



A revision of *Nereimyra* (Psamathini, Hesionidae, Aciculata, Annelida)

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Received 15 February 2011; revised 18 April 2011; accepted for publication 18 April 2011

Nereimyra Blainville, 1828 (Psamathini, Hesionidae, Aciculata, Annelida) is revised based on examination of all available types and newly collected specimens. We assessed the phylogeny of *Nereimyra* in an analysis based on cytochrome oxidase c subunit I (COI), 16S rDNA, 18S rDNA, and 28S rDNA. The genus is delineated to include the three species *Nereimyra aphroditoides* (Fabricius, 1780), *Nereimyra punctata* (O.F. Müller, 1776), and *Nereimyra woodsholea* (Hartman, 1965), which are redescribed. *Nereimyra punctata* has a characteristic pigmentation, but otherwise there are no clear morphological characters for separating the species. Based on the molecular data we obtained strong support both for the monophyly of *Nereimyra* and for each of the three included species. *Nereimyra punctata* and *N. woodsholea* are sister species, and the Kimura two-parameter (K2P)-corrected COI distances between the three species are 16–23%. *Syllidia* Quatrefages, 1866, is sister group to *Nereimyra*. Previous uncertainties regarding the type species of the genus are settled to *Nereis rosea* Fabricius, 1780, junior synonym of *N. aphroditoides*. A neotype is designated for *N. aphroditoides*. The distribution of *Nereimyra* is at present restricted to the Arctic and the boreal parts of the North Atlantic, possibly extending to the Gulf of Mexico on the United States east coast. Records outside this area require verification. *Castalia multipapillata* Théel, 1879, and *Nereimyra alvinae* Blake, 1985, are of uncertain affinity and are treated as *nomina dubia*.

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doi: 10.1111/j.1096-3642.2011.00756.x

ADDITIONAL KEYWORDS: neotype – phylogeny – Polychaeta – redescription – type species.

INTRODUCTION

The hesionid genus *Nereimyra* was introduced by Blainville (1828) for the single species *Nereimyra rosea* (Fabricius, 1780). The animals are common in northern European and Arctic waters and can occur in large numbers, especially in shallow waters. *Nereimyra* has never been revised or properly delineated, and has variously included species that in the recent literature are referred to *Neopodarke* Hartman, 1965, *Ophiodromus* Sars, 1862, *Parasyllidea* Pettibone, 1961, and *Psamathe* Johnston, 1836. Several of these taxa are today not considered to be close to *Nereimyra*

(Pleijel, 1998; Ruta *et al.*, 2007). Furthermore, the type species of *Nereimyra* has variously been stated to be *Nereis rosea* (Fabricius, 1780), *Nereimyra punctata* (Müller, 1776), and *Nereimyra aphroditoides* (Fabricius, 1780). Based on cytochrome oxidase c subunit I (COI), 16S rDNA, 18S rDNA, and 28S rDNA we here assess the phylogeny of *Nereimyra* and the included species, provide redescrptions of the species, and sort out nomenclatural issues within the group.

MATERIAL AND METHODS

Newly collected specimens for standard microscopy were relaxed with 7% magnesium chloride in fresh water, fixed in 10% formaldehyde in sea water for a

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few days, rinsed in fresh water and transferred to 70% alcohol, and specimens for scanning electron microscopy (SEM) were fixed in 1% osmium tetroxide in the magnesium chloride solution for 1 h, rinsed in fresh water, conserved in 70% alcohol, critical point-dried, and sputter-coated. Specimens for DNA sequencing were fixed directly in 95% alcohol. Origin of specimens, GenBank accession numbers, and deposition of vouchers are detailed in Table 1. Eight hesionid species were used as outgroups, together with one chrysopetalid and one nereidid (Table 1). DNA was extracted using a DNAeasy Tissue Kit (Qiagen) following the protocol supplied by the manufacturer. We amplified 627–658 and 467–510 bp of the mitochondrial genes COI and 16S rDNA, respectively, and 744–792 and 1742–1743 bp of the nuclear 28S rDNA and 18S rDNA, respectively. We used the primers LCOI490, HCO2198 (Folmer *et al.*, 1994), and COI-E for COI (Bely & Wray, 2004), 16SarL and 16SbrH for 16SrDNA (Palumbi, 1996), 28SC1' (Dayrat *et al.*, 2001) and 28SD2 for 28S rDNA (Lê *et al.*, 1993), and PCR1F, PCR2F, PCR1R, and PCR2R for 18S rDNA (Nygren & Sundberg, 2003). PCR mixtures contained 21 µl double-distilled H₂O, 1 µl of each primer (10 µM), 2 µl DNA template, and puReTaq Ready-To-Go PCR Beads (Amersham Biosciences). The temperature profile was as follows: 96 °C/240 s–(94 °C/30 s–48–58 °C/30 s–72 °C/60 s)*45 cycles –72 °C/480 s. PCR products were purified with 5 µL mixture of exonuclease I and FastAP thermosensitive alkaline phosphatase (Fermentas) (Werle *et al.*, 1994). Sequencing was performed at Macrogen Inc. facilities (Seoul, Korea). Overlapping sequence fragments were merged into consensus sequences using GENEIOUS 5.1.7 (Drummond *et al.*, 2010). The protein coding COI was trivial to align, whereas the ribosomal genes were aligned using MAFFT v. 6.814b (Katoh *et al.*, 2002) within GENEIOUS 5.1.7 with the following settings: algorithm = E-INS-i, scoring matrix = 200 PAM/k = 2, gap open penalty = 1.53. We used the online GBlocks server v. 0.91b (Castresana, 2002), using the option 'Allow gap positions within the final blocks', to detect alignment-ambiguous sites that were subsequently excluded from the analysis (Gatesy, DeSalle & Wheeler, 1993; Castresana, 2000; Talavera & Castresana, 2007). The nuclear and the mitochondrial data sets were analysed separately and combined. Bayesian analyses were run in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003), and the best-fit models were selected using the Akaike information criterion (AIC) in MrModeltest 2.1 (Nylander, 2004). For the first positions in COI we used a general time reversible model with gamma distributed rate across sites with a proportion of the sites invariable (GTR + G + I), for the second and third positions in COI, as well as for 16S rDNA, and 18S rDNA we used

a GTR + G model, and for 28S rDNA we used a GTR + I model. The partitions were unlinked except for the mitochondrial protein-coding COI where the stationary frequencies and rate matrices were linked for the three positions. The number of generations was set to five million with four parallel chains (three hot, one cold), sample frequencies set to 1000, and numbers of runs set to two. One quarter of the samples was discarded as burn ins. Parameters were altered in the proposal mechanisms to acquire a span of 20–60% acceptance rates for the moves in the cold chain of each run (Gelman *et al.*, 2009). The following changes were made in the analysis of the combined data set: *change (state frequencies) with Dirichlet proposal*, Dirichlet parameter from 300 to 800, *change (gamma shape) with multiplier*, multiplier tuning parameter (lambda) from 0.811 to 2.1, *change (proportion invariable sites) with sliding window*, sliding window size from 0.1 to 0.25, and *change (rate multiplier) with Dirichlet proposal*, Dirichlet parameter from 500 to 3000. The following changes were made in the analysis of the mitochondrial data set: *change (state frequencies) with Dirichlet proposal*, Dirichlet parameter from 300 to 800, *change (gamma shape) with multiplier*, multiplier tuning parameter (lambda) from 0.811 to 3, and *change (prop. invar. sites) with sliding window*, sliding window size from 0.1 to 0.3. The following changes were made in the analysis of the nuclear data set: *change (state frequencies) with Dirichlet proposal*, Dirichlet parameter from 300 to 800, *change (gamma shape) with multiplier*, multiplier tuning parameter (lambda) from 0.811 to 2.5, *change (prop. invar. sites) with sliding window*, sliding window size from 0.1 to 0.15, *change (rate multiplier) with Dirichlet proposal*, Dirichlet parameter from 500 to 250, and *change (topology and branch lengths) with extending tree bisection-reconnection*, extension probability from 0.8 to 0.5, and multiplier tuning parameter 0.94 to 0.5. Proposal rates were not changed. Heating temperature was changed to 0.4 in the analysis of the nuclear data set; otherwise the default value (0.2) was used. Rate prior for the partition rate multiplier was set to be variable, and the prior for branch lengths was changed to Unconstrained: Exponential (100) to avoid the 'land of long trees' (Marshall, 2010). The tree files were analysed in AWTY (Are We There Yet) (Wilgenbusch *et al.*, 2004; Nylander *et al.*, 2008) to interpret visually if the analyses had reached the stationary phase. Numbers of haplotypes were either determined in GENEIOUS 5.1.7 or in TCS 1.21 (Clement, Posada & Crandall, 2000). Amino acid sequence for COI was established in GENEIOUS 5.1.7, and statistical parsimony haplotype networks were generated for COI in TCS 1.21. Genetic variation was calculated in PAUP*4.0b10 (Swofford, 2002) and Microsoft Excel 2004 for Mac,

Table 1. Sequenced specimens, vouchers and GenBank numbers

	Origin	Voucher	18S rDNA	28S rDNA	16S rDNA	COI
<i>Nereis pelagica</i>	Sweden	SMNH83519†	AY340438	AY340407	AY340470	–
<i>Dysponetus bulbosus</i>	Adelaide, Australia	SMNH83517†	–	DQ442599	DQ442570	–
<i>Leocrates chinensis</i>	New Caledonia	SMNH83510†	DQ442589	DQ442605	DQ442575	DQ442565
<i>Ophiudromus flexuosus</i>	Sweden	SMNH83508†	DQ442592	DQ442607	DQ442578	DQ442567
<i>Micropodarke dubia</i>	New Caledonia	SMNH83521†	DQ442590	DQ442597	DQ442576	–
<i>Hesiospina aurantiaca</i>	Croatia (COI)	SMNH-113855*	JF317208	JF317203	–	JF317197
	Sweden (18S, 28S)	SMNH-113856*	–	–	–	–
<i>Syllidia armata</i>	Sweden	SMNH83514†	DQ442596	DQ442612	DQ442583	DQ442568
<i>Psamathe fusca</i>	Sweden	SMNH83516†	DQ442595	DQ442610	DQ442581	DQ513294
<i>Vrijenhoekia balaenophila</i>	Off California	SMNH6305†	JF317209	DQ513306	DQ513301	DQ513296
<i>Sirsoe methanicola</i>	Gulf of Mexico	F. P.'s collection*	JF317210	DQ442611	DQ442582	DQ513295
<i>Nereimyra aphroditoides</i> spm 1	W Greenland	SIO-BIC 2285*	–	JF317204	JF317211	JF317198
<i>Nereimyra aphroditoides</i> spm 2	W Greenland	SIO-BIC 2286*	–	JF317205	JF317212	JF317199
<i>Nereimyra aphroditoides</i> spm 3	W Greenland	Destroyed	–	–	JF317213	JF317200
<i>Nereimyra aphroditoides</i> spm 4	Svalbard	SMNH-113853*	–	–	JF317214	JF317201
<i>Nereimyra aphroditoides</i> spm 5	Svalbard	SMNH-113854*	–	–	JF317206	JF317202
<i>Nereimyra punctata</i> spm 1	Sweden	SMNH76989*	DQ442591	–	DQ442606	DQ442566
<i>Nereimyra punctata</i> spm 2	Sweden	SMNH76989*	–	–	–	AY644789
<i>Nereimyra punctata</i> spm 3	Sweden	SMNH76990*	–	–	–	AY644790
<i>Nereimyra punctata</i> spm 4	Sweden	SMNH76992*	–	–	–	AY644791
<i>Nereimyra punctata</i> spm 5	Sweden	SMNH76991*	–	–	–	AY644792
<i>Nereimyra punctata</i> spm 6	Norway	SMNH76993*	–	–	–	AY644793
<i>Nereimyra punctata</i> spm 7	Norway	SMNH76994*	–	–	–	AY644794
<i>Nereimyra punctata</i> spm 8	Norway	SMNH76995*	–	–	–	AY644795
<i>Nereimyra punctata</i> spm 9	Norway	SMNH76997*	–	–	–	AY644796
<i>Nereimyra woodsholea</i> spm 1	Sweden	SMNH76981*	–	–	–	AY644797
<i>Nereimyra woodsholea</i> spm 2	Sweden	SMNH76982*	–	–	–	AY644798
<i>Nereimyra woodsholea</i> spm 3	Sweden	SMNH76983*	–	–	–	AY644799
<i>Nereimyra woodsholea</i> spm 4	Sweden	SMNH76984*	–	–	–	AY644800
<i>Nereimyra woodsholea</i> spm 5	Norway	SMNH76985*	–	–	–	AY644801
<i>Nereimyra woodsholea</i> spm 6	Norway	SMNH76986*	–	JF317207	–	AY644802
<i>Nereimyra woodsholea</i> spm 7	Norway	SMNH76987*	–	–	–	AY644803
<i>Nereimyra woodsholea</i> spm 8	Norway	SMNH76988*	–	–	–	AY644804
<i>Nereimyra woodsholea</i> spm 9	Middle Atlantic Bight	SMNH76998*	–	–	JF317215	AY644805

*hologenophore.

†paragenophore.

GenBank numbers of new sequences are in bold type. Voucher terminology follows Pleijel *et al.* (2008).

version 11.2.5. Alignments are available at TreeBase and can be accessed at <http://purl.org/phylo/treebase/phyloids/study/TB2:S11227>.

Abbreviations for museums and other depositories are: BIOICE, Benthic Invertebrates of Icelandic Waters, Sandgerdi Marine Centre; LACM-AHF, Los Angeles County Museum of Natural History, Allan Hancock Foundation; SIO-BIC, Scripps Institution of Oceanography, Benthic Invertebrate Collection; SMNH, Swedish Museum of Natural History, Stockholm; and USNM, National Museum of Natural History, Smithsonian Institution, Washington DC.

NOMENCLATURAL SYNOPSIS OF *NEREIMYRA*

1776. Müller described *Nereis punctata*.
 1780. Fabricius described *Nereis aphroditoides* and *Nereis rosea*.
 1822. Savigny described *Castalia* for the single species *Nereis rosea*.
 1828. Blainville described *Nereimyra* for *Nereis longissima* and *Nereis rosea*.
 1843. Ørsted placed *Nereis rosea* in synonymy with *N. punctata* and referred *Nereis punctata* to *Castalia*.
 1843. Rathke described *Halimede* for the single species *Halimede venusta*.
 1862. Sars described *Castalia aurantiaca* and *C. longicornis* and placed *Halimede* in synonymy with *Castalia* and *Halimede venusta* in synonymy with *Castalia punctata*.
 1866. Parfitt described *Psammate* [sic] *pustulata*.
 1867. Malmgren described *Castalia arctica* and *C. fabricii*.
 1879. Théel described *Castalia multipapillata*.
 1883. Wirén placed *Castalia fabricii* and *C. arctica* in synonymy with *C. aphroditoides*.
 1885. Verrill described *Castalia cincinnata*.
 1886. Haswell described *Psamathe crinita*.
 1906. Augener described *Castalia hesionides*.
 1908. McIntosh placed *Nereis rosea* and *Psamathe pustulata* Parfitt, 1866 in synonymy with *Castalia punctata*, and *Nereis aphroditoides* and *Castalia fabricii* in synonymy with *Castalia arctica*.
 1920. Chamberlin described *Psamathe britannica*.
 1948. Støp-Bowitz noted that *Castalia* was preoccupied by *Castalia Lamarck*, 1819 (Mollusca), and that the oldest available name is *Nereimyra*.
 1959. Hartman designated *Nereis punctata* as type species for *Nereimyra*, placed *Nereis rosea* in synonymy with *Nereis punctata*, and transferred *Castalia aurantiaca* Sars, 1862, *Castalia cincinnata* Verrill, 1885, *Castalia hesionides* Augener, 1906, *Castalia longicornis* Sars, 1862, *Castalia multipapillata*, *Nereis aphroditoides*, *Nereis punctata*, *Psamathe britannica*, *Psamathe crinita* Haswell, 1886 to *Nereimyra*. Note: *Castalia hesionides* was also referred by Hartman to *Dalhousiella* in the same study.
 1960. Knox described *Nereimyra blacki*.
 1961. Pettibone (1961) transferred *Nereimyra blacki* to *Parasyllidea* Pettibone, 1961, 1963. Pettibone incorrectly stated that Støp-Bowitz (1948) had designated *Nereis rosea* as type for *Nereimyra*.
 1965. Hartman described *Neopodarke* for the single species *N. woodsholea*.
 1971. Knox & Cameron described *Nereimyra longocirrata*.
 1985. Blake described *Nereimyra alvinae*.
 1998. Pleijel placed *Neopodarke* in synonymy with *Nereimyra* and transferred *Castalia hesionides* to *Dalhousiella*, *Neopodarke woodsholea* to *Nereimyra*, *Nereimyra blacki* to *Parasyllidea*, *Psamathe crinita* to *Gyptis*, *Nereimyra longocirrata* to *Ophiodromus*, and considered *Nereimyra alvinae* to be of uncertain affinity. Pleijel with a questionmark also referred *Castalia cincinnata* to *Podarkeopsis*.
 2004. Pleijel transferred *Castalia aurantiaca* and *C. longicornis* to *Hesiospina* Imajima & Hartman, 1964.
 2006. Ruta & Pleijel placed *Psamathe britannica* in synonymy with *Syllidia armata* Quatrefages, 1966.

PHYLOGENY OF *NEREIMYRA*

PHYLOGENETIC ANALYSIS

The combined data set of COI, 16S rDNA, 28S rDNA, and 18S rDNA consisted of 3832 aligned positions. Amongst the 3646 characters left after excluding alignment ambiguous regions, 1088 are variable, whereof 596 are parsimony-informative. The resulting majority rule consensus tree from the Bayesian analysis has 11 nodes with posterior probabilities (PP) ≥ 0.95 (Fig. 1). The results from the analyses on the separate mitochondrial and nuclear data sets are largely congruent with the combined analysis. There is a single conflicting node with PP ≥ 0.95 amongst the analyses where *Leocrates chinensis* Kinberg, 1866 and *Ophiodromus flexuosus* (Delle Chiaje, 1825) are sister taxa in the mitochondrial phylogenetic tree (PP = 1.0), but consecutive sisters to the remainder hesionids in the phylogenetic trees based on the nuclear (PP = 0.95) and the combined data sets (PP = 0.98). Both separate and combined analyses favour *Syllidia armata* Quatrefages, 1866 as the sister taxon to a monophyletic *Nereimyra* (PP = 1.0 for both nodes in all analyses), and a closer relationship between *N. punctata* (Müller, 1776) and *N. woodsholea* (Hartman, 1965) than either of them has to

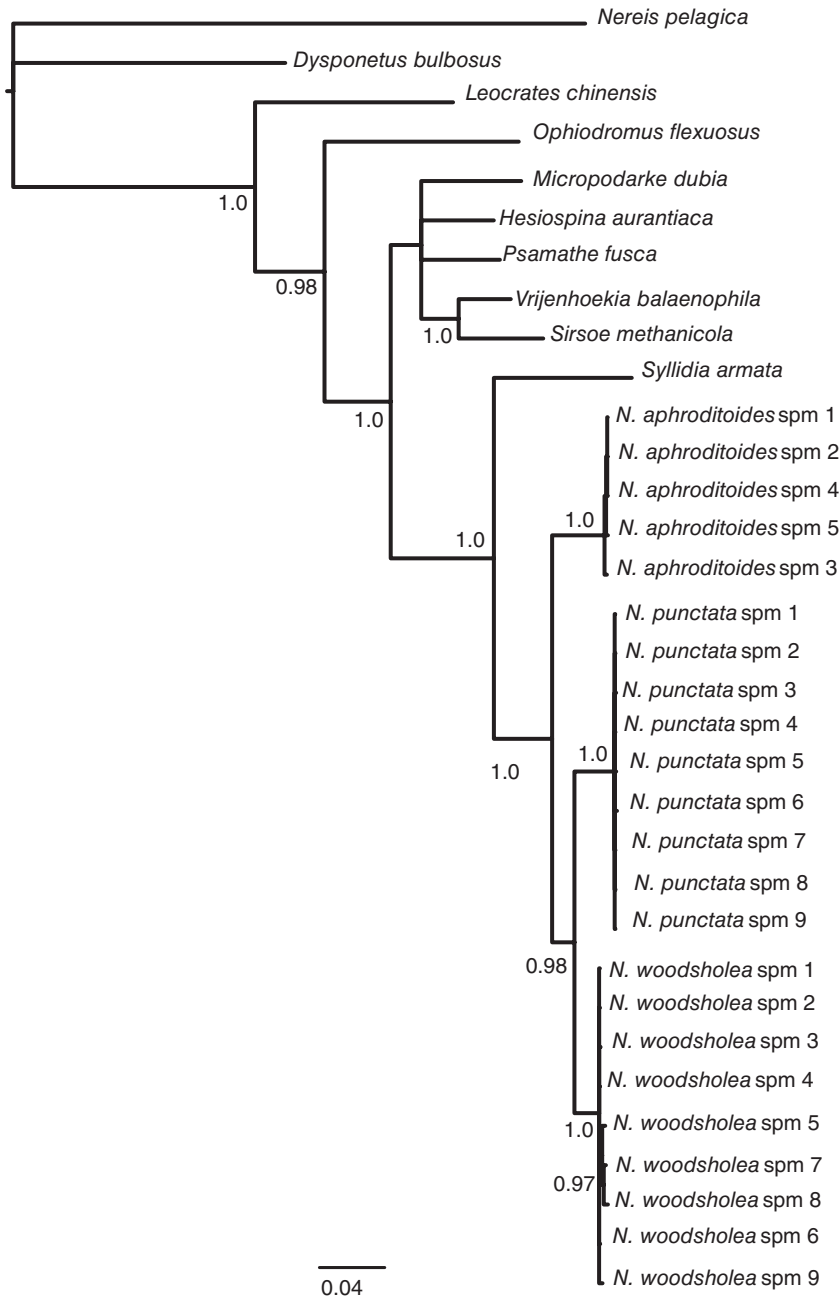


Figure 1. Bayesian majority rule consensus tree from the combined analysis. Posterior probabilities ≥ 0.95 shown.

N. aphroditoides (Fabricius, 1780) (PP = 0.99, 0.82, 0.98 in mitochondrial, nuclear and combined data sets, respectively).

POPULATION GENETIC ANALYSIS

The COI data set consists of 658 aligned positions. Including only *Nereimyra* terminals, 160 characters are variable of which 153 are parsimony-informative. Of those, 19 occur in the first position, and 134 in the

third position. Three of the substitutions separating *N. aphroditoides* from *N. punctata* and *N. woodsholea* result in amino acid changes in amino acid positions 139, 152, and 153. There is also a single amino acid changes within *N. woodsholea* in amino acid position 198. The mean Kimura two-parameter (K2P)-corrected distance between *N. aphroditoides* and *N. punctata* is $23.0 \pm 0.1\%$ (range 22.7–23.2%), the mean K2P-corrected distance between *N. aphroditoides* and *N. woodsholea* is $20.1 \pm 0.3\%$ (range 19.7–

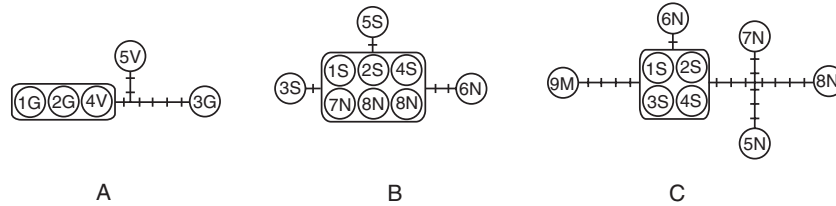


Figure 2. Haplotype networks for cytochrome oxidase c subunit 1. A, *Nereimyra aphroditoides*. B, *Nereimyra punctata*. C, *Nereimyra woodsholea*. Each bar across a line connecting two specimens denotes one mutation. Numbers correspond to specimen numbers in Table 1, and letters indicate origin (G, Greenland; M, Middle Atlantic Bight; N, Norway; S, Sweden; V, Svalbard).

20.8%), and the K2P-corrected distance between *N. punctata* and *N. woodsholea* is $16.6 \pm 0.3\%$ (range 16.0–17.4%). There are three haplotypes in both *N. aphroditoides* and *N. punctata*, and six haplotypes in *N. woodsholea* (Fig. 2). Mean intraspecific variation is $0.47 \pm 0.36\%$ (range 0–0.94%) in *N. aphroditoides*, $0.15 \pm 0.15\%$ (range 0–0.48%) in *N. punctata*, and $0.76 \pm 0.49\%$ (range 0–1.8%) in *N. woodsholea*. Haplotypes are shared between specimens from Greenland and Svalbard in *N. aphroditoides*, and between specimens from Norway and Sweden in *N. punctata*, whereas for *N. woodsholea* the closest haplotypes for specimens from Norway and Sweden are separated by a single mutation (Fig. 2). The 16S data set for *Nereimyra* terminals consists of 503 aligned positions and there are no inferred indel-events present. Of 33 variable characters, 14 are parsimony-informative. The mean K2P-corrected distance between *N. aphroditoides* and *N. punctata* is $5.1 \pm 0.1\%$ (range 4.9–5.1), the mean K2P-corrected distance between *N. aphroditoides* and *N. woodsholea* is $5.6 \pm 0.4\%$ (range 5.0–5.8), and the K2P-corrected distance between *N. punctata* and *N. woodsholea* is 3.1%. Amongst the four specimens that were sequenced for *N. aphroditoides* there are two haplotypes, separated by a single mutation, whereas only single specimens were sequenced for *N. punctata* and *N. woodsholea*. The 28S data set for *Nereimyra* terminals consists of 786 aligned positions; there are no inferred indel-events present. Of 13 variable characters, 12 are parsimony-informative. The mean K2P-corrected distance between *N. aphroditoides* and *N. punctata* is $2.1 \pm 0.0\%$, and the mean K2P-corrected distance between *N. aphroditoides* and *N. woodsholea* is $1.7 \pm 0.0\%$. A single mutation separates *N. punctata* and *N. woodsholea* (K2P-corrected distance = 0.16%). A single haplotype was found in the three specimens that were sequenced for *N. aphroditoides* whereas only single specimens were sequenced for *N. punctata* and *N. woodsholea*. 18S rDNA was only sequenced for *N. punctata* amongst the *Nereimyra* terminals.

TAXONOMY

PSAMATHINI PLEIJEL, 1998

NEREIMYRA BLAINVILLE, 1828

Nereimyra Blainville, 1828: 468.

Castalia Savigny, 1822: 45–46. Type species *Nereis rosea* Fabricius (1780), by monotypy.

Junior homonym of *Castalia* Lamarck, 1819: 66 (Mollusca).

Halimede Rathke, 1843: 161–168. Type species *Halimede venusta* Rathke, 1843, by monotypy. Junior homonym of *Halimede* de Haan in Siebold, 1835: 35 (Crustacea). *Neopodarke* Hartman, 1965: 68. Type species *Neopodarke woodsholea* Hartman, 1965, by original designation.

Type species: *Nereis rosea* Fabricius, 1780, by subsequent designation (Hartman, 1959: 189)

Description: Psamathini with stout body shape, anteriorly truncate and posteriorly tapered. Prostomium quadrangular, with posterior incision, large facial tubercle present, lip glands present. Proboscis with ten terminal papillae, ventral incision, and pair of small ventral jaws. With or without capillary notochaeta, notopodial lobes absent. Neurochaetae and neuropodial lobes from segment 4. Dorsal cirri very long, ventral cirri subdistally inserted. Elevated and slightly stouter dorsal cirri on segment 5, 8, 10, 12, 15, 17, 20, 22, 25, 28, and every third segment thereafter. Pygidial papilla present.

Remarks: The delineation of *Nereimyra* has been unclear and several species have been referred to *Nereimyra* that here are not considered closely related. We here delineate the taxon to include three species, *N. aphroditoides*, *N. punctata*, and *N. woodsholea*. These three species are morphologically similar and we provide a detailed description of *N. punctata* only (being the species of the three for which we have most information) and then

detail the few differentiating characters for the other two species.

There has been some confusion in the literature regarding the type species of *Nereimyra*. Blainville (1828) in his original description of *Nereimyra* included two species, *Nereis rosea* and *Nereis longissima*, of which the latter has by some authors (e.g. Hartman, 1959) been referred to the Phyllodocidae. Hartman (1959: 189) designated *Nereis punctata* as the type species of *Nereimyra*, a species that was not mentioned in Blainville's original description of the genus. However, she also placed *Nereis rosea* in synonymy with *Nereimyra punctata*, and because *Nereis rosea* was included in *Nereimyra* by Blainville, this act then constitutes a valid designation of *Nereis rosea* as type species (International Commission on Zoological Nomenclature, 1999, Article 69.2.2). Pettibone (1963) instead referred the typification to Støp-Bowitz (1948), but this is erroneous because Støp-Bowitz's study made no mention of a type species. See further the Remarks section for *Nereimyra aphroditoides* regarding synonymy between this species and *Nereis rosea*.

Ruta *et al.* (2007) showed that *Syllidia* is the sister group to *Nereimyra*, and that result also has strong support in our study. Morphologically the two taxa can be separated by the much larger and more elaborated dark jaws with serrated, rather than cutting, edges in *Syllidia*, the shorter dorsal cirri on the anterior segments, and the simpler neuropodia without three distinct lobes.

Nereimyra appears to have a distribution limited to the boreal parts of the North Atlantic, possibly extending south in Europe to the Iberian Peninsula and the Mediterranean (unverified records) and on the United States east coast to the Gulf of Mexico.

NEREIMYRA PUNCTATA (O.F. MÜLLER, 1776)
(FIGS 3, 4)

Nereis punctata O.F. Müller, 1776: 217; 1780: pl. LXII, figs 4, 5 ('Punkt-Nereiden'); 1788: 28, 29).

Halimede venusta Rathke, 1843: 168–169, pl. 7, figs 1–4.

Castalia punctata Malm, 1874: 82; McIntosh, 1908: 121–125, pl. 46, fig. 2, pl. 69, fig. 14, pl. 78, fig. 2; Fauvel, 1923: 240–241, fig. 89F–K.

Nereimyra punctata, Ørsted, 1843 (p. 24, figs 15, 63–65, 69); Banse, 1956: 17–24, figs 1–8; Hartmann-Schröder, 1971: 128–129, fig. 40E–H; Hartmann-Schröder, 1996: 134–135, fig. 54; Oug, 1980: 175–191, figs 1–3; Schram & Haaland, 1984: 169–181, figs 1–13, 14I–L, in part; Kirkegaard, 1992: 213–215, fig. 104; Nygren, Pleijel & Sundberg, 2005: 273–276, fig. 1.



Figure 3. *Nereimyra punctata*, dorsal view of live relaxed specimen from Bergen, Norway. Exact scale unknown but specimen is c. 2 cm long.

Psamathe punctata Quatrefages, 1866: 102.

Type material: No type material.

Type locality: Norway, Drøbak.

Material examined: DENMARK. 1 spm (ZMUC), Store Bælt; 1 spm (ZMUC), Fredrikshavn; 1 spm (ZMUC), Helsingør. ICELAND. 8 spms, north Iceland, 66°41,88'N, 20°02,98'W, 148 m, sledge, fine sand, coll. BIOICE 2.x.1994; 1 spm, south-west Iceland, 63°59,01'N, 23°34,13'W, 137 m, sledge, fine sand, coll. BIOICE 3.ix.1992; 2 spms, north Iceland, 66°36,92'N, 18°14,42'W, 110 m, sledge, fine sand, coll. BIOICE 2.x.1994; c. 15 spms, south of Reykjavik, Skejafirði, coll. G.V. Helgason; c. 50 spms, north of Reykjavik, Hvalfjörður coll. G.V. Helgason; 5 spms, north-east Iceland, Langanes, coll. G.V. Helgason. NORWAY. 2 spms (SMNH 76993, 76994; fixed in 95% ethanol), Trondheimsfjorden, Tautra, 63°35.14'N, 10°38.87'E, 30–40 m, dredge, 12.i.2002; 2 spms (SMNH 76995, 76997; fixed in 95% ethanol), Trondheimsfjorden, Tautra, 63°35.09'N, 10°36.39'E, 20–40 m, coll. F. P. 28.i.2002; 100 + spms (F. P.'s collection, fixed in ethanol, formaldehyde and osmium tetroxide), various localities in Trondheimsfjorden, c. 15–300 m, coll. F. P. 1995–2009; 3 spms (F. P.'s collection, fixed in 95% ethanol), Bergen area, Hjeltefjorden, Føllese, 60°24.825'–60°24.667'N, 05°08.478'–05°08.493'E, 101–125 m, dead *Lophelia*, dredge, coll. F. P. 8.iii.2003. SWEDEN. 2 spms (SMNH 76989, 76990; fixed in 95% ethanol), Gullmarsfjorden, Löken, 58°13.154'N, 11°24.416'E, 33–36 m, dredge, coll. F. P. 30.iii.2003; 2 spms (SMNH 76991, 76992; fixed in 95% ethanol), west Gullmarsfjorden, Bondens hamn, 58°12.60'N, 11°18.90'E, 7–12 m, dredge, coll. F. P. 7.iv.2003; 100 + spms (F. P.'s collection, fixed in

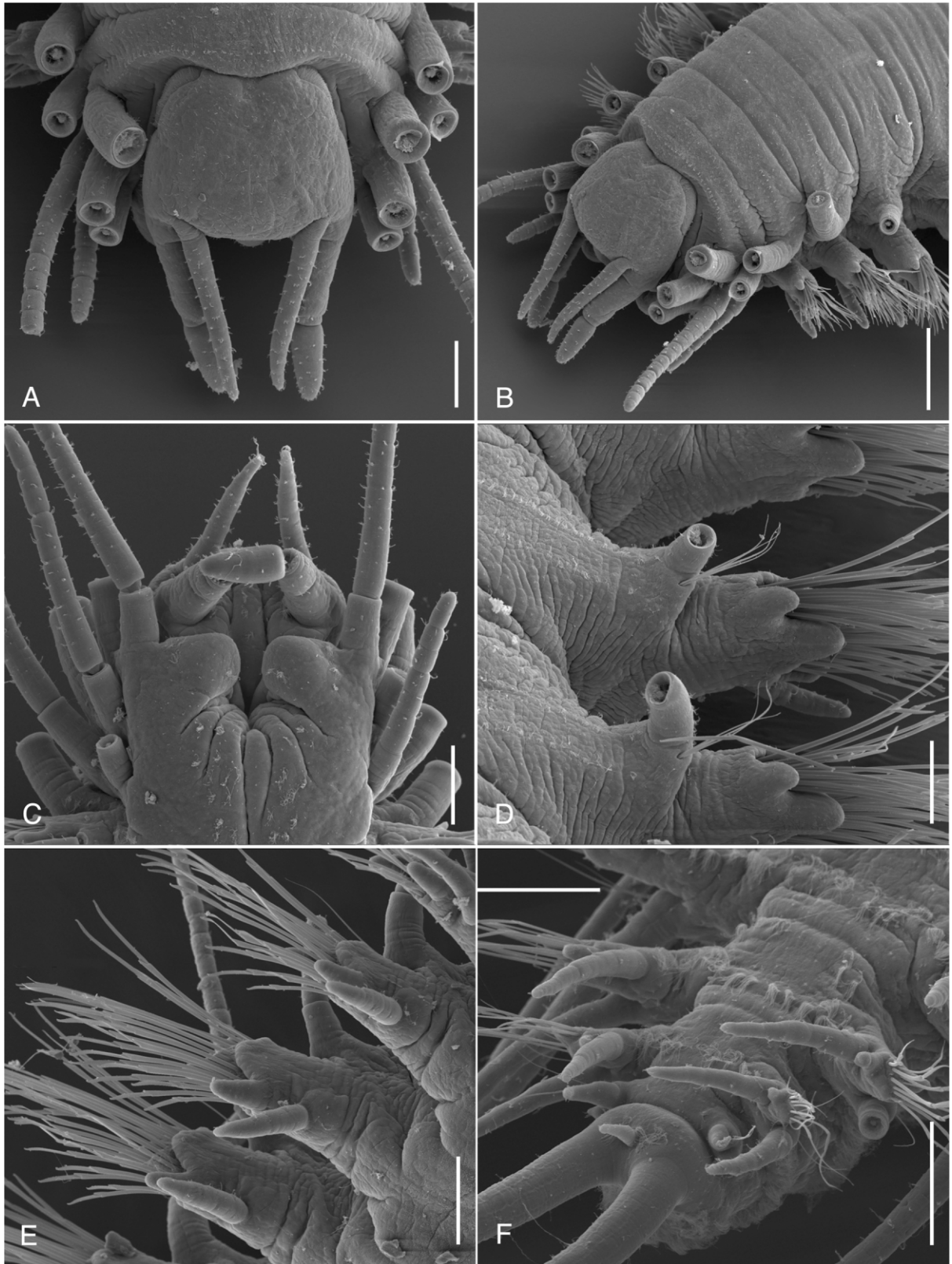


Figure 4. *Nereimyra punctata*, scanning electron microscopy photographs of specimens from Bergen, Norway. A, anterior end, dorsal view. B, anterior end, anterolateral view. C, anterior end, ventral view. D, median parapodia, anterodorsal view. E, median parapodia, ventral view. F, posterior end, ventral side. Scale bars: A, C–F = 100 μ m; B = 200 μ m.

ethanol, formaldehyde and osmium tetroxide), various localities in Kosterhavet, c. 2–50 m, coll. F. P. 1995–2009.

Description: Length up to 24 mm for 49 segments. Live specimens yellowish transparent with green to black transverse stripes across segments (Fig. 3), always present but varying in amount and more dense on anterior part of body; posterior segments ventrally often with broad, dark longitudinal band. Eyes red. Preserved animals yellowish, black to green pigmentation retained. Body outline in dorsal view anteriorly truncated and posteriorly tapered (Fig. 3). Prostomium rounded rectangular, as wide as long, with small median posterior incision (Fig. 4A). Palpophores cylindrical, palpostyles shorter, tapering with rounded tips. Paired antennae as long as palps (Fig. 4A–C). Anterior pair of eyes elongated to kidney-shaped, larger than posterior pair; posterior pair rounded. Nuchal organs follow posterodorsal corners of prostomium (Fig. 4B). Facial tubercle present. Proboscis with smooth surface on proximal and distal ring, opening with terminal ring of ten long and stout papillae. Ventral part of opening with distinct incision. Single pair of sickle-shaped ventral jaws with cutting edges, situated on inside of proboscis incision. Lip glands present. Non-everted proboscis reaching segments 10–11. Segments 1–3 dorsally fused. Dorsal cirri and cirrophores segments 1–5 much longer and stouter than following ones. Ventral cirri segment 1–3 much longer and stouter cirri than on following segments, ventral cirrophores well delineated (Fig. 4C) and absent on following segment. All cirrophores of anterior dorsal and ventral cirri each with one to three aciculae. Segment 4 with neuropodial lobes, neurochaetae, and ventral cirri similar to following segments. Notochaetae from about segment 6. Elevated and slightly stouter dorsal cirri on segments 5, 8, 10, 12, 15, 17, 20, 22, 25, 28, and every third segment thereafter. Dorsal cirri reaching further than neurochaetae. Notopodia consisting of cirrophores only, single acicula and, on most segments, one to five very fine capillaries emerging below base of anterior side of dorsal cirrophores (Fig. 4D). Neuropodia with two pre- and two postchaetal, rounded conical lobes, appearing three-lobed in anterior and posterior view (Fig. 4E). About 50 neurochaetae, all unidentate compounds with shafts with distinct internal chambers and longitudinal canals, dorsal and median blades up to 2.5 times longer than ventral ones. Some median neurochaetae with prolonged teeth on blade. Usually double noto- and neuroaciculae. Ventral cirri tapering with rounded tips, inserted subdistally on underside of neuropodia (Fig. 4E). Pygidium with pair of long cirri, similar to dorsal cirri. Pygidial papillae present (Fig. 4F).

Biology: Gulliksen (1977) reported swarming during autumn in Lübeck Bay in the Baltic, and Banse (1956) and Schram & Haaland (1984) described the larval development of *N. punctata* from Kiel and the Oslofjord, respectively. Schram & Haaland (1984) noted the presence of two colour varieties, and the striped one of these certainly refers to *N. punctata* and the second, unpigmented, to *N. woodsholea*. They examined the larval development of both species but found no consistent differences between them. Larvae of *N. punctata*, like many other hesionids (Pleijel, 1998), have a median antenna that is subsequently lost during ontogeny. However, this occurs late in *N. punctata*, and 6–7-mm-long specimens with 25–26 segments may have a median antenna. Oug (1980) described feeding of *N. punctata*, showing that it is a predator mainly on other polychaetes and small crustaceans, especially harpacticoid copepods.

Habitat: Various hard bottoms and bottoms with shell gravel from shallow waters down to 300 m.

Distribution: Iceland, northern parts of the British Isles (southern limit uncertain), Denmark, Swedish west coast and outer parts of the Baltic, Norway to Trondheim, possibly further north. *Nereimyra punctata* has been reported a number of times from the Iberian Peninsula and the Mediterranean (e.g. Campoy, 1982; Arvanitidis, 1999; Parapar, Besteiro & Moreira, 2004), but, in spite of dense collecting in habitats where the animals normally occur, we have not been able to verify those records. Based on examined specimens it appears that *N. punctata* has a boreal distribution.

Remarks: Müller (1776) in his original description did not mention any type locality, although it can be narrowed down to Denmark or Norway, as these were the areas covered by his study. However, in two later studies (Müller, 1780, 1788), he stated that his specimens were from Drøbak in the Oslofjord and found in oysters. Müller's material of *N. punctata* is not extant, nevertheless we at present see no need for a neotype. The majority of the material examined by us is from Kosterhavet on the Swedish west coast and is situated only 50 nautical miles from Drøbak. In this area F. P. has also observed that *N. punctata* can occur in oysters (*Ostrea edulis*), in agreement with the original description.

The original description of *Psamathe pustulata* Parfitt, 1866 (as *Psammate pustulata*) is brief and without illustrations, and Parfitt (1866) only mentioned the species with reference to a manuscript by Montagu, suggesting that it was a junior synonym of *N. punctata*. Following International Commission on

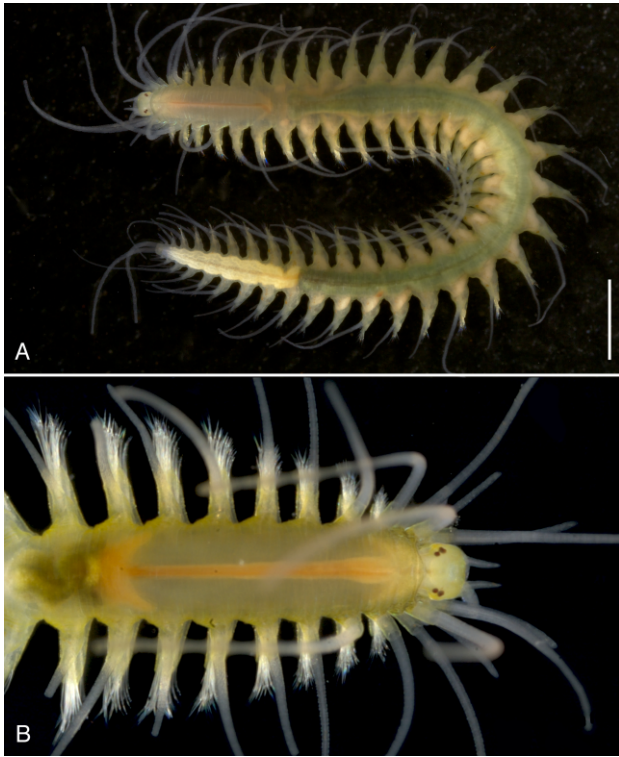


Figure 5. *Nereimyra aphroditoides*, dorsal view of live relaxed specimens. A, neotype, Disko Fjord, Greenland. B, anterior end from Svalbard. Scale bar: A = 1 mm; B, scale unknown.

Zoological Nomenclature (1999), article 11.6, this name is not available and can be disregarded as a *nomen nudum*.

Rathke (1843) described *Halimede venusta* from western Norway. The synonymy with *N. punctata*, rather than with *N. woodsholea*, is based on his description of the pigmentation.

Specimens from deeper waters tend to have weaker transverse stripes. These are nevertheless visible and provide the best feature for separating this species from the partially sympatric *N. woodsholea*. The stripes remain after fixation.

NEREIMYRA APHRODITOIDES
(FABRICIUS, 1780) (FIGS 5, 6)

Nereis aphroditoides Fabricius, 1780: 296–297.

Nereis rosea Fabricius, 1780: 301–302.

Castalia fabricii Malmgren, 1867a: 32, 1867b: 152; Théel 1879: 37–38.

Castalia arctica Malmgren, 1867a: 32, 1867b: 152.

Castalia aphroditoides Augener, 1913: 260, Augener, 1928: 715–716; Grainger, 1954: 511; Uschakov, 1955: 195. fig. 57F–I; Pettibone, 1954: 239–240, fig. 28a–b.



Figure 6. *Nereimyra woodsholea*, dorsal view of live relaxed spm from Kosterhavet, Sweden. Exact scale unknown but visible section of specimen is c. 35 mm long.

Psammate [sic] *aphroditoides* Chamberlin, 1920: 13.

Nereimyra aphroditoides Wesenberg-Lund, 1950: 44–45.

Type material: Neotype (SIO-BIC A2284).

Type locality: Greenland, Disko Fjord, 69°29.059'N, 53°56.342'W, 5–7 m.

Material examined: W GREENLAND. Neotype, entire spm preserved in Bouin's fluid (SIO-BIC 2284 G392 neotype), 1 spm, anterior part preserved in formaldehyde (SIO-BIC A2285 G 392/1) and posterior part in 95% ethanol (used for DNA sequencing), 1 spm, anterior part preserved in formaldehyde (SIO-BIC A2286 G392/2) and posterior part in 95% ethanol (used for DNA sequencing), 1 entire spm preserved in 95% ethanol (destroyed for DNA sequencing), Disko Fjord, 69°29.059'N, 53°56.342'W, 5–7 m, triangular dredge, lumps of calcareous red algae, coll. G. W. R. 2.viii.2010; 10 spms (SMNH types 2434; syntypes for *C. fabricii*), Julianehaab, 46 m, coll. C.T. Amondson 1859; 9 spms (SMNH types 2433; syntypes for *C. fabricii*), Smalesund, 61°34'N, 049°07'W, coll. C.T. Amondson 1859. SVALBARD. 11 spms (SMNH types 2429; syntypes for *C. arctica*), Kongsfjord, 5–50 m, colls Goës and Smitt, Swedish Arctic Expedition 1861; c. 50 spms (SMNH types 2428; syntypes for *C. arctica*), Isfjord, Safe Bay, 36–73 m, 78°10'N 013°30'E, coll. Swedish Arctic Expedition 1861; 3 spms (SMNH types 2427; syntypes for *C. arctica*), Widebay, 73 m, 79°00'N, 15°00'E, colls Goës and Smitt, Swedish Arctic Expedition 1861; 6 spms (SVA03 DNA61, 65, 69, 70, 72, 73, F. P.'s collection, fixed in 95% ethanol), Hinlopen, E Olav V Land, 78°40.623'N, 21°23.796'E, 60 m, detritus sledge, coll. F. P. 23.ix.2003; 1 spm,

preserved in formaldehyde (SVA05 F13) (F. P.'s collection), Olgastret, E Heleysund, 78°40.691'N, 21°25.324'E, stones, gravel with bryozoans, 57 m, detritus sledge, coll. F. P. 4.ix.2005; 7 spms (SVA05 DNA59, 65, 66, F16, 20, 21) (F. P.'s collection; 4 spms preserved in 95% ethanol, 3 spms preserved in formaldehyde), Hinlopen, 79°26.849'N, 20°08.342'E, 52 m, stones and gravel, dredge, coll. F. P. 5.ix.2005.

Description: Neotype entire spm, 11 mm long for 39 segments (Fig. 5A). Live specimens yellowish transparent with more or less distinct green pigmentation dorsally on anterior segments (Fig. 5B); posterior segments ventrally often with broad, dark longitudinal band. Eyes red. Green pigmentation disappears in preserved specimens. Notochaetae a few capillaries occurring sporadically in some segments but completely absent from most examined specimens. In all other features agreeing with the description of *N. punctata* above.

Biology: Nothing known.

Habitat: Mixed bottoms with stones and gravel, 5–73 m.

Distribution: Greenland, east Canada (southern limits uncertain), Svalbard, Franz Josef Land.

Remarks: *Nereis rosea* was treated as a synonym of *Nereimyra punctata* by Hartman (1959: 189). The latter species, however, was described from southern Norway (see Remarks for *N. punctata*) and does not occur in Arctic waters, where instead *N. aphroditoides* is present. Both *N. aphroditoides* and *N. rosea* were described by Fabricius (1780) from Greenland, but his original descriptions does not provide much detail and no types are available. There is nothing in his description that indicates that the two species even are hesionids, but we here accept this because this is how they have been interpreted subsequently, both in contemporary and older literature. We here designate a neotype specimen for *N. aphroditoides* because this name is in current use and was mentioned first as *N. rosea* by Fabricius. There is no original material of either species at the Zoological Museum, University of Copenhagen (D. Eiby-Jacobsen, pers. comm.), and considering the nomenclatural problems involving both these species names and the generic name, we consider the erection of a neotype to be justified. Fabricius did not provide information about type localities, although previous authors have assumed that he did his collecting in the Frederikshåb area. Our specimens come from Disko that is situated further north, where we have been able to recollect animals for live study and preserved for

molecular and morphological analyses. To obtain live specimens from Frederikshåb has not been feasible.

NEREIMYRA WOODSHOLEA
(HARTMAN, 1965) (FIGS 6, 7)

Neopodarke woodsholea Hartman, 1965: 69, pl. 7.

Nereimyra woodsholea Pleijel, 1998: 119–122, 160; Nygren *et al.*, 2005: 273–276.

Nereimyra punctata Schram & Haaland, 1984: 169–181, figs 1–14, in part.

Type material: Holotype (LACM–AHF Poly 0132) and 6 paratypes (LACM–AHF Poly 0133).

Type locality: North Atlantic, slope off Middle Atlantic Bight, 39°58'24"N, 70°40'18"W, 300 m, 28.viii.1962.

Material examined: NORTH ATLANTIC, SLOPE OFF MIDDLE ATLANTIC BIGHT. Holotype (LACM–AHF poly 0132), E upper end of Block canyon, 39°58'24.8N, 70°40'18W, 300 m, 6 paratypes (LACM–AHF Poly 0133), same locality. 1 spm (SMNH 76998; fixed in 95% ethanol), slope off Middle Atlantic Bight, 39°53.879'N, 69°39.38'W, 591 m, coll. A. N. 15.vi.2003. NORWAY. 5 spms (F. P.'s collection; fixed in 95% ethanol, formaldehyde and osmium tetroxide), Trondheimsfjord, Rødberg, 63°28.26'N 10°00.04'E, 500–250 m, dead *Lophelia*, dredge, coll. F. P. 21–25.viii.1995; 3 spms (SMNH 76985, 76986, 76988; fixed in 95% ethanol), Trondheimsfjorden, Rødberg, 63°28.36'N, 10°00.04'E, 180–250 m, coll. F. P. 29.i.2002; 1 spm (SMNH 76987), Trondheimsfjorden, Rødberg, 63°28.36'N, 10°00.04'E, dead *Lophelia*, dredge, 180–250 m, coll. F. P. 18.ii.2003; 12 spms (F. P.'s collection; fixed in 95% ethanol, formaldehyde, and osmium tetroxide), Trondheimsfjorden, Rødberg, 63°28.093'–63°28.329'N, 09°59.990'–09°59.982'E, c. 200 m, dead *Lophelia*, dredge, coll. F. P. 5.xii.2006; 2 spms (F. P.'s collection; fixed in 95% ethanol), Trondheimsfjorden, Rødberg, 63°28.458'–63°28.508'N, 10°00.186'–10°00.192'E, 187–200 m, dead *Lophelia*, dredge, coll. F. P. 7.v.2003. SWEDEN. 4 spms (SMNH 76981–76984; fixed in 95% ethanol), Gullmarsfjorden, Djuphålan, 58°19.50'N, 11°32.50'E, 116 m, detritus sledge, coll. F. P. 5.iv.2003; 50 + spms (F. P.'s collection; fixed in 95% ethanol, formaldehyde and osmium tetroxide), same locality and date; 30 + spms (F. P.'s collection; fixed in 95% ethanol, formaldehyde and osmium tetroxide), various localities in Kosterhavet, coll. F. P. 2000–2009.

Description: Length up to 23 mm for 45 segments. Live specimens yellowish transparent (Fig. 6), ventrally on posterior segments often with broad, dark longitudinal band. A few notochaetae usually present

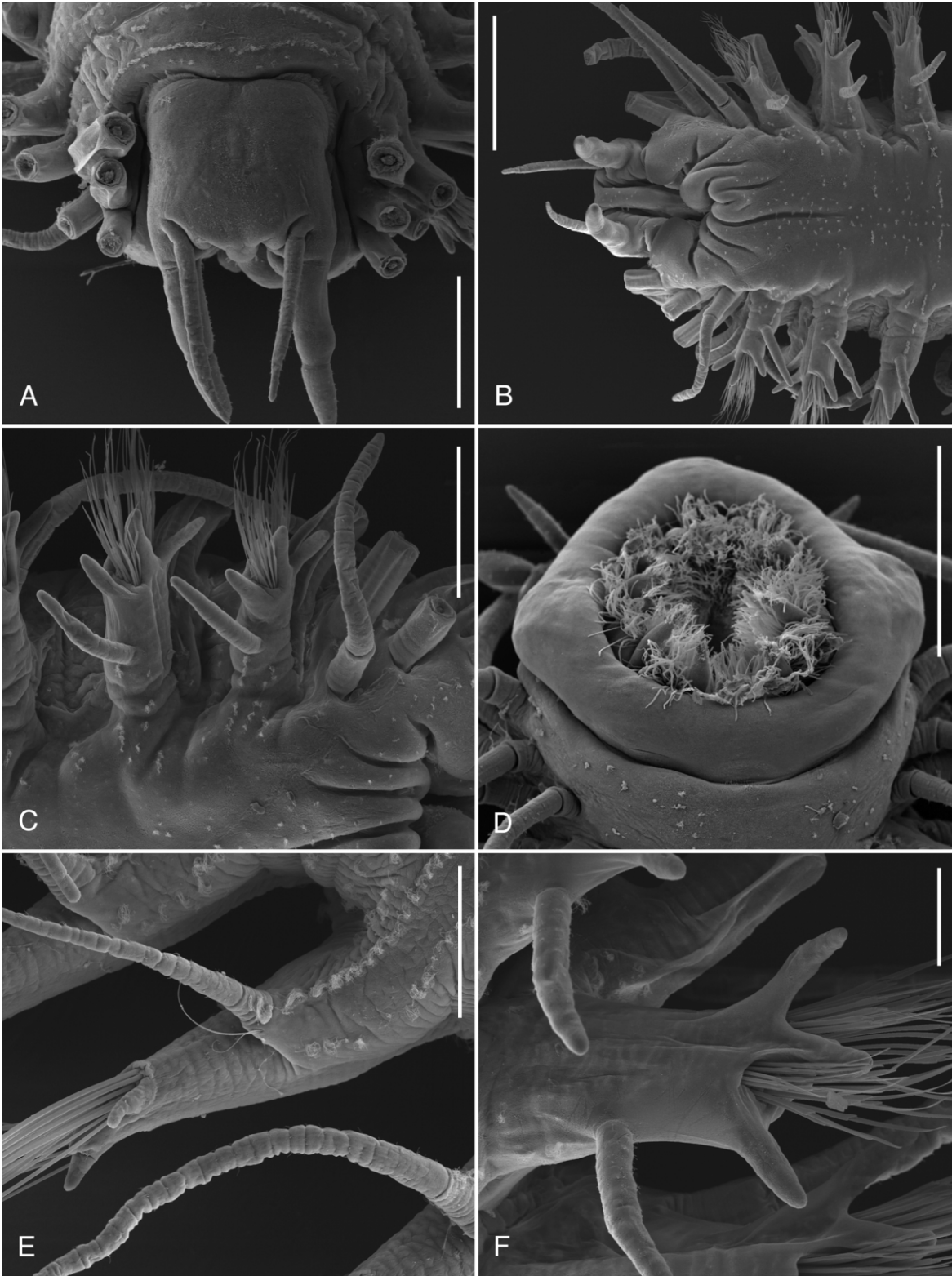


Figure 7. *Nereimyra woodsholea*, scanning electron microscopy photographs of specimens from Kosterhavet, Sweden. A, anterior end, dorsal view. B, anterior end, ventral view. C, parapodia segment 2–5, right side, ventral view. D, proboscis. E, median parapodium, right side, anterodorsal view. F, median parapodium, left side, anteroventral view. Scale bars: A, C–E = 300 μm , B = 600 μm , F = 100 μm .

from about segment 12 (Fig. 7E). In all other features agreeing with the description of *N. punctata* above.

Remarks: The description and illustrations above are based on Swedish specimens, as these were in much better condition than the type material and could also be studied alive and by SEM. They agree both with the types from the Middle Atlantic Bight and a newly collected topotype, and, based on COI analyses by Nygren *et al.* (2005) and this study, the types and the Swedish populations are conspecific.

SPECIES OF UNCERTAIN STATUS

CASTALIA MULTIPAPILLATA (THÉEL, 1879)

NOMEN DUBIUM

Castalia multipapillata Théel, 1879: 38–39, pl. 3, fig. 38.

Nereimyra multipapillata Hartman, 1959: 189.

Type material: Holotype SMNH 2432.

Type locality: Russia, Jenisej Exp 1875 sta 80, Novaya Zemlja, west opening of Matochkin Shar, 72°30'N, 54°40'N, 4–9 m, sandy mud, coll. Stuxberg & Théel, 12.vii.1875.

Material examined: Holotype SMNH 2432. Théel based his description on a single specimen that agrees with *Nereimyra* except that he reported the presence of 24 papillae on the terminal ring of the proboscis (Théel, 1879: pl. 3, fig. 38), rather than ten. Unfortunately the proboscis has been dissected and removed from the type and this feature could therefore not be re-examined. We cannot exclude the possibility that it represents an aberrant specimen of *N. aphroditoides* but treat it as a *nomen dubium* for now. Uschakov (1955) recorded this species from Bering Sea, but his description disagrees with Théel's in that he reports ten terminal proboscis papillae. To our knowledge no further records exist.

NEREIMYRA ALVINA BLAKE, 1985, *NOMEN DUBIUM*

Type material: Holotype USNM 81804, 40 + paratypes USNM 81805.

Type locality: Galapagos Rift, geothermal vents, Garden of Eden, 00°47.7'N, 86°07.7'W, 2482 m, Alvin dive 883, 24.i.1979.

Material examined: Holotype USNM 81804, 40 + paratypes USNM 81805 from type locality; 3 spms, USNM 81806, Galapagos Rift, geothermal vents, 'Mussel bed', 00°47.9'N, 86°09.2'W, 2493 m, Alvin dive 880, 21.i.1979; 2 spms, USNM 81807, Galapagos

Rift, geothermal vents, 'Rose Garden', 00°48.3'N, 86°13.5'W, 2447 m, Alvin Dive 983, 30.xi.1979.

Distribution: Galapagos Spreading Center, Guaymas Basin (Pleijel, 2006)

Remarks: The examined specimens are in too poor condition to assess the affinities of *N. alvinae*, and Blake's (1985) original description does not indicate membership of *Nereimyra*. Until further specimens are available for complementary morphological and molecular studies we regard it as a *nomen dubium*.

NEREIMYRA SP. A

Nereimyra sp. A Uebelacker, 1984: 28–23, figs 28-19, 28-20.

Material examined: GULF OF MEXICO. 1 spm (USNM 75324), West Florida Shelf, 26°45.81'N, 83°32.12'W, medium sand, 56 m; 1 spm (USNM 75325), West Florida Shelf, 26°45.70'N, 84°00.13'W, coarse sand, 91 m.

Remarks. The examined specimens are members of *Psamathe* Johnston, 1836, possibly conspecific with Perkins' (1984) *Kefersteinia* sp.

NEREIMYRA SP. B

Nereimyra sp. B Uebelacker, 1984: 28–25, figs 28-21.

Material examined: No specimens examined.

Remarks. Based on Uebelacker's description the single specimen does not belong to *Nereimyra* but may be a juvenile *Psamathe*.

GENUS A

Genus A Uebelacker, 1984 : 28-5–28-7, fig. 28-2.

Material examined: GULF OF MEXICO. 1 spm (USNM 75239), West Florida Shelf, 26°17.72'N, 83°47.67'W, fine sand, 90 m; 1 spm, (USNM 71775), West Florida Shelf, 26°16.53'N, 84°05.97'W, fine sand, 145 m.

Remarks: The specimens that originally were referred to as Genus A may actually be members of *Nereimyra*, and then probably represent a undescribed species. However, the specimens are juveniles and in poor

condition, and based on this material we can at present only refer them to *Psamathini*.

ACKNOWLEDGEMENTS

Financial support for F. P. was provided by the Swedish Research Council (dnr 2009–5215), the Fulbright Commission (research scholar award), and Carl Tryggers stiftelse för vetenskaplig forskning, and for A. N. by the Swedish Taxonomy Initiative dnr 140/07 1.4 and 166/08 1.4, and Magnus Bergvall foundation. G. W. R. thanks Reinhardt Kristensen, Martin Sørensen, and Katrine Worsaae for the invitation to join the Arctic Workshop 2010: Exploration of a cold trail: Arctic pieces to the puzzle of Evolution (Carlsberg Foundation grant 2009–01-0053) and the Board of the Arctic Station for logistical support. Special thanks to José Ignacio Carvajal for assistance with sequencing and to Alain Dubois for nomenclatural advice.

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