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Four new species of Hesionidae (Annelida, Polychaeta, Phyllodocida) from eastern Pacific
chemosynthetic habitats and reinstatement of *Vrijenhoekia*

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Marine Biology

by

Rachel Kroesche

Committee in charge:

Professor Gregory Rouse, Chair
Professor Ronald Burton
Professor Jennifer Taylor

2025

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University of California San Diego

2025

DEDICATION

For my partner.

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ABSTRACT OF THE THESIS

Four new species of Hesionidae (Annelida, Polychaeta, Phyllodocida) from eastern Pacific
chemosynthetic habitats and reinstatement of *Vrijenhoekia*

by

Rachel Kroesche

Master of Science in Marine Biology

University of California San Diego, 2025

Professor Gregory Rouse, Chair

Hesionid polychaetes are well known at hydrothermal vents, methane seeps, and unusual habitats such as whale falls. In 1985 *Sirsoe grasslei* was the first hesionid to be named from a hydrothermal vent. *Vrijenhoekia* was erected in 2008 for a closely related species from a whalefall. Further species of *Sirsoe* and *Vrijenhoekia* were described in the following decade and

the genera were recovered as reciprocally monophyletic with DNA data. However, *Sirsoe* was made a senior synonym of *Vrijenhoekia* when 10 further new species from the clade were named off the coast of Brazil. To further evaluate the status of *Sirsoe* and *Vrijenhoekia*, we present the first DNA data for the type species of *Sirsoe*, *S. grasslei*. Our results allow the reinstatement of *Vrijenhoekia* and emended diagnoses for *Sirsoe* and *Vrijenhoekia*. Four new species, three in *Sirsoe* and one in *Vrijenhoekia*, are also described.

INTRODUCTION

Hesionidae Grube, 1850 (Annelida) is a globally distributed clade of polychaetes with members found in marine environments from the intertidal to a range of deep-water habitats. Some hesionid taxa are abundant at chemosynthetic environments such as hydrothermal vents, methane seeps, and whale falls [1–9]. *Orseis grasslei* Blake, 1985 is the earliest named of these species, described from a hydrothermal mound in the Guaymas Basin, Gulf of California, Mexico [1]. The “iceworm,” *Hesiocaeca methanicola* Desbruyères and Toulmond, 1998 was subsequently described after being found living in high densities on methane hydrates in the Gulf of California [2]. Pleijel [10], in his major monograph on Hesionidae, established the genus *Sirsoe* Pleijel, 1998 for *O. grasslei* and noted morphological similarities between *S. grasslei* and the then unpublished *H. methanicola*, referring to it as the undescribed *Sirsoe* A. Desbruyères and Toulmond [2] rejected this view and placed their new species in *Hesiocaeca* Hartman, 1965 [11].

Pleijel et al. [3] formally placed *Hesiocaeca methanicola* in *Sirsoe* and published the first DNA sequences for *Sirsoe methanicola*. Molecular data for the type species, *Sirsoe grasslei*, was not available at that time. *Vrijenhoekia balaenophila* Pleijel, Rouse, Ruta, Wiklund & Nygren, 2008 was described in the same study from specimens collected at a whale fall off the coast of California. *Vrijenhoekia balaenophila* was recovered as the sister taxon to *Sirsoe methanicola* and considered as a separate genus based on the absence of an obvious median antenna, presence of glandular lip pads (GLPs), and lack of developed neuropodial lobes on segment three. Subsequently a further three species of *Vrijenhoekia* and a new *Sirsoe* were described from eastern Pacific whale falls, as well as an undescribed *Vrijenhoekia* sp. A [4]. *Sirsoe* and *Vrijenhoekia* formed reciprocally monophyletic clades in that study but unlike *V. balaenophila*,

all the new *Vrijenhoekia* had a median antenna and lacked GLPs, as found in *Sirsoe*. In 2018, Rouse et al. [5] described two more *Sirsoe* from methane seeps off Costa Rica and Mexico, with *Sirsoe* and *Vrijenhoekia* still being recovered as sister clades. In 2019 (and 2021), Shimabukuro et al. [6,9] used DNA data and morphology to describe a further 10 hesionid species from Brazilian whale falls. They recognized three major clades, placing them all within *Sirsoe* and stated that their analyses showed that “*Sirsoe* constitutes a monophyletic group only with the inclusion of *Vrijenhoekia* species,” and that “recognition of *Vrijenhoekia* renders both genera non-monophyletic.” On these arguments they made *Vrijenhoekia* a junior synonym of *Sirsoe*. Examination of their phylogenetic results show that they could have had reciprocally monophyletic *Sirsoe* (Clade I) and *Vrijenhoekia* (Clades II and III) if they had made most of their new species members of *Vrijenhoekia*. Three further new *Sirsoe* were described recently from the South China Sea and were all in Clade I [8]. A new *Vrijenhoekia* was also named recently from a whale fall off Australia, where the synonymy under *Sirsoe* was ignored [7].

To further evaluate the status of *Sirsoe* and *Vrijenhoekia*, we present the first molecular data for type species of *Sirsoe*, *S. grasslei*, collected from the hydrothermal vents in the Pescadero Basin, Mexico, south of the original type locality. Three new species of *Sirsoe* are also described here for specimens collected from the Pescadero Basin and Alaska. The previously informally named *Vrijenhoekia* sp. A. for a single specimen from the Guaymas seeps [4] is described incorporating new material from Costa Rican methane seeps. Our results allow the reinstatement of *Vrijenhoekia* and emended diagnoses for *Sirsoe* and *Vrijenhoekia*.

MATERIALS AND METHODS

SPECIMEN COLLECTION

Specimens described in this study were collected from six cruises. Specimens from the Gulf of California, Mexico were collected with R/V *Falkor* and ROV *SuBastian* on cruises FK181031 (2018) and FK210922 (2021). Specimens from Costa Rica were collected with R/V *Atlantis* with HOV *Alvin* on cruises AT15-44 (2009), AT37-13 (2017), and AT42-03 (2018). Specimens from Alaska were collected on cruise AT50-24 (2024). Specimens from Mexico were collected under CONAPESCA permits PPFE/DGOPA-200/18 (2018) and PPFE/DGOPA-090/21 (2021). Specimens from Costa Rica were under permits issued by CONAGEBIO (Comisión Nacional para la Gestión de la Biodiversidad), INCOPESCA (Instituto Costarricense de Pesca y Acuicultura), and SINAC (Sistema Nacional de Áreas de Conservación) under MINAE (Ministerio de Ambiente y Energía), Government of Costa Rica: INCOPESCA-CPI-003-12-2018, R-070-2018-OT-CONAGEBIO, SINAC-CUSBSE-PI-R-032-2018, SINAC-SE-CUS-PI-R-035-2017.

SPECIMEN FATES AND MORPHOLOGY

Specimens were recovered from the submersibles and after sorting in cold sea water were relaxed with 7% magnesium chloride and photographed live under a stereomicroscope (Leica MZ9.5 or MZ12.5) with a digital camera (Canon EOS M6, Rebel T6i or Rebel T7i). Whole specimens or tissue subsamples for DNA sequencing were preserved in 95% ethanol. Voucher specimens were preserved in 10% formalin in seawater for morphological analysis. Additional post-preservation morphological photographs were taken with one of the aforementioned stereomicroscopes and specimens post-stained with ShirlastainA[®] (SDL Atlas sdlatlas.com) and

chaetae were documented with a Leica DMR interference contrast microscope and Canon EOS Rebel T6i camera. Depth date and locality information can be found in Table 1.

Specimens are deposited at the Scripps Institution of Oceanography, Benthic Invertebrate Collection (SIO-BIC), La Jolla, California, USA, Museo de Zoología, Universidad de Costa Rica (MZUCR), San Jose Costa Rica and the Colección Regional de Invertebrados Marinos (CRIM), Estación Mazatlán UNAM, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México (ICML-EMU), Mazatlán, Sinaloa, Mexico.

Table 1. GenBank accession numbers and catalog numbers of specimens referenced in this study. New data in bold. Abbreviation: **AM** Australian Museum, **MZUSP**, Museu de Zoologia, Universidade de São Paulo, **SY** Repository of the Second Institute of Oceanography, **SIO-BIC** Scripps Institution of Oceanography Benthic Invertebrate Collection, **SMNH** Swedish Museum of Natural History. *Vrijenhoekia mindiae* n. sp. is what was formerly referred to as *Vrijenhoekia* sp. A in Summers et al. [4]. *Vrijenhoekia* BioSuOr was previously referred to as *Sirsoe* BioSuOr [6]. Other COI data generated for this study are listed with the material examined.

Species	Voucher	Locality	COI	16S	18S	28S
<i>Hesiospina vestimentifera</i>	SIO-BIC A2510	Fiji	JN631310	JN631320	JN631330	JN631343
<i>Sirsoe alucia</i>	MZUSP 3359	SW Atlantic	MH935127	MH935204	-	-
<i>Sirsoe dalailamai</i>	SIO-BIC A1767	Costa Rica	MG517498	MG523357	MG649240	MG649245
<i>Sirsoe feitiana</i>	SY 398007	South China Sea	OR126117	OR129662	-	-
<i>Sirsoe grasslei</i>	SIO-BIC A13989	Gulf of California	PQ774161	PQ771110	PQ771116	PQ771120
<i>Sirsoe maximiano</i>	MZUSP 3371	SW Atlantic	MH935151	MH935157	-	-
<i>Sirsoe methanicola</i>	-	Gulf of Mexico	DQ513295	DQ442582	JN631332	DQ442611
<i>Sirsoe nanhaiensis</i>	SY 396P01	South China Sea	OR126101	OR129656	-	-
<i>Sirsoe pleijeli</i> n. sp.	SIO-BIC A13998B	Gulf of California	PQ774167	PQ771113	PQ771119	PQ771123
<i>Sirsoe polita</i>	SY 400001	South China Sea	OR126114	OR129671	-	-
<i>Sirsoe sapote</i> n. sp.	SIO-BIC A14076	Gulf of California	PQ774180	PQ771112	PQ771117	PQ771121
<i>Sirsoe shastae</i> n. sp.	SIO-BIC A10636	Gulf of California	PQ774162	PQ771113	PQ771118	PQ771122
<i>Sirsoe sirikos</i>	SIO-BIC A2323	California	JN571829	JN571882	JN571893	JN571902
<i>Vrijenhoekia balaenophila</i>	SMNH 6305 type	California	DQ513296	DQ513301	JN631333	DQ513306
<i>Vrijenhoekia ahabi</i>	SIO-BIC A2327	California	JN571876	JN571887	JN571898	JN571907
<i>Vrijenhoekia balaenophila</i>	SMNH 6305 type	California	DQ513296	DQ513301	JN631333	DQ513306
<i>Vrijenhoekia</i> cf. <i>balaenophila</i>	SMNH 6307	California	DQ513297	DQ513302	-	DQ513307
<i>Vrijenhoekia mindiae</i> n. sp.	SIO-BIC A3255	Gulf of California	KP745533	KP745536	KP745539	KP745542
<i>Vrijenhoekia ketea</i>	SIO-BIC A2341	California	JN571838	JN571885	JN571896	JN571905
<i>Vrijenhoekia falenothiras</i>	SIO-BIC A2345	California	JN571875	JN571886	JN571897	JN571906
<i>Vrijenhoekia nadir</i> n. comb.	MZUSP 3361	SW Atlantic	MH935129	MH935200	-	-
<i>Vrijenhoekia besnard</i> n. comb.	MZUSP 3370	SW Atlantic	MH935147	MH935199	-	-
<i>Vrijenhoekia alphadelphini</i> n. comb.	MZUSP 2272	SW Atlantic	MH935132	MH935203	-	-

Table 1, Continued.

Species	Voucher	Locality	COI	16S	18S	28S
<i>Vrijenhoekia alphacrucis</i> n. comb.	MZUSP 3363	SW Atlantic	MH935140	MH935191	-	-
<i>Vrijenhoekia yokosuka</i> n. comb.	MZUSP 3369	SW Atlantic	MH935141	MH935196	-	-
<i>Vrijenhoekia ypupiara</i> n. comb.	MZUSP 3357	SW Atlantic	MH935119	MH935179	-	-
<i>Vrijenhoekia pirapuan</i> n. comb.	MZUSP 3455	SW Atlantic	MH935102	MH935189	-	-
<i>Vrijenhoekia ungava</i> n. comb.	MZUSP 3369	SW Atlantic	MH935145	MH935160	-	-
<i>Vrijenhoekia</i> BioSuOr	-	SW Atlantic	MH935146	MH935161	-	-
<i>Vrijenhoekia timoharai</i>	AM W.53702	Australia	OQ801445	OQ820995	OQ803244	-

MOLECULAR DATA

DNA was extracted with the Zymo Research DNA-Tissue Mini- and Microprep kit following the manufacturer's protocol. COI was sequenced for initial species delimitation. Nuclear marker genes (28S rRNA and 18S rRNA) and an additional mitochondrial gene (16S rRNA) were then sequenced from a representative of each of the taxa newly included here. DNA was amplified with 12.5µl Apex 2.0× Taq DNA Polymerase, 1µl each of the forward and reverse primers for each gene, 8.5µl of water, and 2µl of DNA. Primers and profiles used are the same as used in [4]. PCR products were cleaned with ExoSAP-IT and sent to Eurofins Genomics (Louisville, KY, USA) for Sanger sequencing. Sequences were trimmed on Geneious Prime 2023.0.4 (<http://www.geneious.com>). GenBank accession numbers for relevant species and localities are found in Table 1. Additional GenBank numbers for COI data generated for this study are listed with the material examined.

MOLECULAR DATA ANALYSES

Sequences for a terminal listed on GenBank as *Hesiospina vestimentifera* Blake, 1985 were used as outgroup based on previous studies [5,7]. Sequences were aligned using MAFFT [12] with the G-INS-i option via Mesquite v.3.81 [13]. COI, 16S, 18S, and 28S genes were

aligned individually and concatenated using SequenceMatrix [14] into a single matrix. The data was then evaluated with maximum likelihood (ML) inference using RaxML-NG [15] with RAxML GUI v2.0.10 [16] with the GTR+I+G model for all partitions, selected using ModelTest-NG [17]. Support was evaluated by bootstrapping with 1000 replicates. FigTree 1.8 [18] was used to visualize the maximum likelihood tree with bootstrap values. A COI uncorrected distance matrix was constructed with PAUP* 4a (build 168) [19]. COI haplotype networks were created with PopArt [20] using the TCS [21] network option. Morphological transformations for three characters were mapped onto the ML tree topology (with branch length information) via Mesquite using a likelihood transformations under the Mk1 model [22]. The three characters traced were:

1. Median antenna: 0. Absent, 1. Present, 2. Present as mediodorsal tubercle.
2. Frontal tubercle: 0. Absent, 1. Present prominent, 2. Present inconspicuous.
3. Glandular lip pads: 0. Absent, 1. Present.

Scoring for these characters was based on the original descriptions [1–8,10]. We note that the mediodorsal tubercle described for *Vrijenhoekia balaenophila* [3] is positionally in the same place as a median antenna and so may represent a reduced form of this structure. We used the median antenna state ‘Present as mediodorsal tubercle’ to reflect this. Unfortunately for most recently described *Sirsoe* and *Vrijenhoekia* that have been regarded as having no median antenna [6,8], the quality of the preservation and imagery is not adequate to determine if a mediodorsal tubercle may be present. These taxa are scored with median antenna absent. The frontal tubercle, also known as a facial tubercle, is found in a range of hesionids, including other *Psamathinae* such as *Nereimyra* and some *Hesiospina* [10]. We note here that the frontal tubercle described as present for *Sirsoe alucia* Shimabukuro, Carrerette, Alfaro-Lucas, Rizzo, Halanych, and Sumida,

2021 [6,9] and *Sirsoe maximiano* Shimabukuro, Carrerette, Alfaro-Lucas, Rizzo, Halanych, and Sumida, 2021 [6,9] is hardly evident in the labelled figures (Figs 7C, E, 10C, D). We therefore added a state 'Present inconspicuous' for this character. Also, *Sirsoe methanicola* has previously been regarded having a frontal tubercle [3,10], but this feature was not noted nor visible in the original description and figures [2] and was scored as absent here.

RESULTS

PHYLOGENY

The maximum likelihood analysis showed three major clades as recovered in recent analyses [6–8], which are marked as Clades I, II and III (Figure 1).

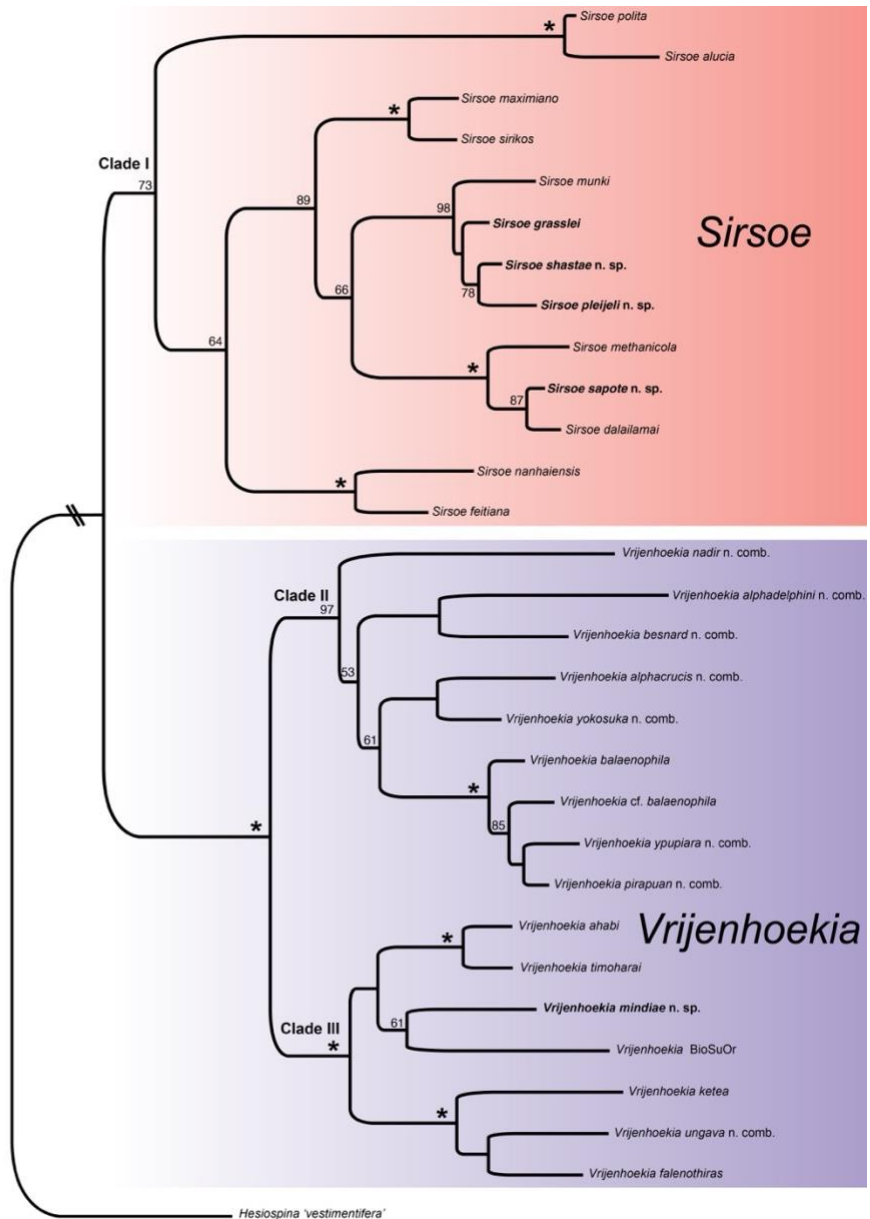


Figure 1. Maximum likelihood (ML) phylogenetic tree from concatenated and partitioned mitochondrial (COI and 16S) and nuclear (18S and 28S) genes. New species are in bold and values on nodes represent ML bootstrap values with an asterisk indicating support of 100%.

Clade I is referred to here as *Sirsoe* and contains the type species *S. grasslei*. Clades II and III formed a clade and are collectively referred to as the reinstated *Vrijenhoekia*. Support values for *Vrijenhoekia* and Clades II and III were high (bootstrap (BS) 97 or above), while that for the *Sirsoe* Clade I was lower with BS 73 (Fig. 1). Three of the new species described here were found in the *Sirsoe* Clade I. Two of the new species, *Sirsoe pleijeli* n. sp. and *Sirsoe shastae* n. sp. formed a clade with reasonable support (BS 78) and this clade was sister group to *S. grasslei*, though with low support. These three taxa formed a well-supported clade with *Sirsoe munki*. The third new *Sirsoe* species, *Sirsoe sapote* n. sp. formed a well-supported clade with *S. dalailama*. The *Vrijenhoekia* species previously known as *Vrijenhoekia* sp. A and described here as *Vrijenhoekia mindiae* n. sp., was recovered as the sister group to the unnamed species from Brazil called here *Vrijenhoekia* BioSuOr (previously called *Sirsoe* BioSuOr [6]), though with low support (BS 61).

HAPLOTYPE NETWORKS

Two haplotypes were present for *Sirsoe pleijeli* n. sp. (Figure 2) among the 21 specimens sequenced for 596 bases of COI. Only one base differed between the specimens found off the Aleutian Archipelago, Alaska, and in the Gulf of California, Mexico. 19 of the sequences were the same haplotype, which were found at both sites. The specimens from Mexico were from around 3700 m at hydrothermal vents while those from Alaska were from a methane seep at around 2000 m. The sampling sites were over 5,500 km apart.

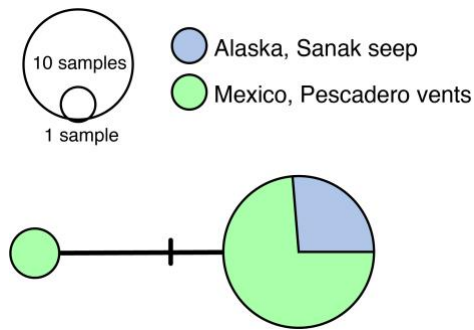


Figure 2. TCS haplotype network for COI from 21 individuals of *Sirsoe pleijeli* n. sp. from the Sanak Islands, Alaska, seeps, and hydrothermal vents in the Pescadero Basin, Gulf of California, Mexico.

Vrijenhoekia mindiae n. sp. Was found at seeps in the Gulf of California, Mexico and off the Pacific coast of Costa Rica from depths of 1000-1500 m. Among the 15 specimens sequenced for 597 bases of COI, six haplotypes were recovered, with one haplotype dominating (Fig. 3). The single specimen from the Gulf of California differed by a minimum of 8 bases from the Costa Rican haplotypes, which differed by no more than 5 bases from each other.

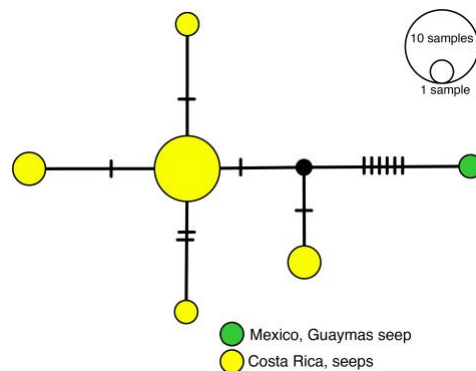


Figure 3. TCS haplotype network for COI from 15 individuals of *Vrijenhoekia mindiae* n. sp. From seeps in the Guaymas Basin, Gulf of California, Mexico, and Costa Rican seeps.

TRANSFORMATIONS

The transformation of the three morphological characters are shown on the ML tree topology in Figures 3, 4, and 5. Figure 4 shows the transformation for the median antenna and under a maximum likelihood model it appears the feature has evolved twice and been lost several times. It appears as apomorphic for subclades within *Sirsoe* and *Vrijenhoekia*, with losses in each

of these subclades. The mediodorsal tubercle form of the median antenna, which has only been seen in *Vrijenhoekia balaenophila* to date, appeared within a clade of *Vrijenhoekia* where the median antenna is otherwise absent (Figure 4).

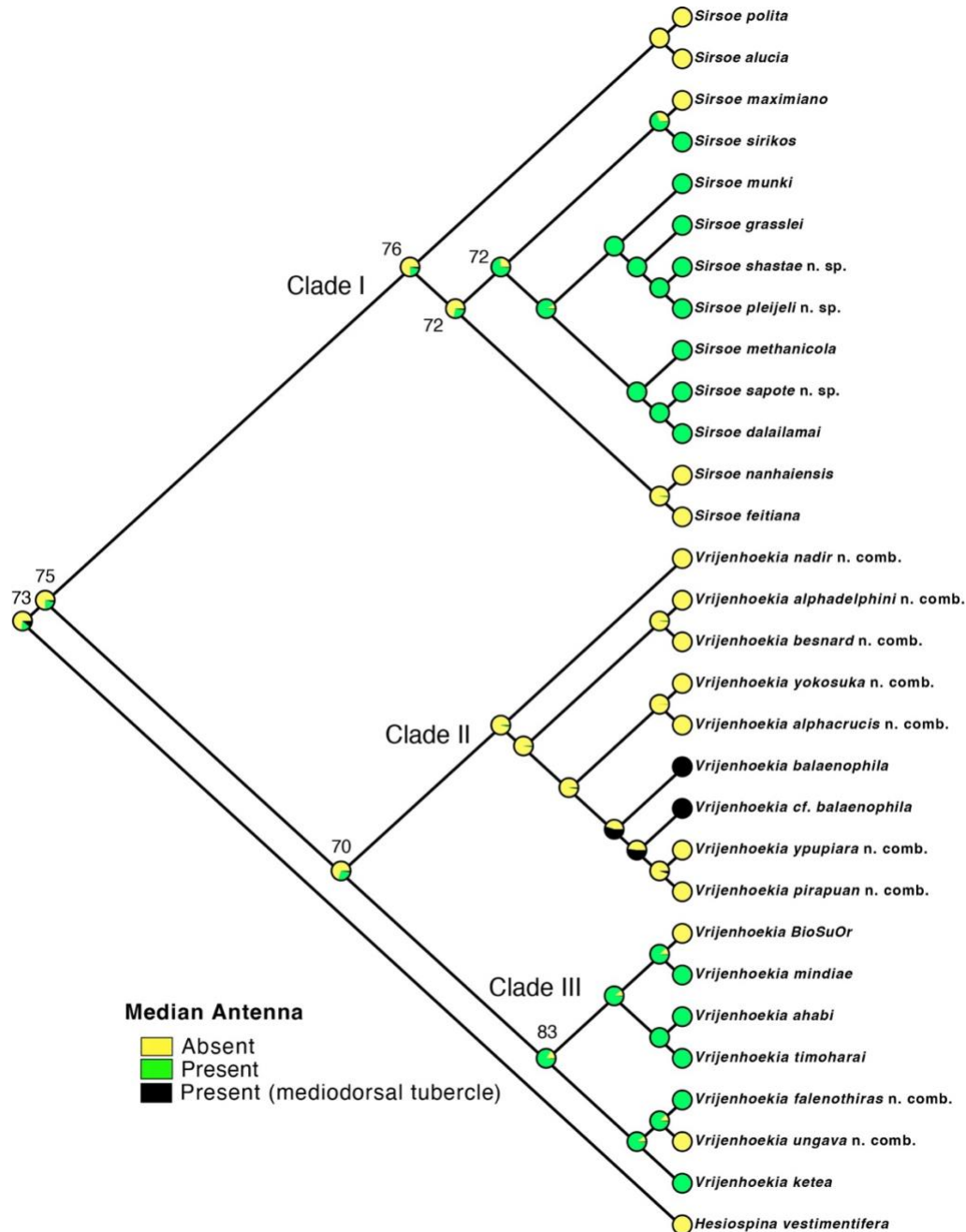


Figure 4. Transformation for the character Median Antenna mapped onto the ML tree topology (with branch length information), visualized in Mesquite 3.81 using likelihood ancestral state reconstruction on ball and sticks tree form, with the Mk1 probability model. Values shown at some nodes represent likelihood for the various states under the model.

The frontal tubercle character transformation (Figure 5) shows that this feature, which is present in the outgroup, may be plesiomorphic for the *Sirsoe*+*Vrijenhoekia* clade.

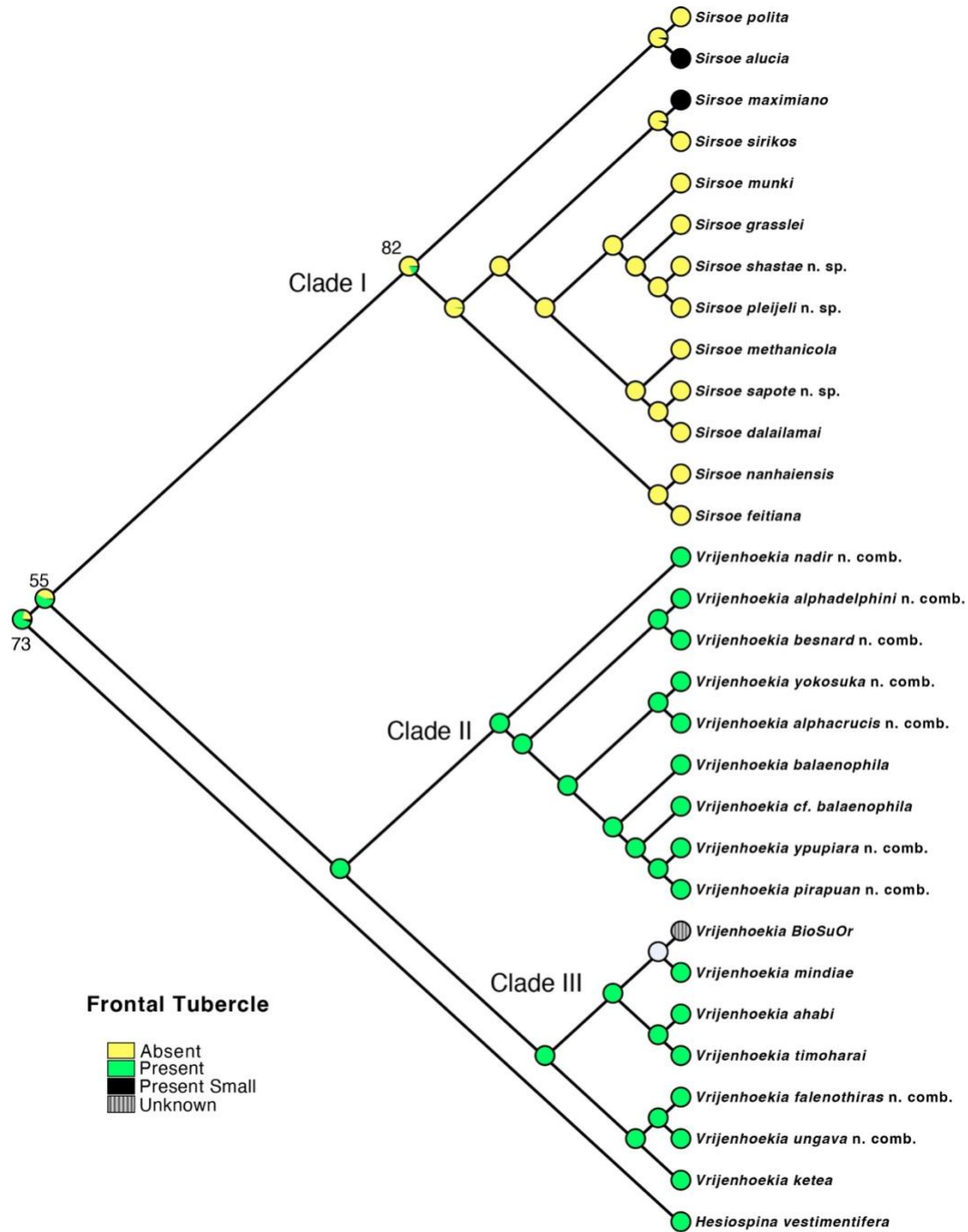


Figure 5. Transformation for the character Frontal Tubercle mapped onto the ML tree topology (with branch length information), visualized in Mesquite 3.81 using likelihood ancestral state reconstruction on ball and sticks tree form, with the Mk1 probability model. Values shown at some nodes represent likelihood for the various states under the model.

If this scenario is accepted then it has been lost in the *Sirsoe* clade and would represent an apomorphic state. *Vrijenhoekia* members can be distinguished by its presence, though this may be plesiomorphic. A less likely scenario is that the presence of the frontal tubercle in *Vrijenhoekia* is apomorphic and its absence in *Sirsoe* is plesiomorphic. The scoring of the frontal tubercle character as ‘small’ showed up independently twice within the *Sirsoe* clade and supports the idea that this is not homologous to the frontal tubercles seen in *Vrijenhoekia*. The glandular lip pads character transformation (Figure 6) suggests that this feature has appeared once or twice within the *Vrijenhoekia* clade. This could either be apomorphic for Clade II with a subsequent loss for the *V. alphadelphini* n. comb.+ *V. besnard* n. comb. clade or independently appearing twice in Clade II.

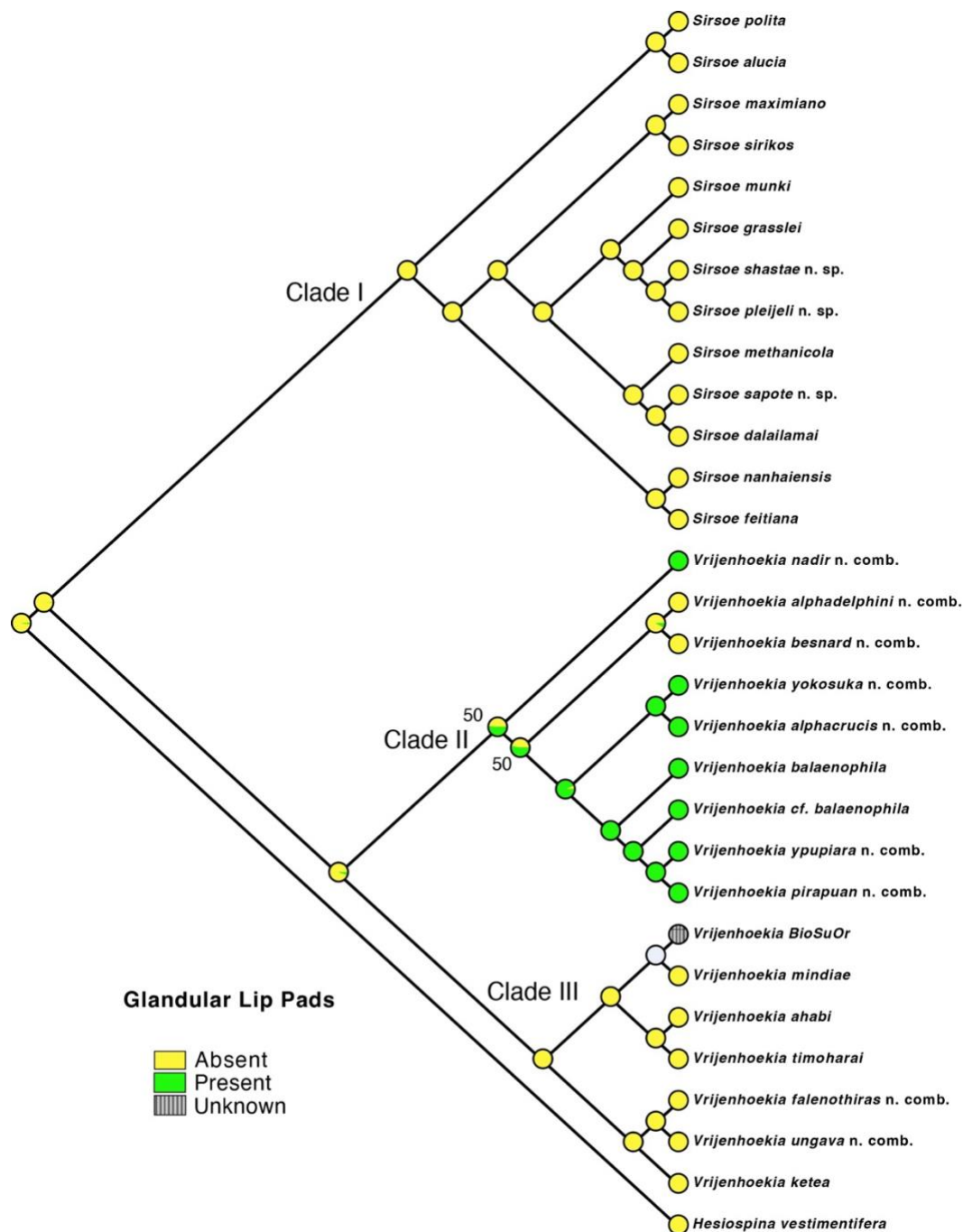


Figure 6. Transformation for the character Glandular Lip Pads mapped onto the ML tree topology (with branch length information), visualized in Mesquite 3.81 using likelihood ancestral state reconstruction on ball and sticks tree form, with the Mk1 probability model. Values shown at some nodes represent likelihood for the various states under the model.

COI DISTANCES

The minimum pairwise distances for COI are shown in Table 2. Of the new species described here, *S. shastae* n. sp. had the smallest uncorrected pairwise COI distance of 4% to *S. grasslei* and these specimens were found in close proximity to each other. This is slightly more than the 3% distance between *S. alucia* and *S. polita*, which are very widely separated geographically. *Sirsoe pleijeli* n. sp. was 8% distant from *S. grasslei* and also 8% from *S. shastae* n. sp., but was found to be the sister group to the latter in the multigene phylogeny (Figure 1). The single specimen of *Sirsoe sapote* n. sp. was 5% divergent from *Sirsoe dalailamai* described from Costa Rican seeps. *Vrijenhoekia mindiae* n. sp. was 15% divergent from the undescribed *Vrijenhoekia* BioSuOr.

Table 2. Minimum uncorrected pairwise distances for COI for all currently known *Sirsoe* and *Vrijenhoekia* species. Orange highlighted cell shows the 3% distance between *S. alucia* from the South Atlantic Ocean and *S. polita* from the South China Sea. The green highlighted cells show distances discussed in the text.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1. <i>S. alucia</i>																												
2. <i>S. dalailamai</i>	0.19																											
3. <i>S. feitiania</i>	0.18	0.15																										
4. <i>S. grasslei</i>	0.20	0.12	0.15																									
5. <i>S. maximiliano</i>	0.20	0.16	0.16	0.14																								
6. <i>S. methanicola</i>	0.21	0.10	0.17	0.14	0.16																							
7. <i>S. munki</i>	0.22	0.14	0.17	0.08	0.15	0.13																						
8. <i>S. nanhaiensis</i>	0.21	0.16	0.11	0.16	0.16	0.19	0.19																					
9. <i>S. pleijeli</i> n. sp.	0.20	0.12	0.15	0.08	0.14	0.13	0.10	0.16																				
10. <i>S. polita</i>	0.03	0.19	0.18	0.20	0.20	0.21	0.21	0.20	0.20																			
11. <i>S. sapote</i> n. sp.	0.19	0.05	0.15	0.13	0.16	0.10	0.13	0.16	0.13	0.18																		
12. <i>S. shastae</i> n. sp.	0.20	0.13	0.15	0.04	0.14	0.13	0.09	0.16	0.08	0.19	0.13																	
13. <i>S. sirikos</i>	0.21	0.15	0.16	0.15	0.08	0.15	0.14	0.16	0.13	0.21	0.15	0.14																
14. <i>V. ahaba</i>	0.21	0.20	0.18	0.20	0.20	0.22	0.22	0.18	0.20	0.21	0.19	0.20	0.20															

Table 2, Continued.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
15. <i>V. alpharucis</i> n. comb.	0. 2 3	0. 1 9	0. 2 0	0. 1 9	0. 1 9	0. 2 2	0. 2 0	0. 2 0	0. 1 9	0. 2 4	0. 2 0	0. 2 0	0. 2 1	0. 1 8	0. 0 7													
16. <i>V. alphadelphini</i> n. comb.	0. 2 3	0. 2 1	0. 2 3	0. 2 1	0. 2 3	0. 2 4	0. 2 4	0. 2 3	0. 2 2	0. 2 4	0. 2 2	0. 2 2	0. 2 3	0. 1 8	0. 1 9													
17. <i>V. balaenophila</i>	0. 1 9	0. 2 0	0. 1 7	0. 1 9	0. 2 0	0. 2 0	0. 2 1	0. 2 9	0. 1 1	0. 2 0	0. 2 9	0. 1 9	0. 1 9	0. 1 6	0. 0 4	0. 0 8												
18. <i>V. cf. balaeophila</i>	0. 2 2	0. 1 9	0. 1 8	0. 1 9	0. 2 1	0. 2 1	0. 2 1	0. 2 0	0. 2 0	0. 2 1	0. 2 0	0. 2 9	0. 1 9	0. 1 6	0. 1 6	0. 0 8	0. 0 8											
19. <i>V. besnard</i> n. comb.	0. 2 1	0. 1 8	0. 2 0	0. 1 9	0. 2 1	0. 2 2	0. 2 2	0. 2 1	0. 2 2	0. 2 2	0. 2 2	0. 1 1	0. 1 1	0. 1 1	0. 1 1	0. 0 6	0. 0 6	0. 0 6										
20. <i>V. falenot</i> n. comb.	0. 2 3	0. 2 0	0. 2 0	0. 2 9	0. 2 9	0. 2 0	0. 2 1	0. 2 0	0. 2 0	0. 2 2	0. 2 9	0. 2 0	0. 2 9	0. 1 6	0. 0 7	0. 0 2	0. 0 8	0. 0 9	0. 0 8	0. 0 4								
21. <i>V. ketea</i>	0. 2 3	0. 2 1	0. 2 0	0. 2 1	0. 2 2	0. 2 2	0. 2 2	0. 2 2	0. 2 2	0. 2 2	0. 2 3	0. 2 1	0. 2 2	0. 1 8	0. 2 0	0. 1 9	0. 1 8	0. 2 0	0. 1 8	0. 2 4								
22. <i>V. mindi</i> n. sp.	0. 2 2	0. 2 0	0. 2 0	0. 2 2	0. 2 2	0. 2 2	0. 2 1	0. 2 2	0. 2 2	0. 2 1	0. 2 2	0. 2 2	0. 1 2	0. 1 1	0. 1 1	0. 1 1	0. 2 1	0. 2 1	0. 0 6	0. 0 8								
23. <i>V. nadir</i> n. comb.	0. 2 2	0. 2 1	0. 2 0	0. 2 1	0. 2 1	0. 2 2	0. 2 3	0. 2 0	0. 2 2	0. 2 2	0. 2 1	0. 2 2	0. 2 0	0. 1 9	0. 0 8	0. 0 7	0. 0 8	0. 0 9	0. 0 0	0. 0 9								
24. <i>V. pirapuan</i> n. comb.	0. 2 2	0. 2 0	0. 1 8	0. 1 9	0. 2 0	0. 2 0	0. 2 0	0. 2 0	0. 2 2	0. 2 2	0. 2 2	0. 2 1	0. 2 2	0. 1 1	0. 1 1	0. 0 7	0. 0 6	0. 0 7	0. 0 8	0. 0 9	0. 0 1	0. 1 1	0. 1 1	0. 1 1	0. 1 1	0. 1 1		
25. <i>V. timoharai</i>	0. 2 2	0. 2 0	0. 1 8	0. 2 0	0. 2 1	0. 2 1	0. 2 1	0. 2 7	0. 2 9	0. 2 1	0. 2 9	0. 2 0	0. 2 9	0. 1 6	0. 0 7	0. 0 8	0. 0 5	0. 0 8	0. 0 6	0. 0 9	0. 0 5	0. 0 7	0. 0 5	0. 0 7	0. 0 5	0. 0 5		
26. <i>V. ungava</i> n. comb.	0. 2 3	0. 1 8	0. 2 9	0. 2 0	0. 2 0	0. 2 1	0. 2 9	0. 2 0	0. 2 3	0. 2 9	0. 2 0	0. 2 9	0. 2 0	0. 1 7	0. 0 5	0. 0 6	0. 0 6	0. 0 9	0. 0 1	0. 0 4	0. 0 6	0. 0 7	0. 0 6	0. 0 7	0. 0 7	0. 0 7		
27. <i>V. yokosuka</i> n. comb.	0. 2 1	0. 1 9	0. 2 0	0. 2 1	0. 2 0	0. 2 3	0. 2 2	0. 2 9	0. 2 2	0. 2 2	0. 2 0	0. 2 1	0. 2 0	0. 1 5	0. 1 1	0. 0 7	0. 0 3	0. 0 4	0. 0 6	0. 0 7	0. 0 8	0. 0 8	0. 0 8	0. 0 4	0. 0 5	0. 0 5		
28. <i>V. yupiaran</i> n. comb.	0. 2 2	0. 2 1	0. 2 8	0. 2 0	0. 2 1	0. 2 1	0. 2 1	0. 2 1	0. 2 1	0. 2 1	0. 2 1	0. 2 1	0. 2 1	0. 1 7	0. 0 7	0. 0 8	0. 0 8	0. 0 7	0. 0 9	0. 0 9	0. 0 8	0. 0 0	0. 1 1	0. 2 0	0. 1 1	0. 1 1		
29. <i>V. BioSu</i> Or	0. 2 1	0. 2 0	0. 2 0	0. 2 0	0. 2 2	0. 2 2	0. 2 2	0. 2 2	0. 2 2	0. 2 2	0. 2 2	0. 2 2	0. 2 2	0. 1 6	0. 1 8	0. 0 0	0. 0 8	0. 0 9	0. 0 5	0. 0 9	0. 0 5	0. 0 9	0. 0 5	0. 0 7	0. 0 5	0. 0 6	0. 0 8	

TAXONOMY

Sirsoe

Type species: *Orseis grasslei* Blake, 1985 (p.78, Figure 6) [1].

Diagnosis (emended)

Psamathinae with or without dorsally inserted median antenna, eyes absent, frontal tubercle and glandular lip pads absent. Notopodial hooks absent.

Remarks

Pleijel 1998 [10] diagnosed *Sirsoe* as ‘Psamathini with dorsally inserted median antenna and eyes absent.’ Pleijel et al. 2008 [3] did not revise the diagnosis for *Sirsoe* when they erected *Vrijenhoekia* and this was not done with subsequent *Sirsoe* descriptions [4,5]. Shimabukuro et al. 2019 [6] emended the diagnosis for *Sirsoe* when they made it a senior synonym of *Vrijenhoekia* to ‘Psamathinae with reduced small depression-like nuchal organs not projected on posterior margin of prostomium, frontal tubercle present with or without dorsally median antenna, eyes absent, with or without glandular lip pads.’ Notably they did not account for the frontal tubercle also being absent in many of the species in their genus, which would have been classified as *Sirsoe* sensu stricto in previous studies [4,5]. Based on the restriction here of *Sirsoe* to Clade I, which includes the type species *S. grasslei*, and the information provided in the morphology transformation (Figure 4-6) we have removed the possible presence of the frontal tubercle and glandular lip pads as diagnostic for the genus. We also removed the shape of the nuchal organs as this is difficult to document without scanning electron microscopy, a tool not always available to labs. The absence of notopodial hooks helps distinguish *Sirsoe* from *Hesiospina*, which also may lack eyes, median antenna, and frontal tubercle [10].

Sirsoe grasslei

Figures 7, 8

Orseis grasslei Blake 1985 [1] (p. 78, Figure 6)

Sirsoe grasslei Pleijel 1998 [10] (pp 124-126, Figure 18)

Material Examined

Voucher: SIO-BIC A13989, Z vent, Auka Vent Field, Gulf of California, 23.956° N, 108.861° W, 3684 m depth, anterior 10% SW formalin fixed, preserved in 50% ethanol, posterior fixed in 95% ethanol, used for DNA sequencing, October 30, 2021, ROV *SuBastian*

dive S0471, collector Greg Rouse [GenBank: COI = PQ774161; other sequences listed in Table 1].

Diagnosis

Smaller *Sirsoe* species with a median antenna and prostomium similar width to following segments. Terminal proboscis ring without ventral incision. Enlarged ventral cirri on segments 1-2, ventral cirri of segment 3 short but with distinct cirrophores. Neuropodial lobes and neurochaetae start on segment 2. Compound chaetal blades quite straight. Ventral cirri five times longer than base width.

Description

Mature specimen 30 or more segments (Figure 7A, B).

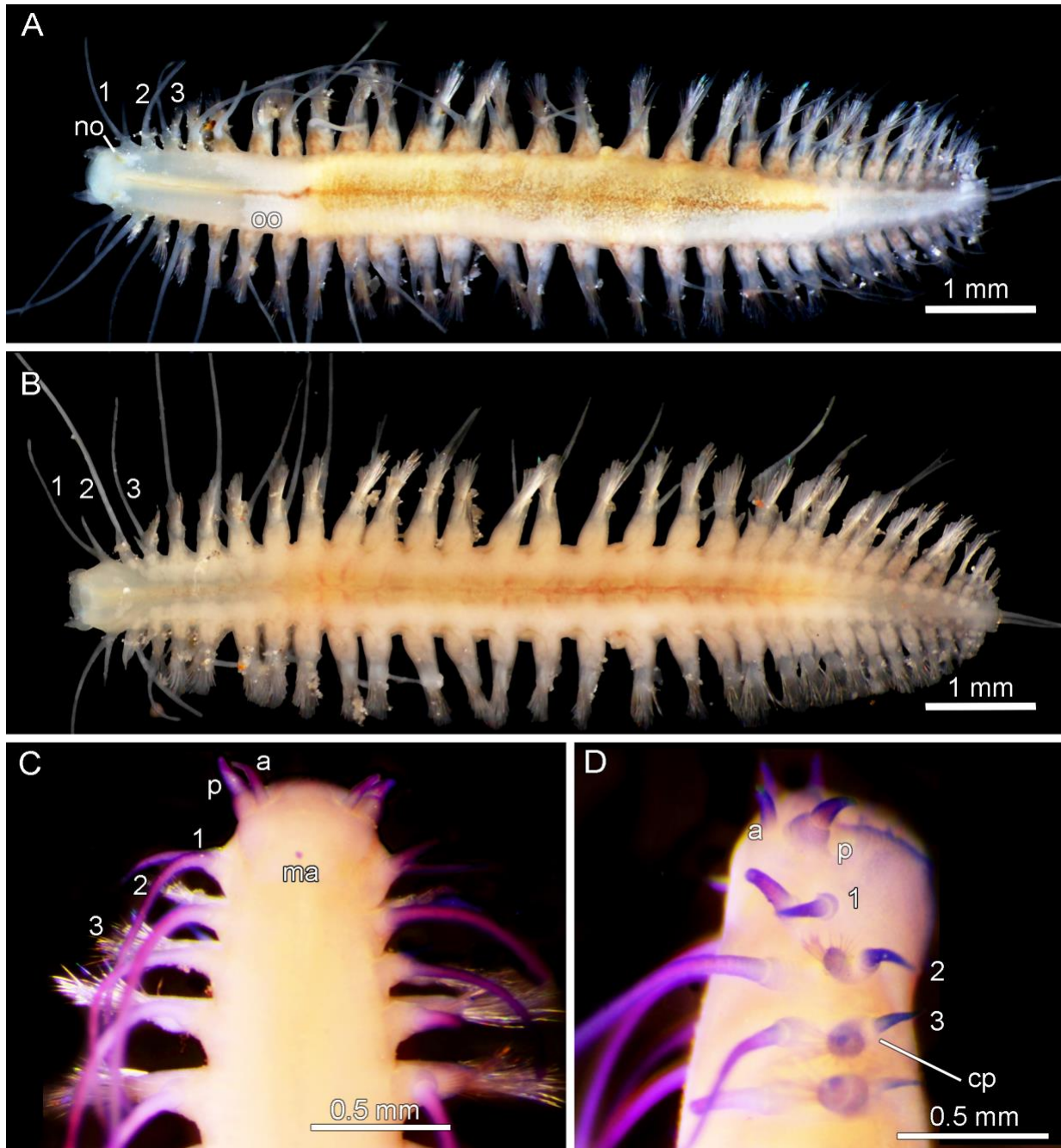


Figure 7. Light microscopy images of *Sirsoe grasslei* (SIO-BIC A13989) from hydrothermal vents of the Pescadero Basin, Gulf of California, Mexico. **(A)** Dorsal view of live, mature, female specimen. **(B)** Ventral view of whole specimen. **(C)** Dorsal view of anterior of preserved specimen stained with ShirlastainA[®]. **(D)** Lateral view of preserved specimen stained with ShirlastainA[®]. Legend: **1, 2, 3:** first three segments; **a:** lateral antenna; **cp:** cirrophore; **ma:** median antenna; **no:** nuchal organ; **oo:** oocytes; **p:** palp.

Gametes (oocytes) found in coelom from segment 5 to most posterior segments. Adult length 8 mm or greater. Body anteriorly truncate, prostomium similar width to following

segments, posterior body tapered. Pigmentation restricted to whitish prostomium and small white spots on dorsal midbody, otherwise translucent. Prostomium rounded. Facial tubercle absent. Palps biarticulated; palpophores as wide as long, cylindrical; palpostyles much longer and thinner, evenly tapering to a point (Figures 7C, D, 8A).

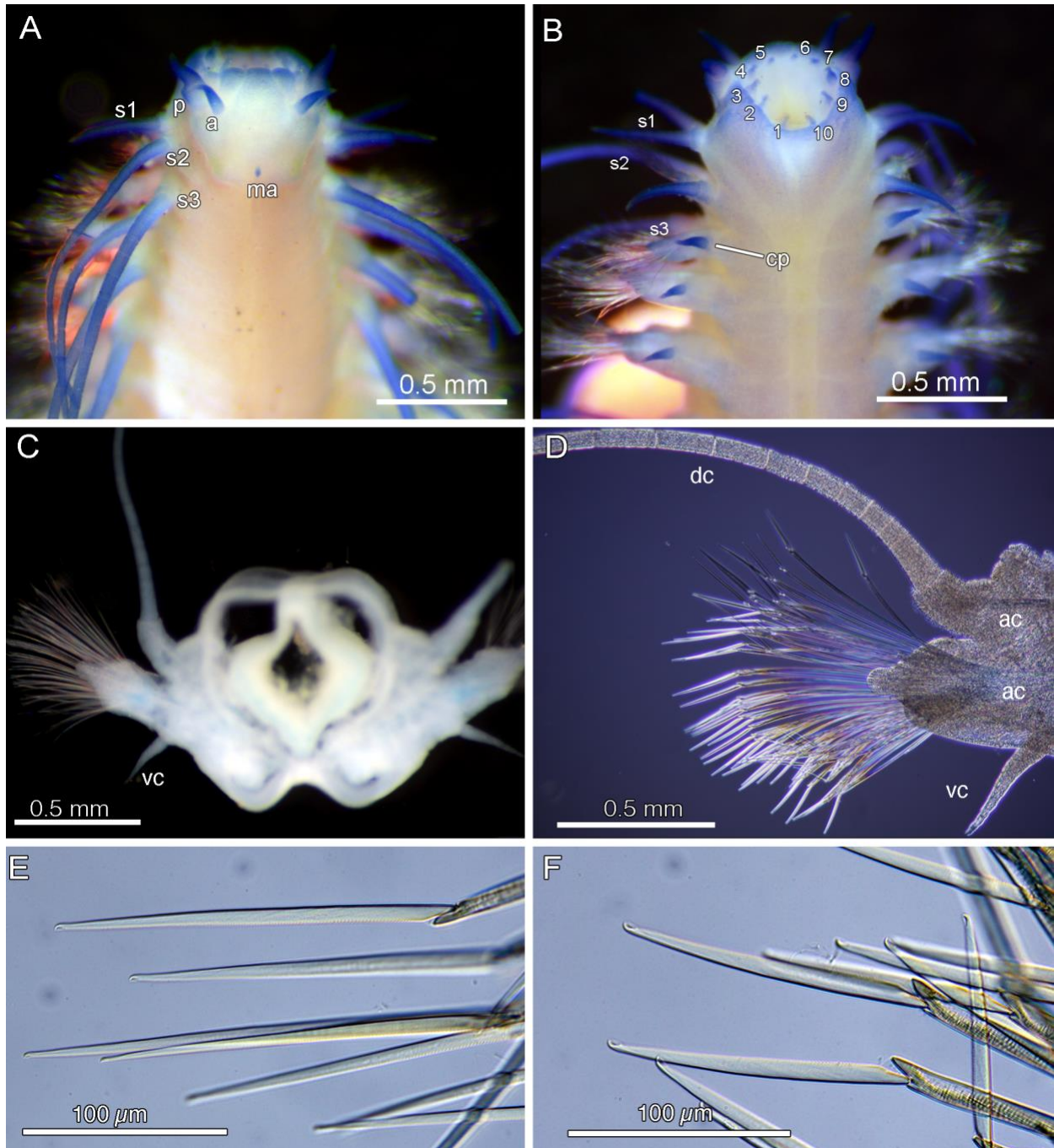


Figure 8. Light microscopy images of *Sirsoe grasslei* (SIO-BIC A13989) from hydrothermal vents of the Pescadero Basin, Gulf of California, Mexico. **(A)** Dorsal view of preserved specimen stained with ShirlastainA[®]. **(B)** Ventral view of preserved specimen with 10 terminal papillae in the proboscis stained with ShirlastainA[®]. **(C)** Segment 12. **(D)** Parapodium of segment 12. **(E)** Superior (dorsal) neurochaetae of segment 12. **(F)** Inferior (ventral) neurochaetae of segment 12. Legend: **1-10**: terminal papillae of proboscis; **a**: lateral antenna; **ac**: aciculae; **cp**: cirrophores; **dc**: dorsal cirrus; **ma**: median antenna; **p**: palpophores; **S1, S2, S3**: segments 1-3; **vc**: ventral cirrus.

Lateral antennae cirriform, lateral to palps, tapering slightly shorter than palps, lacking ceratophores (Figures 7C, D, 8A). Median antenna inserted on dorsal prostomium, posteriorly; median antennal furrows absent (Figures 7C, 8A). Eyes absent. Nuchal organs separated, brown patches in life. (Figure 7A) Prostomium without distinct incision posteriorly. Glandular lip pads absent. Terminal proboscis ring with 10 papillae; ventral incision absent (Figure 8B); jaws absent. Anterior dorsal cirri and cirrophores not obviously differing from following ones (Figures 7A, B, C, 8A); enlarged ventral cirri on segments 1-2 (Fig. 8B), ventral cirri of segment 3 short but differ from following cirri in having distinct cirrophores (Figures 7D, 8B). Notopodial lobes and notochaetae absent. Neuropodial lobes and neurochaetae absent on segment 1 (Figure 7C, D). Dorsal cirri weakly annulated, very long, up to 4mm long in life, cylindrical; elongated cirrophores absent (Figures 7A, 8C, D). Dorsal cirri alternation unknown. Notopodial hooks absent. Neuropodia triangular, with rounded prechaetal lobe distally (Figure 8C, D). Aciculae transparent, notopodial and neuropodial (Fig. 8D). Neurochaetae ~50 in chaetiger 12, all compound with distinctly internally chambered shafts (Fig. 8D), ending in rounded hooked tip, superior (dorsal) and median blades up to 3 times longer than inferior (ventral) ones, in all cases blades quite straight (Fig 8D, E, F). Ventral cirri subdistally inserted on neuropodium, without cirrophores, five times longer than base width (Fig. 8B, C, D). Paired pygidial cirri present (Fig. 7A, B), like dorsal cirri; median pygidial papilla absent.

Distribution

Hydrothermal vents of the Gulf of California, Mexico.

Remarks

This redescription is largely based on Pleijel's 1998 [10] study of the type specimens from the Guaymas Basin, several hundred kilometers north of the Pescadero Basin vents where

the single specimen we had available for study was obtained. Our specimen (SIO-BIC A13989) matched Pleijel's redescription in all respects and allowed for some further observations since the animal was observed alive and was a mature female. Blake [1] stated the lateral antennae had ceratophores but we see no evidence of this (Figure 7C,D) and the point was not commented on by Pleijel [10]. We provide here the first DNA sequences for *Sirsoe grasslei* and its placement in Clade I (Fig. 1) is valuable in delineating the membership of *Sirsoe*. Obtaining sequence data for *Sirsoe grasslei* from the type locality in the Guaymas Basin would be valuable.

Sirsoe pleijeli new species

Figures 9, 10

Material Examined

Holotype: SIO-BIC A14068 (to be ICML-EMU XXXX), Bejeweled Mound, south of the JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.936° N, 108.853° W, 3634.6 - 3646.0 m depth, anterior 10% SW formalin fixed, preserved in 50% ethanol, posterior fixed in 95% ethanol, used for DNA sequencing, November 7, 2021, ROV *SuBastian* dive S0479, collector Greg Rouse [GenBank: COI = PQ774173]. **Paratypes:** SIO-BIC A13998A, Z Vent, Auka Vent Field, Pescadero Basin, Gulf of California, 23.956° N, 108.861° W, 3684 m depth, fixed in 95% ethanol, October 21, 2021, ROV *SuBastian* dive S0472, collector Greg Rouse [GenBank: COI = PQ774166; other sequences listed in Table 1]; SIO-BIC A13998B, A13998C, Z Vent, Auka Vent Field, Pescadero Basin, Gulf of California, 23.956° N, 108.861° W, 3684 m depth, fixed in 95% ethanol, October 21, 2021, ROV *SuBastian* dive S0472, collector Greg Rouse [GenBank: COI = PQ774167, PQ774168]; SIO-BIC A13991, Z Vent, Auka Vent Field, Pescadero Basin, Gulf of California, 3.956° N, 108.861° W, 3684 m depth, anterior 10% SW formalin fixed, preserved in 50% ethanol, posterior fixed in 95% ethanol, used for DNA

sequencing, October 30, 2021, ROV *SuBastian* dive S0471, collector Greg Rouse [GenBank: COI = PQ774169]; SIO-BIC A14074A, A14074B, Matterhorn and Z vent, Auka Vent Field, Pescadero Basin, Gulf of California, 23.956° N, 108.860° W, 3635 - 3664 m depth, fixed in 95% ethanol, November, 8, 2021, ROV *SuBastian* dive S0480, collector Greg Rouse [GenBank: COI = PQ774170, PQ774171]; SIO-BIC A14001, Midway between Auka and JaichMaa 'ja'ag Vent Fields, Pescadero Basin, Gulf of California, 23.948° N, 108.858° W, 3687 m depth, anterior 10% SW formalin fixed, preserved in 50% ethanol, posterior fixed in 95% ethanol, used for DNA sequencing, November 1, 2021, ROV *SuBastian* dive S0473, collector Greg Rouse [GenBank: COI = PQ774172]; SIO-BIC A14050, Sisters, JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.943° N, 108.855° W, 3695 m depth, fixed in 95% ethanol, November 6, 2021, ROV *SuBastian* dive S0478, collector Greg Rouse [GenBank: COI = PQ774174]; SIO-BIC W10406A, W10406B, W10406C, W10406D, Sanak Islands seep, Aleutian Archipelago, Alaska, 53.748° N, 162.588° W, 2014 m depth, fixed in 95% ethanol, May 31, 2024, HOV *Alvin* dive AD5278, collectors Tina Treude and Emily Klonicki [GenBank: COI = PQ774175, PQ774176, PQ774177, PQ774178]; SIO-BIC W10501A, Sanak seep, Aleutian Archipelago, Alaska, 53.748° N, 162.588° W, 2014 m depth, fixed in 95% ethanol, June 1, 2024, HOV *Alvin* dive 5279, collectors Victoria Orphan and Shana Goffredi [GenBank: COI = PQ774179]; SIO-BIC A10015, Weey 'kual (Red Hill), JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.940° N, 108.855° W, 3674 m depth, anterior 10% SW formalin fixed, preserved in 50% ethanol, posterior fixed in 95% ethanol, used for DNA sequencing, November 20, 2018, ROV *SuBastian* dive S0199, collectors Greg Rouse and Ekin Tilic [GenBank: COI = PQ800516]; SIO-BIC A10631, Top of Matterhorn red bacterial mat, Auka Vent Field, Pescadero Basin, Gulf of California, 23.953° N, 108.863° W, 3650 m depth, fixed in 95% ethanol,

November 14, 2018, ROV *SuBastian* dive S0193, collectors Greg Rouse and Ekin Tilic [GenBank: COI = PQ800517]; SIO-BIC A9984, Two Sisters Mounds, JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.943° N, 108.856° W, 3684 m depth, anterior 10% SW formalin fixed, preserved in 50% ethanol, posterior fixed in 95% ethanol, used for DNA sequencing, November 16, 2018, ROV *SuBastian* dive S0195, collectors Greg Rouse and Ekin Tilic [GenBank: COI = PQ800518]; SIO-BIC A10032, A10637, A10638, A10639, A10640, A10641, Z Mound area, Auka Vent Field, Pescadero Basin, Gulf of California, 23.956° N, 108.861° W, 3687 m depth, fixed in 95% ethanol, November 21, 2018, ROV *SuBastian* dive S0200, collectors Greg Rouse and Ekin Tilic [GenBank: COI = PQ800524, PQ800523, PQ800519, PQ800522, PQ800521, PQ800520]; SIO-BIC A10632, A10633, A10634, Weey 'kual (Red Hill), JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.940° N, 108.855° W, 3674 m depth, fixed in 95% ethanol, November 20, 2018, ROV *SuBastian* dive S0199, collectors Greg Rouse and Ekin Tilic [GenBank: COI = PQ800528, PQ800526, PQ800525]; SIO-BIC A14080A, Red Hill (Weey 'kual), JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.940° N, 108.855° W, 3682 m depth, fixed in 95% ethanol, November 9, 2021, ROV *SuBastian* dive S0481, collector Greg Rouse [GenBank: COI = PQ800527]. **Other materials:** SIO-BIC A13998D - H, Z Vent, Auka Vent Field, Pescadero Basin, Gulf of California, 23.956° N, 108.861° W, 3684 m depth, fixed in 95% ethanol, October 21, 2021, ROV *SuBastian* dive S0472, collector Greg Rouse; SIO-BIC A13998I, Z Vent, Auka Vent Field, Pescadero Basin, Gulf of California, 23.956° N, 108.861° W, 3684 m depth, 10% SW formalin fixed, preserved in 50% ethanol, October 21, 2021, ROV *SuBastian* dive S0472, collector Greg Rouse; SIO-BIC A13998J, Z Vent, Auka Vent Field, Pescadero Basin, Gulf of California, 23.956° N, 108.861° W, 3684 m depth, frozen for isotopes, October 21, 2021, ROV

SuBastian dive S0472, collector Greg Rouse; SIO-BIC A14074C, A14074D, Matterhorn and Z vent, Auka Vent Field, Pescadero Basin, Gulf of California, 23.956° N, 108.860° W, 3635 - 3664 m depth, fixed in 95% ethanol, November, 8, 2021, ROV *SuBastian* dive S0480, collector Greg Rouse; SIO-BIC A14074E, A14074E, Matterhorn and Z vent, Auka Vent Field, Pescadero Basin, Gulf of California, 23.956° N, 108.860° W, 3635 - 3664 m depth, 10% SW formalin fixed, preserved in 50% ethanol, November, 8, 2021, ROV *SuBastian* dive S0480, collector Greg Rouse; SIO-BIC W10406E, Sanak Islands seep, Aleutian Archipelago, Alaska, 53.748° N, 162.588° W, 2014 m depth, 10% SW formalin-fixed, preserved in 50% ethanol, May 31, 2024, HOV *Alvin* dive 5278, collectors Tina Treude and Emily Klonicki; SIO-BIC W10406F, Sanak Islands seep, Aleutian Archipelago, Alaska, 53.748° N, 162.588° W, 2014 m depth, frozen for isotopes, May 31, 2024, HOV *Alvin* dive 5278, collectors Tina Treude and Emily Klonicki; SIO-BIC W10501B, W10501C, Sanak Islands seep, Aleutian Archipelago, Alaska 53.748° N, 162.588° W, 2014 m depth, fixed in 95% ethanol, June 1, 2024, HOV *Alvin* dive 5279, collectors Victoria Orphan and Shana Goffredi; SIO-BIC A9973, Top of Matterhorn red bacterial mat, Auka Vent Field, Pescadero Basin, Gulf of California, 23.953° N, 108.863° W, 3650 m depth, 10% SW formalin fixed, preserved in 50% ethanol, November 14, 2018, ROV *SuBastian* dive S0193, collectors Greg Rouse and Ekin Tilic; SIO-BIC A14080B - H, Red Hill (Weey 'kual), JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.940° N, 108.855° W, 3682 m depth, fixed in 95% ethanol, November 9, 2021, ROV *SuBastian* dive S0481, collector Greg Rouse.

Diagnosis

Moderate-sized *Sirsoe* species with a median antenna, prostomium similar width to following segments. Terminal proboscis ring without ventral incision. Enlarged ventral cirri on

segments 1-2, ventral cirri of segment 3 short, with distinct cirrophores. Neuropodial lobes and neurochaetae start on segment 2. Compound chaetal blades curved. Ventral cirri five times longer than base width.

Description

Holotype 32 segments, a mature female, 16 mm long (Figure 9A). Gametes (sperm) found in coelom from segment 7 to most posterior segments.

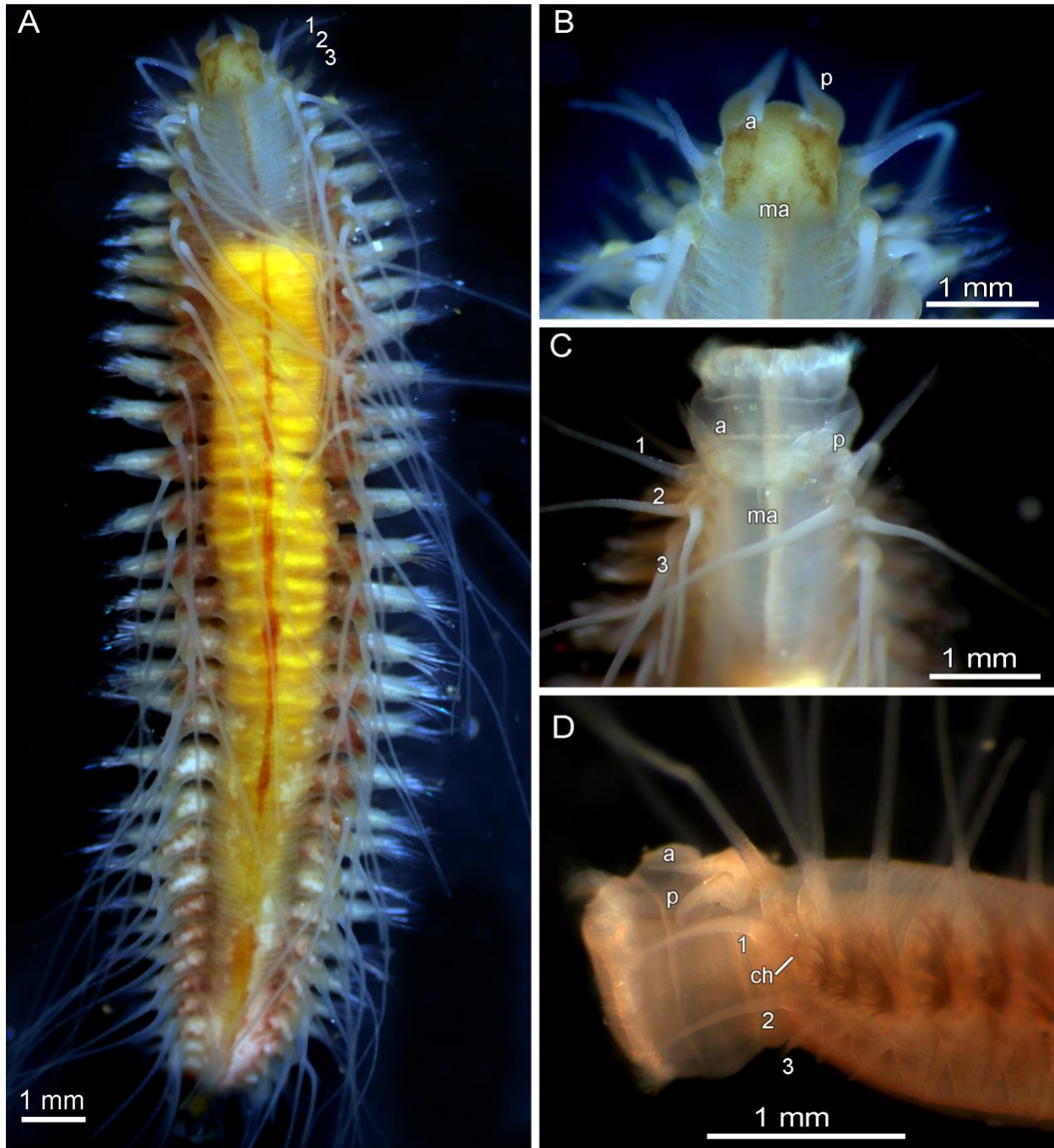


Figure 9. Light microscopy images of *Sirsoe pleijeli* n. sp. (A) Holotype (SIO-BIC A14068, to be ICML-EMU XXXX), dorsal view of live specimen. (B) Holotype, dorsal view of anterior living specimen. (C) Paratype (SIO-BIC A14080A) dorsal view of anterior of live specimen with everted proboscis. (D) Paratype (SIO-BIC A14080A) lateral view of live specimen with everted proboscis and first three ventral cirri labeled. Legend: 1, 2, 3: first three segments; a: lateral antenna; ch: chaetae of segment 2; ma: median antenna; p: palp.

Body anteriorly and posteriorly tapered. Pigmentation restricted to brownish patches on prostomium and small brown spots on dorsal midbody, otherwise translucent with red blood

vessels visible in life (Fig. 9A, B). Prostomium rectangular, narrower than segments behind (Fig. 9A, B). Facial tubercle absent. Palps biarticulated; palpophores as wide as long, cylindrical; palpostyles much longer and thinner, evenly tapering to a point (Figure 9C, D). Lateral antennae cirriform, lateral to palps, tapering slightly shorter than palps, lacking ceratophores (Figure 9B, C). Median antenna inserted on dorsal prostomium, posteriorly; median antennal furrows absent (Figure 9C).

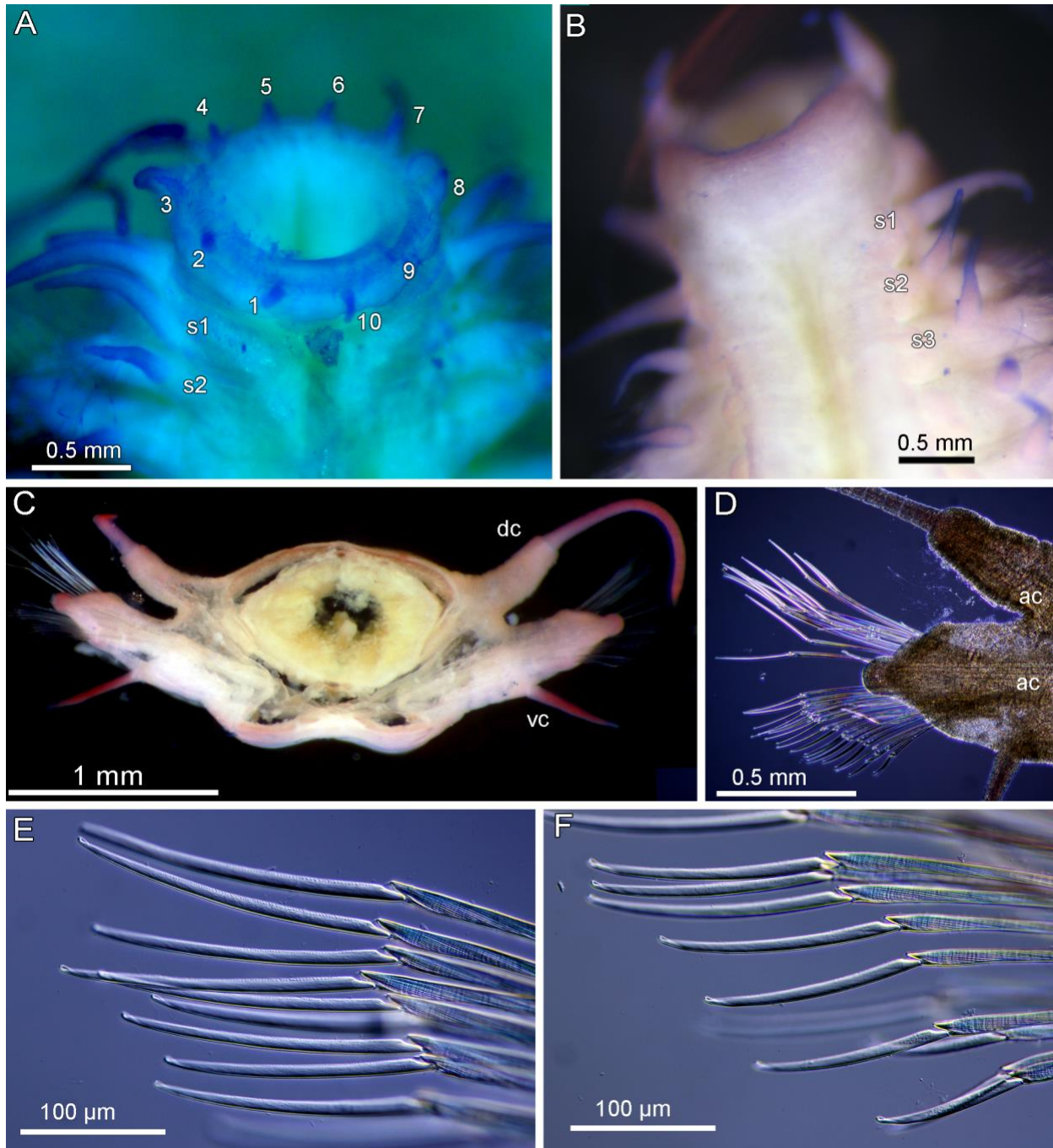


Figure 10. Light microscopy of *Sirsoe pleijeli* n. sp. (A) Paratype (SIO-BIC A14074) ventral view of preserved specimen with everted proboscis and 10 terminal papillae stained with ShirlastainA®. (B) Paratype (SIO-BIC A13998) ventral view of preserved specimen stained with ShirlastainA®. (C) Holotype (SIO-BIC A14068, to be ICML-EMU XXXX), segment 12. (D) Holotype, segment 12 parapodium. (E) Holotype, superior (dorsal) neurochaetae segment 12. (F) Holotype, inferior (ventral) neurochaetae segment 12. Legend: 1, 2, 3: first three segments; ac: aciculae; dc: dorsal cirrus; S1, S2, S3: segments 1-3; vc: ventral cirrus.

Eyes absent. Nuchal organs not distinct. Prostomium without distinct incision posteriorly.

Glandular lip pads absent. Terminal proboscis ring ciliated with 10 papillae; ventral incision

absent (Figures 9C, D, 10A); jaws absent. Anterior dorsal cirri and cirrophores not obviously differing from following ones, all extremely long (Figures 9A, C, D); enlarged ventral cirri on segments 1-2 (Fig. 9D, 10A, B), ventral cirri of segment 3 short, like following cirri in having no cirrophores (Figure 10B). Notopodial lobes and notochaetae absent. Neuropodial lobes and neurochaetae absent on segment 1 (Figures 9D, 10B). Dorsal cirri weakly annulated, very long, up to 8 mm in life, cylindrical; elongated cirrophores absent (Figures 9A, 10C, D). Dorsal cirri alternation unknown. Notopodial hooks absent. Neuropodia triangular, with rounded prechaetal lobe distally (Figure 10C, D). Aciculae transparent, notopodial and neuropodial (Fig. 10D). Neurochaetae ~30 in chaetiger 12 all compound with distinctly internally chambered shafts (Fig. 8D), ending in rounded tip, superior (dorsal) and median blades up to 4 times longer than inferior (ventral) ones, in all cases blades curved (Fig 10D, E, F). Ventral cirri subdistally inserted on neuropodium, without distinct cirrophores (Fig. 10C, D). Paired pygidial cirri present (not shown), very long, like dorsal cirri; median pygidial papilla absent.

Variation

As seen in the haplotype network (Figure 2) there was very little variability on COI among the 21 specimens sequenced across a 5,500 km range. Paratypes were smaller than the holotype, usually less than 10 mm and with ~24 segments. Some specimens had less brown pigmentation on the prostomium than the holotype and the brown pair of curved nuchal organs was visible.

Distribution

Hydrothermal vents at ~3700 m in the Pescadero Basin, Gulf of California, Mexico, and methane seeps at ~2000 m off the Sanak Islands, Aleutian Archipelago, Alaska.

Etymology

This species is named for Fredrik Pleijel who erected the genus *Sirsoe* and had devoted much time to the study of Hesionidae.

Remarks

Sirsoe pleijeli n. sp. was found to be the sister group to another of the new species described here, *S. shastae* n. sp., and is additionally very similar to *S. grasslei*. Apart from the COI distance of 8% in each case (Table 2), *Sirsoe pleijeli* n. sp. can be distinguished from both species by its lack of a cirrophore on the ventral cirri of segment 3 (Figure 10B), extremely long dorsal cirri, and compound chaetae with curved blades. It differs also from *S. grasslei* in that the ventral cirri are proportionally longer.

Sirsoe shastae new species

Figures 11, 12

Material Examined

Holotype: SIO-BIC A10636 (to be ICML-EMU XXXX), Weey 'kual (Red Hill), JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.940° N, 108.855° W, 3674 m depth, fixed in 95% ethanol, September 20, 2018, ROV *SuBastian* dive S0199, collectors Greg Rouse and Ekin Tilic [GenBank: COI = PQ774162; other sequences listed in Table 1].

Paratypes: SIO-BIC A14065A, A14065B, A14065C, Bejeweled Mound, south of the JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.936° N, 108.8534° W, 3635 - 3646 m depth, fixed in 95% ethanol, September 7, 2021, ROV *SuBastian* dive S0479, collector Greg Rouse [GenBank: COI = PQ774163, PQ774164, PQ774165]. **Other materials:** SIO-BIC A14065D, A1406E, Bejeweled Mound, south of the JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.936° N, 108.853° W, 3635 - 3646 m depth, 10% SW formalin fixed, preserved in 50% ethanol, September 7, 2021, ROV *SuBastian* dive S0479, collector Greg

Rouse; SIO-BIC A14065F Bejeweled Mound, south of the JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.936° N, 108.853° W, 3635 - 3646 m depth, frozen for isotopes, September 7, 2021, ROV *SuBastian* dive S0479, collector Greg Rouse; SIO-BIC A10016A, Weey 'kual (Red Hill), JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.9404° N, 108.8558° W, 3674 m depth, 10% SW formalin fixed, preserved in 50% ethanol, September 20, 2018, ROV *SuBastian* dive S0199, collectors Greg Rouse and Ekin Tilic; SIO-BIC A10016B, Weey 'kual (Red Hill), JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.9404° N, 108.8558° W, 3674 m depth, RNAlater, September 20, 2018, ROV *SuBastian* dive S0199, collectors Greg Rouse and Ekin Tilic; SIO-BIC A10635, Weey 'kual (Red Hill), JaichMaa 'ja'ag Vent Field, Pescadero Basin, Gulf of California, 23.940° N, 108.855° W, 3674 m depth, fixed in 95% ethanol, September 20, 2018, ROV *SuBastian* dive S0199, collectors Greg Rouse and Ekin Tilic.

Diagnosis

Small-sized *Sirsoe* species with a median antenna, prostomium similar width to following segments. Enlarged ventral cirri on segments 1-2, ventral cirri of segment 3 short, with distinct cirrophores. Neuropodial lobes and neurochaetae start on segment 2. Compound chaetal blades straight. Ventral cirri ten times longer than base width.

Description

Holotype with 30 segments, length 11 mm in life; gametes (oocytes) found in coelom from segment 7 to most posterior segments (Fig. 11A). Body anteriorly truncate, prostomium similar width to following segments, posterior body tapered.

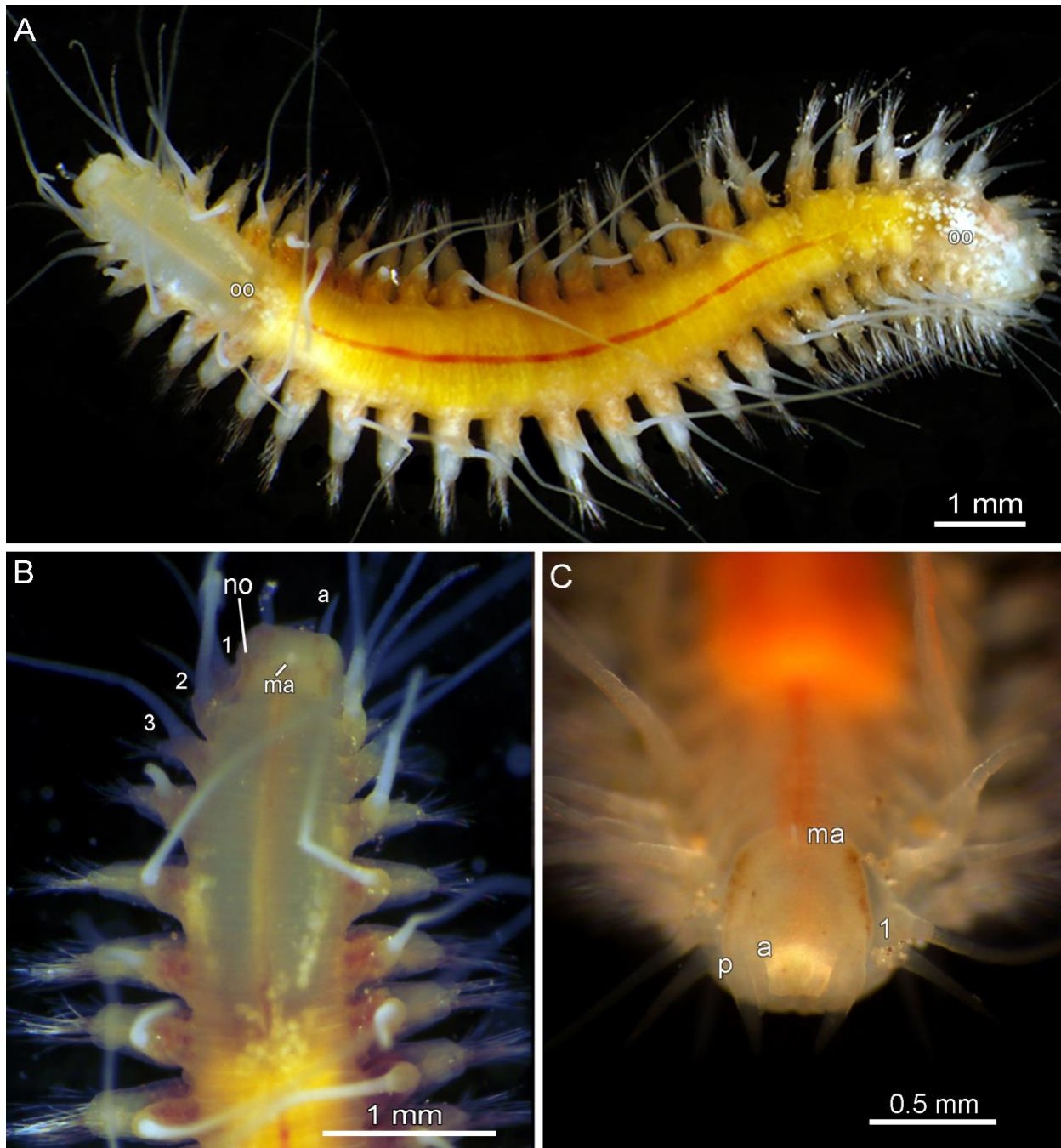


Figure 11. Light microscopy images of *Sirsoe shastae* n. sp. from the Pescadero Basin hydrothermal vent fields. (A) Holotype (SIO-BIC A10636, to be ICML-EMU XXXX), dorsal view of live specimen. (B) Holotype, dorsal view of anterior of living specimen. (C) Paratype (SIO-BIC A14065A) prostomium of live specimen in frontal view. Legend: **1, 2, 3**: first three segments; **a**: lateral antenna; **ma**: median antenna; **no**: nuchal organ; **oo**: oocytes; **p**: palp.

Pigmentation restricted to yellowish gut, otherwise translucent. Prostomium rounded.

Facial tubercle absent. Palps biarticulated; palpophores as wide as long, cylindrical; palpostyles much longer and thinner, evenly tapering to a point (Figures 11C, 12B). Lateral antennae

cirriform, lateral to palps, tapering slightly shorter than palps, lacking ceratophores (Figures 11B, C, 12A). Median antenna inserted on dorsal prostomium, posteriorly; median antennal furrows absent (Figures 11B, C, 12A). Eyes absent. Nuchal organs separated, brown patches in life. (Figure 11A) Prostomium without distinct incision posteriorly. Glandular lip pads absent. Terminal proboscis not observed. Anterior dorsal cirri and cirrophores not obviously differing from following ones (Figure 11A, B); enlarged ventral cirri on segments 1-2 (Fig. 12B), ventral cirri of segment 3 short but differ from following cirri in having distinct cirrophores (Figure 12B). Notopodial lobes and notochaetae absent. Neuropodial lobes and neurochaetae absent on segment 1 (Figure 11B, C). Dorsal cirri weakly annulated, very long, up to 4.7 mm in life, cylindrical; elongated cirrophores absent (Figures 11A, B, 12C, D). Dorsal cirri alternation unknown. Notopodial hooks absent. Neuropodia triangular, with rounded prechaetal lobe distally (Figure 12C, D). Notopodial and neuropodial aciculae transparent (Figure 12D). Neurochaetae ~30 in chaetiger 12, all compound with distinctly internally chambered shafts (Fig. 12E, F), ending in rounded hooked tip, superior (dorsal) and median blades up to 3 times longer than inferior (ventral) ones, in all cases blades quite straight (Figure 12D, E, F). Ventral cirri subdistally inserted on neuropodium, without cirrophores, up to ten times longer than base width (Figure 12B, C, D). Paired pygidial cirri present (not shown), like dorsal cirri; median pygidial papilla absent.

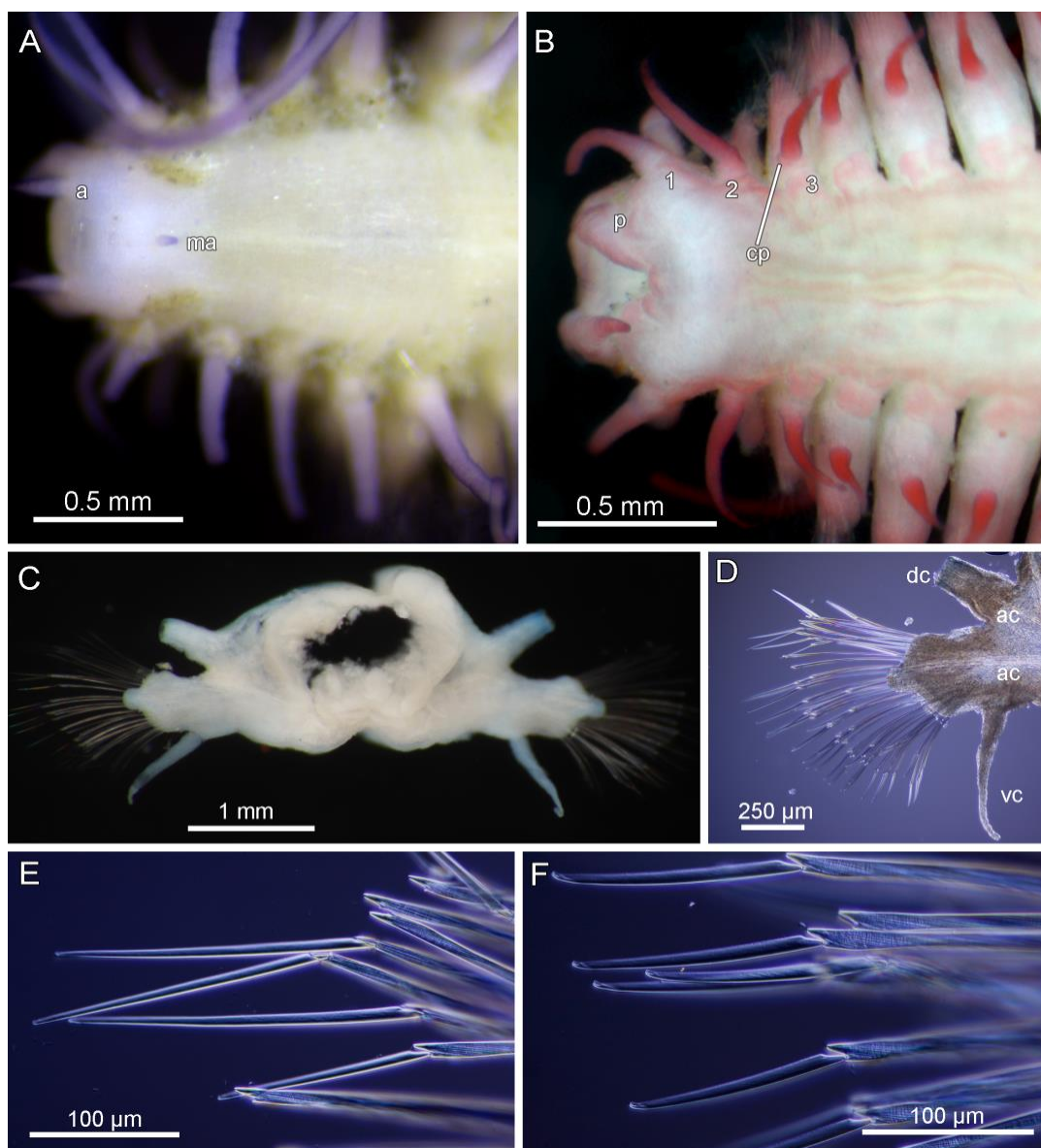


Figure 12. Light microscopy images of holotype (SIO-BIC A10636) of *Sirsoe shastae* n. sp. (A) Dorsal view of preserved specimen stained with ShirlastainA[®]. (B) Ventral view of preserved specimen stained with ShirlastainA[®]. (C) Segment 12. (D) Segment 12 parapodium. (E) Superior (dorsal) neurochaetae segment 12. (F) Inferior (ventral) neurochaetae segment 12. Legend: **1, 2, 3**: first three segments; **a**: lateral antenna; **ac**: aciculae; **cp**: cirrophore; **dc**: dorsal cirrus; **ma**: median antenna; **p**: palp; **vc**: ventral cirrus.

Distribution

Hydrothermal vents at ~3700m in the Pescadero Basin, Gulf of California.

Etymology

This species is named after one of the first author's female cats for the cirri's similarities to her whiskers.

Remarks

Sirsoe shastae n. sp. was found to be the sister group to *S. pleijeli* n. sp. (Fig. 1), from which it is 8% divergent with COI (Table 2). It can be distinguished from *S. pleijeli* n. sp. by its cirrophore on the ventral cirri of segment 3, shorter dorsal cirri, and straight compound chaetae blades. However, *S. shastae* n. sp. is most similar *S. grasslei* morphologically and is only 4% divergent from it with COI (Table 2). *Sirsoe shastae* n. sp. can be distinguished from *S. grasslei* in that it has fewer chaetae per parapodium, and the ventral cirri are much longer in proportion to the width.

Sirsoe sapote new species

Figures 13, 14

Material Examined

Holotype: SIO-BIC A14076 (to be ICML-EMU XXXX), Matterhorn and Z Vent, Auka Vent Field, Pescadero Basin, Gulf of California, 23.954° N, 108.862°, 3655 m depth, 10% SW formalin fixed, preserved in 50% ethanol piece fixed in 95% ethanol for DNA sequencing, November 8, 2021, ROV *SuBastian* dive S0480, collector Greg Rouse [GenBank: COI = PQ774166; other sequences listed in Table 1].

Diagnosis

Large-sized *Sirsoe* species with a median antenna, prostomium similar width to following segments. Enlarged ventral cirri on segments 1-3 with distinct cirrophores. Segment 3 without small triangular (neuropodial?) lobes dorsal to ventral cirri. Neuropodial lobes and neurochaetae start on segment 4. Proboscis opening midventrally with distinct incision and small rounded knob. Compound chaetal blades straight.

Description

Holotype with at least 28 segments, at least 30 mm long in life (Fig. 13A). Body anteriorly truncate, prostomium similar width to following segments, but shape obscured by everted proboscis. Pigmentation bright orange in life with whitish gut visible through body wall; fixed specimen white. Facial tubercle absent. Palps biarticulated; palpophores cylindrical and palpostyles tapering, palpostyles much shorter than palpophores (Figure 13A, C). Lateral antennae cirriform, lateral to palps, tapering slightly, shorter, much thinner than palps, lacking ceratophores (Figure 13C). Median antenna inserted on dorsal prostomium, posteriorly; median antennal furrows absent (Figures 13C). Eyes absent. Nuchal organs forming two short slits postero-laterally on prostomium. (Figure 13A). Prostomium without distinct incision posteriorly. Glandular lip pads absent. Proboscis with 10 tapering papillae situated on dorsal half of the proboscis opening; papillae elongated, tapering, decreasing in size towards the ventral side. Proboscis opening midventrally with distinct incision and small rounded knob (Figure 13A, B, D).



Figure 13. Holotype (SIO-BIC A14076 (to be ICML-EMU XXXX)), of *Sirsoe sapote* n. sp. from hydrothermal vents of the Pescadero Basin, Gulf of California, Mexico. (A) Dorsal view of live specimen with everted proboscis. (B) Ventral view of everted proboscis of preserved holotype with 10 terminal papillae stained with ShirlastainA[®]. (C) Anterior dorsal view of preserved holotype stained with ShirlastainA[®]. (D) Lateral view of preserved holotype stained with ShirlastainA[®]. Legend: 1-10: terminal papillae of proboscis; a: lateral antenna; k: knob; ma: median antenna; no: nuchal organ; oo: oocytes; p: palp; S1, S2, S3, S4: first four segments; vi: ventral incision of proboscis.

Anterior dorsal cirri and cirrophores not obviously differing from following ones (Figure 13A, C, D); enlarged ventral cirri on segments 1-3 (Figure 13D), all with distinct cirrophores. Notopodial lobes and notochaetae absent on all segments. Neuropodial lobes and neurochaetae absent on segment 1-3, first chaetiger segment 4 (Figure 13D). Segment 3 also without small triangular (neuropodial?) lobes dorsal to ventral cirri. Dorsal cirri weakly annulated, very long, up to 8 mm in life, cylindrical; elongated cirrophores absent (Figures 13A, D, 14A). Dorsal cirri alternation unknown. Notopodial hooks absent. Neuropodia triangular, with rounded prechaetal lobe distally (Figure 14A, B). Noto- and neuro-aciculae not visualized owing to thickness of parapodia. Neurochaetae ~25 in chaetiger 12, all compound with distinctly internally chambered shafts (Figure 14C, D), ending in rounded hooked tip, superior (dorsal) and median blades up to 3 times longer than inferior (ventral) ones, in all cases blades quite straight (Fig 14C, D). Ventral cirri subdistally inserted on neuropodium, without cirrophores, up to five times longer than base width (Figure 14A, B). Paired pygidial cirri present (not shown), like dorsal cirri; median pygidial papilla absent.

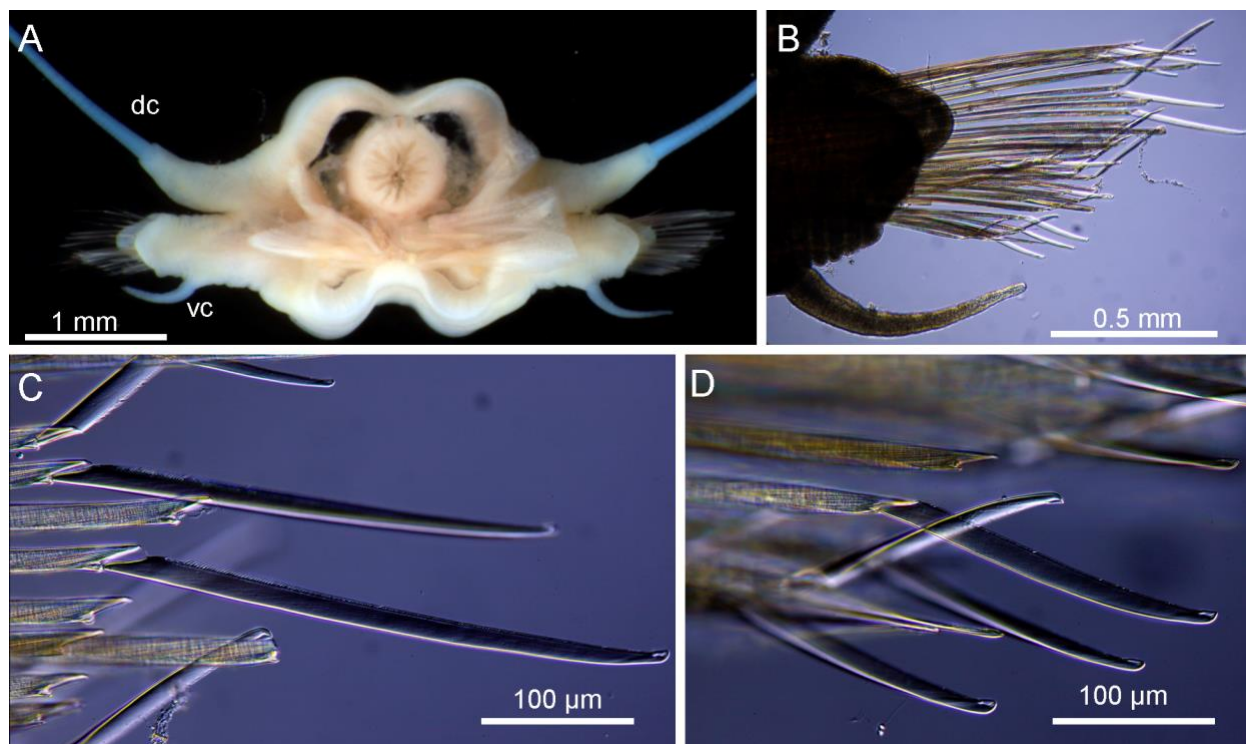


Figure 14. Holotype (SIO-BIC A14076 (to be ICML-EMU XXXX)), of *Sirsoe sapote* n. sp. from hydrothermal vents of the Pescadero Basin, Gulf of California, Mexico. (A) Segment 12. (B) Segment 12 parapodium. (C) Superior (dorsal) neurochaetae segment 12. (D) Inferior (ventral) neurochaetae segment 12. Legend: **dc**: dorsal cirrus; **vc**: ventral cirrus.

Distribution

Hydrothermal vents at ~3700m in the Pescadero Basin, Gulf of California.

Etymology

This species is named as a noun in apposition for sapote, a type of fruit native to Mexico. The mamey sapote, *Pouteria sapota*, has an orange flesh like the color of the *S. sapote* n. sp. species described.

Remarks

Sirsoe sapote n. sp. was found to be the sister group to *S. dalailamai* known from Costa Rican methane seeps (Fig. 1) and this clade was then sister group to *Sirsoe methanicola* (Gulf of Mexico). *Sirsoe sapote* n. sp. was found to be 5% divergent from *S. dalailamai* with COI and 10% from *Sirsoe methanicola* (Table 2). It is morphologically very similar to *S. dalailamai*, even

with regards to color in life. Rouse et al. 2018 [5] could not provide any obvious differences between *S. dalailamai* and *S. methanicola* and the erection of the former was justified on molecular and geographical divergence. Here we can distinguish *Sirsoe sapote* n. sp. from *S. dalailamai* in that segment 3 lacks small triangular (neuropodial?) lobes dorsal to ventral cirri and it has fewer chaetae (~25 compared to 30-50) in midbody parapodia. A clear difference distinguishing *Sirsoe sapote* n. sp. and *S. dalailamai* from *S. methanicola* is that both have far fewer neurochaetae in the parapodia than the more than 90 reported for the latter species [2].

Vrijenhoekia Pleijel, Rouse, Ruta, Wiklund & Nygren, 2008 [3]

Type species: *Vrijenhoekia balaenophila* Pleijel, Rouse, Ruta, Wiklund & Nygren, 2008 [3]

(p.78, Figure 6)

Diagnosis (emended)

Psamathinae with or without dorsally inserted median antenna, may be present as mediodorsal tubercle, eyes absent, frontal tubercle present, glandular lip pads absent or present. Notopodial hooks absent.

Remarks

Pleijel et al. [3] did not diagnose (a mixture of apomorphies and plesiomorphies) *Vrijenhoekia* when they established the genus for *V. balaenophila*, but instead listed a proposed set of apomorphic features as follows: ‘Three pairs of large glandular lip pads surrounding mouth opening, papilla-shaped neuropodial lobes on segment 3, very long dorsal cirri, and growth pattern with up to about 35 segments where after segments increase in size but no new segments are added.’ In their remarks they did note that *Vrijenhoekia* lacked a median antenna compared to members of *Sirsoe*, which also had developed neuropodial lobes on segment 3, while lacking glandular lip pads. Species of *Vrijenhoekia* and *Sirsoe* that were described later introduced more

variability in terms of the presence or absence of the median antenna and glandular lip pads (Figures 4, 5) and led in part to Shimabukuro et al. [6] arguing for *Vrijenhoekia* to be a junior synonym of *Sirsoe*. Here our revised diagnosis of *Vrijenhoekia* allows for clear identification of members of the *Vrijenhoekia* clade (Figure 1) by the presence of an obvious frontal tubercle, which is arguably absent in members of *Sirsoe* (Figure 5).

Vrijenhoekia mindiae new species

Vrijenhoekia sp. A Summers et al. 2015 [4](pp. 120-121, Fig. 3H)

Vrijenhoekia sp. A Seid et al. 2025 [23](pp. 29 Fig. 11B).

Holotype: SIO-BIC A9606, Mound 12, bone, wood, and chips deployment, Costa Rica, 8.93° N, 84.311° W, 992 m depth, anterior 10% SW formalin fixed, preserved in 50% ethanol, posterior fixed in 95% ethanol, used for DNA sequencing, October 20, 2018, HOV *Alvin* dive AD4974, collectors Lisa Levin and Kyle Metcalfe [GenBank: COI = PQ800508]. **Paratypes:** SIO-BIC A3255 (to be ICML-EMU XXXX), seep at Pinkie's 'Vent' Guaymas Basin, Mexico, 27.587° N 111.473° W, 1565 m depth, anterior 10% SW formalin fixed, preserved in 50% ethanol, posterior fixed in 95% ethanol, used for DNA sequencing, April 15, 2012, ROV *Doc Ricketts* dive 388, collectors G. Rouse and S. Katz, [GenBank: COI = PQ774162; other sequences listed in Table 1]; SIO-BIC A1406, Parrita Seep, Costa Rica, 9.029° N, 84.623° W, 1419 m depth, on wood, posterior and anterior 10% SW formalin fixed, preserved in 50% ethanol, midpiece fixed in 95% ethanol, used for DNA sequencing, March 1, 2009, HOV *Alvin* dive 4508, collectors Andrew Thurber and Jason Waggoner [GenBank: COI = PQ814685]; SIO-BIC A9608A (to be MZUCR XXXX), A9608B, A9608C, Mound 12, bone, wood, and chips deployment, Costa Rica, 8.93° N, 84.3117° W, 992 m depth, fixed in 95% ethanol, October 20, 2018, HOV *Alvin* dive 4974, collectors Lisa Levin and Kyle Metcalfe

[GenBank: COI = PQ800507, PQ800509, PQ800510]; SIO-BIC A9612A - F, Mound 12, bone, wood, and chips deployment, Costa Rica, 8.93° N, 84.311° W, 992 m depth, fixed in 95% ethanol, October 20, 2018, HOV *Alvin* dive 4974, collectors Lisa Levin and Kyle Metcalfe [GenBank: COI = PQ800506, PQ800511, PQ800512, PQ800513, PQ800514, PQ800515]; SIO-BIC A9615, Mound 12, bone, wood, and chips deployment, Costa Rica, 8.93° N, 84.311° W, 992 m depth, fixed in 95% ethanol, October 20, 2018, HOV *Alvin* dive 4974, collectors Lisa Levin and Kyle Metcalfe [GenBank: COI = PQ800505]; SIO-BIC A9926A, Mound 11, naturally occurring wood fall, Costa Rica, 8.922° N, 84.304° W, 1010 m depth, fixed in 95% ethanol, November 3, 2018, HOV *Alvin* dive 4988, collectors Victoria Orphan and Hang Yu [GenBank: COI = PQ800504]. **Other materials:** SIO-BIC A9608D, Mound 12, bone, wood, and chips deployment, Costa Rica, 8.93° N, 84.311° W, 992 m depth, 1 fixed in 95% ethanol, October 20, 2018, HOV *Alvin* dive 4974, collectors Lisa Levin and Kyle Metcalfe; SIO-BIC A9608E - G, Mound 12, bone, wood, and chips deployment, Costa Rica, 8.93° N, 84.311° W, 992 m depth, 10% SW formalin fixed, preserved in 50% ethanol, October 20, 2018, HOV *Alvin* dive AD4974, collectors Lisa Levin and Kyle Metcalfe; SIO-BIC A9926B, Mound 11, naturally occurring wood fall, Costa Rica, 8.922° N, 84.304° W, 1010 m depth, fixed in 95% ethanol, November 3, 2018, HOV *Alvin* dive AD4988, collectors Victoria Orphan and Hang Yu.

Diagnosis

Moderate-sized *Vrijenhoekia* species with a median antenna and prostomium similar width to following segments. Proboscis lacking terminal papillae, jaws, or teeth. Enlarged ventral cirri on segments 1-3, ventral cirri with distinct cirrophores segments 1-5. Segment 3 with a small triangular neuropodial lobes dorsal to ventral cirri and neurochaetae. Compound chaetal blades straight.

Description

Holotype with at least 33 segments, 12 mm long, though other specimens reach 15 mm (Fig. 15A, B).



Figure 15. Collection site and individual representative of *Vrijenhoekia mindiae* n. sp. (A) Paratype SIO-BIC A9615 in situ on decaying vertebrate bone fragment at Costa Rica seep at 992 m depth. (B) Holotype (SIO-BIC A9606) dorsal view of live, relaxed specimen. (C) Anterior end of holotype. Legend: 1, 2, 3, 4: first four segments; a: lateral antenna; ch: chaetae of segment 3; ft: frontal tubercle; p: palp.

Body stout anteriorly tapering steadily to posterior. Prostomium rounded rectangular, much wider than long, posterior incision absent. In life anterior body in pharyngeal region translucent followed by bright orange gut wall visible through body wall, posteriorly turning to white (Fig. 15A, B); fixed specimens white. Facial tubercle present (Figures 15C, 16A).

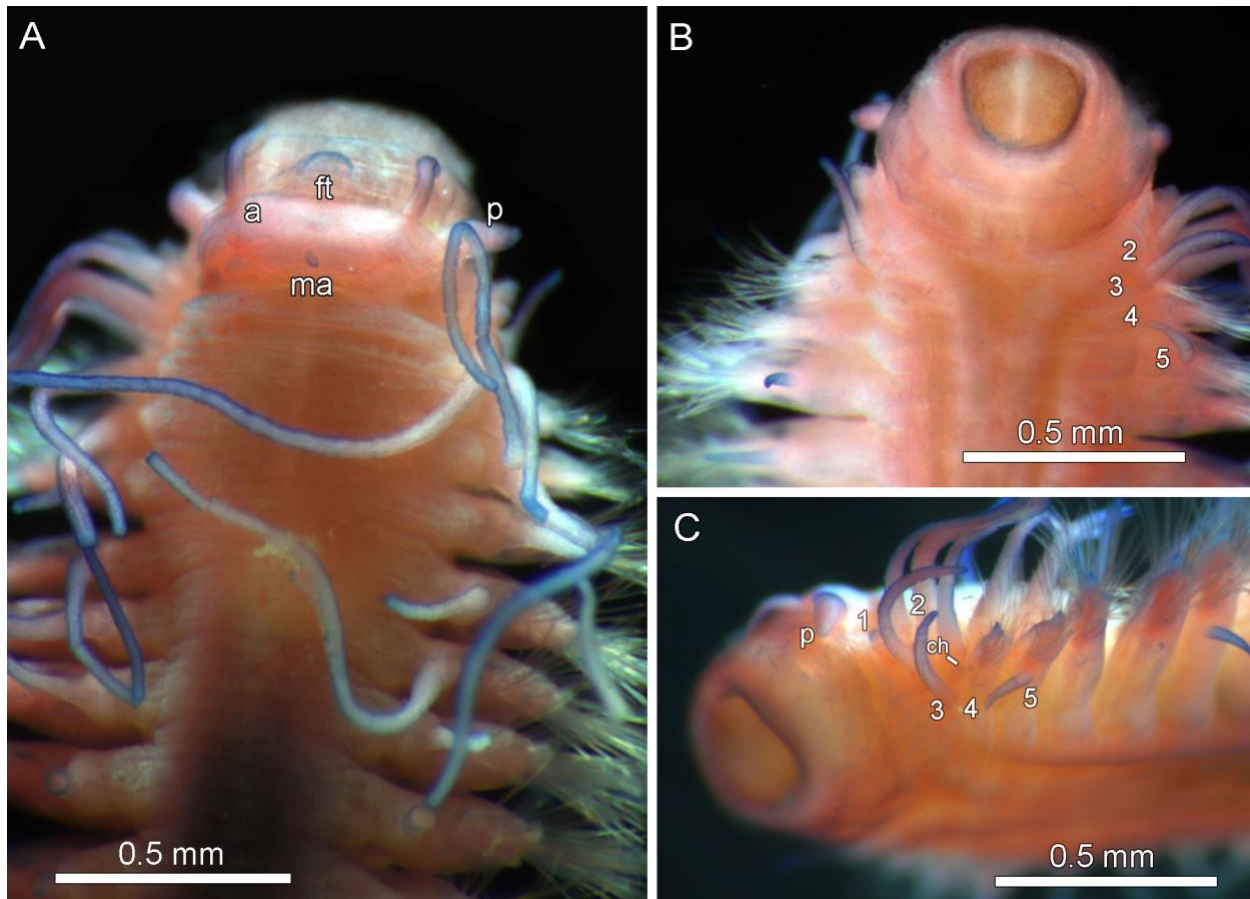


Figure 16. Paratype (SIO-BIC A9612F) of *Vrijenhoekia mindiae* n. sp. stained with ShirlastainA® (A) Dorsal view of preserved specimen anterior region. (B) Ventral view of partially everted proboscis and anterior segments. (C) Lateral view showing partially everted proboscis and anterior segments. Legend: **1, 2, 3, 4, 5**: first five segments; **a**: lateral antenna; **ch**: chaetae; **ft**: frontal tubercle; **ma**: median antenna; **p**: palp.

Biarticulated palps: palpophores cylindrical, longer than wide, slightly longer than palpostyles, which taper (Fig. 15C). Lateral antennae cirriform, lateral to palps, tapering slightly, shorter, much thinner than palps, lacking ceratophores (Figure 13C). Median antenna inserted on dorsal prostomium, posteriorly; median antennal furrows absent (Figures 16A). Eyes absent.

Nuchal organs not discernable with light microcopy. Proboscis without terminal papillae, jaws or teeth. Proboscis opening midventrally without distinct incision or small rounded knob (Figure 16B, C). Glandular lip pads absent. Anterior dorsal cirri and cirrophores not obviously differing from following ones (Figures 15A, B, C, 16A); enlarged ventral cirri on segments 1-3 (Figure 16C), all with distinct cirrophores. Segments 4-5 with shorter cirri and distinct cirrophores, remaining ventral cirri without cirrophores (Figure 16C). Notopodial lobes and notochaetae absent on all segments. Neuropodial lobes and neurochaetae absent on segment 1-2, first chaetiger segment 3 (Figure 13D). Segment 3 with small neuropodial lobe dorsal to ventral cirri. Dorsal cirri weakly annulated, very long, up to 5 mm in life, cylindrical; elongated cirrophores absent (Figures 15A, B, 17A). Dorsal cirri alternation unknown.

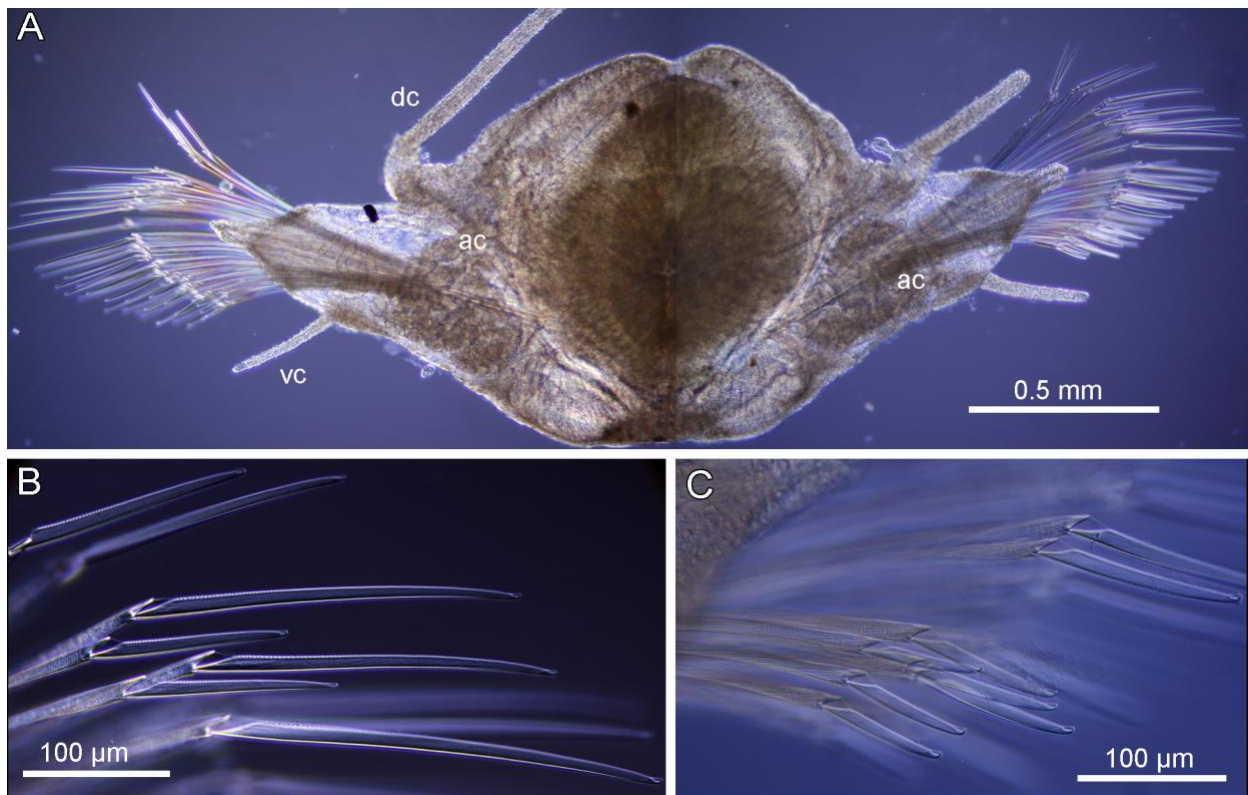


Figure 17. Holotype (SIO-BIC A9606) of *Vrijenhoekia mindiae* n. sp. (A) Segment 12. (B) Superior (dorsal) neurochaetae segment 12. (C) Inferior (ventral) neurochaetae segment 12. Legend: **ac**: aciculae; **dc**: dorsal cirrus; **vc**: ventral cirrus.

Notopodial hooks absent. Neuropodia triangular, with rounded prechaetal lobe distally inserted (Figure 17A). Noto- and neuro-aciculae present. Neurochaetae ~40 in chaetiger 12, all compound with distinctly internally chambered shafts (Fig. 17B, C), ending in rounded hooked tip, superior (dorsal) and median blades up to 5 times longer than inferior (ventral) ones, in all cases blades quite straight (Fig 17B, C). Ventral cirri subdistally inserted on neuropodium, without cirrophores, up to 10 times longer than base width (Fig. 17A). Paired pygidial cirri present (Figure 15A), like dorsal cirri; median pygidial papilla not observed.

Distribution

Methane seeps at ~990-1400 m off the Pacific coast of Costa Rica and at ~1500 m in the Guaymas Basin, Gulf of California, Mexico.

Etymology

This species is named in honor of Mindi Summers for her work on *Sirsoe* and *Vrijenhoekia* and who first informally led the description of this species as *Vrijenhoekia* sp. A [4].

Remarks

Vrijenhoekia mindiae n. sp. was originally described but not named from a single specimen from the Guaymas Basin seeps [4]. Owing to there being only a single specimen in poor condition, the authors chose to refer to it as *Vrijenhoekia* sp. A and published several sequences for the species that clearly showed it belonging in *Vrijenhoekia*. The acquisition of many more specimens, all associated with wood or bone on the seafloor at seep locations off the coast of Costa Rica, has allowed for the species to now be described. The haplotype network for this species showed six haplotypes for the 15 specimens sequenced (Figure 3). The single Guaymas Basin haplotype was separated by at least six base pairs from the Costa Rican

specimens, which showed little variation. The description here largely matches the original informal description but the newly acquired specimens here were mostly much larger.

Vrijenhoekia mindiae n. sp. is the sister group to the as yet undescribed *Vrijenhoekia* BioSurOr from bones deployed off the Brazilian coast. It was 15% divergent on COI (Table 2).

Vrijenhoekia mindiae n. sp. lies in the clade of *Vrijenhoekia* (Clade III, Figure 1) that mainly have a median antenna and lack glandular lip pads. Like *V. ketea* and *V. timoharai*, it lacks the terminal proboscis papillae [4] that is seen in *Sirsoe* spp. and in *V. balaenophila*, *V. besnard* n. comb., *V. alphacrucis* n. comb., *V. alphadelphini* n. comb., *V. nadir* n. comb., and *V. yokosuka* n. comb. [3,6], all members of *Vrijenhoekia* Clade II. Only one member of *Vrijenhoekia* Clade III has been described as having terminal papillae, *V. ungava* n. comb. [6]. *Vrijenhoekia mindiae* n. sp. appears to be unique in having ventral cirri on segments 1-5 with cirrophores.

DISCUSSION

The availability of an appropriately fixed and recently collected specimen of *Sirsoe grasslei*, the type species for the genus [10], allowed for it to be sequenced and placed into a molecular phylogeny (Figure 1). This facilitated a reassessment of the recent proposal to make *Vrijenhoekia* a junior synonym of *Sirsoe* [6]. In their arguments for the synonymy, the authors erroneously stated that *Sirsoe* could only be monophyletic with the inclusion of *Vrijenhoekia* species and that recognition of *Vrijenhoekia* made both genera non-monophyletic. Examination of their phylogenetic results showed that, allowing for the new species included, their tree was not markedly different from the previously published phylogeny [5] showing reciprocally monophyletic *Sirsoe* and *Vrijenhoekia*. Their Clade I could have been retained as *Sirsoe* and their Clades II and III (sister taxa) as *Vrijenhoekia*. Concerns about the diagnosis of each genus also seemed to be an issue and the authors opted for an expanded genus with a diagnosis with a series of variable features. This was unfortunate in that four species changed genus name from *Vrijenhoekia* to *Sirsoe* when a main goal of taxonomy is the stability of taxon names.

The phylogenetic results here show *Sirsoe grasslei* clearly falls (Figure 1) with what was previously regarded as *Sirsoe* [3,5], which is not surprising given its morphological similarity to taxa such as *Sirsoe methanicola*. As type species for *Sirsoe*, this subjectively allows for members of Clade I alone to be in the genus (Figure 1), a decision we follow here. We additionally reinstate *Vrijenhoekia* here for Clades II and III, also a subjective decision. Our new diagnoses for each genus are clear and should hopefully allow for morphological identification (see sections 3.5.1 and 3.5.6) in the absence of DNA data. An unfortunate consequence of this is that eight species named as *Sirsoe* will now be referred to as *Vrijenhoekia* (Figure 1) but hopefully with the two genera preserved, there will be long term stability.

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