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ORIGINAL PAPER

Description and distribution of *Desmacella hyalina* sp. nov. (Porifera, Desmacellidae), a new cryptic demosponge in glass sponge reefs from the western coast of Canada

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Abstract

Glass sponges (Porifera, Hexactinellida) form globally unique reefs that support deep-sea biodiversity in the Canadian northeast Pacific. In February 2017, the largest known reefs were protected within the Hecate Strait and Queen Charlotte Sound Glass Sponge Reefs Marine Protected Area (HSQCS-MPA). Many studies that have established baseline biodiversity data for the MPA have focused on describing the crustaceans and fish living in the reefs, but the relationship between glass sponges and sponge epibionts has often been overlooked. We studied one of the more conspicuous sponge epibionts of the genus *Desmacella* Schmidt, 1870, a demosponge that encrusts the surface of reef-forming glass sponges. Using a remotely operated vehicle, samples of an encrusting sponge with three color morphotypes (yellow, white, and mauve) were collected from the northern reef complex of the HSQCS-MPA. Spicule and DNA analyses of COI sequences revealed the white morphotype to be distinct from the previously described species, *D. austini* Lehnert, Conway, Barrie & Krautter, 2005. Comparisons with other *Desmacella* samples collected from other regions in British Columbia waters since 1976 confirmed this to be a new species, which we describe here as *Desmacella hyalina* sp. nov. We also mapped the spatial distribution of the color morphotypes on the reefs and found that *Desmacella* spp. formed nearly 20% of live sponge cover at some sampling sites indicating its potential importance in the reefs. Our results expand on knowledge of the diversity of sponge epibionts in glass sponge reefs and highlight the importance of understanding cryptic species diversity especially for future monitoring in marine protected areas.

Keywords Glass sponges · Porifera · Cryptic diversity · Marine protected areas · *Desmacella* · Epibionts · Hecate Strait and Queen Charlotte Sound · Hexactinellida

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Introduction

Glass sponges (Porifera, Hexactinellida) are typically deep-water invertebrates that can be found in shallow waters (< 500 m) in a few locations globally (Barthel and Gutt 1992; Vacelet et al. 1994; Vacelet and Boury-Esnault 1995; Hogg et al. 2010). Of these locations, the Canadian northeast Pacific is home to glass sponges that have formed reefs stretching tens of kilometers across the seafloor. The largest reefs occur at 150–250 m depth in the Hecate Strait and Queen Charlotte Sound, but many smaller reef complexes are also found in the Strait of Georgia (SoG) at 90–200 m depth (Conway et al. 1991; Conway 1999; Conway et al. 2005) and within fjords (Stone et al. 2014; Dunham et al. 2018). More reefs are anticipated to exist since reef-forming sponges are common inhabitants of fjord walls (Leys et al. 2004) and many other locations remain unexplored.

Sponge reefs are formed by three species of glass sponge: *Aphrocallistes vastus* Schulze, 1886; *Heterochone calyx* (Schulze, 1886); and *Farrea occa* Bowerbank, 1862 (Krautter et al. 2001; Conway et al. 2005). These species differ from other glass sponges in the area by having a fused skeleton of siliceous spicules (Leys et al. 2007), which remains relatively intact after the death of the sponge. The skeletons provide the framework for building the reefs as clay-rich sediments bury and cement them over time (Conway et al. 1991; Conway et al. 2005; Kahn et al. 2016), but they are also substrate for settlement of juvenile glass sponges and for a host of other invertebrates including a diversity of sponge epibionts (Conway et al. 2005; Krautter et al. 2006; Guillas et al. 2019). Although several studies have documented the motile megafauna (animals > 5 cm) inhabiting reefs (Cook 2005; Cook et al. 2008; Chu and Leys 2010; Du Preez and Tunnicliffe 2011; Law 2018), including commercially important species such as spot prawns (*Pandalus platyceros* Brandt, 1851), squat lobsters (*Munida quadrispina* Benedict, 1902), Pacific halibut (*Hippoglossus stenolepis* Schmidt, 1904), and several rockfish species (*Sebastes* spp.), less is known about sponge epibionts in glass sponge habitat (Lehnert et al. 2005; Cook et al. 2008).

Desmacella austini Lehnert, Conway, Barrie, & Krautter, 2005 is one of the few sponge epibionts that has been studied in some detail because it grows directly and conspicuously on reef-forming glass sponges. The first samples of *D. austini* were collected in the SoG reefs and described as a thin encrusting sponge with two color morphotypes: yellow and mauve (Lehnert et al. 2005). The yellow form was found "overtaking" live *H. calyx*, while the mauve form was typically observed growing on dead *H. calyx* (Lehnert et al. 2005). However, we observed a white color morphotype also growing in the reefs, which until now, has remained unidentified. In 2015 and 2017, the SoG and Hecate Strait reefs were surveyed using a remotely operated vehicle (ROV), during which a surprisingly large portion of glass sponge was found encrusted with sponges of all three color morphotypes (i.e., yellow, white, and mauve). Samples of these morphotypes were opportunistically collected since 1976 during research cruises and by divers along the British Columbia coast, and stored at the Royal British Columbia Museum (RBCM) where they were identified by expert sponge taxonomists H.M. Reiswig, B.S. Ott, and W.C. Austin. A number of these samples were classified as *D. austini*, but a small subset was identified as a different *Desmacella* species. This has raised many questions about whether multiple species of *Desmacella* Schmidt, 1870 exist in the reefs and if each species can be distinguished by color alone.

Many sponge reefs have historically been damaged due to bottom trawling (Conway 1999; Jamieson and Chew 2002; Cook et al. 2008). In light of this, Fisheries and Oceans Canada established the Hecate Strait and Queen Charlotte Sound Glass Sponge Reefs Marine Protected Area (HSQCS-MPA) in February 2017, protecting 2410 km^2 of reef habitat (Fisheries and Oceans Canada 2017). The effective management and monitoring of protected areas, such as the HSQCS-MPA, hinges on the ability to identify and document baseline biodiversity (Wheeler 1995; Brooks et al. 2004). Therefore, to better understand the diversity of animals living in the reefs, we focused on documenting and describing sponge epibionts in glass sponge habitat. We collected encrusting sponges of different color morphotypes (yellow, white, and mauve) and used spicule and molecular analyses of COI sequences, combined with a study of past collections, to distinguish between morphotypes. We also used imagery from ROV to create high-resolution maps of the distribution and abundance of *Desmacella* species at three regions in the northern reef complex of the HSQCS-MPA. Our findings provide fundamental groundwork for understanding sponge epibiont relationships in glass sponge reef ecosystems. They also highlight the importance for continued investigations into sponge reef biodiversity to better inform HSQCS-MPA management and monitoring efforts.

Materials and methods

Field surveys

Three field sites in the northern reef complex of the HSQCS-MPA were surveyed in October 2015 and May 2017 on the *CCGS John P. Tully*. We named the three sites Farrea 2015 (53° 11.6′ N, 130° 28.4′ W, mean depth 170 m), Peloponnesus (53° 8.9′ N, 130° 25.6′ W, mean depth 191 m), and Sponge Ridge West (53° 6.31′ N, 130° 29.6′ W, mean depth 178 m) (Fig. 1a, b). Field sites were mapped extensively using the Canadian ROV ROPOS (ropos.com) along a grid of stratified georeferenced points separated 25 m apart. Non-overlapping photos were captured 1 to 2 m above the seafloor

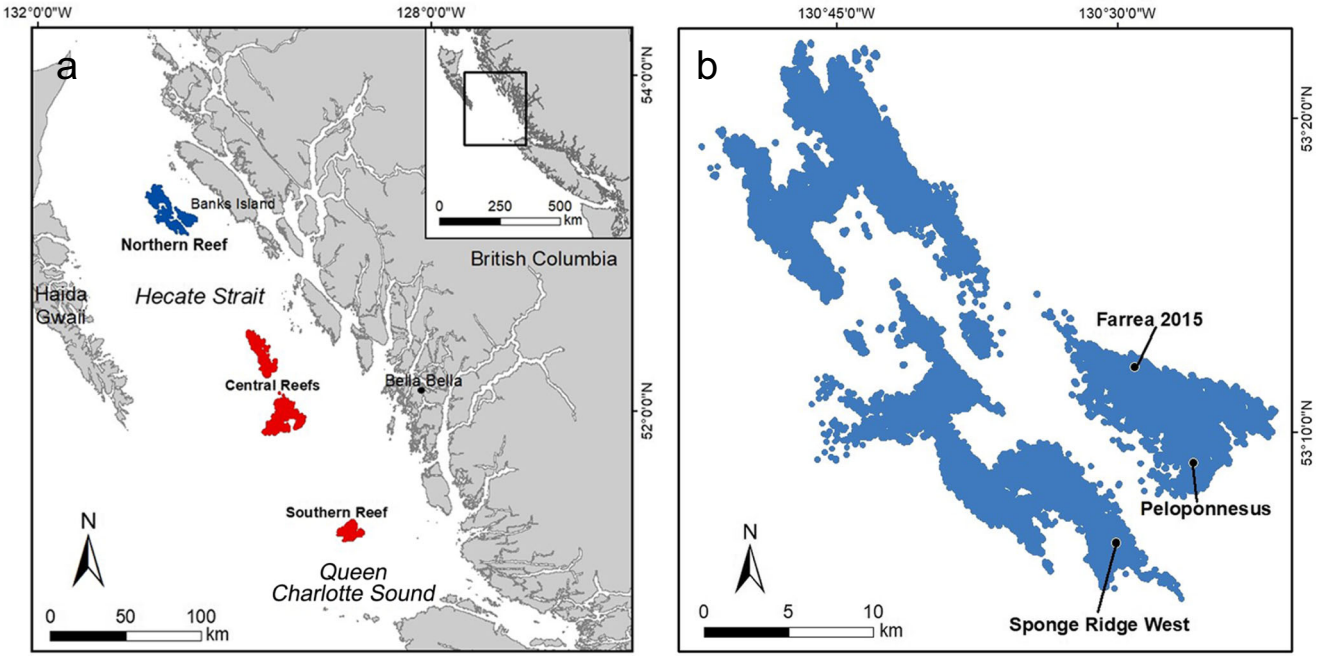

Fig. 1 Locations of sponge reefs in the Hecate Strait and Queen Charlotte Sound (QCS). **a** The Hecate Strait and QCS reefs are comprised of four massive reef complexes grouped as the Northern, Central, and Southern reefs. All reefs lie on the continental shelf between Haida Gwaii and mainland British Columbia, Canada. Field sampling was conducted in the northern reef (blue); **b** Sampling locations in the northern reef complex at field sites Farrea 2015, Peloponnesus, and Sponge Ridge West. Distribution of sponge areas in the Hecate Strait and QCS are shown in blue and red (courtesy K.W. Conway, Natural Resources Canada)

from birds-eye view with a 12.4-megapixel digital still camera (DSC, Nikon D7000) mounted on a pan and tilt function on ROPOS, while high-definition video was captured throughout the duration of the survey. Lasers 10 cm apart on the two cameras provided a scale in the images.

Spatial mapping

Maps of live and dead sponge cover were interpolated with kriging from semivariogram models of sponge cover measured at each dive site (Supplementary Table 1). For live reef cover, still framegrabs were extracted at 20 s time intervals from ROPOS video imagery and analyzed for percent cover using Yen auto-thresholding in ImageJ v1.52k (Schindelin et al. 2012; Schneider et al. 2012). Percent dead sponge cover was quantified from still DSC images captured every 25 m during ROPOS dives. We measured dead cover in two different ways: for the Farrea 2015 and Peloponnesus reef sites, manual delineation (i.e., tracing) of dead sponge cover was carried out in Adobe Photoshop CS5. For the Sponge Ridge West reef site, we overlaid a 10 cm^2 grid on each DSC image and summed all grid cells that contained > 50% dead sponge cover to get an estimate of total percent dead cover. Difference between estimates from the two methods was found to be minimal. Zone 9 Universal Transverse Mercator (UTM) coordinates and percent cover for all framegrabs were imported into R 3.5.2 (R Core Team 2018). Percent cover was log-transformed for normality when necessary (all cases except for dead cover at Farrea 2015 and Peloponnesus). The high-resolution imagery of the live cover data allowed us to test different sampling scales (i.e., minimum distance between any two sample points) by removing nearest neighbors closer than a set Euclidean distance (ranging from 1 to 25 m) using the spdep package in R (Bivand and Wong 2018). Optimal sampling scales were determined by examination of spatial structure using correlograms of Moran's I coefficient and plotted using the pgirmess package (Giradoux 2018). We chose a live cover sampling scale of 7 m for all three sites.

To determine the amount of *Desmacella* cover in the reefs, areas of the yellow, white, and mauve color morphotypes were manually delineated from live reef cover in Adobe Photoshop CS5. These areas were first measured in pixel units in ImageJ v.1.52k and then converted into area per meter-square using the 10 cm laser dots for scale. The relative abundance of *Desmacella* spp. was determined from the total percentage of live reef cover at each field site. The spatial distribution of *Desmacella* spp. was mapped and analyzed using ArcMap 10.6.1 (ESRI) and compared with the distribution of live and dead glass sponge cover interpolated by kriging.

Variography was performed with the geoR package (Ribeiro and Diggle 2001). We explored exponential, spherical, circular, and Gaussian models to fit empirical semivariograms, and the best-fitting model was chosen for each site by comparing Akaike's Information Criterion values. We used the best-fitting model for the three sites: Farrea 2015

(live cover, exponential; dead cover, spherical), Peloponnesus (live cover, spherical; dead cover, circular), and Sponge Ridge West (live cover, spherical; dead cover, circular). Ordinary kriging interpolation was conducted separately for live and dead cover in ArcMap 10.6.1. (ESRI) using model parameters from R, and interpolation maps for each site were converted to raster and added together using the Raster Calculator tool (Spatial Analyst tools). The North American Datum 1983 coordinate system was used for all mapping and spatial analyses. A Spearman rank correlation was performed to determine how live sponge cover influences the percent cover of *Desmacella* in the reefs (STATISTICA 13.3).

Specimen collections and preparation for microscopy

Specimens of the yellow ($n = 6$), white ($n = 6$), and mauve ($n = 5$) sponge morphotypes were collected opportunistically during ROV dives at each field site. Samples were collected using a suction tube or manipulator arm and placed into separate collection boxes. Samples were stored in 95% ethanol on the ship and transported to the University of Alberta for processing. Pieces of sponge tissue 1 cm × 0.5 cm were dissolved in undiluted household bleach overnight to isolate spicules. Spicules were rinsed four times in distilled water and twice with 95% ethanol. Spicule suspensions were pipetted onto glass slides and dried before mounting in DPX with a coverslip. Spicules were imaged using a Zeiss Axioskop2 Plus compound microscope with a QiCam camera using Northern Eclipse software. Spicule dimensions were measured using ImageJ v.1.52k and these dimensions were compared with published descriptions of other *Desmacella* species.

Sponge spicules were studied using scanning electron microscopy (SEM). Circular coverslips were mounted onto aluminum SEM stubs using double-sided adhesive tabs, then ethanol-spicule suspensions were pipetted onto the coverslips and left to dry for 3–5 h. The stubs were sputter coated with gold using the Nanotek SEMprep 2 sputter coater and imaged using a Zeiss Sigma 300 VP-FESEM. SEM images were processed in Corel PaintShop Pro X3.

Additional material studied included *Desmacella* spp. samples ($n = 33$) that were collected since 1976 from other regions in British Columbia waters and stored at the RBCM. These were added to our *Desmacella* species inventory list (Table 1).

DNA sequencing and phylogenetic analysis

Tissue approximately 1 cm^2 in size was cut from sponge samples ($n = 19$) and DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen, Germany) according to the manufacturer instructions. DNA concentrations (ng/μL) were evaluated using a Nanodrop 1000 spectrophotometer and amplified using the degenerate primers dgLCO1490: 5′-GGT CAA CAA ATC ATA AAG AYA TYG G-3′ and dgHCO2198: 5′-TAA ACT TCA GGG TGA CCA AAR AAY CA-3′ modified from Meyer et al. (2005). Primer dgLCO1490 was 5′ tailed with M13F sequence 5′-GTA AAA CGA CGG CCA GTG-3′ and dgHCO2198 was 5′ tailed with M13R sequence 5′-GGA AAC AGC TAT GAC CAT G-3′. The reaction mix (50 μL) contained 1X PCR buffer, 2.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.5 μM of each primer, 0.3 U Platinum Taq polymerase (Invitrogen) and 4 μL of template genomic DNA. PCR conditions were as follows: 95 °C for 2 min (95 °C for 30 s, 50 °C for 30 s, 72 °C for 60 s) × 40 cycles followed by a final elongation of 10 min at 72 °C. A 750-bp band was excised and DNA purified using the Qiagen QIAquick gel extraction column kit. Sequencing reactions used 7 μL of purified PCR product with the BigDye 3.1 kit (Applied Biosystems) and were run on an ABI 3730DNA Analyzer. Sequences were manually edited in DNASTAR. ML trees were constructed in MEGA 7.0 based on the Jukes-Cantor model with 500 bootstraps.

Two specimens (RBCM 018-00148-008 and RBCM 018-00225-001) from the RBCM were incorporated into our molecular analyses. DNA could not be extracted from other RBCM specimens as these samples were either too small or preserved for considerable amounts of time in 70% isopropanol, thus reducing the amount and quality of DNA that could be recovered.

Results

In situ observations

All three color morphotypes occurred as thin encrusting sponges. Glass sponges colonized by these encrusting sponges had a "dirty" appearance with wrinkled and/or broken edges at the lip of the osculum (Fig. 2a–c). The yellow morphotype appeared as off-white and was often associated with live and dead *H. calyx*, but examples of this sponge growing on live and dead *A. vastus* were also seen (Fig. 2a). The white morphotype was snow-white in color, often speckled with mud, and frequently found growing in association with both live and dead *H. calyx* and *A. vastus* (Fig. 2c, d). The mauve morphotype was not found in association with any living reef-forming species and was typically found growing at the base of dead reef skeleton or in patches of mud (Fig. 2b).

Spatial distribution of color morphotypes in the reefs

The yellow morphotype comprised 10.7% of the live sponge cover at Farrea 2015 and 7.2% at Sponge Ridge West, but presence of this color morph was rarely observed at the Peloponnesus site (0.3%) (Table 2). The white morphotype was also common at Farrea 2015 forming 6.4% of the live sponge cover; however, this morphotype was found in

Table 1 Inventory of *Desmacella* specimens collected off the west coast of British Columbia, Canada, from 1976 to 2017. List includes specimens from the RBCM catalogue (courtesy H.M. Reiswig) and samples collected during the scientific research cruises in October 2015 and May 2017 aboard the *CCGS John P. Tully*

Identifier	Collector	Year	Location	Depth (m)	Latitude	Longitude	Species	Sigmas
RBCM 018-00219-001	W.C. Austin	1976	Jervis Inlet, BC	40	49° 47.6′ N	124° 06.6′ W	*D. austini*	3
HMR 82-10-20.01A	H.M. Reiswig	1982	Fitzhugh Sound, BC	191	51° 24.0′ N	129° 42.0′ W	*D. austini*	3
HMR 82-10-21.1A	H.M. Reiswig	1982	Fitzhugh Sound, BC	---	51° 43.5′ N	127° 58.8′ W	*D. austini*	3
RBCM 014-00179-001	W.C. Austin; H.M. Reiswig	1982	Fitzhugh Sound, BC	30.5	51° 43.5′ N	127° 47.2′ W	*D. austini*	3
RBCM 018-00220-001	W.C. Austin	1983	Muchalaht Inlet, BC	160	49° 39.1′ N	126° 14.7′ W	*D. austini*	3
RBCM 018-00221-001	W.C. Austin	1984	Jervis Inlet, BC	264	49° 51.0′ N	123° 52.0′ W	*D. austini*	3
RBCM 018-00222-001	W.C. Austin	1985	Jervis Inlet, BC	132	50° 05.2′ N	123° 47.5′ W	*D. austini*	3
RBCM 018-00223-001	V. Bierl	1999	Hecate Strait, BC	200	52° 25.0′ N	129° 42.0′ W	*D. austini*	3
HMR 02-09-05.10	H.M. Reiswig	2002	Hecate Strait, BC	179	53° 6.0′ N	130° 29.9′ W	*D. austini*	3
HMR 02-09-05.11	H.M. Reiswig	2002	Hecate Strait, BC	179	53° 6.0′ N	130° 29.9′ W	*D. austini*	3
HMR 02-09-05.12	H.M. Reiswig	2002	Hecate Strait, BC	179	53° 6.0′ N	130° 29.9′ W	*D. austini*	3
HMR 02-09-05.16A	H.M. Reiswig	2002	Hecate Strait, BC	192	53° 7.8′ N	130° 31.1′ W	*D. austini*	3
HMR 02-09-06.11B	H.M. Reiswig	2002	Hecate Strait, BC	198	53° 8.2′ N	130° 32.1′ W	*D. austini*	3
HMR 02-09-06.15B	H.M. Reiswig	2002	Hecate Strait, BC	176	53° 10.4′ N	130° 25.6′ W	*D. austini*	3
HMR 02-09-06.15C	H.M. Reiswig	2002	Hecate Strait, BC	176	53° 10.4′ N	130° 25.6′ W	*D. austini*	3
HMR 02-09-06.16A	H.M. Reiswig	2002	Hecate Strait, BC	185	53° 10.4′ N	130° 26.4′ W	*D. austini*	3
HMR 02-09-06.17	H.M. Reiswig	2002	Hecate Strait, BC	185	53° 10.4′ N	130° 26.4′ W	*D. hyalina* sp. nov.	2
HMR 02-09-06.18	H.M. Reiswig	2002	Hecate Strait, BC	185	53° 10.4′ N	130° 26.4′ W	*D. austini*	3
HMR 02-09-06.19A	H.M. Reiswig	2002	Hecate Strait, BC	185	53° 10.4′ N	130° 26.4′ W	*D. austini*	3
HMR 02-09-06.19CA	H.M. Reiswig	2002	Hecate Strait, BC	185	53° 10.4′ N	130° 26.4′ W	*D. austini*	3
HMR 02-09-09.06A	S.P. Leys	2002	Barkley Sound, BC	157.1	48° 54.1′ N	125° 02.6′ W	*D. hyalina* sp. nov.	2
HMR 03-07-14.02	H.M. Reiswig	2003	Barkley Sound, BC	---	----------	----------	*D. austini*	3
HMR 03-07-14.06	H.M. Reiswig	2003	Barkley Sound, BC	---	----------	----------	*D. austini*	3
HMR 04-10-25.13C2	G. Schmahl	2004	Welker Seamount, AK	774	55° 03.6′ N	140° 18.9′ W	*D. austini*	3
HMR 06-01-15.07B	R. Stone	2005	Juneau, AK	160	58° 14.1′ N	138° 52.7′ W	*D. austini*	3
HMR 07-06-26.01A	J. Rose	2007	Grays Canyon, WA	160	46° 50.0′ N	124° 45.0′ W	*D. austini*	3
HMR 07-11-08.04	S. Leys	2007	Galiano Ridge, BC	---	----------	----------	*D. hyalina* sp. nov.	2
HMR 07-11-08.05A	S. Leys	2007	Galiano Ridge, BC	---	----------	----------	*D. hyalina* sp. nov.	2
RBCM 018-00224-001	S. Ensor	2007	Saanich Inlet, BC	---	48° 35.5′ N	123° 29.15′ W	*D. austini*	3
HMR 08-11-22.23A	J. Rose	2008	Learmonth Bank, BC	---	----------	----------	*D. hyalina* sp. nov.	2
RBCM 018-00148-008	N. McDaniel	2011	Howe Sound, BC	21	49° 32.0′ N	123° 17.4′ W	*D. hyalina* sp. nov.	2
RBCM 018-00225-001	N. McDaniel	2017	Howe Sound, BC	30	49° 34.7′ N	123° 16.2′ W	*D. hyalina* sp. nov.	2
RBCM 018-00226-001	N. McDaniel	2017	Howe Sound, BC	30	49° 34.7′ N	123° 16.2′ W	*D. hyalina* sp. nov.	2
RBCM 019-00113-001	L. Law	2017	Hecate Strait, BC	174.3	53° 11.6′ N	130° 28.6′ W	*D. hyalina* sp. nov.	2
RBCM 019-00113-002	L. Law	2017	Hecate Strait, BC	174.4	53° 11.6′ N	130° 28.6′ W	*D. austini*	3
RBCM 018-00114-001	L. Law	2017	Hecate Strait, BC	176	53° 11.7′ N	130° 28.3′ W	*D. austini*	3
RBCM 019-00115-001	L. Law	2017	Hecate Strait, BC	182	53° 6.3′ N	130° 29.7′ W	*D. austini*	3
RBCM 019-00115-002	L. Law	2017	Hecate Strait, BC	182	53° 6.3′ N	130° 29.7′ W	*D. hyalina* sp. nov.	2
RBCM 019-00116-001	L. Law	2017	Hecate Strait, BC	184.6	53° 6.3′ N	130° 29.6′ W	*D. hyalina* sp. nov.	2
RBCM 019-00117-001	L. Law	2017	Hecate Strait, BC	183.2	53° 6.3′ N	130° 29.5′ W	*D. hyalina* sp. nov.	2
RBCM 019-00117-002	L. Law	2017	Hecate Strait, BC	180.3	53° 6.3′ N	130° 29.5′ W	*D. hyalina* sp. nov.	2
RBCM 019-00118-001	L. Law	2017	Hecate Strait, BC	172.2	53° 11.6′ N	130° 28.5′ W	*D. austini*	3
RBCM 019-00113-003	L. Law	2017	Hecate Strait, BC	169.8	53° 11.6′ N	130° 28.6′ W	*D. hyalina* sp. nov.	2
RBCM 019-00113-004	L. Law	2017	Hecate Strait, BC	170.5	53° 11.6′ N	130° 28.6′ W	*D. austini*	3
RBCM 019-00118-002	L. Law	2017	Hecate Strait, BC	170.5	53° 11.6′ N	130° 28.5′ W	*D. austini*	3
RBCM 019-00119-001	L. Law	2017	Hecate Strait, BC	172.6	53° 11.6′ N	130° 28.3′ W	*D. hyalina* sp. nov.	2

substantially lower amounts at Peloponnesus (2.4%) and Sponge Ridge West (2.9%). The mauve morphotype was present in only a few of the reef areas we surveyed, with less than 1% of this morphotype comprising live sponge cover at each field site. The percent cover of all three morphotypes was greatest in areas where percent live and dead reef-forming glass sponge cover was high (Fig. 3a–c) and cover of these encrusting sponges was strongly correlated with the presence of live and dead glass sponges (Spearman rank correlation, $\rho = 0.702$, $p < 0.0001$).

Taxonomic analysis

Spicule types of all three color morphotypes collected from the field sites and from RBCM samples are summarized in Table 3. Specimens of the white morphotype contained slight, but distinct differences in spicules from the yellow morphotype that suggest this is a new cryptic *Desmacella* species. Two of the samples classified as the mauve morphotype have the sample spicule complement as the white morphotype and are thus considered the same species, while the other three specimens do not contain *Desmacella* spicules.

Systematic description

Class Demospongiae Sollas, 1885
Order Desmacellida Morrow & Cárdenas, 2015
Family Desmacellidae Ridley & Dendy, 1886
Genus *Desmacella* Schmidt, 1870

Desmacella hyalina sp. nov.

http://zoobank.org/4F81B9AE-1F62-46C4-86E2-8F1C800CC9D9

Type locality

Hecate Strait, British Columbia, Canada

Material examined

Holotype: RBCM 019-00119-001, near Banks Island, BC (53° 11.6′ N, 130° 28.3′ W; 172.6 m), *CCGS John P. Tully*, May 2017.

Paratypes

RBCM 019-00115-002 (53° 6.3′ N, 130° 29.7′ W; 182 m), RBCM 019-00116-001 (53° 6.3′ N, 130° 29.6′ W; 184.6 m), RBCM 019-00117-001 (53° 6.3′ N, 130° 29.5′ W; 183.2 m), RBCM 019-00113-003 (53° 11.6′ N, 130° 28.6′ W; 169.8 m), and RBCM 019-00113-001 (53° 11.6′ N, 130° 28.6′ W; 174.3 m) were collected in the northern Hecate Strait reef in May 2017 by suction sampler or manipulator arm using ROPOS. Collection information and additional specimens are listed in Table 1.

Comparative material examined

Samples HMR 02-09-06.17 (Hecate Strait, BC; 53° 10.4′ N, 130° 26.4′ W; 185 m), HMR 02-09-09.06A (Barkley Sound, BC; 48° 54.1′ N, 125° 02.6′ W; 157.1 m), HMR 07-11-08.04 (Galiano Ridge, BC; unknown coordinates and depth), HMR 07-11-08.05A (Galiano Ridge, BC; unknown coordinates and depth), and HMR 07-11-22.23A (Learmonth Bank, BC; unknown coordinates and depth) were collected from 2002 to 2008. RBCM 018-00148-008 (49° 32.0′ N, 123° 17.4′ W; 21 m), RBCM 018-00225-001 (49° 34.7′ N, 123° 16.2′ W; 30 m), and RBCM 018-00226-001 (49° 34.7′ N, 123° 16.2′ W; 30 m) were collected in Howe Sound, BC in 2017. Two of these samples (RBCM 018-00148-008 and RBCM 018-00225-001) were included in our COI analyses. DNA could not be recovered from all other samples.

External morphology (Fig. 2c, d)

Desmacella hyalina sp. nov. is an encrusting sponge with a hispid surface and non-apparent oscules. This species grows directly on live and dead *H. calyx* and *A. vastus*. Color in situ is snow-white or mauve. Color preserved in ethanol is yellow to off-white or light mauve.

Spicules (Fig. 4)

Tylostyles (185–289.6–478 × 5–6.72–10 μm; min-mean-max, length × width) are long, thin, and smooth with a straight or slightly curved form. An elliptical tyle is situated at the base of each tylostyle. Sigmas I (22–30.3–58 μm; min-mean-max, chord length) and sigmas II (8–16.3–20 μm; min-mean-max, chord length) are both terminally microspined.

Skeleton (Fig. 5)

The skeleton consists of tylostyles forming dense bundles, appearing as bouquets, with points facing outward from the glass sponge surface.

Remarks

The only other *Desmacella* species known from the northeastern Pacific Ocean is *D. austini*. *Desmacella hyalina* sp. nov. differs from *D. austini* by having two categories of sigmas, while *D. austini* has three size classes of sigmas. Other species with two sigma size categories include *Desmacella annexa* Schmidt, 1870; *Desmacella digitata* (Lévi, 1960); *Desmacella lampra* de Laubenfels, 1954; *Desmacella polysigmata* van Soest, 1984; *Desmacella pumilio* Schmidt,

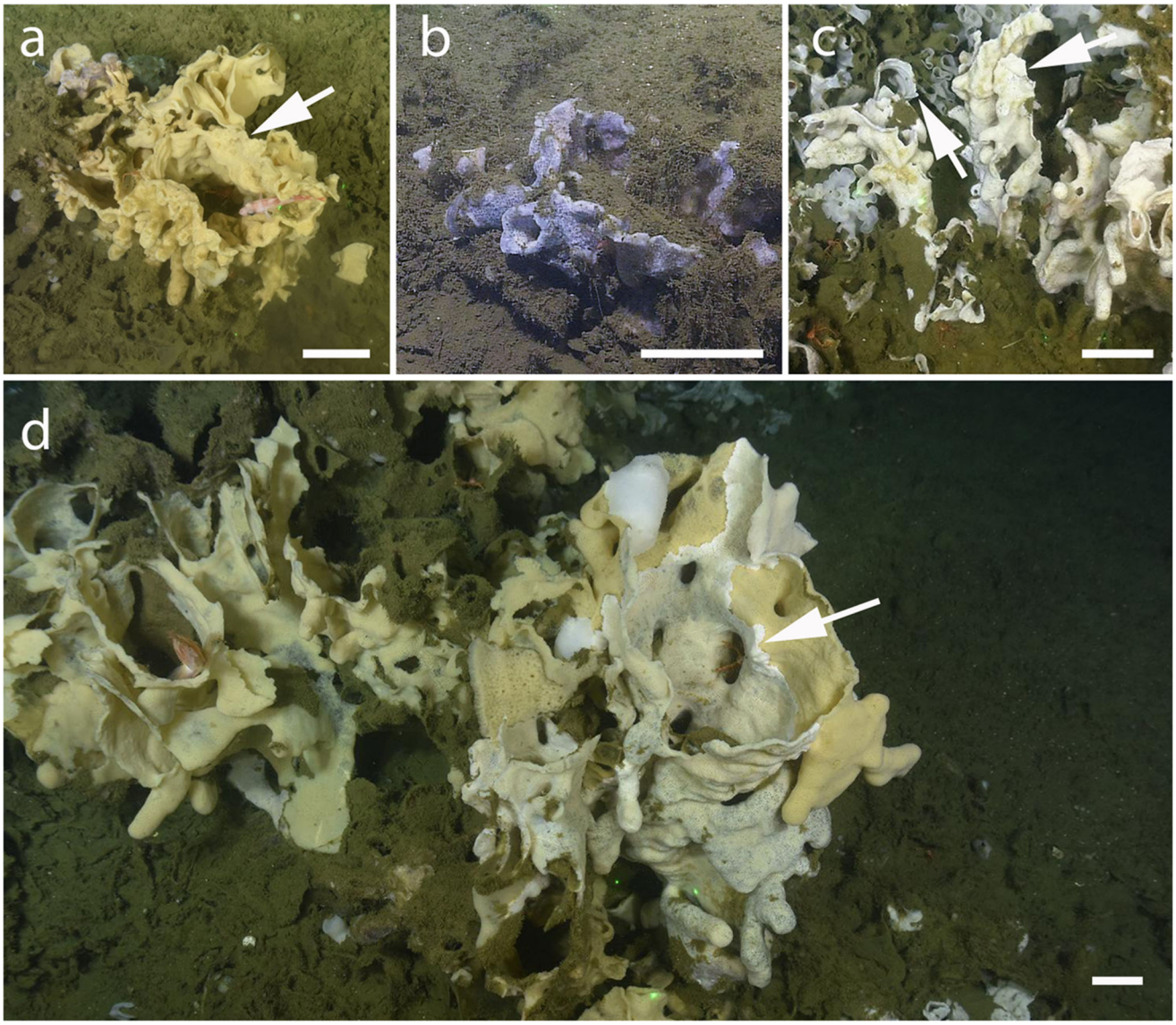

Fig. 2 Color morphotypes of encrusting sponges observed on reef structures. **a** Yellow morphotype; **b** mauve morphotype; **c** white morphotype; **d** Image showing the distinct interface between the white morphotype overgrowing live *Aphrocallistes vastus*. All arrows point at the osculum with characteristic "wrinkling" and/or broken edges at the lip where the encrusting sponge is overtaking the glass sponge. Scale bars, 10 cm

1870; and *Desmacella vicina* Schmidt, 1870; however, all these species are found in different geographic locations such as tropical, shallow (< 150 m) water environments or substantially deeper waters (472 m).

Table 2 Estimates of non-reef-forming sponge cover for each color morphotype (i.e., yellow, white, and mauve) in the HSQCS-MPA northern reef complex. Percentages in parentheses represent the proportion of area at each site covered by the yellow, white, and mauve morphotypes relative to the total live cover of reef-forming glass sponges. Reef-forming sponges include the species *Heterochone calyx*, *Aphrocallistes vastus*, and *Farrea occa*

Reef	Live sponge cover (m^2)	Area covered by morphotypes (m^2)			Total proportion of *Desmacella* (%)
		Yellow	White	Mauve	
Farrea 2015	89.2	9.5 (10.7%)	5.7 (6.4%)	0.5 (0.6%)	17.7
Peloponnesus	29.5	0.1 (0.3%)	0.7 (2.4%)	3.0×10^{-3} (0.01%)	2.7
Sponge Ridge West	90.5	6.5 (7.2%)	2.6 (2.9%)	0.1 (0.1%)	10.2

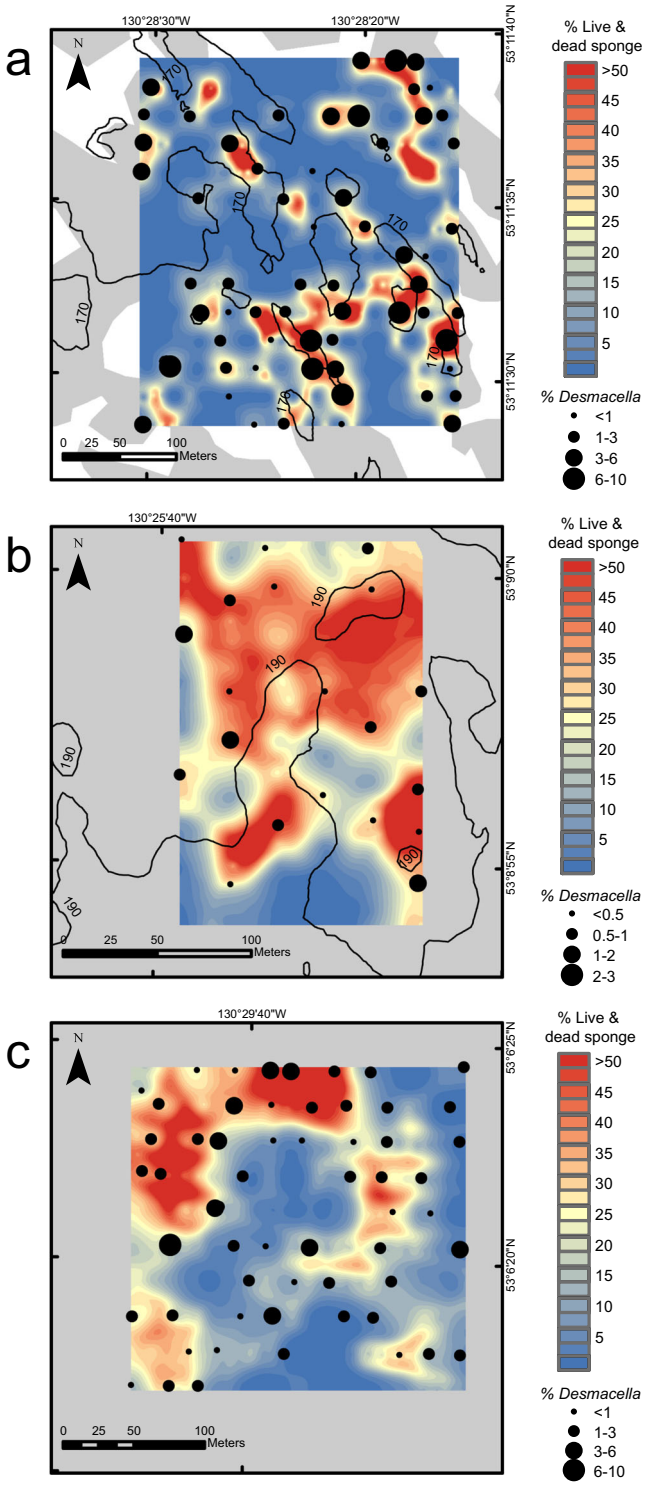

Fig. 3 Spatial distribution of the yellow, white, and mauve color morphotypes combined at each field site. The percent cover of all encrusting sponges was strongly correlated with the distribution of live and dead reef-forming glass sponges ($p < 0.0001$) at field sites: **a** Farrea 2015, **b** Peloponnesus; **c** Sponge Ridge West. Areas predicted to be reef based on multibeam mapping are shown in light gray (courtesy K.W. Conway, Natural Resources Canada)

The skeleton of the yellow morphotype match descriptions of *Desmacella austini* Lehnert, Conway, Barrie & Krautter, 2005 and is comprised of megascleres of long, thin tylostyles and microscleres of sigmas. Tylostyles were extremely abundant, straight to curved, with one end pointed and an elliptical tyle (a globular swelling) at the base ranging from 166 to 548 μm long (mean = 312.2 μm; SD = 87.4; $n = 180$) and 5–10 μm wide (mean = 7.2 μm; SD = 1.0; $n = 180$) (Fig. 6a, b). Sigmas were c-shaped and divided into three size classes. The chord length of large sigmas I ranged from 50 to 80 μm (mean = 60.8 μm; SD = 5.2; $n = 180$); medium sigmas II, 24–49 μm (mean = 36.6 μm; SD = 6.0; $n = 180$); and small sigmas III, 13–23 μm (mean = 18.6 μm; SD = 2.3; $n = 180$) (Fig. 6c–e). Microspines were present at the ends for all size classes of sigmas (Fig. 6f–h).

The other three mauve samples (not accessioned), R1995_0243, R1995_0251, and R1995_0255 (Supplementary Table 2), do not fit the description of *Desmacella* and have megascleres of long, thin styles with one end pointed and the other end blunt ranging from 160 to 578 μm long (mean = 389.3 μm; SD = 56.6; $n = 90$) and 4–9 μm wide (mean = 7.1 μm; SD = 0.8; $n = 90$) (Fig. 7a, b), and oxeas pointed at both ends were also found and ranged from 88 to 312 μm long (mean = 169.9 μm; SD = 47.5; $n = 90$) and 3–7 μm wide (mean = 4.9 μm; SD = 0.9; $n = 90$) (Fig. 7c, d). The genus of these specimens remains to be determined.

Geographical distribution

Desmacella hyalina sp. nov. is currently known only in the northeast Pacific off the coast of British Columbia, Canada. Specimens were collected from the northern reef complex of the Hecate Strait and Queen Charlotte Sound Glass Sponge Reefs Marine Protected Area at three locations: (1) 53° 11.6′ N, 130° 28.4′ W, mean depth 170 m; (2) 53° 8.9′ N, 130° 25.6′ W, mean depth 191 m; and (3) 53° 6.3′ N, 130° 29.6′ W, mean depth 178 m.

Genetic data

COI sequences were obtained for 17 samples and deposited in GenBank. Genbank accession numbers, RBCM numbers, and sample codes of the sequences used in the phylogenetic tree can be found in Table 4. Phylogenetic analyses of COI supported the distinction found in spicule complement between the yellow and white color morphotypes (Fig. 8). Species-specific groupings for the yellow, white, and mauve morphotypes had high bootstrap support (> 90%). However, one mauve sample (RBCM 019-00117-002) was grouped with the white samples and contained spicule types characteristic of the white morphotype (i.e., tylostyles and sigmas of two size classes). DNA extracted from two mauve samples (R1989_0112 and R1995_0251) was of low quality and could

Table 3 Data comparing the spicule types and sizes between yellow (*D. austini*), white (*Desmacella hyalina* sp. nov.), and mauve color morphotypes and two RBCM specimens (RBCM 018-00148-008 and RBCM 018-00225-001) courtesy of H.M. Reiswig. All specimens were collected using the ROV ROPOS. Type 1 mauve specimens contained spicule complement matching *Desmacella hyalina* sp. nov. (white). Type 2 mauve specimens contained spicules of styles and oxeas, typically not found in the genus *Desmacella*. The RBCM 018-00148-008 and RBCM 018-00225-001 samples also contained spicule complements matching that of *Desmacella hyalina* sp. nov. (white). Lehnert et al.'s (2005) spicule description of *D. austini* is provided for reference. Values are in micrometers (μm), expressed as follows: min-max or min-mean-max. All values for sigma types represent chord lengths

Specimen	Tylostyles I		Other spicules		Sigmas I	Sigmas II	Sigmas III
	Length	Width	Length	Width			
D. austini[(1)]	170–495	6–10	None	None	55–65	26–42	15–20
Yellow ($n = 6$)	166–312.2–548	5–7.2–10	None	None	50–60.8–80	24–36.6–49	13–18.6–23
White ($n = 6$)	185–289.6–478	5–6.7–10	None	None	22–30.3–58	8–16.3–20	None
Mauve type 1 ($n = 2$)	220–310.5–528	5–7.1–10	None	None	24–30.9–40	8–17.6-20	None
Mauve type 2 ($n = 3$)	None	None	Styles: 160–389.3–578; oxeas: 88–169.9–312	4–7.1–9; 3–4.9–7	None	None	None
RBCM 018-00148-008	133–259.4–470	3–6.7–13	None	None	23–27.4–33	13–16.5–21	None
RBCM 018–00225–001	195–319.7–495	5–8.6–13	None	None	26–32.4–44	13–18.1–25	None

[(1)] Lehnert et al. (2005)

not be amplified for phylogenetic analysis. The other two mauve samples, R1995_0243 and R1995_0255, grouped separately from the yellow and white morphotypes with high bootstrap support (100%) and contained styles and oxeas that are typically not found in *Desmacella* specimens. The RBCM samples, RBCM 018-00148-008 and RBCM 018-00225-001, were originally identified by H.M. Reiswig as a possible new *Desmacella* species and contained tylostyles and two sizes of sigmas characteristic of the white morphotype. Analyses of COI sequences from these RBCM samples grouped them with samples of the white form with high bootstrap support (100%). Our analyses of spicule complement and COI sequences strongly suggest the white morphotype is a new cryptic *Desmacella* species; however, *Desmacella hyalina* sp. nov. can occasionally exhibit a mauve coloration in situ, but possible explanations for this remain unclear.

Etymology

The name is derived from the word hyalinus, borrowed from the Ancient Greek word *huálinos* meaning "of crystal or glass." This species name refers to its growth on glass sponges.

Discussion

Encrusting sponges exhibiting three color morphotypes (yellow, white, and mauve) were identified using spicule complement and molecular analyses. The yellow and white morphotypes were affirmed to be *D. austini* and *Desmacella hyalina* sp. nov., respectively. Our findings were further supported with analyses of sponge samples previously collected since 1976 from other regions in British Columbia waters. Specimens of the mauve morphotype can be assigned to a possible third species not in the genus *Desmacella*, while a few of the mauve specimens contained spicule types consistent with those found in *Desmacella hyalina* sp. nov. These discrepancies remain unresolved and should be considered in future studies. *Desmacella* spp. comprised a surprisingly high amount of live reef cover (nearly 20% at one site) and was found growing in close association with live and dead glass sponge. Here we discuss possible reasons for distinct patterns of *Desmacella* growth and explore factors behind the different color morphotypes that exist.

Desmacella spp. distribution and abundance

Sponge reefs form multistoried frameworks that provide three-dimensional habitat for recruiting sponge epibionts. Past studies have shown the remains of dead hexactinellid sponges can host higher levels of sponge-sponge associations than surrounding featureless environments (Barthel and Gutt 1992). In the Weddell Sea, Antarctica, large mats comprised mainly of hexactinellid spicules contained much higher diversities of sponge epibionts than on neighboring muddy substrate (Barthel and Gutt 1992). Likewise, our study found sponge reef skeletons provided significant recruitment sites for *Desmacella* species. Live and dead *H. calyx* and *A. vastus* form massive biogenic structures in the deep sea, and we observed the greatest abundance of *Desmacella* (10–20% for *D. austini* and *Desmacella hyalina* sp. nov. combined) on glass sponge skeletons. In contrast, the mauve morphotype made up only a small fraction (< 1%) of live reef cover and was

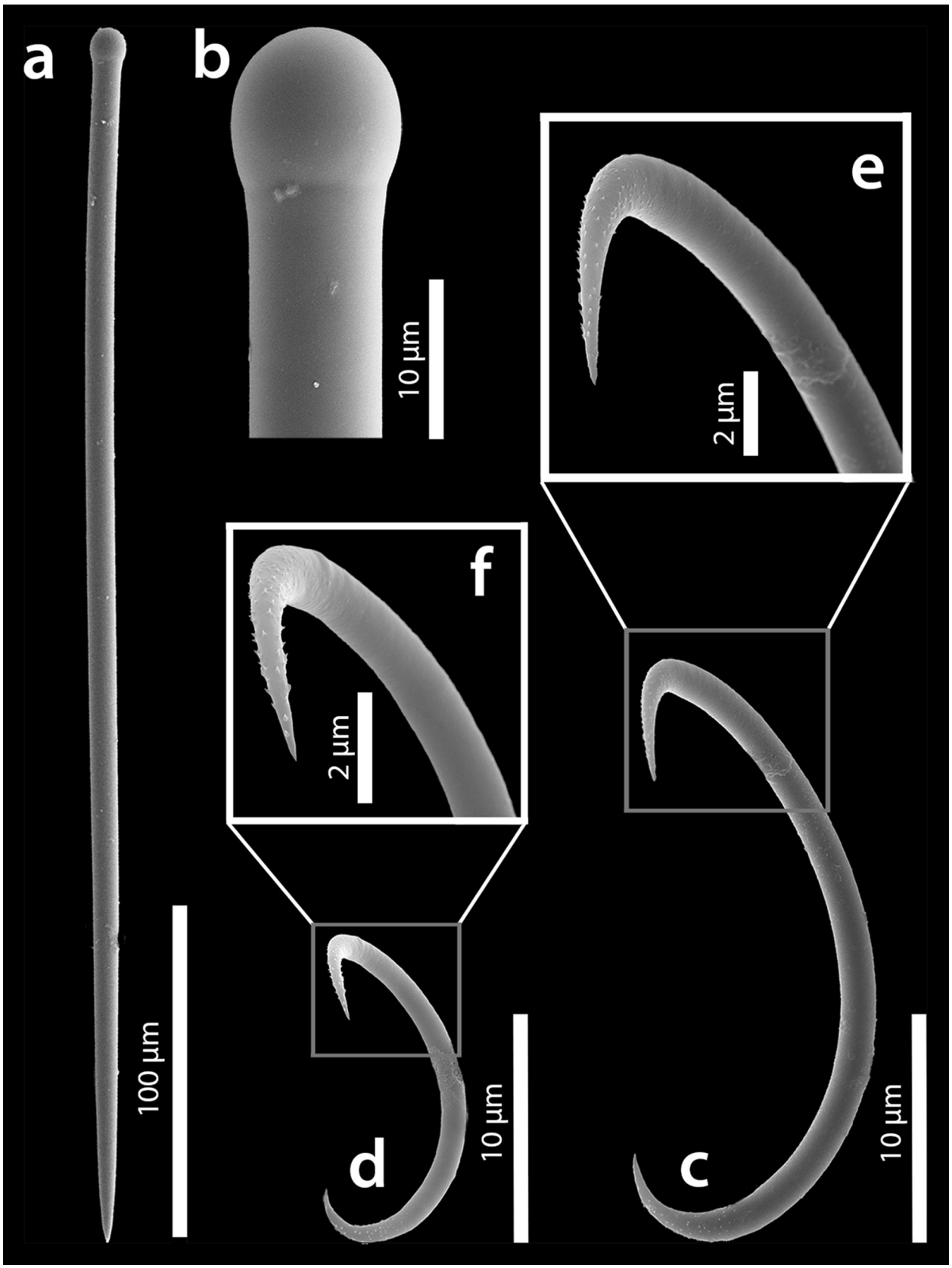

Fig. 4 SEM images of spicule types of *Desmacella hyalina* sp. nov., the white morphotype. **a** Full length tylostyle; **b** tylostyle base; **c** sigma I; **d** sigma II; **e** details of sigma I microspines; **f** details of sigma II microspines

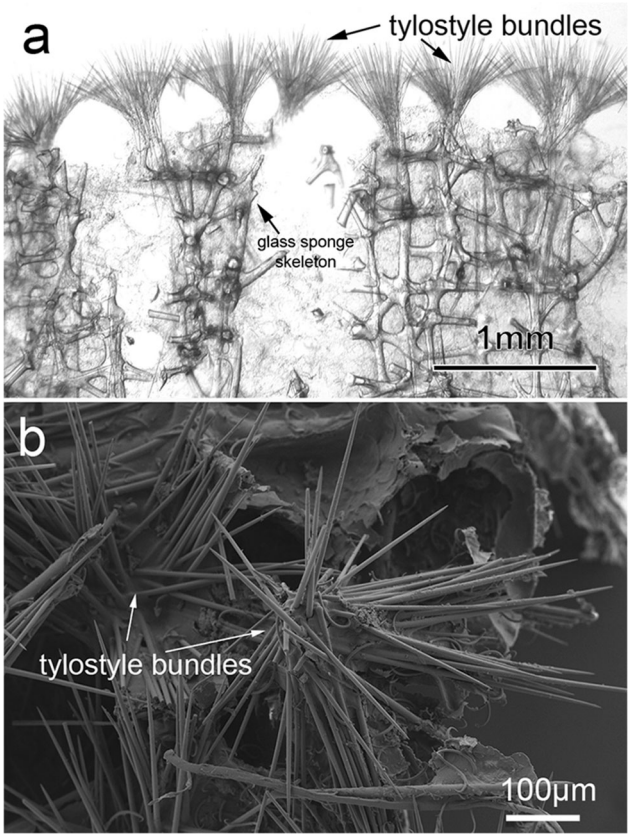

Fig. 5 *Desmacella hyalina* sp. nov. on reef-forming glass sponges. **a** Cross section of *Desmacella hyalina* sp. nov. tylostyles forming tight bundles on the surface of glass sponge skeleton (image courtesy of H.M. Reiswig); **b** Scanning electron microscopy image of *Desmacella* tylostyle bundles with points facing outwards to form bouquets. C-shaped sigmas are shown embedded in *Desmacella* tissue

found primarily growing on the seafloor in muddy substrate. Interestingly, in ROV images, we did not observe *Desmacella* growth on *F. occa* skeletons, which instead typically hosted a sponge epibiont with "finger-like" projections that remains to be identified (Law, L., pers. obs.). Our observations differ from those of Guillas et al. (2019) who found 11 distinct individuals of *D. austini* growing on *F. occa* in the HSQCS-MPA. This discrepancy can be explained by the incomparable methodologies which quantified *Desmacella* growth at different spatial resolutions. Guillas et al. (2019) measured the presence and absence of individual *Desmacella* specimens based on samples found on the underside of individual specimens collected by ROV, whereas we quantified the proportion of *Desmacella* growth relative to live and dead sponge cover in ROV imagery.

Desmacella may use reef structures to reach heights outside of the benthic boundary layer, where there are higher rates of water flow that offer greater access to food. Similar interactions have been observed in other sponges such as *Amphimedon compressa* Duchassaing de Fonbressin & Michelotti, 1864 and *Iotrochota birotulata* (Higgin, 1877), which are specifically associated with the upper portion of octocoral skeletons (McLean and Lasker 2013). These sponges were thought to use the octocoral for support and had higher growth rates when they were 60 cm above the seafloor, compared with 5 cm above (McLean and Lasker 2013).

The functional role of reef skeleton is not only significant for sponge epibionts, it is also important substrate for juvenile glass sponge recruits. The siliceous skeletons left behind by dead glass sponges serve an ecological role comparable with that of nurse logs in an old-growth forest. Nurse logs in temperate forest ecosystems are especially important for the recruitment of seedlings, which in turn initiates forest regeneration and succession (Sanchez et al. 2009). Kahn et al. (2016) found higher densities of juvenile sponges in the SoG reefs near adult sponges and dead glass sponge skeletons than in nearby mud patches. Since both *Desmacella* spp. and juvenile reef sponges grow on dead reef skeleton, it is likely that they compete for settling space.

Although it remains uncertain whether reef sponges experience competitive or beneficial interactions with sponge epibionts, the abundance and composition of *Desmacella* in the reefs could serve as a management tool for monitoring changes in reef ecosystem dynamics. For instance, coral reef ecosystems undergoing stress by global warming and ocean acidification have shifted to sponge-dominated communities (Bell et al. 2013). Perhaps observations of higher sponge epibiont abundances in the reefs might indicate a successional transition brought on by disturbance regimes; however, such interpretations should be made with caution since no studies have assessed sponge succession in glass sponge habitats.

Interactions between sponge-sponge associates

The interaction between *Desmacella* species and reef-forming glass sponges could have implications for reef growth and recruitment. We saw a noticeable interface and distinct color change where *D. austini* and *Desmacella hyalina* sp. nov. had encrusted live and dead *H. calyx* and *A. vastus*. Glass sponges overtaken by *Desmacella* were "wrinkled" with broken tissue and skeleton at the lip of their oscula. Past studies have proposed *D. austini* competes for and/or limits the availability of growing space for the main reef-forming glass sponge species (Lehnert et al. 2005). Since glass sponge larvae require hard substrata for settlement (Kahn et al. 2016), and considering that dead and live glass sponges are the most accessible hard substrata within a sponge reef, this competition could severely limit reef expansion. Particularly in disturbed ecosystems, species with a capacity for rapid colonization and high growth rates can outcompete other benthic organisms (González-Rivero et al. 2011). Many sponge reefs in the HSQCS-MPA have been damaged due to bottom trawling (Conway 1999; Jamieson and Chew 2002; Cook et al. 2008) and where *Desmacella* growth is prevalent, the ability of juvenile glass

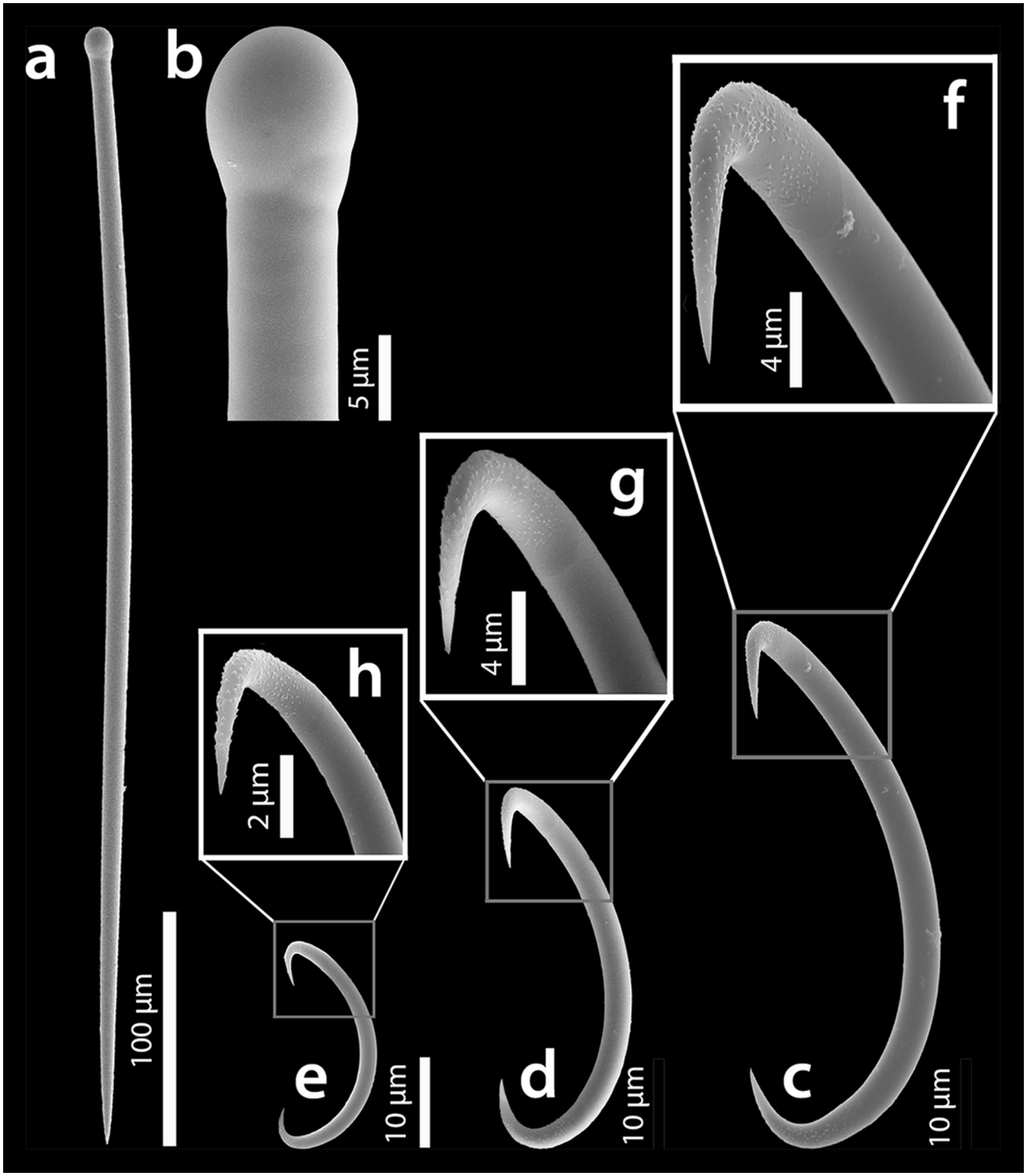

Fig. 6 SEM images of spicule types of *Desmacella austini*, the yellow morphotype. **a** Full length tylostyle; **b** tylostyle base; **c** sigma I; **d** sigma II; **e** sigma III; **f** details of sigma I microspines; **g** details of sigma II microspines; **h** details of sigma III microspines

sponges to re-colonize damaged reef areas may be hindered. More studies are warranted to measure the colonization rates of *Desmacella* and compare *Desmacella* growth rates in disturbed and undisturbed glass sponge habitats.

Although space is commonly a limiting resource among sessile benthic organisms, mutualism between sponge associates is known to exist in sponge-dominated ecosystems. A body of evidence suggests sponges receive

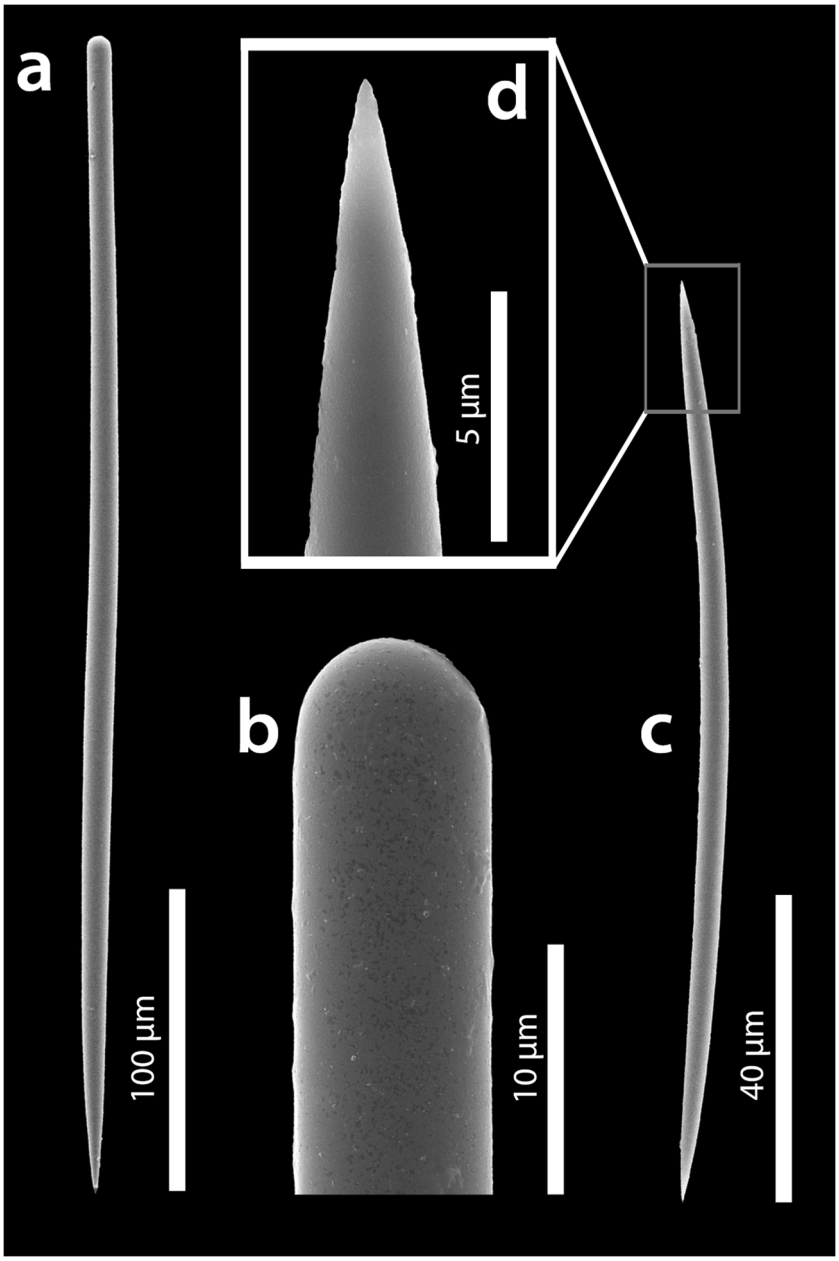

Fig. 7 SEM images of spicule types in the mauve morphotype. **a** Full length style; **b** style base; **c** oxea; **d** details of smooth oxea ends

benefits from the colonization of predator-deterring encrusting sponges (Pawlik et al. 1995; Wilcox et al. 2002; Wulff 2008). Numerous predators including sea stars (Dayton et al. 1974), nudibranchs (Chu and Leys 2012), and a variety of fishes (Randall and Hartman 1968), consume sponges. In the Florida Keys seagrass meadows, Wilcox (2002) studied the overgrowth of *Geodia* sp. Lamarck, 1815 (0.075–0.91 individuals per m^2) by a species of *Haliclona* Grant, 1841, a sponge genus thought to be chemically defended with toxic metabolites. Wulff (2008) also documented collaborative sponge associations in Belize, where sea star predation on *Lissodendoryx colombiensis* Zea & van Soest, 1986 was significantly reduced for individuals overgrown with unpalatable seagrass sponges. The growth of *Desmacella* on reef-forming glass sponges might confer benefits to both participating sponges (i.e., defense from predators for reef sponges and growing space for *Desmacella*), but whether a species of *Desmacella* produces chemical deterrent compounds remains a compelling topic for future assessment.

Overgrowth and many other forms of intimate sponge-sponge associations have been reported from around the world (Rützler 1970; Wilcox et al. 2002). One seemingly facultative and symbiotic sponge association was described in the Adriatic Sea and Florida Keys (Rützler 1970; Wilcox et al.

Table 4 Genbank accession numbers for sequences obtained using degenerate Folmer fragment primers (dgLCO1490 and dgHCO2198) of the COI gene and sample numbers for specimens deposited at the Royal British Columbia Museum

Species	Color morph	Sample	Accession no.
Desmacella austini	Yellow	RBCM 019-00113-002	MN417058
	Yellow	RBCM 018-00114-001	MN417061
	Yellow	RBCM 019-00115-001	MN417071
	Yellow	RBCM 019-00118-001	MN417065
	Yellow	RBCM 019-00113-004	MN417067
	Yellow	RBCM 019-00118-002	MN417059
Desmacella hyalina sp. nov.	White	RBCM 018-00148-008	MN417057
	White	RBCM 018-00225-001	MN417069
	White	RBCM 019-00113-001	MN417060
	White	RBCM 019-00115-002	MN417062
	White	RBCM 019-00116-001	MN417072
	White	RBCM 019-00117-001	MN417063
	Mauve	RBCM 019-00117-002	MN417064
	White	RBCM 019-00113-003	MN417066
	White	RBCM 019-00119-001	MN417068
Unknown	Mauve	R1995_0243	MN417073
	Mauve	R1995_0255	MN417070

2002), where several sponges were capable of surviving while being fully overgrown with other sponge species in a relationship referred to as epizoism. The most fascinating feature of such sponge-sponge symbioses is the ability of the internal sponge to maintain its feeding despite being fully covered by an external sponge. Most sponges feed by pumping large volumes of water through their body wall and any impediment to water flow would presumably impact sponge health negatively (Reiswig 1971). However, in the Florida Keys, microscopic sections of the interface between two adhering sponges in an epizoic relationship revealed the presence of a small interstitial space, which might permit high enough water flow for the internal sponge to continue feeding (Wilcox et al. 2002). Although *Desmacella* growth was primarily observed on glass sponge skeletons in this study, *D. austini* has been described in past studies to grow directly on living glass sponges (Lehnert et al. 2005). It is still unclear whether growth of *Desmacella* in the reefs is a symbiotic or parasitic association, but further ultrastructure examinations at the interface between glass sponge and *Desmacella* may reveal a unique adaptation for overgrowth.

Cryptic species diversity of *Desmacella hyalina* sp. nov.

Both spicule morphology and COI sequence analyses confirmed that the yellow and white morphotypes were *D. austini* and *Desmacella hyalina* sp. nov., respectively. Tylostyles were comparable in both *D. austini* and *Desmacella hyalina* sp. nov. and did not serve as a diagnostic tool for separating the species. The key feature that differentiated *Desmacella hyalina* sp. nov. was the presence of only two size classes of sigmas rather than the three found in *D. austini*. While several other species of *Desmacella* have two size categories of sigmas (Table 5), these species are generally found in shallow (< 150 m) waters in the tropics, and thus it is unlikely from a biogeographical standpoint that they are conspecific with *Desmacella hyalina* sp. nov. from our deep-water sites. Another deep-water *Desmacella* species containing two sigma

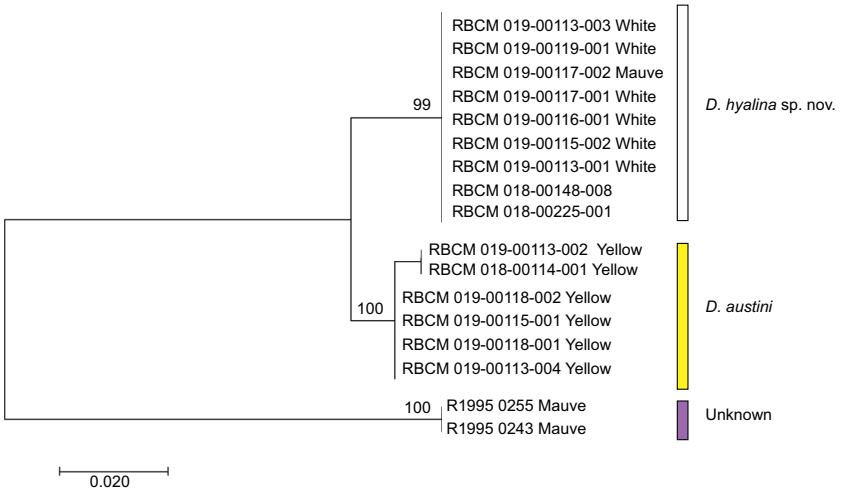

Fig. 8 Phylogenetic analysis of sponge COI Folmer fragments. Samples of the white (*Desmacella hyalina* sp. nov.) ($n = 8$), yellow (*D. austini*) ($n = 6$), and mauve ($n = 3$) color morphotypes were collected using the ROV ROPOS in the HSQCS-MPA northern reef complex. Samples RBCM 018-00148-008 and RBCM 018-00225-001 were obtained from the Royal British Columbia Museum in Victoria, BC (courtesy H.M. Reiswig). The maximum likelihood tree was based on the Jukes-Cantor model using MEGA v. 7.0. Values at each node indicate bootstrap support generated from 500 replicates

Table 5 Comparative spicule morphology for species of *Desmacella* Schmidt, 1870. Values are in micrometers (μm), expressed as minimum-maximum or minimum-mean-maximum; length × width from sources listed below as well as Lehnert et al. (2005), Cavalcanti et al. (2015), Li (1986), and the World Porifera Database (2020)

Species	Type locality/depth (m)	Tylostyles I	Tylostyles II	Sigmas I	Sigmas II	Sigmas III	Other spicules
Desmacella hyalina sp. nov.	Northeastern Pacific Ocean/150-250	185–289.6–478 × 5–6.7–10	None	22–30.2–58	8–16.3–20	None	None
D. alba (Wilson, 1904)	Galapagos, Kerguelen, Philippines/195-320	216–1275 × 6.5–36	None	18.7–137 × 2–6.4	None	None	None
D. ambigua Bergquist & Fromont, 1988	New Zealand/intertidal	390–530 × 10–13	280–360 × 7.5–10	None	None	None	Rhaphides, 113-145; tylostyles, 160-250 × 5-9
D. annexa Schmidt, 1870	Florida/350-357	Present, size not given	None	14–100+	None	None	Thin oxeas, size not given
D. arenifibrosa Hentschel, 1911	Australia/14-18	160–344 × 3–6 (styles and subtylostyles)	None	None	None	None	Rhaphides, 304-342; toxa, 21-26
D. austini Lehnert, Conway, Barrie & Krautter, 2005	Northeastern Pacific Ocean/160-205	170–495 × 6–10	None	55–65	26-42	15-20	Rhaphides, 20-30 (sometimes missing)
D. democratica (Sollas, 1902)	Sunda Shelf/not recorded	180–560 × 2.5–6	None	10–80 × 3	None	None	None
D. dendyi de Laubenfels, 1936	New Zealand/not recorded	140–630 × 6–12	None	10–44	None	None	None
D. digitata (Lévi, 1960)	Sahelian Upwelling/25-30	180–270 × 1–2	None	22–26	14-18	None	None
D. grimaldii (Topsent, 1890)	Azores, Canaries, Madeira/927	390–1900 × 8–30	None	28–45	None	None	None
D. informis (Stephens, 1916)	Ireland/457-1024	180–1300 × 8–27	None	26–45	None	None	None
D. infundibuliformis (Vosmaer, 1885)	Arctic Ocean/228.6	250 × 500	None	25	None	None	None
D. inornata (Bowerbank, 1866)	North Sea/100-270	190–1000 × 6–18	None	20–45	None	None	None
D. ithystela Hooper, 1984	Australia/40	135–222 × 4–10	100-164 × 1-4	12–20 × 0.5–2	29-55 × 2.5-4	96-192 × 5-10	None
D. jania Verrill, 1907	Bermuda, Caribbean Sea, Mexico/not recorded	220–250 (styles to tylostyles)	None	37–40	None	None	None
D. koltuni Göcke & Janussen, 2013	Weddell Sea/602.1	810–1030–1175 × 20–28–32.5 (styles)	370-428-500 × 8.75-11-12.5 (styles)	30–34–37.5 × 16.25–18–20	None	None	S-shaped sigmas (rare), size not given
D. lampra de Laubenfels, 1954	East Caroline Islands/4	250 × 2.5	None	30–33	13	None	None
D. meliorata Wiedenmayer, 1977	Bahamas, Caribbean Sea/not recorded	210–230 × 3.5–4.5	None	37 × 2 (rare)	None	None	None
D. microsigma (Lévi, 1964)	Philippines/not recorded	500–1000 × 15–25	None	11–15 × 2	None	None	None

Table 5 (continued)

Species	Type locality/depth (m)	Tylostyles I	Tylostyles II	Sigmas I	Sigmas II	Sigmas III	Other spicules
D. microsigmata Cavalcanti, Santos & Pinheiro, 2015	Northeastern Brazil/157	177–286.3-425 × 2–3.9–7	None	12–14.6–19	None	None	None
D. peachi sensu Ferrer-Hernández, 1914	Spain, South European Atlantic Shelf/not recorded	Present, long and sinuous, size not given	None	None	None	None	Rhaphides, size not given
D. polysigmata van Soest, 1984	Belize, Caribbean Sea/100	513–575.4–635 × 10–15.2–19 (styles to strongyles)	None	30–37.3–42	10–11.6–15	None	None
D. pumilio Schmidt, 1870	Florida, Caribbean Sea, Greater Antilles, Gulf of Mexico/98.7	320–1400 × 9–17	None	30–46	12–27	None	None
D. suberea (Schmidt, 1870)	Atlantic, Portugal/not recorded	mainly oxeas and styles, tylostyles present, size not given	None	612.8	None	None	None
D. suberitoides (Burton, 1932)	Tristan Gough, South Atlantic/80-140	1000 × 18 (choanosomal)	600 × 12 (ectosomal)	28	None	None	None
D. topsenti (Burton, 1930)	Azores/not recorded	250–730 × 5–10	None	43	None	None	None
D. toxophora Lévi, 1993	New Caledonia/540-600	300–600 × 10–12	None	None	None	None	Toxa, 90–140
D. tylostrongyla (Li, 1986)	Hong Kong/not recorded	199–286 × 4–6 (smooth subtylostyle)	185-210 × 5-7 (subtylostrongyles)	34-42 × 2-3	None	None	None
D. tylovariabilis Cavalcanti, Santos, Pinheiro, 2015	Eastern Brazil/1130	315–616–1050 × 6–11–16	None	25–34.2-48	None	None	None
D. vagabunda Schmidt, 1870	Florida/30-44 m	600 long	None	14–over 100	None	None	None
D. vestibularis (Wilson, 1904)	Galapagos, Pacific, Antarctica, Namibia, Philippines/16-97	240–630 × 8–16	None	12–36	None	None	None
D. vicina Schmidt, 1870	Florida/not recorded	600 × 12	None	36	12	None	None

size categories is *D. vicina* Schmidt, 1870, but this species is found in substantially deeper water (472 m) and has tylostyles that are much longer and wider (600 × 12 μm).

Lehnert et al. (2005) described *D. austini* as having two dominant color morphotypes: yellow and mauve. We found one mauve sample (RBCM 019-00117-002) with spicules and COI sequence matching that of *Desmacella hyalina* sp. nov. The range of color morphotypes might reflect other factors such as predator deterrence, environmental changes, and the presence of symbiotic microorganisms affecting sponge color (Palumbi 1984; Pawlik et al. 1995; Thacker and Starnes 2003; Reveillaud et al. 2010). All other mauve samples (R1995_0243, R1995_0251, and R1995_0255) lacked tylostyles and instead contained styles and oxeas, and clearly grouped apart from *Desmacella hyalina* sp. nov. and *D. austini* in molecular analyses. COI sequences from mauve morphotypes were compared with those in the GenBank database using the BLAST search program (http://blast.ncbi.nlm.nih.gov/) and were found to group closest to sponges in the family Suberitidae; however, gene similarities were low at 94%. The mauve morphotype may be a successional species growing on *Desmacella*; however, the only evidence of succession described by Lehnert et al. (2005) was by the species *Topsentia disparilis* (Lambe, 1893). Mauve samples are not representative of *T. disparilis* given this species consists only of oxeas, whereas mauve samples in this study contained oxeas and styles.

Various theories have been postulated to explain why cryptic species are observed in an ecosystem. One theory suggests cryptic speciation is an evolutionary adaptation for species occurring in severe environmental extremes, including deep-sea environments (Bickford et al. 2007). "Extremophiles" are expected to converge in physical characteristics given there is a limited number of ways an organism can adapt to harsh conditions. Although glass sponge reefs occur in deeper waters, they are not considered "extreme" habitats; however, reefs are limited to specific environmental conditions including low sedimentation rates, high silica concentrations, low light levels, and water temperatures usually 10 °C or less (Leys et al. 2004). These conditions may limit variations in morphology for *Desmacella* species, and perhaps the high specificity of *Desmacella* growth on glass sponges also limits morphological changes in the genus.

Implications for conservation

There are several reasons that underscore the importance of focusing on sponge epibionts in sponge reef studies, but one of the most important reasons is for conservation management. Glass sponges are slow-growing (1 to 3 cm year^{-1}) (Leys and Lauzon 1998; Austin et al. 2007) and long-lived species with siliceous skeletons that make them vulnerable to physical damage. Over the last decade, impacts of bottom trawling have been well documented in sponge reefs, which prompted calls for their protection (Conway 1999; Jamieson and Chew 2002; Cook et al. 2008). To date, the HSQCS-MPA is the only large-scale marine protected area for glass sponge habitat, with the exception of a few small marine refuges (total 32.6 km^2) in the SoG, recently established in 2019.

MPAs are a widely prescribed strategy for protecting marine biodiversity, but can often be implemented without prior knowledge of the diversity of species being protected (Agardy et al. 2003; Chape et al. 2005; Heck et al. 2012). The success of MPAs is commonly measured through effectiveness evaluations, but programs designed to monitor sponge reefs can miss changes if knowledge of biodiversity is lacking, particularly when cryptic sponge species exist. Therefore, accurate and comprehensive inventories of baseline biodiversity are essential for the adaptive management and long-term monitoring of sponge reef protected areas.

This study is the first to describe sponge epibiont relationships in glass sponge habitat since Lehnert et al. (2005) and Kahn et al. (2016). Considering we sampled only three areas of the northern reef of the HSQCS-MPA, there are likely to be more occurrences of these species in other reef areas as well as many other sponge epibionts remaining to be discovered and quantified. Given sponge epibiont communities can have major influence on reef function, recruitment, and overall ecosystem health, we suggest future ecological assessments of glass sponge habitat focus additional surveying efforts on non-reef-forming sponges.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

Field studies and sampling Sampling was carried out with collection permits XR 197, 237, 228, 230, and 164 from 2012 to 2018 to S.P.L.

Data availability The sequence data generated during this analysis have been deposited in GenBank and are listed in Table 5 and are available at the University of Alberta Education and Research Archive (ERA): doi.org/10.7939/r3-awh0-7967. Samples of specimens have been deposited with the Royal British Columbia Museum. Accession numbers for DNA and samples are provided in Table 5 and are available at the University of Alberta Education and Research Archive: doi.org/10.7939/r3-awh0-7967.

Author contributions L.K.L. and S.P.L. conceived and designed the research. B.S.O. and N.M. collected additional specimens; H.M.R. carried out spicule analysis. K.C.G. conducted spatial analysis. A.S.K. assisted with field collections. C.D. carried out gene analysis and data management. L.K.L. and S.P.L. wrote the manuscript. All authors read and approved the manuscript.

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