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Nephtyidae (Annelida, Polychaeta) from southern Europe

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Abstract

Eighteen nephtyid species belonging to four different genera are known from southern Europe. In this study we revise the nephtyids from this area and provide descriptions of all the known species. Geographical and bathymetrical distributions are given, together with ecological notes. *Inermonephtys foretmontardoi*, new species, is described, *Micronephthys maryae* is newly synonymized with *M. stammeri* and *Aglaophamus rubellus* with *A. agilis*. New diagnoses are provided for southern European genera and a key to all species from the region is included.

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

Introduction

Nephtyidae is a common family of polychaetes comprising five genera and over 100 described species (Ravara *et al.* 2010). 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, 1843a), Malmgren (1865), Ehlers (1868), Malm (1874), Théel (1879), Michaelsen (1896) and McIntosh (1900b, 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 one study from the region of Marseille, southern France (Foret-Montardo 1969), and a study of the Iberian fauna (Laborda 2004), up to date no major studies have been carried out 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), ten of which belong to the genus *Nephtys*, five to *Aglaophamus*, three to *Micronephthys*, and one to *Inermonephtys*. In this study we provide diagnoses of the four 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* and *Aglaophamus rubellus* with *A. agilis*. A key for southern European species is also included.

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 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), Göteborgs naturhistoriska museum (GNHM), Naturhistoriska riksmuseet, Stockholm (SMNH), Zoologisk Museum, Copenhagen (ZMUC), the United States National Museum of Natural History (USNM), the Museum of Comparative Zoology, Harvard University (MCZ) and the Muséum national d'Histoire naturelle (MNHN).

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 diagrams that relate body length, number of chaetigers and other variables.

Systematics

Nephtyids have an elongated body, wider anteriorly in the phraynx region and tapering posteriorly, 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 (Fig. 4A) (papillae are absent in *Inermonephtys*). In some species a single longer middorsal and midventral papilla are also present between the terminal and subterminal papillae (Fig. 20A). Proximally the proboscis is either smooth or covered with small warts (Fig. 12A). 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 (Fig. 4A). 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 (Fig. 4A). A pair of nuchal organs is present near the posterior corners of prostomium (Fig. 4A).

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 ventrally placed cirrus. The parapodia of the first chaetiger are usually anteriorly directed, and their lamellae are less developed than the following ones (Fig. 14A). 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 cirrus), have ciliated margins and may be involute, straight or recurved. A papilliform projection may be present dorsally at the base of the branchiae. Chaetae are simple and form dense, fan-shaped fascicles in pre- and postacicular positions. They are usually barred (or chambered) in preacicular position (Fig. 4H), and spinulated in postacicular position (Fig. 4I). In some species of *Aglaophamus*, *Inermonephtys* and *Micronephthys*, a few lyriform chaetae may be present in postacicular position of both rami (Fig. 6H). 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*) (Fig. 4J).

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

Key to the southern European species of Nephtyidae

The main distinctive characters used in this key include parapodial features (acicular lobes and pre- and postchaetal lamellae shape and size), branchiae shape and location, and pharynx structure. 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. 6A); pharynx without papillae; jaws spindle-shaped; branchiae start at chaetiger 4.....*Inermonephtys foretmontardoi* **sp. nov.** (Fig. 6)

- Prostomium with antennae; nuchal organs rounded; pharynx papillae present; jaws conical, hook-like 2
2 Branchiae absent or present on a few chaetigers only, 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 on chaetigers 6–9 to 10–14..... *M. minuta*
- Branchiae absent..... 4
4 Modified chaetae present on notopodia of first chaetiger (Fig. 9E); two pairs of coalescent eyes present at the level of chaetiger 3 (Fig. 9C)..... *M. stammeri* (Fig. 9)
- Modified chaetae absent; one pair of small subdermal eyes may be visible at the level of chaetiger 2–3..... ..... *M. sphaerocirrata* (Fig. 8)
5 Acicular lobes acutely pointed (Figs. 1, 3–5); neuropodial superior lobes may be present (Fig. 4F); 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. 21E, G), rounded or bilobed (Figs. 12B–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 lobes distinctly present; branchiae involute, from chaetiger 2 ..... *A. agilis* (Fig. 1)
- Prechaetal lamellae simple; postchaetal lamellae shorter or not much longer than acicular lobes; neuropodial superior lobes, if present, very small and difficult to observe; branchiae start at or posteriorly to chaetiger 5..... 7
7 Notopodial postchaetal lamellae poorly developed, rounded; branchiae involute, starting at chaetiger 11–13; pharynx with 20–22 rows of 6–11 subterminal papillae, extending to base of pharynx..... *A. elamellatus* (Fig. 3)
- Notopodial postchaetal lamellae well developed, bilobed at least in middle parapodia 8
8 Branchiae involute, starting at chaetiger 11–13; pharynx with 22 rows of 2–17 short subterminal papillae extending over 1/2 length of pharynx..... *A. malmgreni* (Fig. 4)
- Branchiae recurved, starting at chaetiger 5–7; pharynx with 14 well defined rows of 10–15 subterminal papillae, extending to base of pharynx ..... *A. pulcher* (Fig. 5)
9 Notopodial acicular lobes rounded with rudimentary prechaetal lamellae; neuropodial acicular lobes conical with well developed prechaetal lamellae; branchiae from chaetiger 4 to near end of body; dorsal cirri in posterior chaetigers as long as branchiae (Fig. 15G); pharynx with 22 rows of 4–9 subterminal papillae extending to base of pharynx (Fig. 15A)..... *N. cirrosa* (Fig. 15)
- 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. 10D–E); postacicular chaetae finely spinulated; branchiae start at chaetigers 4–7 11
- Acicular lobes rounded to bilobed; prechaetal lamellae rudimentary or poorly developed (Fig. 12B–D); postacicular chaetae coarsely spinulated; branchiae start at chaetigers 3–14 15
11 Acicular lobes with a papilliform outgrowth (Fig. 10C, 17E–F); postchaetal lamellae of neuropodia extending well beyond acicular lobes (Fig. 10D–E, 17G–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.18A)..... 13
12 Acicular lobes with low papilliform outgrouth (Fig. 10C); branchiae start at chaetiger 4; neuropodial postchaetal lamellae broadly rounded with internal vascular structure (Fig. 10D); interramal region of posterior chaetigers with prominent raised ciliary pads (Fig. 10E)..... *N. assimilis* (Fig. 10)
- Acicular lobes with prominent papilliform outgrouth (Fig. 17E–F); branchiae start at chaetiger 4 or 5 (rarely 6); neuropodial postchaetal lamellae slender without vascular structure; interramal region of posterior chaetigers with ciliated patches ..... *N. hombergii* (Fig. 17)
13 Postchaetal lamellae more than twice as long as acicular lobes; acicular lobes with rugose area near aciculae (Fig. 21D, F, H); branchiae start at chaetiger 4 to near posterior end; conspicuous papilla-like projection present at the base of the branchiae..... *N. kersivalensis* (Fig. 21)
- Postchaetal lamellae shorter or no longer than twice the length of acicular lobes; acicular lobes without rugose area; branchiae start at chaetiger 5–10, absent from posterior chaetigers; basal projection of the branchiae reduced or absent 14
14 Postchaetal lamellae up to twice the length of acicular lobes; branchiae start at chaetigers 5–7, usually at chaetiger 6 ..... *N. hystricis* (Fig. 18)
- Postchaetal lamellae shorter than or as long as acicular lobes; branchiae start at chaetigers 9–10…*N. incisa* (Fig. 20)
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 start at chaetigers 7–14, reduced

in posterior chaetigers 17
16 Postchaetal lamellae well developed in notopodia and neuropodia; branchiae start at chaetiger 4 (rarely 5); pharynx proximal region with numerous warts ..... *N. caeca* (Fig. 12)
- Notopodial postchaetal lamellae of median and posteror chaetigers much shorter than in neuropodia; branchiae start at chaetiger 3; pharynx proximal region smooth ..... *N. longosetosa* (Fig. 22)
17 Branchiae cirriform, starting at chaetigers 7–11; acicular lobes of anterior and middle chaetigers distinctly bilobed; pharynx proximal region with numerous warts (Fig. 14A) ..... *N. ciliata*
- Branchiae foliaceous (Fig. 23C), start at chaetigers 9–14; acicular lobes rounded in anterior and median parapodia, conical in posterior parapodia; pharynx proximal region smooth ..... *N. paradoxa*

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.* 2010). Lyriform chaetae may be present or absent. All aciculae have curved tips. Antennae present. Pharynx usually with rows of more than 10 closely together subterminal papillae, of which the proximal ones are sometimes arranged in small groups; longer middorsal papilla absent; proximal region smooth. Jaws conical, hook-like. Nuchal organs rounded.

Aglaophamus agilis (Langerhans, 1880)
Figures 1, 2

Nephthys agilis Langerhans, 1880: 304, pl. XVI, fig. 39; Fauvel 1923: 372, fig. 145C–G.
Nephthys rubella Michaelsen, 1896: 19, pl. I, figs. 5–8; Heinen 1911: 31, fig. 9, map 1; Fauvel 1914: 196; Fauvel 1923: 373, fig. 145H–I; not Berkeley and Berkeley 1945: 327.
Aglaophamus agilis Fauvel 1923: 372–373, fig. 145c–g; Friedrich 1964: 135, fig. 1; Guille and Laubier 1966: 266; Hartmann-Schröder 1982: 9; Campoy 1982: 507; Laborda 2004: 412, fig. 151A.
? *Nephthys squamosa* Fauvel 1936: 41.
Nephtys rubella Eliason 1962: 249.
Nephthys (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; Wolff 1968: 6, fig. 12; Kirkegaard 1992: 327, fig. 159; Hartmann-Schröder 1974: 205 (partim); Hartmann-Schröder 1996: 216, fig. 93. 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. Funchal, Madeira Island, Portugal.

Material examined. Atlantic Ocean. Norwegian waters: 1 incomplete spm (ZMH V-3960, holotype of *A. rubellus*). 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 as *A. rubellus*). 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 as *A. rubellus*); off Cascais: 38º39'–38º42'N, 9º25'–9º30'W, 40 m, Jun 1998, 1 incomplete spm (DBUA 00871 as *A. rubellus*) and 1 incomplete spm (MB36000132 as *A. rubellus*); Madeira, Câmara de Lobos: 30 m, haul net, Jun 2000, 1 complete spm in poor condition (MMF.36457); Porto Santo: subtidal, May 1991, 1 complete and 2 incomplete spms (in collection of J. Gil).

Mediterranean Sea. France, Banyuls: RV *Nereis*, 42º29.75'N, 3º8.40'E, 24 m, dredge, Jul 2004, 3 complete spms (DBUA 01048) and 1 incomplete spm (MB36000142 as *A. rubellus*).

Description. Examined specimens up to 24 mm long (for 45 chaetigers), and up to 59 chaetigers. See Fig. 2 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 (Fig. 1A); antennae and palps long and conical with cirriform tip; palps slightly longer than antennae (Fig. 2C), 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 (Fig. 2D); 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 (Fig. 1B–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 (Fig. 1H), spinulated chaetae in postacicular position (Fig. 1I), and capillary chaetae in the neuropodia of chaetiger 1. One acicula with curved tips per ramus (Fig. 1J).

Remarks. The only specimen previously identified as *A. agilis* and examined in this study (MMF.36457), is in very poor condition and the observation of several important features was not possible. All the Langerhans's material from Madeira is deposited in the Museum of Natural History of Wien, however no specimens of *A. agilis*, including the holotype, could be found there. No other material was available for examination. *Aglaophamus agilis* 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* (including *A. rubellus*). He considered 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), reported the same species from the Mediterranean Sea, although without any further comments. According to Friedrich (1964), the species *A. agilis* and *A. rubellus* differ in the development of the prechaetal lamellae that are rudimentary in *A. agilis* and well developed and bilobed in *A. rubellus*, and in the shape of the notopodial postchaetal lamellae that are entire in *A. agilis* and bilobed in *A. rubellus*. However, Langerhans (1880) and Friedrich (1964) mentioned the presence of a pair of eyes in the anterior chaetigers of *A. agilis*, a feature typical of 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* (Fig. 1D–E). Three *Aglaophamus* specimens collected in Porto Santo Island were examined and match the description of *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 *A. rubellus* as a junior synonym of *A. agilis*. However, we have chosen not to designate a neotype for *A. agilis*. The synonymy with *A. rubellus* is based on a few formalin-preserved specimens from Madeira, and a designation in this case should preferably be associated to the deposition of material suitable for molecular analyses.

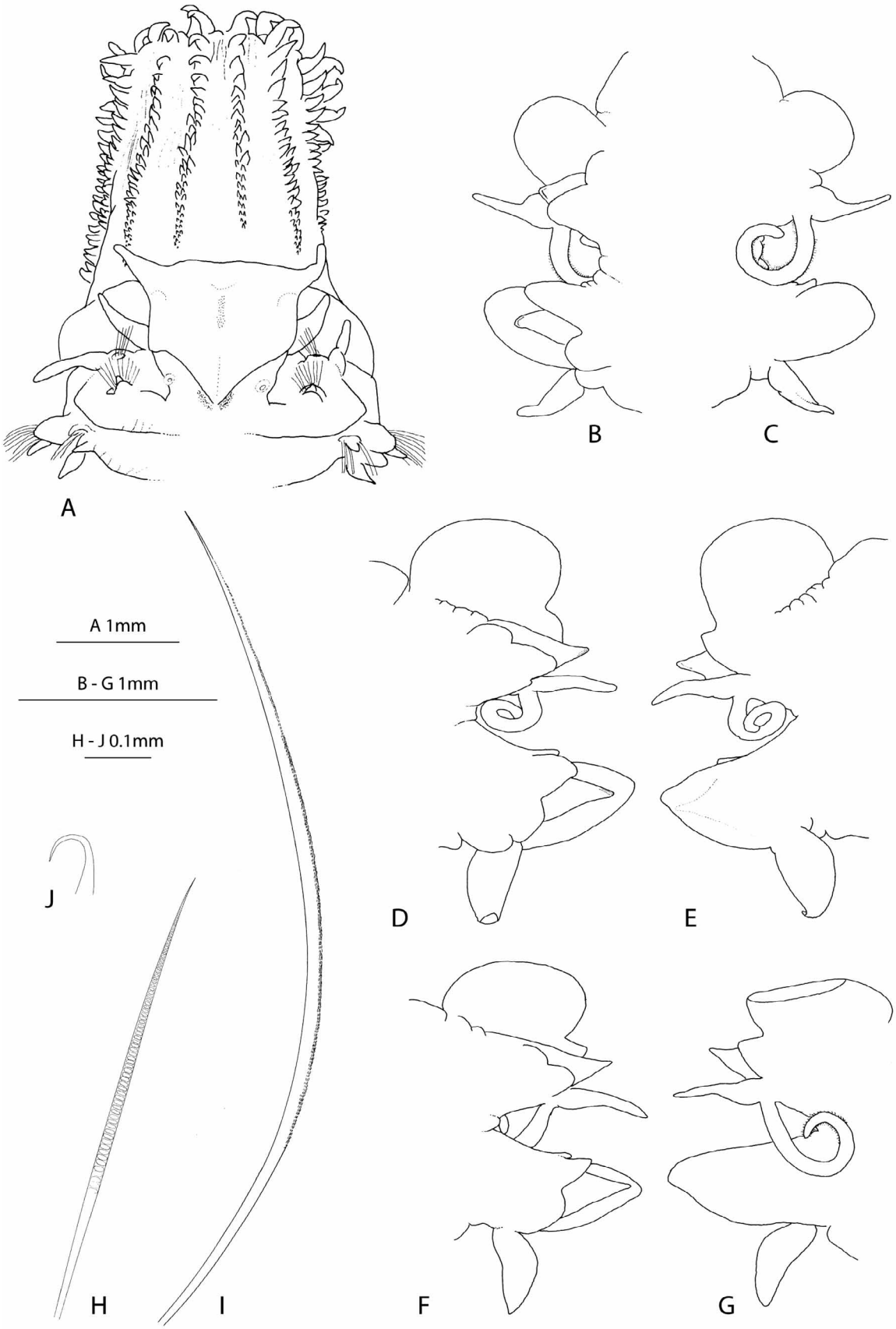

FIGURE 1. *Aglaophamus agilis*. A. Pharynx and prostomium, dorsal view. B. Right parapodium of chaetiger 10, anterior view. C. Same, posterior view. D. Right parapodium of chaetiger 29, anterior view. E. Same, posterior view. F. Right parapodium of chaetiger 45, anterior view. G. Same, posterior view. H. Pre-acicular chaeta from chaetiger 29. I. Postacicular chaeta from chaetiger 29. J. Acicula from chaetiger 10.

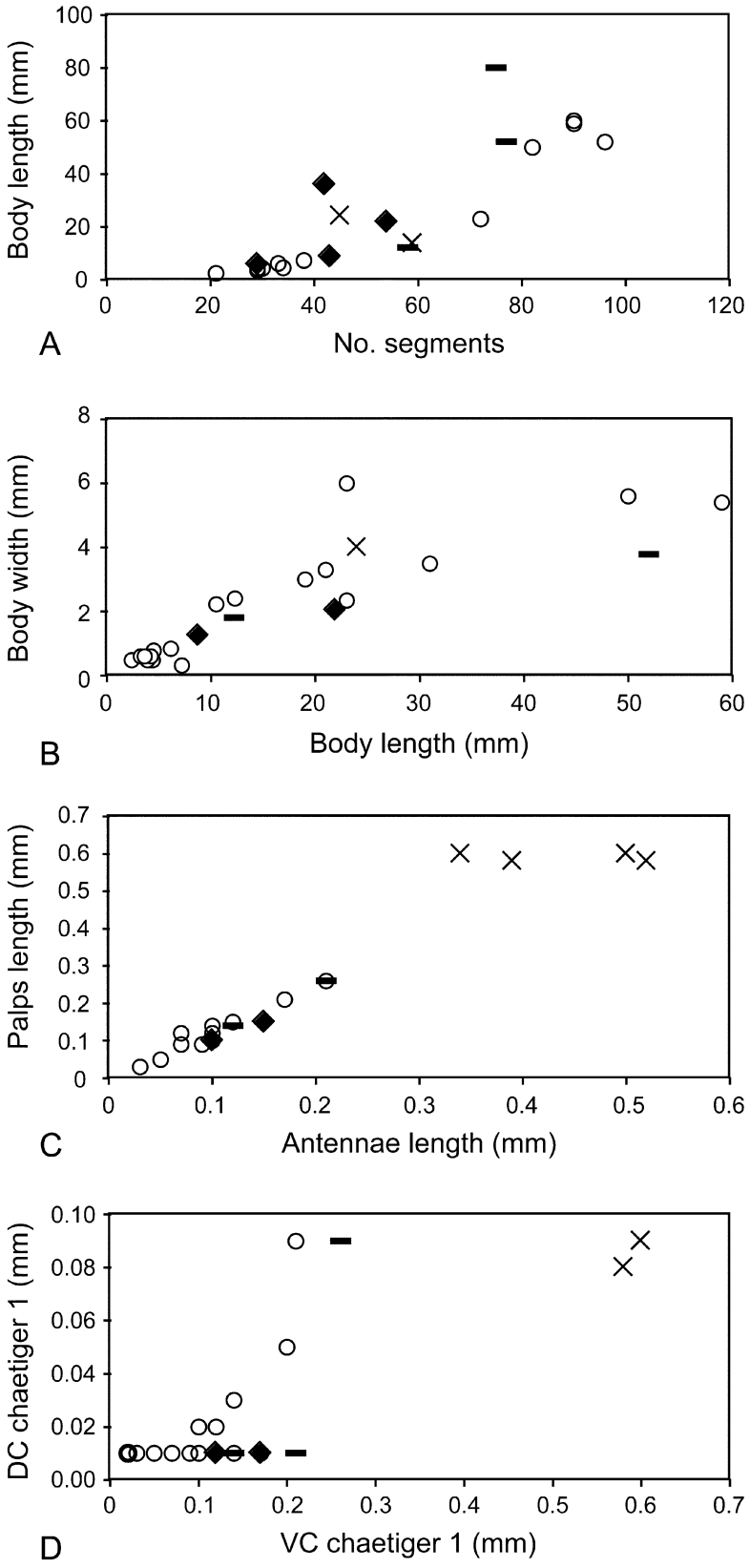

FIGURE 2. Relationships between: A. Number of segments and body length. B. Body length and body width. C. Antennae and palps length. D. Length of ventral cirri (VC) and dorsal cirri (DC) of chaetiger 1. ◆ *Aglaophamus elamellatus*. - *A. malmgreni*. ○ *A. pulcher*. *A. rubellus*. Minute dorsal cirri 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).

Aglaophamus agilis 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 3). From the measurements shown in Figure 2, it is also evident the greater length of antennae, palps and first chaetiger ventral cirri of *A. agilis* in comparision to other species.

Distribution. Atlantic Ocean (from Norway to Mauritania); Mediterranean Sea (NE Spain; S France; Sicily, Corsega, Gulf of Génova) (Fauchald 1963; Foret-Montardo 1969; Campoy 1982; Laborda 2004).

Habitat. Fine sand and mud, 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*.

***Aglaophamus elamellatus* (Eliason, 1951)**
Figures 2, 3

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).

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 Fig. 2 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 (Fig. 3A–B); proximal region without warts. Jaws conical (Fig. 3C). Prostomium subpentagonal, anterior margin straight or slightly convex, posterior margin V-shaped, extending over first chaetiger (Fig. 3D); antennae and palps conical, subequal in length (Fig. 2C), 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

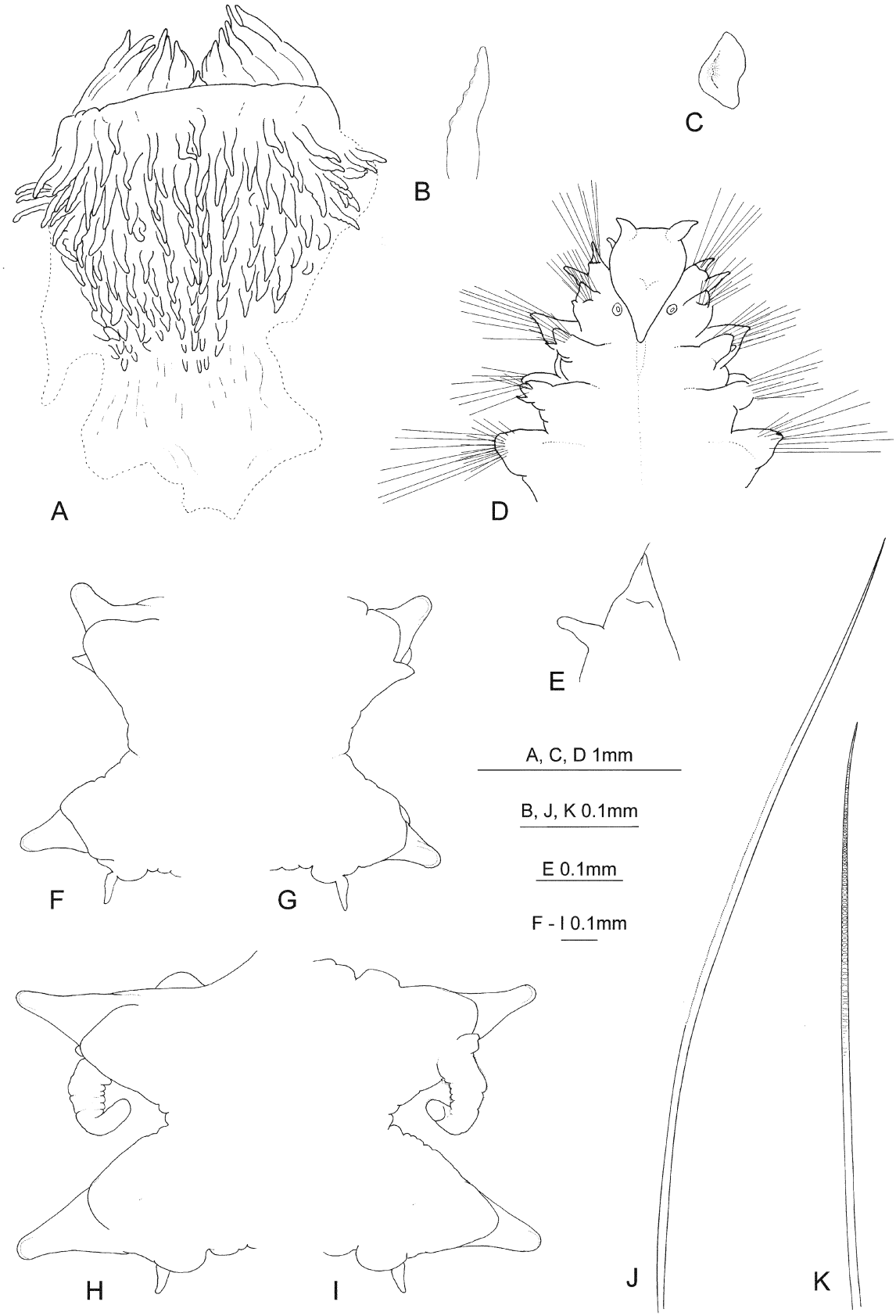

FIGURE 3. *Aglaophamus elamellatus*. A. Dissected pharynx, dorsal view. B. Detail of pharynx subterminal papillae. C. Jaw. D. Prostomium and anterior chaetigers, dorsal view. E. Left neuropodium of chaetiger 1. F. Right parapodium of chaetiger 10, anterior view. G. Same, posterior view. H. Right parapodium of chaetiger 20, anterior view. I. Same, posterior view. J. Postacicular chaeta from chaetiger 15. K. Preacicular chaeta from chaetiger 15.

TABLE 1. *Aglaophamus elamellatus.* Branchiae occurrence and development according to the number of chaetigers.

Local	Depth	No. chaetigers	Branchiae start and end	Posterior chaetigerous without branchiae	Observation on branchial 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	-	--	

pointed; pre- and postchaetal lamellae rudimentary; acicula of neuropodia protruding from acicular lobes (fig. 3E); dorsal cirri rounded, minute (Fig. 2D); 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 parapodia; dorsal cirri short, conical to rounded, with broad base; ventral cirri digitiform (fig. 3F–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 (Fig. 3K), finely spinulated chaetae in postacicular position (Fig. 3J), 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 has 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 1). 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).

Aglaophamus malmgreni (Théel, 1879)

Figures 2, 4

Nephthys malmgreni Théel, 1879: 26, pl. I, fig. 17, pl. II, fig. 17; Marenzeller 1904: 304–308; Heinen 1911: 29, fig. 8, map 2 (partim); Augener 1912: 206; not Treadwell 1914: 192; Fauvel 1914: 196; 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; Hansen 1882: 31, pl. 4, figs. 1–4.

Nephthys grubei McIntosh, 1900a: 33; 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, 3G, 4, 8A, 9, table 1; Pettibone 1963: 191, fig. 48B; Wolff 1968: 6, fig. 13; Hartmann-Schröder 1971: 224; Hartmann-Schröder 1974: 205, fig. 26 (partim); Jirkov 1989: 73, fig. 15.2 and 15.3; Kirkegaard 1992: 326, fig. 158; Hartmann-Schröder 1996: 216; 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.

Nephtys longisetosa Malmgren 1865: 106, pl. 12, fig. 20 (not Ørsted 1842).

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).

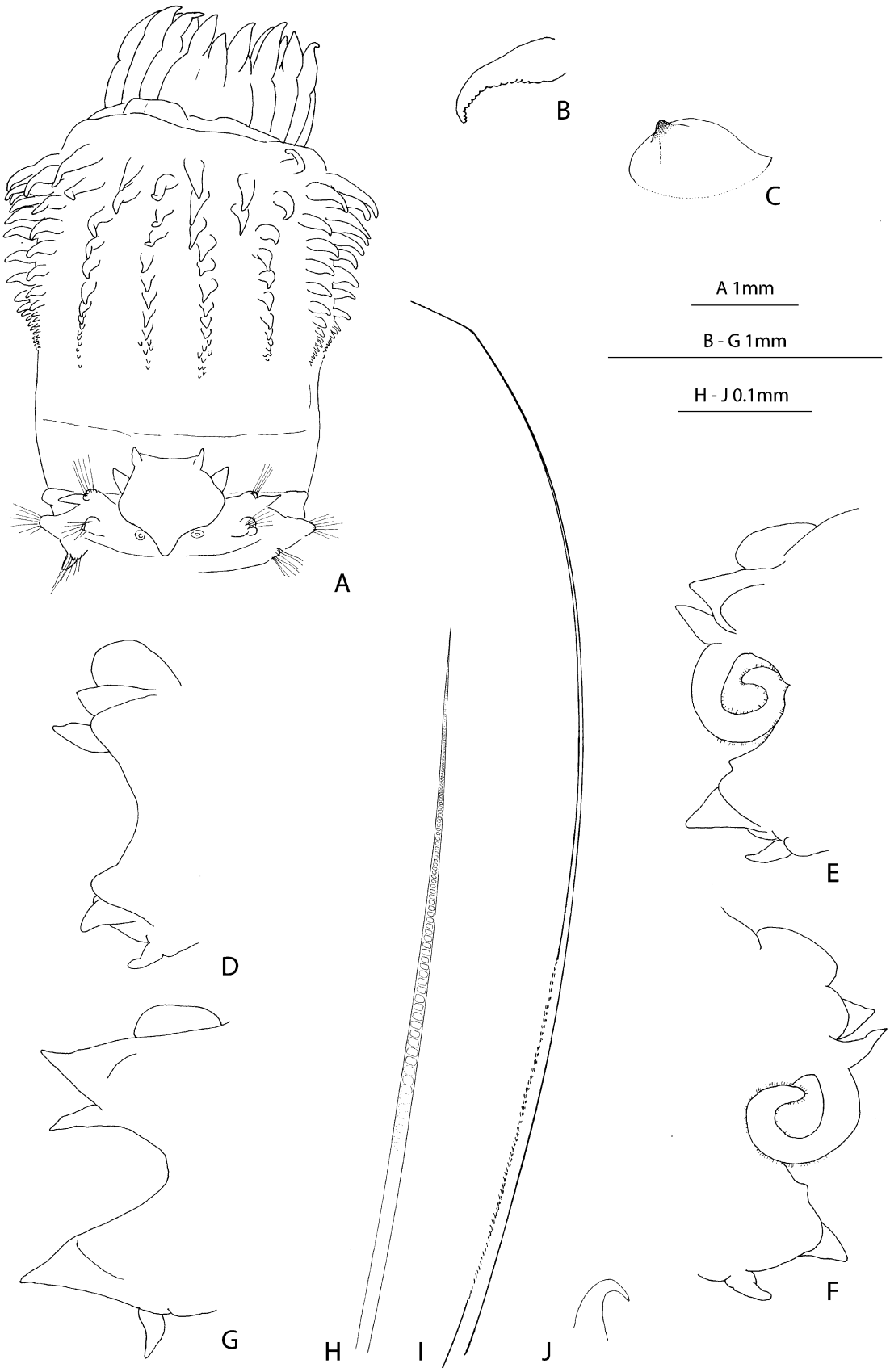

FIGURE 4. *Aglaophamus malmgreni*. A. Pharynx and prostomium, dorsal view. B. Detail of pharynx subterminal papilla. C. Jaw. D. Right parapodium of chaetiger 10, anterior view. E. Right parapodium of chaetiger 20, anterior view. F. Same, posterior view. G. Right parapodium of chaetiger 40, anterior view. H. Preacicular chaeta from chaetiger 20. I. Postacicular chaeta from chaetiger 20. J. Acicula from chaetiger 20.

Description. Examined specimens up to 52 mm long for up to 77 chaetigers. See Fig. 2 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 (Fig. 4A–B); proximal region smooth. Jaws conical (Fig. 4C). Prostomium subpentagonal, anterior margin slightly concave, tapered, forming membrane between antennae; posterior margin V-shaped, extending over first chaetiger (Fig. 4A); antennae and palps conical, palps slightly longer than antennae (Fig. 2C), 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 (Fig. 2D); 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 (Fig. 4D–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 (Fig. 4H), spinulated chaetae in postacicular position (Fig. 4I), and capillary chaetae in neuropodia of chaetiger 1. One acicula with curved tip per ramus (Fig. 4J).

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*, although Campoy did not examine specimens of this species. 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)

Aglaophamus pulcher (Rainer, 1991)

Figures 2, 5

Nephtys pulchra Rainer, 1991: 83, fig. 1A–F; Hartmann-Schröder 1996: 232; Arvanitidis 2000: 79; Dnestrovskaya and Jirkov 2001: 210, fig.; Laborda 2004: 410, fig. 150C–D.
Nephthys hystricis McIntosh 1900b: 259 (partim); McIntosh 1908: 27 (partim).
Nephtys incisa Fauchald 1963: 15, figs. 1H, 2C, 3B (partim).
Aglaophamus malmgreni Hartmann-Schröder 1974: 205 (partim) (not Théel 1879).
Aglaophamus rubella Hartmann-Schröder 1974: 205 (partim) (not Michaelsen 1896).

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 Fig. 2 for length and width measurements. Body small, slightly wider anteriorly, gradually tapering posteriorly. 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 (Fig. 5A); 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 (Fig. 5B); antennae conical, with broad base and cirriform tip; palps conical, similar to antennae but longer and with broader base (Fig. 2C), 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

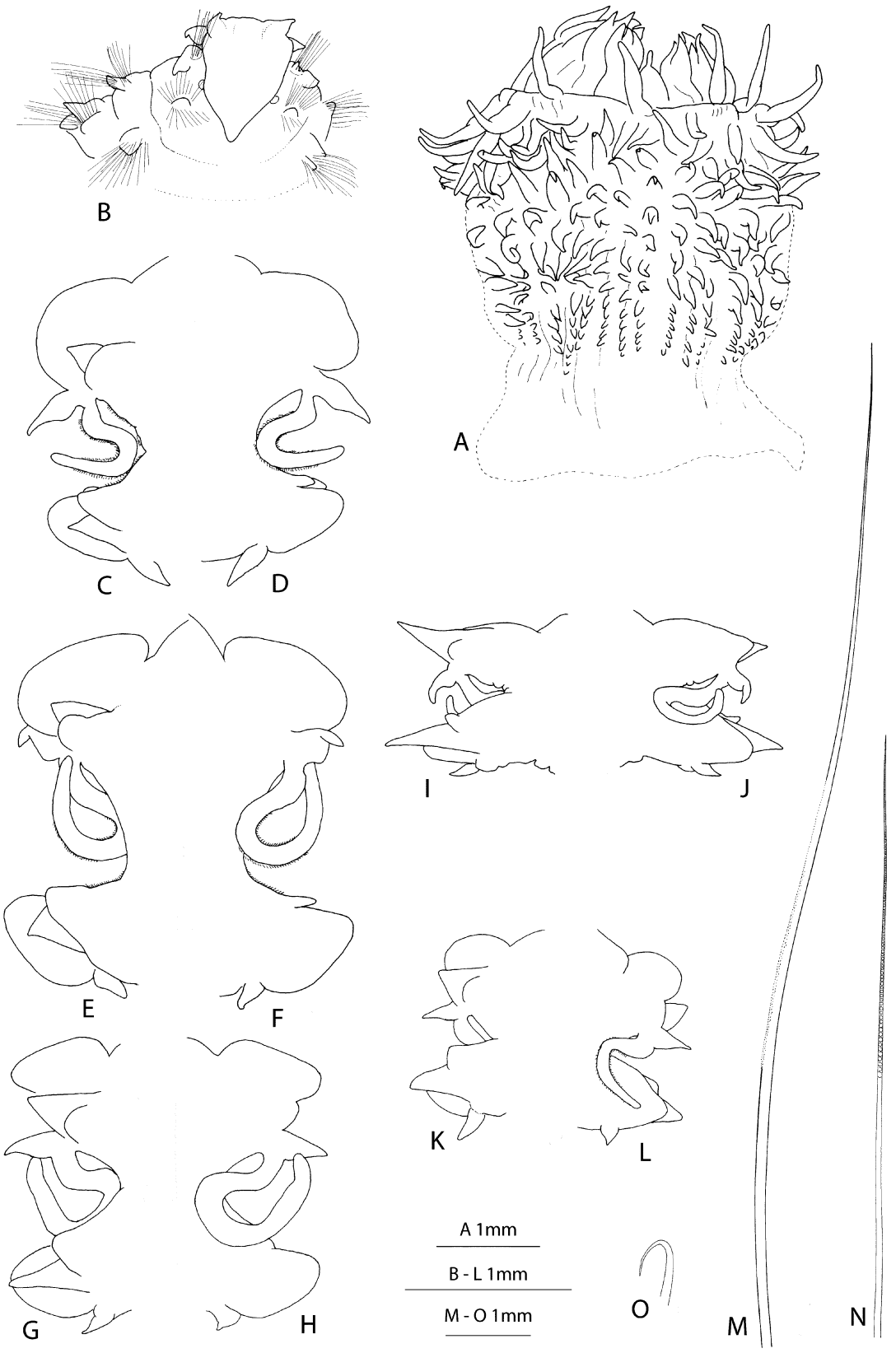

FIGURE 5. *Aglaophamus pulcher*. A. Dissected pharynx, dorsal view. B. Prostomium, dorsal view. C. Right parapodium of chaetiger 10, anterior view. D. Same, posterior view. E. Right parapodium of chaetiger 20, anterior view. F. Same, posterior view. G. Right parapodium of chaetiger 40, anterior view. 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. Postacicular chaetae from chaetiger 20. N. Preacicular chaeta from chaetiger 20. O. Acicula from chaetiger 20.

cirri conical, small (Fig. 2D); ventral cirri with broad bases and cirriform tips. Acicular lobes of following parapodia acutely pointed; prechaetal lamellae shorter than acicular lobes, rounded in notopodia, conical in neuropodia, becoming poorly developed posteriorly; postchaetal lamellae extending beyond acicular lobes in anterior parapodia, rounded, becoming shorter than acicular lobes in posterior parapodia; dorsal cirri long and conical, with bulbous bases and tapering tips; ventral cirri conical (Fig. 5C–L). In some middle parapodia, the notopodial postchaetal lamellae gradually shift to a more dorsal position giving the lamellae a bilobed appearance (Fig. 5G–H). This effect is more appearent in smaller specimens (Fig. 5K–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. Chaetae long and thin, of three kinds: barred chaetae in preacicular position (Fig. 5N), minutely spinulated chaetae in postacicular position (Fig. 5M), and capillary chaetae in neuropodia of chaetiger 1. One acicula with curved tip per ramus (Fig. 5O).

TABLE 2. *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 developed
Nazaré Canyon	38	7 / 7	0	-	Poorly developed
Gulf of Cadiz	> 36	5 / 5	-	+ (rudim.)	Rounded/bilobed
Sweden	> 35	5 / 5	-	+	Rounded/bilobed
Nazaré Canyon	34	8 / 8	4	-	Poorly developed
Cascais Canyon	33	18 / 19	7	-	Rudimentary
Cascais Canyon	32	19 / 20	10	-	Rudimentary
Cascais Canyon	32	19 / 19	8	-	Rudimentary
Cascais Canyon	30	-	-	-	Rudimentary
OS, off Sines	30	-	-	-	Rudimentary
OS, off Sines	29	-	-	-	Rudimentary
Cascais Canyon	29	-	-	-	Rudimentary
Cascais Canyon	29	-	-	-	Rudimentary
OS, off Sines	21	9 / 9	2	-	Rudimentary
Cascais Canyon	21	-	-	-	Rudimentary

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.* (2010), according to the results of 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 distinctive character for genera is discussed below, in the discussion section.

The description presented herein 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 (Fig. 4G–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 2). 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 posteriorly 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 3 for differences in the number of rows of pharynx papillae).

A comparison between *A. pulcher* and the other *Aglaophamus* species is summarized in Table 3. *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*.

Distribution. Atlantic Ocean (Norway, Oslofjord, Skagerrak, NW Spain, Portugal and Gulf of Cadiz); Mediterranean Sea (abyssal plains and canyons of the western Mediterranean, Aegean Sea) (Rainer 1991; Arvanitides 2000; Laborda 2004; J. Gil pers. com.; this study).

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

TABLE 3. Diagnostic characteristics of south European *Aglaophamus* species.

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

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.

***Inermonephtys foretmontardoi* sp. nov.**
Figure 6

Nephthys (Aglaophamus) inermis McIntosh 1900b: 262; Foret-Montardo 1969: 820, pl. V, figs. 1–5; Bellan 1964b: 75 (not Ehlers, 1887).
Nephthys inermis Marenzeller 1904: 296, 305; Fauvel 1923: 375, fig. 147 (partim); Bellan 1959: 326; Bellan 1960: 13; Bellan 1961: 169; Bellan 1964a: 275; Augener 1932: 679, fig. 3; not Fauvel 1933b: 47–50, fig. 3; Fauvel 1940: 11.
Nephtys (Aglaophamus) inermis Intes and Le Lœuff 1975: 303.
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 *Nephthys (Aglaophamus) inermis* Ehlers, 1887 (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, 1 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*). SW Portugal: 37º14.1'N, 9º05.3'W, 145 m, May 1981, 1 incomplete spm (in collection of João Gil); 37º38.9'N, 8º53.1'W, 113 m, Oct 1981, 1 incomplete spm (in collection of João Gil); 37º38.9'N, 8º52.9'W, 113 m, Oct 1981, 1 incomplete spm (in collection of João Gil); 37º49.9'N, 8º56.8'W, 130 m, Dec 1981, 1 incomplete spm (in collection of João Gil).

Mediterranean Sea. Adriatic Sea: collection Pierre Fauvel (1948), 1 complete and 1 incomplete spm (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 (Fig. 6A); 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) (Fig. 6B–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 Fig. 6F–G), lyriform chaetae with subequal rami in postacicular position (Fig. 6H) and capillary chaetae in the neuropodia

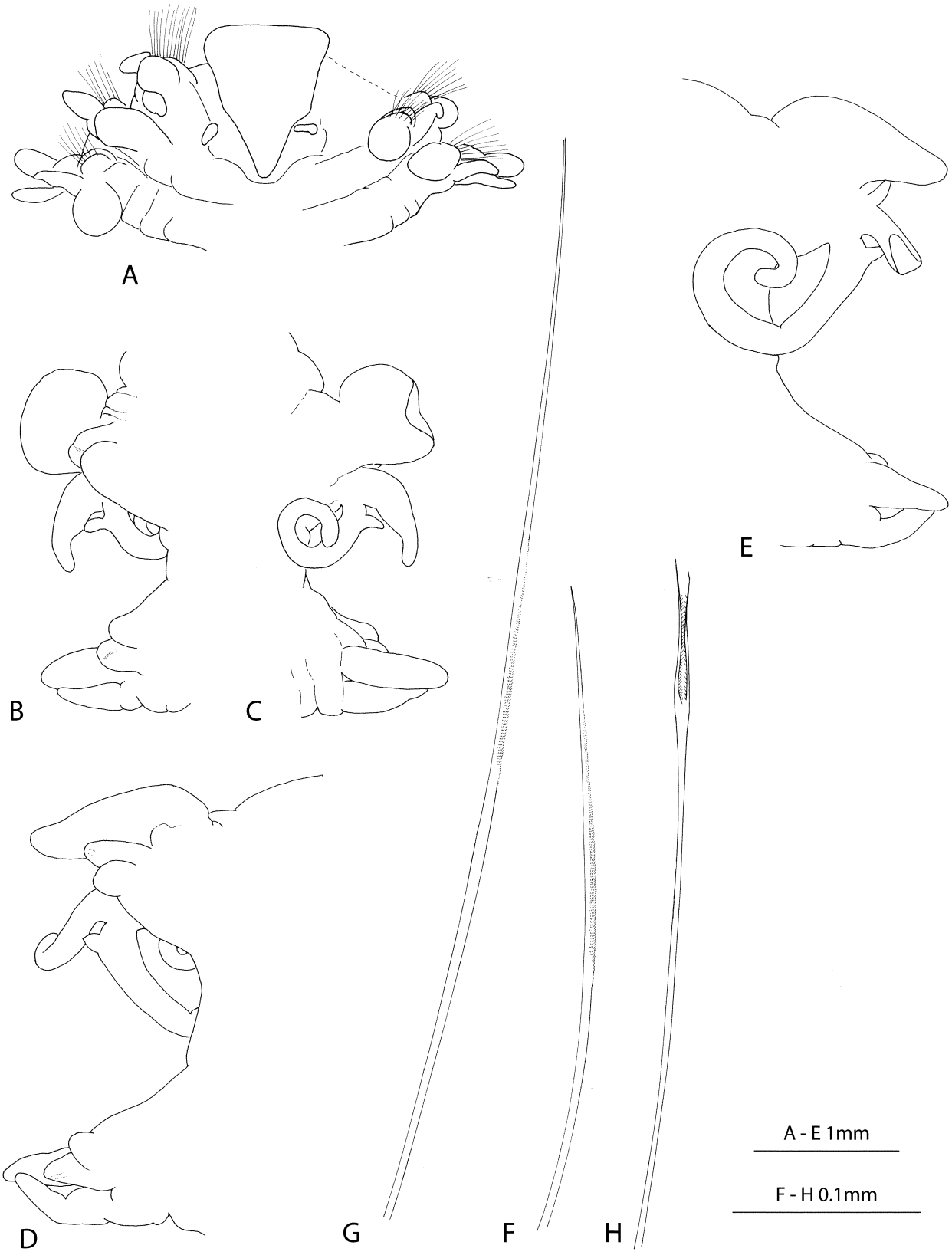

FIGURE 6. *Inermonephtys foretmontardoi* **n. sp.** A. Prostomium and anterior chaetigers, dorsal view. B. Right parapodium of chaetiger 10, anterior view. C. Same, posterior view. D. Right parapodium of chaetiger 30, anterior view. E. Same, posterior view. F. Preacicular chaeta from a posterior chaetiger. G. Postacicular chaetae from a posterior chaetiger. H. Lyriform chaeta from a posterior chaetiger.

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 4).

TABLE 4. *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. *Inermonephtys foretmontardoi* **sp. nov.** is here 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* **sp. nov.**). The main difference is the presence of well-developed neuropodial postchaetal lamellae (extending well beyond acicular lobes) in *I. foretmontardoi* sp. nov., 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 (McIntosh 1900b; Quatrefages 1904; 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 *I. foretmontardoi* sp. nov.. 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).

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 minuta* (Théel, 1879)**
Figure 7

Nephthys minuta Théel, 1879: 28, pl. II, fig. 18; Augener 1913: 206; Uschakov 1955: 218, fig. 68G.
Nephtys minuta Annenkova 1937: 164; Annenkova 1938: 162; Gorbunov 1946: 38; Zatsepin 1948: 122, table 30 (partim); Uschakov 1955: 217, fig. 68 (partim).
Micronephthys minuta Friedrich 1939: 123, fig. 3–4; Taylor 1984: 35-5, fig. 35-1 and 2A–E; Jirkov 1989: 74, fig. 15.4 (partim); not 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 minuta Hartman 1950: 130; Reish 1965: 139; Curtis 1979: 1; Tzetlin 1980: 25 (partim).
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. Barents Sea. Novaya Zemlya, Besimennïa Bay: 72º53'N, 52º53'E, 4–5 fms, N. Semlja Expedition 1875, Jul 1875, 29 complete and 13 incomplete spms, syntypes (SMNH-type-2463). White Sea. Kondalaksha Fiord: 40 m, 1 incomplete spm (DBUA 01137.01).

Description. Examined specimens up to 14.5 mm long for up to 34 chaetigers. See Fig. 7 for length and width measurements. Body small, slightly wider anteriorly, gradually tapering from middle region to pygidium. Colour in ethanol white; chaetae and aciculae amber. Eyes not visible. Pharynx distal region with 9 pairs of terminal, bifid papillae, separated by dorsal and ventral gap; long middorsal papillae present; subdistal region with 20 rows of 3–7 small subterminal papillae; proximal region smooth. Prostomium subquadrangular, anterior margin slightly convex, posterior margin poorly defined; antennae conical with a broad base and a cirriform tip; palps inserted ventrolaterally on anterior region of prostomium, slightly behind antennae, conical to cirriform, with a small papilla ventrally at the base. Nuchal organs rounded. Parapodia biramous. Parapodia of chaetiger 1 anteriorly directed, parallel to prostomium; noto- and neuropodial acicular lobes conical; pre- and postchaetal lamellae rudimentary; dorsal cirri very small; ventral cirri well developed, cirriform. Acicular lobes of following parapodia conical; pre- and postchaetal lamellae rudimentar; dorsal and ventral cirri conical, very small. Branchiae straight or slightly involute, strongly ciliated; present from chaetiger 6 to 13–14; well developed in all branchiate chaetigers; occupies 1/2 to 2/3 of interramal space when fully developed. Chaetae of three kinds: barred chaetae in preacicular position of the first 20 chaetigers, very finely spinulated chaetae in postacicular position, capillary chaetae in neuropodia of first chaetiger and in preacicular position of the posterior chaetigers. One acicula per ramus, median and posterior ones with curved tips.

Remarks. *Micronephthys minuta* was recorded a few times in local unpublished studies from Portugal. However, no material from South Europe was examined in this study, and those records should be considered with caution. This species was described from the Barents Sea and seems to be frequent in Arctic and Subarctic regions (Jirkov 1989; Jirkov & Paraketsova 1996). Parapar *et al*. (1993) recorded two specimens from Ceuta (N Africa) that differ from *M. minuta* in having 12 rows of large subterminal papillae in the pharynx, sphaerical to oval dorsal and ventral cirri, and branchiae absent. Thus, the specimens from Ceuta are here considered to belong to a different species.

Théel (1879) and Jirkov and Paraketsova (1996) mention the presence of branchiae on chaetigers 6–9 to 10–14. From the specimens examined in this study, only one (from the White Sea) has branchiae on chaetigers

7–11. All the other 42 specimens (syntypes) have branchiae from chaetiger 6 to 13–16 (to 13 on 16 spms, 14 on 23 spms, 15 on 2 spms and 16 on 1 spm).

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).

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).

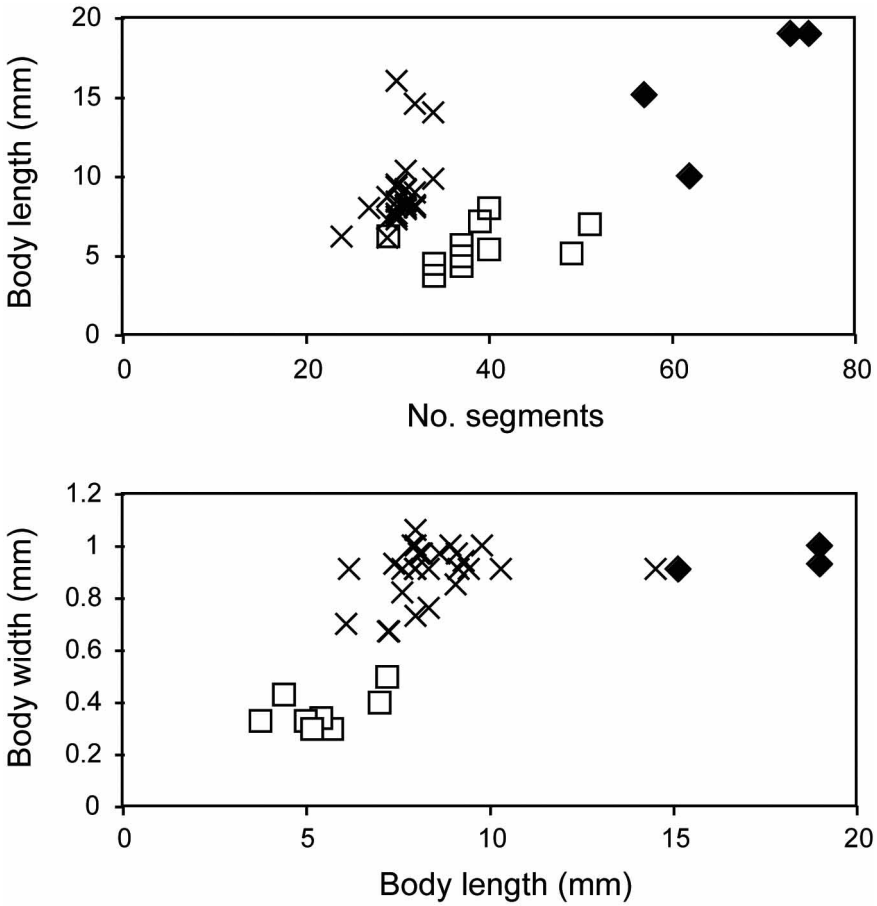

FIGURE 7. Relationships between: A. Number of segments and body length. B. Body length and body width. × *M. minuta*. ◆ *M. sphaerocirrata*. □ *M. stammeri*. *M. minuta* plot is based on the literature (Théel, 1879; Pettibone, 1963; Jirkov & Paraketsova, 1996). *M. sphaerocirrata* plot includes measurements from Wesenberg-Lund (1949) and Rainer & Hutchings (1977). *M. stammeri* plot includes measurements from Banse (1959), San Martín (1982) (original description of *M. maryae*) and Rainer & Kaly (1988) (for *M. maryae*).

Micronephthys sphaerocirrata (Wesenberg-Lund, 1949)

Figures 7, 8

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: 116, 121; Rullier 1972: 96; Campoy 1982: 506; ?Nateewathana and Hylleberg 1986: 209; Laborda 2004: 415.

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).

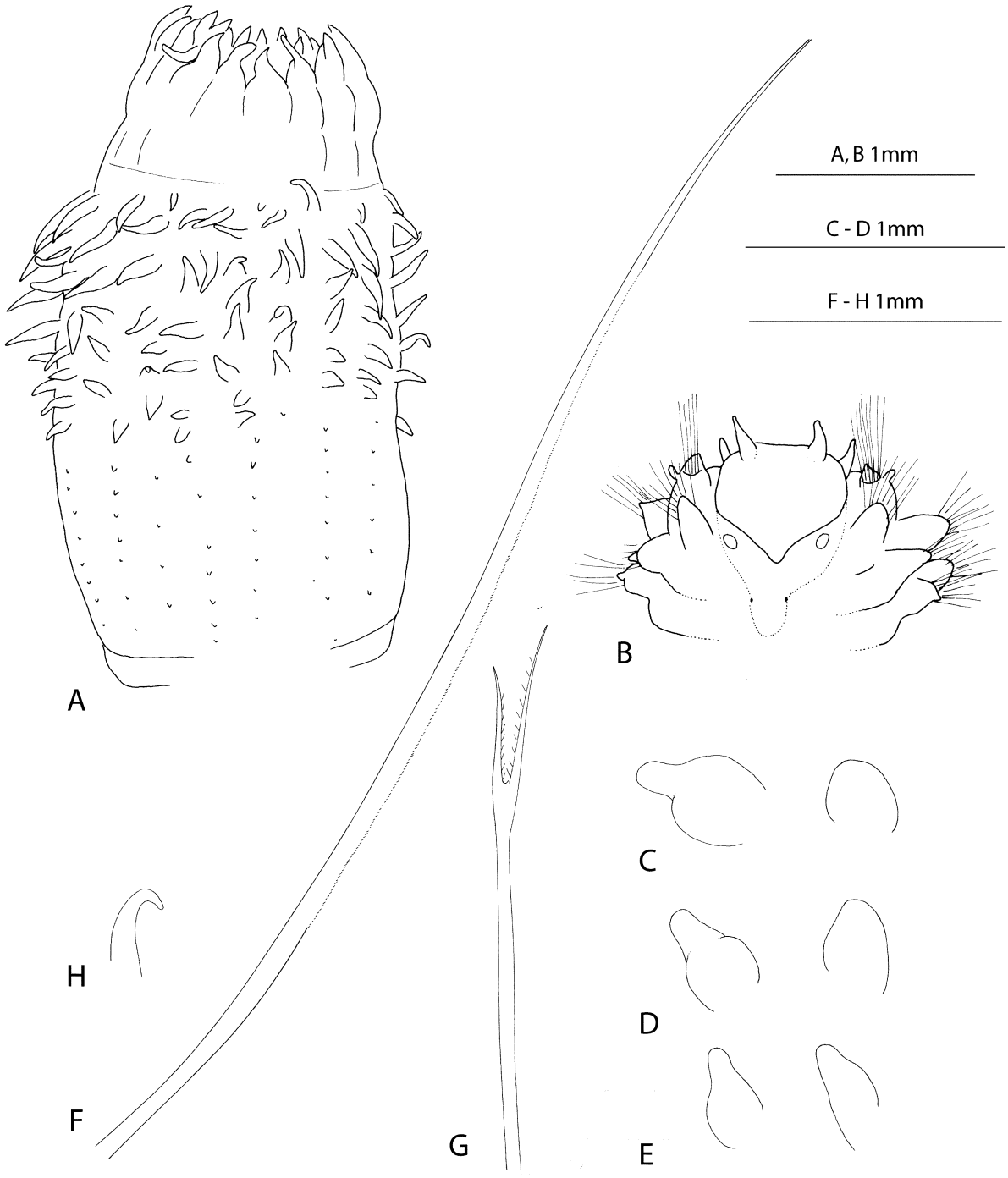

FIGURE 8. *Micronephthys sphaerocirrata*. A. Pharynx, dorsal view. B. Prostomium and anterior chaetigers, dorsal view. C. Dorsal (left) and ventral (right) cirrus from anterior parapodia. D. Dorsal (left) and ventral (right) cirrus from median parapodia. E. Dorsal (left) and ventral (right) cirrus from posterior parapodia. F. Postacicular chaeta. G. Lyriform chaeta. H. Acicula from posterior chaetiger.

Description. Examined specimens up to 19 mm long for up to 73 chaetigers. See Fig. 7 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 (Fig. 8A); 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 (Fig. 8B). 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 (Fig. 8C–E). Branchiae absent. Chaetae of four kinds: barred chaetae in preacicular position, finely spinulated chaetae (Fig. 8F) and lyriform chaetae with unequal rami (Fig. 8G) in postacicular position, capillary chaetae in the neuropodia of first chaetiger. One acicula per ramus, posterior ones with curved tips (Fig. 8H).

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 have not been able to verify the identity of the South African and Australian records. But the South African specimens were examined and the identification confirmed. As for the NE Australia, Rainer and Hutchings (1977) could not detect any differences 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 conform with *M. stammeri* and *M. oculifera*, respectively. The specimens recorded from Vietnam (Fauchald, 1968) were already by Lee and Jae (1983) referred to the subspecies *M. sphaerocirrata orientalis*, described from Korea. This subspecies differs 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 specimens from Thailand as *M. sphaerocirrata* despite some minor differences in the parapodial lamellae proportions. The Thailand specimens differ in having the neuropodial prechaetal lamellae well developed (as long as the acicular lobes) and the notopodial postchaetal lamellae larger than the 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 treat this record 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 7, 9

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 Martín, 1982: figs. 1–3; Rainer and Kaly 1988: 696, figs. 5A–E and 6B; Laborda 2004: 416, fig. 152A–C.

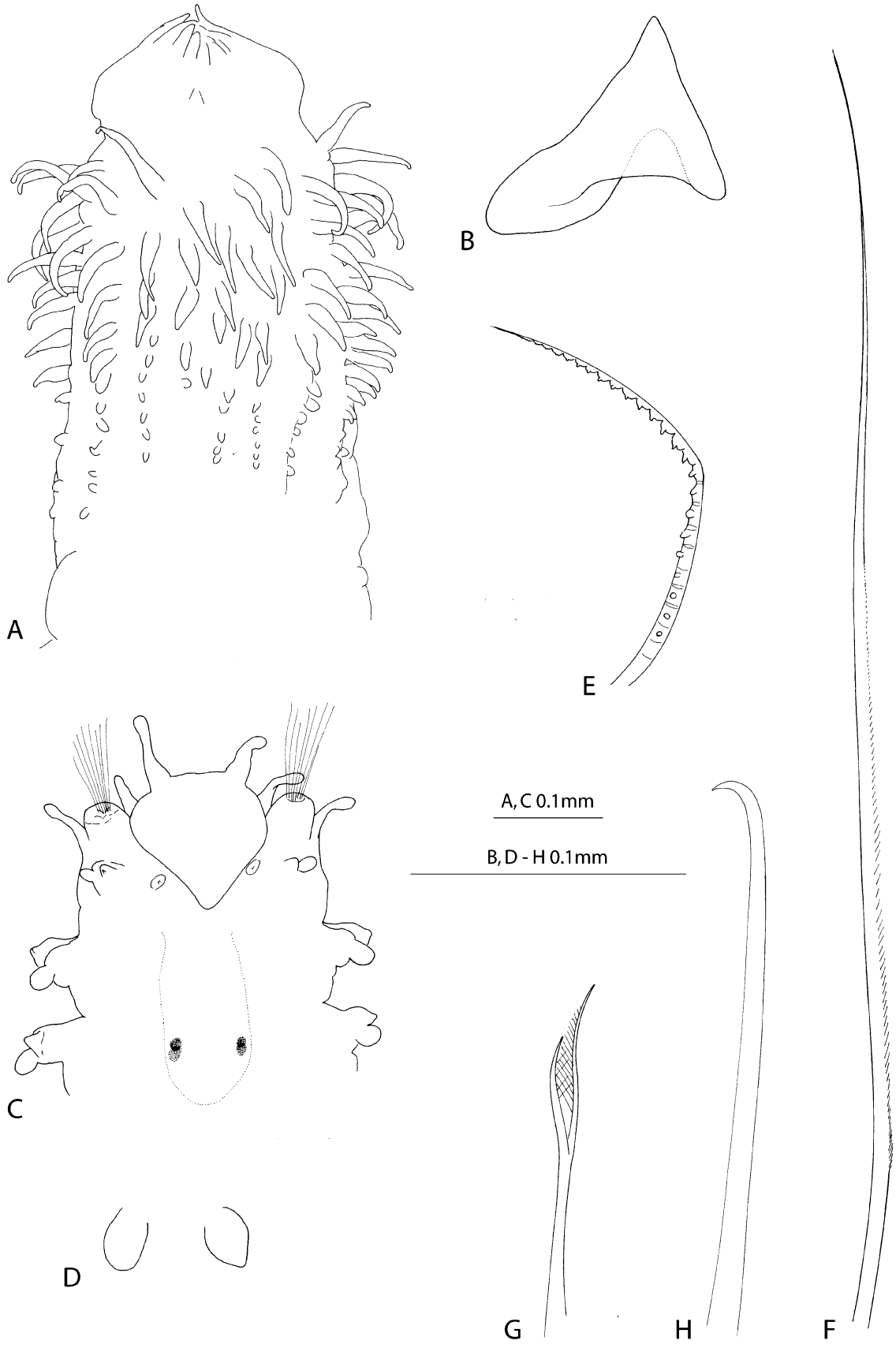

FIGURE 9. *Micronephthys stammeri*. A. Pharynx, dorsal view. B. Jaw. C. Prostomium and anterior chaetigers, dorsal view. D. Dorsal (left) and ventral (right) cirrus from median parapodia. E. Barred chaeta from notopodia of chaetiger 1. F. Postacicular chaeta of median chaetiger. G. Lyriform chaeta. H. Acicula from median chaetiger.

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 Fig. 7 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 (Fig. 9A); proximal region smooth. Jaws conical (Fig. 9B). Prostomium subpentagonal, anterior margin slightly convex; antennae and palps subequal in length, cirriform with swollen tips; palps inserted ventrolaterally on median region of prostomium (Fig. 9C). 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 (Fig. 9D). 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 (Fig. 9E); simple barred chaetae in preacicular position of following parapodia; finely spinulated chaetae in postacicular position of all parapodia (Fig. 9F); lyriform chaetae with unequal rami and thin and long spines on the internal side, in postacicular position of parapodia from chaetiger 3 (Fig. 9G), and capillary chaetae in the neuropodia of chaetiger 1. One acicula with curved tips per ramus (Fig. 9H).

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 features: 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 Martín described a new species, *M. maryae*, for specimens collected in the Mediterranean Sea. However, he did 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 Martín to distinguish these two species are exactly the characters added here to 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 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 the 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 (Fig. 7). *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 Martín 1982; Rainer & Kaly 1988; Laborda 2004).

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

Nephtys Cuvier, 1817

Type species. *Nephtys hombergii* Savigny *in* Lamarck, 1818 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 10, 11

Nephthys assimilis Örsted, 1843a: 33, pl. VI, figs. 93 and 100; Malmgren 1865: 105, pl. XII, fig. 19; not Treadwell 1914: 192; not Berkeley 1924: 290; not Hartman 1940: 239, pl. 39, figs. 87–88.
Nephtys assimilis Rainer 1989: 877, fig. 1A–E; Rainer 1991: 66, fig. 2A; Hartmann-Schröder 1996: 218, fig. 94; 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.
Nephthys hombergii Saint-Joseph 1894: 3, pl. 1, figs. 1–13 (partim) (not Savigny *in* Lamarck, 1818).
Nephthys hombergi Augener 1913: 197 (partim).
Nephtys hombergii 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).
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); Fauvel 1923: 370, fig. 144B.
Nephthys breogani Laborda and Viéitez, 1984: 211, figs. 2–6; Laborda 1987: 131.

Type locality. Hellebæk, Øresund, 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

(in collection of M. Pardal); 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*).

Atlantic/Indian Ocean. 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 spms (NHM 1961.19.76/81 as *N. hombergii*).

Description. Examined specimens up to 124 mm long for up to 117 chaetigers. See Fig. 11 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 of chaetiger 2. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by dorsal and ventral gap (Fig. 10A); middorsal papilla cirriform, long (Fig. 11D); 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 (Fig. 10B). 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", posteriorly with ciliation in raised pads. 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 the acicular lobes; dorsal cirri poorly developed, rounded (Fig. 11C); ventral cirri conical, with broad base and tapered distally. Acicular lobes of anterior parapodia rounded, with low papilliform outgrowth on interramal side of aciculae (Fig. 10C), 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 (Fig. 10C–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 (Fig. 10F), finely spinulated chaetae in postacicular position (Fig. 10G), 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 (Fig. 10H).

Remarks. *Nephtys assimilis* was originally described by Örsted (1843a), but the type material was appearently 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

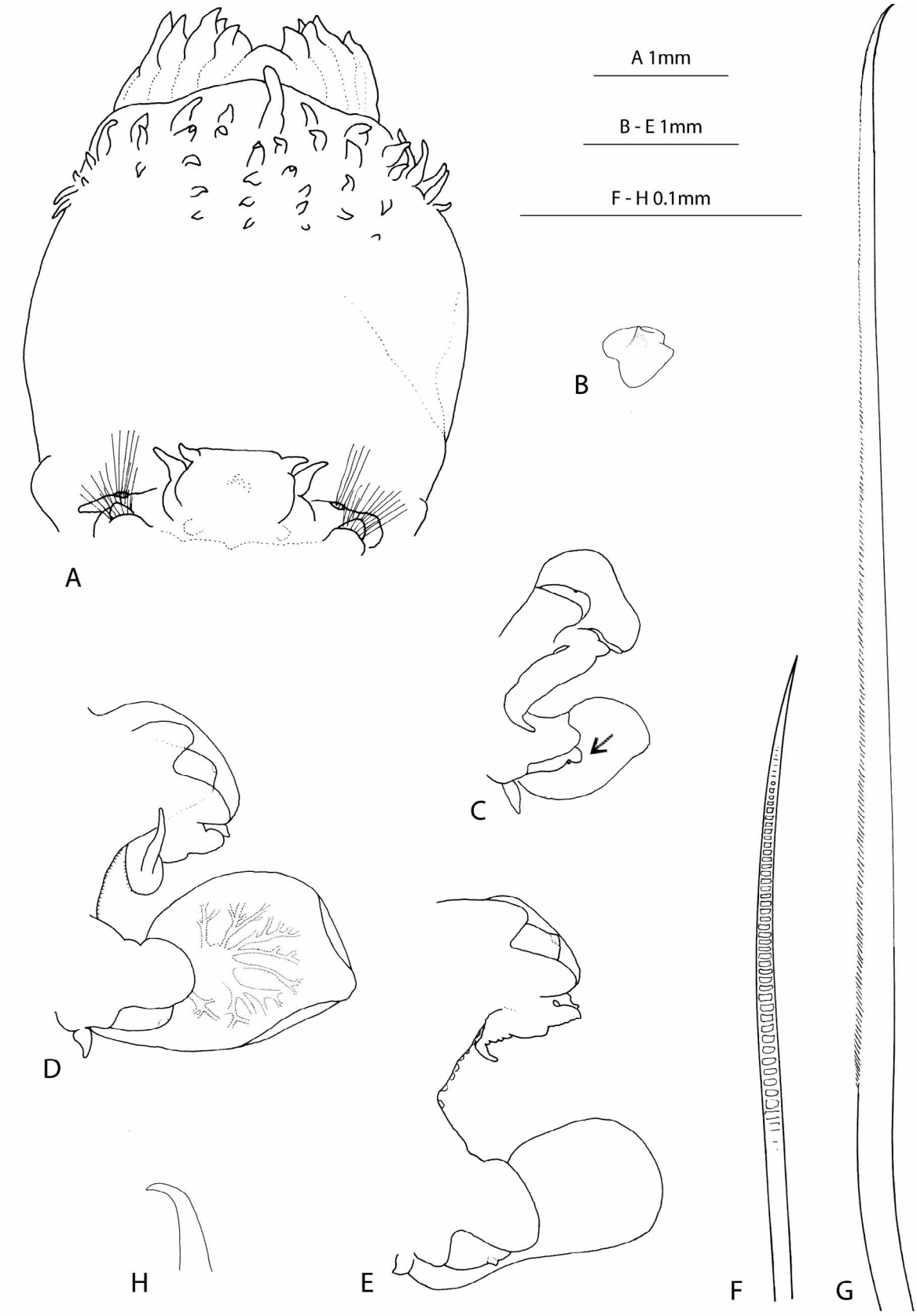

FIGURE 10. *Nephtys assimilis*. A. Pharynx, prostomium and first chaetiger, dorsal view. B. Jaw. C. Left parapodium of chaetiger 10, anterior view. D. Left parapodium of chaetiger 40, anterior view. E. Left parapodium of chaetiger 80, anterior view. F. Preacicular chaeta from chaetiger 40. G. Postacicular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

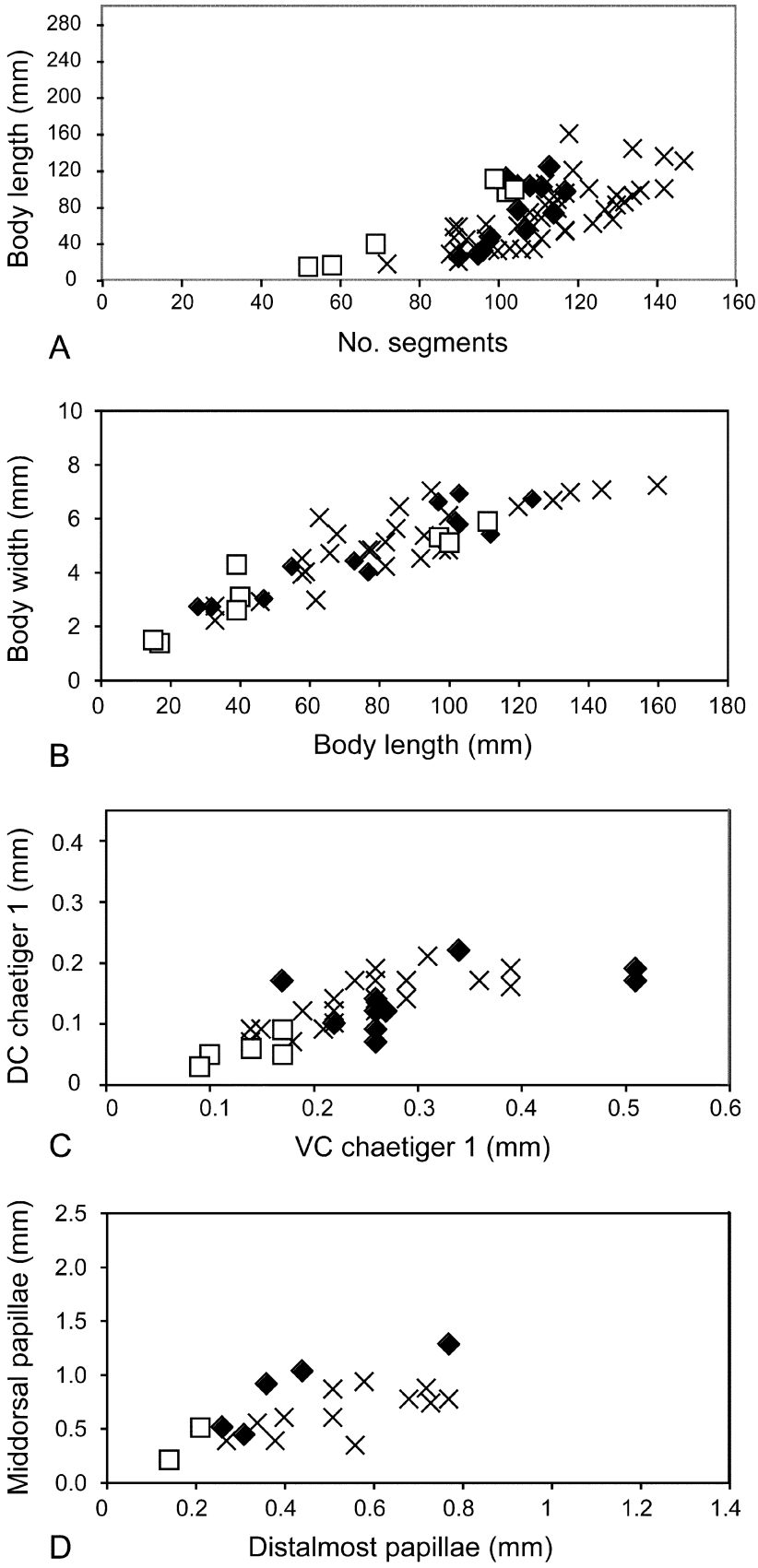

FIGURE 11. Relationships between: A. Number of segments and body length. B. Body length and body width. C. Length of ventral cirri (VC) and dorsal cirri (DC) of chaetiger 1. D. Length of pharynx distalmost subterminal papillae and middorsal papilla. ◆ *Nephtys assimilis*. × *N. hombergii*. □ *N. kersivalensis*.

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 morphologically close related species with similar geographical distribution are summarized in Table 5. *Nephtys hystricis* and *N. kersivalensis* are smaller species (Figs. 11, 19) with noto- and neuropodial postchaetal lamellae similar in size, 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 deeper waters, while *N. kersivalensis* occurs frequently in shallow waters, together with *N. hombergii* and *N. assimilis*.

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).

TABLE 5. Diagnostic characters of 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 papilliform 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 papillae	20–22 rows of 2–5 papillae	22 rows of 2–5 papillae	22 rows of 3–6 papillae	22 rows of 3–6 papillae
Depth	Intertidal – 100m	Intertidal – 1000m	100 – 800m	Shallow subtidal – 300m

***Nephtys caeca* (Fabricius, 1780)**
Figures 12, 13

Nereis caeca Fabricius, 1780: 304.
Aonis caeca Savigny 1822: 45.
Nephtys margaritacea Johnston, 1835: 341, fig. 33; Quatrefages 1865: 423.
Nephtys ingens Stimpson, 1853: 33.
Portelia caeca Quatrefages 1865: 433.
Nephtys bononensis Quatrefages, 1865: 425.
Nephtys oerstedi Quatrefages, 1865: 427.

Nephthys cæca [misspelling of *caeca*] Malmgren 1865: 104, pl. XII, fig. 18; Saint-Joseph 1894: 16, Pl. I, fig. 14–18.
Nephtys nudipes Ehlers, 1868: 635, pl. XXIII, fig. 61.
Nephthys caeca Ehlers 1868: 588, fig. 10–34; Möbius 1875: 168 (partim); Verrill 1881: 294, 307, 314; Webster and Benedict 1887: 709; Whiteaves 1901: 82; McIntosh 1908: 8; Heinen 1911: 10, fig. 1; Izuka 1912: 213; Fauvel 1923: 365, fig. 142A–L; Okuda 1938: 123; Okuda and Yamada 1954: 186, fig. 4.
Nephtys coeca [misspelling of *caeca*] Michaelsen 1896: 25; Johnson 1901: 401 (partim); Nordgaard 1905: 162, 235; Augener 1912: 191, pl. 6, figs. 24–25; Gorbunov 1946: 38; Thorson 1946: 71, fig. 34; Wesenberg-Lund 1950a: 20; Wesenberg-Lund 1950b: 57; Wesenberg-Lund 1951: 43.
Nephthys johnstoni McIntosh 1908: 34 (partim).
Nephthys hombergi Heinen 1911: 16 (partim).
Nephthys longisetosa Heinen 1911: 26 (partim).
Nephtys caeca 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; Wolff 1968: 4, fig. 7; 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; Kirkegaard 1992: 331, fig. 161; Hartmann-Schröder 1996: 220, fig. 95; Böggemann 1997: 80, fig. 54; Dnestrovskaya and Jirkov 2001: 196,1 fig; Laborda 2004: 398, fig. 146C.
Nephtys caeca var. *ciliata* McIntosh 1908: 13, pl. LXVI, fig. 3; Heinen 1911: 13, fig. 2; ?Okuda 1939: 231, fig. 6.
Nephtys hombergii var. *ehlersi* Augener 1939: 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 Fig. 13 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 (Fig. 13D); 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 pharynx (Fig. 12A); 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 (Fig. 12A). 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 (Fig. 13C); 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 towards median segments; postchaetal lamellae extending well beyond acicular lobes, rounded and directed ventrally in notopodium, triangular in

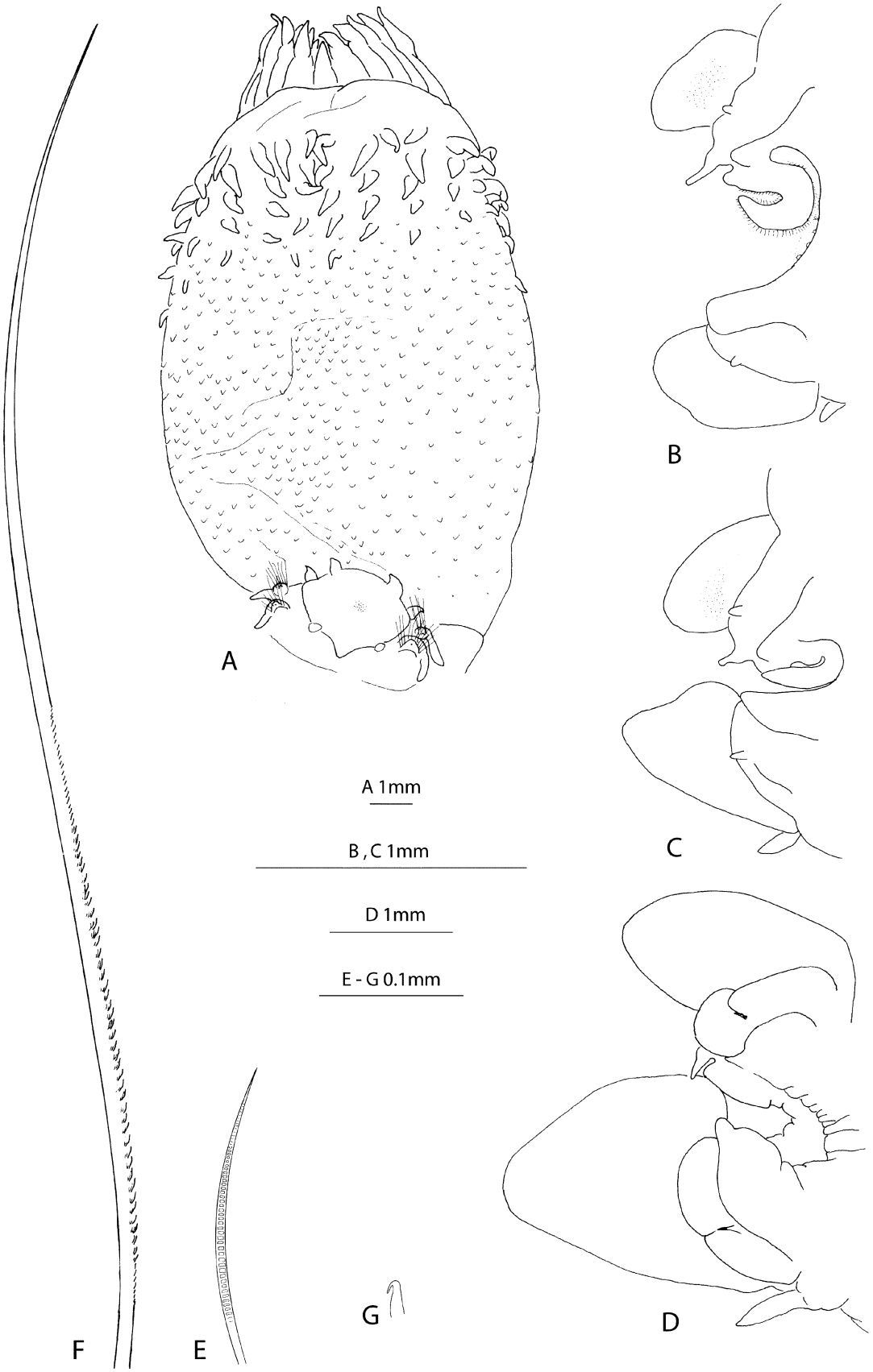

FIGURE 12. *Nephtys caeca*. A. Pharynx, prostomium and first chaetiger, dorsal view. B. Right parapodium of chaetiger 10, anterior view. C. Right parapodium of chaetiger 20, anterior view. D. Median parapodium of a larger specimen, anterior view. E. Pre-acicular chaeta from chaetiger 20. F. Post-acicular chaeta from chaetiger 20. G. Acicula from chaetiger 20.

neuropodium; dorsal cirri small, lameliform, with enlarged base and acute tip; ventral cirri conical (Fig. 12B–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 (Fig. 12E), coarsely spinulated chaetae in postacicular position (Fig. 12F), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips (Fig. 12G).

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 to be 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 (Fig. 13) 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, the middorsal papilla is 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 assess.

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 13, 14

Nereis ciliata Müller, 1776: 17; Müller 1789: 14, pl. LXXXIX, figs. 1–4.

Nephtys borealis Örsted, 1843a: 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: 162, 235; not McIntosh 1908: 23; Heinen 1911: 21, fig. 5 (partim); Izuka 1912: 215; not Augener 1912: 192; 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; Wolff 1968: 4, fig. 9; not Kirkegaard 1969: 46, fig. 19 (= *N. pente*); Hartmann-Schröder 1971: 218, fig. 71A (partim); not Banse and Hobson 1974: 75, fig. 19I (?= *N. pente*); Campoy 1982: 511; ?Imajima and Takeda 1987: 67; Jirkov 1989: 77, Figs. 16.4 and 16.5; Rainer 1991: 70, fig. 3A; Kirkegaard 1992: 333, fig. 162; Hartmann-Schröder 1996: 221, fig. 96; Dnestrovskaya and Jirkov 2001: 197,1 fig; Laborda 2004: 399, fig. 146D; not McIntosh 1908: 23.

Nephthys hombergi Augener 1913: 202 (partim).

Nephtys ciliata form *longosetosa* not Augener 1939: 137.

Nephtys hombergii var. *ehlersi* Augener 1939: 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, 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 Fig. 13 for length and width measurements. Body segments of about the same width, last segments tapering abruptly. Poor dorsal delineation between anterior segments. Colour in ethanol cream; chaetae amber; aciculae of anterior segments with red tips and in median and posterior segments with dark tips. Eyes not visible. Pharynx distal region with 10 pairs of terminal bifid papillae, separated by small dorsal and ventral elevations; middorsal papilla long and cirriform (Fig. 13D); 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 (Fig. 14A). Jaws conical (Fig. 14B). Prostomium subquadrangular, anterior margin straight, posterior margin V-shaped (Fig. 14A); 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 (Fig. 14C–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 (Fig. 14I), spinulated chaetae in postacicular position (Fig. 14J), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips (difficult to see in all specimens observed; Fig. 14L).

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).

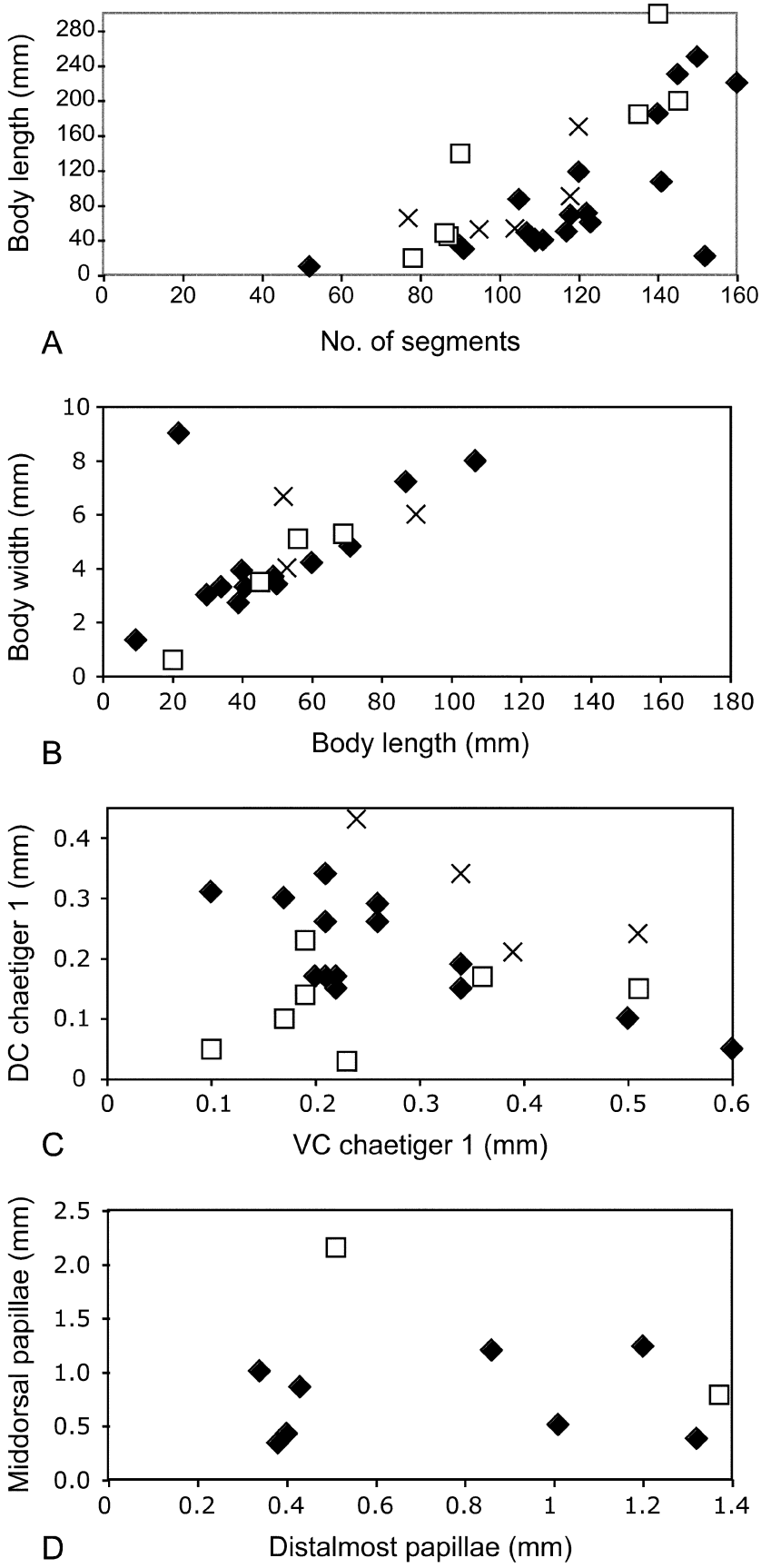

FIGURE 13. Relationships between: A. Number of segments and body length. B. Body length and body width. C. Length of ventral cirri (VC) and dorsal cirri (DC) of chaetiger 1. D. Length of pharynx distalmost subterminal papillae and middorsal papilla. ◆ *Nephtys caeca*. □ *N. ciliata*. × *N. longosetosa*.

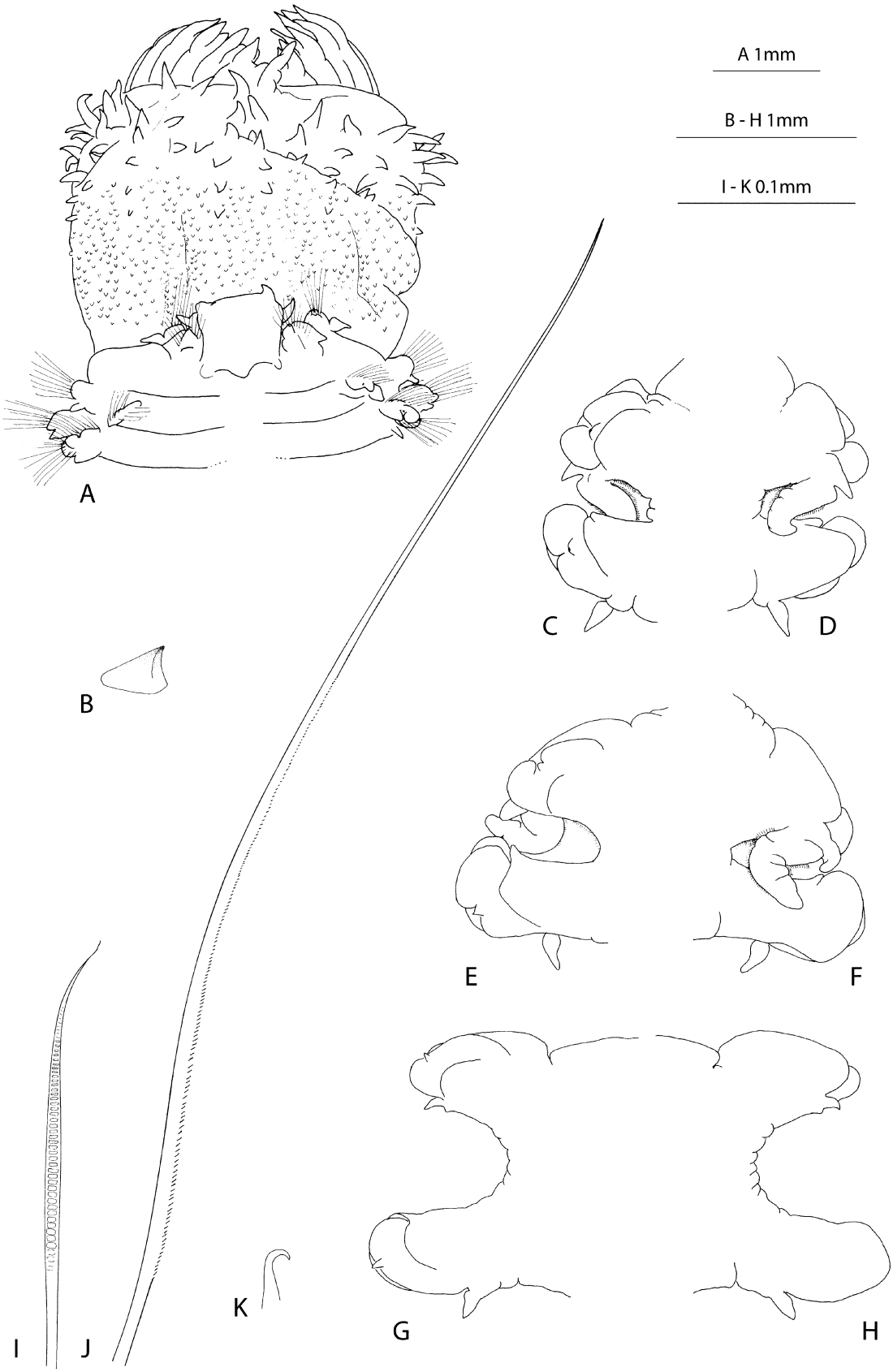

FIGURE 14. *Nephtys ciliata*. A. Pharynx, prostomium and anteriormost chaetigers, dorsal view. B. Jaw. C. Right parapodium of chaetiger 10, anterior view. D. Same, posterior view. E. Right parapodium of chaetiger 40, anterior view. F. Same, posterior view. G. Right parapodium of chaetiger 70, anterior view. H. Same, posterior view. I. Preacicular chaeta from chaetiger 20. J. Postacicular chaeta from chaetiger 20. K. Acicula from chaetiger 20.

***Nephtys cirrosa* Ehlers, 1868**
Figures 15, 16

? Portelia rosea Quatrefages, 1865: 431, pl. VII, fig. 12–15.
Nephthys cirrosa Ehlers, 1868: 624, pl. XXIII, figs. 6–7, 37, 38; Saint-Joseph 1894: 20, pl. 1 fig. 19; McIntosh 1908: 36; Augener 1912: 199; Fauvel 1923: 369, fig. 144C–H; Fauvel 1936: 40; La Greca 1946: 277; Guille and Laubier 1966: 267; Gibbs 1969: 320 (juvenile stages); Foret-Montardo 1969: 812, pl. II, fig. 117; Hartmann-Schröder 1971: 214, fig. 69A–E; Hartmann-Schröder 1974: 208.
Nephtys cirrosa Wolff 1968: 4, fig. 5; Kirkegaard 1969: 46, fig. 19; Campoy 1982: 512; Laborda 1987: 132, figs. 1, 3, 6, 11and12; Rainer 1991: 72, fig. 3F; Kirkegaard 1992: 334, fig. 163; Hartmann-Schröder 1996: 222, fig. 97; Dnestrovskaya and Jirkov 2001: 199, 1 fig; Laborda 2004: 400, fig. 147A–C.
Nephthys johnstoni McIntosh 1908: 34 (partim).
Nephtys ehlersi Heinen, 1911: 34, pl. I, fig. 1 and 2.
Nephthys longisetosa Heinen 1911: 26 (partim).
Nephtys cf. cirrosa Böggemann 1997: 80, fig. 55.

Type locality. England.

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, (in collection of M. Pardal); 40º07'57.270"N, 08º51'07,744"W, 2.0 m, Nov 2005, 11 incomplete spms (in collection of M. Pardal), and Mar 2006, 2 complete spms (in collection of M. Pardal); 40º07'29.447"N, 08º50'47.313"W, 2.5 m, Nov 2005, 13 incomplete spms (in collection of M. Pardal); 5.2 m, Nov 2005, 2 incomplete spms (in collection of M. Pardal); 40º08'33.179"N, 08º49'38.073"W, 4.5 m, Nov 2005, 10 incomplete spms (in collection of M. Pardal), and Mar 2006, 4 complete spms (in collection of M. Pardal); 40º08'21,405"N, 08º48'55.126"W, 5.2 m, Nov 2005, 5 incomplete spms (in collection of M. Pardal), and Mar 2006, 2 complete spms (in collection of M. Pardal); 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 Fig. 16 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 (Fig. 16D); 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) (Fig. 15A); proximal region smooth. Jaws conical (Fig. 15B). Prostomium subpentagonal; anterior and lateral margins convex, giving prostomium a rounded appearance; 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 (Fig. 16C); 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 (Fig. 15C–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 (Fig. 15H), very finely spinulated chaetae in postacicular position (Fig. 15I), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips (very dificult to see; Fig. 15J).

Remarks. *Nephtys cirrosa* was erected by Ehlers (1868) for specimens having acicular lobes rounded to bilobed and notopodial prechaetal lamellae rudimentary, apart from the other diagnostic features that separate 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 specimens of *N. cirrosa* from the North Sea. Foret-Montardo (1969) and Böggemann (1997) also 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 (Fig. 15C–G). Form B (described as *N. ehlersi* by Heinen 1911) has acicular lobes rounded to conical, notopodial prechaetal lamellae well developed and bilobed, and pharynx middorsal papilla longer than the other subterminal papillae (Fig. 15K–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 that make the distinction difficult between the two potentially different species.

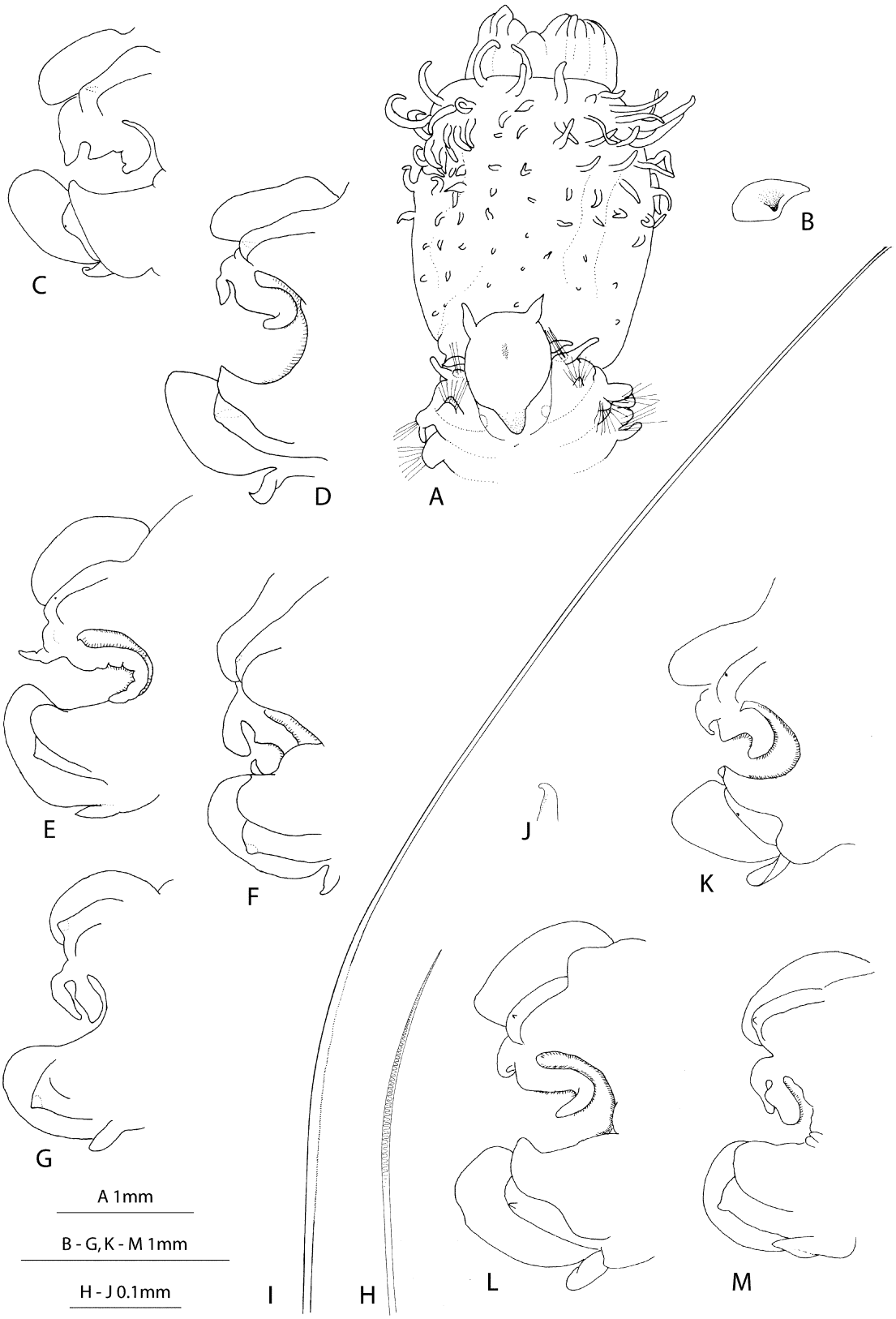

FIGURE 15. *Nephtys cirrosa* (form A). A. Pharynx, prostomium and anteriormost chaetigers, dorsal view. B. Jaw. C. Right parapodium of chaetiger 10, anterior view. D. Right parapodium of chaetiger 21, anterior view. E. Right parapodium of chaetiger 40, anterior view. F. Right parapodium of chaetiger 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. *Nephtys cirrosa* (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.

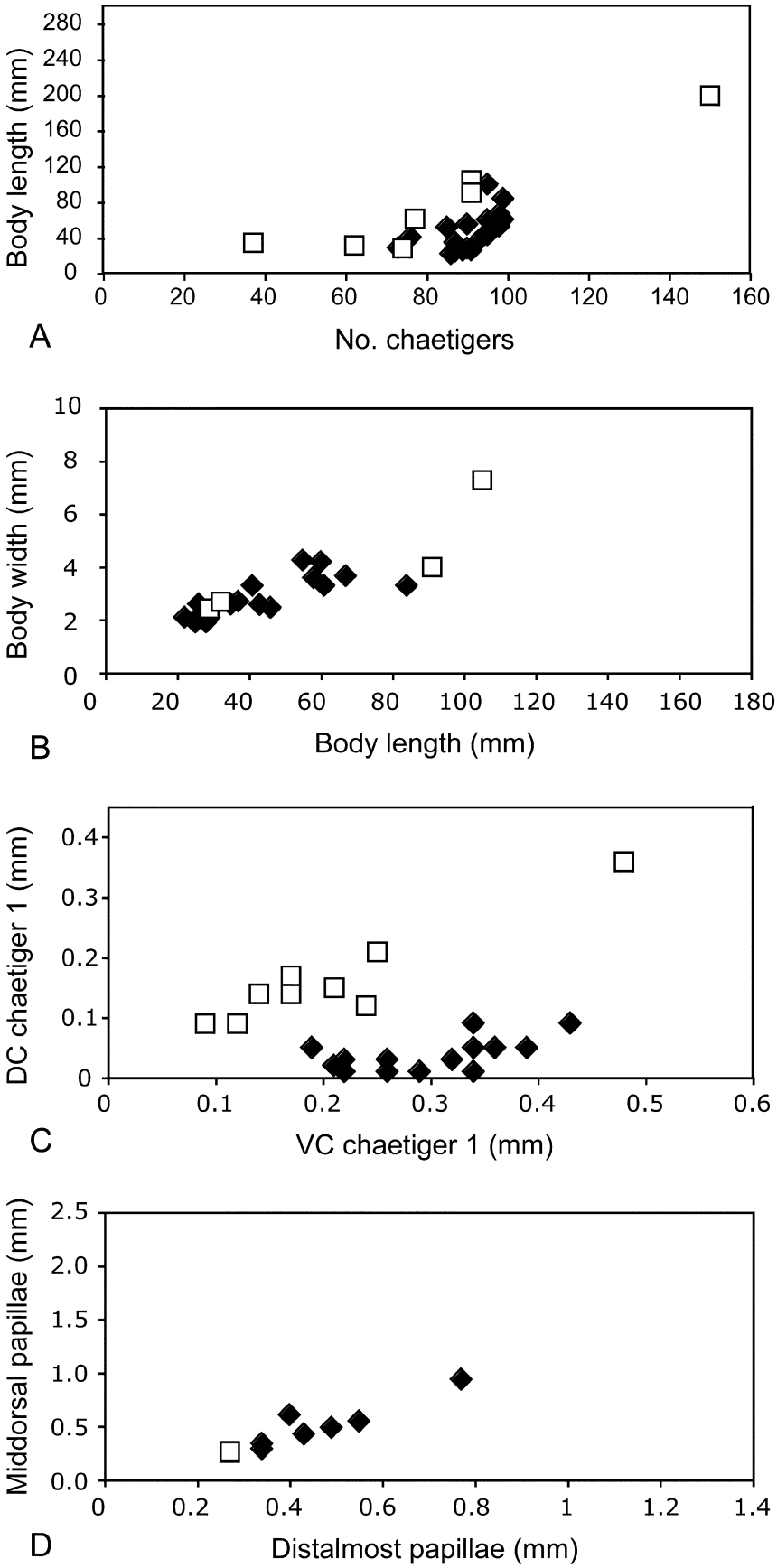

FIGURE 16. Relationships between: A. Number of segments and body length. B. Body length and body width. C. Length of ventral cirri (VC) and dorsal cirri (DC) of chaetiger 1. D. Length of pharynx distalmost subterminal papillae and middorsal papilla. ◆ *Nephtys cirrosa*. □ *N. paradoxa*. Minute dorsal cirri were scored as 0.01.

Although we have 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, Germany, 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 *in* Lamarck, 1818

Figures 11, 17

Nephthys hombergii Savigny *in* Lamarck, 1818: 314; 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); Fauvel 1923: 367, fig. 143A–D (partim); Fauvel 1936: 40; Ditlevsen 1929: 20; Day 1953: 431; Tebble 1955: 102; Foret-Montardo 1969: 810, pl. I, figs. 6–7; Rullier and Amoureux 1970: 124.

Nereis scolopendroides Chiaje 1822: pl. XXVII, figs. 8, 13 and 22–27; Chiaje 1825: 401, 424.

Nephthys neapolitana Grube 1840: 71.

Nephthys macandrewi Baird 1873: 94.

Nephthys scolopendroides Audouin and Milne Edwards 1833: 260; Michaelsen 1896: 57 (partim).

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

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

Nephthys hombergi Augener 1913: 197, 202, fig. 26 (partim).

Nephtys hombergi Fauchald 1963: 3, figs. 1G, 2D and 3E; Wolff 1968: 4, fig. 6; Kirkegaard 1992: 336, fig. 164 (partim).

Nephtys hombergii Hartman 1950: 101, pl. 17, fig. 2; Eliason 1962: 249; Gibbs 1969: 320 (juvenile stages); Hartmann-Schröder 1971: 215, fig. 70A–B (partim); Hartmann-Schröder 1974: 88 (partim); Clay 1974; Hartmann-Schröder 1977: 88 (partim); not Hartmann-Schröder 1981: 31; not Hartmann-Schröder 1982 (= *N. assimilis*): 10; Campoy 1982: 515; Laborda 1987: 132, figs. 2, 5, 10, 14, 16; 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, fig. 70C.

Type locality. Le Havre, 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 (in collection of M. Pardal), and Mar 2006, 1 complete spm (in collection of M. Pardal); 40º08'36.600"N, 08º51'23.972"W, 7.5 m, Oct 2005, 2 incomplete spms (in collection of M. Pardal), and Mar 2006, 3 complete and 2 incomplete spms (in collection of M. Pardal); 40º07'57.270"N, 08º51'07.744"W, 2.0 m, Mar 2006, 3 complete spms (in collection of M. Pardal); Foz do Arelho: intertidal, Apr 2006, 6 complete and 7 incomplete spms, (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 (in collection of A. Ravara); 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 Fig. 11 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 (Fig. 11D); midventral papilla normally absent (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 (Fig. 17A); proximal region smooth. Jaws conical, deeply incised at base (Fig. 17B). Prostomium subrectangular, anterior margin slightly convex, posterior margin V-shaped extending over first chaetiger (not very well deliniated; Fig. 17C); 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 (Fig. 17D) 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 (Fig. 11C); ventral cirri conical, with broad base and tapering distally. Acicular lobes of following parapodia conical to rounded, with a distinct papilliform outgrowth on interramal

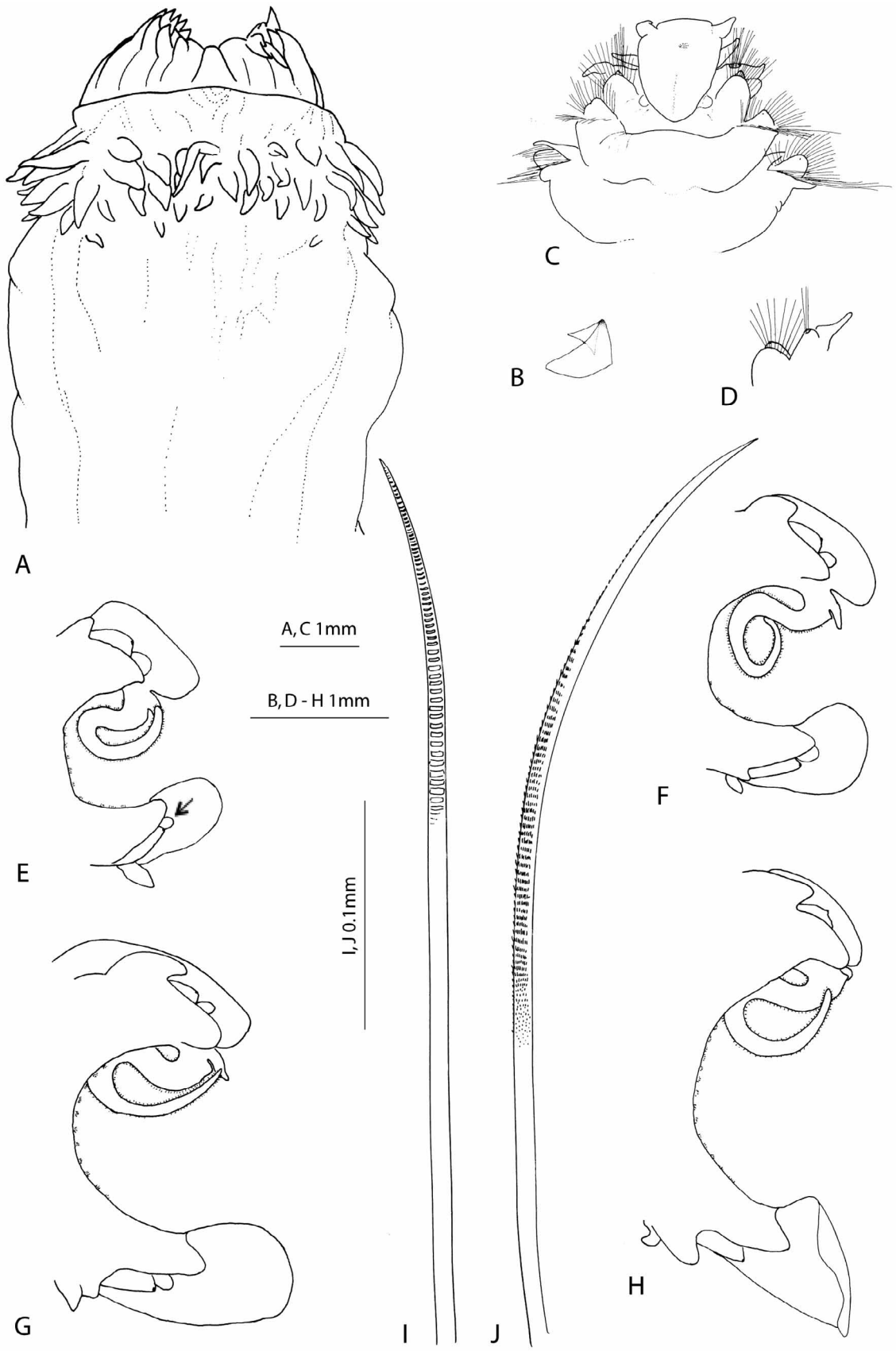

FIGURE 17. *Nephtys hombergii*. A. Pharynx, dorsal view. B. Jaw. C. Prostomium and anteriormost chaetigers, dorsal view. D. Right parapodium of chaetiger 1, posterior view. E. Left parapodium of chaetiger 10, anterior view. F. Left parapodium of chaetiger 20, anterior view. G. Left parapodium of chaetiger 40, anterior view. H. Left parapodium of chaetiger 80, anterior view. I. Preacicular chaeta from chaetiger 40. J. Postacicular chaeta from chaetiger 40.

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 (Fig. 17E–H). Branchiae recurved, long and cirriform, moderately ciliated, with papilliform 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 (Fig. 17I), spinulated chaetae in postacicular position (Fig. 17J), 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 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 minor 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 18, 19

Nephthys hystricis McIntosh, 1900b: 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 (= *N. incisa*); 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, pl. XVIII, fig. 3; 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); Fauvel 1923: 370, fig. 144B.

Nephtys incisa Fauchald 1963: 15, figs. 1H, 2C, 3B, 7B, 9 (partim); Wolff 1968: 4, fig. 10; Kirkegaard 1969: 51, fig. 23 (partim); Hartmann-Schröder 1971: 217, fig. 70d–e; Hartmann-Schröder 1974: 207 (partim); ?Campoy 1982: 516; Kirkegaard 1992: 338, fig. 165.

Nephtys (Nephtys) hystricis not Day 1967: 345.

Nephtys incisa bilobata Campoy 1982: 518.

? *Nephtys hystricis* not Guille and Laubier 1966: 267; not Wolff 1968: 6, fig. 11 (= *N. incisa*); Laborda 2004: 402, fig. 147D–E.

Nephtys hystricis not Campoy 1982: 514; Rainer 1990: 362, fig. 1A–E; Rainer 1991: 75, fig. 2C; Hartmann-Schröder 1996: 225, fig. 99; Dnestrovskaya and Jirkov 2001: 201,1 fig.

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 Fig. 19 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 (Fig. 19D); midventral papillae absent; subdistal region with 22 rows of 3–6 very small, conical subterminal papillae, extending over 1/3 length of pharynx (Fig. 18A); proximal region smooth. Jaws conical. Prostomium subpentagonal (Fig. 18A), 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 (Fig. 19C). 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 (Fig. 18B–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 (Fig. 18G), finely spinulated chaetae in postacicular position (Fig. 18H), 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 (1900b) 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)

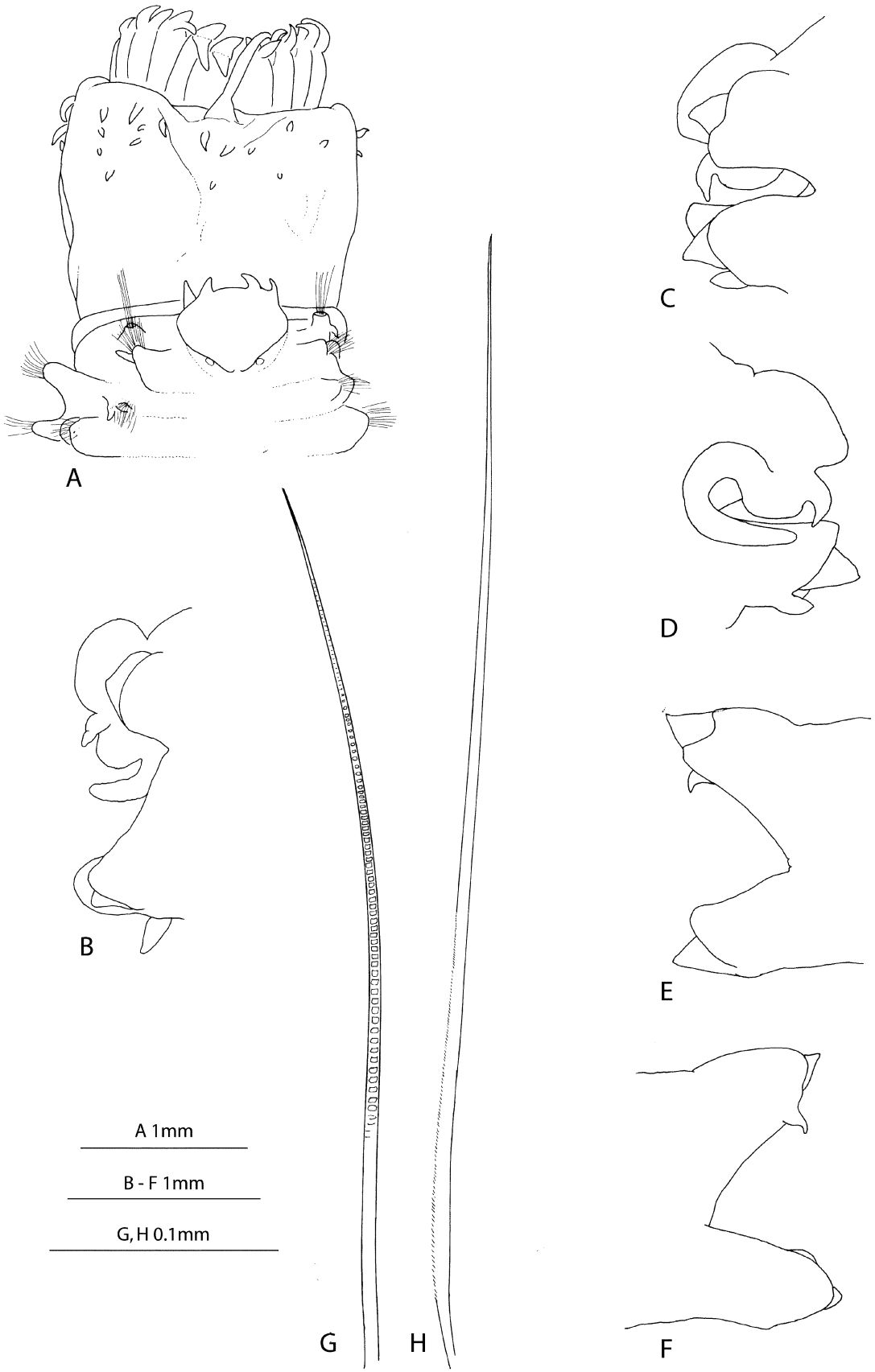

FIGURE 18. *Nephtys hystricis*. A. Pharynx, prostomium and anteriormost chaetigers, dorsal view. B. Right parapodium of chaetiger 10, anterior view. C. Right parapodium of chaetiger 20, anterior view. D. Same, posterior view. E. Right parapodium of a posterior chaetiger, anterior view. F. Same, posterior view. G. Preacicular chaeta from chaetiger 20. H. Postacicular chaeta from chaetiger 20.

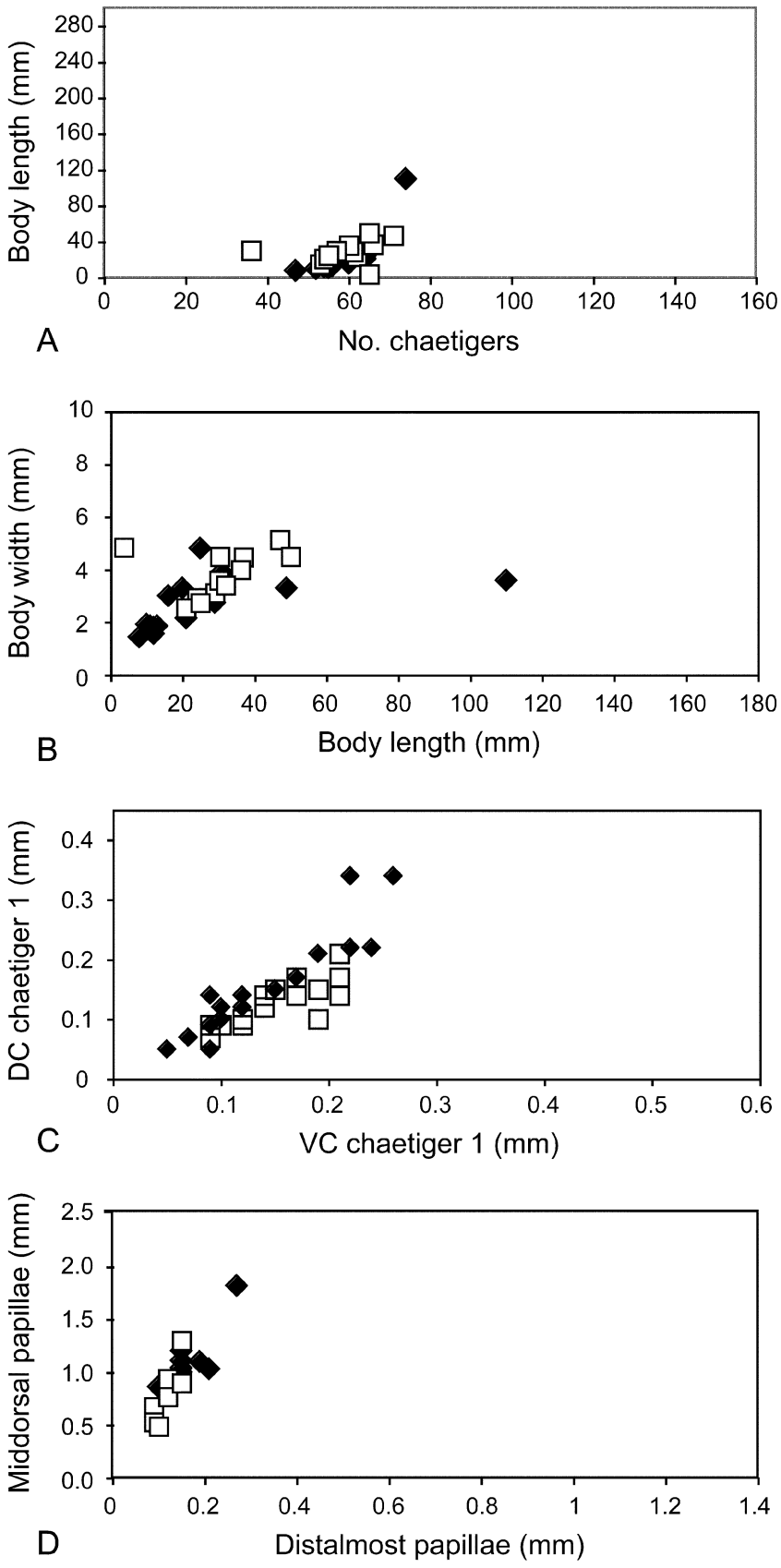

FIGURE 19. Relationships between: A. Number of segments and body length. B. Body length and body width. C. Length of ventral cirri (VC) and dorsal cirri (DC) of chaetiger 1. D. Length of pharynx distalmost subterminal papillae and middorsal papilla. ◆ *Nephtys hystricis*. □ *N. incisa*.

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 shorter than the acicular lobes, and the postchaetal lamellae are larger than the 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 has fewer 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 a larger variation; 11–21 posterior chaetigers without branchiae in *N. hystricis* (4 entire specimens examined) and 19–30 in *N. incisa* (9 entire specimens examined). We also found differences in the preacicular chaetae of the two species; in *N. hystricis* they are barred in all its extension (Fig. 18G), while in *N. incisa* they are only distally barred (Fig. 20H).

Nephtys kersivalensis is another species that is morphologically similar to *N. hystricis*. However, the two species can be differentiated by the chaetiger number 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*. Besides, *N. 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. One specimen from off Mozambique (NHM 1934.1.19) 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 the 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).

Nephtys incisa Malmgren, 1865

Figures 19, 20

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 1913: 203 (partim); not Treadwell 1914: 193; not Fauvel 1914: 198, pl. XVIII, fig. 3; not Fauvel 1923: 369, fig. 144A–B (= *N. hystricis*).

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

Nephthys hystricis McIntosh 1908: 27, pl. LVII, figs. 8 and 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; not Wolff 1968: 4, fig. 10; ?Foret-Montardo 1969: 814, pl. III, figs. 8–10; Kirkegaard 1969: 51, fig. 23 (partim); not Hartmann-Schröder 1971: 217, fig. 70D–E; Day 1973: 43; not Hartmann-Schröder 1974: 207; Gardiner 1976: 154, fig. 16C, D; Campoy 1982: 516; Hartmann-Schröder 1982: 11; not Taylor 1984: 35-7, figs. 35-3 and 4A–D; Rainer 1990: 366, fig. 2A–E; Rainer 1991: 76, fig. 3G; not Kirkegaard 1992: 338, fig. 165 (= *N. hystricis*); Hartmann-Schröder 1996: 225, fig. 100; Böggemann 1997: 80, fig. 57; Dnestrovskaya and Jirkov 2001: 202, 1 fig; Laborda 2004: 405, fig. 148C–D.

Nephtys (Nephtys) hystricis Day 1967: 345.

Nephtys hystricis Wolff 1968: 6, fig. 11; ?Foret-Montardo 1969: 816, pl. III, figs. 1–4; Campoy 1982: 514.

Aglaophamus malmgreni Hartmann-Schröder 1974: 205 (partim) (not Théel, 1879).

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 condition (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 Fig. 19 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 (Fig. 19D); midventral papillae absent; subdistal region with 20 rows of 1–5 very small subterminal papillae, extending over 1/3 length of pharynx (Fig. 20A); proximal region smooth. Jaws conical (Fig. 20B). Prostomium subpentagonal, anterior margin slightly concave, posterior margin rounded (Fig. 20A); 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 (Fig. 19C). 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 (Fig. 20C–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 (Fig. 20H), finely spinulated chaetae in postacicular position (Fig. 20I), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips (Fig. 20J).

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, but also reported from depths to 1700 m in the western Atlantic (Rainer 1990, 1991; Laborda 2004).

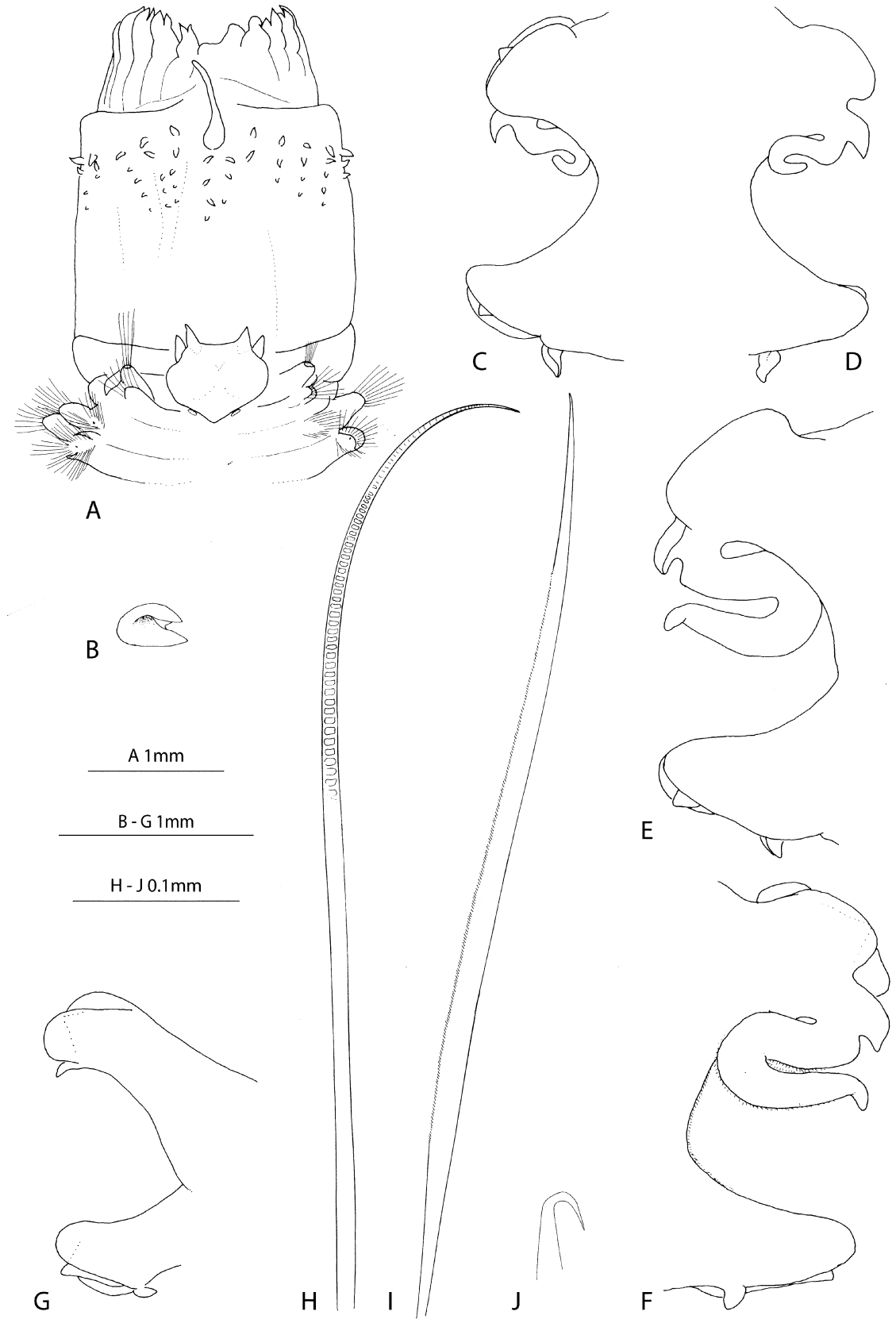

FIGURE 20. *Nephtys incisa*. A. Pharynx, prostomium and anteriormost chaetigers, dorsal view. B. Jaw. C. Right parapodium of chaetiger 11, anterior view. D. Same, posterior view. E. Right parapodium of chaetiger 20, anterior view. F. Same, posterior view. G. Right parapodium of chaetiger 40, anterior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

***Nephtys kersivalensis* McIntosh, 1908**
Figure 11, 21

Nephthys hombergii var. *kersivalensis* McIntosh, 1908: 20 (partim).
Nephthys incisa Michaelsen 1896: 59 (partim); Augener 1913: 203 (partim); George 1979: 198 (not Malmgren 1865).
Nephthys hombergii forma *ehlersii* Fage and Legendre 1927: 124, fig. 15.
Nephtys incisa Fauchald 1963: 15 (partim).
Nephtys hombergi kersivalensis Fauchald 1963: 5.
Nephtys hombergii var. *kersivalensis* Hartmann-Schröder 1971: 217, fig. 70C.
Nephtys kersivalensis Rainer 1989: 882, fig. 2A–F; Rainer 1991: 78, fig. 2D; Hartmann-Schröder 1996: 229, fig. 101; 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 Fig. 11 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 (Fig. 11D), midventral papilla absent; subdistal region with 22 rows of 3–6 small, conical subterminal papillae, extending over 1/3 length of pharynx (Fig. 21A); proximal region smooth. Jaws not examined. Prostomium subpentagonal, anterior margin slightly convex, posterior margin V-shaped extending over first chaetiger (Fig. 21A); 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 (Fig. 11C), rounded; ventral cirri conical, with broad base and tapering distally. Acicular lobes of following parapodia conical with rugose area on ventral side, near acicula (Figs. 21D, 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 (Figs. 21B, 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 (Fig. 21I), finely spinulated chaetae in postacicular position (Fig. 21J), and capillary chaetae in the neuropodia of chaetiger 1. One acicula per ramus, middle and posterior ones with curved tips (Fig. 21D, 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 north 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). Besides, the Portuguese specimens are usually smaller and 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* (Figs. 11, 19).

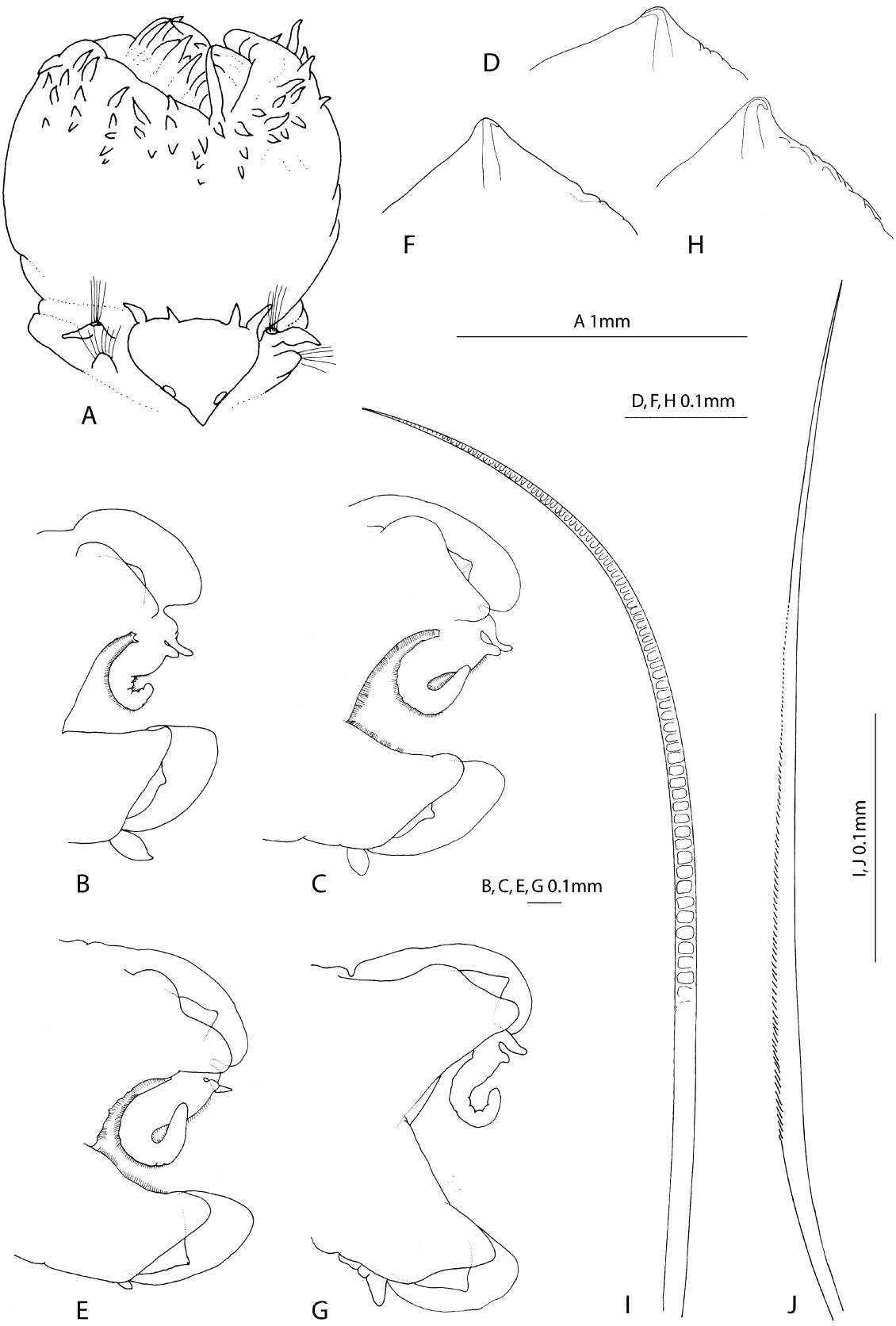

FIGURE 21. *Nephtys kersivalensis*. A. Pharynx, prostomium and first chaetiger, dorsal view. B. Left parapodium of chaetiger 10, anterior view. C. Left parapodium of chaetiger 20, anterior view. D. Detail of notopodial acicular lobe of chaetiger 20. E. Left parapodium of chaetiger 40, anterior view. 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.

Distribution. Atlantic Ocean (Outer Hebrides, lreland, North Sea, Kattegat, W France, W and S Portugal) (Rainer 1991; Laborda 2004; this study); Mediterranean Sea (J. Gil pers. com.).

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

Nephtys longosetosa Örsted, 1842

Figure 13, 22

Nephthys longosetosa Örsted, 1842: 123; Örsted 1843b: 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: 172, fig. 5 (partim); not Malmgren 1865: 106, tab. XII, fig. 20; Verrill 1881: 295, 319; Michaelsen 1896: 24; Heinen 1911: 26, fig. 7; Augener 1913: 193; Okuda 1939: 231; not McIntosh 1908: 29, pl. LVII, figs. 10–12, pl. LXVI, fig. 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 (partim).

Nephthys ciliata Augener 1913: 193 (partim) (not Müller 1776).

Nephthys ciliata form. *longosetosa* Augener 1939: 137.

Nephtys 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, figs. 71C, 73A–B; Wolff 1968: 4, fig. 8; Kirkegaard 1969: 52, figs. 24–26; 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, figs. 10A–I, 14; Jirkov 1989: 78, Figs. 16.10 and 16.11; Rainer 1991: 80, fig. 3D; Kirkegaard 1992: 339, fig. 166; Hartmann-Schröder 1996: 229, fig. 102; 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 Fig. 13 for length and width measurements. Body long and slender, of about same width, 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 (Fig. 13D); 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 (Fig. 22A); 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 the anterior border of the first chaetiger. 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 (Fig. 13C), 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 median ventral incision giving it a typical S-shaped appearence; dorsal cirri slender, with broad base and a cirriform tip; ventral cirri conical somewhat flattened (Figs. 22B–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 is another report of this species from the Strait of Magellan (Imajima & Takeda 1987), but this record requires confirmation.

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).

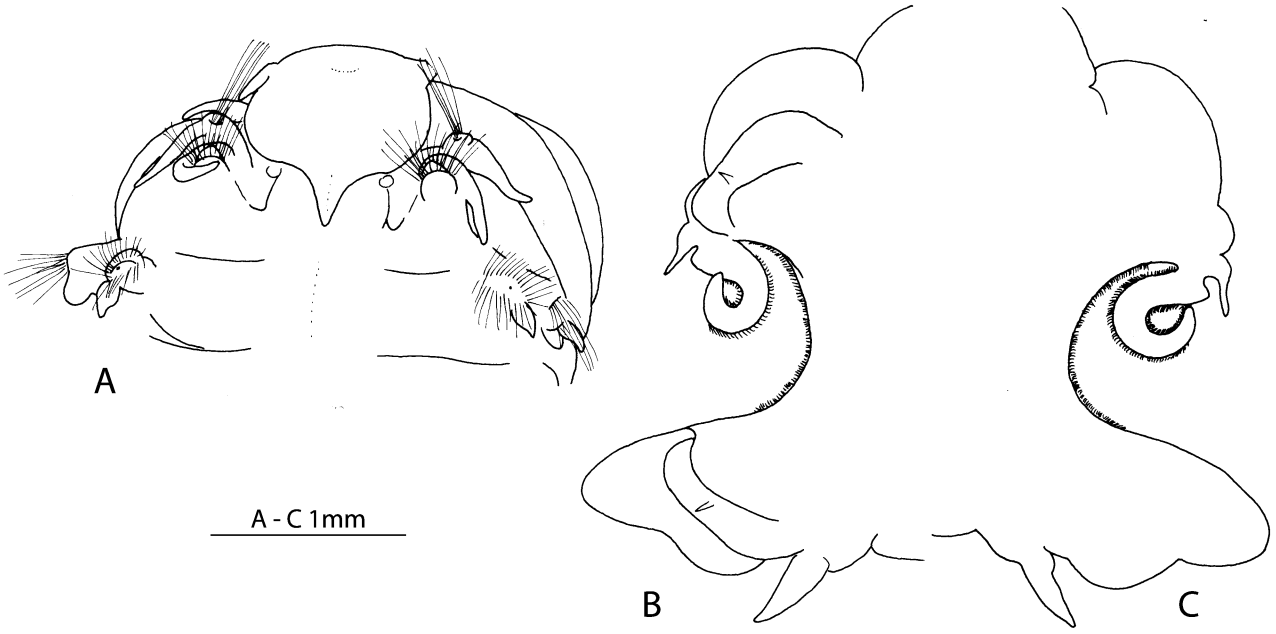

FIGURE 22. *Nephtys longosetosa*. A. Prostomium and first chaetigers, dorsal view. B. Right parapodium of chaetiger 39, anterior view. C. Same, posterior view.

***Nephtys paradoxa* Malm, 1874**
Figure 16, 23

Nephthys paradoxa Malm, 1874: 78, pl. I, fig. 2; Levinsen 1887; Heinen 1911: 36; Augener 1912: 204; Fauvel 1914: 199; Fauvel 1923: 375, fig. 146F–I; Augener 1928: 701; Ditlevsen 1937: 19; Bellan 1960: 13; Bellan 1961: 265; Foret-Montardo 1969: 818.

Nephthys pansa [*nomen oblitum*] Ehlers, 1874: 293; Ehlers 1875: 40, pl. III, figs. 1 and 2; Horst 1881: 7; McIntosh 1908:

40, figs. 39, 40.

Nephthys 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) (not Savigny *in* Lamarck, 1818).

? *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; Wolff 1968: 4, fig. 4; Kirkegaard 1969: 55, fig. 19; 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, fig. 16.6; Rainer 1991: 81, fig. 3E; Kirkegaard 1992: 341, fig. 167; Kirkegaard 1995: 39; Hartmann-Schröder 1996: 230; Dnestrovskaya and Jirkov 2001: 206, 1 fig; Laborda 2004: 408, fig. 150A–B.

Nephtys brachycephala Uschakov 1955: 216, fig. 69F–G (not Moore 1903).

Nephtys (Nephtys) paradoxa Day 1967: 347, fig. 15.2N–O.

Type locality. Koster, Bohuslän, 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, 2300 m, 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 Fig. 16 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 (Fig. 16D); midventral papillae, if present, similar in size and shape to subterminal ones; subdistal region with 22 rows of (3)4–6 conical subterminal papillae, extending over 1/3 length of pharynx (Fig. 23A); 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 (Fig. 16C). 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,

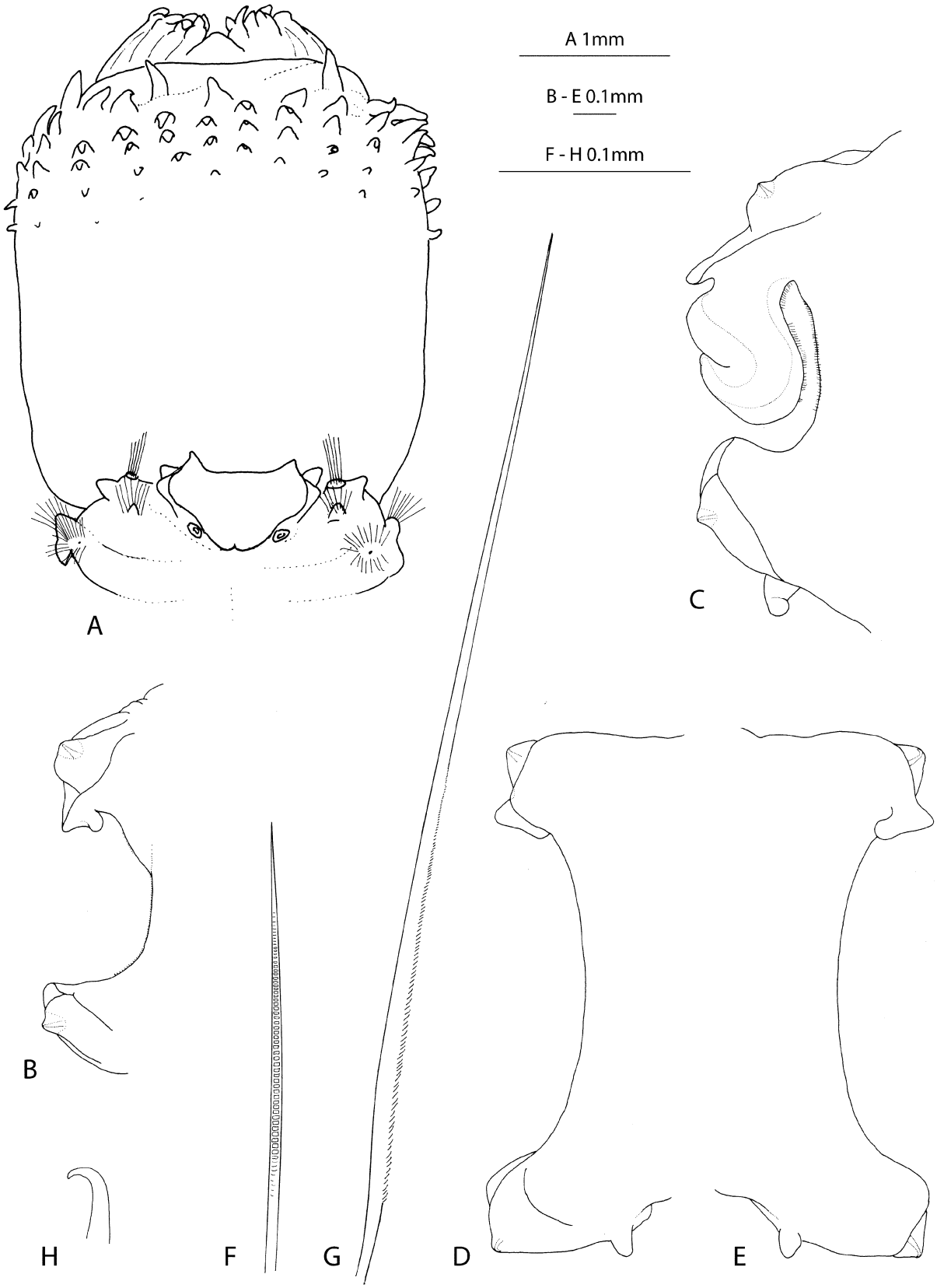

FIGURE 23. *Nephtys paradoxa*. A. Pharynx, prostomium and first chaetigers, dorsal view. B. Right parapodium of chaetiger 10, anterior view. C. Right parapodium of chaetiger 29, anterior view. D. Right parapodium of chaetiger 50, anterior view. E. Same, posterior view. F. Preacicular chaeta from chaetiger 10. G. Postacicular chaeta from chaetiger 10. H. Acicula of chaetiger 50.

small (Figs. 23B–E). Branchiae recurved, with membranous expansions externally and internally when fully developed; moderately ciliated; present from chaetigers 9–14, where it is still very rudimentary, well visible from chaetigers 13–15; become 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 (Fig. 23F), spinulated chaetae in postacicular position (Fig. 23G), and capillary chaetae in neuropodia of chaetiger 1. One acicula per ramus, posterior ones with curved tips (Fig. 23H).

Remarks. Fauchald (1963) provided an earlier history of the synonyms of *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 had 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 differed 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 specimens of *N. paradoxa* from Europe (including the type locality) and the eastern coast of USA. Apart from slightly better developed postchaetal lamellae in the specimens of *N. schmitti*, no consistent differences were found between these specimens and the European ones referred to *N. paradoxa*. 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 was observed in all specimens examined (including the ones from USA). Significant differences in the length of subterminal papillae in the two species were not found, although in the specimens of *N. schmitti* and the European ones of *N. paradoxa* the papillae seem to be slightly broader basally. Both *N. schmitti* and the European specimens of *N. paradoxa* have foliaceous branchiae between chaetigers 12–42. However, in the specimens of *N. paradoxa* from USA the branchiae start being foliaceous only in the middle chaetigers (from 25–26 until 40–64), and the postchaetal lamellae are of the same size or slightly larger than the acicular lobes (instead of poorly developed as in the specimens from Europe). Therefore, *N. schmitti* is here considered to belong to a *N. paradoxa* species complex. According to the many records from deep-waters from very different geographical regions *N. paradoxa* seems to have a worldwide distribution. However, many of these records including *N. paradoxa* from North America should be carefully revised with examination of more specimens. The taxonomical status of this species complex can possibly be resolved only by molecular analyses.

Distribution. Arctic Ocean; Atlantic Ocean (Greenland; from Iceland to South Africa and from Gulf of St. Lawrence to off Delaware); Mediterranean Sea (SE 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).

Discussion

Due to the close morphological similarities between species, nephtyids are very easily recognized 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.* (2010) 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, present in southern Europe, are suggested, as summarized in Table 6.

TABLE 6. Diagnostic characteristics for the genera of Nephtyidae from South Europe.

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

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 differ distinctly 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 juvenile stages of all species. The same situation occurs with the poor development or absence of branchiae. As mentioned above for *A. elamellatus* and *A. pulcher*, there are species for which the number of branchiate chaetigers 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 the 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 junior synonym of *Nephtys* by Ravara *et al*. (2010).

From the eighteen nephtyid species reported up to date from South European waters, only one has its distribution restricted to this region. *Inermonephtys foretmontardoi* **sp. nov.** occurs from southern England to the Mediterranean Sea. *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. agilis*, *A. pulcher*, *N. assimilis*, *N. hystricis*, *N. incisa* and *N. kersivalensis*, have their distributions extending all around Europe, and 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 have 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.

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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 Russian]. *In: Reports of the Japan Sea Hydrobiological Expedition of the Academy of Sciences of the USSR in 1934, pt. 1* pp. 81–230.

Arvanitidis, C. (2000) Polychaete fauna of the Aegean Sea: inventory and new information. *Bulletin of Marine Science*, 66(1), 73–96.

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. (1913) 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. (1939) Beitrag zur Polychaetenfauna der Ostsee. *Kieler Meeresforschungen*, 3, 133–147.

Baird, M.D. (1873) 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.

Banse, K. & Hobson, K.D. (1974) Benthic errantiate polychaetes of British Columbia and Washington. *Bulletin of the Fisheries Research Board of Canada*, 185, 1–111.

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

Bellan, G. (1960) Annélides Polychètes. *Résultats Scientifiques de la Campagne du N.R.P. "Faial" dans les eaux cotières du Portugal (1957)*, 2, 1–31.

Bellan, G. (1961) Résultats Scientifiques des Campagnes de la Calypso. XVI. Campagne 1955 en Méditerranée Nord-Orientale (suite). 4. Annélides Polychètes. Campagne de la Calypso (Septembre-Octobre l955). *Annales de l'Institut Océanographique*, 39(5), 161–178.

Bellan, G. (1964a) Résultats Scientifiques des Campagnes de la «Calypso». Méditerranée Nord-Orientale. 6. Annélides Polychètes. *Annales de l'Institut Océanographique*, 41(6), 271–288.

Bellan, G. (1964b) Contribution a l'étude systématique, bionomique et écologique des annélides polychètes de la Méditerranée. *Recueil des Travaux de la Station Marine d'Endoume*, 33(49), 1–371.

Bellan, G. (1969) Annélides polychètes recueillies dans l'archipel de Madère 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) Annelida. Polychaeta Errantia. *Canadian Pacific Fauna*, 9b(1), 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. Figure.* Napoli: Stamperia delle Societá Tipografica.

Chiaje, S., delle (1825) *Memoria sulla storia e notomia degli animali senza vertebre del Regno di Napoli*. Stamperia della Societá Tipografica, Napoli, 2, 185–444.

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), 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 im 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) Pêches 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 pélagiques provenant des campagnes de l'Hirondelle et de la Princesse-Alice (1885–1910). *Résultats des campagnes scientifiques accomplies sur son yacht par Albert I^er^ Prince Souverain de Monaco*, 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. *Publications du Musée Hoang ho 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) Annélides 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. Zur Polychaeten-Fauna der Barents-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 Biological 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 eigenen Sammlungen beschrieben.* Königsberg: J.H. Bon.
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.S., "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, einschließlich 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 während der Fahrten des "Willem Barents" in den Jahren 1878 und 1879. *Niederländisches Archiv für Zoologie, Supplementband* 1(1), 1–26.
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.
Intes, A. & Le Lœuff, P. (1975) Les annélides polychètes de Côte d'Ivoire. I. Polychètes errantes. *Compte rendu systématique. Cahiers ORSTOM, Série Océanographie*, 13(4), 267–321.
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. [In Russian].
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. *Magazine of Natural History and Journal of Zoology, Botany, Mineralogy, Geology and Meteorology*, 8, 341–343.
Johnston, G. (1865) *A catalogue of the British non-parasitical worms in the collection of the British Museum*. London: Taylor and Francis.
Jung, R.-H. & Hong, J.-S. (1997) Nephtyidae (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. (1992) Havbørsteorme I. Errantia. *Danmarks Fauna*, 83, 1–416.
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, Annelida. Die Expedition zurphysikalisch-chemischen und biologischen Untersuchung der Ostsee im Sommer 1871 auf S.M. Avisodampfer Pommerania. *Jahresbericht der Kommission zur wissenschaftlichen Untersuchungen 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 Martín (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. Publicación Técnica*, 7, 207–221.
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. 612.
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*, 21, 51–110.
Malmgren, A.J. (1867) *Annulata Polychaeta Spetsbergiae, Groelandiae, Islandiae et Scandinaviae Hactenus Cognita*. Helsingforsiae: Ex Officina Frenckelliana.
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.
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, Series 2, Zoology*, 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 during the years 1873–76*, 12, 1–554.
McIntosh, W.C. (1900a) Nemertea and Polychaeta: Amphinomidae to Sigalionidae. *A monograph of British Annelids*, Ray Society of London, 1(2), 1–442.
McIntosh, W.C. (1900b) Notes from the Gatty Marine Laboratory, St. Andrews. *Annals and Magazine of Natural History (Ser. 7)*, 5, 254–268.
McIntosh, W.C. (1908) Polychaeta. Nephthydidae to Syllidae. A Monograph of the British Annelids, Ray Society, London, *2(1)*, 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. *Jahresbericht der Kommission zur wissenschaftlichen Untersuchungen 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 Bergens Museum as a separate Volume) Vermes*, 161–164, 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. Fourth Series (Biology)*, 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. (1843a) *Annulatorum Danicorum Conspectus. Fasc. 1. Maricolæ, Hafniæ* (Copenhagen): Sumtibus Librariæ Wahlianæ.
Örsted, A.S. (1843b) Grönlands Annulata Dorsibranchiata. *Kongelige Danske Videnskabernes Selskabs Naturhistorisk-Mathematiske Afhandliger*, 10, 153–216.
Paik, E.-I. (1973) Some benthic polychaetous annelids from the Yellow Sea. *Bulletin of the Korean Fisheries Society*, 6, 123–131.
Parapar, J., San Martín, 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 Biological 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 Biological 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. *Helgoländer 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. (2010) Phylogenetic relationships within Nephtyidae (Polychaeta, Annelida). *Zoologica Scripta*, 39, 394–405.
Reish, D.J. (1965) Benthic polychaetous annelids from Bering, Chukchi, and Beaufort Seas. *Proceedings of the United States National Museum*, 117, 131–158.
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. *Expédition Française sur les Récifs Coralliens de la 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'Égypte, Histoire Naturelle*, 1, 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. (1853) 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, Section B*, 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), Zoology*, 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.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).
Uschakov, P.V. & Wu, B.-L. (1962) Polychaete worms of the Yellow Sea II. Fam. Chrysopetalidae, Glyceridae and Nephtyidae (Polychaeta, Errantia). *Studia Marina Sinica*, 1, 1–32.
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. *Annual Report of the United States Commission of Fish and Fisheries*, 1885, 707–755.
Wesenberg-Lund, E. (1949) Polychaetes of the Iranian Gulf. *Danish Scientific Investigations in Iran*, 4, 247–400.
Wesenberg-Lund, E. (1950a) Polychaeta. *The Danish Ingolf-Expedition*, 4, 1–80.
Wesenberg-Lund, E. (1950b) 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 of the 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.