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

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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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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 redescriptions 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 pointdried, 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' (Davrat 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 H₂0, 1 µl of each primer (10 µM), 2 µl DNA template, and puReTag 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) multiplier, multiplier tuning parameter with (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 datas et: 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 bisectionreconnection, 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,

DQ442565 DQ442567 JF317197 **JQ**513296 00513295JF317198 JF317199 JF317200 JF317202 DQ442566 AY644798 DQ442568 Q513294 JF317201 AY644789 AY644790 AY644792 AY644793 AY644795 4Y644799 AY644800 AY644803 AY644805 AY644794 AY644796AY644797 4Y644802 4Y644804AY644791AY64480 COI 6S rDNA 00442570 00442575 00442578 00442576 JF317213 JF317206 DQ442606 **JQ442582** JF317212 JF317214 JF317215 AY340470 00442583 JQ513301 JF317211 0044258 28S rDNA DQ442605 JQ442597 JQ442612 00442610 00513306 00442599 DQ442607 JF317203 DQ442611 JF317204 JF317205 JF317207 AY340407 8S rDNA JQ442589 JQ442590 00442596 DQ442595 JF317209 JF317210 00442592 JF317208 DQ442591 AY340438 SMNH-113856* F. P.'s collection* SMNH-113853* SMNH-113854* SMNH-113855* SIO-BIC 2285* SIO-BIC 2286* SMNH83519+ SMNH83517† SMNH83510+ 3MNH83508 SMNH83521+ SMNH83514[†] SMNH83516+ *68697HNMS *68697HNMS *06697HNMS *SMNH76992 *16691HNI SMNH76994* *2669LHNMS *SWINH76982 *SWINH76983 SMNH76984* *28697HVIMS *98697HNMS *18697HNMS *8869LHNINS *8669LHNINS *E6692HNWS *INH76981 *L669LHNMS SMNH6305+ Destroyed Voucher Middle Atlantic Bight Sweden (18S, 28S) Adelaide, Australia New Caledonia New Caledonia Gulf of Mexico Off California Croatia (COI) W Greenland W Greenland W Greenland Svalbard Svalbard Norway Norway Sweden Norway Norway Norway Sweden Norway Norway Origin Vereimyra aphroditoides spm 1 $^{\circ}$ Nereimyra aphroditoides spm 3 Nereimyra aphroditoides spm 4 Nereimyra aphroditoides spm 5 Nereimyra aphroditoides spm Nereimyra woodsholea spm 3 Nereimyra woodsholea spm 5 Vereimyra woodsholea spm 8 Vereimyra woodsholea spm 9 Nereimyra woodsholea spm 1 Nereimyra woodsholea spm 2 Nereimyra woodsholea spm 4 Vereimyra woodsholea spm 6 Vereimyra woodsholea spm Nereimyra punctata spm 5 Nereimyra punctata spm 9 Nereimyra punctata spm 1 Nereimyra punctata spm 2 ೧ Nereimyra punctata spm 4 Nereimyra punctata spm 6 Nereimyra punctata spm 7 Nereimyra punctata spm 8 7rijenhoekia balaenophila Nereimyra punctata spm Ophiodromus flexuosus Hesiospina aurantiaca Asponetus bulbosus Micropodarke dubia Leocrates chinensis Sirsoe methanicola Syllidia armata Psamathe fusca Vereis pelagica

GenBank numbers of new sequences are in bold type. Voucher terminology follows Pleijel $et \, al.$ (2008). paragenophore.

hologenophore.

version 11.2.5. Alignments are available at TreeBase and can be accessed at http://purl.org/phylo/treebase/phylows/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 punc-

tata, 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 $(PP) \ge 0.95$ (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

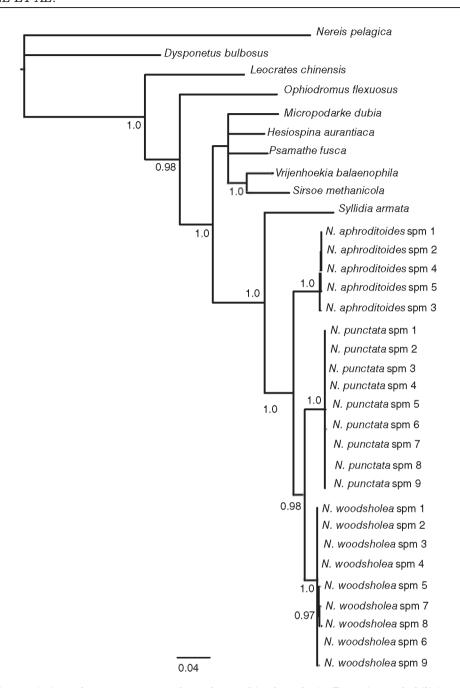


Figure 1. Bayesian majority rule consensus tree from the combined analysis. Posterior probabilities ≥ 0.95 shown.

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-

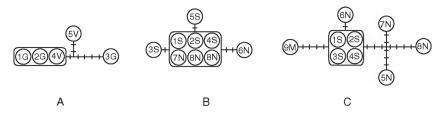


Figure 2. Haplotype networks for cytochrome oxidase c subunit 1. A, *Nereimyra aphroditoides*. B, *Nereimyra punctata*. C, *Nereimyra woodsholea*. Each bar across a line connecting two specimens denotes one mutation. Numbers correspond to specimens numbers in Table 1, and letters indicate origin (G, 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 indelevents 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 K2Pcorrected distance between N. aphroditoides and N. punctata is $2.1 \pm 0.0\%$, and the mean K2Pcorrected 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, $63^{\circ}59{,}01'\mathrm{N},\,23^{\circ}34{,}13'\mathrm{W},\,137\;\mathrm{m},\,\mathrm{sledge},\,\mathrm{fine}$ 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, Skejafir∂i, coll. G.V. Helgason; c. 50 spms, north of Reykjavik, Hvalfjör∂ur 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 tetraoxide), 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, Hieltefjorden, 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

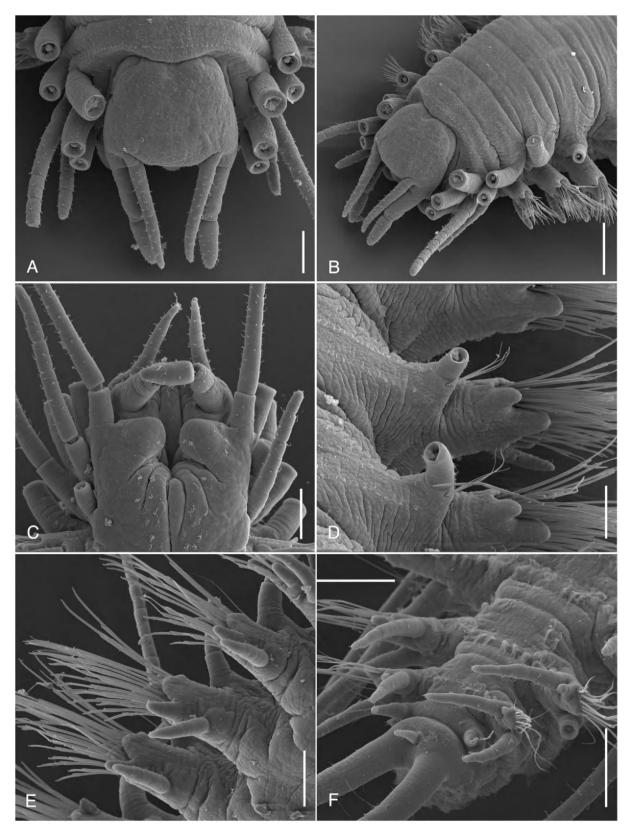


Figure 4. Nereimyra punctata, scanning electron microscopy photographs of specimens from Bergen, Norway. A, anterior end, dorsal view. B, anterior end, anterolateral view. C, anterior end, ventral view. D, median parapodia, anterodorsal view. E, median parapodia, ventral view. F, posterior end, ventral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

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ethanol, formaldehyde and osmium tetraoxide), 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. Eves red. Preserved animals vellowish, 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 kidneyshaped, 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 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 Oslofford, 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

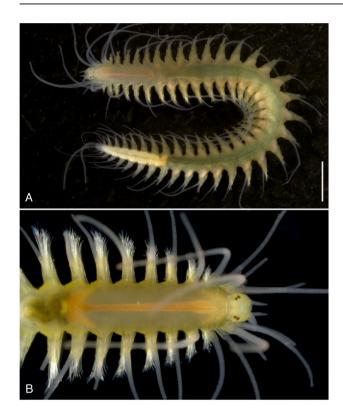


Figure 5. Nereimyra aphroditoides, dorsal view of live relaxed specimens. A, neotype, Disko Fjord, Greenland. B, anterior end from Svalbard. Scale bar: A = 1 mm; B, scale unknown.

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, $69^{\circ}29.059'N$, $53^{\circ}56.342'W$, 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. Amondsen 1859; 9 spms (SMNH types 2433; syntypes for C. fabricii), Smalesund, 61°34′N, 049°07′W, coll. C.T. Amondsen 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. Eibye- 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 tetraoxide), 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. 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 tetraoxide), Trondheimsfjorden, Rødberg, 09°59.990′ 63°28.093′-63°28.329′N, 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 tetraoxide), same locality and date; 30 + spms (F. P.'s collection; fixed in 95% ethanol, formaldehyde and osmium tetraoxide), 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

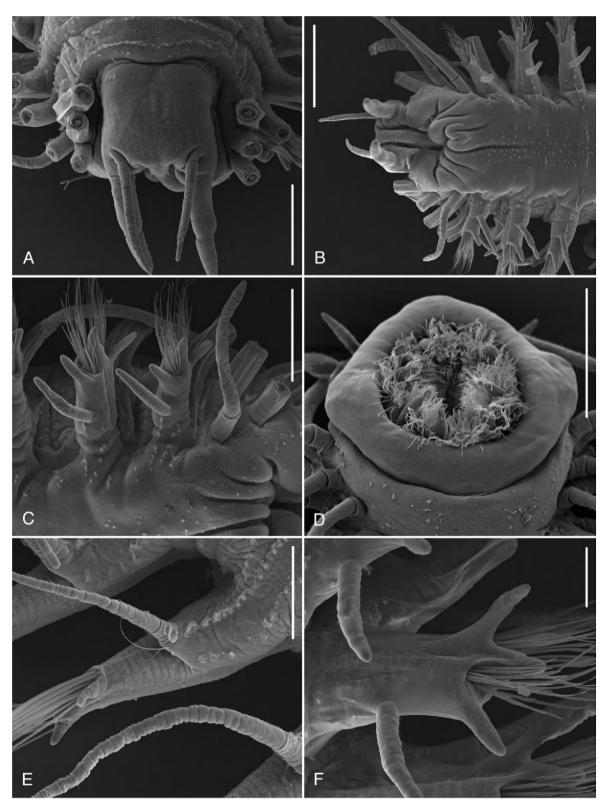


Figure 7. Nereimyra woodsholea, scanning electron microscopy photographs of specimens from Kosterhavet, Sweden. A, anterior end, dorsal view. B, anterior end, ventral view. C, parapodia segment 2–5, right side, ventral view. D, proboscis. E, median parapodium, right side, anterodorsal view. F, median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

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 ALVINAE 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.

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