



A partial revision of *Gyptis* (Gyptini, Ophiodrominae, Hesionidae, Aciculata, Annelida), with descriptions of a new tribe, a new genus and five new species

FREDRIK PLEIJEL^{1*}, GREG W. ROUSE², TOBIAS SUNDKVIST³ and ARNE NYGREN⁴

¹Fredrik Pleijel, University of Gothenburg, Department of Marine Ecology – Tjärnö, SE-452 96 Strömstad, Sweden

²Greg Rouse, Scripps Institution of Oceanography, University of California, San Diego, CA 92093-0202, USA

³Tobias Sundkvist, MMT, Vita gavelns väg 6, SE-426 71 Västra Frölunda, Sweden

⁴Arne Nygren, University of Gothenburg, Department of Zoology, Systematics and Biodiversity, Box 463, SE-405 30 Göteborg, Sweden

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Phylogenetic analyses of molecular data (COI, 16SrDNA, 18SrDNA, and 28SrDNA) show that the hesionid genus *Gyptis* Marion & Bobretzky in Marion, 1874, and the tribe Gyptini Pleijel, 1998, are nonmonophyletic as currently delineated. We introduce the new tribe Amphidurini and the new genus *Neogyptis* to accommodate these new findings. Amphidurini is sister to Gyptini and Ophiodromini and includes *Amphiduros* Hartman, 1959, *Amphiduroopsis*, Pleijel, 2001, *Neogyptis* **gen. nov.**, and, possibly, *Parahesion* Pettibone, 1956. Morphologically, Amphidurini can be separated from Gyptini by the distally, rather than subdistally, inserted ventral cirri, and *Neogyptis* by the combination of this feature, the presence of a median antenna, and a distal ring with papillae on the proboscis. We redescribe and transfer the four species *Gyptis crypta* Pleijel, 1993, *Gyptis mediterranea* Pleijel, 1993, *Gyptis plurisetis* Hilbig, 1992, and *Gyptis rosea* (Malm, 1874) from *Gyptis* to *Neogyptis* **gen. nov.**, and describe five new species from shallow waters in Belize, Hong Kong, off Vladivostok, and deep-sea hydrothermal vents in the Lau Basin off Fiji.

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INTRODUCTION

The genus *Gyptis* was introduced by Marion & Bobretzky in Marion (1874) for the single species *Gyptis propinqua* Marion & Bobretzky, 1875, and today includes about 20 described species (Pleijel, 1998). The genus has never been revised world-wide, although Pleijel (1993a) reviewed the European species, and provided a brief review in a revision of

Hesionidae (Pleijel, 1998). Based on differences in morphology the members of *Gyptis* can be split into two groups, where the nominotypical group has distinct lip pads and subdistally inserted ventral cirri on the neuropodium, and the second group usually lacks lip pads and always has distally inserted ventral cirri. In a previous analysis, although with limited taxon sampling for the question at hand (Ruta *et al.*, 2007), these two groups came out as nonmonophyletic. We here assess the phylogeny of members of Gyptini, including *Amphiduros* Hartman, 1959, *Gyptis*, and *Parahesion* Pettibone, 1956, in an analysis based on COI, 16S rDNA, 18S rDNA, and 28S rDNA. In order

*Corresponding author. E-mail: fredrik.pleijel@marecol.gu.se

to accommodate our new findings we introduce the new tribe Amphidurini and the new genus *Neogyptis*, including five new species from shallow waters in Belize, Hong Kong, and deep-sea hydrothermal vents in the Lau Basin off Fiji, and four new combinations for species transferred from *Gyptis* to *Neogyptis* (for simplicity these will be referred to with their new names hereafter in this paper), namely *Neogyptis crypta* Pleijel, 1993b, comb. nov., *Neogyptis mediterranea* Pleijel, 1993a, comb. nov., *Neogyptis plurisetis* Hilbig, 1992, comb. nov., and *Neogyptis rosea* (Malm, 1874) comb. nov.

MATERIAL AND METHODS

Specimens for standard microscopy were relaxed with 7% magnesium chloride in fresh water, preserved in 10% formaldehyde in sea water for a 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. For transmission electron microscopy (TEM), specimens were fixed in 3% glutaraldehyde, with 0.2 M sodium cacodylate buffer (pH 7.4) and 0.3 M sucrose. They were then rinsed in buffer at least three times and postfixes with 1% osmium tetroxide in buffer at 4 °C for 80 min. Samples were rinsed in buffer three times before dehydration with increasing concentrations of ethanol (finally three times of 100% ethanol). Specimens were infiltrated and embedded in Spurr's resin and 500–800 nm sections were cut and stained for 20 min in alcoholic uranyl acetate, rinsed in distilled water, stained for 10 min in lead citrate, rinsed, and examined in a Philips EM400 transmission electron microscope. Specimens for DNA sequencing were preserved directly in 95% alcohol. Origin of specimens, GenBank accession numbers, and deposition of vouchers are detailed in Table 1. DNATable 2 was extracted using DNAeasy Tissue Kit (Qiagen) following the protocol supplied by the manufacturer. We amplified 334–658 bp and 402–519 bp of the mitochondrial genes cytochrome oxidase subunit I (COI) and 16S rDNA, respectively, and 739–790 bp and 1638–1778 bp of the nuclear 28S rDNA and 18S rDNA, respectively. We used the primers LCO1490, HCO2198 (Folmer *et al.*, 1994) and COI-E for COI (Bely & Wray, 2004), 16SarL and 16SbrH for 16S rDNA (Palumbi, 1996), 28SC1' (Dayrat *et al.*, 2001) and 28SD2 for 28S rDNA (Lê, Lecointre & Perasso, 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 of 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 a 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 (Kato *et al.*, 2002) within GENEIOUS 5.1.7 with the following settings: algorithm = E-INS-i, scoring matrix = 200PAM/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). Bayesian analyses (BAs) of the combined data set were run in MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003), and the best-fit models were selected using the Akaike information criterion in MrModeltest 2.1 (Nylander, 2004). For all partitions except for the third 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 third positions in COI we used a GTR + G model. Stationary base frequency priors were set to be equal for the first positions in COI. All partitions were unlinked. The number of generations was set to 15 million with four parallel chains (three hot, one cold), sample frequency was set to 1000, and number of runs was set to two. One third 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 (in italics) were made: *change (topology and branch lengths) with extending tree-bisection reconnection (TBR)*, extension probability from 0.8 to 0.45, and multiplier tuning parameter 0.94 to 0.45, *change (gamma shape) with multiplier*, multiplier tuning parameter (lambda) from 0.811 to 1.7, *change (topology and branch lengths) with LOCAL*, multiplier tuning parameter (lambda) from 0.191 to 0.06, *change (proportion of invariable sites) with sliding window*, sliding window size from 0.1 to 0.25, *change (rate multiplier) with Dirichlet proposal*, Dirichlet parameter from 500 to 2900, and *change (state frequencies) with Dirichlet proposal*, Dirichlet parameter from 300 to 650. Proposal rates were not changed. 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; Nylander *et al.*, 2008) to interpret

Table 1. Origin of sequenced terminals, specification of vouchers and GenBank accession numbers. New sequences are in bold. All vouchers are hologenophores unless otherwise stated (Pleijel *et al.*, 2008)

Taxon	Origin	Voucher	COI	16S	18S	28S
<i>Nereis pelagica</i>	Sweden	–	–	AY340470	AY340438	AY340407
<i>Dysponetus caecus</i>	Sweden	–	AF221568	EU555047	AY839568	EU555028
<i>Hesion</i> sp.	New Caledonia	–	–	DQ442615	DQ442617	DQ442619
<i>Hesiospina aurantiaca</i>	Sweden	SIO-BIC A2513*	–	JN631319	JN631329	JN631342
<i>Hesiospina vestimentifera</i>	Fiji	SIO-BIC A2510*	JN631310	JN631320	JN631330	JN631343
<i>Leocrates chinensis</i>	New Caledonia	–	DQ442565	DQ442575	DQ442589	DQ442605
<i>Micropodarke dubia</i>	New Caledonia	–	–	DQ442576	DQ442590	DQ442597
<i>Nereimyra punctata</i>	Sweden	–	DQ442566	DQ442577	DQ442591	DQ442606
<i>Ophiudromus flexuosus</i>	Sweden	–	DQ442567	DQ442578	DQ442592	DQ442607
<i>Ophiudromus pallidus</i>	Sweden	–	–	DQ442579	DQ442593	DQ442608
<i>Podarkeopsis arenicolus</i>	France	–	–	–	DQ442594	DQ442609
<i>Podarkeopsis helgolandicus</i>	Sweden	SIO-BIC A2511*, A2512†	JN631311	–	JN631331	JN631344
<i>Psamathe fusca</i>	Sweden	–	DQ513294	DQ442581	DQ442595	DQ442610
<i>Sirsoe methanicola</i>	Gulf of Mexico	–	DQ513295	DQ442582	JN631332	DQ442611
<i>Syllidia armata</i>	Sweden	–	DQ442568	DQ442583	DQ442596	DQ442612
<i>Vriejenhoekia balaenophila</i>	California	–	DQ513296	DQ513301	JN631333	DQ513306
<i>Amphiduros fuscescens</i>	France	–	DQ442561	DQ442569	DQ442584	DQ442598
<i>Amphiduros pacificus</i>	California	SIO-BIC A2514*, A2515†	JN631312	JN631324	JN631334	JN631345
<i>Gyptis brunnea</i>	California	FP collection	JN631313	JN631323	JN631335	JN631346
<i>Gyptis golikovi</i>	Svalbard	SIO-BIC A2509*, paragenophore	–	JN631321	JN631336	JN631347
<i>Gyptis pacifica</i>	Japan	SIO-BIC A2516*, A2517†	JN631314	JN631322	JN631337	JN631348
<i>Gyptis paucilineata</i>	Australia, Adelaide	–	EU498243	–	–	–
<i>Gyptis polymorpha</i>	Australia, Adelaide	–	EU498247	–	–	–
<i>Gyptis propinqua</i>	France, Sweden	–	EU498229	DQ442573	DQ442586	DQ442602
<i>Gyptis simpsonorum</i>	Australia, Adelaide	–	EU498237	–	–	–
<i>Neogyptis carriebowcayi</i> sp. nov.	Belize	SIO-BIC A2468‡, paragenophore	JN631315	JN631325	JN631338	JN631349
<i>Neogyptis fauchaldi</i> sp. nov.	Belize	SIO-BIC A2485, paragenophores	JN631316	JN631326	JN631339	–
<i>Neogyptis hinehina</i> sp. nov.	Off Fiji	SIO-BIC A2493, holo- and paragenophores	JN631317	JN631328	JN631340	JN631350
<i>Neogyptis mediterranea</i>	France	–	DQ442563	DQ442572	–	DQ442601
<i>Neogyptis rosea</i>	Norway	–	DQ442564	DQ442574	DQ442587	DQ442603
<i>Neogyptis</i> sp. A	Florida	SIO-BIC A2505	JN631318	JN631327	JN631341	JN631351

COI, cytochrome oxidase subunit I.

*Anterior end, preserved in formaldehyde.

†Posterior end, preserved in ethanol.

‡Entire specimen, preserved in formaldehyde.

Table 2. Summary of morphological characters of species of *Neogyptis*

Species	Eyes	Proboscis papillae	Lip pads	Enlarged vc	Neurochaetae start	Notochaetae start	One-side serrated notochaetae	Dorsal ridges	Maximum known length (mm)/no. of segms
<i>Neogyptis rosea</i> comb. nov.	Brown-black	35–80	Absent	Segm 1–4	Segm 5	Segm 6	Present	Weak	11/36
<i>Neogyptis carriebowcayi</i> sp. nov.	Red	10	Absent	Segm 1–4	Segm 5	Segm 6	Present	Absent	6.5/28
<i>Neogyptis crypta</i> comb. nov.	Red	10	Absent	Segm 1–4	Segm 5	Segm 5	Present	High	7.5/39
<i>Neogyptis fauchaldi</i> sp. nov.	Brown-black	10	Absent	Segm 1–4	Segm 5	Segm 6	Present	Weak	4.5/24
<i>Neogyptis hinehina</i> sp. nov.	Absent	10	Absent	Segm 1–3	Segm 4	Segm 6	Present	High	4.5/27
<i>Neogyptis hongkongensis</i> sp. nov.	Black	10	Present	Segm 1–4	Segm 5	Segm 6	Absent	Absent	2.6/25
<i>Neogyptis mediterranea</i> comb. nov.	Red	20–32	Absent	Segm 1–4	Segm 5	Segm 6	Present	High	7/32
<i>Neogyptis plurisetis</i> comb. nov.	Red	35–40	Unknown	Segm 1–4	Segm 5	Segm 6	Present	Uncertain	Unknown
<i>Neogyptis vostokensis</i> sp. nov.	Black	10	Absent	Segm 1–4	Segm 5	Segm 6	Absent	Weak	4.5/27
<i>Neogyptis</i> sp. A	Red	10	Absent	Segm 1–4	Segm 5	Segm 6	Present	Uncertain	Incomplete

Segm, segment; vc, ventral cirri.

visually if the analyses had reached the stationary phase.

Maximum parsimony analyses (PAs) of the concatenated data set were executed in PAUP* v. 4.0b10 (Swofford, 2001) using a heuristic search, TBR branch swapping, with 1000 random-addition starting tree replicates, and assessed support via 1000 jackknife replicates (37% deletion according to Farris *et al.*, 1996). Two PAs were performed, one with and one without the third positions of COI included. The maximum likelihood (ML) result was inferred using RAxML 7.2.3 (Stamatakis, 2006) with the GTR-GAMMA model for each of the gene partitions. The proportion of invariable sites and gamma distribution shape parameter for the variable sites were estimated during the ML analysis. 'Multiparametric' bootstrapping (command $-b$ = nonparametric bootstrapping) with random seed value 12345 was carried out with 1000 replicates using the same model as the ML search. Alignments are available from the last author.

Abbreviations used for museums and other depositories are NHMG, Gothenburg Museum of Natural History; SAM, South Australian Museum, Adelaide; SIO-BIC, Scripps Institution of Oceanography, Benthic Invertebrate Collection, La Jolla; SMNH, Swedish Museum of Natural History, Stockholm; USNM, National Museum of Natural History, Smithsonian Institution, Washington DC; ZMUB, Zoological Museum, University of Bergen; ZMUU, Zoological Museum, University of Uppsala; NMW, National Museum of Wales, Cardiff.

PHYLOGENETIC ANALYSIS OF GYPTINI

In order to assess positions and delineations of Amphidurini, new tribe, and *Neogyptis* gen. nov., we performed Bayesian, maximum likelihood, and parsimony analyses of the mitochondrial COI and 16SrDNA, and the nuclear 18SrDNA and 28SrDNA from a number of putative members of these two taxa and outgroups.

The combined data set of COI, 16S rDNA, 28S rDNA, and 18S rDNA consists of 4090 aligned positions. Amongst the 3596 characters left after excluding alignment ambiguous regions, 1224 are variable and 820 are parsimony-informative.

The topologies from the BA and ML are fully congruent (Fig. 1) and show that Gyptini and *Gyptis* as traditionally delineated (e.g. Pleijel, 1998) are non-monophyletic. The nominotypical group of *Gyptis*, characterized morphologically by subdistally inserted ventral cirri, is the sister taxon to *Ophiiodromus* M. Sars, 1862 and *Podarkeopsis* Laubier, 1961, whereas those *Gyptis* species that have distally inserted ventral cirri instead are the sister group to *Amphiduros* Hartman, 1959. We refer these to the new

genus *Neogyptis*, and together with *Amphiduros*, to the new tribe Amphidurini. *Neogyptis* has strong support in all three analyses, whereas Amphidurini has highest possible support in BA, but only 0.78 in ML and PA. Together with the five new species (of which only three are included in Fig. 1 because we lack molecular data for two of them), the taxon *Neogyptis* at present includes nine species.

Our initial parsimony analysis differed from BA and ML mainly in that *Neogyptis*, as delineated here, was paraphyletic with the exclusion of *Amphiduros* (result not shown). However, when removing the third positions of COI the result was identical to the two other analyses with *Neogyptis* and *Amphiduros* as non-nested taxa, and we attributed the first result to the higher sensitivity of noise in PA. Following the removal of the third positions a monophyletic *Neogyptis* also received high support in PA (support values for this second analysis are shown in Fig. 1). We therefore chose to delineate *Neogyptis* as in Figure 1. Furthermore, and with due consideration to differences in terminals, the topology in Figure 1 is also fully congruent with the analysis of Ruta *et al.* (2007).

Although not within the scope of this study, *Hesiospina* Imajima & Hartman, 1964, in the analysis is represented by the two species *Hesiospina auran-tiaca* (M. Sars, 1862) and *Hesiospina vestimentifera* Blake, 1985, and these appear in a grade together with *Micropodarke* Okuda, 1938, and *Psamathe* Johnston, 1836, thus bringing into question the monophyly of *Hesiospina*. The matter warrants further study based on more dense taxon sampling of *Hesiospina* and relatives.

TAXONOMY

OPHIODROMINAE PLEIJEL, 1998

AMPHIDURINI NEW TRIBE

Description: Median antenna dorsally inserted, terminal ring of proboscis papillae present or absent, lip pads absent or present, enlarged dorsal cirri on segment 1–5, enlarged ventral cirri and cirrophores on segment 1–3 or 1–4, neurochaetae from segment 4 or 5, notochaetae from segment 5 or 6, notochaetae and notopodial lobes well developed, dorsal ridges absent or present, elevated dorsal cirri on segment 5, 8, 10, 12, 15, 17, 19, 21, and 23, distally inserted ventral cirri, and pygidial papilla absent.

Remarks: Amphidurini, new tribe, includes *Amphiduros* Hartman, 1959, *Amphiduroopsis* Pleijel, 2001, and *Neogyptis* gen. nov. *Paraheisione* Pettibone, 1956, may or may not be a member of Amphidurini; it shares the distally inserted ventral cirri but lacks a median antenna.

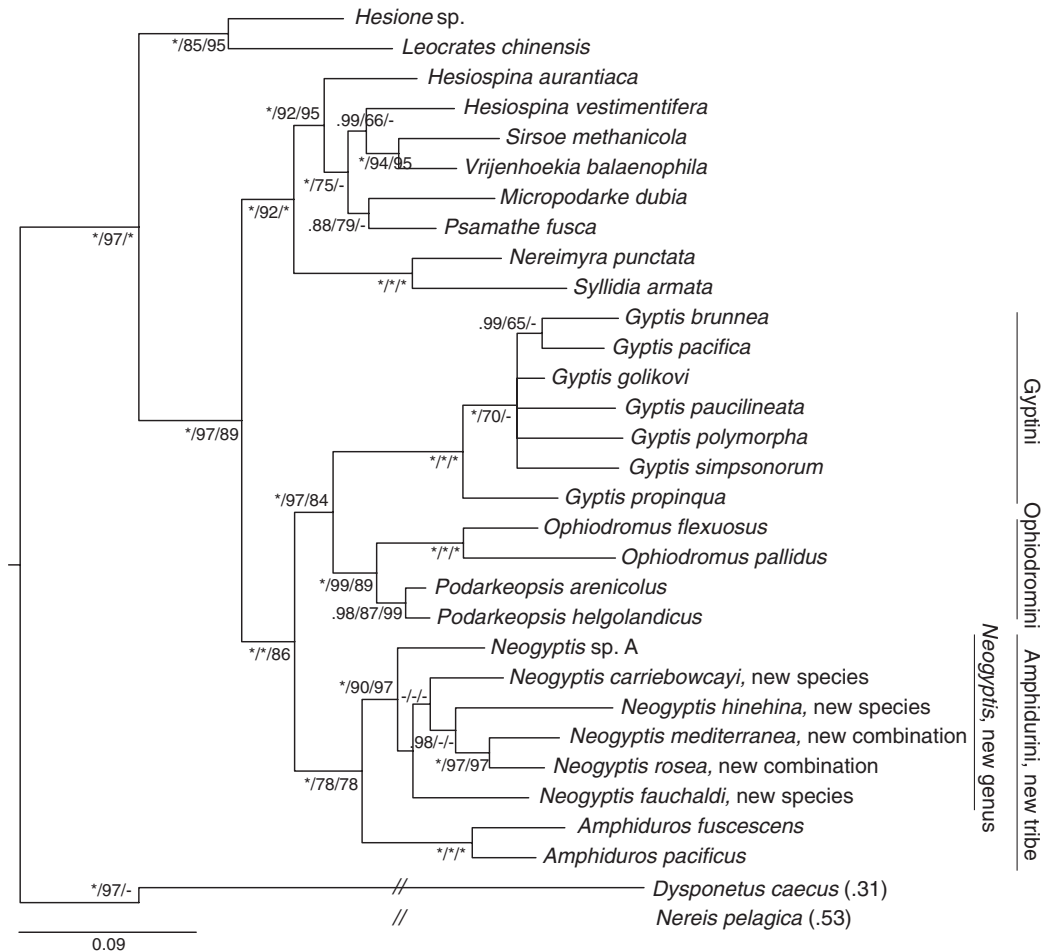


Figure 1. Phylogenetic relationships of Amphidurini, new tribe, and *Neogyptis* gen. nov. Majority rule consensus tree from the Bayesian analysis together with support values from the maximum likelihood and parsimony analyses (with the third positions excluded). First node values represent posterior probabilities from the Bayesian analysis, second bootstrap support from the maximum likelihood analysis, and third jackknife support from the parsimony analysis. Asterisks denote 1.0 posterior probabilities or 100% bootstrap support. Only values ≥ 0.75 and 75%, respectively, are displayed. Branch length of the two outgroups are truncated and the values are instead given within parentheses after the taxon names.

NEOGYPTIS GEN. NOV.

Type species: Ophiidromus roseus Malm, 1874: 82.

Etymology: ‘neo’ is Latin for new, ‘Gyptis’ is the genus to which several of the *Neogyptis* members were previously allocated. Gender feminine.

Description: Terminal ring of proboscis papillae present, lip pads usually absent (present in *Neogyptis hongkongensis* sp. nov.), neurochaetae usually from segment 5 (from segment 4 in *Neogyptis hinehina* sp. nov.), notochaetae usually from segment 6 (from segment 5 in *Neogyptis crypta* sp. nov.), transverse dorsal ridges absent or present.

Remarks: *Neogyptis* includes *Neogyptis carriebowcayi* sp. nov., *N. crypta* Pleijel, 1993b, comb. nov., *Neogyptis*

fauchaldi sp. nov., *N. hinehina* sp. nov., *N. hongkongensis* sp. nov., *N. mediterranea* Pleijel, 1993a, comb. nov., *N. plurisetis* Hilbig, 1992, comb. nov., *N. rosea* (Malm, 1874) comb. nov., *Neogyptis vostokensis* sp. nov., and *Neogyptis* sp. A. A summary of characters separating the species is provided in Table 2.

There are no currently known morphological apomorphies for *Neogyptis* at the exclusion of *Amphiduros*. However, the molecular data provide strong support for a sister group relationship between the two taxa.

NEOGYPTIS ROSEA (MALM, 1874) COMB. NOV. (FIGS 2, 3)

Ophiidromus roseus Malm, 1874: 82.

Gyptis rosea Eliason, 1962: 238–240, figure 9; Haaland & Schram, 1982: 107–118, figures 1–9;



Figure 2. *Neogyptis rosea* **comb. nov.**, live relaxed mature female from Bohuslän, Sweden, 10.5 mm long excluding cirri. A, dorsal view. B, ventral view.

Pleijel, 1993a: 172–176, figures 9, 10: figure 26; Hartmann-Schröder, 1996: 132 [not *G. rosea sensu* Hartmann-Schröder (1971: 132–134, figure 43, and Helgason *et al.* (1990)]

Type material: Holotype (NHMG 901).

Type locality: Sweden, Bohuslän, Gullmarsfjorden, 82 m, mud.

Material examined: SWEDEN. Holotype (NHMG 901), Bohuslän, Gullmarsfjorden, 82 m, mud; two specimens (spms; NHMG 12805a, b), Gullmarsfjorden, Skår,

110 m, mud, 25.v.1963; one spm (FP collection, fixed in formaldehyde), Bohuslän, Singlefjord, 59°04'N, 11°10'E, 80–84 m, mud, detritus sledge, collected by (coll.) FP 27.xii.1988; two spms (FP collection, fixed in formaldehyde), same locality data, coll. FP 14.vi.1989; six spms (FP collection, four fixed in formaldehyde), same locality data, coll. FP 11.iv.1990; three spms (FP collection, fixed in osmium and mounted on SEM stubs), same locality data, coll. FP 26.ii.1991; five spms (FP collection, fixed in formaldehyde), same locality data, coll. FP 2.ix.1991; five spms (FP collection, fixed in formaldehyde), same locality data, coll. FP 15.ix.1991; six spms (FP collection, four fixed in form-

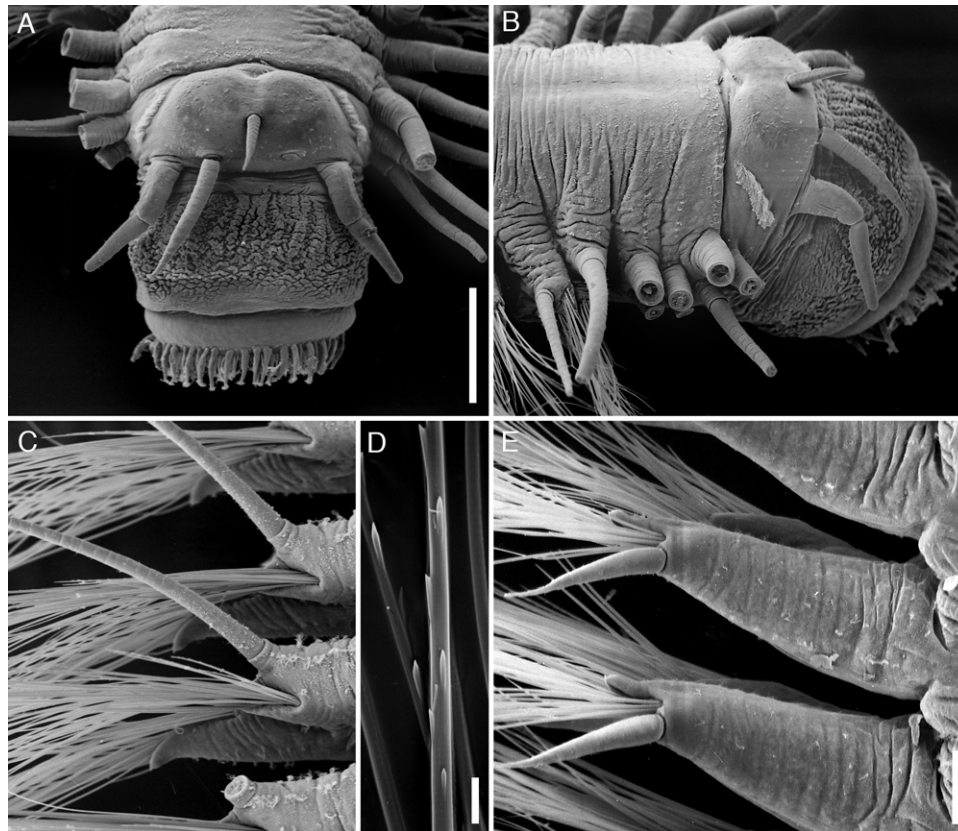


Figure 3. *Neogyptis rosea* **comb. nov.**, scanning electron microscopy photographs of specimens from Bohuslän, Sweden. A, anterior end, anterodorsal view. B, anterior end, right side. C, median parapodia, anterodorsal view. D, capillary notochaetae with alternating rows of teeth. E, median parapodia, ventral view. Scale bars: A = 250 µm, C and E 100 µm, D 10 µm; A and B same scale.

aldehyde, two fixed in osmium and mounted on SEM stubs), Bohuslän, Koster area, W Svartskär, 58°54.5'N, 11°05.0'E, 100–150 m, mud, dredge, coll. FP 22.ix.1989; one spm (FP collection, fixed in formaldehyde), Bohuslän, Koster area, South of Yttre Vattenholmen, 58°52'N, 11°06'E, 50–140 m, mud, dredge, coll. FP 1.x.1990; four spms (FP collection, fixed in 95% ethanol), Bohuslän, Koster area, S Yttre Vattenholmen, 58°52.31'N, 11°05.89'E, 196–210 m, mud, detritus sledge, coll. FP 28.xi.1995; one spm (FP collection, fixed in osmium and mounted on stub), same locality data, coll. FP 17.viii.1991; two spms (one fixed in formaldehyde and one in osmium and mounted on SEM stub), same locality data, coll. FP 7.ix.1991; three spms (ZMUU), Skagerrak, 58°08'N, 10°07'E, 295 m, grab, 27.vi.1933; two spms (ZMUU), Skagerrak, 58°02.5'N, 09°29.5'E, 478 m, grab, 30.vi.1933; one spm (ZMUU), Skagerrak, 58°02.5'N, 09°29.5'E, 427 m, grab, 1.vii.1933; one spm (ZMUU), Skagerrak, 58°21'N, 08°56'E, 225 m, grab, 2.vii.1933; one spm (ZMUU), Skagerrak, 58°02.7'N, 08°13.5'E, 241 m, grab, 4.vii.1933; four spms (ZMUU), Skagerrak, 57°50'N, 08°51'E, 358 m, grab, 5.vii.1933; one spm

(ZMUU), Skagerrak, 57°45'N, 08°07'E, 421 m, grab, 6.vii.1933; three spms (ZMUU), Skagerrak, 57°52'N, 08°01'E, 510 m, Agassiz trawl, 6.vii.1933; two spms (ZMUU), Skagerrak, 57°58'N, 06°44'E, 384 m, grab, 7.vii.1933; one spm (ZMUU), Skagerrak, 58°59.5'N, 06°27'E, 290 m, dredge, 12.vii.1933; six spms (ZMUU), Skagerrak, 58°22'N, 10°34'E, 270 m, Agassiz trawl, 14.vii.1933; five spms (ZMUU), Skagerrak, 58°30'N, 10°26'E, 300 m, Agassiz trawl, 15.vii.1933; one spm (ZMUU), Skagerrak, 58°30'N, 10°32.5'E, 175 m, Agassiz trawl, 15.vii.1933; one spm (FP collection, fixed in 95% ethanol), Bohuslän, Persgrunden, 58°43.014'–58°42.96'N, 10°51.89.044'–10°51.790'E, 44–64 m, mud and stones, dredge, coll. FP 3.ix.2004; one spm (FP collection, fixed in 95% ethanol), Bohuslän, Koster area, North of Nord Hällsö, 58°58.335'–58°58.415'N, 11°04.348'–11°04.414'E, 134–129 m, mud, dredge, coll. FP 26.iii.2007; one spm (FP collection, fixed in osmium and mounted on SEM stub), Bohuslän, Koster area, S Yttre Vattenholmen, 58°52.132'–58°51.809'N, 11°06.235'–11°06.434'E, 170 m, mud, detritus sledge, coll. FP 16.i.2006; two spms (FP collection, fixed in formaldehyde), Bohuslän,

Koster area, S Yttre Vattenholmen, 58°51.905'N, 11°06.511'E, 125 m, mud, detritus sledge, coll. FP 26.vi.2007; two spms (FP collection, fixed in formaldehyde), Bohuslän, Koster area, S Yttre Vattenholmen, 58°52.425'–58°51.905'N, 11°06.053'–11°06.511'E, 130–140 m, mud, detritus sledge, coll. FP 5.x.2007; two spms (FP collection, fixed in formaldehyde), same locality data, coll. FP 10.x.2007; one spm (FP collection, fixed in 95% ethanol), Bohuslän, Koster area, S Yttre Vattenholmen, 58°52.238'N, 11°06.274'E, 110–133 m, mud, detritus sledge, coll. FP 15.xii.2009. NORWAY. One spm (ZMUB), Skagerrak, 57°49.5'N, 08°12.5'E, 500 m, RP-sledge, 15.iii.1990; one spm (ZMUB), Skagerrak, 57°59'N, 08°40'E, 500 m, RP-sledge, 15.iii.1990; one spm (FP collection), Trondheimsfjorden, 63°27.90'N, 10°06.40'E, 503 m, mud, detritus sledge, coll. FP 21.viii.1995; ten spms (FP collection, fixed in ethanol, four destroyed for DNA sequencing), Trondheimsfjorden, 63°29.24'N, 10°22.43'E, 271–334 m, mud, detritus sledge, coll. FP 15.i.2002.

Description: Length up to 11 mm for 36 segments. Live animals transparent with light yellow gut; eyes brownish black. Body outline in dorsal view elliptical with median parapodia much longer than anterior and posterior ones (Fig. 2A, B). Prostomium rounded rectangular, wider than long (Fig. 3A). Palpophores cylindrical, palpostyles evenly tapering to rounded tips; palpophores and palpostyles of equal length (Fig. 3A, B). Paired antennae as long as palps but much thinner, tapering, distal-most third forming demarcated tips. Median antenna of similar shape to paired antennae but much shorter, inserted centrally on dorsal part of prostomium (Fig. 3A). Eyes small, anterior pair larger and positioned slightly further apart. Nuchal organs ciliated bands along lateral sides of prostomium (Fig. 3A, B). Lip pads absent. Proboscis with rugose surface on proximal ring, distal ring smooth, opening with terminal ring of long, thin papillae (Fig. 3A, B), number 35–80 (size-dependent). Non-everted proboscis reaching segment 10. Anterior segmental delineations indistinct, most part of segment 1 dorsally reduced. Dorsal cirri and cirrophores segment 1–5 much longer and stouter than following ones, with dorsal cirri segment 1 reaching about segment 10, dorsal cirri segment 2 reaching about segment 18, dorsal cirri segment 3 reaching about segment 12, dorsal cirri segment 4 reaching about segment 18, and dorsal cirri segment 5 reaching about segment 17 (Fig. 2A, B). Ventral cirri segment 1–4 with well-delineated cirrophores and longer and stouter cirri than on following segments, with ventral cirri segment 1 reaching about segment 7, ventral cirri segment 2 reaching about segment 9, ventral cirri segment 3 reaching about segment 7, and ventral cirri segment 4

reaching about segment 10 (Fig. 2A, B). Segment 5 with neuropodial lobes, neurochaetae, and ventral cirri similar to following segments, segment 6 with notopodial lobes and notochaetae. Elevated and slightly stouter dorsal cirri on segment 8, 12, 15, 17, 19, 21, and 23. Dorsal cirri reaching as far as or slightly further than chaetae. Weakly developed transverse dorsal ridges across median and posterior segments. Notopodial acicular lobes conical. Notochaetae of three kinds; few dorsally bent acicular chaetae emerging near tip of acicula, large number of capillary chaetae with two alternating rows of teeth (Fig. 3D), and few, ventrally positioned curved chaetae with conical side subdistally serrated (Pleijel, 1993a: fig. 1H). Prechaetal neuropodial lobes elongated rounded to conical (Fig. 1C). Forty to 50 neurochaetae, all unidentate compounds, dorsal and median blades up to five times longer than ventral ones. Usually double noto- and neuroaciculae. Ventral cirri inserted distally near tip of neuropodium, tapering to fine points (Fig. 3E). Pygidium with long pygidial cirri, similar in shape to dorsal cirri; pygidial papilla absent.

Biology: Females with eggs found in Sweden in April to August, the former immature. Mature eggs pink (Fig. 2A, B), about 50–60 µm in diameter (the colour of mature females explains Malm's choice of the specific epithet 'rosea'). Haaland & Schram (1982) provide descriptions of both adults and juvenile stages from the Oslofjord.

Habitat: Mud, 44–510 m.

Distribution: Northern part of the Swedish west coast, Skagerrak, the Oslofjord, and the Trondheimsfjord.

Remarks: Records and descriptions of *N. rosea* (as *Gyptis rosea*) by Hartmann-Schröder (1971) and Helgason *et al.* (1990) refer to members of *Gyptis sensu stricto*, rather than to *Neogyptis*, possibly to *G. propinqua*.

***NEOGYPTIS CARRIEBOWCAYI* SP. NOV. (FIGS 4, 5)**

Type material: Holotype (SIO-BIC A2467), + 100 paratypes (SIO-BIC 2468–2476, 2508).

Type locality: Belize, north of Carrie Bow Cay, 16°48.805'N, 88°04.902'W, 1 m, sand and amongst *Halimeda* algae.

Etymology: Named after Carrie Bow Cay, the type locality.

Material examined: BELIZE. Holotype (SIO-BIC A2467, fixed in formaldehyde), Carrie Bow Cay, 16°48.2'N, 88°04.5'W, 1 m, sand and *Thalassia*,



Figure 4. *Neogyptis carriebowcayi* sp. nov., dorsal view of live relaxed paratype (SIO-BIC A2475), 3.7 mm long excluding cirri.

SCUBA, coll. FP 18–26.ix.1997; 13 paratypes (SIO-BIC A2468, fixed in formaldehyde), same collection data; five spms fixed in osmium and mounted on SEM stubs (FP collection), same collection data; + 30 paratypes (SIO-BIC A2469, fixed in formaldehyde), Carrie Bow Cay, off reef, 26 m, *Halimeda* sand, SCUBA, coll. FP 23.ix.1997; + 25 paratypes (SIO-BIC A2470, fixed in formaldehyde), Curley Cay, 16°47.4'N, 88°04.8'W, 1 m coarse sand, SCUBA, coll. FP 22.ix.1997; three paratypes (SIO-BIC A2506, one spm fixed in 95% ethanol); one spm (SIO-BIC A2471, fixed in formaldehyde), Carrie Bow Cay, 16°48.162'N, 88°04.913'W, 1 m, sand, SCUBA, coll. FP 3.xi.2006; one paratype (SIO-BIC A2472, fixed in formaldehyde) and six spms (fixed in 95% ethanol, destroyed for DNA sequencing), Twin Cays, Lair Channel, 16°49.675'N, 88°06.047'W, 0.5 m, mangrove, SCUBA, coll. FP 5.xi.2006; nine paratypes (SIO-BIC A2507, two spms fixed in 95% ethanol, SIO-BIC A2473, eight spms fixed in formaldehyde), and 11 spms (FP collection), fixed in osmium and mounted on SEM stubs, Carrie Bow Cay, outside reef, 16°48.190'N, 88°04.669'W, 15 m, *Halimeda* sand, SCUBA, coll. GR 8.xi.2006; 20 paratypes (SIO-BIC A2474, five spms fixed in 95% ethanol; SIO-BIC A2475, six spms fixed in formaldehyde), south of Carrie Bow Cay, Curlew Bank, 16°47.311'N, 88°04.575'W, 15 m, coll. GR 10.xi.2006; six paratypes (SIO-BIC A2508, fixed in 95% ethanol), north of Carrie Bow Cay, 16°48.805'N, 88°04.902'W, 2 m, *Halimeda* sand, coll. FP 11.xi.2006; ten paratypes (SIO-BIC A2476, fixed in formaldehyde), same collection data; ten spms (FP collection, fixed in osmium and mounted on SEM stubs), same collection data.

Description: Length up to 6.5 mm for 28 segments (holotype, measured live, relaxed). Live animals transparent with light yellow gut (Fig. 4). Preserved animals whitish, some with dark dorsal and ventral

cirri. Eye colour red, pigment often lost in preserved specimens. Body outline elongated elliptical to cylindrical (Fig. 4) Prostomium slightly wider than long (Fig. 5A). Palpophores cylindrical, palpostyles elongated, evenly tapering to rounded tips; palpostyles longer than palpophores (Fig. 5A, B). Paired antennae slightly thinner and shorter than palps, of even width with last third tapering to fine tips. Median antenna similar to paired antennae but much shorter (Fig. 5B), inserted well in front of eyes. Eyes large, anterior pair twice as large as posterior and positioned further apart, both pairs almost coalescing. Nuchal organs ciliated bands along lateral sides of prostomium, almost meeting mid-dorsally (Fig. 5A). Lip pads absent. Proboscis smooth, with proximal and distal ring, opening with terminal ring of ten conical papillae (Fig. 5C). Non-everted proboscis reaching segment 8–9 (Fig. 4). Segment 1 dorsally reduced, following segments fully developed. Dorsal cirri and cirrophores segment 1–5 longer and stouter than following ones, with dorsal cirri segment 1 reaching about segment 8–9, dorsal cirri segment 2 reaching about segment 11, dorsal cirri segment 3 reaching about segment 11–12, dorsal cirri segment 4 reaching about segment 11, and dorsal cirri segment 5 reaching about segment 11–12. Ventral cirri segment 1–4 with well-delineated cirrophores and much longer and stouter cirri than on following segments, with ventral cirri segment 1 reaching about segment 5–6, ventral cirri segment 2 reaching about segment 6–7, ventral cirri segment 3 reaching about segment 7, and ventral cirri segment 4 reaching about segment 7–8. Segment 5 with neuropodial lobes, neurochaetae, and ventral cirri similar to following segments, segment 6 with notopodial lobes and notochaetae. Elevated and longer dorsal cirri on segment 8, 12, 15, 17, 19, 21, and 23. Shorter dorsal cirri reaching as far as or slightly further than chaetae (Fig. 5D). Transverse dorsal ridges absent. Notopodial

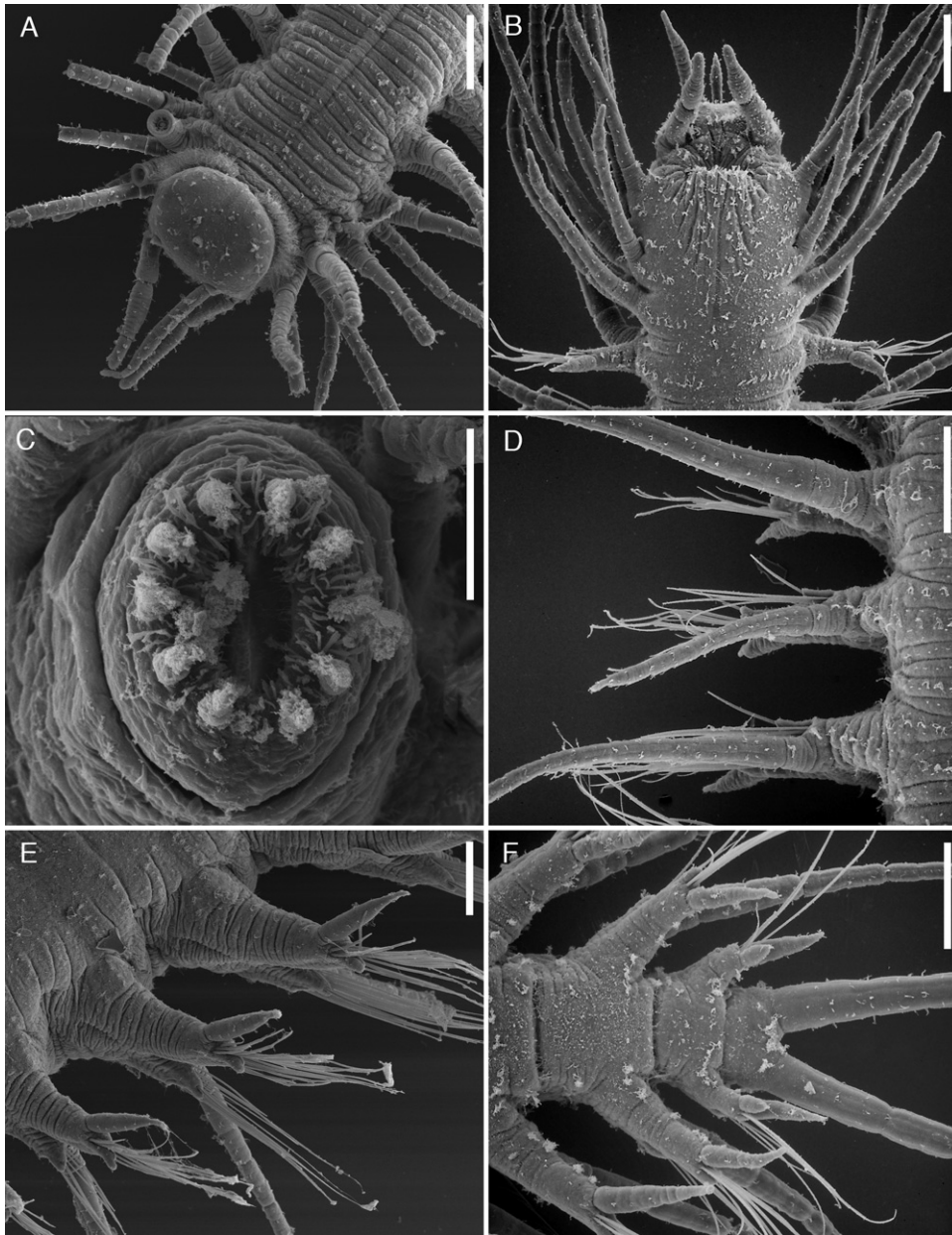


Figure 5. *Neogyptis carriebowcayi* sp. nov., scanning electron microscopy photographs of specimens from the type locality. A, anterior end, dorsal view. B, anterior end, ventral view. C, proboscis opening. D, parapodia segment 5–7, left side, dorsal view. E, parapodia segment 6–8, right side, anteroventral view. F, posterior end, ventral view. Scale bars = A, B, D–F = 100 μ m, C = 50 μ m.

aciculary lobes conical. Notochaetae of three kinds, single bent chaeta emerging near tip of acicula, about 25 capillary chaetae with two alternating rows of teeth, and two to three ventrally positioned curved chaetae with conical side subdistally serrated. Prechaetal neuropodial lobes elongated triangular. About 25 neurochaetae, all unidentate compounds, dorsal and median blades up to four times longer than ventral. Usually single noto- and neuroaciculae. Ventral cirri

inserted distally on neuropodium, tapering to fine points (Fig. 5E). Pygidial cirri much longer than dorsal cirri; pygidial papilla absent (Fig. 5F).

Biology: Not fully mature females and males observed in September and November (the only months when specimens were collected).

Habitat: Found in sand and coarse sand at 1–26 m depth.

Distribution: Only known from Carrie Bow Cay and Twin Cays in Belize.

Remarks: *Neogyptis carriebowcayi* shares red eye colour with *N. crypta* and *N. mediterranea*, but differs from the former in having notochaetae from segment 6, rather than from segment 5, and from the latter in having ten papillae in the terminal proboscis ring, rather than 20–32, and in the absence of high dorsal ridges on the posterior half of dorsum.

NEOGYPTIS CRYPTA (PLEIJEL, 1993b) **COMB. NOV.**

Gyptis crypta Pleijel, 1993b: 238–242, figure 2.

Gyptis vittata Gardiner, 1976: 119, figure 81; Uebelacker, 1984: 28.29–28.31, figure 28 [not *Gyptis vittata* Webster & Benedict, 1887].

Type material: Holotype (USNM 52893) and 31 paratypes (USNM 52892–52894, 45534, 75478, 75319, 157615).

Type locality: USA, North Carolina, Wrightsville Beach, Banks Channel, intertidally in burrow of *Noto-mastus lobatus*.

Material examined: NORTH CAROLINA. One paratype (USNM 52892), Wrightsville Beach, Banks Channel, intertidal in burrow of *N. lobatus*, 20.vii.1974; holotype (USNM 52893) and five paratypes (USNM 157615), same locality, 18.viii.1974; five paratypes (USNM 52894), same locality, 27.ii.1975. FLORIDA. 18 paratypes (USNM 45534), Tampa Bay, 1963; one paratype (USNM 75319), off south-west Florida, 24°47.5'N, 82°13.16'W, 24 m, vii.1981; MISSISSIPPI. One paratype (USNM 75478), off Mississippi, 30°16.27'N, 88°36.42'W, 3.4 m, 24.x.1980).

Description: Length up to 7.5 mm for 39 segments. Live animals opaque with yellowish gut; eyes red. Body outline in dorsal view slightly elliptical, posteriorly tapered. Prostomium rounded rectangular, wider than long. Palpophores cylindrical, palpostyles thinner, tapering to rounded tips; palpophores as long as or slightly longer than palpostyles. Paired antennae tapering, slightly longer than or as long as palps, distal-most third forming well-demarcated tips. Median antenna similar to paired antennae but much shorter, inserted on or just in front of line between anterior pair of eyes. Eyes small, anterior pair larger and positioned slightly further apart. Nuchal organs ciliated bands along lateral sides of prostomium. Lip pads absent. Proboscis smooth, with proximal and distal ring, opening with terminal ring of ten conical papillae. Non-everted probos-

cis reaching segment 9. Segment 1 dorsally reduced, segments 2 and 3 possibly dorsally fused. Dorsal cirri and cirrophores segment 1–5 much longer and stouter than following ones, with dorsal cirri segment 3 and 4 reaching about segment 10–11. Ventral cirri segment 1–4 with well-delineated cirrophores and longer and stouter cirri than on following segments. Segment 5 with notopodial lobes and notochaetae, and neuropodial lobes and neurochaetae. Transverse dorsal ridges across median and posterior segments. Dorsal cirri reaching as far or slightly further than chaetae. Notopodial acicular lobes conical. Notochaetae of three kinds; five to ten dorsally bent acicular chaetae inserted anterior to other chaetae, large number of capillary chaetae with two alternating rows of teeth, and few, ventrally positioned curved chaetae with conical side subdistally serrated. Prechaetal neuropodial lobes elongated conical. Twenty to 40 neurochaetae, all compound and unidentate, with dorsal and median blades up to five times longer than ventral. Usually double noto- and neuroaciculae. Ventral cirri inserted distally near tip of neuropodium, tapering to fine points. Pygidium with long pygidial cirri, longer than dorsal cirri; pygidial papilla absent.

Habitat: Sand and mixed bottoms intertidally to 24 m depth, reported several times from burrows of the polychaete *N. lobatus* (Gardiner, 1976; Uebelacker, 1984).

Distribution: North Carolina, Florida, and off Mississippi.

Remarks: The description above is based on Pleijel (1993b), which also includes illustrations of the species. *Neogyptis crypta* comb. nov. is unique amongst Amphidurini in having both noto- and neuropodial lobes and chaetae starting on segment 5; usually in related taxa the notopodial lobes and notochaetae do not appear until on the following segment.

NEOGYPTIS FAUCHALDI SP. NOV. (FIGS 6–8)

Type material: Holotype (SIO-BIC A2477), + 60 paratypes (SIO-BIC 2478–2490).

Type locality: Belize, Carrie Bow Cay, 16°48.162'N, 88°04.913'W, 1 m, sand.

Etymology: Named after maestro Kristian Fauchald.

Material examined: BELIZE. Holotype (SIO-BIC A2477, fixed in formaldehyde), Carrie Bow Cay, 16°48.162'N, 88°04.913'W, 1 m, sand, SCUBA, coll. FP 2.xi.2006; six paratypes (SIO-BIC A2478, fixed in



Figure 6. *Neogyptis fauchaldi* sp. nov., dorsal view of live relaxed female paratype (SIO-BIC A2490) from Carrie Bow Cay, Belize, 4.6 mm long excluding cirri.

formaldehyde), Carrie Bow Cay, 16°48'N, 88°04'W, 1 m, sand and *Thalassia*, SCUBA, coll. FP 10.v.1993; four paratypes (SIO-BIC A2479, fixed in formaldehyde), Carrie Bow Cay, 16°48.2'N, 88°04.5'W, 1 m, sand and *Thalassia*, SCUBA, coll. FP 3–10.v.1997; 15 spms (in authors' collections, fixed in glutaraldehyde and osmium for TEM and SEM), same collection data; seven paratypes (SIO-BIC A2480, fixed in formaldehyde), reef 200 m east of Carrie Bow Cay, 10–15 m, sand, SCUBA, coll. FP 19.ix.1997; three paratypes (SIO-BIC A2481, fixed in formaldehyde), east of Carrie Bow Cay, off First Reef, 30 m, sand, SCUBA, coll. FP 21.ix.1997; five spms (FP collection, fixed in osmium for SEM), same collection data; six paratypes (SIO-BIC A2482, fixed in formaldehyde), Curley Cay, 16°47.4'N, 88°04.8'W, 1 m, coarse sand, SCUBA, coll. FP 22.ix.1997; ten paratypes (SIO-BIC A2483, fixed in formaldehyde), Carrie Bow Cay, off First Reef, East Carrie Bow Cay, 26 m, sand, SCUBA, coll. FP 23.ix.1997; three spms (fixed in 95% ethanol, destroyed for DNA sequencing), same collection data; six paratypes (SIO-BIC A2484, fixed in formaldehyde), East Carrie Bow Cay, off First Reef, 12 m, sand, SCUBA, coll. FP 23.ix.1997; two paratypes (SIO-BIC A2485, fixed in 95% ethanol), same collection data as holotype; two spms (fixed in 95% ethanol, destroyed for DNA sequencing), same collection data as holotype; one paratype (SIO-BIC A2486, fixed in formaldehyde), Twin Cays, 16°49.991'N, 88°06.240'W, 1 m, sand, SCUBA, coll. FP 3.xi.2006; two paratypes (SIO-BIC A2487, fixed in formaldehyde), Carrie Bow Cay, off reef, 16°48.190'N, 88°04.669'W, 15 m, *Halimeda* sand, SCUBA, coll. GR 8.xi.2006; one paratype (SIO-BIC A2488, fixed in 95% ethanol), same collection data; ten paratypes (SIO-BIC A2489, fixed in formalde-

hyde), Curlew Bank, 16°47.311'N, 88°04.575'W, 1 m, sand, SCUBA, coll. FP 10.xi.2006; five paratypes (SIO-BIC A2490, fixed in formaldehyde), Carrie Bow Cay, off reef crest, 16°48.065'N, 88°08.847'W, 3 m, sand, SCUBA, coll. FP 13.xi.2006.

Description: Length up to 4.5 mm for 24 segments. Live animals transparent with yellow gut; eyes brownish black. Body outline cylindrical with tapering posterior-most end (Fig. 6). Prostomium rounded quadrangular, as wide as long. Palpophores cylindrical, palpostyles evenly tapering to rounded tips; palpophores shorter than palpostyles (Fig. 7A, B). Paired antennae as long as palps but slightly thinner, tapering, distal-most third forming demarcated tips. Median antenna weakly club-shaped, much shorter than paired antennae (Fig. 7B), inserted anterior to anterior pair of eyes. Eyes medium-sized, anterior pair kidney-shaped, posterior pair smaller and rounded; both pairs positioned almost along transverse line (Fig. 6). Nuchal organs ciliated bands along dorsolateral sides of prostomium (Fig. 7A, C). Proboscis with smooth distal and terminal rings, opening with terminal ring of ten very small papillae (Fig. 7C). Lip pads absent. Non-everted proboscis reaching segment 10. Anterior segmental delineations indistinct, most part of segment 1 reduced. Dorsal cirri and cirrophores segment 1–5 longer and stouter than following ones, distinctly annulated. Ventral cirri segment 1–4 with well-delineated cirrophores and longer and stouter cirri than on following segments. Segment 5 with neuropodial lobes, neurochaetae and ventral cirri similar to following segments, segment 6 with notopodial lobes and notochaetae. Alternation in length and direction of dorsal cirri not observed. Dorsal cirri reaching as long as or slightly beyond chaetae. Weakly developed transverse dorsal ridges across posterior

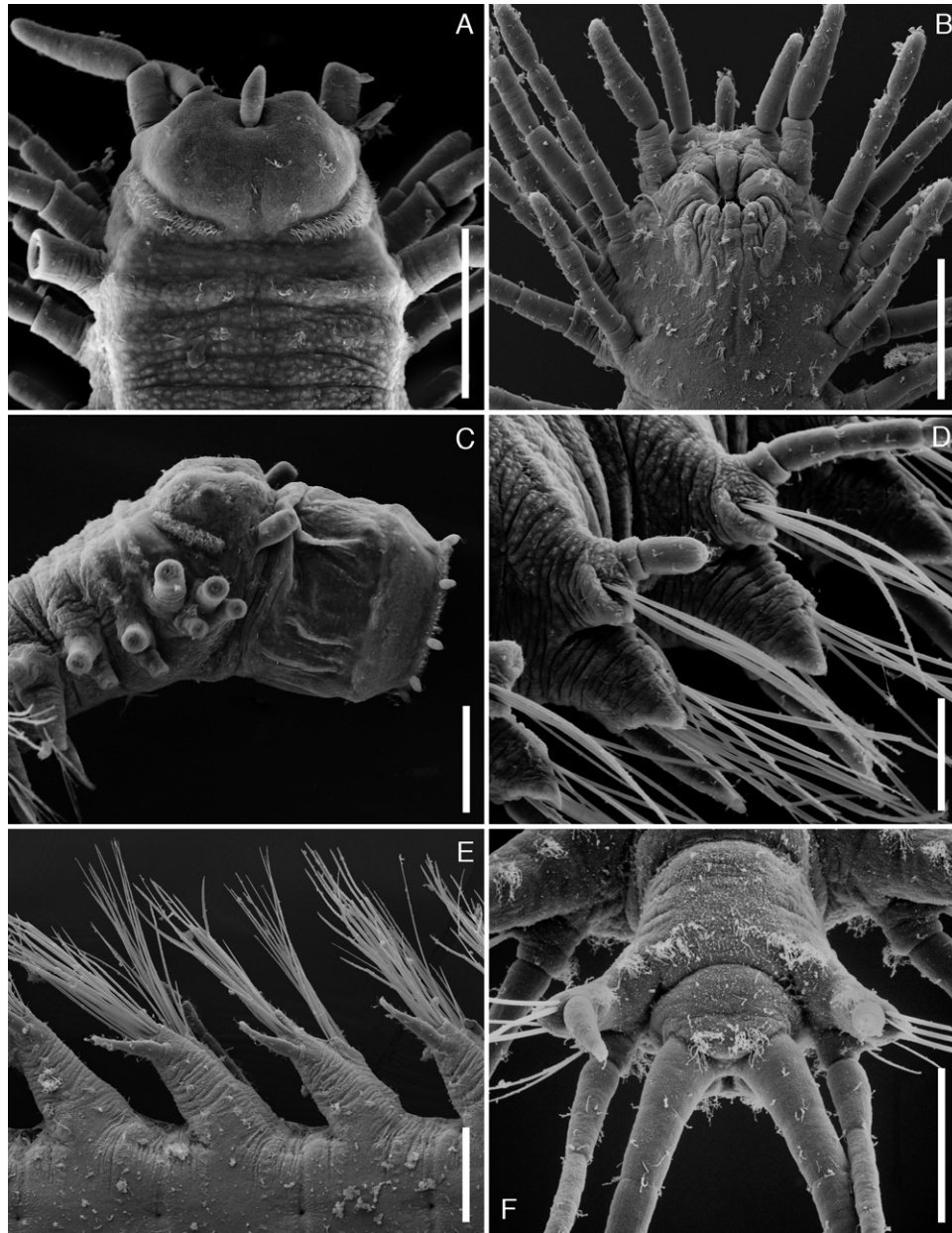


Figure 7. *Neogyptis fauchaldi* sp. nov., scanning electron microscopy photographs of specimens from the type locality. A, anterior end, dorsal view. B, anterior end, ventral view. C, anterior end, right side. D, median parapodia, anterodorsal view. E, median parapodia, right side, ventral view. F, posterior end, ventral view. Scale bars: A, B, C, E = 100 μ m, D = 50 μ m, F = 60 μ m.

segments. Notopodial acicular lobes conical (Fig. 7D). Notochaetae of three kinds; single dorsally bent acicular chaetae inserted near tip of notoacicular, *c.* ten capillary chaetae with two alternating rows of teeth, and few, ventrally positioned curved chaetae with conical side subdistally serrated. Prechaetal neuropodial lobes conical (Fig. 7D). About 15 neurochaetae, all compound and unidentate, with dorsal and median blades up to three times longer than ventral. Single

noto- and neuroacicular. Ventral cirri inserted distally on neuropodium, tapering to fine points (Fig. 7E). Pygidial cirri much longer than dorsal cirri; pygidial papilla absent (Fig. 7F).

Biology: Mature specimens observed both in May and November. Mature eggs weak pink, size 80 μ m. The sperm of *N. fauchaldi* sp. nov., appears to be that of an animal with broadcast spawning. It has a spheri-



Figure 8. *Neogyptis fauchaldi* sp. nov., specimen from the type locality, transmission electron micrograph of a section through several mature sperm. The sperm have spherical nucleus, flat cap-like acrosome and several spherical mitochondria surrounding the anchoring apparatus and 9 + 2 axoneme. Scale bar = 500 nm.

cal electron-dense nucleus capped by a simple acrosome and the midpiece is simple with a few mitochondria surrounding the anchoring apparatus. The flagellum consists of the axoneme and plasma membrane only.

Habitat: Sand and coarse sand at 1–30 m depth.

Distribution: Only known from Carrie Bow Cay and surroundings in Belize.

Remarks: *Neogyptis fauchaldi* sp. nov., shares brown-black eye colour with *N. rosea* comb. nov., *N. hongkongensis* sp. nov., and *N. vostokensis* comb. nov. It differs from *N. rosea* comb. nov. in having ten, rather than 35–80, papillae terminally on the proboscis, from *N. hongkongensis* sp. nov. in lacking lip pads but having curved notochaetae with conical side subdistally serrated, and from *N. vostokensis* comb. nov. in having slimmer ventral cirri with well-demarcated tips.

***NEOGYPTIS HINEHINA* SP. NOV.** (FIGS 9, 10)

Type material: Holotype (SIO-BIC A2491). c. 70 paratypes (SIO-BIC 2492–2495).

Type locality: Off Fiji, Lau Basin, 22°31.94'S, 176°43.11'W, 1821 m, RV Melville, ROV Jason, II dive J2-145, on vent site Hine Hina.

Etymology: Named after Hine Hina, the type locality.

Material examined: Holotype (SIO-BIC A2491, fixed in formaldehyde), off Fiji, Lau Basin, 22°31.94'S, 176°43.11'W, 1821 m, RV Melville, ROV Jason II dive J2-145, on vent site Hine Hina, 22.v.2005; c. 70 paratypes (SIO-BIC A2492, fixed in formaldehyde), same collection data as holotype; five spms (preserved in 95% ethanol, destroyed for DNA sequencing), same collection; five paratypes (SIO-BIC A2493, preserved in 95% ethanol), same collection data; three paratypes (SIO-BIC A2494, fixed in formaldehyde), off Fiji, Lau Basin, 22°32.33'S, 176°43.07'W, 1845 m, RV Melville, ROV Jason II dive J2-146, on vent site Hine Hina, 23.v.2005; five specimens (FP collection, fixed in osmium and mounted on SEM stubs), same collection data; three paratypes (SIO-BIC A2495, fixed in formaldehyde), off Fiji, Fiji Basin, 16°59.43'S, 173°54.95'W, 1973 m, RV Melville, ROV Jason II dive J2-150, on vent site White Lady, 29.v.2005.

Description: Length up to 4.5 mm for 27 segments. Live animals opaque with yellow gut, red dorsal blood vessel distinct. Body outline elongated elliptical with tapering posterior end (Fig. 9). Prostomium rounded, as wide as long (Fig. 10A). Palpophores cylindrical, palpostyles evenly tapering to rounded tips; palpostyles longer than palpophores (Fig. 10A–C). Paired antennae thinner and slightly shorter than palps, distal-most third forming well-demarcated tips. Median antenna similar in shape to paired antennae but shorter, inserted on anterior third of prostomium (Fig. 10A, B). Eyes absent. Nuchal organs short ciliated bands along lateral sides of prostomium (Fig. 10B). Lip pads absent. Proboscis opening with terminal ring of ten elongated papillae (Fig. 10C). Non-everted proboscis reaching segment 8. Segment 1 dorsally reduced, segment 2 fully developed. Dorsal cirri and cirrophores segment 1–5 much longer and stouter than following ones; longest dorsal cirri reaching segment 11–12. Ventral cirri segment 1–3 with well-delineated cirrophores and longer and stouter cirri than on following segments (Fig. 10C). Segment 4 and 5 with neuropodial lobes, neurochaetae and ventral cirri similar to following segments, segment 6 with notopodial lobes and notochaetae. Dorsal cirri thin (Fig. 10D), reaching about as far as or slightly



Figure 9. *Neogyptis hinehina* sp. nov., dorsal view of live relaxed paratype (SIO-BIC A2492), 4.5 mm long.

further than chaetae. Dorsal cirri alternation uncertain. Transverse dorsal ridges across median and posterior segments (Fig. 10D). Notopodial acicular lobes conical. Notochaetae of three kinds: one to four bent acicular chaetae, large number of capillary chaetae with alternating rows of teeth, and few, ventrally positioned curved chaetae with conical side subdistally serrated. Neuropodial lobes conical. Neurochaetal blades of three kinds: with prolonged teeth, with smooth long blades positioned medially in bundle, and with short serration. Notochaetae except acicular chaetae and shaft of neurochaetae twisted along longitudinal axis. One to three notoacaculae and usually two neuroacaculae, one smaller and one larger. Ventral cirri tapering to fine points (Fig. 10E). Pygidial cirri similar to dorsal cirri; pygidial papilla absent (Fig. 10F).

Habitat: Hydrothermal vents, 1821–1973 m.

Distribution: Only known from the hydrothermal vent sites Hine Hina and the White Lady in the Lau Basin off Fiji.

Remarks: *Neogyptis hinehina* sp. nov. is unique within Amphidurini in lacking eyes, in having neurochaetae from segment 4, and in having twisted noto- and neurochaetae.

***NEOGYPTIS HONGKONGENSIS* SP. NOV. (FIG. 11)**

Gyptis sp. A, Pleijel (1998), figure 22A–F.

Type material: Holotype (SIO-BIC A2496) and 21 paratypes (SIO-BIC A2497).

Type locality: Hong Kong, Cape D'Aquilar, Lobster Bay, 22°12.4'N, 114°15.5'E, 1 m.

Etymology: Named after Hong Kong, the type locality.

Material examined: Holotype (SIO-BIC A2496, fixed in formaldehyde), Hong Kong, Cape d'Aquilar, Lobster Bay, 22°12.4'N, 114°15.5'E, coarse sand, 1 m, 10–15.vii.1995; 21 paratypes (SIO-BIC A2497; fixed in formaldehyde), same collection data as holotype; ten spms (FP collection; fixed in osmium and mounted on stubs for SEM), same locality and date.

Description: Length up to 2.6 mm for 25 segments. Body outline cylindrical with tapering posterior end. Live animals transparent; eyes brown-black. Prostomium rounded quadrangular, as wide as long (Fig. 11A). Palpophores cylindrical, palpostyles tapering to rounded tips; palpostyles longer than palpophores. Paired antennae as long as palps but thinner, with tapering distal part (Fig. 11B). Median antenna much shorter than paired antennae, inserted on anterior third of prostomium, weakly club-shaped. Eyes medium-sized, anterior pair twice as large as posterior and situated anterolaterally to posterior pair. Nuchal organs ciliated bands along lateral sides of prostomium (Fig. 11A, D). Distinct lip pads present (Fig. 11C). Proboscis with smooth distal and terminal rings, opening with terminal ring of

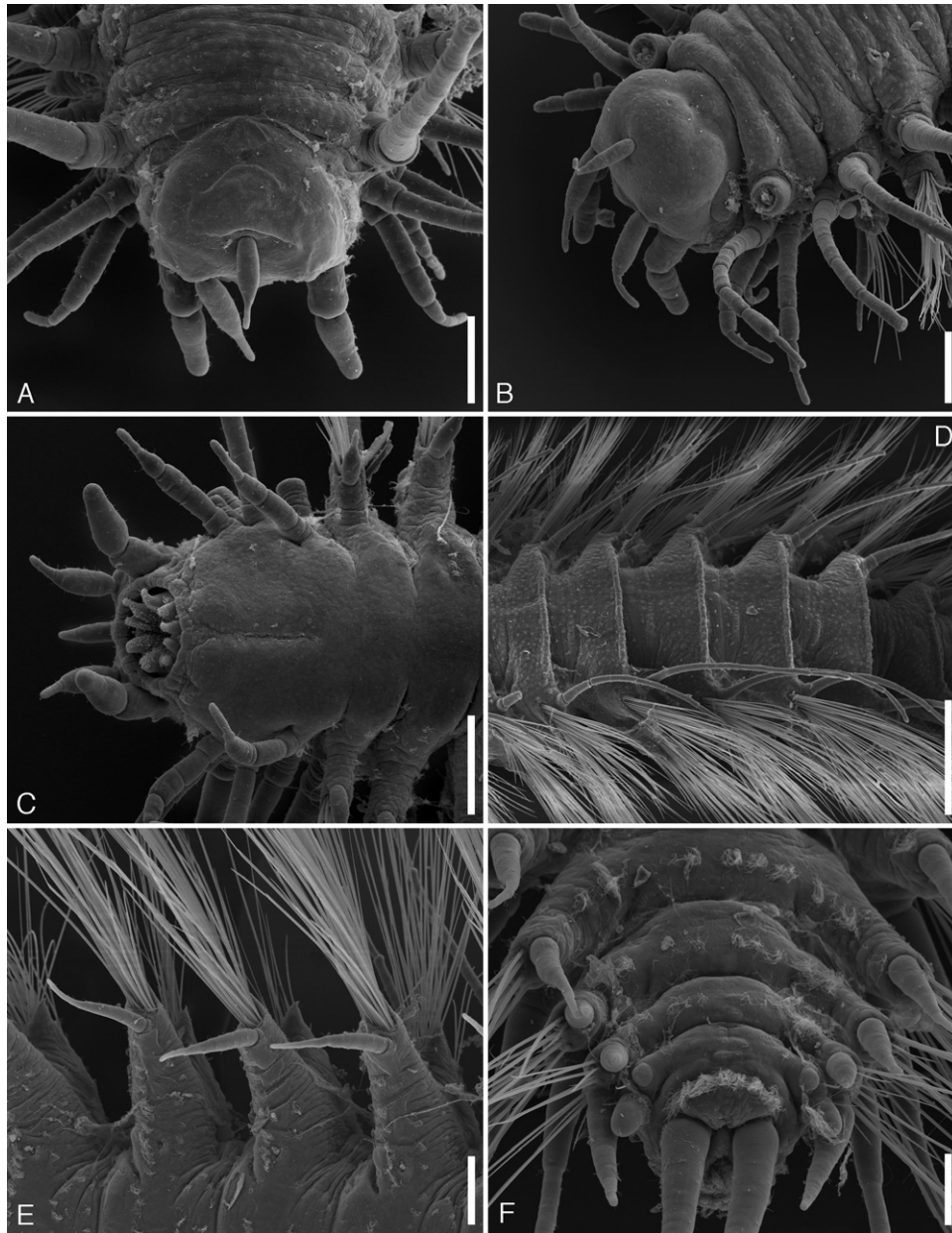


Figure 10. *Neogyptis hinehina* sp. nov., scanning electron microscopy photographs of specimens from the type locality. A, anterior end, dorsal view. B, anterior end, left side. C, anterior end, ventral view. D, posterior segments with dorsal ridges, dorsal view. E, median parapodia, right side, ventral view. F, posterior end, posteroventral view. Scale bars: A, B, D, F = 100 μ m, C = 50 μ m, E = 200 μ m. Scale bars: A–C, E = 100 μ m, D = 300 μ m, F = 50 μ m.

ten small papillae. Non-everted proboscis reaching segment 7–8. Segment 1 dorsally reduced, segment 2 fully developed. Dorsal cirri and cirrophores segment 1–5 longer and stouter than following ones, distinctly annulated. Ventral cirri segment 1–4 with well-delineated cirrophores and longer and stouter cirri than on following segments. Segment 5 with neuropodial lobes, neurochaetae and ventral cirri similar to following segments, segment 6 with noto-

podial lobes and notochaetae. Elevated and slightly stouter dorsal cirri on segment 8, 12, 15, 17, 19, 21, 23, and 25. Transverse dorsal ridges absent. Dorsal cirri short, not reaching beyond notochaetae. Transverse ridges absent (Fig. 11E). Notopodial acicular lobes conical. Notochaetae of two kinds; single or several dorsally bent acicular chaetae inserted near tip of notoaciculae, and *c.* ten capillary chaetae with two alternating rows of teeth. Prechaetal neuropo-

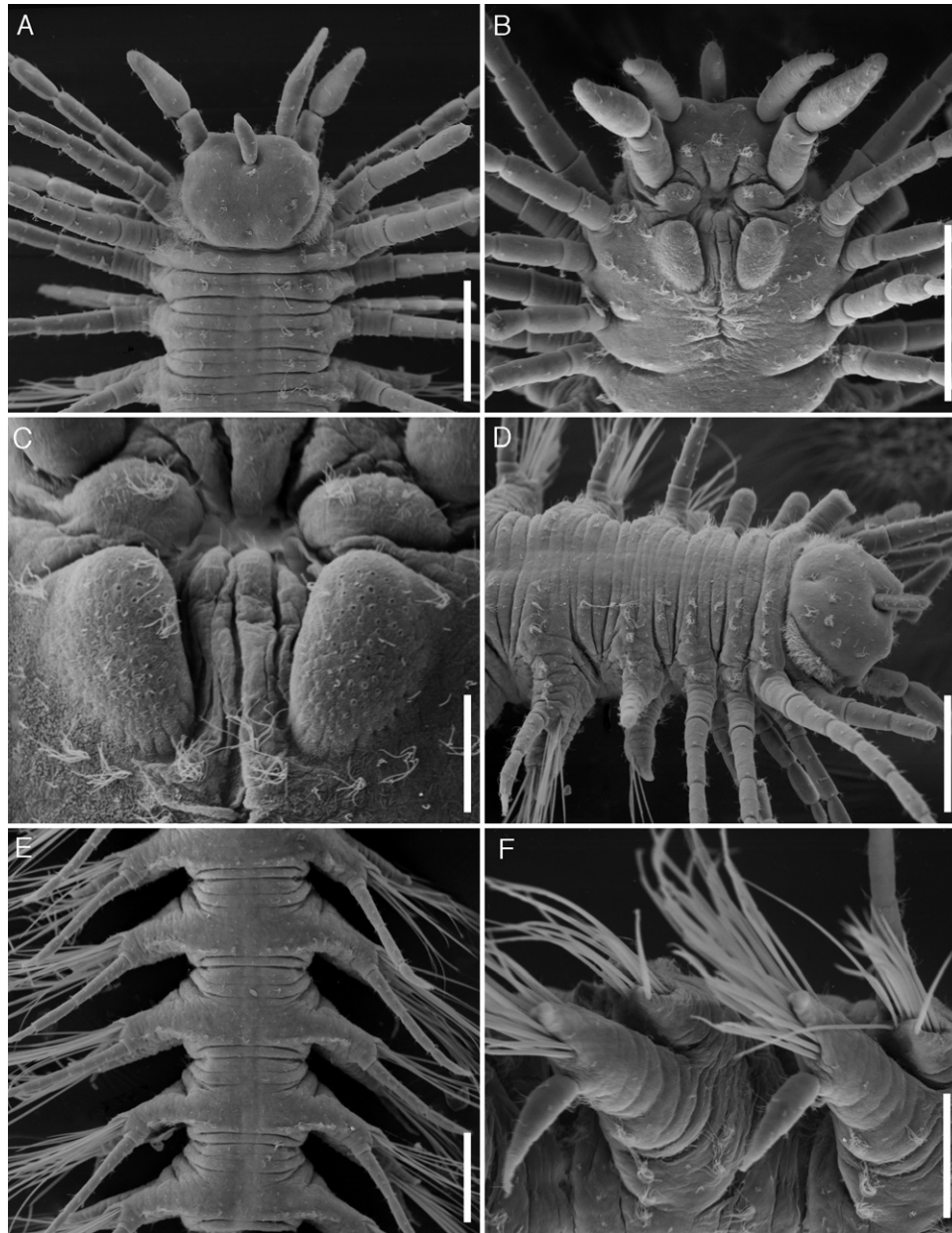


Figure 11. *Neogyptis hongkongensis* sp. nov., scanning electron microscopy photographs of specimens from the type locality. A, anterior end, dorsal view. B, anterior end, ventral view. C, lip pads. D, anterior end, right side. E, median segments, dorsal view. F, median parapodia, anteroventral view, right side. Scale bars: A, B, D, E = 100 μm , C = 25 μm , F = 50 μm .

dial lobes conical. About 15 neurochaetae, all compound and unidentate, with dorsal and median blades up to four times longer than ventral. Single noto- and neuroaciculae. Ventral cirri tapering to fine points (Fig. 11F). Pygidial cirri much longer than dorsal cirri; pygidial papilla absent.

Habitat: Coarse sand at 1 m depth.

Distribution: Only known from the type locality.

Remarks: *Neogyptis hongkongensis* sp. nov., shares brown-black eye colour with *N. rosea* comb. nov., *N. fauchaldi* sp. nov., and *N. vostokensis* comb. nov. It differs from *N. rosea* comb. nov. in having ten, rather than 35–80, papillae terminally on the proboscis, from *N. fauchaldi* sp. nov. in lacking curved notochaetae with conical side subdistally serrated, and from *N. vostokensis* comb. nov. in having slimmer ventral cirri with well-demarcated tips. Furthermore, it differs from all Amphidurini in having lip pads, a

feature that otherwise is present in *Gyptis*. The species is referred to *Neogyptis* based on the presence of distally inserted ventral cirri. However, at least one of these features must be homoplastic, and the preference of *Neogyptis*, rather than *Gyptis*, is somewhat arbitrary. Unfortunately no specimens were available for molecular study.

This is the smallest known member of *Neogyptis* and, as no mature specimens were observed and all were collected within a limited time period, we cannot exclude the possibility that they may attain a larger size. However, the absence of notochaetae on segment 1–5 and neurochaetae on segment 1–4, together with the development of the dorsal and ventral cirri on segment 1–5 and 1–3, respectively, indicate that they indeed are adults (see e.g. Pleijel, 1998, on the development of hesionids).

NEOGYPTIS MEDITERRANEA (PLEIJEL, 1993a)

COMB. NOV. (FIG. 12)

Gyptis mediterranea Pleijel, 1993a: 168–172, figures 6, 7.

Type material: Holotype (SMNH 4398) and 20 paratypes (SMNH 4399–4401).

Type locality: South France, Banyuls-sur-Mer, 42°29.92'N, 03°09.22'E, 35 m, sandy mud with detritus.

Material examined: FRANCE. Holotype (SMNH 4398), seven paratypes (SMNH 4399, 4400, fixed in formaldehyde) and four spms (FP collection, fixed in osmium and mounted on stub), Banyuls-sur-mer, 42°30.17'N, 03°09.48'E, 40 m, mud, dredge, colls Andy Mackie and FP 7.x.1991; three paratypes (NMW.Z. 1992.007.3, fixed in formaldehyde), Banyuls-sur-mer, 42°29.92'N, 03°09.22'E, 35 m, sandy mud with detritus, dredge, colls Andy Mackie and FP 3.x.1991; 13 paratypes (SMNH 4401, fixed in formaldehyde), Banyuls-sur-mer, 42°30.00'N, 03°11.75'E, 80 m, mud, dredge, colls Andy Mackie and FP 13.x.1991; six spms (FP collection, fixed in osmium and mounted on stub), Banyuls-sur-mer, 42°29.55'N, 03°09.90'E, 45 m, mud, dredge, coll. FP 15.v.1997; one spm (FP collection, fixed in 95% ethanol) Banyuls-sur-mer, 42°29.55'N, 03°09.90'E, 45 m, sandy mud, dredge, colls AN and FP 13.vii.2004. ITALY. One spm (FP collection, fixed in formaldehyde), east Sicily, Brucoli, 37°17'N, 15°13'E, 60 m, mud, dredge, coll. FP 21.v.1990.

Description: Length up to 7 mm for 32 segments. Live animals transparent; eyes red. Body outline elliptical with median parapodia much longer than anterior and posterior ones. Prostomium rounded rectangular, wider than long, with very small dorsoposterior inci-

sion (Fig. 12A, B). Palpophores cylindrical, palpophores thinner, evenly tapering to rounded tips; palpophores and palpostyles of equal length. Paired antennae thinner and slightly shorter than palps, distal-most third forming demarcated tips (Fig. 12A, B). Median antenna cylindrical, much shorter than paired antennae and without demarcated tip, inserted on line between anterior pair of eyes. Eyes medium-sized, anterior pair larger and situated further apart. Nuchal organs ciliated bands along lateral sides of prostomium (Fig. 12B). Lip pads absent. Proboscis with rugose surface on proximal ring, distal ring smooth, opening with terminal ring of conical papillae, number 20–32 (size-dependent) (Fig. 12C). Anterior segmental delineations indistinct, most part of segment 1 dorsally reduced, segment 2 and 3 dorsally fused. Dorsal cirri and cirrophores segment 1–5 much longer and stouter than following ones, dorsal cirri segment 2 longest, reaching about segment 10–12. Ventral cirri segment 1–4 with well-delineated cirrophores and longer and stouter cirri than on following segments. Segment 5 with neuropodial lobes, neurochaetae, and ventral cirri similar to following segments, segment 6 with notopodial lobes and notochaetae. Elevated and slightly stouter dorsal cirri on segment 8, 12, 15, 17, 19, 21, and 23. Dorsal cirri reaching about as far as chaetae. Transverse dorsal ridges across segments, higher on median and posterior segments (Fig. 12D, E). Notopodial acicular lobes conical. Notochaetae of three kinds: few dorsally bent acicular chaetae inserted anterior to other chaetae, large number of capillary chaetae with two alternating rows of teeth, and few, ventrally positioned curved chaetae with conical side subdistally serrated. Prechaetal neuropodial lobes elongated rounded to conical. Twenty to 40 neurochaetae, all unidentate compounds, dorsal and median blades much longer than ventral ones. Usually double noto- and neuroaciculae. Ventral cirri inserted distally near tip of neuropodium, tapering to fine points (Fig. 12F). Pygidium with long pygidial cirri, similar in shape to dorsal cirri; pygidial papilla absent.

Biology: Several mature females collected in Banyuls in October, eggs 50–60 µm in diameter.

Habitat: Mud, 35–80 m.

Distribution: Only known from southern France and the east coast of Sicily.

NEOGYPTIS PLURISSETIS (HILBIG, 1992) COMB. NOV.

Gyptis plurissetis Hilbig, 1992: 712–713, figure 2.

Amphiduros sp. A, Uebelacker, 1984: 28–34, figures 28–30.

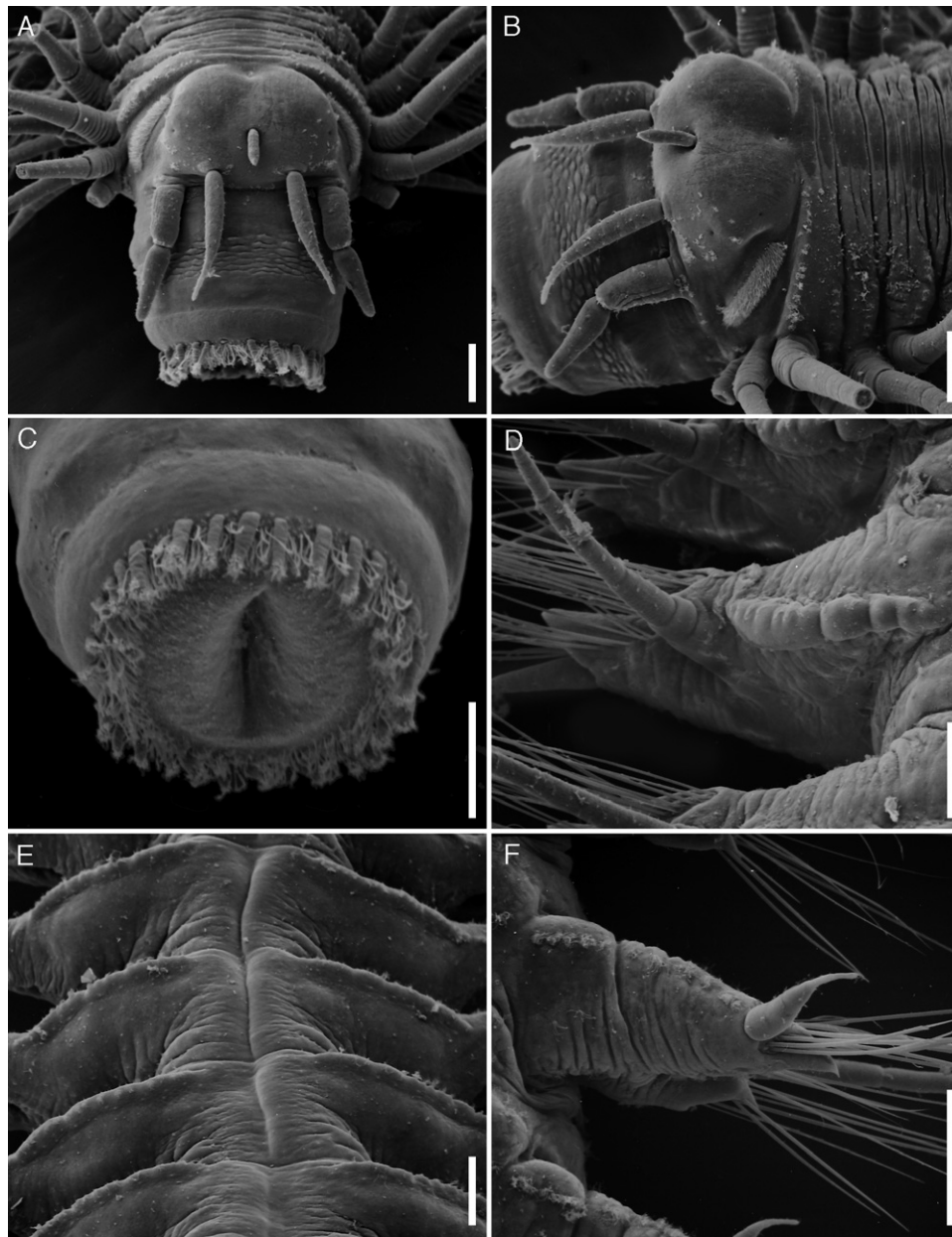


Figure 12. *Neogyptis mediterranea* **comb. nov.**, scanning electron microscopy photographs of specimens from Banyuls-sur-mer, south France. A, anterior end, anterodorsal view. B, anterior end, left side. C, proboscis opening. D, median parapodium, right side, dorsal view. E, dorsal ridges on median segments, anterodorsal view. F, median parapodium, right side, ventral view. All scale bars = 100 μ m.

Type material: Holotype (USNM 75314) and three paratypes (USNM 75212, 75315, 148702).

Type locality: Gulf of Mexico, south Florida, 25°45.70'N, 83°11.07'W, 54 m.

Material examined: GULF OF MEXICO. Holotype (USNM 75314), south Florida, 25°45.70'N, 83°11.07'W, 54 m; one paratype (USNM 75212), off

Texas, 27°24'N, 96°29'W, 98 m; one paratype (USNM 75315), same as type locality. CALIFORNIA. One paratype (USNM 148702), California, Santa Maria Basin, 35°05.83'N, 120°49.16'W, 91 m.

Description: Length up to 2 mm for eight chaetigers (only anterior fragments present). Prostomium rounded rectangular, wider than long. Palpophores cylindrical, palpostyles evenly tapering to rounded

tips; palpophores and palpostyles of about equal length. Paired antennae tapering, much thinner than palps. Median antenna of similar shape to paired antennae but much shorter, inserted between anterior pair of eyes. Eyes red, large, anterior pair twice as large as posterior pair. Nuchal organs ciliated bands along lateral sides of prostomium. Lip pads unknown. Proboscis divided in proximal and distal ring, opening with terminal ring of long, thin papillae, number 35–40 (USNM 75212 and 75315). Dorsal cirrophores segment 1–5 stouter than on following segments. Ventral cirrophores well delineated on segment 1–4, indistinct on following segments. Segment 5 with neuropodial lobes and neurochaetae only, notopodial lobes and notochoetae from segment 6. Transverse dorsal ridges uncertain. Notochaetae of four kinds (not examined, according to original description and Uebelacker, 1984); two dorsally bent acicular chaetae, five capillary chaetae with two alternating rows of teeth, about five ventrally positioned curved chaetae with conical side subdistally serrated, and one or two very fine and smooth capillaries. Neurochaetae all compounds. Scars from ventral cirri indicate distal insertion near tip of neuropodium.

Remarks: The description above is based solely on the holotype and paratypes from the Gulf of Mexico. The type material also included a paratype from California; however, this specimen is certainly not conspecific. Although all type specimens are in poor condition, they can be separated from the Gulf of Mexico specimens by having black rather than red eyes, and by having ten papillae in the terminal proboscis ring rather than a higher number. The original description reported four different kinds of notochoetae, but only three could be verified here.

Referred to Amphidurini and *Neogyptis* based on the absence of lip pads and distally inserted ventral cirri.

***NEOGYPTIS VOSTOKENSIS* SP. NOV. (FIG. 13)**

Type material: Holotype (SIO-BIC A2498), *c.* 75 paratypes SIO-BIC A2499–A2504).

Type locality: Sea of Japan, Peter the Great Bay, Vostok Bay, Vostok Marine Biological Station, 42°53.7'N, 132°44.0'E, 0.5–1 m, amongst lumps of *Modiolus modiolus* (Linnaeus, 1758).

Etymology: Named for Vostok Bay, the type locality.

Material examined: Russia, Sea of Japan, Peter the Great Bay, Vostok Bay, Vostok Marine Biological Station. Holotype (SIO-BIC A2498, fixed in formaldehyde), 42°53.7'N, 132°44.0'E, 0.5–1 m, amongst lumps

of *M. modiolus*, colls FP and Radashevsky 11.v.1994; 17 paratypes (SIO-BIC A2499, fixed in formaldehyde), same collecting data as holotype; eight spms (FP collection, fixed in formaldehyde; mounted on SEM stubs for SEM), same collecting data as holotype; *c.* 25 paratypes (SIO-BIC A2500, fixed in formaldehyde), 42°53'N, 132°44'E, 6–8 m, amongst lumps of *M. modiolus* and mud with H₂S, SCUBA, coll. Belokonev 13.v.1994; nine paratypes (SIO-BIC A2501, fixed in formaldehyde), 42°53'N, 132°44'E, 3–5 m, amongst *Crassostrea gigas* (Thunberg, 1793), SCUBA, coll. Belokonev 15.v.1994; ten paratypes (SIO-BIC A2502, fixed in formaldehyde), 42°53.7'N, 132°44.0'E, 0.5–1 m, amongst *Mytilus* sp. growing on buoy, colls FP and Radashevsky 17.v.1994; three paratypes (SIO-BIC A2503, fixed in formaldehyde), 42°53.5'N, 132°44.1'E, 3 m, sand, SCUBA, coll. Radashevsky 19.v.1994; *c.* 25 paratypes (SIO-BIC A2504, fixed in formaldehyde), Point Pashennikov, 42°53.0'N, 132°43.9'E, 6–8 m, coarse gravel with some detritus, SCUBA, coll. Radashevsky 20.v.1994.

Description: Length up to 4.5 mm for 27 segments. Live animals transparent yellowish white, eyes black; preserved yellowish white. Body outline in dorsal view of equal width with tapering posterior end (Fig. 13A). Prostomium rounded rectangular, slightly wider than long (Fig. 13B). Palpophores cylindrical, palpostyles cylindrical to elongated ovoid with rounded tips; palpophores and palpostyles of equal length. Paired antennae about as long as palps but slightly thinner, cylindrical with tapering, rounded tips. Median antenna much shorter than paired antennae, elliptical with rounded tip, inserted anterior to anterior pair of eyes. Eyes medium-sized, anterior pair twice as large and positioned slightly further apart. Nuchal organs ciliated bands along lateral sides of prostomium (Fig. 13B). Lip pads absent. Proboscis smooth, with terminal ring of ten small, elongated papillae. Segment 1 dorsally reduced, segment 2 fully developed. Dorsal cirri and cirrophores segment 1–5 much longer and stouter than following ones, with dorsal cirri segment 2 and 4 reaching about segment 10–11. Ventral cirri segment 1–4 with well-delineated cirrophores and longer and stouter cirri than on following segments (Fig. 13C). Segment 5 with neuropodial lobes, neurochaetae and ventral cirri similar to following segments, segment 6 with notopodial lobes and notochoetae. Elevated and slightly stouter dorsal cirri on segment 8, 12, 15, 17, 19, 21, and 23. Median segments with dorsal cirri reaching as far as chaetae (Fig. 13A). Weakly developed transverse dorsal ridges across median and posterior segments (Fig. 13A, D). Notopodial acicular lobes small, conical. Notochaetae of two kinds, single dorsally bent acicular chaeta inserted anterior to

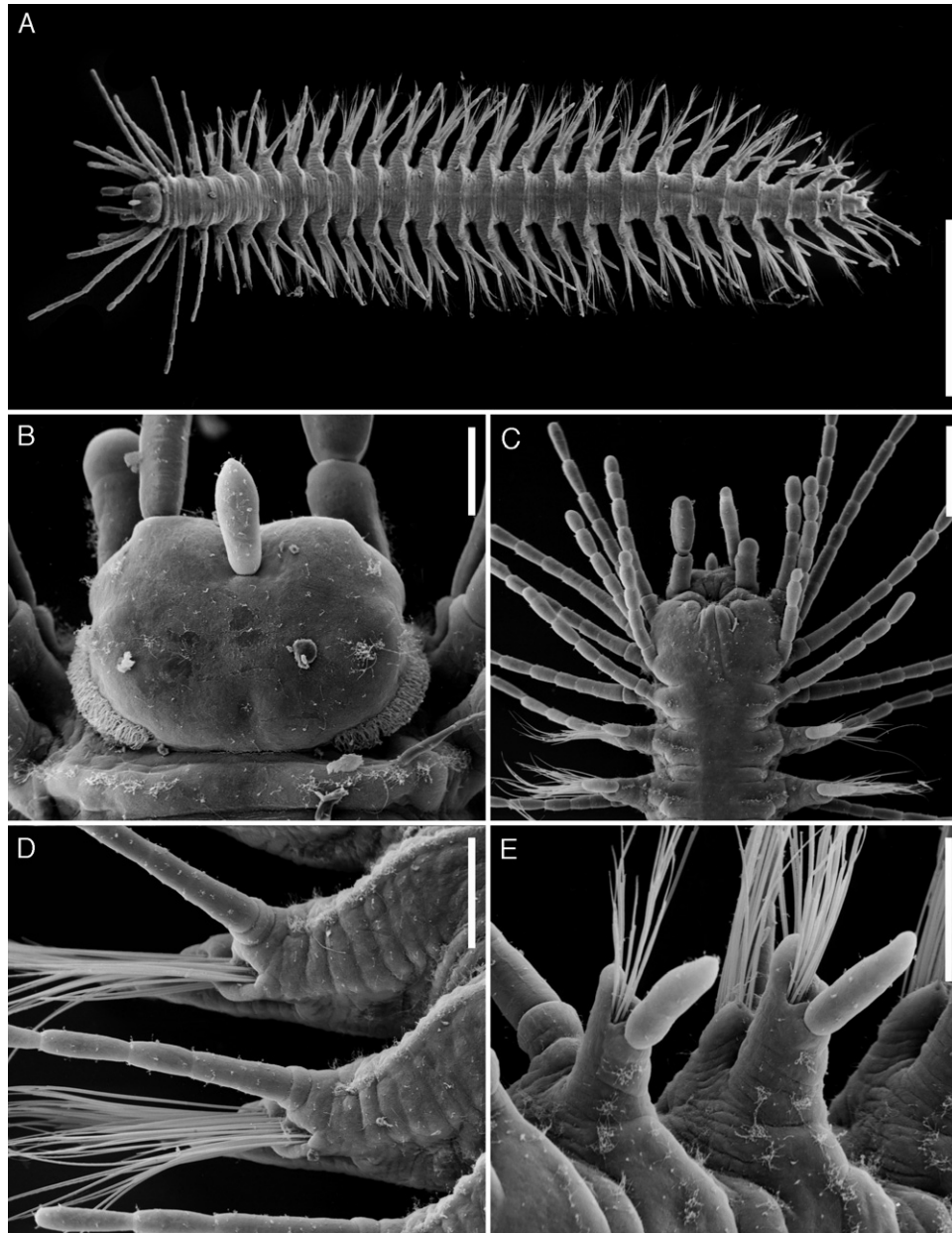


Figure 13. *Neogyptis vostokensis* sp. nov., specimens from the type locality, scanning electron microscopy photographs. A, entire specimen, dorsal view. B, prostomium, dorsal view. C, anterior end, ventral view. D, median parapodia, right side, anterodorsal view. E, segment 5 and 6, right side, anteroventral view. Scale bars: A = 500 μ m, B = 50 μ m, C = 200 μ m, D, E = 100 μ m.

other chaetae, and *c.* 25 capillary chaetae, both with two alternating rows of teeth. Neuropodial lobes elongated triangular. Neurochaetae *c.* 25, all unidentate compounds with shafts with distinct internal chambers and longitudinal canals, dorsal and median blades up to seven times longer than ventral ones. Single or double noto- and neuroaciculae. Ventral cirri inserted distally near tip of neuropodium, with distinct, elongated tips (Fig. 13E; usually with more

elongated tips than on picture). Pygidium with long pygidial cirri, similar in shape to dorsal cirri; pygidial papilla absent.

Habitat: Sand and mud, amongst mussels and oysters, 0.5–8 m.

Distribution: Only known from Vostok Bay in Peter the Great Bay, Sea of Japan.

Remarks: Morphologically, *N. vostokensis* sp. nov. belongs to a group of small *Neogyptis* species that have brown-black eyes, and that also includes *N. fauchaldi* sp. nov., from Belize, and *N. hongkongensis* sp. nov. It can be separated from the latter by the absence of lip glands, from the former by the absence of notochaetae with the conical side subdistally serrated, and from both by the shape of the ventral cirri, which are stouter and lack well-demarcated tips. Unfortunately, no specimens were available for molecular study.

NEOGYPTIS SP. A

Material examined: One spm fixed in 95% ethanol, posterior part used for molecular analysis (SIO-BIC A2505), US, Florida Keys, Spanish Harbor Key Borrow, 24°39.430'N, 81°18.155'W, intertidal, amongst sand, stones, and *Halimeda* sp., colls FP and GR, 5.iii.2010.

Description: Posteriorly incomplete, 3.5 mm long for 18 segments. Live specimen transparent whitish; eyes red. Prostomium rounded rectangular, about as wide as long.

Palpophores cylindrical, palpostyles tapering; palpophore length 1/3 of palpostyles. Paired antenna as long as palps but thinner, cylindrical, with demarcated tips. Median antenna without distinct tip, length 1/3 of paired antennae, inserted anterior to anterior pair of eyes. Anterior pair of eyes larger than posterior pair, weakly kidney-shaped; posterior pair rounded. Nuchal organs not observed. Lip pads absent. Proboscis terminal ring with ten papillae. Non-everted proboscis reaching segment 8. Dorsal cirri and cirrophores segment 1–5 much longer and stouter than following ones, ventral cirri segment 1–4 with well-delineated cirrophores and longer and stouter cirri than on following segments. Segment 5 with neuropodial lobes, neurochaetae and ventral cirri similar to following segments, segment 6 with notopodial lobes and notochaetae. Dorsal cirri reaching slightly further than neurochaetae. Notochaetae of two kinds only observed, about 20 capillary chaetae with two alternating rows of teeth, and single chaetae with one side subdistally serrated. Neurochaetae about 20, all unidentate compounds, dorsal median blades much longer than ventral ones. Ventral cirri inserted distally near tip of neuropodium, with distinct tips.

Habitat: Sand and *Halimeda*, intertidal.

Distribution: Known only from a single specimen from Spanish Harbor Key Borrow, Florida Keys.

Remarks: *Neogyptis* sp. A may be close to *N. plurisetis* but we have at present not enough information to assess this; the number of proboscis papillae appears to be smaller in *Neogyptis* sp. A, although this may be size-related.

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