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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

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ABSTRACT: Twelve species of *Nephtys* now known from northern Europe are described, including one new species, *N. pulchra* sp. n. A key is provided to the 14 species of Nephtyidae from the region. Geographic changes in the setiger in which interramal cirri first occur are recognized in *N. caeca* (Fabricius), *N. ciliata* (Müller), *N. hombergii* Savigny and *N. pente* Rainer.

INTRODUCTION

Nephtyid polychaetes occur in most marine environments. The first nephtyid described was *Nephtys ciliata* (O. F. Müller, 1776); by 1843, the three common shallow-water and intertidal species in northern Europe had been described (*Nephtys caeca* [Fabricius, 1780], *N. hombergii* Savigny, 1818 and *N. longosetosa* Örsted, 1843). Between 1865 und 1911, many nephtyid species were described from material collected from northern European waters, by Malmgren (1865), Ehlers (1868), Malm (1874), Hansen (1878), Théel (1879), Michaelsen (1896), McIntosh (1900, 1908) and Heinen (1911). The studies by Michaelsen (1896) and Heinen (1911), and those by McIntosh (1908) and Fauvel (1914), placed many of these in synonymy with previously described species, and provided the basis for the present systematic status of European nephtyids. Descriptions of northern European nephtyids given by Fauchald (1963), Woolf (1968) and Hartmann-Schröder (1971) are based on these studies.

The descriptions of some species of *Nephtys*, especially *N. ciliata*, have encompassed a wide range of apparently intraspecific variation in taxonomic features such as the segment on which interramal cirri first occur, and the form and size of pre- and postsetal lamellae. With the recent description of *N. pente* Rainer, 1984, intraspecific variation in *N. ciliata* is now similar to most other species of nephtyids.

Two other *Nephtys* species, *N. hombergii* and *N. incisa* Malmgren, 1865, have been considered to have a wide range of variation in some characters. Examination of museum collections of these species, and of extensive ecological collections from the North Sea and from Danish waters (Rainer, 1991), has shown that three closely related species have been variously identified as *N. hombergii* or *N. incisa*. Recent studies on *Nephtys* have

resulted in the redescription of *N. hystricis* and *N. incisa*, two species that have often been confused in northern European collections (Rainer, 1990), and of *N. kersivalensis* (originally erected as a variety of *N. hombergii*) and *N. assimilis* (Rainer, 1989). The present paper (1) describes the currently known species of *Nephtys* from northern European waters, including a new deepwater species closely related to *N. incisa*, (2) provides a key to the northern European nephtyids and (3) discusses geographically related variation in individual species of *Nephtys*. The number of nephtyid species now known from northern European waters is increased to 14, comprising two species of *Aglaophamus* and 12 species of *Nephtys*.

The nephtyid material examined came from collections in the Natural History Museum, London (BMNH), the Departamento de Zoología, Universidad de Alcalá de Henares (DZAH), the Museum für Naturkunde, Berlin (MNB), the Muséum National d'Histoire Naturelle, Paris (MNHN), the Naturhistoriska Riksmuseet, Stockholm (NRS), the Smithsonian Institution (USNM), the Zoologisches Museum, Hamburg (ZMH), the Zoologisches Museum, Kiel (ZMK), the Zoologisk Museum, Copenhagen (ZMC) and the Zoologisk Museum, Oslo (ZMO). Type material of *N. pulchra* sp. n. (Fig. 1) is deposited in the BMNH and the ZMH.

SYSTEMATICS

Nephtys Cuvier, 1817 (sensu Hartmann-Schröder, 1971)

Synonymy. *Aonis* de Savigny, 1818 [partim]
Nephthys de Savigny, 1818
Portelia de Quatrefages, 1865
Diplobranchus de Quatrefages, 1865

Diagnosis. Eyes absent, or present as two eyespots visible posterior to the prostomium. Pharynx with 14, 20 or 22 rows of subterminal papillae, usually with an unpaired dorsal median cirrus and sometimes with an unpaired ventral median cirrus. First setiger with or without a dorsal cirrus, with a ventral cirrus. Parapodia with conical, rounded or bilobed acicular lobes; presetal lamellae well developed or rudimentary; postsetal lamellae usually well developed. Interramal cirri flattened or cirriform, recurved. No superior neuropodial cirrus. No furcate setae. Aciculae with straight or recurved tips.

Nephtys assimilis Örstedt, 1843
(Fig. 2A)

Nephthys assimilis Örsted, 1843: 33; – Malmgren, 1865: 105–106; 1867: 19; – ?Malm, 1874: 78; – Rainer, 1989: 877–882. Non – Treadwell, 1914: 192; – Hartman, 1940: 239.
? *Nephtys cuvieri* de Quatrefages, 1865: 421–423.
Nephthys scolopendroides – Michaelsen, 1896: 57 [partim].
Nephthys hombergii var. *vasculosa*, McIntosh, 1908: 21–22 [partim].
Nephthys caeca – Heinen, 1911: 13 [partim].
Nephtys incisa var. *bilobata* Heinen, 1911: 25 [partim].
Nephthys hombergii – de Saint-Joseph, 1894: 3–16 [partim]; – Augener, 1912: 197 [partim].
Nephtys hombergii – Kirkegaard, 1969: 47–51 [partim]; – Hartmann-Schröder, 1971: 215–216 [partim]; – Hartmann Schröder, 1974: 206–207 [partim]; – Hartmann-Schröder, 1977: 88 [partim]; – Hartmann-Schröder, 1981: 31; – Hartmann-Schröder, 1982: 10–11.
Nephthys breogani Laborda & Viéitez, 1984: 211–218.
Nephtys breogani – Laborda, 1987: 131–145.

Material examined. >454 animals, including the following (see Rainer, 1989 for complete details). Neotype, ZMC collection, complete, ovigerous, 102 setigers, 112 mm long, coll. 05. 07. 1963 from Stns 225–227, 18 m, off Hornbæk Bay, Øresund, Denmark.

Kattegatt/Skagerrak. – ZMC: >80 animals from the Øresund, off Hornbæk Bay and off Hellebæk, all ident. as *N. hombergii.*

Baltic Sea. – ZMK: 20 animals from Kiel Bay (Po 0181), ident. as *N. caeca* by H. Michaelsen.

North Sea/English Channel. 379 animals, including – BMNH: ZK 1969.15, 1 animal, Drake Is, Plymouth Sound, intertidal, ident. by P. Gibbs as *N. cirrosa.*

U. K. (West), Ireland. 8 animals, including – BMNH: ZK 1921.5.1.810–813, 5 animals, syntypes of *Nephthys hombergii* var. *vasculosa*, Montrose Bay, Ireland, 1870.

Portugal/N. W. Spain. 2 animals, including – DZAH: Paratype of *Nephthys breogani* Laborda & Viéitez, 1984 – entire, 110 setigers, 58 mm long.

Mediterranean. – ZMH: V1053, 1 entire animal, Mediterranean, ident. by H. Michaelsen as *N. scolopendroides*, by H. Augener as *N. hombergii.*

North-West Africa. 3 animals, including – ZMH: P-17422, 2 animals, Meteor Stn 176, 20°43′ S, 17°10′ W, 16. 03. 1972, 40 m, ident. by Hartmann-Schröder as *N. hombergii.*

Description. Body up to 115 mm long, for 110 setigers. Body colour cream in alcohol, lightly iridescent in anterior setigers, no eyespots visible, midventral groove darker than rest of body; pharynx with orange distal aperture and subterminal papillae. Setae light olive in anterior body, becoming dark olive in posterior setigers. Aciculae visible laterally on parapodia as dark brown or (in anterior setigers) red points.

Prostomium pentagonal, length about 1.5 times width, usually with slightly rounded sides; anterior margin may be straight, slightly convex, or concave. Antennae inserted at anterolateral angles of prostomium, conical, broadly separated; palps, conical with bulbous base, inserted well behind and below antennae.

Pharynx subcylindrical, with 22 rows of subterminal papillae, 2–5 per row (mostly 3–4), and a long median dorsal papilla. Median dorsal papilla reaching as far as terminal papillae, 3 times longer than longest subterminal papillae. Surface of pharynx otherwise smooth.

Parapodia well-developed from setiger 10 (Fig. 2A). Acicular lobes rounded-conical; interramal portion with a broadly based, rounded protuberance adjacent to the aciculae, best developed in anterior setigers. Presetal lamellae equally developed in notopodia and neuropodia, bilobed with dorsal and ventral portions not extending much past acicular lobes. Postsetal lamellae mainly developed above level of aciculae, in noto- and neuropodia; in neuropodia, narrow in anterior and posterior setigers, broad in midbody setigers, projecting well beyond acicular lobes, with an internal vascular structure present in all postsetal lamellae after setiger 15. Dorsal and ventral cirri short, conical, similar in size along body. Interramal cirri first present on setiger 4, with stout proximal half, separated from dorsal cirri only by a notch; in posterior setigers, distal portion becomes shortened more than basal portion. Interramal region with a broken line of 10–15 ciliated pads between noto- and neuropodia, situated on the posterior surface of parapodia in anterior setigers and forming prominent ciliated papillae on the lateral surface of the interramal region of parapodia in midbody and posterior setigers.

Setae comprise barred preacicular setae, capillary and spinulose postacicular setae

and capillary or very finely spinulose setae in position nearest the interramal space. Preacicular setae short, not extending past postsetal lamellae; postacicular and medial setae longer, projecting beyond postsetal lamellae. Capillary and spinulose setae not clearly differentiated, particularly in posterior setigers. The number of setae in each parapodium increases along the body to quite near the tail. The posterior setigers of large animals may have 45–50 barred setae and 100–110 capillary/spinulose setae in each ramus.

Remarks on morphology. Over 500 animals were examined, between 12 mm long (1.2 mm body width) and 112 mm long (8.7 mm body width). The number of setigers increases with body length, from 80–90 setigers in animals 20–25 mm long to 100–110 setigers (max. 111) in animals over 50 mm long. The first interramal cirri were present on setiger 4 in all animals.

Remarks on taxonomy. The features that uniquely differentiate *Nephtys assimilis* from other European species of *Nephtys* are the well-developed ventral postsetal lamellae with broadly rounded tips and strong internal vascularisation, and the presence of numerous ciliated papillae in the interramal region of posterior setigers. The vascular structure of the neuropodial postsetal lamellae in *N. assimilis* is usually very clear in large animals. In having parapodia with bilobed presetal lamellae, a medial papilla on the acicular lobes, and well-developed postsetal lamellae, *N. assimilis* is close to *N. hombergii*, and the species has usually been identified as *N. hombergii*.

Differentiation of *N. assimilis* from the other northern European species of *Nephtys* with well-developed postsetal lamellae is easily made with large animals, because vascular postsetal lamellae are characteristic of *N. assimilis*. Differentiation of small animals of *N. assimilis* from morphologically similar species may be more difficult, since all except *N. longosetosa* have interramal cirri that first occur on setiger 4. *N. caeca* has well-developed postsetal lamellae in both noto- and neuropodia, and lacks a medial bulb or papilla on the acicular lobe. *N. kersivalensis* also lacks a medial bulb or papilla on the acicular lobes, but has narrower neuropodial postsetal lamellae and lacks the raised ciliated papillae in the interramal region of midbody and posterior setigers. *N. hombergii* has a generally much better developed medial bulb than *N. assimilis*, has narrower neuropodial postsetal lamellae, and has low, rounded ciliated pads in the interramal region of midbody setigers rather than prominent, raised pads. There are also differences in the pharyngeal papillae. *N. caeca* lacks a median dorsal papilla and has warty processes on the pharynx. The other three species have a median dorsal papilla and lack warty processes. The pharyngeal papillae of *N. assimilis* and *N. kersivalensis* are similar to each other. However, *N. hombergii* has a median dorsal papilla that is almost the same size as the other subterminal papillae, rather than much longer and more slender.

Distribution. Coasts of west Africa, Mediterranean and north-eastern Atlantic, including English Channel, North Sea, Skagerrak, Øresund, western Baltic.

Ecology. Intertidal to about 100 m, in sandy to muddy substrata but most abundant in muddy sands with good tidal currents (e.g. Dogger Bank, Øresund). *N. assimilis* frequently occurs with *N. hombergii*, and may also occur with *N. kersivalensis*. Mature animals have been found in March (Øresund), in April and May (North Sea), and in August (Mediterranean, Øresund).

Nephtys caeca (Fabricius, 1780) (Fig. 3C)

Nereis caeca Fabricius, 1780: 304.
Aonis caeca de Savigny, 1818: 45.
Nephthys margaritacea Johnston, 1835: 341.
Nephtys bononensis de Quatrefages, 1865: 425.
Nephtys oerstedii de Quatrefages, 1865: 427.
Portelia caeca de Quatrefages, 1865: 433.
Nephthys nudipes Ehlers, 1868: 635–637.
Nephthys coeca – Michaelsen, 1896: 25–27.
Nephthys caeca – Möbius, 1875: 168–169 [partim]; – McIntosh, 1908: 8–17; – Heinen, 1911: 10–12.
Nephthys caeca var. *ciliata* McIntosh, 1908: 13–14.
Nephthys hombergii – Heinen, 1911: 16–20 [partim].
Nephthys longisetosa – Heinen, 1911: 26–29 [partim].
Nephthys hombergi var. *ehlersi* – Augener, 1940: 137 [partim].
Nephtys caeca – Fauchald, 1963: 11–13; – Hartmann-Schröder, 1971: 220–221; – Hartmann-Schröder, 1974: 208.

Material examined. 60 specimens, including the following.

Greenland. – BMNH: ZK 1921.5.1.704, 2 animals; – ZMC: 2 animals, 6. 10. 1855; – ZMH: PE-542, 1 animal, 1866.

Iceland: – ZMC: 1 animal, Dana Stn 5596, Skardsfjord.

Norway. – BMNH: ZH 1865.9.23.9, 1 animal, Finmarken.

Kattegatt/Skagerrak. – ZMC: 1 animal, Fornæs.

Baltic Sea. – ZMH: V12271, 1 animal, Kieler Förde, ident. by Augener as *Nephthys incisa*; P-13127, 6 animals, Wesermündung, July 1969.

Denmark. – BMNH: ZH 1882.5.12.10, 1 animal.

North Sea/English Channel. – BMNH: ZK 1928.4.26.275, 1 animal, ident. by Fauvel as *N. caeca* var. *ciliata*, Cherbourg; ZK 1928.4.26.753–755, 3 animals, St Vaast-la-Houge; – ZMH: PE-539, 1 animal, Helgoland, 1980; PE-541, 1 animal, British coast, 1883; P-13184, 1 animal, Anton Dohrn Stn 29, 57°04′ N, 1°56′ W; P-13376, 1 animal, Anton Dohrn Stn 5, 56°04′ N, 6°21′ E; P-15314, 3 animals, Nordergründe, Helgoland 8.07.65; P-15315, 2 animals, Deutsche Bucht, 1964; – ZMK: Po 0191 – 1 animal, 04.HVII Stn 46, North Sea, ident. by Heinen as *N. hombergii*; – 1 animal, 05.V.N6, North Sea, ident. by Heinen as *N. hombergii*; Po 0607, 1 animal, 03.V.N11, North Sea, ident. by Heinen as *N. longosetosa*.

U.K. (West), Ireland. – BMNH: ZK 1921.5.1.712, 1 animal, St Magnus Bay; ZK 1921.5.1.716, 1 animal, ident. by McIntosh as *Nephthys caeca* var. *setosissima*, Montrose.

Description. Body up to 250 mm long, for up to 150 setigers. Body whitish, yellowish-grey, greenish or greenish-brown, with lightly iridiscent cuticle; gills red. Pharynx often dark, frequently dark brown. Eyespots dark brown when present.

Prostomium pentagonal with slightly convex anterior margin and straight or convex lateral margins, longer than wide. Antennae and palps conical to cirriform, the antennae about half as long as the width of the prostomium, the palps longer and stouter, inserted immediately behind the antennae.

Pharynx subcylindrical or slightly clavate, with 22 rows of subterminal papillae, 4–6 per row, often with a slender dorsal median papilla; large animals may have a similar median ventral papilla. Surface of pharynx with abundant wart-like papillae.

Parapodia well developed from setigers 20–25 (Fig. 3C). Acicular lobes simple, rounded, or more-or-less distinctly bilobed, particularly in notopodia. Presetal lamellae

small or rudimentary. Postsetal lamellae simple, large, in notopodia nearly twice as long as acicular lobes, obliquely oval in shape, in neuropodia much longer than the acicular lobes, with ventral and dorsal sides evenly rounded; in anterior neuropodia these come together to form an obtuse tip, but in middle and posterior setigers the postacicular lamellae are broadly rounded. Dorsal and ventral cirri slender cirriform or conical, ventral cirri the larger. Interramal cirri stout and relatively short, first occurring on setiger 4 or occasionally 5, reduced posteriorly but distinct to near the pygidium.

Setae comprise barred preacicular setae and spinose postacicular setae. Preacicular setae short and stiff, postacicular setae slender, with a finely tapered tip, shorter than the postacicular lobes.

Remarks on morphology. *Nephtys caeca* is reported to have interramal cirri first present on setigers 4–6 (e.g. Hartmann-Schröder, 1971). In the animals that I examined, the interramal cirri are first present on setiger 4 in animals from the latitude of the North Sea, and on either setiger 4 or 5 (usually 5) in animals from Arctic waters (e.g. Greenland). No animals were found with interramal cirri first present on setiger 6. The interramal cirri are usually small on setiger 4, sometimes very small, and are usually well-developed only by setiger 5.

A median dorsal subterminal papilla is often present, about as long as the longest distal subterminal papillae; it may be similar in shape and thickness to the subdistal papillae or somewhat more slender, and be directed towards the aperture of the pharynx.

Remarks on taxonomy. *Nephthys nudipes* Ehlers is here newly considered to be a junior synonym of *N. caeca*, not *N. ciliata* as considered by Hartmann (1959) and other authors. *Nephthys nudipes* was described for two small animals that had a pharynx with flattened papillae, parapodia fully formed by the fourth segment [= setiger], and bilobed acicular lobes. *Nephtys caeca* is the only known European species with these characteristics; the reduced development of the postsetal lamellae in *N. nudipes* is consistent with the animals described being early juveniles of *N. caeca*.

Distribution. North Atlantic from the Arctic to the English Channel, including the North Sea, Skagerrak, Kattegat and western and middle Baltic Sea. Reported from the Mediterranean as far as the Black Sea, and from the North Pacific.

Ecology. Reported from a wide variety of sediments, between the lower intertidal and nearly 1000 m depth.

Nephtys ciliata (O. F. Müller, 1776)
(Fig. 3A)

Nereis ciliata O. F. Müller, 1776: 17.
Nephtys borealis Örsted, 1843: 32.
Nephthys ciliata – Heinen, 1911: 21–23 [partim]. Non – McIntosh, 1908: 23–27; – Kirkegaard, 1969: 46.
Nephthys hombergii – Augener, 1912: 202 [partim].
Nephthys ciliata form. *longosetosa* non – Augener, 1940: 137.
Nephthys hombergi var. *ehlersi* – Augener, 1940: 137 [partim].
Nephtys ciliata – Fauchald, 1963: 5–8; – Hartmann-Schröder, 1971: 218–220.

Material examined. >100 specimens, including the following.

Arctic. – BMNH: ZH 1853.4.18.2, 1 animal, Arctic Sea; ZK 1923.3.22.66–69, 3 animals, Spitzbergen; ZK 1934.5.17.59, 2 animals, Klaas Billen Bay, West Spitzbergen.

Greenland. – ZMC: 3 animals, Lindenaufjord, 25. 07. 1935; 2 animals, Uvdle Thüle, 30. 07. 1939.

Iceland. – BMNH: ZK 1954.1.1.198, 1 animal, NW Iceland.

Norway. – BMNH: ZK 1900.5.1.279, 1 animal, Finmark; ZK 1921.5.1.758, 1 animal, off Bergen.

Kattegatt/Skagerrak. – ZMH: V12239, 2 animals, Drøback-Sund, Oslofjord, ident. by Augener as *Nephthys hombergii*; – ZMK: Po 0180 – Stn 1910.V K4 (1 animal); Po 0186 – Stns 1910.V K3 (1 animal).

Baltic Sea. – ZMH: V1043, 1 animal, Hornphaff, ident. by Michaelsen as *Nephthys ciliata*, by Augener as *Nephthys hombergii*; V10638, 7 animals, Kiel Bay, ident. by Augener as *Nephthys hombergi* var. *ehlersi*; – ZMK: Po 0180 – Stns 04.XI O4 (6 animals), 1910.IV O (7 animals); Po 0186 – Stns 07.V O3 (4 animals), 04.V O5 (8 animals), 07.VIII A67 (1 animal), 07.VIII A66 (2 animals), 03.VIII O4 (5 animals), 22.V O between Stollergrund and Bülk (7 animals).

Description. Body up to 300 mm long, for up to 140 setigers. Colour in alcohol white, yellowish or brownish, dorsum of anterior setigers often with a reddish-brown hue. Eyespots usually visible in small animals, occasionally in larger animals.

Prostomium pentagonal, somewhat longer than wide, with a straight or slightly convex anterior margin. Antennae and palps much shorter than half the width of the prostomium, the palps slightly longer than the antennae and arising close behind them.

Pharynx clavate, with a short, stout dorsal median papilla and 22 rows of subterminal papillae, 3–7 in each row; a ventral median papilla may be present in large animals. Surface of pharynx covered with flat, warty papillae.

Parapodia (Fig. 3A) fully developed from setiger 15. Acicular lobes in anterior and middle setigers distinctly bilobed, in posterior setigers rounded or weakly bilobed. Presetal lamellae small or rudimentary. Postsetal lamellae simple, rounded to oval, as long as or slightly longer than the acicular lobes. Dorsal and ventral cirri cirriform. Interramal cirri stout to cirriform, without a basal swelling, first present on setigers 7–10, then much reduced or rudimentary in the last 20–30 setigers.

Setae comprise barred setae in preacicular group and setae with spinulose margins in postacicular group; postacicular setae may include some capillary setae. Preacicular setae somewhat longer than the acicular lobes, postacicular setae usually slightly more than twice as long as the acicular lobes.

Remarks. Variation in the setiger on which interramal cirri are first present appears to be geographically related, with animals from the most northern latitudes having interramal cirri beginning furthest from the prostomium (Rainer, 1984). The number of setigers is rarely more than 110, and usually fewer than 90.

Distribution. Arctic and North Atlantic, including coasts of Greenland, Iceland, Norway, Skagerrak, Kattegat, and the western and middle Baltic Sea. Also reported from the North Pacific, the North Sea and the Mediterranean as far as the Black Sea; all records that I have checked for the North Sea refer to *N. pente*.

Ecology. Abundant in muddy sand substrata in shallow areas of the Baltic, and in deeper waters further north. Reported from the lower intertidal to 950 m depth.

Nephtys cirrosa Ehlers, 1868
(Fig. 3F)

Nephthys cirrosa Ehlers, 1868: 624–626; – McIntosh, 1908: 36–39; Hartmann-Schröder, 1974: 208–209.
Nephthys ehlersi Heinen, 1911: 34–36.
Nephthys longisetosa – Heinen, 1911: 26–29 [partim].

Material examined. 20 specimens, including the following.

North Sea/English Channel. – BMNH: ZK 1910.2.136-7, 1 animal, Plymouth; – ZMH: V9237, 1 animal, Helgoland; P-13310, 1 animal, Anton Dohrn Stn 465, North Sea, 54°17′ N, 7°43′ E, 13. 05. 1970; – ZMK: Po 0193, 4 animals, including 1 from Stn 03.VII 73, type of *Nephthys ehlersi* Heinen, 1911 (labelled "Beschriebenes Exemplar"); Po 0601, 4 animals, Stn 02.VIII N15, North Sea, ident. by Heinen as *Nephthys longisetosa*; 7 animals, Stn 03.VII 59, North Sea, ident. as *Nephthys longisetosa*.

U.K. (West), Ireland. – BMNH: ZK 1914.12.12.12, 4 animals, Blacksod Bay, Eire.

Description. Body up to 100 mm long, for up to 95 setigers. Body yellowish-white, gills red. Eyespots visible in small animals, sometimes also in larger animals.

Prostomium pentagonal, with slightly convex anterior and lateral margins, longer than wide. Length of antennae 0.5–0.7 times, palps about 1.0 times, the width of the anterior margin of the prostomium; palps arise well behind the antennae.

Pharynx with a slender median dorsal papilla and 22 rows of up to 9–10 subterminal papillae extending to the base of the everted pharynx; longest subterminal papillae about as long as median dorsal papilla; last 3–4 papillae are small, slender, widely separated cirri.

First parapodium directed anteriorly, with rudimentary dorsal cirrus and slender ventral cirrus as long as the prostomial palps; remaining parapodia directed laterally, well-developed (Fig. $3F_1$) from setiger 10. Acicular lobes in anterior and posterior parapodia simple, rounded, in middle parapodia unequally bilobed. Presetal lamellae bilobed or rudimentary, towards interramal region usually extending beyond the interramal region. Notopodial postsetal lamellae simple, rounded, a little longer than the acicular lobes; neuropodial postsetal lamellae oval to cordiform, about as long as notopodial lamellae. Dorsal cirri cirriform, as long as or longer than the interramal cirri in posterior setigers (Fig. $3F_2$); ventral cirri shorter, cirriform to conical. Interramal cirri from setiger 4, without basal papilla, much reduced in size towards the pygidium but distinct.

Setae comprise preacicular barred setae and two types of postacicular setae. Preacicular setae short, somewhat longer than the parapodial lamellae; most postacicular setae about three times as long as barred setae, curved, finely spinulose to smooth; remaining setae (12–15) shorter, sharply bent and with strongly spinulose margins.

Remarks on morphology. This description of *N. cirrosa* is based on material from the North Sea and English Channel. It differs from previous descriptions particularly in recognizing an increased number of subterminal papillae on the pharynx (9–10, rather than 5–8), in rows that extend to the base of the pharynx. The base of the pharynx is otherwise smooth. The presetal lamellae may in some animals be clearly bilobed, as described by Heinen (1911) for *N. ehlersi*, and as illustrated by Foret-Montardo (1969) for *N. cirrosa* from Marseilles.

Remarks on taxonomy. *Nephtys ehlersi* has had a complex history of synonymy, but has most recently been synonymized with *N. kersivalensis* (Augener,

1940; Hartman, 1959; Hartmann-Schröder, 1971) rather than with *N. cirrosa*. Augener (1912) suggested that both *N. ehlersi* and *N. hombergii* var. *kersivalensis* might be transitional forms between *N. cirrosa* and *N. hombergii*. Fauvel (1923) considered *N. ehlersi* to be a variety of *N. hombergii*, and Fage & Legendre (1927) suggested that *N. hombergii* forma *ehlersii* was the epitokous form of *N. hombergii* var. *kersivalensis*. Hartman (1950) then accepted *N. ehlersi* as a synonym of *N. hombergii kersivalensis*. The present synonymy with *N. cirrosa* is based on examination of the type of *N. ehlersi*. This conforms to the accepted descriptions of *N. cirrosa* except for having bilobed presetal lamellae and lacking elongated dorsal cirri in posterior setigers. However, a bilobed presetal lamella is present in at least some of the North Sea *N. cirrosa* examined in this study, and apparently also in animals from around Marseilles (Foret-Montardo, 1969). The type of *N. ehlersi* has only 75 setigers, the last few of which are narrower and have reduced parapodial lamellae, suggesting that these segments were in the process of regenerating. The elongated dorsal cirri usually characteristic of *N. cirrosa* would not therefore be expected to be present in this animal.

Distribution. North-eastern Atlantic, including the English Channel and the North Sea. Reported also from the Mediterranean and the Black Sea.

Ecology. Occurs in clean to muddy coarse and fine sands; commonest in clean, fine sand in the lower intertidal and in shallow waters to 45 m depth.

Nephtys hombergii de Savigny, 1818
(Fig. 2B)

Nephthys hombergii de Savigny, 1818: 314; – de Saint-Joseph, 1894: 3–16 [partim]; – McIntosh, 1908: 17–23 [partim]; – Heinen, 1911: 16–20 [partim]; – Augener, 1912: 197–199, 202 [partim]; – Ditlevsen, 1929: 20–21.
Nereis scolopendroides delle Chiaje, 1822: 401, 424, in Audouin & Milne Edwards, 1833: 260.
Nephthys neapolitana Grube, 1840: 71.
Nephthys macandrewi Baird, 1873: 94.
Nephtys scolopendroides Michaelsen, 1896: 57 [partim].
Nephthys hombergii var. *kersivalensis* McIntosh, 1908: 20–21 [partim].
Nephthys hombergii var. *vasculosa* – McIntosh, 1908: 21–22 [partim].
Nephtys hombergii – Fauchald, 1963: 3–5 [partim]; – Hartmann-Schröder, 1971: 215–216 [partim]; – Hartmann-Schröder, 1974: 88 [partim]. Non – Hartmann-Schröder, 1981: 31; Hartmann-Schröder, 1982: 10–11.
non – *Nephtys hombergii* var. *kersivalensis* Hartmann-Schröder, 1971: 217.

Material examined. >440 specimens, including the following.

Kattegatt/Skagerrak. – ZMC: >10 animals, Frederickshavn, Kattegat, 05. 07. 1967; – ZMH: V13209, 3 animals, Anton Dohrn Stn 741, Skagerrak.

Baltic Sea. – ZMH: V1051, 2 animals, Kiel Bay, ident. by Michaelsen as *N. scolopendroides*.

North Sea/English Channel. – BMNH: ZK 1889.9.16.12, 1 animal, Herm, Channel Islands; ZK 1928.4.26.815, 1 animal, Îles St Marcouf, Cherbourg, ident. by Fauvel as *Nephthys ehlersi*; ZK 1969.11, ~30 animals, Stonehouse Ck, Devon; – MNHM: A1(R.)-1868-N°105a, b, 1 complete and 1 anterior fragment, Le Hâvre, ident. as *Nephtys cuvieri* by de Quatrefages; – ZMC: >170 animals, Dana Stns, North Sea, 1963–64; – ZMH: V3909, 1 animal, 55°52′ N, 6°21′ E, North Sea, ident. by Michaelsen as *N. scolopen-*

droides; V3943, 1 animal, 53°40′ N, 5°27′ E, North Sea, ident. by Michaelsen as *N. longisetosa*; V11216, 1 animal, Westerbalg, Zuiderzee, Holland.

U. K. (West), Ireland. – BMNH: ZK 1921.5.1.815, 1 animal of 2 syntypes of *Nephthys hombergii* var. *vasculosa* McIntosh, "Porcupine", Bono Bay, 1870, 250 fm; ZK 1921.5.1.802–804, 6 animals, off Valentia, 1869, 160 fm, included among syntypes of *N. hombergii* var. *kersivalensis*; ZK 1921.5.1.4704, 1 animal, Connemara, Ireland, included among syntypes of *N. hombergii* var. *kersivalensis*.

North Atlantic. – ZMC: 1 animal, 63°05′ N, 20°07′ W, coll. 1903, 557 m, ident. as *Nephthys incisa* var. *bilobata*; 1 animal, Dana Stn 3070, 63°37′ N, 17°39′ W, ident. by Wesenberg-Lund as *Nephthys coeca* var. *ciliata*.

Portugal/N. W. Spain. – BMNH: ZH 1863.9.19.12, 1 animal, Coruña, Spain, type of *Nephthys macandrewi* Baird, 1873; – ZMH: P13715, 2 animals, Meteor Stn 62, off Portugal, 38°22′ N, 8°56′ W, 08. 02. 1967, 85–90 m.

Mediterranean. – MNB: Q.4228, 1 complete and 2 anterior fragments, Naples, syntypes of *Nephthys neapolitana* Grube, 1840, p. 71; – ZMH: PE-573, 1 animal, Naples, ident. by Ehlers as *Nephthys scolopendroides*; V1053, 1 animal, Mediterranean, ident. by Michaelsen as *N. scolopendroides*; V12998, 1 animal, Venice, ident. by Laubier as *Nephthys incisa*.

Description. Body up to 200 mm long, with up to 135 setigers. Colour pink to flesh-coloured, with a pearly sheen; gills red. A dorsal patch of dark pigment frequent in the centre of the prostomium; tips of the pharyngeal papillae, and dorsal parts of notopodial postsetal lamellae, often dark pigmented in larger specimens. A pair of eyespots usually visible only in small specimens.

Prostomium pentagonal, nearly twice as long as wide, with straight or weakly convex anterior margin. Antennae and palps cirriform to conical, the palps somewhat longer and arising somewhat behind the antennae.

Pharynx cylindrical, with a median dorsal and 22 rows of well-developed triangular subterminal papillae, 3–6 papillae in each row. Median dorsal papillae similar to the subterminal papillae but about twice their greatest length. Proximal surface of the pharynx smooth.

Parapodia (Fig. 2B) fully developed from setigers 25–30. Acicular lobes simple, rounded in anterior setigers, conical in posterior setigers, with a distinctive papilliform outgrowth on the interramal side of the aciculae in both noto- and neuropodia, first apparent on the setiger on which the interramal cirri begin and well developed on the succeeding 35–40 setigers; presetal lamellae bilobed, with a deep V separating dorsal and ventral portions, which are often longer than the acicular lobes; notopodial postsetal lamellae simple, rounded, somewhat longer than the acicular lobes, neuropodial postsetal lamellae simple, oval, broadly rounded and up to twice the length of acicular lobes, often directed dorsolaterally in posterior setigers. Dorsal cirri small, cirriform, ventral cirri larger and stouter. Interramal cirri cirriform, with distinct basal papilla, present from setigers 4–6 to the end of the body; if present from setiger 4, usually markedly smaller on first one or two setigers than on subsequent setigers.

Setae include preacicular barred setae and postacicular capillary and finely spinulose setae, the latter slender with a long tapering smooth tip. Preacicular setae usually longer than the acicular lobes, postacicular setae always longer.

Remarks on morphology. The number of setigers has been reported to be

90–200 (Fauvel, 1923). Except in small individuals, the number is usually 120–130; animals with fewer or more setigers than this should be identified as *N. hombergii* only with caution. Interramal cirri are usually present by setiger 4 in animals from the intertidal down to about 20 m depth, and in *N. hombergii* collected from deeper water they are usually first present on setiger 5, or setiger 6 in large animals. In northern European animals, the basal papilla of the interramal cirri is distinct, usually similar in size to the closely related *N. assimilis* and *N. kersivalensis*.

Remarks on taxonomy. *Nephtys cuvieri* de Quatrefages, 1865 is accepted by most authors (e.g. Fauvel, 1923; Hartman, 1950, 1959; Hartmann-Schröder, 1971) as a junior synonym of *N. hombergii*. The two animals identified by de Quatrefages as *N. cuvieri*, held by the MNHN, were both *N. hombergii*. Neither of these is the type on which de Quatrefages based his description, a 7-cm long animal with about 80 setigers. An animal of this size is unlikely to be *N. hombergii*, but could well be *N. assimilis*.

Distribution. Mediterranean and eastern Atlantic north to the Barents Sea, including the North Sea, Skagerrak, Kattegat, and outer Baltic. Reported from as far south as South Africa.

Ecology. Tolerant of a wide range of salinity and temperature; occurs from the intertidal to continental shelf depths, particularly in muddy or clayey sand.

Nephtys hystricis McIntosh, 1900
(Fig. 2C)

Nephthys hystricis McIntosh, 1900: 259–260; – McIntosh, 1908: 27–29. Non – Fauvel, 1914: 200–201; – Fauvel, 1923: 373–375.
Nephtys hombergii var. *kersivalensis* McIntosh, 1908: 20–21 [partim].
Nephtys hystricis – Rainer, 1990: 362–366. Non – Woolf, 1968: 6; – Day, 1967: 345.
Nephthys malmgreni – Heinen, 1911: 29–31 [partim].
Nephthys incisa – Heinen, 1911: 23–25 [partim]; – Fauvel, 1914: 198–199; – Fauvel, 1923: 369–370.
Nephthys incisa var. *bilobata* Heinen, 1911: 25 [partim].
Nephtys incisa – Fauchald, 1963: 15–16 [partim]; – Kirkegaard, 1969: 51–52 [partim]; – Hartmann-Schröder, 1971: 217–218; – Hartmann-Schröder, 1974: 207 [partim].

Material examined. More than 62 animals, including the following (see Rainer, 1990 for complete details). Lectotype BMNH: ZK 1921.5.1.791: anterior fragment of 44 setigers, Norway.

Norway. 12 animals, including – paralectotypes: BMNH: ZK 1921.765–766, anterior fragments of 33, 34, 34 setigers, Bergen, Norway.

Kattegatt/Skagerrak. 5 animals, including – ZMK: 1 entire (orig. ident. as *N. incisa*), 72 setigers, Stn 1910.V N10, dredge.

North Sea/English Channel. >25 animals, including – ZMH: P-13182, 2 entire and 8 anterior fragments (ident. as *N. incisa*), Anton Dohrn Stn 448, 58°16′ N, 5°50′ E, 346 m.

U.K. (West), Ireland. 19 animals, including– BMNH: ZK 1921.5.1.784–789, 8 anterior fragments, Porcupine Stn 1, 51°51′ N, 11°50′ W, 1869, 370 fm.

Description. Body fragile, fragmenting easily, up to 40 mm long, for up to 70 (occasionally 75) setigers. Body colour cream in alcohol, with a light brown pharynx, no eyespots visible, midventral groove yellow in anterior setigers; surface of anterior setigers slightly iridescent. Setae light brown, aciculae visible laterally on parapodia as black points.

Prostomium longer than wide, with concave anterior margin and gently convex lateral margins. Antennae and palps arise near anterolateral angles of prostomium, antennae conical, inserted on anterior margin, palps conical with bulbous base, inserted ventrally behind and below antennae near anterolateral margin of prostomium.

Pharynx with long median dorsal papilla and 22 rows of short subterminal papillae on the distal ⅓ of the basal region. Median dorsal papilla slender, long, extending past aperture of pharynx. Subterminal papillae 4–6 per row, conical, small. Surface of pharynx otherwise smooth.

Parapodia (Fig. 3C) fully developed by setiger 10, best developed in anterior setigers. Acicular lobes conical. Presetal lamellae bilobed, extending slightly past acicular lobes in notopodia and neuropodia after setiger 5, best developed above and below the acicular lobes, with medial portion low or absent. Postsetal lamellae of anterior notopodia form an auricular lamella above and lateral to acicular lobes, decreasing in size to extend only as far as acicular lobes by posterior setigers; postsetal lamellae of neuropodia similar in size but more rounded than notopodial postsetal lamellae, more-or-less equally developed above and below the level of the acicular lobes. Dorsal and ventral cirri conical to cirriform, varying little in size along the body. Interramal cirri first present on setigers 6 or 7, as a strongly recurved cirriform lobe occupying the interramal space in anterior setigers then decreasing in size and curvature in posterior setigers.

Setae comprise preacicular barred setae, postacicular spinulose setae and capillary setae in position nearest and furthest from the interramal region. Preacicular setae relatively short, not extending past postsetal lamellae of anterior and middle setigers; postacicular and medial setae project well beyond postsetal lamellae. Setal numbers are greatest around setiger 20, decreasing slowly thereafter.

Remarks on morphology. Entire animals measured were between 25 and 35 mm long, with 62–72 setigers; larger animals are unlikely to have significantly more setigers. A delicate pygidial cirrus may be present, about as long as the last five setigers.

The first interramal cirri were found on setiger 6 or setiger 7 on all animals examined, sometimes on setiger 6 on one side and setiger 7 on the other. The interramal cirri decrease in size past setiger 40, to become the same length as the dorsal cirri over the next 5–15 setigers; interramal cirri are absent on the last 15–18 setigers.

Distribution. North-eastern Atlantic, including the North Sea and Skagerrak, from Norway to Cape Sagres, Portugal, in depths of 100–600 m.

Ecology. Found in mud or sandy mud.

Nephtys incisa Malmgren 1865
(Fig. 3G)

Nephthys incisa Malmgren, 1865: 105 [partim]; – Michaelsen, 1896: 58–59 [partim]; – McIntosh, 1908: 38–40; – Heinen, 1911: 23–25 [partim]; – Augener, 1912: 203 [partim]. Non – Fauvel, 1914: 198–199; – Fauvel, 1923: 369–371.

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

Nephthys hystricis – McIntosh, 1908: 27–29 [partim]; – Fauvel, 1914: 200–201; – Fauvel, 1923: 373–375.

Nephtys hystricis – Woolf, 1968: 6.

Nephtys incisa – Fauchald, 1963: 15–16 [partim]; – Kirkegaard, 1969: 51–52 [partim]; – Hartmann-

Schröder, 1982: 11; Rainer, 1990: 366–370. Non – Woolf, 1968: 4; – Hartmann-Schröder, 1971: 217–218; Hartmann-Schröder, 1974: 207.
Aglaophamus malmgreni – Hartmann-Schröder, 1974: 205–206 [partim].

Material examined. 103 specimens, including the following (see Rainer, 1990 for complete details). Lectotype BMNH: ZH 1865.923.8: entire, 61 setigers, 32 mm long, mature female, Väderöarne (Skagerrak coast, Bohuslän, Sweden), 107 m, argillaceous bottom, coll. S. Lovén.

Iceland. – ZMC: 1 anterior fragment, Ykerasaggssüak, Iceland, Bertelsen Stn 12, 235 m, ident. by Wesenberg-Lund as *Nephthys coeca* var. *ciliata*.

Norway. 2 animals, including – ZMO: C 1693, 1 anterior fragment, G.M. Dannevig Stn 37, Torungen-Homborsund, 19. 07. 1950.

Kattegat/Skagerrak. 28 animals, including paralectotype – NRS 258, Typ samml. 2459, entire, 51 setigers, 16 mm long, Bohuslän, coll. S. Lovén.

North Sea/English Channel. 9 animals, including – ZMH: V3937, 5 anterior fragments, Anton Dohrn Stn 190, North Sea, 54°14′ N, 5°40′ E, 31. 08. 1890.

U.K. (West), Ireland. 3 animals, including – BMNH: ZK 1894.9.27.1, entire animal, upper Loch Foyle, N. Ireland, ident. as *N. ciliata*.

Portugal/N.W. Spain. 10 animals, including – BMNH: ZK 1921.5.1.769/770, 4 anterior fragments, "Porcupine", off Cape Sagres, 1870, ident. by McIntosh as *Nephthys hystricis*.

North-West Africa. – ZMH: P-17760, 1 anterior fragment, Anton Dohrn Stn 122, off NW Africa, 33°17′ N, 8°34′ W, 65 m.

Description. Body delicate, easily fragmented, up to 60 mm long for up to 70 (occasionally 75) setigers. Body colour cream in alcohol, no eyespots visible, midventral region iridescent. Setae golden, aciculae visible laterally on parapodia as dark brown points.

Prostomium about 1.5 times wider than long, broadest in anterior half; anterior margin slightly concave, sides broadly convex. Antennae and palps inserted near anterolateral angles of prostomium, antennae conical, inserted on anterior margin of prostomium, palps long, conical with bulbous base, inserted below and behind antennae.

Pharynx short, cylindrical, with median dorsal papilla and 20 rows of subterminal papillae. Dorsal median papilla slender, reaching to terminal papillae, 6–8 times as long as longest subterminal papillae. Subterminal papillae small, conical, 1–5 per row, decreasing in size towards base of pharynx. Surface of pharynx otherwise smooth.

Parapodia (Fig. 3G) fully developed from setigers 10–15. Acicular lobes conical. Presetal lamellae rounded, well developed over most setigers, their length approximately that of the acicular lobes, which they do not obscure. Postsetal lamellae rounded, best developed away from the interramal region, better developed than presetal lamellae over the anterior half of the body, then posteriorly decreasing in size to become obscured by the presetal lamellae and acicular lobes. Dorsal cirri best developed over setigers 15–30, flattened-conical with broad base; ventral cirri tapered, varying little in size along body. Interramal cirri cirriform, first present on setiger 9–10 (occasionally 8–11), fully developed by setiger 15, then gradually decreasing in size to be absent on last 25 setigers.

Setae comprise preacicular barred setae, spinulose postacicular setae and capillary setae in position adjacent to and away from the interramal space. Preacicular setae generally short, not extending much beyond presetal lamellae; postacicular and medial

setae longer, projecting well beyond postsetal lamellae. Numbers of all setal types decrease gradually from the middle of the body towards the pygidium.

Pygidial cirrus slender, about the length of the last 5–6 setigers or up to one quarter as long as the body.

Remarks on morphology. Significant variation occurs in the degree of development of the interramal cirri and in the pharyngeal papillae.

The number of posterior setigers lacking interramal cirri is relatively constant, at about 25 setigers. Small animals, with relatively few setigers, may have interramal cirri present only to setigers 20–22, while large animals may have interramal cirri present up to setigers 48–50. Interramal cirri were first present mainly from setigers 9 (80 %) or 10 (15 %), occasionally on setigers 8 or 11.

The number of rows of subterminal pharyngeal papillae varies. Fourteen rows have 3–4 papillae in each row. The remaining eight rows consist of only 1 or 2 papillae. In some animals, some of these papillae may be lacking, so that only 18 rows of papillae are present; larger animals are more likely to have 22 rows.

Remarks on taxonomy. Two other species of *Nephtys* in northern Europe have short postsetal lamellae and conical acicular lobes: *N. pulchra* sp. n. and *N. hystricis*. They are readily differentiated from *N. incisa* on the basis of the setigers on which the first interramal cirri are found: *N. pulchra*, setigers 5 or 6, *N. hystricis*, setigers 6 or usually 7, *N. incisa*, setigers 8–11, usually 9–10. Small animals could be confused with *N. paradoxa*, in which the interramal cirri may not have developed a lamellate appearance. *N. incisa* has interramal cirri over fewer setigers, only 1–4 papillae rather than 5–6 papillae in each row of subterminal papillae, and postacicular setae with spinulose rather than spinose margins.

Distribution. Western Atlantic from off north-west Africa to Iceland, including the North Sea, Skagerrak and Kattegat. Also recorded from the north-western and western Atlantic, and from the Mediterranean as far as the Bosphorus; possible confusion of *N. incisa* with other species suggests that these records require confirmation.

Ecology. Occurs in soft substrata ranging from gravel and mud to soft silts, from the shallow subtidal to 930 m, reported from depths to 1700 m; most commonly found in silty sand and or mud substrata.

Nephtys kersivalensis McIntosh, 1908
(Fig. 2D)

Nephthys incisa – Michaelsen, 1896: 59 [partim]; – Augener, 1912: 203; – Fauchald, 1963: 15–16 [partim]; – George, 1979: 198.
Nephthys hombergii var. *kersivalensis* McIntosh, 1908: 20–21 [partim].
Nephthys hombergii forma *ehlersii* Fage & Legendre, 1927: 124–126.
Nephtys hombergi kersivalensis Fauchald, 1963: 5.
Nephtys hombergii var. *kersivalensis* Hartmann-Schröder, 1971: 217.
Nephtys kersivalensis – Rainer, 1989: 882–886.

Material examined. 45 animals, including the following (see Rainer, 1989 for complete details). Lectotype: BMNH: ZK 1921.5.1.807, Connemara, Ireland; 20 paralectotypes of *Nephtys kersivalensis* McIntosh (see below).

Kattegat/Skagerrak. 21 animals, including – ZMH: P-19235, entire animal, Stn 343, Hornbæk Bay, 06. 01. 1964, 18 m.

North Sea/English Channel. – ZMH: V3967, 2 anterior fragments, oyster bank south-east of Helgoland, coll. 16. 08. 1892, ident. by H. Michaelsen, H. Augener, as *Nephthys incisa*.

U. K. (West), Ireland. – Paralectotypes: BMNH: ZK 1921.5.1.796–806, 19 animals, off Valentia, 1869, 160 fm; ZK 1921.5.1.808, 1 animal, Connemara, Ireland.

Description. Body up to 40 mm long, for up to 80 (maximum 85) setigers. Body colour cream in alcohol; dorsal and ventral surfaces of anterior segments iridescent; paired eyespots frequently visible through dorsum of setiger 2. Setae pale brown, aciculae visible laterally on parapodia as dark points.

Prostomium about 1.5 times longer than wide, with gently convex anterior margin and broadly rounded lateral margins. Antennae inserted at anterolateral angles of prostomium, conical; palps shorter, conical with bulbous base, inserted below and behind antennae about half way along anterolateral margin of prostomium.

Pharynx cylindrical, with a long median dorsal papilla and 22 rows of subterminal papillae extending over one quarter length of subdistal region of pharynx, 3–6 per row. Median dorsal papilla strong, reaching to gap between terminal papillae, about five times as long as largest subterminal papillae. Median field of pharynx otherwise smooth.

Parapodia (Fig. 2D) fully developed from setiger 10. Acicular lobes rounded to conical in anterior setigers, conical from middle setigers to the tail; surface of lobes with minutely rugose region on interramal side of acicular tips. Presetal lamellae well-developed, bilobed, medially not extending past acicular lobe. Postsetal lamellae extending well beyond acicular lobes, elongate in notopodia, rounded in neuropodia, relatively elongate with a sharply rounded tip in setigers 10–40. Dorsal and ventral cirri short, conical, varying little in size along body. Interramal cirri cirriform, present from setiger 4 to tail, largest in anterior setigers then decreasing slowly in size to the tail. Interramal cirri and interramal region lightly ciliated.

Setae include barred preacicular setae, capillary and spinulose postacicular setae and capillary setae in the interramal (medial) position. Preacicular and medial setae not extending much past postsetal lamellae in anterior setigers; postacicular setae longer, projecting well beyond postsetal lamellae. Number of barred setae greatest at about setiger 10, other setae not decreasing much until posterior setigers.

Pygidial cirrus may be as long as the length of the last six setigers.

Remarks on morphology. Animals 2.1–2.6 mm wide comprised 70–81 setigers, with lengths of up to 39 mm. The animal with the greatest body width measured (4.3 mm) was 39 mm long, with only 69 setigers. If *N. kersivalensis* follows the usual growth pattern for *Nephtys* species, then larger animals are unlikely to have more than 85 setigers.

The morphology of animals varied with size. In small animals, the postsetal lamellae were more rounded, approaching the shape of postsetal lamellae in small animals of *N. assimilis*, while the median dorsal papilla of the pharynx was less well developed. A pair of eyespots was visible dorsally on the hindbrain in setiger 2 on all the Hornbæk Bay animals, which were up to 4.2 mm wide. Eyespots were visible only in the smallest animal (2.0 mm wide) from the other locations.

Remarks on taxonomy. Differentiation of *N. kersivalensis* from other northern European species with closely related characteristics (*N. assimilis, N. hombergii, N. hystricis, N. incisa*) may be made from a number of characteristics. The minutely rugose

area on the acicular lobes is visible at moderate magnifications (× 400); in contrast, in the same area *N. assimilis* has a low, rounded expansion, and *N. hombergii* has a more distinct rounded bulb or even a cirriform extension of the acicular lobes. In all *N. kersivalensis* examined, the interramal cirri were first present on setiger 4. This differentiates *N. kersivalensis* from *N. hystricis*, which has conical acicular lobes and apparently bilobed presetal lamellae, but interramal cirri from setigers 6 or 7, and from *N. incisa*, which has conical acicular lobes but entire, rounded presetal lamellae and interramal cirri from setigers 9–11.

Distribution. North-eastern Atlantic: Outer Hebrides, Ireland, North Sea, Kattegat; western France(?). This distribution is likely to be extended as the species is more widely recognized.

Ecology. *Nephtys kersivalensis* may occur with *N. assimilis* and *N. hombergii* in silty sand or clean sand; it also occurs in muddy sand and gravel. Known from the shallow subtidal to 295 m depth. Apparently mature animals known from August to November.

Nephtys longosetosa Örsted, 1842
(Fig. 3d)

Nephthys longosetosa Örsted, 1842: 123; – Örsted, 1843: 195.
Nephthys emarginata Malm, 1874: 77.
Nephthys johnstoni Ehlers, 1874: 293; – McIntosh, 1908: 34–36.
Nephthys longisetosa – Michaelsen, 1896: 58; – Heinen, 1911: 26–29; – Augener, 1912: 193. Non – McIntosh, 1908: 29–32.
Nephthys ciliata form. *longosetosa* – Augener, 1940: 137.
Nephtys longosetosa – Fauchald, 1963: 8–11; – Hartmann-Schröder, 1971: 221–223.

Material examined. 45 specimens, including the following.

Greenland. – ZMC: 4 animals, Ingolf Stn 31, 66°35′ N, 55°54′ W, 11. 07. 1895.

Iceland. – ZMC: 1 animal, Borqarfjord, Iceland, 30. 05. 1899.

Norway. – BMNH: ZK 1900.5.1.280/1, 3 animals, Hardangerfjord, Norway, ident. as *Nephthys emarginata*.

Kattegat/Skagerrak. – MNB: Q.5549, 1 animal, posterior fragment only, Kattegat, syntype of *Nephthys emarginata* Malm, 1874; – ZMC: 6 animals, Kattegat, ident. as *Nephtys emarginata*.

Baltic Sea. – ZMH: V10698, 1 animal, Kiel Bay, ident. by Augener as *Nephthys ciliata* form. *longosetosa*.

North Sea/English Channel. – BMNH: ZH 1865.3.9.17, 1 animal, North Sea, ident. as *Nephthys caeca*; – ZMH: V3931, 1 animal, North Sea, ident. by Michaelsen and Augener as *Nephthys longisetosa*; – ZMK: Po 0608, 1 animal, Stn 04.VII 50, North Sea, ident. by Heinen as *Nephthys hombergii*.

U. K. (West), Ireland. – BMNH: ZK 1921.5.1.837, 1 animal, Porcupine Bank, Ireland, ident. as *Nephthys johnstoni*.

Description. Body up to 170 mm long, for up to 120 setigers. Colour cream to colourless in alcohol. A pair of eyespots usually visible dorsally.

Prostomium pentagonal, longer than broad, with straight or convex anterior margin. Antennae and palps cirriform to conical, the antennae about half as long as the width of the prostomium, the palps somewhat longer and arising approximately half way along the lateral margins of the prostomium.

Pharynx with a long median dorsal papilla and 22 rows of 5–7 papillae; a median ventral papilla may be present in large animals. Surface of pharynx smooth.

Parapodia (Fig. 3D) well developed from setiger 25. Acicular lobes simple, broadly rounded in notopodia, more-or-less clearly bilobed in neuropodia. Presetal lamellae rudimentary. Postsetal lamellae in anterior notopodia large, rounded to bilobed, in middle and posterior notopodia shorter, about as long as acicular lobes or slightly longer; postsetal lamellae of neuropodia about twice as long as acicular lobes, broadly rounded but with a normally distinct ventral incision. Dorsal cirrus small, slender; ventral cirrus larger, conical. Interramal cirri cirriform, slender, present from setiger 3 to the end of the body, best developed from setigers 10–15, reduced posteriorly but distinct even in the last setigers.

Setae comprise preacicular barred setae and postacicular setae with spinose margins. Preacicular setae about as long as acicular lobes or a little longer; postacicular setae up to four times longer than postsetal lamellae.

Distribution. Arctic and North Atlantic, including the North Sea, Skagerrak, Kattegat and western Baltic. Also reported from the North Pacific and the Straits of Magellan, and the Mediterranean as far as the Black Sea.

Ecology. Occurs in a wide variety of sediments, from the lower intertidal down to 1000 m depth. It is most common in well-sorted fine or medium sands.

Nephtys paradoxa Malm, 1874
(Fig. 3E)

Nephthys paradoxa Malm, 1874: 77; – Augener, 1928: 701.
Nephthys hombergii – Heinen, 1911: 16–20 [partim].
Nephtys paradoxa – Fauchald, 1963: 13–15; – Hartmann-Schröder, 1971: 214; – Hartmann-Schröder, 1974: 207–208; – Hartmann-Schröder, 1977: 88.

Material examined. 25 specimens, including the following.

Greenland. – ZMC: 1 animal, Yulianehaabsfjord, Greenland, 26. 07. 1930, 280 m.

North Sea/English Channel. – ZMH: P-13156, 10 animals, Anton Dohrn Stn 131.8, NW North Sea, 20. 09. 1968; – ZMK: Po 0604, 1 animal, Stn 04.III N9, North Sea, 142–147 m, ident. by Heinen as *Nephtys hombergii*.

North Atlantic – ZMC: 1 animal, Shackleton Stn 1899, 50°43′ N, 11°18′ W, 26. 04. 1977, 1160 m.

Portugal/Bay of Biscay. – ZMH: P-13725, 1 animal, Meteor Stn 11, off Portugal, 37°41′ N, 9°12′ W, 20. 01. 1967, 500 m.

Description. Body stout, up to 200 mm long, with up to 150 setigers. Colour in alcohol yellow to greyish white, lacking eyespots in larger animals.

Prostomium square to pentagonal, with straight or slightly convex anterior margin. Antennae and palps short to moderately long, conical, the palps somewhat larger than and arising immediately posterior to the antennae.

Pharynx subcylindrical, with 22 rows of short subterminal papillae, 5–6 per row. Median dorsal and ventral papillae present, little larger than subterminal papillae. Proximal surface of pharynx smooth.

Parapodia (Fig. 3E) fully developed from setigers 20–25. Acicular lobes obliquely rounded in notopodia, conical in neuropodia; presetal lamellae rudimentary, postsetal

lamellae simple, rounded, not longer than the acicular lobes. Dorsal and ventral cirri short, rounded to triangular. Interramal cirri present from setigers 5–14, usually from setigers 8–10, small, increasing in size to setigers 25–27, then reducing after setigers 40 to become absent by setigers 55–60; fully developed interramal cirri equipped with lateral foliaceous lobes that may be smooth or undulated along the edge.

Setae relatively short and stout; preacicular setae barred, little longer than the acicular lobes, postacicular setae with strongly dentate margins, about twice the length of preacicular setae.

Distribution. Arctic; North Pacific; North Atlantic to the Mediterranean, including the northern North Sea, Skagerrak and Kattegat.

Nephtys pente Rainer, 1984
(Fig. 3B)

Nephthys caeca Möbius, 1875: 168–169 [partim].
Nephthys ciliata – von Marenzeller, 1889: 127 [partim]; – Michaelsen, 1896: 58 [partim]; – McIntosh, 1908: 23–27; – Heinen, 1911: 21–23 [partim]; – Augener, 1912: 193 [partim].
Nephthys incisa – Heinen, 1911: 23–25 [partim].
Nephtys ciliata – Kirkegaard, 1969: 46.
Nephtys pente Rainer, 1984: 901–905.
Nephtys zatsepini Jirkov, 1986: 39.

Material examined. 32 specimens, including the following. Additional material examined is given in Rainer (1984).

Labrador. – BMNH: ZK 1941.1.1.59, 1 animal, Rosaura Stn 10, 52°13′ N, 55°07′ W, Horn Bay, Labrador, ident. as *Nephthys ciliata*.

Greenland. – BMNH: ZH 1877.12.10.10, 3 animals, Godhavn, Greenland, ident. as *Nephthys ?incisa*; ZK 1941.1.1.53–58, 8 animals, Rosaura Stn 6, 60°06′ N, 45°25′ W, off Nanortilik, Greenland, ident. as *Nephthys ciliata*; – ZMC: 1 animal, Nov Sbromsfjord, Nordmann Stn 29, 26. 07. 1911, ident. by Wesenberg-Lund as *Nephtys coeca* var. *ciliata*; 1 animal, Nordmann Stn 2, off Strömfjord, 23. 06. 1911, 375–380 m, ident. by Wesenberg-Lund as *Nephtys coeca* var. *ciliata*.

Kattegat/Skagerrak. – ZMC: 1 animal, Helsingør, Denmark, 1971.

North Sea/English Channel. – ZMK: 0187, 1 animal, 03.V Stn 6, North Sea, ident. by Heinen as *Nephthys incisa*.

U. K. (West), Ireland. – BMNH: ZK 1921.5.1.757, 1 animal, Bressay Sound, Shetland, ident. as *Nephthys ciliata*; ZK 1921.5.1.764, 2 animals, St Magnus Bay, Shetland, ident. as *Nephthys ciliata*.

Description. Body stout, broadest at setigers 5–20 and tapering slowly to near pygidium, up to 140 mm long, with up to 90 setigers. Colour cream in alcohol, with faint brown dorsal epidermal pigmentation on anterior setigers, eyespots apparent only in small animals.

Prostomium longer than wide, with straight anterior margin and convex sides. Antennae short, conical, arising near anterolateral margin of prostomium; palps conical, with bulbous base, about 1.5 times length of antennae.

Pharynx with a median dorsal papilla and 22 rows of subterminal papillae; subterminal papillae 3–5 per row, median dorsal papilla about ⅔ length of distal region of pharynx. Median field of pharynx densely covered with warty outgrowth.

Parapodia (Fig. 3B) fully developed from about setiger 10. Acicular lobes divided equally in notopodium, with more expanded dorsal portion in neuropodium; presetal lamellae inconspicuous or rudimentary; postsetal lamellae rounded, projecting beyond the acicular lobes in anterior setigers, expanded dorsally in notopodia. Dorsal and ventral cirri short, conical, with bulbous bases. Interramal cirri stout, from setiger 5 (rarely 6) to near end of body, increasing in size in first 5–10 setigers and remaining large over most of the body length.

Setae include preacicular barred setae, postacicular setae with spinulose or spinose margins, medial setae capillary or with finely spinulose margins. Preacicular setae not extending much past postsetal lamellae, postsetal and medial setae somewhat longer, usually extending beyond postsetal lamellae.

Distribution. North-eastern Atlantic, between the North Sea and the Arctic (Greenland to the Murman coast), including the Baltic. *Nephtys pente* has frequently been identified as *N. ciliata*, and may have a wider distribution than indicated here.

Ecology. Silty sand, from shallow subtidal locations to 380 m.

Nephtys pulchra sp. n.
(Fig. 1A–F)

Nephthys hystricis McIntosh, 1900: 259–260 [partim]; – McIntosh, 1908: 27–29 [partim].
Nephtys incisa – Fauchald, 1963: 15–16 [partim].
Aglaophamus malmgreni – Hartmann-Schröder, 1974: 205–206 [partim].
Aglaophamus rubella – Hartmann-Schröder, 1974: 205 [partim].

Material examined. Holotype: BMNH: ZK 1921.5.1.794 (syntype of *N. hystricis*), entire, 59 mm long, mature male, Norway. Paratypes: 1 – BMNH: ZK 1921.5.1.795 (syntype of *N. hystricis*), anterior fragment of 78 setigers, 53 mm, Norway; 2 – BMNH: ZK 1921.5.1.767 (syntype of *N. hystricis*), anterior fragment of 35 setigers, Knight Errant Stn 10, 510 fm [author's note: no Stn 10 is known to have been sampled by the Knight Errant]; 3 – ZMH: V12238, entire, 60 mm long, mature female, Drøback-Sund, Oslofjord, coll. H. Brock, ident. by H. Augener as *Nephthys rubella*; 4 – ZMH: P-13438, entire (41 setigers + regenerated pygidium), Anton Dohrn Stn 459b, 58°02′ N, 9°23′ E, 12. 05. 1970, 490 m, mud, ident. by Hartmann-Schröder as *N. malmgreni*; 5 – ZMH: P-19234, 1 anterior fragment, 31 setigers, Anton Dohrn Stn 12b, Norwegische Rinne, 58°21′ N, 5°26′ E, 06. 01. 1968, 345 m, silt and clay, ident. by Hartmann-Schröder as *A. rubella*; 6–9 – BMH: ZK 1940.12.27.9–11, one entire, 50 mm long, 90 setigers, and three anterior fragments of 42, 60, 53 setigers, Rödberg, Trondheim Fjord, Norway, 250–300 fm, ident. as *Nephthys caeca*?.

Norway. – ZMH: P-13180, 18 anterior fragments (poor condition), Anton Dohrn Stn 12 II, Norwegische Rinne, 58°21′ N, 5°26′ E, 06. 01. 1968, 345 m, silt and clay, ident. by Hartmann-Schröder as *A. rubella*; P13400, 1 anterior fragment, Anton Dohrn Stn 12 II, Norwegische Rinne, 58°21′ N, 5°26′ E, 06. 01. 1968, 345 m, silt and clay, ident. by Hartmann-Schröder as *N. rubella*; P13474, 6 anterior fragments, Anton Dohrn Stns 729 and 453, Norwegische Rinne, 345 and 500 m, mud, ident. by Hartmann-Schröder as *N. malmgreni*; – ZMO: C 1696, 5 anterior fragments, Brændtangen, 100 fv., 02. 08. 1910, ident. by Fauchald as *N. incisa*.

Kattegat/Skagerrak. – ZMH: V12238, 3 anterior fragments, Drøback-Sund, Oslo-

fjord, coll. H. Brock, ident. by H. Augener as *Nephthys rubella*; P-13228, 14 anterior fragments, Anton Dohrn Stns 1212 (24. 11. 1968, 598 m) and 1231 (25. 11. 1968, 196 m), Skagerrak, ident. by Hartmann-Schröder as *A. malmgreni*.

Description. Entire animal of 90 setigers, 59 mm long (pharynx partly everted). Body broadest at setigers 8–25, width including parapodia 5.4 mm, excluding parapodia 3.2 mm; body tapers slowly to 2.2 mm wide (excluding parapodia) at setiger 40, then to 0.8 mm wide by setiger 80; pygidial cirrus not seen. Width of anterior setigers about 8 times length at level of pharynx, reducing gradually to equal length of setiger by setiger 80. Dorsum rounded, ventrum with midventral groove from setiger 7 to pygidium. Mouth ventral with rugose posterior margin at level of setiger 3; rugose area extending to setigers 5–6. Body colour creamish brown in alcohol, with midventral groove darker brown, anterior dorsum and midventral groove moderately iridescent, no eyespots visible. Setae very pale, glistening, aciculae visible laterally on parapodia as brown points.

Prostomium (Fig. 1A) wider than long (1.0 mm by 0.5 mm), broadest in middle, anterior margin gently concave, anterolateral margins straight, posterior margin indistinctly separated from setiger 1. Antennae inserted at anterolateral angles of prostomium, 0.07 mm long, conical with narrow tips, palps 0.2 mm long, conical with bulbous base and slender tips, inserted below and behind antennae, on ventral surface of prostomium and visible dorsally at about half way along the anterolateral margins of prostomium.

Pharynx with paired jaws, 20 bifid and 2 simple terminal papillae, and 14 rows of subterminal papillae extending over most of the length of the pharynx; no median dorsal papilla. Jaws typical of the genus: brown, elongate conical, bilaterally symmetrical, set within the dorsoventrally flattened aperture. Bifid terminal papillae radially flattened, with outer portion longer than inner, 10 on each side of the pharynx separated by low, simple, mid-dorsal and midventral terminal papillae. Distal subterminal papillae, 20 or 22, large, reaching as far as the terminal papillae. Subsequent subterminal papillae in rows, 14–16 per row, decreasing in size towards base of pharynx. Surface of pharynx otherwise smooth.

Parapodia biramous, projecting about one quarter body width in anterior setigers (Fig. 1A), 1–1.5 body widths in posterior setigers. First three parapodia reduced, parapodia of setiger 1 directed anteriorly, adjacent to prostomium, parapodia of setiger 2 and 3 becoming more lateral in position and directed anterolaterally, remaining parapodia directed laterally. Setiger 1 (Fig. 1B), notopodium with conical acicular lobe and indistinct pre- and postsetal lamellae; neuropodium with pre- and postsetal lamellae forming a low cylinder around a projecting conical acicular lobe; dorsal cirrus is a low triangular flap, ventral cirrus similar in size and shape to palps. Setiger 2, notopodium and neuropodium with low, broadly conical acicular lobes and rudimentary pre- and postsetal lamellae; dorsal and ventral cirri similar to setiger 1 except that the ventral cirrus is about 1.5 times longer. Setiger 3 similar to setiger 2 except that neuropodium now has a low presetal and a distinct postsetal lamella, and dorsal cirri are bulbous with a short terminal filament. Setiger 4 with low presetal lamella in notopodium; postsetal lamellae distinct in both rami, extending beyond acicular lobe in neuropodium; dorsal cirri flatter, with terminal portion as long as basal portion. By setiger 10 (Fig. 1C), pre- and postsetal lamellae have increased in size; notopodial presetal lamellae are low and rounded, reaching half as far as the acicular lobe, neuropodial presetal lamellae better developed towards interramal

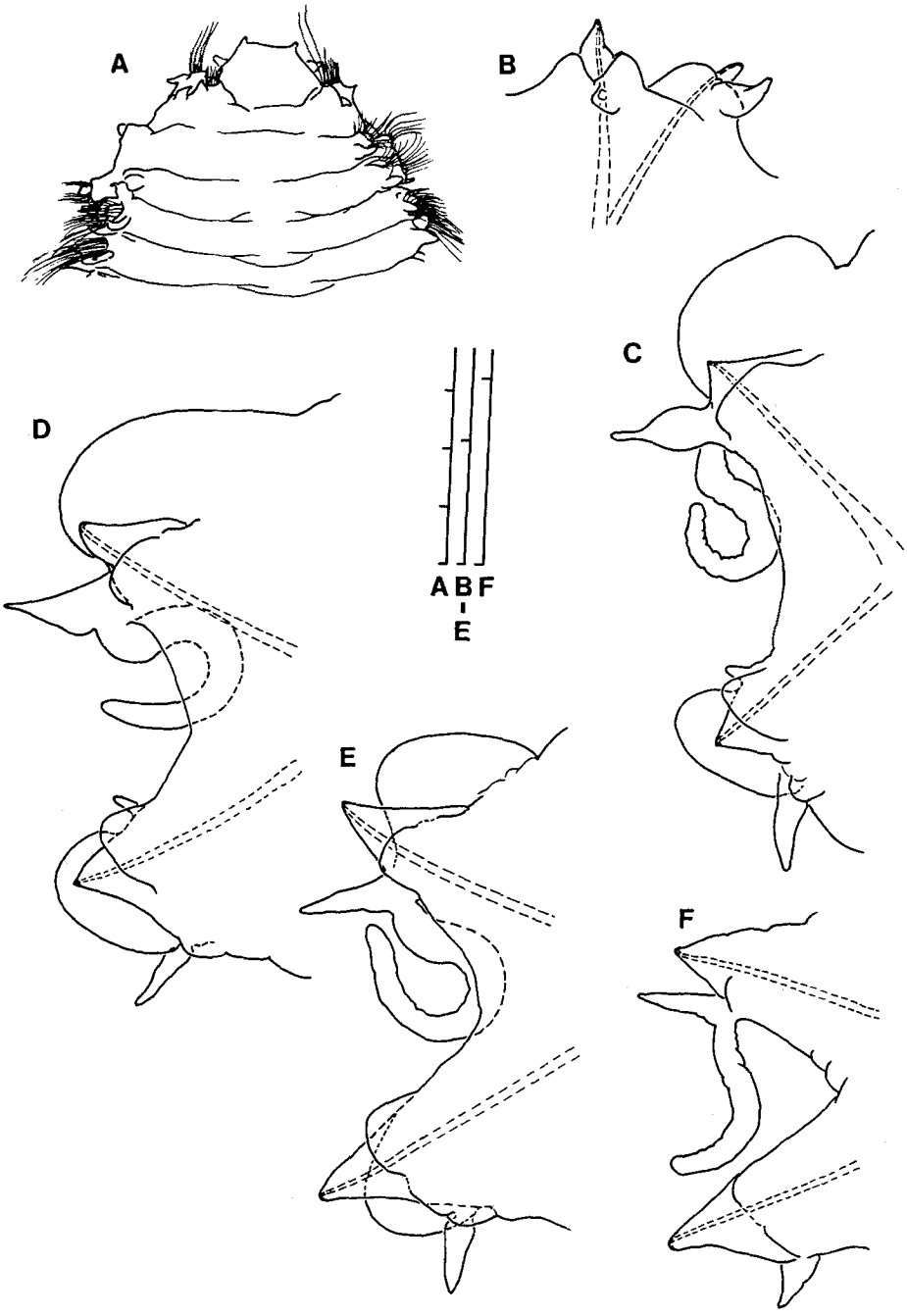

Fig. 1. *Nephtys pulchra* sp. n. A: Prostomium and anterior setigers, dorsal aspect. B: Parapodium of setiger 1. C: Parapodium of setiger 10. D: Parapodium of setiger 20. E: Parapodium of setiger 40. F: Parapodium of setiger 80. Parapodia are from the right side, Fig. 1B from anterior aspect, Fig. 1C–F from posterior aspect; intervals on scale bars are 0.5 mm long

region, also reaching half as far as acicular lobe; postsetal lamellae of both rami are broadly rounded and project well beyond the acicular lobes. Presetal lamellae from setiger 20 (Fig. 1D) best developed towards interramal region, but continue as an obscure ridge that develops to form a low lamella covering the bases of postacicular setae (see below); presetal lamellae become smaller after about setiger 30, and become inconspicuous (Fig. 1E) or, in posterior setigers, rudimentary (Fig. 1F). Postsetal lamellae are best developed in setigers 10–30, but reach to only about half the length of the acicular lobes in posterior setigers. Distance between notopodia and neuropodia changes little along the body, although decreasing somewhat in posterior setigers. Dorsal and ventral cirri long and tapered, varying little in size along body; dorsal cirri longer than in most other species, projecting beyond the acicular lobes along much of the body.

Interramal cirri first present on setiger 5 (right) and 6 (left), as a slender recurved lobe occupying about one quarter (setiger 5) or half (setiger 6) of interramal space; interramal cirri rapidly increase in length to become completely recurved by setiger 10, usually occupying only the dorsal half of the interramal region (Fig. 1C, D). Interramal cirri and dorsal cirri become progressively smaller and more slender towards the tail, but are distinct up to the last few setigers. The interramal cirrus and interramal region are ciliated in anterior setigers. A short, unciliated, dorsal neuropodial lobe is present in anterior setigers (Fig. 1C, D).

Aciculae of moderate thickness, tapering, with fine, posteriorly directed tips; aciculae of posterior setigers are slender; a single acicula in notopodium and in neuropodium. Aciculae translucent, light brown when viewed in transmitted light.

Setae of noto- and neuropodium arranged in an uneven "U" around each acicular lobe, with pre- and postacicular limbs of the "U" directed away from the interramal space; postacicular limbs much longer, with the end of the limb curving around the base of the acicular lobe to occupy an anterior position. Setae in this position are separated from preacicular setae proper by a small space, and usually have a separate, low presetal lamella. Setae of two types only: barred and capillary. Notopodium of setiger 1 with preacicular row of barred setae and postacicular row of capillary setae, neuropodium with capillary setae only. Setae of subsequent setigers have preacicular barred setae and postacicular capillary setae; capillary setae, about as long as the barred setae, are present with the barred setae, as a small group furthest from the interramal region. Preacicular setae relatively long (exposed length 0.8–1.0 mm), extending past acicular lobes and postsetal lamellae of all setigers. Postacicular setae longer (exposed length 0.8–1.0 mm in anterior setigers, 0.8–2.0 mm in middle setigers), projecting beyond postsetal lamellae. Number of setae per parapodium, expressed as number of barred (B) and capillary (C), for notopodium/neuropodium respectively: setiger 1, 12C/17B, 26C; setigers 10–40, 33–41B, 90–120C/33–45B, 95–115C; setae remain numerous to near end of body, with setiger 80, 12B, 30C/6B, 30C. Barred setae of posterior setigers slender, with barred pattern much lighter than in anterior setigers.

Remarks on morphology. Three complete animals were found, together with one in which the pygidium had regenerated. The complete animals were between 50 and approx. 60 mm long, with 90 setigers in two animals and 93 in the third. The parapodia in these animals were complete to almost the last setiger, suggesting larger animals would have few if any more setigers. None of the three complete animals had a pygidial cirrus. A short, filamentous pygidial cirrus about as long as the last setiger was

Table 1. Diagnostic characteristics of northern European species of *Nephtys*

Species	Parapodial characters					Pharyngeal characters			Size	Notes*
	Preacicular lamellae	Acicular lobes	Post-acicular lamellae*	Setigers with interramal cirri	Post-acicular setae	Mid-dorsal cirrus	Subterminal papillae: rows, #/row	Surface of pharynx	No. of setigers	
N. assimilis	bilobed	lateral bulb	expanded, neuro > noto	4 to pygidium	spinulose	long	22, 2–5	smooth	< 115	vascular neuropodial lamellae
N. caeca	small to rudimentary	rounded to bilobed	expanded, neuro > noto	4–5 to pygidium	spinose	short, stout (if present)	22, 4–6	warty	< 150	interramal cirri usually from set. 4
N. ciliata	small to rudimentary	bilobed	moderate, neuro ≈ noto	7–10 to last 20–30	spinulose	stout	22, 3–7	warty	< 140	interramal cirri usually from set. 4
N. cirrosa	rudimentary to bilobed	rounded to bilobed	moderate, neuro ≈ noto	4 to pygidium	spinulose	long, slender	22, 9–10	smooth	< 95	set. 1, dorsal cirrus v. small, ventral cirrus long
N. hombergii	bilobed	lateral bulb	expanded, neuro ≫ noto	4–6 to pygidium	spinulose	short	22, 3–6	smooth	< 135	prostomium length ≫ width
N. hystricis	bilobed	conical	expanded, neuro ≈ noto	6–7 to last 15–18	spinulose	long	22, 4–6	smooth	< 75	interramal cirri usually from set. 7
N. incisa	simple, small	conical	moderate, neuro ≈ noto	8–11 to last 25	spinulose	long, slender	14–22 (24?), 1–5	smooth	75	interramal cirri usually from set. 9
N. kersivalensis	bilobed	rounded to conical	expanded, neuro ≈ noto	4 to pygidium	spinulose	long, strong	22, 3–6	smooth	< 85	1 pr eyespots occas. in setiger 2
N. longosetosa	rudimentary	rounded to bilobed	expanded, neuro > noto	3 to pygidium	spinose	long	22, 5–7	smooth	< 120	1 pr eyespots usual in setiger 2
N. paradoxa	rudimentary	rounded to conical	moderate, neuro ≈ noto	5–14 to 55–60	spinose /dentate	short	22, 5–6	smooth	< 150	interramal cirri usually from set. 9
N. pente	rudimentary	bilobed	moderate, neuro ≈ noto	5–6 to pygidium	spinulose /spinose	stout	22, 3–5	warty	< 90	interramal cirri usually from set. 5
N. pulchra sp. n.	simple, small	conical	small, neuro ≈ noto	5–6 to pygidium	capillary	none	14, 14–16	smooth	< 95	dorsal neuropodial lobe present

* Abbreviations: neuro – neuropodial; noto – notopodial; set. – setiger.

present on the animal with the regenerated pygidium, and a short, filamentous cirrus was also seen on a posterior end identified as belonging to *N. pulchra* sp. n.

The shape of the prostomium and anterior body depends on the extent to which the pharynx is everted. In animals in which the pharynx is present well back from the prostomium, setiger 1 is about one quarter the maximum body width, and the body increases gradually in size towards the position of the pharynx, at about setigers 12–21, thereafter decreasing gradually towards the posterior. The prostomium in these specimens is 1.5–2 times longer than wide, with a straight, gently convex or gently concave anterior margin, and gently concave lateral margins, with the greatest width about ⅓ of the distance from the anterior margin. Eyespots were not seen even in small specimens (e.g. ZMH: P13438, 1.8 mm body width).

The first interramal cirri were consistently present on setigers 5 or 6, continuing to the end of the body. In most animals, the interramal cirri were first present on setiger 5; in several of these, the interramal cirri were first present on setiger 5 on one side of the body, setiger 6 on the other. In small animals the cirri were less strongly involute than in the larger animals, and the dorsal neuropodial lobe may be absent.

Remarks on taxonomy. *Nephtys pulchra* sp. n. is uniquely characterised among *Nephtys* species from northern Europe in having only 14 rows of subterminal papillae on the pharynx and in the presence of a small dorsal papilla on the neuropodium of anterior setigers. In these characters, it is similar to many species of *Aglaophamus*. However, it lacks the furcate setae common in *Aglaophamus* species, and the recurved interramal cirrus clearly identifies it as a species of *Nephtys*. *N. pulchra* sp. n. shares many points of parapodial morphology with *N. hystricis* and *N. incisa*, with which it has been confused. It is most easily distinguished from these species by the interramal cirri beginning on setiger 5 rather than 6 or 9. It also differs from *N. hystricis* in having simple, not bilobed, presetal lamellae, and from *N. incisa* in the greater development of the postsetal lamellae. In many respects, *N. pulchra* sp. n. is also close to *N. cirrosa*, from which it differs in having interramal cirri from setiger 5, not 4, and in having more conical acicular lobes.

Distribution. North Atlantic, including coasts of Norway, Oslofjord and Skagerrak.

Ecology. 200–930 m, from mud and clay substrata.

Etymology. The specific name is the Latin *pulchra* (fem.), referring to the attractive colour of the setae.

KEY TO NORTHERN EUROPEAN SPECIES OF NEPHTYIDAE

Fourteen species of Nephtyidae are now known from northern European waters, including the twelve species of *Nephtys* considered above. All species can be consistently differentiated on the basis of parapodial characters: the size and form of the acicular lobes and the pre- and postsetal lamellae, and the form and position of the interramal cirri (Table 1). Pharyngeal characteristics and body size (particularly number of setigers) are useful as secondary morphological characters to differentiate the species.

The key relies mainly on parapodial features; dissection of the pharynx should not normally be required. The parapodial characteristics used are those of midbody setigers, unless otherwise stated. The relative development of the parapodial lamellae and lobes

may vary with the size of the animals and with the geographic area from which they were collected; provisional identifications made from the key should therefore be checked against a complete description.

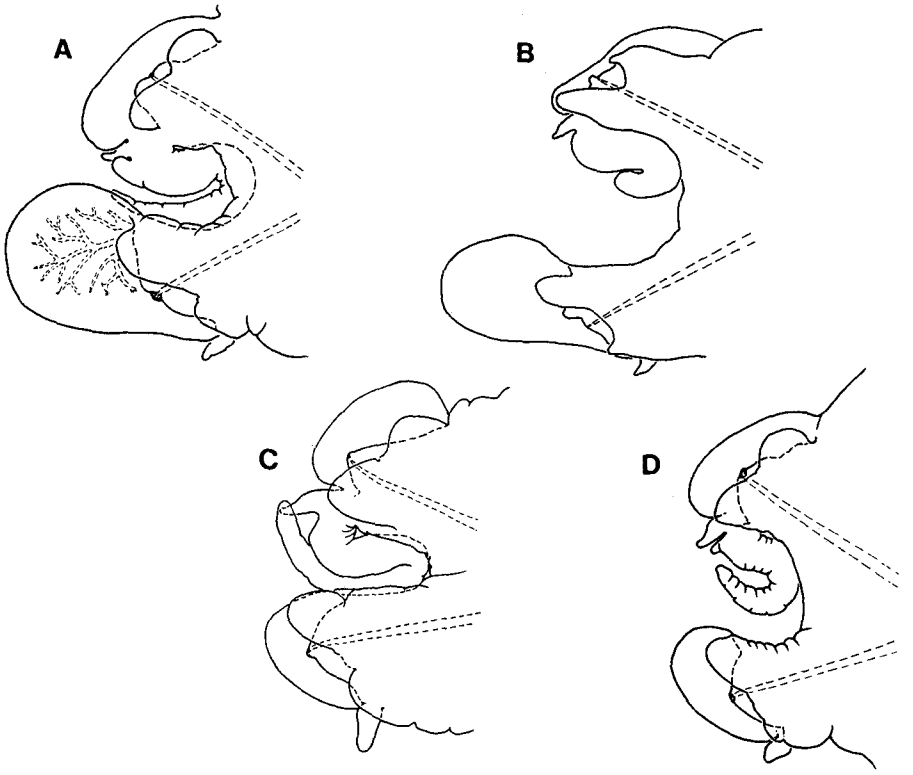

Fig. 2. Parapodia of northern European species of *Nephtys* having bilobed presetal lamellae. A: *N. assimilis* Örsted, 1843. B: *N. hombergii* Savigny, 1818. C: *N. hystricis* McIntosh, 1900. D: *N. kersivalensis* McIntosh, 1908. All parapodia are from midbody setigers. B redrawn after Hartmann-Schröder, 1971

1. Interramal cirri involute, cirriform; pharynx with 14 rows of subterminal papillae ..... *Aglaophamus* .. 2
   Interramal cirri recurved, foliaceous or cirriform; pharynx with 14, 20 or 22 rows of subterminal papillae ..... *Nephtys* .. 3
2. Presetal lamellae rudimentary, more-or-less distinctly bilobed; dorsal postsetal lamellae much longer than acicular lobes, ventral postsetal lamellae about as long as acicular lobes; dorsal interramal cirri from setiger 2, ventral interramal cirri present on neuropodia; up to 120 setigers ..... *Aglaophamus rubella* (Michaelsen, 1896)
   Presetal lamellae rudimentary, simple; postsetal lamellae shorter than acicular lobes; dorsal interramal cirri from setigers 8–15 to the last 15–40 setigers, no ventral interramal cirri; up to 90 setigers ..... *Aglaophamus malmgreni* Théel, 1879
3. Presetal lamellae of notopodia well developed, bilobed, with dorsal and medial portions extending beyond acicular lobes; interramal cirri from setigers 4–7 4
   Presetal lamellae rudimentary or simple; interramal cirri from setigers 3–14 7

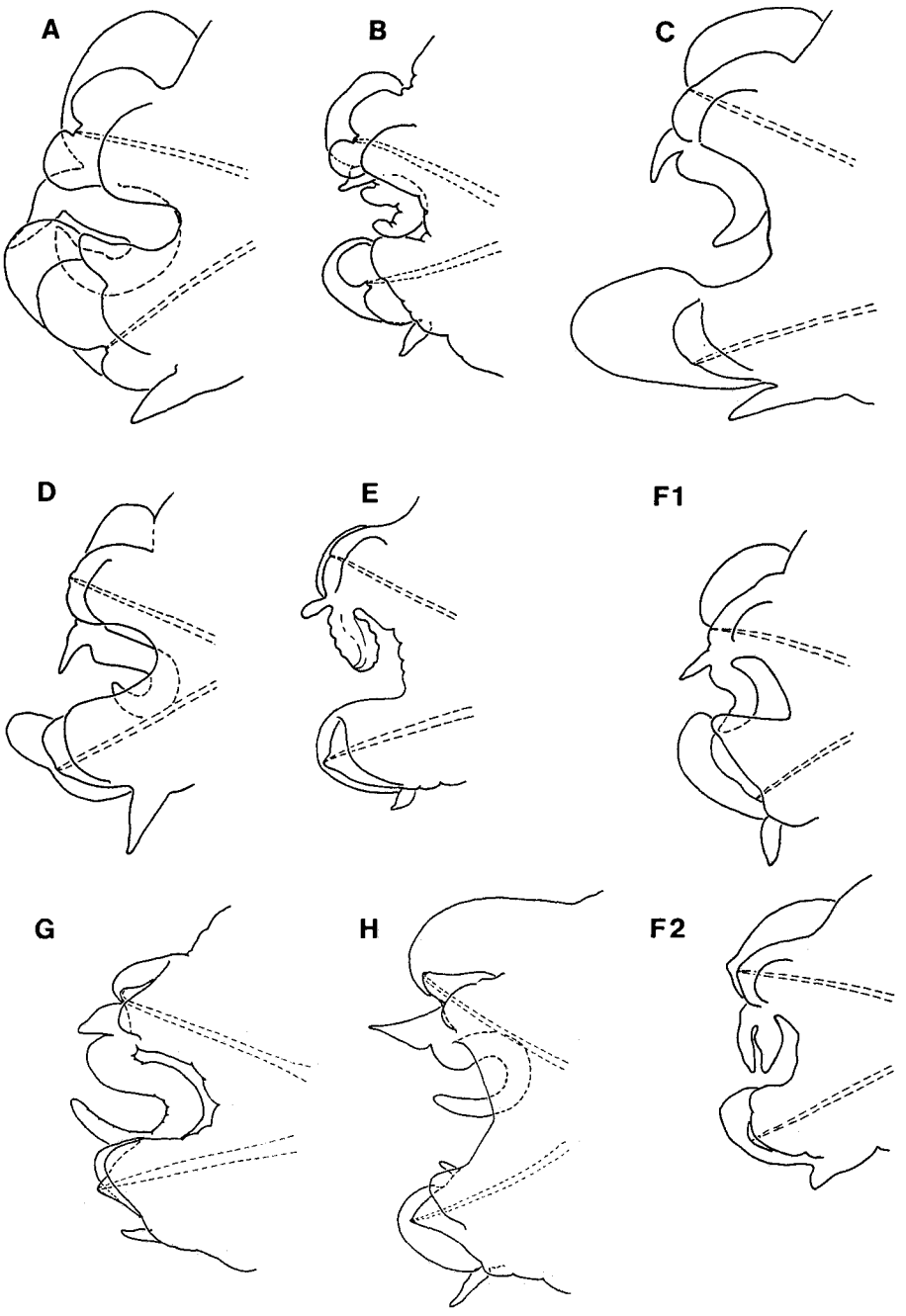

Fig. 3. Parapodia of northern European species of *Nephtys* having simple or rudimentary presetal lamellae. A: *N. ciliata* (O. F. Müller, 1776). B: *N. pente* Rainer, 1984. C: *N. caeca* (Fabricius 1780). D: *N. longosetosa* Örsted, 1843. E: *N. paradoxa* Malm, 1874. F_1: *N. cirrosa* Ehlers, 1868. F_2: *N. cirrosa* (posterior setiger). G: *N. incisa* Malmgren, 1865. H: *N. pulchra* sp. n. All parapodia are from midbody setigers except Fig. 3G. A and B redrawn after Rainer, 1984; C and F redrawn from Hartmann-Schröder, 1971; E redrawn after Fauvel, 1923

4. Acicular lobes with medial bulb or papilla; postsetal lamellae more than twice as long as acicular lobes; pharynx with median dorsal papilla long or short 5
   Acicular lobes simple, rounded to conical; postsetal lamellae well or poorly developed; pharynx with median dorsal papilla at least twice as long as subterminal papillae 6
5. Acicular lobes with low medial bulb; interramal cirri from setiger 4; prostomium broadest anteriorly or with parallel sides; ventral postsetal lamellae broadly rounded with internal vascular structure (Fig. 2A); interramal region of posterior setigers with prominent raised ciliary pads; up to 110 setigers ..... *Nephtys assimilis* Örsted, 1843
   Acicular lobes with prominent medial bulb or papilla; interramal cirri from setiger 4, 5 or 6; prostomium narrowest anteriorly, with convex anterior margin; ventral postsetal lamellae expanded medially, with acutely rounded distal margins (Fig. 2B); interramal region of posterior setigers with low ciliary pads; up to 145 setigers ..... *Nephtys hombergii* de Savigny, 1818
6. Postsetal lamellae up to twice length of acicular lobes (Fig. 2C), which lack a rugose area; interramal cirri from setigers 6 or 7, usually 7, reduced or absent in last 15 setigers; up to 70, occasionally 75 setigers ..... *Nephtys hystricis* McIntosh, 1900
   Postsetal lamellae more than twice as long as acicular lobes (Fig. 2D), which have a rugose area near aciculae; interramal cirri from setiger 4, with basal papilla below dorsal cirrus; up to 85 setigers ..... *Nephtys kersivalensis* McIntosh, 1908
7. Presetal lamellae rudimentary; acicular lobes of anterior and middle setigers distinctly bilobed (Fig. 3A, B); pharynx with numerous warty processes or minute papillae; up to 140 setigers ... 8
   Presetal lamellae rudimentary or moderately developed, acicular lobes of anterior and posterior setigers conical or rounded; pharynx with or lacking warty processes or minute papillae; up to 150 setigers 9
8. Interramal cirri from setigers 7–10, reduced or absent in last 20–30 setigers; up to 140 setigers ... . *Nephtys ciliata* (O. F. Müller, 1776)
   Interramal cirri from setigers 5 or 6, not markedly reduced in posterior setigers; up to 90 setigers . ..... *Nephtys pente* Rainer, 1984
9. Postsetal lamellae more than twice as long as acicular lobes; interramal cirri from setigers 3–5, usually from 3 or 4; postacicular setae with strongly denticulate distal region 10
   Postsetal lamellae less than twice as long as acicular lobes; interramal cirri from setigers 4–14; postacicular setae usually with spinulose or smooth margins 11
10. Postsetal lamellae well-developed in notopodia and neuropodia (Fig. 3C); interramal cirri from setigers 4–5, usually from 4; prostomium broad, with straight or gently concave anterior margin; pharynx with numerous warty papillae; up to 150 setigers ..... *Nephtys caeca* (Fabricius, 1780)
    Presetal lamellae of notopodia in middle and posterior setigers much shorter than in neuropodia (Fig. 3D); interramal cirri from setiger 3; prostomium broadest anteriorly, with strongly concave anterior margin; pharynx lacking warty papillae, up to 120 setigers .... *Nephtys longosetosa* Örsted, 1843
11. Interramal cirri foliaceous or cirriform, from setigers 8–14, reduced or absent in posterior setigers; up to 110 setigers 12
    Interramal cirri cirriform, from setigers 4–6 to near end of body; up to 95 setigers 13
12. Interramal cirri foliaceous, usually present from setigers 8–10, well-defined from setigers 14–16 (Fig. 3E), absent from last 30–50 setigers; postacicular setae with denticulate proximal region; up to 110 setigers ..... *Nephtys paradoxa* Malm, 1874
    Interramal cirri cirriform (Fig. 3G), from setigers 8–10, reduced or absent in last 20–25 setigers; postacicular setae with spinulose or smooth margins; up to 70, occasionally 75 setigers .... *Nephtys incisa* Malmgren, 1865
13. Interramal cirri from setiger 4; acicular lobes in anterior and posterior setigers simple, rounded, in middle setigers unequally bilobed (Fig. $3F_1$); dorsal cirri in posterior setigers as long as interramal cirri (Fig. $3F_2$); pharynx with 22 rows of 9–10 subterminal papillae extending to proximal end of pharynx; postacicular setae smooth or very finely denticulate .... *Nephtys cirrosa* Ehlers, 1868
    Interramal cirri from setigers 5 or 6, usually 5; acicular lobes conical; dorsal cirri shorter than interramal cirri; neuropodium with a small dorsal lobe in anterior setigers (Fig. 3H); pharynx with 14 rows of 10–12 papillae per row; setae long, flowing, with barred and capillary setae only . ..... *Nephtys pulchra* sp. n.

DISCUSSION

Early descriptions of nephtyid polychaetes were marked by considerable disagreement about the appropriate morphological features to define individual species. Workers such as Möbius (1875), Wirén (1883) and Schack (1886) considered the then known European species to fall within a broadly defined *Nephtys caeca*. Subsequent revisions led to the acceptance of 11 species of *Nephtys* (Fauvel, 1923), eight of which are now accepted within the genus as currently defined (Fauchald, 1963; Woolf, 1968; Hartmann-Schröder, 1971). The setiger on which interramal cirri first occur was relatively constant in *N. longosetosa* (setiger 3–4), *N. cirrosa* (setiger 4) and *N. hystricis* (setiger 9[!]). In the remaining five species, however, this character varied over three or more setigers; *N. caeca* (setigers 4–6), *N. hombergii* (setigers 4–6), *N. ciliata* (setigers 4–10), *N. paradoxa* (setigers 5–14) and *N. incisa* (setigers 6–8).

Some of the variability in this character was reduced in *N. ciliata*, with the description of *N. pente* (Rainer, 1984). The present study reduces this variability for *N. incisa*, and recognizes three further species in which the interramal cirri regularly begin on a particular setiger: *N. assimilis*, *N. kersivalensis* and *N. pulchra* sp. n. (all on setiger 4). *N. caeca* should be regarded as a species in which the interramal setae first occur regularly on setigers 4–5, rather than 4–6.

Two species, *N. paradoxa* and *N. hombergii*, are still relatively variable. Some of the variation in *N. paradoxa* of European waters may be due to the presence of a second species (Fauchald, 1963). The recognition of *N. assimilis* as a valid species and the removal of *N. kersivalensis* from varietal status within *N. hombergii* result in a narrower characterisation of *N. hombergii*, but do not change the range over which the interramal cirri first occur.

With the description of *Nephtys pente*, it has become clearer that some variability in species of *Nephtys* may be geographically related. At the latitude of the North Sea or Baltic Sea, *N. pente* and *N. ciliata* have interramal cirri first present on setigers 5 and 7 respectively. Further north, towards Spitzbergen, *N. pente* may have interramal cirri beginning on setiger 6, and *N. ciliata*, interramal cirri beginning on setigers 8, 9 or even 10. *N. caeca* has interramal cirri that first occur on setiger 4 at the latitude of the North Sea, but usually on setiger 5 in animals from Greenland.

Some of the variation within *N. hombergii* may be accounted for in this way also. The majority of the animals examined from the Mediterranean have interramal cirri commencing on setiger 4 or, in deeper water, setiger 5. Animals from 50–55° N regularly have interramal cirri first present on setiger 4 in shallow water (e.g. around Kiel Bay, or in the Limfjord), and on setiger 5 or 6 in deeper water (e.g. around the Dogger Bank). Further north, in Norwegian waters, the interramal cirri occur first on setigers 5 or 6 only (Fauchald, 1963). Some variability in the form of the postsetal lamellae in particular is also characteristic of *N. hombergii*. The species is common in intertidal mud flats (Warwick & Price, 1975) and sand flats (Olive, 1977), from the upper half of the tidal zone (Woolf, 1973) down to depths of 400 m, and it is found in sediments ranging from medium sand to soft mud (Hartmann-Schröder, 1971), and in locations from the Black Sea to the Barents Sea. This suggests that *N. hombergii* may well possess a higher degree of genetic richness than other European species of *Nephtys*. The morphological differences found in *N. hombergii* may reflect both phenotypic differences associated with different habitats

and perhaps also genetic differences associated with different geographical locations. Schubert & Reise (1986) have suggested, on the basis of differences in the diet of various populations, that more than one species may exist under the name *N. hombergii*. The more consistent morphology of most of the other European nephtyids suggests that this may still be correct, even for *N. hombergii* as redefined here.

While examining material for the present study, I also examined animals from the south-eastern and north-western Atlantic, variously identified as species originally described from northern European waters. The morphology of these animals usually differed significantly from the northern European animals, but the extent to which this represents ecologically or geographically related variation cannot be assessed with any certainty. As yet, we know little about the ecology of several of even the shallow-water species, including *N. assimilis, N. kersivalensis* and *N. pente*. We know even less about the ecology of the deeper-water species, *N. incisa, N. hystricis, N. paradoxa* and *N. pulchra* sp. n. We also know very little about geographic variation in most of the northern European species. The narrow geographic distribution of *N. ciliata, N. hombergii, N. incisa, N. longosetosa* and *N. paradoxa* accepted in this paper, compared with Fauchald (1963) and Hartmann-Schröder (1971), reflects a conservative approach to the problem of morphological variability in nephtyids.

The broader distribution of most of the northern European species of *Nephtys* is best known from the deeper-water species. Eight of the twelve northern European species of *Nephtys* have been found in continental slope (>200 m) or deeper waters: *N. caeca, N. ciliata, N. hystricis, N. incisa, N. longosetosa, N. paradoxa, N. pente* and *N. pulchra* sp. n. *N. caeca, N. ciliata, N. longosetosa* and *N. paradoxa* have been recorded from the northern waters of the Pacific Ocean (Imajima & Takeda, 1987), while *N. caeca, N. ciliata, N. incisa* and *N. paradoxa* have been recorded from the eastern Atlantic Ocean (Hartman, 1950). Some doubt exists about the identifications of *N. ciliata* and *N. incisa*, which may include or refer to *N. pente* and *N. hystricis* respectively. However, one would expect deep-water species of *Nephtys* to have a distribution that includes a boreal or Arctic component, and thus to be relatively widely distributed.

The situation for the shallow-water species, *N. assimilis, N. cirrosa, N. hombergii* and *N. kersivalensis*, is less clear, partly because of the previous general inclusion of *N. assimilis* and *N. kersivalensis* within *N. hombergii*. *N. cirrosa* is accepted as Lusitanean, and reaching its northern limit at the latitude of the British Isles (Kirkegaard, 1969; Olive & Morgan, 1983). *N. hombergii* is widespread, but common in the Mediterranean. *N. assimilis* is also known from the Mediterranean. It thus seems that species of *Nephtys* reported only from relatively shallow waters in north-eastern Europe comprise a Lusitanean element in the nephtyid fauna, while the species of wide bathymetric distribution or that occur only in deeper waters have stronger boreal or Arctic affinities.

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LITERATURE CITED

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

Augener, H., 1912. Beitrag zur Kenntnis verschiedener Anneliden und Bemerkungen über die nordischen *Nephthys*-arten und deren epitoke Formen. – Arch. Naturgesch. *78A*(10), 162–212.

Augener, H., 1928. Ergänzungen zu den Polychaeten von Spitzbergen. – Fauna arct. *5*, 647–834.

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

Baird, W., 1873. Description of some new species of Annelida and Gephyrea in the collection of the British Museum. – J. Linn. Soc. *11*, 94–97.

Cuvier, G., 1817. La règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Deterville, Paris, *2*, 1–532.

Day, J. H., 1967. A monograph on the Polychaeta of southern Africa. Part 1. Errantia. British Museum (Natural History), London, 458 pp.

Delle Chiaje, S., 1822–1825. Memorie sulla storia e notomia degli animali senza vertebre, del Regno di Napoli. Societa tipografica, Naples, 444 pp.

Ditlevsen, Hj., 1929. Polychaeta. – Zoology Faroes *16*, 1–83.

Ehlers, E., 1868. Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Untersuchungen. Engelmann, Leipzig, *1*, 269–748.

Ehlers, E., 1874. Annulata nova vel minus cognita in Expeditione "Porcupine" capta. – Ann. Mag. nat. Hist. (Ser. 4) *13*, 292–298.

Fabricius, O., 1780. Fauna Groenlandica, systematice sistens, animalia Groenlandiae occidentalis hactenus incognita, quod nomen specificum, triviale, vernaculumque; synonyma auctorum plurium, descriptionem, locum, victum, generationem, mores, usum, capturumque singuli; pro ut detegendi occasio fuit, maximaque parti secundum proprias observationes. Rothe, Hafniae et Lipsiae, 452 pp.

Fage, L. & Legendre, R., 1927. Pêches planctoniques à la lumière effectuées à Banyuls-sur-Mer et à Concarneau. I. Annélides polychètes. – Archs Zool. exp. gén. *67*, 23–222.

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

Fauvel, P., 1914. Annélides polychètes non pélagiques provenant des campagnes de l'Hirondelle et de la Princesse-Alice (1885–1910). – Résult. Camp. scient. Prince Albert I *46*, 1–432.

Fauvel, P., 1923. Polychètes errantes. – Faune Fr. *5*, 1–488.

Foret-Montardo, P., 1969. Étude systématique et écologique des Nephthydidæ (polychètes errantes) des parages de Marseille. – Tethys *1*, 807–832.

George, J. D., 1979. The polychaetes of Lewis and Harris with notes on other marine invertebrates. – Proc. R. Soc. Edinb. *77B*, 189–216.

Grube, A.-E., 1840. Actinien, Echinodermen und Würmer des Adriatischen und Mittelmeeres. Bon, Königsberg, 61–88.

Hansen, G. A., 1878. Annelider fra den norske Nordhavsexpedition i 1876. – Nyt Mag. Naturvid. *24*(1), 1–16.

Hartman, O., 1940. Chrysopetalidae to Goniadidae. – Allan Hancock Pacif. Exped. *7*, 173–287.

Hartman, O., 1950. Goniadidae, Glyceridae and Nephtyidae. – Allan Hancock Pacif. Exped. *15*, 1–181.

Hartman, O., 1959. Catalogue of the polychaetous annelids of the world. Part. I. – Occ. Pap. Allan Hancock Fdn *23*, 1–353.

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

Hartmann-Schröder, G. 1974. Polychaeten von Expeditionen der "Anton Dohrn" in Nordsee und Skagerrak. – Veröff. Inst. Meeresforsch., Bremerh. *14*, 169–274.

Hartmann-Schröder, G. 1977. Polychaeten aus dem Sublitoral und Bathyal vor der portugiesischen und marokkanischen Küste. – Meteor Forsch. Ergebn. (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 Forsch. Ergebn. (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 Forsch. Ergebn. (D)*35*, 1–20.

Heinen, A., 1911. Die Nephtyideen und Lycorideen der Nord- und Ostsee, einschließlich der verbindenden Meeresteile. – Wiss. Meeresunters. (Abt. Kiel) *13*, 1–87.

Imajima, M. & Takeda, Y., 1987. Nephtyidae (Polychaeta) from Japan. II. The genera *Dentinephtys* and *Nephtys*. – Bull. natn. Sci. Mus., Tokyo (Ser. A) *13*(2), 41–77.

Jirkov, I. A., 1986. *Nephtys zatsepini* sp. nov. (Polychaeta, Nephtyidae) iz Barentseva Morya. – Biol. Nauky, *1*, 39–42.

Johnston, G., 1835. Illustrations in British Zoology. *Nephtys* Cuvier. – Nat. Hist. Mag. *8*, 341–343.

Kirkegaard, J. B., 1969. A quantitative investigation of the central North Sea Polychaeta. – Spolia zool. Mus. haun. *29*, 1–285.

Laborda, A. J., 1987. Estudio con el SEM (scanning electron mycroscopy) de tres especies del género *Nephtys*. – Cah. Biol. mar. *28*, 131–146.

Laborda, A. J. & Viéitez, J. M., 1984. Anélidos poliquetos intermareales endémicos de Galicia (con la descripción de una nueva especie del género *Nephtys*). – Cuard. marisqu., Publ. téc. de la Consellaria de Agricultura, Pesca e Alimentacion, Xunta de Galicia, *7*, 207–221.

McIntosh, W. C., 1900. Notes from the Gatty Marine Laboratory, St. Andrews. – Ann. Mag. nat. Hist. (Ser. 7) *5*, 254–268.

McIntosh, W. C. 1908. A monograph of the British annelids. Ray Soc., London, *2*(1), 1–232.

Malm, A. W., 1874. Annulater i hafvet utmed Sverges vestkust och omkring Göteborg. – Göteborgs VetenskAkad., Samh. Handl. *14*, 67–105.

Malmgren, A. J., 1865. Nordiska hafs-Annulater. – K. svenska VetenskAkad. Forh. *21*, 51–110.

Malmgren, A. J., 1867. Annulata Polychaeta Spetsbergiae, Grönlandiae, Islandiae et Scandinaviae hactenus incognita. – K. svenska VetenskAkad. Forh. *24*, 127–235.

Marenzeller, E. von, 1889. Spitzbergische Anneliden. Beiträge zur Fauna Spitzbergens. – Arch. Naturgesch. *55*(1), 127–132.

Michaelsen, W., 1896. Die Polychaetenfauna der deutschen Meere einschliesslich der benachbarten und verbindenden Gebiete. – Wiss. Meeresunters. (Abt. Helgoland) *2*(1), 1–218.

Möbius, K., 1875. Vermes. – Jber. Commn wiss. Unters. dt Meere in Kiel für die Jahre 1872, 1873. *2–3*, 153–172.

Müller, O. F., 1776. Zoologica danicae prodromus seu animalium Daniae et Norvegiae indigenarum characters, nomine et synonyma imprimis popularium. Hafniae, 274 pp. [published in 1777.]

Olive, P. J. W., 1977. The life-history and population structure of the polychaetes *Nephtys caeca* and *Nephtys hombergii* with special reference to the growth rings in the teeth. – J. mar. biol. Ass. U.K. *57*, 133–150.

Olive, P. J. W. & Morgan, P. J., 1983. A survey of the age structure of beach populations of *Nephtys* spp. in the British Isles. The basis of population fluctuations. – Oceanologica Acta (Vol. spéc.), 141–145.

Örsted, A. S., 1842. Udtog af en Beskrivelse af Grønlands Annulata dorsibranchiata. – Naturhistorisk Tidsk. (Ser. 1) *4*, 109–127.

Örsted, A. S., 1843. Maricolae. Annulatorum danicorum conspectus. Hafniae, *1*, 52.

Quatrefages, A. de, 1865. Histoire naturelle des annelés marins et d'eau douce. Annélides et Géphyriens. Libr. Encycl. de Rôret, Paris, *1*, 1–588.

Rainer, S. F., 1984. *Nephtys pente* sp. nov. (Polychaeta: Nephtyidae) and a key to *Nephtys* from northern Europe. – J. mar. biol. Ass. U.K. *64*, 899–907.

Rainer, S. F., 1989. Redescription of *Nephtys assimilis* and *N. kersivalensis* (Polychaeta: Phyllodocida) and a key to *Nephtys* from northern Europe. – J. mar. biol. Ass. U.K. *69*, 875–889.

Rainer, S. F., 1990. The genus *Nephtys* (Polychaeta: Phyllodocida) of northern Europe: redescription of *N. hystricis* and *N. incisa*. – J. nat. Hist. *24*, 361–372.

Rainer, S. F., 1991. Distribution, growth and production of *Nephtys hombergii* and *N. assimilis* (Polychaeta: Nephtyidae) in benthic communities of the North Sea. – Bull. mar. Sci. *48* (in press.).

Saint-Joseph, A. de, 1894. Les annélides polychètes des côtes de Dinard. 3me partie. – Annls Sci. nat., Zool. Paléontol. (Sér. 7) *17*, 1–395.

Savigny, J. C. de, 1818. Annelids. In: Histoire naturelle des animaux sans vertèbres, Ed. par J. B. de Lamarck. Deterville, Paris *5*, 1–612.

Schack, F., 1886. Anatomisch-histologische Untersuchung von *Nephtys coeca* Fabricius. Ein Beitrag zur Kenntnis der Fauna der Kieler Bucht. Lipsius & Tischer, Kiel, 38 pp.

Schubert, A. & Reise, K., 1986. Predatory effects of *Nephtys hombergii* on other polychaetes in tidal flat sediments. – Mar. Ecol. Progr. Ser. *34*, 117–124.

Théel, H. J. 1879. Les Annélides polychètes des mers de la Nouvelle-Zemble. – K. svenska VetenskAkad. Handl. *16*(3), 3–75.

Treadwell, A. L., 1914. Polychaetous annelids of the Pacific coast in the collections of the zoological museum of the University of California. – Univ. Calif. Publs Zool. *13*, 175–234.

Warwick, R. M. & Price, R., 1975. Macrofauna production in an estuarine mud flat. – J. mar. biol. Ass. U.K. *55*, 1–18.

Wirén, A., 1883. Chaetopoder fran Sibirska Ishafvet och Berings Hav insamlade under Vega-Expeditionen 1878–79. – Vega-Expedition-Vetenskapliga Iakttagelser *2*, 383–428.

Woolf, W. J., 1968. De familie Nephtyidae (Polychaeta). – Tabellenserie van de Strandwerkgemeenschap *22*, 1–7.

Woolf, W. J., 1973. The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse and Scheldt. – Zool. Verhand., Leiden *126*, 1–242.