The minimal endosymbiosis between *Spurilla braziliana* (Aeolidiidae, Nudibranchia) and Symbiodiniaceae

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Abstract

Symbiotic relationships between dinoflagellates of the family Symbiodiniaceae and marine invertebrates underpin the functioning of marine ecosystems. Although the Symbiodiniaceae-Cladobranchia nudibranch association has been proposed as a promising model for symbiosis research, interspecific variation in the extent of this association remains poorly resolved. Here, we assessed the algal-symbiotic capacity of the nudibranch *Spurilla braziliana*. Histological analyses revealed only limited branching of the digestive gland that accommodates algal cells. Metagenomic profiling further showed a complete absence of *Endozoicomonas*—bacteria typically linked to Symbiodiniaceae symbioses—in this species. These findings indicate that *S. braziliana* can harbor Symbiodiniaceae but exhibits only minimal morphological and microbial adaptations to the symbiotic state. Consequently, *S. braziliana* may bridge the evolutionary gap between symbiotic and non-symbiotic nudibranchs, providing a valuable reference point for studies on the evolution of animal–algal symbioses.

Introduction

Dinoflagellates of the family Symbiodiniaceae establish symbiotic partnerships with a wide range of marine invertebrates, including cnidarians[1], molluscs[2], and foraminiferans[3]. The hosts provide the algae with inorganic nutrients[1] and a light environment conducive to photosynthesis[4], while the algae

reciprocate with photosynthetically derived organic compounds[1]. In the best-studied cnidarian hosts, this association dates back at least 385 million years[5], and Symbiodiniaceae supply not only most of the metabolic substrates required for host energy production[6] but also the amino acids essential for somatic growth[7]. Consequently, Symbiodiniaceae–host symbioses underpin the functioning of shallow-water marine ecosystems. In recent decades, however, the breakdown of this relationship—most conspicuously manifested as mass bleaching in coral hosts—has become increasingly evident[8], highlighting the urgent need to clarify the universal mechanisms that govern Symbiodiniaceae–marine invertebrate symbioses.

Cladobranch nudibranchs are considered promising host models for investigating Symbiodiniaceae symbiosis[9]. Their relatively large body size and well-developed anatomical features make them easy to observe, and importantly, the degree of symbiosis varies markedly among species. Some species are capable of maintaining healthy Symbiodiniaceae cells intracellularly for over 200 days[10], while others retain the algae for only a few weeks or do not internalize them at all[11,12]. By documenting host traits histologically in closely related species and conducting genetic and ecological comparisons, it may be possible to identify the mechanisms driving symbiosis with greater precision. However, the diversity of algal symbiotic capacity in nudibranchs has been described only in a limited number of species. Although the genera *Berghia*, *Spurilla*, and *Baeolidia*—closely related to the widely used model species *Berghia stephanieae*[12–15]—have been relatively well studied[11,16–23], many species within these groups remain unexamined, continuing to hinder broader comparative research.

Here, we provide the first detailed description of the Symbiodiniaceae symbiotic state in the nudibranch *Spurilla braziliana*. Through comprehensive histological and metagenomic analyses, we show that while *S. braziliana* possesses the capacity to host Symbiodiniaceae, this ability appears comparatively limited relative to its close relatives. This study not only offers new data on an understudied species but also highlights the potential of *S. braziliana* as an evolutionary model for understanding the diversity and development of algal symbiosis.

Materials and methods

Sample collection

Two live specimens of *Spurilla braziliana* (designated as individual A and individual B) were collected from the intertidal zone in Miura, Kanagawa Prefecture, Japan, on June 10 and October 5, 2021, respectively. Individual A is the same specimen previously used in our mitochondrial genome sequencing study[24] and was preserved in NucleoProtect RNA solution (MACHEREY-NAGEL). Individual B was maintained in an artificial seawater aquarium (33 g/L, Instant Ocean Premium,

NAPQO, Ltd.) equipped with an external filtration system, under constant light conditions and a water temperature of 25°C.

Fluorescence Microscopy Observation

Fluorescence microscopy was conducted following the same protocol as described in a previous study[25]. The cerata of individual A were excised on the day of sampling (prior to immersion in NucleoProtect RNA) and chemically fixed in 4% paraformaldehyde (PFA). After washing with PBS, the samples were cleared using the CUBIC Trial Kit (FUJIFILM Wako Pure Chemical Corporation), according to the protocol provided by the manufacturer. During the clearing process, nuclear staining was performed using DAPI solution (FUJIFILM Wako Pure Chemical Corporation). Chlorophyll autofluorescence from Symbiodiniaceae and DAPI fluorescence were observed under a fluorescence microscope (KEYENCE BZX-810).

Light and Transmission Electron Microscopy of Tissue Sections

Transmission electron microscopy (TEM) was carried out following the same protocol as described in a previous study[25]. The cerata, tentacles, and rhinophores of individual B, which had been maintained for 15 days, were dissected and fixed in an aldehyde-based fixative solution (2% paraformaldehyde, 2% glutaraldehyde, 50 mM HEPES, 33 g/L Instant Ocean Premium, NAPQO Ltd.). After rinsing with distilled water, the tissues were post-fixed in 1% osmium tetroxide at 4℃ for 1 hour. Following washing and dehydration through a graded ethanol series, the samples were transferred to propylene oxide and subsequently embedded in epoxy resin (Quetol 812, Nisshin EM). The resin blocks were sectioned using an ultramicrotome (Leica Ultracut UCT). Semi-thin sections (500 nm thick) were stained with toluidine blue and observed under a light microscope (KEYENCE BZX-810). Ultrathin sections (60 nm thick) were stained with 4% aqueous uranyl acetate and Reynolds' lead citrate, and observed using a transmission electron microscope (JEOL JEM-1010).

Identification of the Symbiotic Symbiodiniaceae Genus

Raw whole-genome shotgun sequence reads from individual A (GenBank Accession ID: DRR450785)[24] were assembled using CLC Genomics Workbench version 8.5 (QIAGEN Aarhus A/S). To identify symbiotic Symbiodiniaceae sequences, we used the reference dataset published by Pochon et al.[26] and conducted blastn searches against all contigs in the primary assembly for six genetic markers: nuclear 28S rRNA, nuclear elf2, mitochondrial COI, mitochondrial cob, chloroplast 23S rRNA, and chloroplast psbA genes. Contigs identified as Symbiodiniaceae-derived were subsequently aligned to the reference dataset using MAFFT v7.490[27,28] on Geneious Prime. Based on these alignments, maximum likelihood phylogenetic trees were constructed using IQ-TREE version 2.3.3[29] with 1000 bootstrap replicates. To reduce overestimation of branch support, the -bnni

option was applied. Additionally, SH-aLRT[30] and aBayes[31] tests were performed to provide a more stringent assessment of node support. The final phylogenetic trees were visualized using Interactive Tree of Life version 6[32].

Visualization of the Hologenome Structure

Raw reads were mapped to the primary assembly using BWA-MEM[33], and the resulting alignments were processed into BAM files with samtools version 1.17[34]. The BAM files were analyzed with CoverM version 0.6.1 (https://github.com/wwood/CoverM) to calculate the mean coverage for each contig. Contig lengths were determined using seqkit version 2.3.0[35] and GNU Awk version 4.0.2 (https://www.gnu.org/software/gawk/). The 4-mer composition of each contig was calculated using Perl scripts included in the Multi-metagenome[36]. Feature data from each contig were visualized as scatter plots using the matplotlib package in Python version 3.10.4. Contig coverage and length were used as the x- and y-axis coordinates, respectively. The 256-dimensional 4-mer vectors were reduced to three dimensions using UMAP (umap-learn module, version 0.5.3)[37], normalized, and converted into RGB color values that were applied to the data points in the plot.

Identification of Organisms Present in the Holobiont

Each contig in the primary assembly was taxonomically characterized by homology search against the NCBI nr database (downloaded on May 19, 2021; https://ftp.ncbi.nlm.nih.gov/blast/db/) using DIAMOND version 2.0.9[38]. Only hits with an E-value of 0.0 and a bit score within 95% of the top hit were retained. Taxonomic assignments for each contig were determined using the lowest common ancestor (LCA) approach. A scatter plot was then redrawn using contig coverage and length as the x- and y-axes, respectively, with each contig colored according to its assigned taxon.

Results

Whole-Mount Localization of Symbiodiniaceae in the Cerata

Whole-mount fluorescence microscopy revealed the internal structure of the ceras in *Spurilla braziliana*. While most cells within the ceras exhibited only blue fluorescence from DAPI staining, red autofluorescence—potentially derived from chlorophyll of Symbiodiniaceae—was observed in the slightly branched digestive gland located at the center of the ceras (Fig. 1). In contrast, no autofluorescence was detected in the cnidosacs, which are extensions of the digestive gland.

Light and Transmission Electron Microscopy of Tissue Sections

Observation of toluidine blue-stained sections under a light microscope allowed examination of the two-dimensional tissue architecture in the cerata, tentacles, and rhinophores of *S. braziliana* (Fig. 2). A gently branched digestive gland extended through the center of each ceras, and multiple

Symbiodiniaceae cells were observed in its epithelial layer (Fig. 2a). All five branches of the digestive gland exhibited similar structure, although algal cells were not observed in the central branch within the limits of our observations. No algal cells were detected outside the digestive gland epithelium within the ceras. In both the tentacles and rhinophores, no penetration of the digestive gland was observed, and no algal cells were present (Fig. 2b, c).

Transmission electron microscopy (TEM) was used to examine the ultrastructure of algal symbiosis within the digestive gland epithelium of the ceras in *S. braziliana* (Fig. 3). The lumen of the digestive gland was lined with microvilli, and its epithelial cells contained numerous vacuole-like structures. In some of these epithelial cells, algal cells were enclosed within the vacuole-like compartments. Many of the algal cells appeared to retain intact cellular architecture, with clearly distinguishable internal structures.

Clade Affiliation of Symbiodiniaceae in *S. braziliana*

Using blastn searches followed by manual alignment inspection, one contig each was identified as homologous to the mitochondrial COI and cob genes based on similarity to reference sequences. In contrast, the remaining four genes (nuclear and chloroplast markers) either produced no significant hits or showed clearly low sequence similarity. Phylogenetic trees were constructed for the two contigs with confirmed homology to the reference dataset (Fig. 4). In both the COI and cob gene trees, the contigs derived from *S. braziliana* formed a monophyletic group with *Symbiodinium* (clade A) species, indicating that the symbiotic algae associated with *S. braziliana* belong to *Symbiodinium*.

Hologenomic Structure in *Spurilla braziliana*

In the *S. braziliana*–Symbiodiniaceae symbiotic system, not only the dinoflagellates but also a broader microbiome may contribute to symbiotic adaptation. To explore this possibility, we visualized the major microbiome components present within the nudibranch using previously obtained whole-genome shotgun sequencing data (Fig. 5). Each contig from the primary assembly was plotted using its coverage and length as spatial coordinates, and its color was determined by dimensional reduction (3D UMAP) of its 4-mer sequence composition. This visualization revealed four clearly distinct peaks, each representing contigs with differing compositional properties (Fig. 5a).

Using DIAMOND blastx searches and taxonomic assignment via the lowest common ancestor (LCA) method, we were able to infer the likely source organisms for 1,294 out of 850,960 contigs in the primary assembly. Among these, taxa represented by more than 50 contigs included *Vibrio* (977 contigs), *Photobacterium* (134 contigs), and Gastropoda (77 contigs), corresponding to the host itself.

An additional 56 bacterial contigs were attributed to taxa other than the two dominant genera. Other notable assignments included Embryophyta (24 contigs) and Symbiodiniaceae (4 contigs). When taxonomic assignments were overlaid onto the coverage–contig length scatter plot, it became evident that distinct taxa underlie the four prominent peaks observed in Fig. 5a (Fig. 5b). Peak 1 was primarily composed of contigs assigned to the genus *Photobacterium*, while Peak 2 was dominated by *Vibrio*. Peak 3 corresponded to Gastropoda, reflecting sequences derived from the host organism. Peak 4, though less sharply defined, exhibited the highest coverage and was attributed to a heterogeneous group of other bacterial taxa. Contigs matching Symbiodiniaceae or other non-bacterial organisms did not form distinct peaks in the plot.

Among the bacteria other than *Photobacterium* and *Vibrio*, seven families were identified through LCA-based analysis at the family level: Cyclobacteriaceae, Enterobacteriaceae, Flammeovirgaceae, Marinifilaceae, Marinilabiliaceae, Prolixibacteraceae, and Pseudomonadaceae. Of these, contigs assigned to Enterobacteriaceae and Pseudomonadaceae tended to have relatively low coverage (Fig. 5c).

Discussion

Symbiotic Structure of *Spurilla braziliana* in the Context of Cladobranchia Symbioses

Whole-mount fluorescence microscopy provided a coarse-resolution view of internal structures within the ceras of *S. braziliana* (Fig. 1). In *Pteraeolidia semperi*, a species within the same superfamily Aeolidioidea and known for its highly developed symbiotic capacity with Symbiodiniaceae[10], previous observations[25] revealed intense chlorophyll autofluorescence just beneath the cerata epidermis. This pattern is attributed to the extensive branching of the digestive gland that houses the algal cells. In contrast, no such peripheral fluorescence was observed in *S. braziliana*, where red autofluorescence was detected exclusively in the central digestive gland running through the ceras. Follow-up histological and ultrastructural observations (Figs. 2, 3) confirmed that, consistent with general patterns reported in Cladobranchia–Symbiodiniaceae symbioses[9], algal cells are located within the epithelial cells of the digestive gland.

Histological observations confirmed the findings from whole-mount fluorescence imaging: algal cells were found exclusively within the digestive gland in the cerata, with no presence in other tissues. The digestive gland penetrating the cerata exhibited only limited branching (Fig. 1), and among the five branches observed in Fig. 2a, algal cells were absent only in the central canal. In contrast, species such as *Pteraeolidia semperi*, *Phyllodesmium briareum*, and *Melibe engeli* possess highly branched digestive gland systems within the cerata, forming networks of structurally distinct fine tubules, in which algal symbionts are harbored within epithelial cells of the branches[10,25,39,40].

The branching structure observed in *S. braziliana* bears some resemblance to this organization. However, unlike *Pteraeolidia*, in which fine tubules extend into both the rhinophores and tentacles[25], or *P. briareum* and *M. engeli*, where they penetrate at least the rhinophores[39,40], no such branching structures were found in the rhinophores or tentacles of *S. braziliana* (Fig. 2b, c). Moreover, the degree of branching in *S. braziliana* was limited (Fig. 1), and no structural differentiation was evident between the central canal and lateral branches (Fig. 2a). Given that the extent of digestive gland branching in *Phyllodesmium* has been suggested to correlate with symbiotic efficiency[10,41], the relatively simple morphology of the digestive gland in *S. braziliana* indicates a lower morphological capacity for algal symbiosis.

In our field sampling, *P. semperi* was also found in the same coastal area, but whereas *P. semperi* was collected from sunlit areas, *S. braziliana* was found beneath rocks. This ecological distinction further suggests that *S. braziliana* may be less adapted to light-dependent symbiosis.

Symbiotic Structure of Spurilla braziliana in the Context of Aeolidiidae Symbioses

Within the family Aeolidiidae, to which *Spurilla* belongs[17,22,42–49], Symbiodiniaceae have been explicitly reported from 16 nudibranch species and absent in 2 species[11,16–23,47,50,51] (Fig. 6, Supplementary Table 1). Among them, the genus *Berghia*, which is phylogenetically close to *Spurilla*[42,48], has been the most frequently used model for studying Cladobranchia–Symbiodiniaceae symbioses in recent years[12–15]. Previous studies have suggested that the symbiotic capacity of *Berghia* is relatively primitive, with algal cells being retained for only about one week[11,18]. The symbiosis observed in *Spurilla* may represent a similar state.

Among *Spurilla* and *Baeolidia* species more closely related to *S. braziliana* than *Berghia*, detailed histological studies of *S. neapolitana*[16], *Baeolidia australis*[19], and *Baeolidia moebii*[19] have reported penetration of the digestive gland into the rhinophores. In contrast, *S. braziliana* exhibited no such penetration into the rhinophores, suggesting an even lower level of adaptation to symbiosis. Supporting this, a previous study based on external morphology reported that *S. neapolitana* displayed pigmentation likely derived from Symbiodiniaceae, while such coloration was inconsistent or unstable in *S. braziliana*[22]—further reinforcing the interpretation that *S. braziliana* exhibits relatively limited symbiotic capacity. However, this time we did not assess the algal retention capacity directly. Future investigations that track temporal changes in algal load under controlled conditions—specifically, in the complete absence of potential cnidarian prey—will be essential to clarify the symbiotic capacity of *S. braziliana* in greater detail.

In any case, the observation that symbiotic capacity varies at intra- and interspecific, as well as intergeneric levels strongly suggests that comparative analyses among *Spurilla*, *Baeolidia*, and

Berghia provide a powerful evolutionary model for studying animal–algal symbiosis. In this context, *S. braziliana* may serve as a critical intermediate, bridging the gap between symbiotic and non-symbiotic nudibranchs. Notably, *Baeolidia salaamica*—the only species among the three genera for which a lack of symbiotic capacity has been reported[19]—could also serve as an important comparative reference in future studies.

Microbiome Composition in *Spurilla braziliana*

From the whole-genome shotgun (WGS) assembly of *S. braziliana*, single contigs corresponding to the COI and cob genes of dinoflagellates were identified. Phylogenetic analysis showed that both sequences belong to the genus *Symbiodinium* (clade A) (Fig. 4). Nudibranchs within the suborder Cladobranchia have been reported to form symbioses with Symbiodiniaceae clades A through D—*Symbiodinium*, *Breviolum*, *Cladocopium*, and *Durusdinium*—with the specific clade often reflecting the host's geographic distribution[52–58]. *Symbiodinium* (clade A) is frequently detected in nudibranchs from temperate regions[53] and has previously been reported in *Pteraeolidia semperi* from Hayama[52], a locality very close to the present sampling site. This finding aligns with known biogeographic trends in Cladobranchia–Symbiodiniaceae associations.

Regarding the bacterial community of *S. braziliana*, contigs assigned to the genera *Photobacterium* and *Vibrio* were detected at relatively low coverage. These genera are commonly reported as intestinal bacteria in marine gastropods[59]. In addition, members of the families Cyclobacteriaceae, Enterobacteriaceae, Flammeovirgaceae, Marinifilaceae, Marinilabiliaceae, Prolixibacteraceae, and Pseudomonadaceae were identified. Among these, Enterobacteriaceae and Pseudomonadaceae have been reported to co-occur with certain clades of Symbiodiniaceae in coral hosts[60]. However, their functional roles remain poorly understood, and the study has specifically noted a lack of co-occurrence with *Symbiodinium* (clade A)[60]. Therefore, caution is warranted in interpreting any direct contribution of these bacterial taxa to algal symbiosis in *S. braziliana*.

Among bacterial taxa associated with photosymbiosis, the genus *Endozoicomonas* has attracted the most attention. In cnidarian hosts, members of this family are thought to positively influence algal symbiosis by modulating host immunity and supplying essential metabolites that support Symbiodiniaceae photosynthesis[61–63]. In nudibranch hosts as well, *Endozoicomonas* has been identified in species with both advanced (*Pteraeolidia semperi*)[64] and rudimentary (*Berghia stephanieae*)[65] symbiosis. However, in the present study, no contigs assigned to Endozoicomonadaceae were detected from *S. braziliana*. This absence of symbiosis-associated bacterial taxa may further support the interpretation that *S. braziliana* possesses a low level of symbiotic adaptation. That said, the actual functional roles of bacterial communities in marine

invertebrate–Symbiodiniaceae symbioses remain poorly understood. As our understanding of host–symbiont–microbiome interactions deepens, it will become possible to more precisely evaluate the symbiotic potential of species like *S. braziliana*.

Conclusion

The study of nudibranch-Symbiodiniaceae symbiosis remains in its early stages, and the diversity of symbiotic capacity across species is still poorly understood. In this study, we conducted the first histological and metagenomic analyses of endosymbiosis in *Spurilla braziliana*, a species previously unexamined in this context. The combination of a simple digestive morphology for algal retention and the absence of bacterial taxa typically associated with algal symbiosis suggests that *S. braziliana* exhibits only minimal algal symbiotic capacity. These findings contribute new insight into the diversity of nudibranch–Symbiodiniaceae interactions and underscore the value of *S. braziliana* as a potential model for exploring the evolutionary origins and acquisition of photosymbiosis. As comparative analyses of related species continue to expand, we will be better equipped to bridge interspecific and intergeneric gaps and identify the key factors underlying the emergence of symbiotic capacity in marine invertebrates.

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Author contributions

H.M. conceived the study. H.M., R.Y., and K.H. conducted sampling and maintenance of live nudibranchs. H.M., K.T., and K.H. performed histological observations. H.M. carried out microbiome analyses. H.M. interpreted the results and wrote the manuscript. All authors contributed to discussions and revised the manuscript.

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Figure captions

Figure 1. Whole-mount fluorescence microscopy image of a *Spurilla braziliana* ceras.
Red autofluorescence is visible exclusively in the digestive gland. Blue fluorescence indicates DAPI staining.

Figure 2. Toluidine blue-stained sections of various tissues in *Spurilla braziliana*.
a. Cross-section of a ceras. The digestive gland divides into five diverticula, within which algal cells are located in the epithelium. Arrowheads indicate algal cells.
b. Cross-section of a tentacle. No penetration of the digestive gland or presence of algal cells is observed.
c. Cross-section of a rhinophore. No penetration of the digestive gland or presence of algal cells is observed.

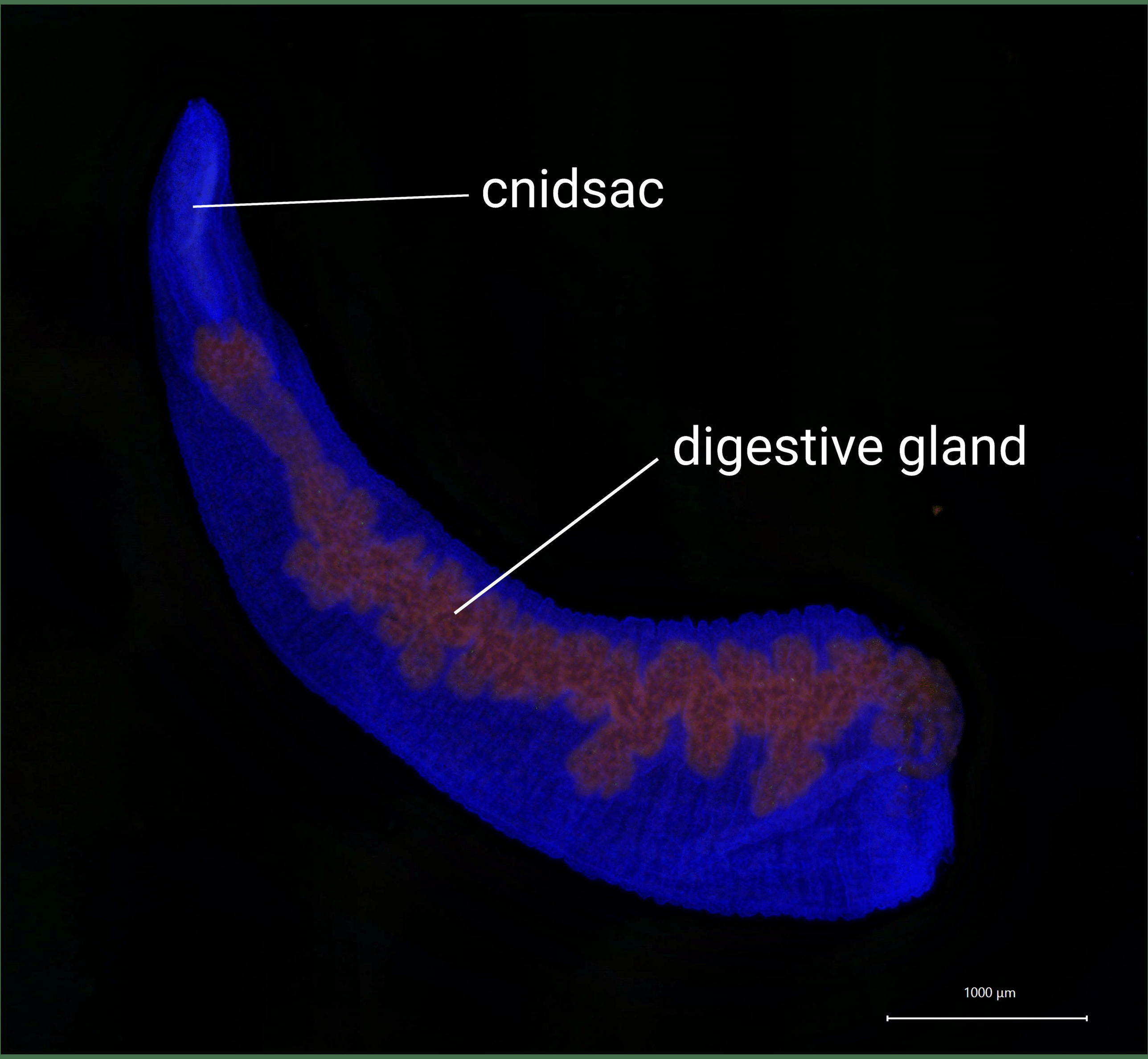
Figure 3. Cross-section of the digestive gland within a ceras.
Algal cells are enclosed within the epithelial cells. Arrows: algal cells; dg: digestive gland lumen; vls: vacuole-like structures. Scale bar: 5 μm.

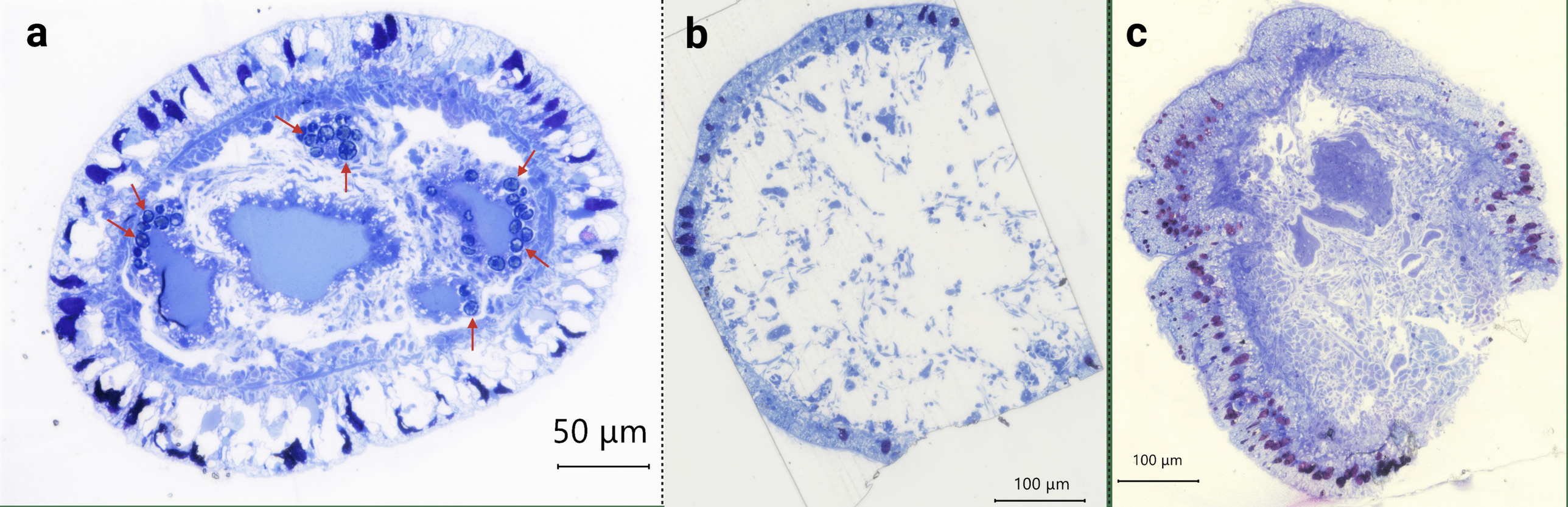
Figure 4. Phylogenetic placement of Symbiodiniaceae-derived sequences detected in *Spurilla braziliana*.
Branch lengths are not to scale for clarity. For full trees with branch lengths, see Supplementary Data 1. a. COI gene; b. cob gene.

Figure 5. Hologenomic structure of the *Spurilla braziliana* – Symbiodiniaceae holobiont.
a. Coverage–contig length scatter plot colored by sequence composition.
b. Coverage–contig length scatter plot colored by taxonomic assignment. Each peak corresponds to a different biological origin. Black: no hit; yellow: *Photobacterium*; blue: *Vibrio*; red: Gastropoda; brown: other bacteria; green: Embryophyta; light green: Symbiodiniaceae; gray: others.
c. Coverage–contig length scatter plot focusing on contigs assigned to bacterial taxa.

Figure 6. Presence of Symbiodiniaceae in the family Aeolidiidae.
The species list of Aeolidiidae follows MolluscaBase as accessed via WoRMS on June 30, 2025[49]. Green: species for which the presence of Symbiodiniaceae has been reported. Gray: species for

which the absence of Symbiodiniaceae has been reported. No color: species for which neither presence nor absence has been confirmed. Red box: present study. See Supplementary Table 1 for references supporting phylogenetic placement and symbiont status.


cnidsac
digestive gland
1000 µm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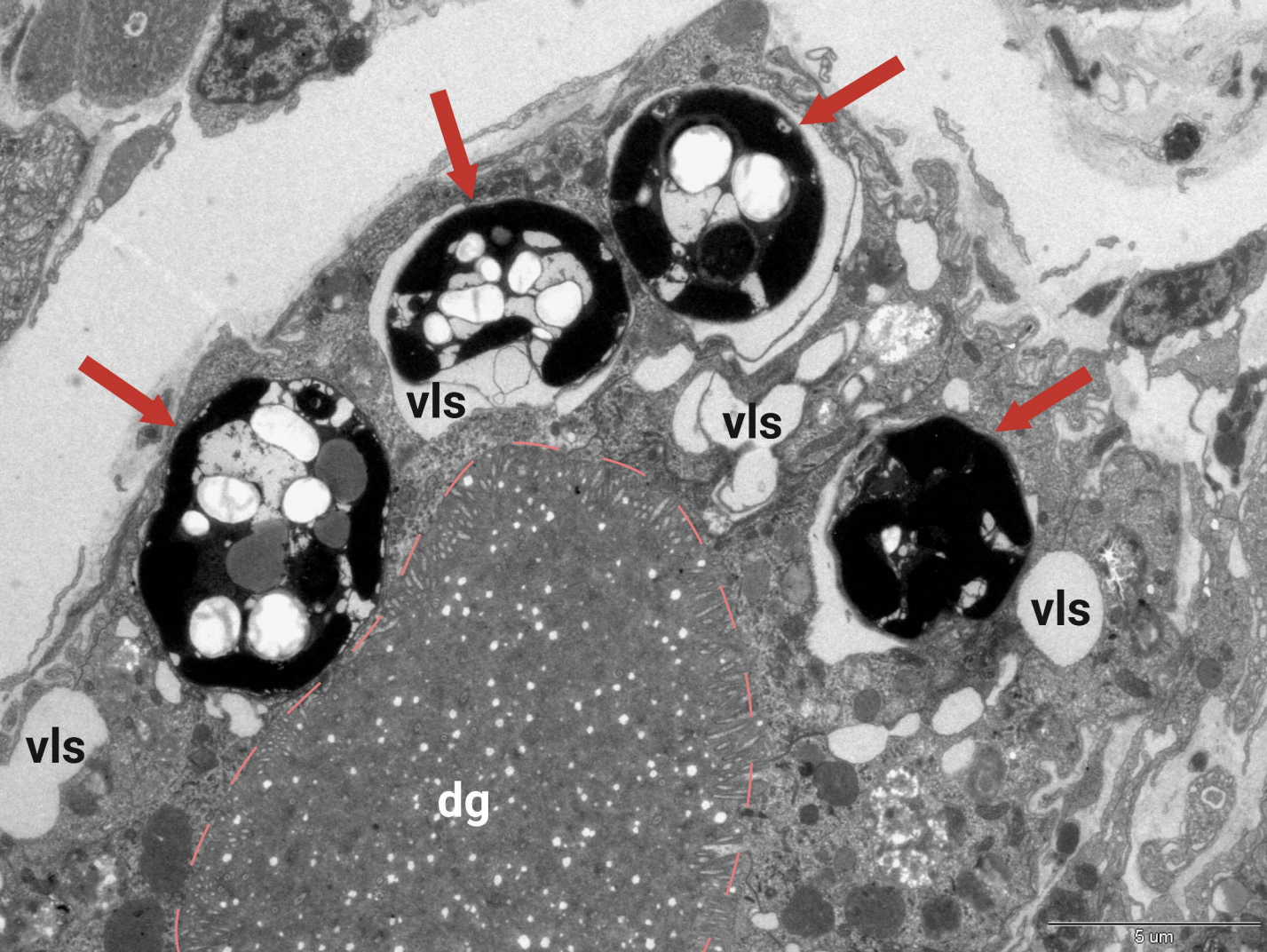
c
100 µm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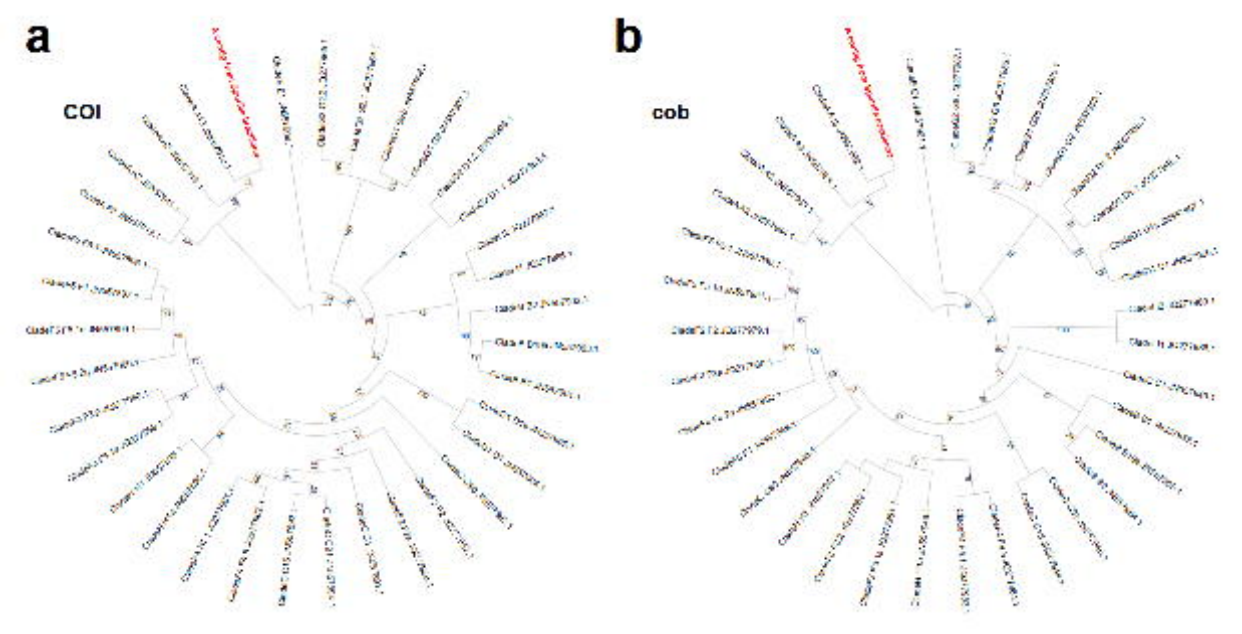
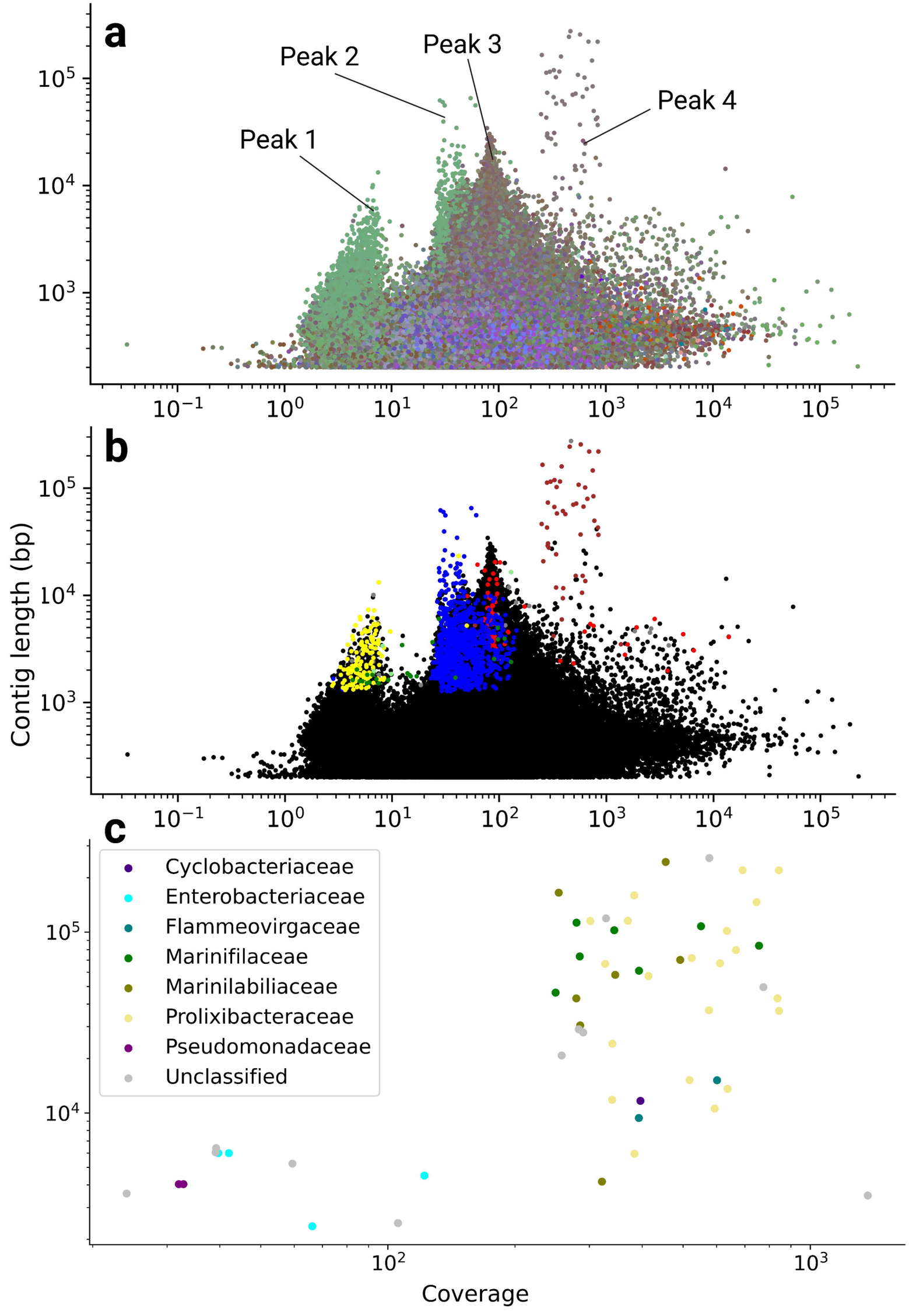
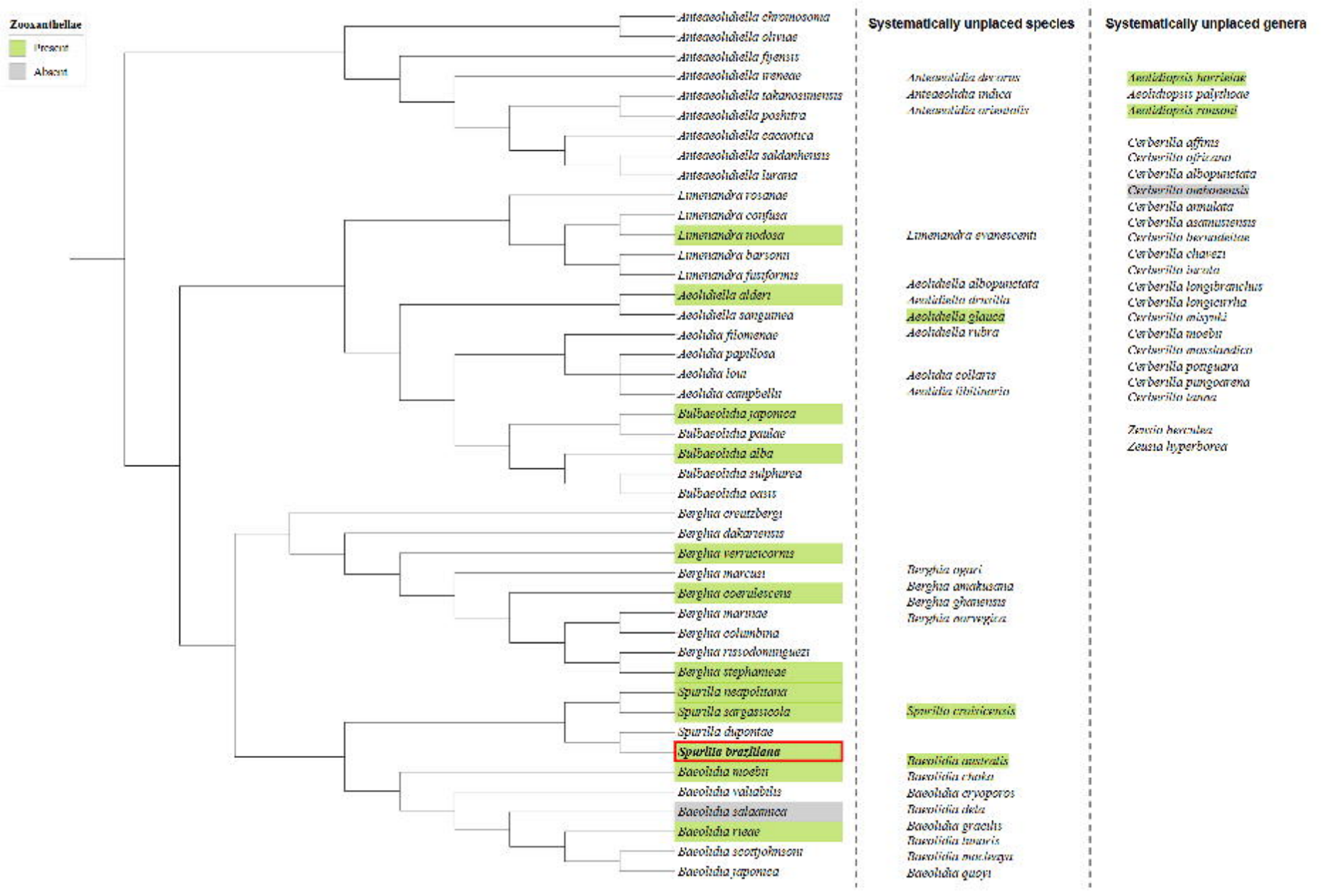

a
COI
b
cob


a
Peak 1
Peak 2
Peak 3
Peak 4
b
Contig length (bp)
c
Cyclobacteriaceae
Enterobacteriaceae
Flammeovirgaceae
Marinifilaceae
Marinilabiliaceae
Prolixibacteraceae
Pseudomonadaceae
Unclassified
Coverage


Zooxanthellae
Present
Absent
Anteaeolidiella chromosoma
Anteaeolidiella oliviae
Anteaeolidiella fijensis
Anteaeolidiella ireneae
Anteaeolidiella takanosimensis
Anteaeolidiella poshitra
Anteaeolidiella cacaotica
Anteaeolidiella saldanhensis
Anteaeolidiella lurana
Limenandra rosanae
Limenandra confusa
Limenandra nodosa
Limenandra barsonii
Limenandra fusiformis
Aeolidiella alderi
Aeolidiella sanguinea
Aeolidia filomenae
Aeolidia papillosa
Aeolidia loui
Aeolidia campbelli
Bulbaeolidia japonica
Bulbaeolidia paulae
Bulbaeolidia alba
Bulbaeolidia sulphurea
Bulbaeolidia oasis
Berghia creutzbergi
Berghia dakariensis
Berghia verrucicornis
Berghia marcusi
Berghia coerulescens
Berghia marinae
Berghia columbina
Berghia rissodominguezi
Berghia stephanieae
Spurilla neapolitana
Spurilla sargassicola
Spurilla dupontae
Spurilla brazilana
Baeolidia moebii
Baeolidia valiabilis
Baeolidia salaamica
Baeolidia rieae
Baeolidia scottjohnsoni
Baeolidia japonica
Systematically unplaced species
Anteaeolidia decorus
Anteaeolidia indica
Anteaeolidia orientalis
Limenandra evanescenti
Aeolidiella albopunctata
Aeolidiella drusilla
Aeolidiella glauca
Aeolidiella rubra
Aeolidia collaris
Aeolidia libitinaria
Berghia ogari
Berghia amakusana
Berghia ghanensis
Berghia norvegica
Spurilla cruisicensis
Baeolidia australis
Baeolidia choko
Baeolidia cryoporos
Baeolidia dela
Baeolidia gracilis
Baeolidia tunaris
Baeolidia mosleaya
Baeolidia quoyi
Systematically unplaced genera
Aeolidiopsis harrieiae
Aeolidiopsis palythoae
Aeolidiopsis ronsoni
Cerberilla affinis
Cerberilla africana
Cerberilla albopunctata
Cerberilla ambonensis
Cerberilla annulata
Cerberilla asamusiensis
Cerberilla bernadettae
Cerberilla chavezi
Cerberilla incata
Cerberilla longibranchus
Cerberilla longicirrha
Cerberilla misyuki
Cerberilla moebii
Cerberilla mossiaodica
Cerberilla potiguara
Cerberilla pungoarena
Cerberilla tanga
Zeusia beculea
Zeusia hyperborea