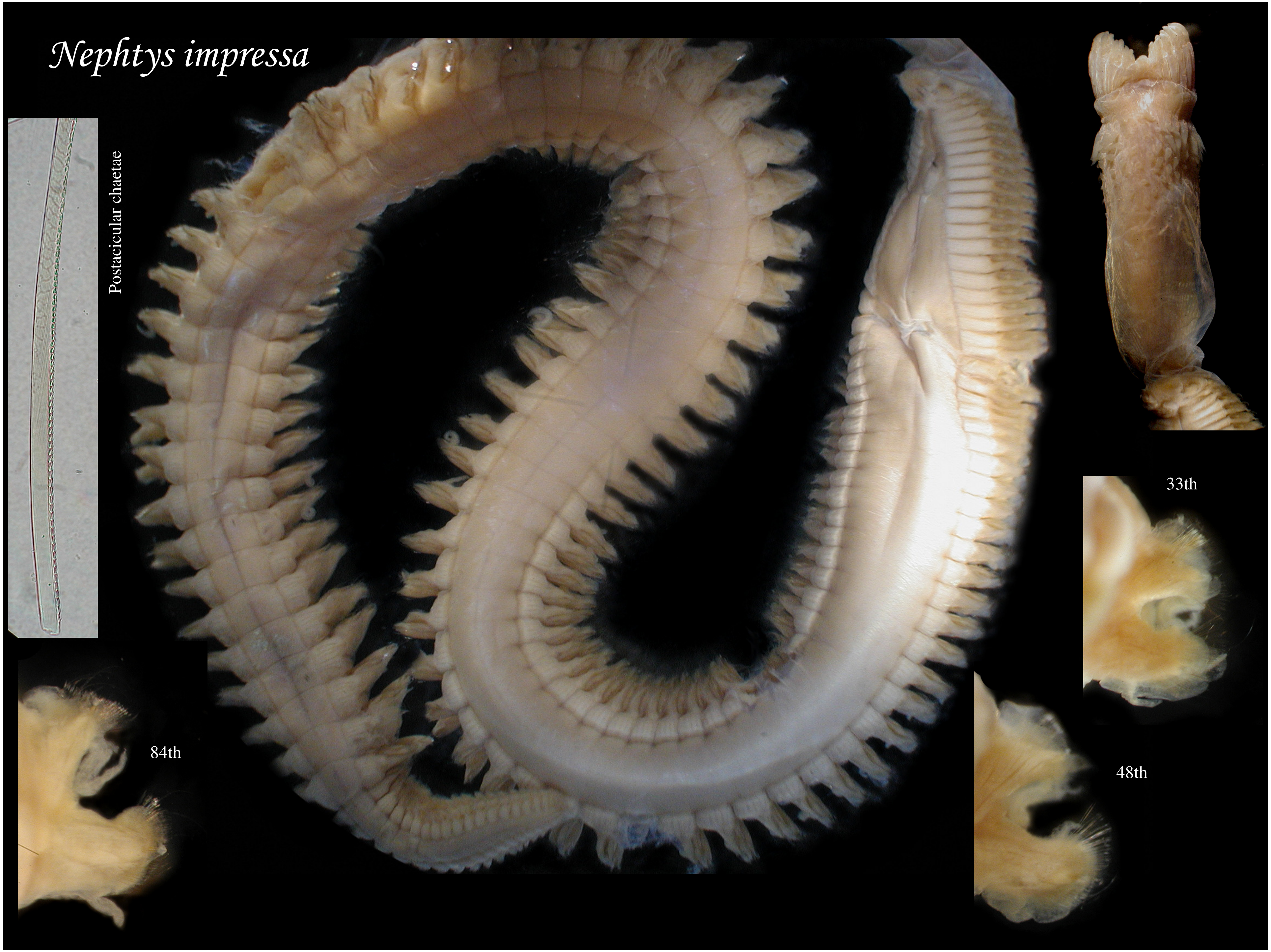
Aciculum



Posterior

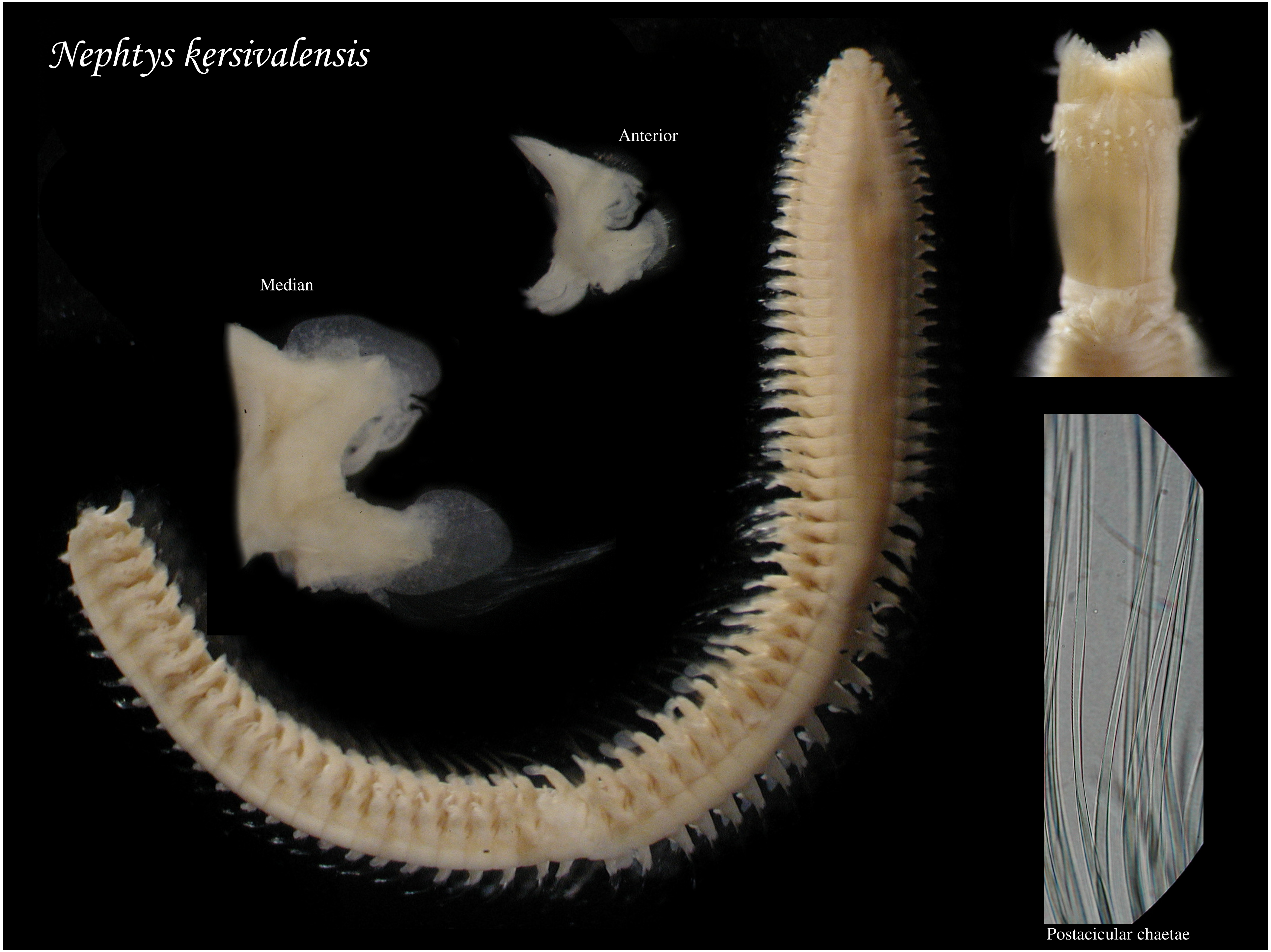


Nephtys impressa

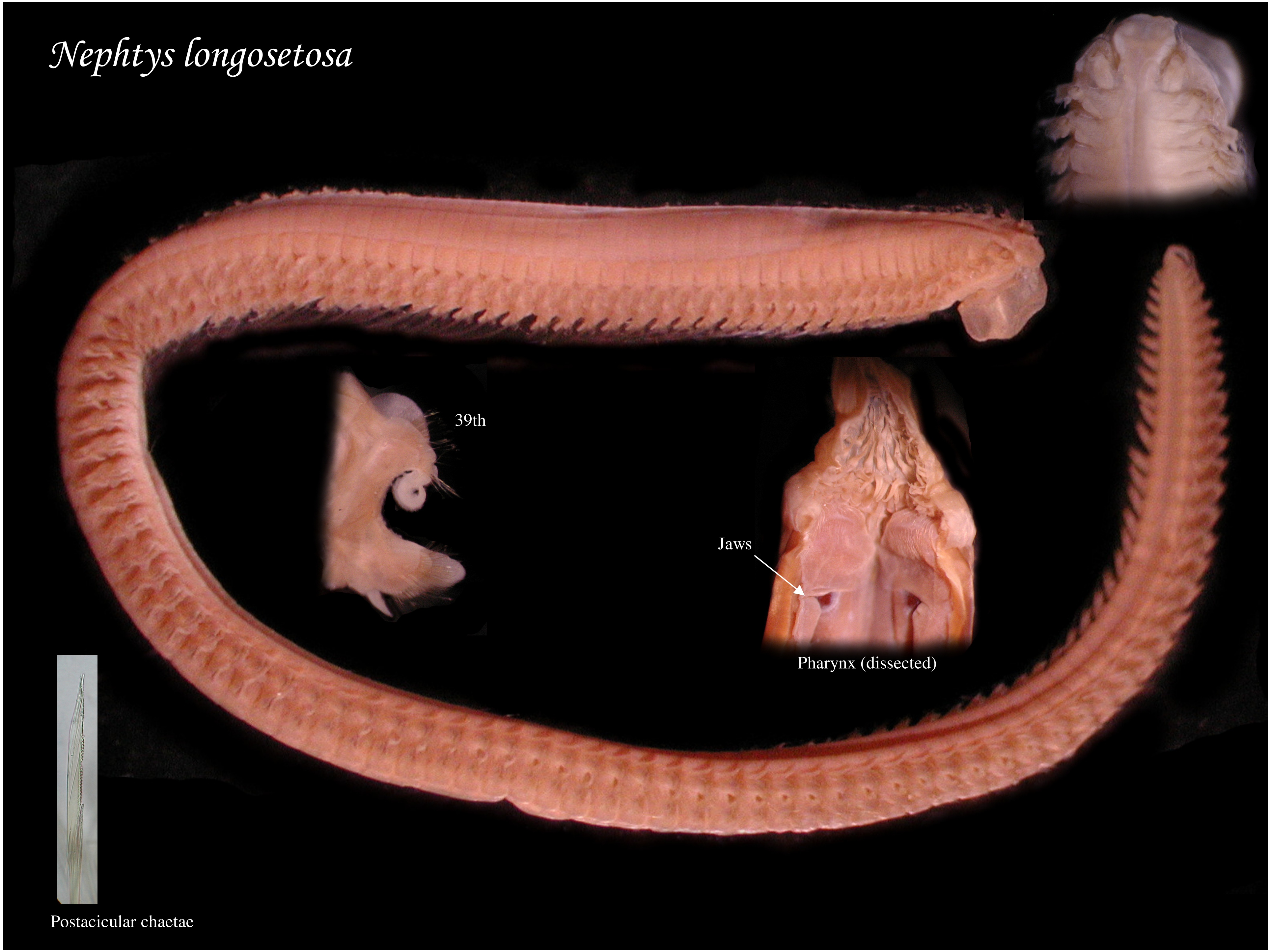


Nephtys incisa

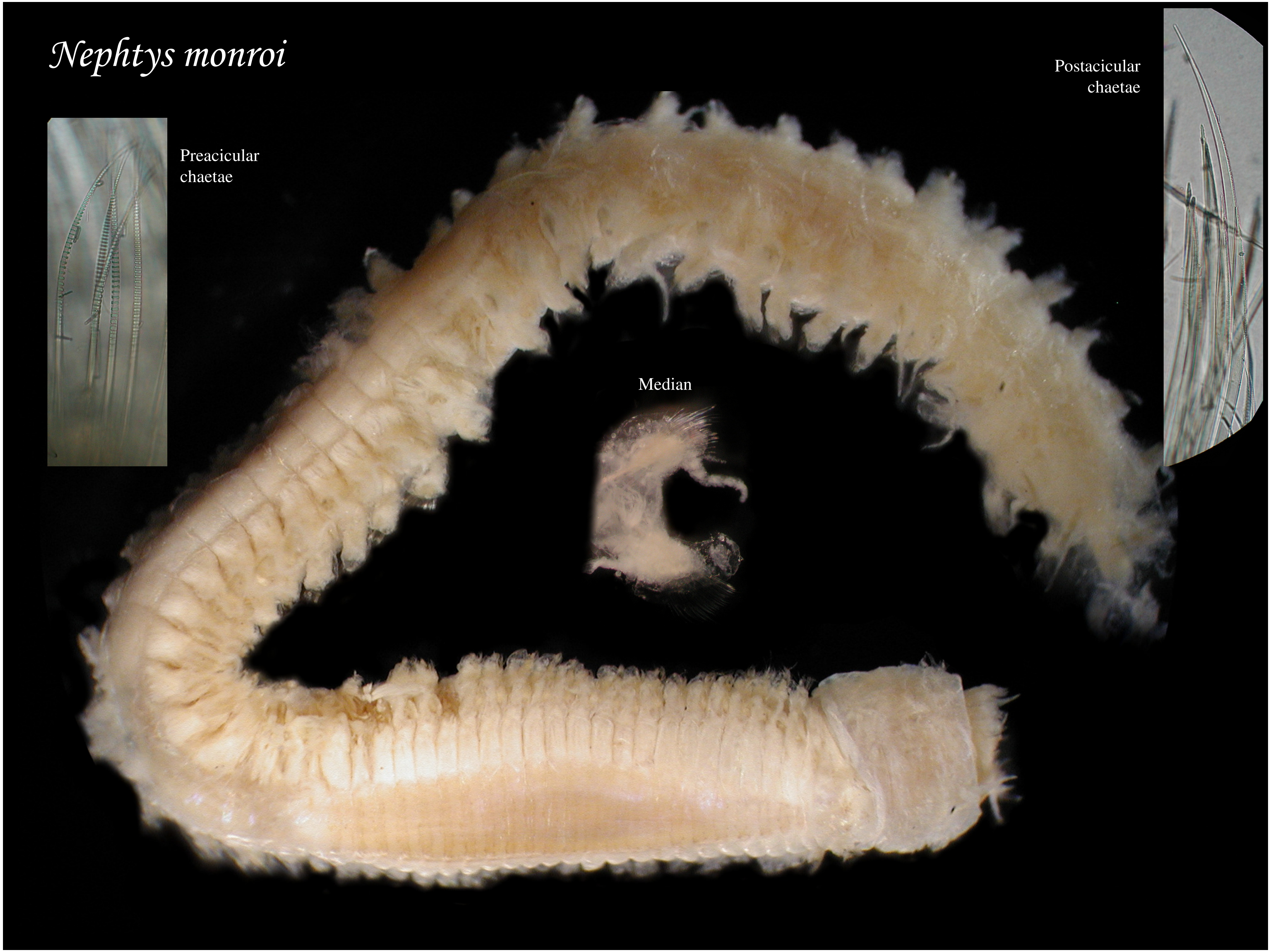
Nephtys kersivalensis



Nephtys longosetosa

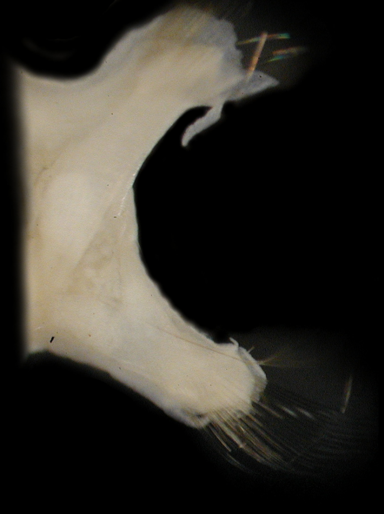


Nephtys monroi

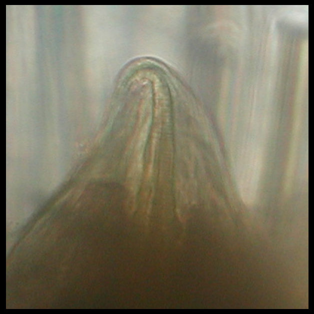


Nephtys panamensis

60th

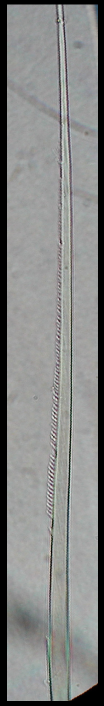


Aciculum



24th

Preacicular chaetae

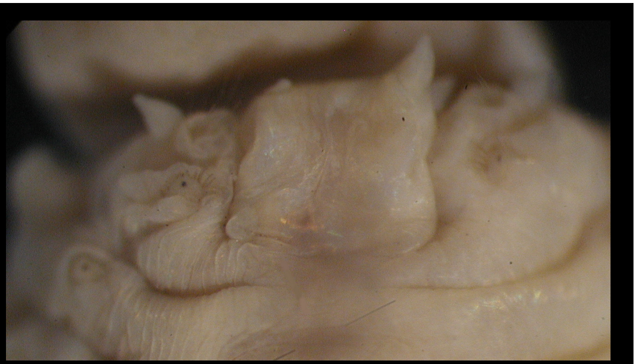


Postacicular chaetae

Nephtys paradoxa

20th

39th

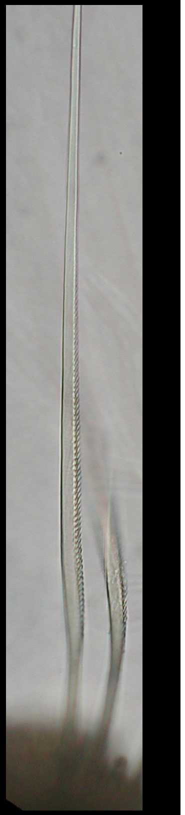


Nephtys paradoxa (Gulf of Cadiz)

50th

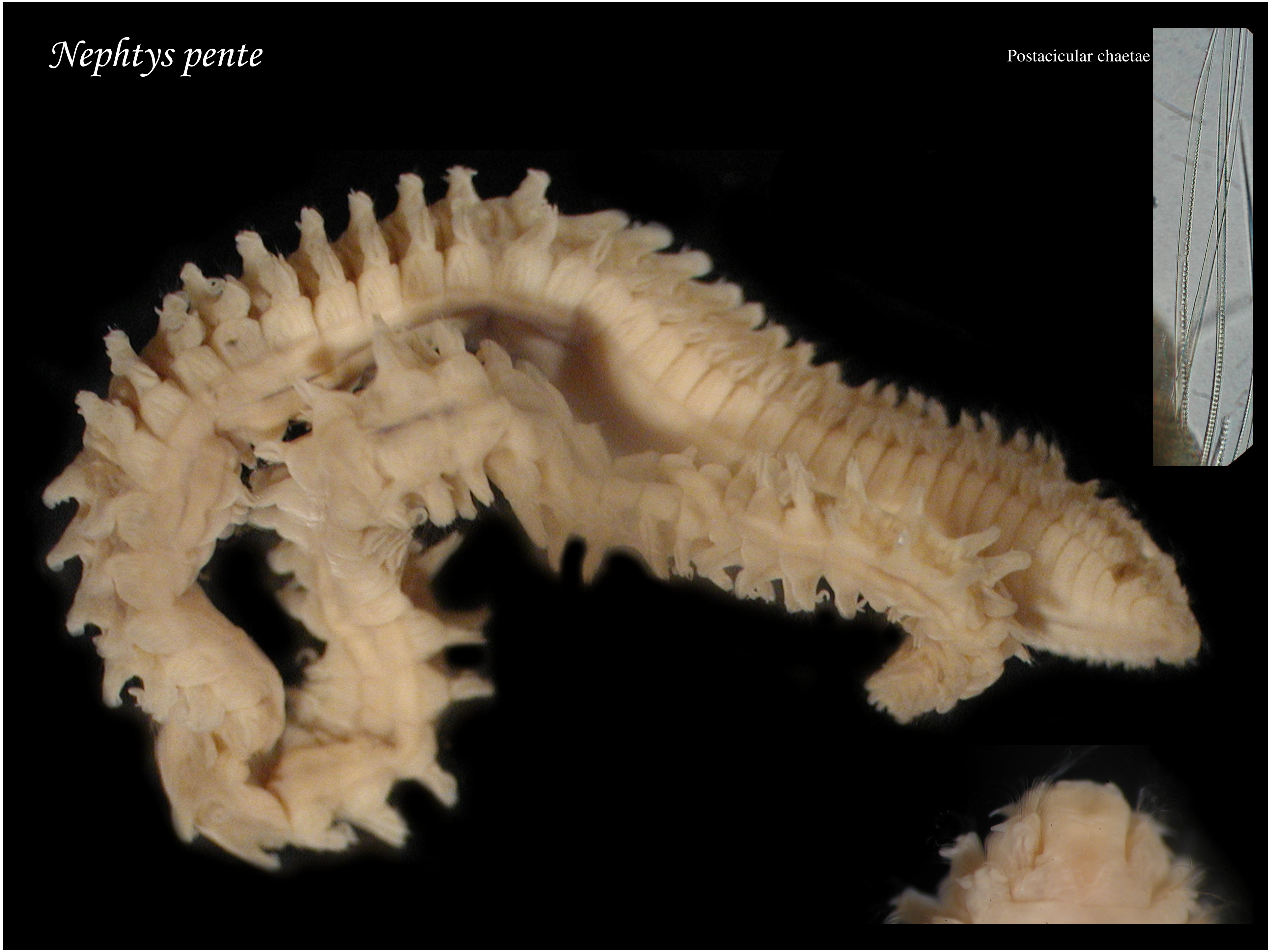
29th

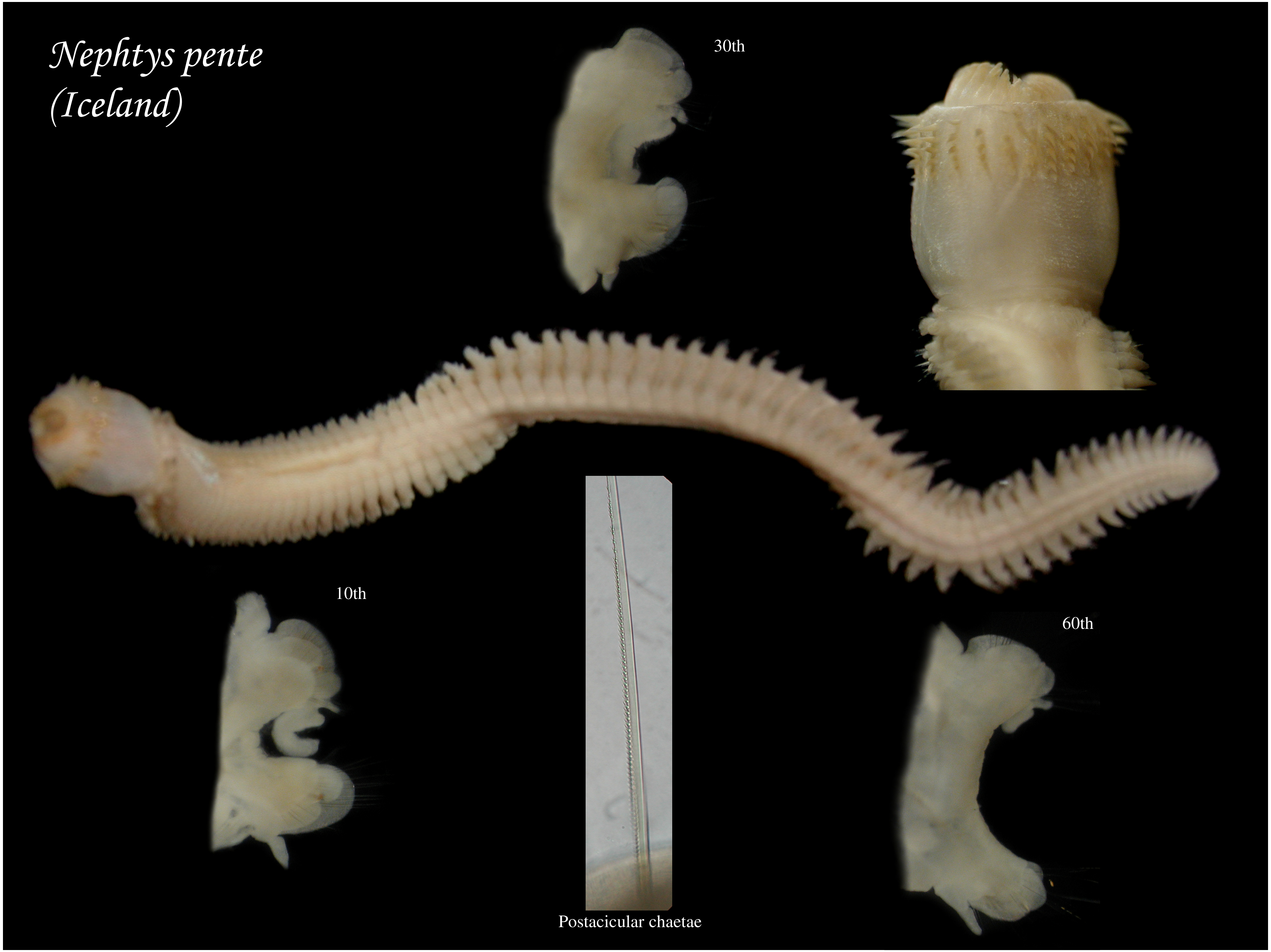
10th



Postacicular chaetae

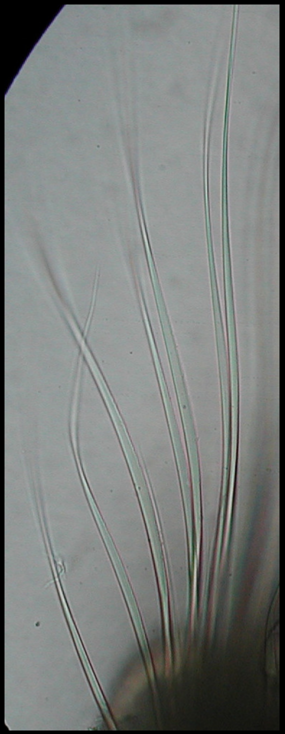
Nephtys pente





Nephtys pente
(Iceland)

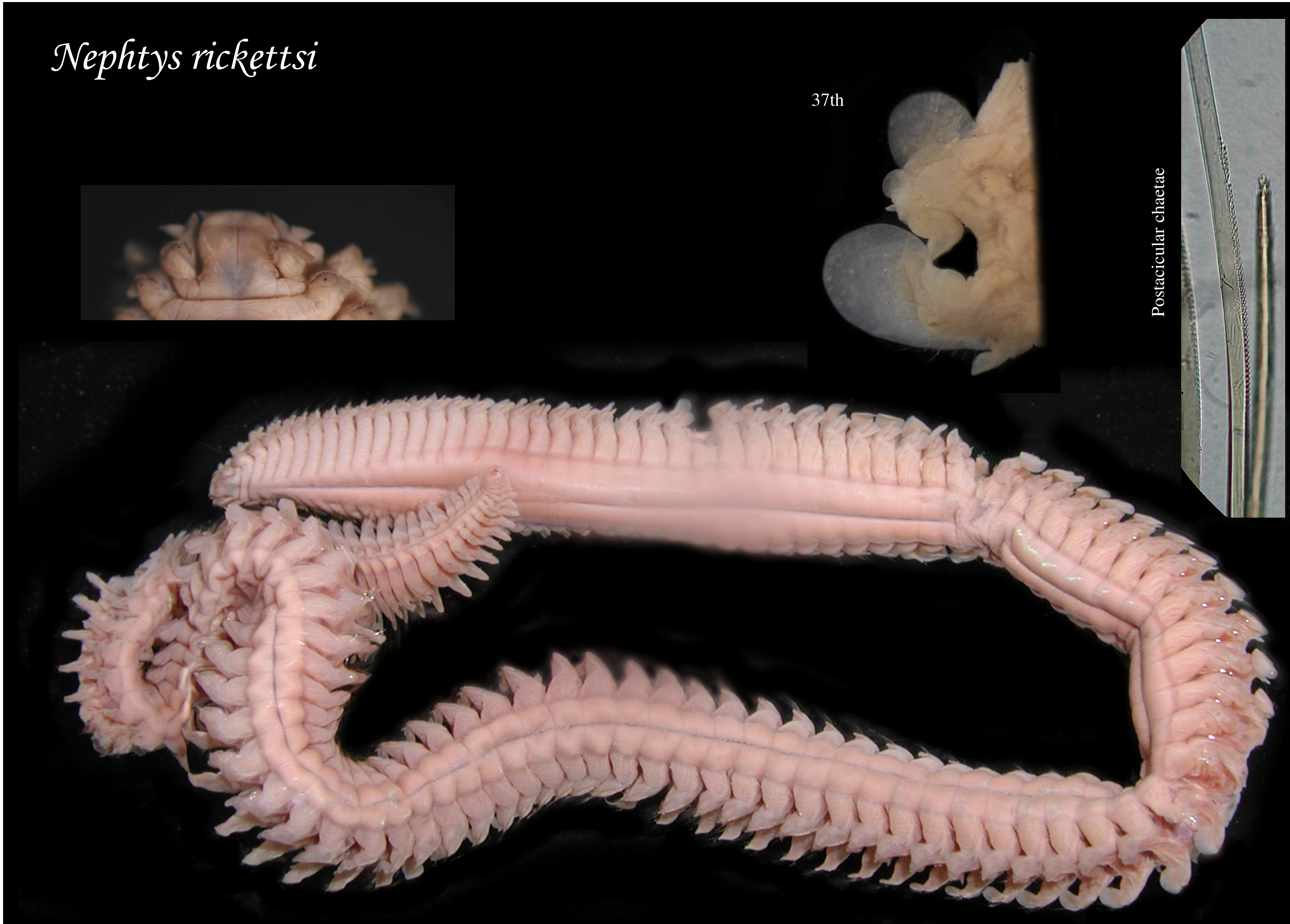
Nephtys polybranchia



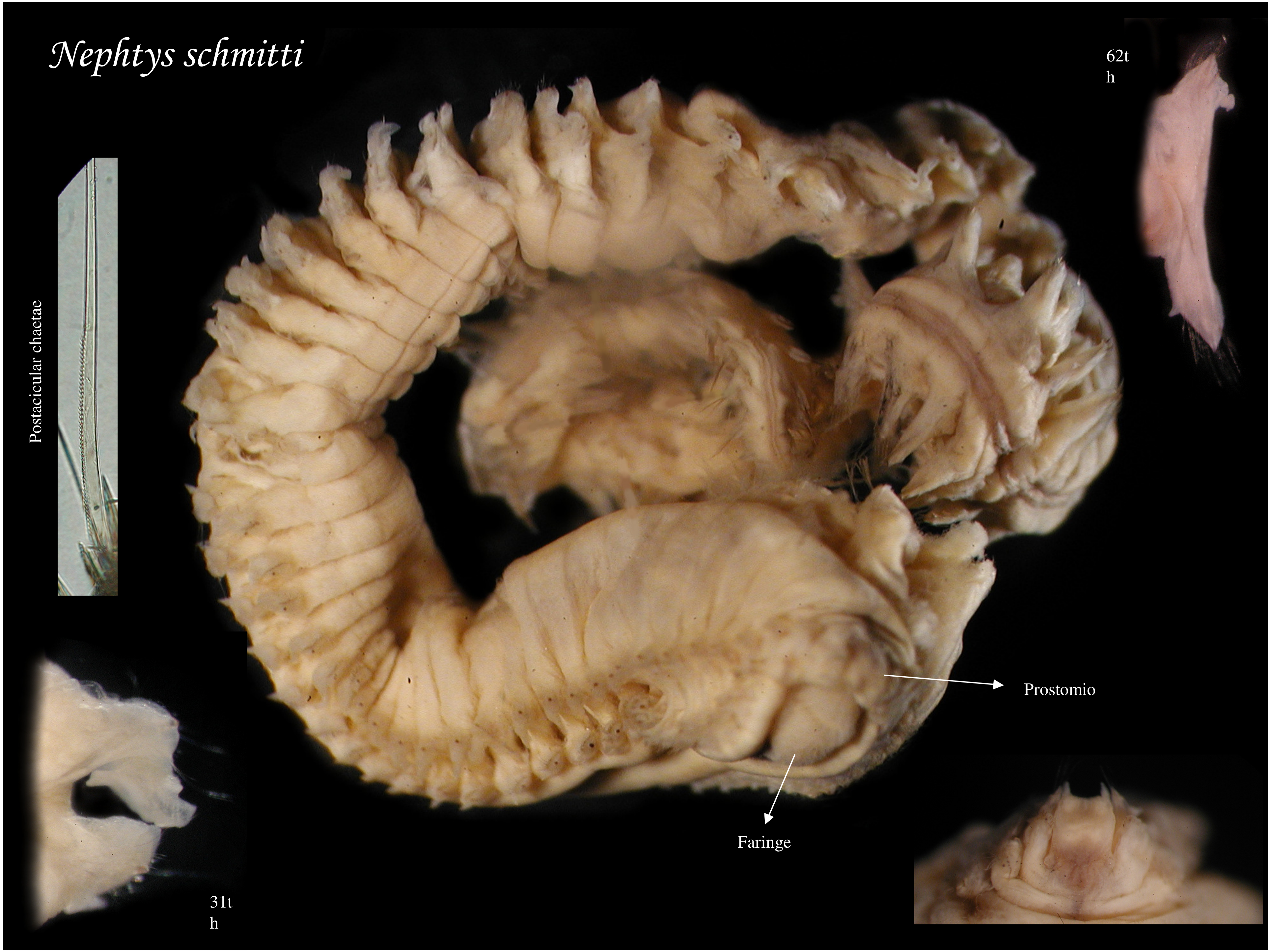
Postacicular chaetae

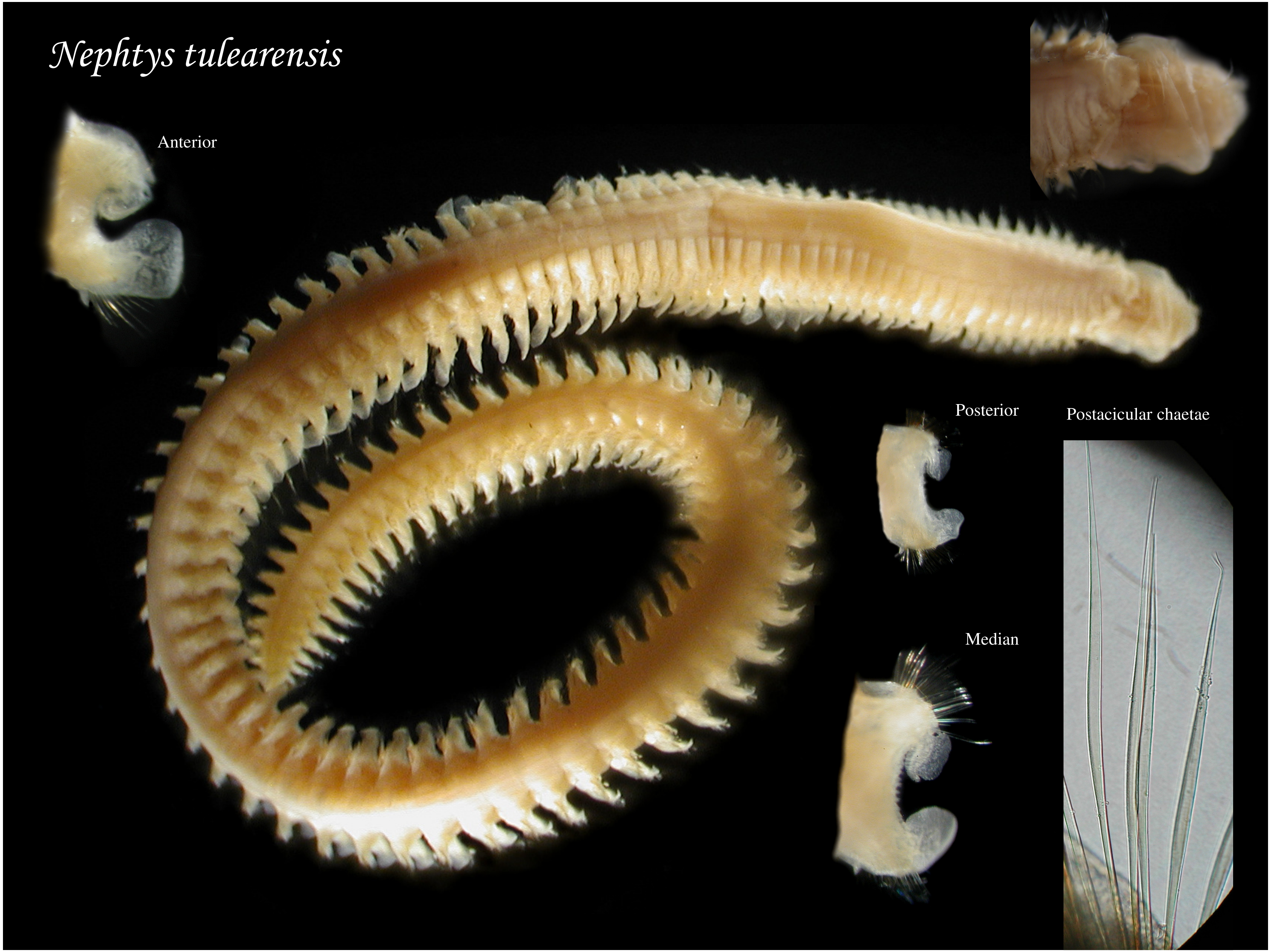
Nephtys punctata

Nephtys rickettsi



Nephtys schmitti




Nephtys tulearensis
Anterior
Posterior
Postacicular chaetae
Median