Description of a stauromedusa commonly seen on the Pacific Coast of the United States and Canada, *Haliclystus sanjuanensis* new species (Cnidaria: Staurozoa) (#85426)

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Description of a stauromedusa commonly seen on the Pacific Coast of the United States and Canada, *Haliclystus sanjuanensis* new species (Cnidaria: Staurozoa)

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Haliclystus "*sanjuanensis*" *nomem nudum* is the most common staurozoan on the west coast of the United States and Canada. This species was described in an unpublished M.S. Thesis by Gellermann (1926) and although that name has been in use nearly continuously since that time, no published description exists. Furthermore, the most popular operative name for this species has wandered over several related species names over time, leaving much confusion in the literature. We provide here a detailed description and synonymy of *Haliclystus sanjuanensis* n. sp., whose distribution is verified from Unalaska Island in the Aleutians (53.4° N, 166.8° W), in the northwest, to Santa Barbara County, California, just north of Point Conception (34.5° N), in the south. *Haliclystus sanjuanensis* n. sp. is compared with the twelve other described species of *Haliclystus* and illustrations of both macroscopic and microscopic anatomy are provided. *Haliclystus sanjuanensis* n. sp. is unique among all species of *Haliclystus* in the arrangement of the bright-white nematocysts spots in its calyx and the pattern of dark stripes running the length of the stalk and up the outside of the calyx.

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ABSTRACT

Haliclystus "*sanjuanensis*" *nomem nudum* is the most common staurozoan on the west coast of the United States and Canada. This species was described in an unpublished M.S. Thesis by Gellermann (1926) and although that name has been in use nearly continuously since that time, no published

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Keywords: Stauromedusae, Haliclystidae, *H. antarcticus*, *H. auricula*, *H. stejnegeri*, *H. octoradiatus*, stalked jellyfish, taxonomy, diversity.

INTRODUCTION

Staurozoa is a cnidarian class with about 50 valid species (Miranda *et al*. 2018). They are a rare group of marine animals, which are generally found attached to algae or rocks in intertidal pools or in the shallow subtidal (Miranda *et al*. 2018), occasionally in great numbers. *Haliclystus* James-Clark, 1863 is currently the most diverse genus of the class, with 12 valid species and one additional species assigned as a *nomen nudum* (i.e., a Latin term referring to a species name that was not described in conformance with the International Code of Zoological Nomenclature; ICZN, 1999), *Haliclystus “sanjuanensis”* (see Miranda *et al*. 2018).

The reader will discover that this little animal has been known by naturalists and scientists since at least the 1920s and has appeared in most guidebooks to the NE Pacific coastal fauna for the last nearly one hundred years. The synonymy that we present here for this species is both impressively long and indicative of the confusion over what to call this stalked jellyfish that has persisted nearly as long as it has been known.

This animal was first described in an unpublished Master's Thesis by Gellermann (1926), a student at the University of Washington Friday Harbor Laboratories in Friday Harbor, Washington, USA. That species name was subsequently used by other visitors to the Friday Harbor Laboratories including Guberlet (1936, 1949) and Hyman (1940a, b) as if it had been formally described, sneaking its way into the literature. In fact, Hyman (1940b) has sometimes been indicated as the author/descriptor of *H. "sanjuanensis"* (e.g., Kramp 1961; Hirano 1997; Collins & Daly 2005), although Hyman was apparently unaware of the necessity to formally describe *H. "sanjuanensis"* and her work did not address the requirements for species descriptions (e.g., a complete description and the designation of a type, see also ICZN, 1999, Article 13).

At some point in the literature, *H. "sanjuanensis"* was synonymized with *Haliclystus auricula* James-Clark, 1863, increasing the misunderstanding. After morphological considerations, Gwilliam (1956) synonymized *H. "sanjuanensis"* (which he had studied in False Bay on San Juan Island, Washington, USA) with *H. auricula* in his unpublished Ph.D. dissertation. Gwilliam never published his taxonomic conclusions, but he used the same identification in an article derived from that dissertation on the neuromuscular physiology (Gwilliam 1960) of *H. "sanjuanensis"* (as *H. auricula*) collected on San Juan Island, Washington. Kramp (1961) followed Gwilliam's conclusions and included *H. "sanjuanensis"*, mentioned by Hyman (1940b), in the synonym list of *H. auricula*, and that species name was also selected for the much-used keys for identification of Pacific Northwest invertebrates by Kozloff (1974).

Meanwhile, on another front, many authors misidentified specimens of *H. "sanjuanensis"* collected between British Columbia (Canada) and California (USA) as *Haliclystus stejnegeri* Kishinouye, 1899 (e.g., Ricketts *et al.* 1968; Otto 1976, 1978; and a number of guidebooks written for the Pacific coast of mainland USA from the 1920s into the 1960s, see synonymies below), perhaps based on stauromedusae (correctly?) identified as *H. stejnegeri* by Bigelow (1920) from 2–3 fathoms deep at Port Clarence, Alaska (USA, near the Bering Strait).

Contributing to this chaotic scenario, *H. "sanjuanensis"* has also been called *Haliclystus octoradiatus* James-Clark, 1863 (e.g., Eckelbarger & Larson 1993) and there is at least one other not formally described species of *Haliclystus* in the same region (partially sympatric), also proposed by Gellermann (1926) in her unpublished Master's Thesis (this species later referred to as *Haliclystus salpinx* James-Clark, 1863 in many publications including Otto 1976, 1978; Mills 1987; Strathmann 1987; Wrobel & Mills 1998, 2003; Mills & Larson 2007; but this synonymy is yet to be tested and is to be dealt with in a future publication).

On the other hand, there is information in the literature supporting the validity of *H. "sanjuanensis"*. Hirano (1997) morphologically revalidated *H. "sanjuanensis"* as different from *H. auricula* based on the presence of prominent white spots (sacs) composed of masses of nematocysts in *H. "sanjuanensis"*; these nematocyst-filled structures are absent in *H. auricula*. Hirano (1997) also distinguished *H. "sanjuanensis"* from *H. stejnegeri* and *H. octoradiatus* based on the distribution of the white nematocyst spots in the subumbrella.

Phylogenetic analyses based on ribosomal and mitochondrial genes corroborate that *H. "sanjuanensis"* is clearly distinct from *H. stejnegeri* and *H. octoradiatus* and closely related to *Haliclystus antarcticus* Pfeffer, 1889 and *H. auricula* (Miranda *et al*. 2010, 2016a; Holst & Laakmann 2019; Holst *et al*. 2019).

Based on this evidence, and since "*nomina nuda"* and other unavailable names can be made available if they are published again in a way that meets the criteria of availability (ICZN, 1999; see http://iczn.org/content/what-nomen-nudum), our aim in this study is to formally describe Gellerman's *Haliclystus "sanjuanensis"* using the species name that she originally applied. We also here provide a table comparing *Haliclystus sanjuanensis* n. sp. with the other twelve described-species in the genus *Haliclystus*.

MATERIAL AND METHODS

Animal collection

We hand-collected hundreds of live specimens of *Haliclystus sanjuanensis* n. sp. at low tides on the south end and west side of San Juan Island and the south end of Lopez Island, San Juan County, Washington State, USA and along the southern shore of Victoria, British Columbia, Canada (approximately 30 km to the west of San Juan Island) for study over a period of many years. Our primary collection locations were the type locality at Cattle Point on San Juan Island, Washington (48.452131 N, −122.961750 W) from the late 1970s–2019 and on the shoreline of the Chinese Cemetery in Victoria, British Columbia (48.406356 N, −123.323467 W) between May and September of 2013–2015. The waters of San Juan County and Cypress Island [the San Juan Archipelago], Washington, are a designated Marine Biological Preserve, with the University of Washington Friday Harbor Laboratories as the managing agency (Washington State House Bill 68, 1923; R.C.W.28.77.230,1969; Revision R.C.W.28B.20.320, 2023); since 1923, the Director of the Friday Harbor Laboratories FHL grants approval of scientific collection of marine plants and animals within the Marine Biological Preserve and C.E.M. has been granted such permission for collection of the marine animals reported in this study. Staurozoa were collected in Victoria, British Columbia, Canada, under Scientific License XR 30 2013-15 issued by the Department of Fisheries and Oceans Canada to Professor Louise Page, academic advisor of H.E.W during those years.

A type series of *H. sanjuanensis* n. sp. specimens including holotype and paratypes was collected on July 3, July 15, and July 29, 2019 on low tides at Cattle Point, San Juan Island. Animals were hand-collected from surfgrass or algae around the −50 cm (−1.5 foot) level in shallow water. The animals were transported back to the laboratory and preserved either in formalin or ethanol. Formalin-preserved animals were first relaxed in 50% seawater:50% isotonic magnesium chloride for 30–60 minutes, and then formalin was gradually added to a final concentration of 10% formalin. Animals preserved in ethanol for future molecular genetic studies were left in clean cold seawater for six hours; each animal was then lifted out individually with forceps, blotted briefly on a tissue, and dropped directly into 95% ethanol.

The electronic version of this article in Portable Document Format (PDF) will represent a published work according to the International Commission on Zoological Nomenclature (ICZN), and hence the new names contained in the electronic version are effectively published under that Code from the electronic edition alone. This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for this publication is: urn:lsid:zoobank.org:pub:BF343A8D-DB31-4150-840C-6CDA5A5B121E. The online version of this work is archived and available from the following digital repositories: PeerJ, PubMed Central SCIE and CLOCKSS.

Morphology and cnidome

Many animals were studied live in small bowls under a dissecting microscope. In general, they did not survive well in the laboratory, remaining in good condition for only a few days, even when fed daily with *Artemia* nauplii.

Photos of live animals were taken with an Olympus SZX9 dissecting microscope with Olympus DP72 camera attachment and DP2-BSW software (Version 2.2, Build 6212) and under a Nikon stereomicroscope using a Q Imaging digital camera and Q Capture software.

Observations and measurements of nematocysts from secondary tentacles, white nematocyst spots, gastric filaments, and exumbrellar surface were made on tissues preserved in 10 % formalin in seawater solution, squashed in a drop of fresh water on a microscope slide, covered by a cover slip, and gently compressed to further dissociate the cells (Gwilliam 1956; Mejía-Sánchez & Marques 2013). Undischarged capsules of each type of nematocyst were isolated and photographed using brightfield (Zeiss Axioskop, Zeiss Primo Star with Zeiss AxioCam ERc5s) and Nomarski differential interference contrast (DIC) (Leitz Aristoplan) microscopy. Measurements were made using ImageJ software (Version 1.48). Nematocyst terminology follows Östman (2000).

Histology

Animals for histological analyses were preserved in 10% formalin solution in seawater. We followed the resin technique, described in Miranda *et al*. (2017). The samples were dehydrated and embedded in glycol methacrylate following the instructions provided with the kit ("Leica Historesin Embedding Kit", Leica Microsystems Nussloch GmbH, Germany). Thin transversal sections (3.0–5.0 µm) were cut with a Leica RM2255 microtome and stained with hematoxylin-eosin and toluidine blue (see Miranda *et al*. 2017). Slides were observed and photographed under a Zeiss microscope Primo Star (AxioCam ERc5s). The slides are deposited in the collection of the Laboratory of Biology and Evolution of Cnidaria (catalog number LABEC 001, voucher deposited at the Taxonomic Collections Center of the Federal University of Minas Gerais, Brazil, UFMG-INV 2000003; Table 1), Department of Zoology, Institute of Biological Sciences, Federal University of Minas Gerais, Brazil.

Distribution

In addition to searching the scientific literature, the geographic range of *H. sanjuanensis* n. sp. has been determined by contacting many colleagues who work in the intertidal in British Columbia, Washington, Oregon, and California and by searching the web for images posted online and subsequently contacting and discussing the images with the photographers. Images posted on iNaturalist.org were useful in verifying some field locations (Table S1). All locations were verified with photographs or specimens. The distributional map was constructed using Q-GIS 3.28. Geographic data were georeferenced mostly by our colleagues who provided images which we examined, and occasionally from site names described in the literature (Table S1) using Google™ Earth (Pro, v7) or Google Maps using satellite view so that shoreline locations could be precisely determined.

SYSTEMATIC ACCOUNT

Phylum Cnidaria Verrill, 1865

Subphylum Medusozoa Petersen, 1979

Class Staurozoa Marques & Collins, 2004

Order Stauromedusae Haeckel, 1879

Suborder Myostaurida Miranda, Hirano, Mills, Falconer, Fenwick, Marques & Collins, 2016a

Family Haliclystidae Haeckel, 1879

Genus *Haliclystus* James-Clark, 1863

***Haliclystus sanjuanensis* new species**

Synonymy.

“*Haliclystus sanjuanensis* n. sp.” in Gellermann 1926 (pp. 80–84, Plate XX figures 20, 20a, Plate XXXVI figures 49, 50, 51) San Juan Island, Washington.

“*Haliclystus stejnegeri*” in Ricketts 1929 (p. 20).

“*Haliclystus*” in Ricketts & Calvin 1939 (p. 87).

“*Haliclystus* (probably *stejnegeri*)” in Ricketts & Calvin 1939 (p. 195) Port Townsend and Friday Harbor, Washington, and from Point Joe, Monterey, and Carmel Bay, California.

“*Haliclystus stejnegeri*” in Ricketts & Calvin 1939 (Figure 86 and p. 261).

“*Haliclystus”* in Hyman 1940a (Figure 165E and caption on p. 510, pp. 534, 535) Puget Sound (San Juan Island), Washington.

“*Haliclystus”* in Hyman 1940b (Figure 8 caption and text on p. 292, pp. 282, 293, 295) San Juan Island, Washington.

“*Haliclystus sanjuanensis”* in Hyman 1940b (p. 292) San Juan Island, Washington.

“Stalked Jelly Fish *Haliclystus sanjuanensis”* in Guberlet 1936, 1949 (pp. 46, 47, 409).

“*Haliclystus*” in Ricketts & Calvin 1948 (p. 87).

“*Haliclystus* (probably *stejnegeri*)” in Ricketts & Calvin 1948 (p. 195) Port Townsend and Friday Harbor, Washington, and from Point Joe, Monterey, and Carmel Bay, California.

“*Haliclystus stejnegeri*” in Ricketts & Calvin 1948 (Figure 86 and p. 296).

“*Haliclystus stejnegeri*” in MacGinitie & MacGinitie 1949 (Figure 19 on p. 120, p. 121) found in great numbers in Puget Sound and occasionally in Monterey Bay.

“*Haliclystus sanjuanensis”* in Knapp 1950, Neptune State Park, Oregon.

"*Haliclystus*" in Ricketts *et al*. 1952 (p. 85).

"*Haliclystus* (probably *stejnegeri*)" in Ricketts *et al*. 1952 (p. 249) Port Townsend and Friday Harbor, Washington, and from Point Joe, Monterey, and Carmel Bay, California.

"*Haliclystus stejnegeri*" in Ricketts *et al*. 1952 (Figure 86 on p. 284, p. 416).

"Two species of *Haliclystus* are found in the Friday Harbor region" in Smith *et al.* 1954 (p. 41) San Juan Islands, Washington.

"*Haliclystus auricula*" in Smith 1955, Field Notebook #3, June 24, 1955, Davis Bay, Lopez Island, Washington.

"*Haliclystus auricula* (Rathke)" in Gwilliam 1956 (pp. 2, 8, 17, 20, 21, 43–55, 56, 57, 61–66, 79, 80, 94–97, 110–180) San Juan Island, Washington.

"*Haliclystus sanjuanensis*" in Gwilliam 1956 (pp. 13, 14, 20) San Juan Island, Washington.

"*Haliclystus auricula*" in Anonymous 1958 (p. 2) San Juan County, Washington.

"*Haliclystus auricula* (Rathke)" in Gwilliam 1960 (pp. 454–473) San Juan Island, Washington.

"*Haliclystus auricula* (Rathke, 1806)" [in part] in Kramp 1961 (pp. 292–293).

"*Haliclystus* sp." in McLean 1962 (p. 106) scarce on rock walls along the open coast of the Monterey Peninsula, nine miles south of Carmel near Granite Creek, California.

"*Haliclystus*" in Ricketts *et al*. 1962 (p. 85).

"*Haliclystus* (probably *stejnegeri*)" in Ricketts *et al*. 1962 (p. 249) Port Townsend and Friday Harbor, Washington, and from Point Joe, Monterey, and Carmel Bay, California.

"*Haliclystus stejnegeri*" in Ricketts *et al*. 1962 (Figure 86 on p. 284, p. 416).

"*Haliclystus* sp." in MacGinitie & MacGinitie 1968 (Figure 19 on p. 120, p. 123) abundant in Puget Sound waters.

"*Haliclystus"* in Ricketts *et al*. 1968 (p. 130).

“*Haliclystus* (probably *H. stejnegeri*)” in Ricketts *et al*. 1968 (pp. 299–300) Port Townsend and Friday Harbor, Washington, and from Point Joe, Monterey, and Carmel Bay, California.

“*Haliclystus stejnegeri*” in Ricketts *et al*. 1968 (Figure 221 on p. 299, p. 462).

“*Haliclystus*” in Westfall 1968 (p. 803), San Juan Island, Washington.

“*Haliclystus auricula*” in Westfall 1968 (p. 804), San Juan Island, Washington.

“Two species of *Haliclystus* are found in the Friday Harbor region” in Smith 1970 (p. 41) San Juan Islands, Washington.

“*Haliclystus auricula*” in Westfall *et al*. 1970 (p. 545), San Juan Island, Washington.

“*Haliclystus auricula*” in Westfall 1973 (pp. 239–243), San Juan Island, Washington.

“*Haliclystus auricula*” in Kozloff 1973 (Figure 206 and text, p. 247).

“*Haliclystus auricula*” in the Bodega Marine Lab Synoptic Collection, collected in 1973 at Shell Beach, Sonoma County, California.

“*Haliclystus auricula* (Rathke, 1806)” in Kozloff 1974 (pp. 22, 219).

“*Haliclystus auricula*” in Smith 1975 (Figure 21 on p. 88, p. 96).

“21, *Haliclystus*, from False Bay near Friday Harbor, Wash.” in Smith 1975 (caption on p. 89).

“*Haliclystus auricula* (Rathke, 1806) (= *H. sanjuanensis* of several authors)” in Smith 1975 (p. 96) Friday Harbor, Washington.

“*Haliclystus auricula*” in Smith 1976 (Figure 121 on p. 115) Pacific Northwest.

“*Haliclystus stejnegeri*” in Otto 1976 (pp. 319–322, 328) San Juan Island, Washington.

“*Haliclystus stejnegeri*” in Singla 1976 (pp. 533–539) on eelgrass, Victoria, British Columbia.

“*Haliclystus auricula*” in Flora & Fairbanks 1977 (Figure 48 on p. 56) on kelp and eelgrass in protected bays in Puget Sound.

“*Haliclystus stejnegeri*” in Otto 1978 (p. 22) San Juan Island, Washington.

"*Haliclystus auricula*" in Snively 1978 (p. 162).

not *"Haliclystus auricula*" = *Manania handi* in Snively 1978 (Figure 79 on p. 43).

"*Haliclystus*" in Brusca & Brusca 1978 (pp. 52–54, Figure 24 on p. 53) in Northern California attached to seaweeds in quiet tidepools, or to eelgrass in Humboldt Bay.

"*Haliclystus auricula*" in Caine 1980 (p. 162) San Juan Island, Washington.

"*Haliclystus* sp." in Barr & Barr 1983 (Figure 32 on p. 9, pp. 81–82) Yakobi Island, Southeast Alaska.

"*Haliclystus stejnegeri* and *H. auricula*" in Phillips 1984 (p. 40) Pacific Northwest.

"*Haliclystus auricula* (Rathke, 1806)", in part, in Austin 1985 (p. 70).

"*Haliclystus steinegeri* Kishinouye, 1899", in part, in Austin 1985 (p. 70).

"*Haliclystus"* in Ricketts *et al*. 1985 (pp. 154–155) common "in the north" and rare to occasional at Monterey.

"*Haliclystus auricula*" in Ricketts *et al*. 1985 (pp. 343–344, Figure 267 on p. 344, p. 513) on eelgrass in Puget Sound and northern California.

"*H. stejnegeri*" in Ricketts *et al*. 1985 (p. 513).

"*H. sanjuanensis*" = *Haliclystus auricula* (Rathke, 1806) in Hirano 1986 (p. 183).

"*Haliclystus*" in Westfall 1987 (pp. 9, 11, 12), San Juan Island, Washington.

"*Haliclystus stejnegeri* Kishinouye, 1899" in Mills 1987 (p. 67).

"*Haliclystus stejnegeri* Kishinouye (= *H. sanjuanensis* and *H. auricula*, E. Kozloff pers. comm.)" in Strathmann 1987 (p. 79) San Juan Island, Washington.

"*Manania* (?)" in Abbott 1987 (p. 22) July 2, 1974, 15–20 feet deep on *Plocamium*, off Malpaso Creek, Monterey County, California.

"*Haliclystus octoradiatus* (Lamarck, 1816)" in Larson 1990 (pp. 546–550, Figure 1A on p. 551) Alaska to central California.

"*Haliclystus stejnegeri* Kishinouye, 1899" in Cairns *et al.* 1991 (p. 11 [in part], Figure 1 on p. 77).

"*Haliclystus octoradiatus*" in Eckelbarger & Larson 1993 (pp. 225–236) Victoria, British Columbia, Canada.

"*Haliclystus salpinx*" in Eckelbarger 1994 (p. 16, Figure 2.3.d on p. 19, pp. 20, 26) Victoria, British Columbia, Canada.

"*Haliclystus*" in Kozloff 1996 (pp. 322, 323).

"*Haliclystus stejnegeri*" in Kozloff 1996 (p. 323, Figure 345 on p. 324).

"*Haliclystus stejnegeri* Kishinouye, 1899" in Mills 1996 (pp. 67, 489).

"*H. sanjuanensis* Hyman, 1940" in Hirano 1997 (pp. 247, 249–251).

"*Haliclystus stejnegeri*" in Heeger 1998 (p. 74).

"*Haliclystus stejnegeri*" in O'Clair & O'Clair 1998 (Figure 13 on p. 15, pp. 15–16) Bertha Bay, west side of Chichagof Island, Southeast Alaska.

"*Haliclystus sanjuanensis*" in Wrobel & Mills 1998 and 2003 (p. 49).

"*Haliclystus "sanjuanensis*" Gellermann, 1926 or Hyman, 1940 or Hirano, 1997 or undescribed?" in Mills 1999–present accompanied by C.E. Mills photograph of two stauromedusae on one piece of eelgrass (accessed March 2023).

"*Haliclystus sanjuanensis*" in Collins 2000 (pp. 10, 11, 14–16).

"*Haliclystus* sp. undescribed "*sanjuanensis*"" in Cairns *et al.* 2002 (pp. 9, 47).

"*Haliclystus stejnegeri*" in Cairns *et al.* 2002 (Figure 3 on p. 109).

"*Haliclystus sanjuanensis*" in Collins 2002 (p. 420).

"*Haliclystus sanjuanensis* Hyman, 1940" in Zagal 2004 (table 2 on p. 339).

"*Haliclystus sanjuanensis* Hyman, 1940" in Collins & Daly 2005 (pp. 221, 222, 225, 226, 229).

"*Haliclystus sanjuanensis*" in Collins *et al*. 2006a (p. 3).

“*Haliclystus sanjuanensis*” in Collins *et al*. 2006b (Figure 2 on p. 101, Figure 3 on p. 102, Figure 4 on p. 103, Figure 6 on p. 106, p. 115).

“Oval-anchored stalked jelly *Haliclystus stejnegeri*” in Lamb & Hanby 2005, 2015 (p. 111 photo and text) intertidal to 10 m, Sekiu, Olympic Peninsula, Washington.

“*Haliclystus* sp.” in Mills & Hirano 2007 (Figure 1 on p. 541).

“*Haliclystus* sp. (undescribed species)” in Mills & Larson 2007 (p. 170).

“*Haliclystus* sp. (“*sanjuanensis*”)” in Mills & Larson 2007 (Plate 63A on p. 171).

“*Haliclystus* sp. (=*H. “sanjuanensis,” nomen nudum*)” in Mills & Larson 2007 (p. 172).

“*Haliclystus “sanjuanensis”* (*nomen nudum*)” in Miranda *et al*. 2009 (pp. 1507, 1508, 1513–1515).

“*Haliclystus “sanjuanensis”* (*nomen nudum*)” in Miranda *et al*. 2010 (pp. 3–5, 7).

“*H. sanjuanensis*” in Miranda *et al*. 2010 (p. 4).

“*Haliclystus* “sanjuanensis” *nomen nudum*” in Kahn *et al*. 2010 (pp. 49, 52, 54–57).

“Oval-anchored stalked jelly (*Haliclystus stejneger*i)” in Brewer *et al*. 2011 (p. 40 photo and text) Cape Prominence, Unalaska Island in the Aleutians.

“*Haliclystus “sanjuanensis”*” in Kayal *et al*. 2012 (pp. 2–4, 11).

“*Haliclystus sanjuanensis*” in Kayal *et al*. 2013 (Figure 2 on p. 5, table 3 on p. 13).

“*H. “sanjuanensis”*” in Miranda *et al*. 2013 (p. 1381).

“*Haliclystus sanjuanensis*” in Zapata *et al.* 2015 (pp. 5, 9, Figure 4 on p. 7) San Juan Island, Washington.

“*Haliclystus ‘sanjuanensis’ nomen nudum”* in Westlake 2015 (185 pp.) Victoria, British Columbia, Canada.

“*H. “sanjuanensis” nomen nudum*” in Miranda *et al*. 2016a (pp. 6, 13–15, 17, 19, 37).

“*H. “sanjuanensis”* (*nomen nudum*)” in Miranda *et al*. 2016b (pp. 3, 72, 73).

“*Haliclystus sanjuanensis*” in Li *et al*. 2016 (pp. 113–114).

“*Haliclystus ‘sanjuanensis’ nomen nudum*” in Westlake & Page 2017 (pp. 29–49) Victoria British Columbia, Canada.

“*Haliclystus “sanjuanensis”*” in Kayal *et al*. 2018 (pp. 4, 13, 15, Figures 1b on p. 2, Figure 5 on p. 7, Figure 6 on p. 9) from Cattle Point, San Juan Island, Washington.

“*H. “sanjuanensis” nomen nudum*” in Miranda *et al*. 2018 (pp. 1697, 1699, 1703, 1706, 1707, 1709).

“*Haliclystus* sp.” in Jensen *et al*. 2018 (p. 28) British Columbia to central California.

“*Haliclystus sanjuanensis*” in Nicosia *et al*. 2018 (Table 2 on p. 5, Figure 6 on p. 13).

“*Haliclystus “sanjuanensis”*” and “*Haliclystus sanjuanensis*” in Holst & Laakmann 2019 (Table 1 on p. 1062, Figure 2 on p. 1064).

“*Haliclystus “sanjuanensis”*” in Holst *et al*. 2019 (Figure 6 on p. 1787, Table 4 on p. 1788, pp. 1789, 1793, 1794).

“*Haliclystus “sanjuanensis”* (*nomen nudum*)” in Miranda & Collins 2019 (p. 8).

“*Haliclystus sanjuanensis*” in Koch & Grimmelikhuijzen 2019 (Table 1 on p. 3, Table 3 on p. 5, Figure 3 on p. 9, Figure 4 on p. 10).

“*Haliclystus sanjuanensis*” in Lewandowska *et al*. 2020 (p. 11).

“*Haliclystus sanjuanensis*” in Gornik *et al*. 2021 (p. 1755).

“*Haliclystus sanjuanensis*” in Hartigan *et al*. 2021 (Figure 4 on p. 11).

“*Haliclystus “sanjuanensis”* (nomen nudum)” in Holst *et al*. 2021 (p. 249)

“*Haliclystus sanjuanensis*” in Adriansyah *et al*. 2022 (Figure 8A on p. 265, Table 2 on p. 269).

“*Haliclystus sanjuanensis*” in Santander *et al*. 2022 (Figure 1C on p. 2).

“*Haliclystus sanjuanensis*” in Vöcking *et al*. 2022 (p. 11).

“*Haliclystus sanjuanensis*” in Zhang & Jacob 2022 (Table 1 on p. 5, Figure 4 on p. 8).

"*Haliclystus sanjuanensis*" in Steinworth *et al*. 2023 (Table 2 and text on p. 3, p. 9).

WE REMAIN UNSURE whether the following records refer to *H. sanjuanensis*:

"*Haliclystus stejnegeri* Kishinouye" in Bigelow 1920 (p. 12H and Plate 2 figure 4 on p. 20H) Port Clarence, Alaska, 2–3 fathoms. There is insufficient information to distinguish if this was *H. stejnegeri* or *H. sanjuanensis*.

"*Haliclystus*" in 1946 field notes by Ed Ricketts (*Transcript of the 1946 trip to West Vancouver Island and to the Queen Charlotte Islands*), Massett, Queen Charlotte Islands, June 27, 1946 and July 2, 1946, "lots of *Haliclystus*" on eelgrass in two locations near Massett in the very low intertidal, in Steinbeck *et al*. 1978 (pp. 115, 118), and Rodger 2006 (pp. 306, 310).

"*Haliclystus auricula* (Rathke, 1806)" in Anonymous, Pacific Gas & Electric Environmental Report ~2001, table 2.3-5, Sheet 7 of 23, p. 173 of 202, from coastline near Diablo Canyon, California (confirmed by personal communication from David Behrens, who did much of the collecting and identifying for that report, but since he could not locate a photograph of the specimen for us in 2019, we cannot be positive of this material, which would otherwise represent one of the southernmost collection locations of *H. sanjuanensis*).

"*Haliclystus stejnegeri*" Royal British Columbia Museum (RBCM) #015-00395-001. Single animal collected from Egeria Bay, Langara Island, Haida Gwaii, British Columbia May 22, 2015 by Heidi Gartner, Melissa Frey, Gavin Hanke, Tommy Norgard, Leslie Barton and Vanessa Hodes is too young to determine whether it is *H. sanjuanensis* or *H. stejnegeri*. Claudia Mills notes upon inspection of the specimen, April 26, 2019.

Holotype. Smithsonian Institution, National Museum of Natural History, USNM 1522349 (Table 1). Northeast Pacific, collected July 15, 2019 at Cattle Point, San Juan Island, San Juan County, Washington, USA (48.452131 N, −122.961750 W) on a blade of algae at approximately −0.5 m deep. Preserved in 10% formalin in seawater. Collector Claudia E. Mills.

Other material examined. Paratypes and additional specimens (Table 1) were collected July 3, July 15 and July 29, 2019 on low tides at Cattle Point, San Juan Island, San Juan County, Washington, USA (48.452131 N, −122.961750 W) on red or green algae or surfgrass *Phyllospadix* at approximately −0.5 m deep, collector Claudia E. Mills. The animals were preserved in 10% formalin in seawater or preserved directly into 95% ethanol. Both formalin and ethanol preserved paratypes and additional specimens were deposited at the Smithsonian Institution, National Museum of Natural History in DC; the Florida Museum at the University of Florida in Gainesville; the Royal British Columbia Museum in Victoria, British Columbia; the California Academy of Sciences in San Francisco, California; and the Synoptic Collection of the University of Washington Friday Harbor Laboratories in Friday Harbor, Washington (Table 1).

Further evidence. Photographs (mainly from https://www.inaturalist.org/), specimens in public and particular collections, and personal communications, not otherwise published, South to North, are available in Table S1.

Diagnosis. *Haliclystus* with broadly conical calyx, wider than high (Figs 1, 2). Calyx well demarcated from the stalk, where the profile goes from conical to cylindrical (Figs 1, 2). Stalk length variable, from as long as the calyx is tall to about 1/2 length of calyx. Gonads extending from base of the calyx to tips of each of eight arms (Figs 1, 2); 200 to 300 tightly-packed gonadal vesicles comprising each gonad, with 10 to 22 abreast at the widest (Figs 1, 2). The gonads are broadly leaf-shaped, filling much of the available subumbrellar surface, and slightly folded over upon themselves in larger animals; the proximal half of each gonad may be turned over upon itself in the perradii and the distal half turned over in a similar manner in the interradii (Figs 1, 2). Each arm tipped with a cluster of usually up to 130 (but may be more than 200 in larger specimens) capitate secondary tentacles (Figs 1–3). Eight anchors along the calyx margin on interradial and perradial axes, alternating with the eight adradial arms — the anchors are roughly oval in outline and vary from fairly spherical to elongate, sometimes with a remnant of the primary tentacle in the center, usually disappearing in older animals (Figs 1, 2, 3A–E). The eight marginal notches between arms are all approximately equal in size (Figs 1, 2). Bright-white nematocyst spots about the same size as the gonadal vesicles (Fig. 4E–G), closely grouped in a single row along the distal perradial edges of the gonads from the tips of the arms to the widest point of the gonads or a little further down, but also rarely seen along the perradial calyx margin (Figs 1–4). Often, but not always, with four dark pigment stripes running up the perradii of the stalk and bifurcating (into eight stripes) at the stalk-calyx junction, extending halfway up the calyx on the exumbrella along the interradial edge of each gonad, and sometimes also with lighter stripes running along both upper edges of the gonads near the calyx margin (Fig. 2).

Description. (General description using Gellermann 1926; Gwilliam 1956; Westlake 2015; photographs by the authors and online, and observation of living and preserved individuals.) Calyx broadly conical, with eight arms; arms sometimes recurved toward the stalk in life; calyx usually up to about 30 mm wide (rarely to 40 mm wide) and clearly demarcated from the stalk, wider than high (Figs 1, 2). Stalk narrow and varies from about 1/2 the length of calyx to as long as the calyx is tall, rarely a little longer than the calyx is tall (Figs 1, 2, 5). Well-developed basal pedal disc at base of stalk (Fig. 5B, C). Stalk quadratic in cross section, with four usually darkly-pigmented perradial gastric chambers (delimited by gastrodermis) and four interradial longitudinal muscle bands, embedded in mesoglea (Figs 5, 6A). Perradial chambers fusing into one single chamber at stalk-calyx connection, with four interradial septa associated with the four interradial longitudinal muscle bands (Figs 6B, C; 7). Four infundibula funnel-shaped with blind end, delimited by epidermis, deeply developed down to base of calyx, widening apically, with broad apertures on subumbrella (Fig. 7). Gastrovascular cavity without claustrum. Numerous gastric filaments in gastrovascular cavity (Fig. 3F, G). At base of infundibula, the four interradial longitudinal muscle bands of the stalk divide into eight bands (Figs 6C–G; 7D, E), continuing up through the calyx along interradii, reaching out into the eight adradial arms. Gastrovascular cavity divided into four perradial gastric pockets at the manubrium region (Fig. 6F, G), where gonadal vesicles are located in mature individuals. Four perradial gastric pockets bifurcating distally to form eight adradial branches, each of which is running into each arm. The manubrium is short and quadrangular, with dark-pigmented perradial corners, and with the four oral lobes thin and folded (Figs 4A–D; 6F, G).

Eight adradial arms, all alike, and notches between arms are all approximately equal in size (Figs 1, 2). However, arms occasionally exhibit some perradial pairing, with the perradial notches between arms sometimes a little narrower than the interradial notches. Tip of each arm with a cluster of up to 130 (or more than 200 in larger specimens) knobbed (capitate) secondary tentacles; all tentacles are short, from 1 to 3 mm long (Figs 1–3, 8A–H).

Intertentacular lobules at the internal tip of the arms (at the base of tentacular clusters) (Fig. 8A–C). Each secondary tentacle in the arms is ensheathed with longitudinal muscle fibers (Fig. 8D–F). Four groups of perradial muscular fibers extend from the manubrium lips (Fig. 4C, D) down to the four perradial corners of the manubrium. The coronal muscles lie beneath the subumbrellar surface at the periphery of the calyx and are comprised of four interradial and four perradial segments.

Eight anchors on the exumbrella, near the margin, one between each pair of arms in the interradii and perradii outside of the low-point of each notch (Figs 1, 2, 3A–E). The anchors are irregularly oval in outline and about half as long as the diameter of the stalk, but quite variable in shape and size between animals. The primary tentacle (the developmental origin of the anchor) capitulum usually disappears in older specimens, but is present in developing animals to a greater or lesser extent depending on animal size (Figs 3A–E, 6H). The anchors may be fairly flat in profile or rather elongate, but they are never flaring or trumpet-shaped with thickened or rolled edges (Figs 1, 2, 3A–E); the cavity of each anchor communicates with the general body cavity of the animal by means of a very short canal through the anchor peduncle (Fig. 3E).

The eight adradial gonads extend the full length of the eight arms, are very broad in the middle, filling much of the available subumbrellar surface, and in large specimens slightly folding over on themselves, and narrower at both ends (Figs 1, 2, 4E–G). The gonads in the largest animals are composed of 200 to 300 tightly-packed gonadal vesicles that are roughly spherical, but may be so tightly packed together that their shape may be modified (Figs 1, 2, 4E–G). The gonadal vesicles are not arranged in rows; there are 10 to 22 vesicles abreast at the broadest part of each gonad (usually 12-16) (Figs 1, 2). In the largest animals, the proximal half of each gonad is turned over upon itself in the perradii and the distal half is turned over in a similar manner in the interradii (Figs 1A, E). The gonads are separated in the interradii, but are closer at their bases in the perradii, making four pairs of gonadal bands (Figs 1, 2).

The exumbrellar surface is finely granulated with numerous, scattered nematocyst clusters (Fig. 9L). The subumbrella is marked with distinctive bright-white nematocyst spots that are about the same size as the gonadal vesicles (Fig. 4E–G) — these white spots are arranged in the perradii, mostly closely grouped in a single row along the distal perradial edges of the gonads from the tips of the arms to the widest point of the gonads or a little further down, but also occasionally located along the calyx margin (perradial center) in large specimens (Figs 1, 4E–H, 8I). The subumbrellar epidermis is raised in slight bulges over each white nematocyst spot (Figs 4H, 8I).

Overall color in life is highly variable, but each individual is of a single color, from brown or beige to orangey red to peach, rusty or wine red, or greenish, usually cryptically matching the color of its eelgrass or algal substrate (Figs 1, 2); young (small) animals are less pigmented. Gonads and anchors golden brownish to green to orange to wine red, bright-white nematocyst spots along perradial edges of gonads and (rarely) subumbrellar margin; tentacles greenish to golden yellow to reddish or pink (Figs 1, 2). Often, but not always, with four dark brown to orange longitudinal stripes of varying intensity on the perradial corners of the manubrium (Fig. 4A–D) and on the perradii of the stalk, bifurcating at the stalk-calyx junction (Figs 1, 2, 5F), extending halfway up the calyx on the exumbrella along the interradial edge of each gonad, and sometimes also with lighter stripes running along both upper edges of the gonads near the calyx margin (Fig. 2B, C). Muscles whitish to colorless in the stalk and calyx (Fig. 5D, E).

Cnidome. Secondary tentacles with two types of nematocysts: isorhiza (abundant), length 9.54–13.50 μm (mean 12.11 μm, number of capsules measured n = 62), diameter 2.26–4.18 μm (mean 3.51 μm, n = 62); and microbasic eurytele (scarce), length 15.69–19.85 μm (mean 17.73 μm, n = 24), diameter 7.39–9.36 μm (mean 8.52 μm, n = 24) (Fig. 9A–F). White nematocyst spots with one type of nematocysts: birhopaloid type II (two dilatations close together) (abundant), length 11.63–17.13 μm (mean 14.60 μm, n = 50), diameter 7.95–11.39 μm (mean 9.96 μm, n = 50) (Fig. 9G–I). Gastric filaments with one type of nematocysts: rhopaloid (not enough information to identify them as eurytele, stenotele, or birhopaloid) (abundant), length 7.10–10.70 µm (mean 8.90 µm, n = 11), diameter 4.13–6.80 µm (mean 5.47 µm, n = 11) (Fig. 9J, K). Exumbrella with one type of nematocysts: rhopaloid (not enough information to identify them as eurytele, stenotele, or birhopaloid), mean length 11.04 µm (n = 13), mean diameter 4.46 µm (n = 13) (Fig. 9L, M).

Behavior. This animal is almost always attached to the substrate by its pedal disc; some use of the anchors and secondary tentacles for anchorage has also been observed (Figs 1, 2). Only once or twice in many visits to the seashore have we seen a specimen free in the water. This stauromedusa produces a periderm in the form of a thin transparent cup that encases the pedal disc and is left behind when the staurozoan moves (Fig. 10); a new periderm is formed when the staurozoan reattaches. Small (usually arthropod) prey was captured by flexing (not contracting) one or more secondary tentacles on one or more adjacent arms, which immediately then bent in to the manubrium to transfer the captured prey to the mouth. Bending of an arm or arms was often accompanied by bending or twisting of the stalk. Spontaneous bending of single and multiple arms was typically observed. The anchors did not participate in feeding behaviors; their sole purpose appears to be as adhesive organs. One animal spawned spontaneously in the laboratory in May 2015, releasing many 35 µm diameter eggs in sticky mucus strands through its mouth opening of the manubrium (Fig. 11).

Etymology. The specific name, originally assigned by Gellermann (1926) in her unpublished M.S. Thesis, refers to the San Juan Archipelago, San Juan County, Washington State, where this animal is abundant in some more-exposed areas, and she studied it in detail. This location in NW Washington is approximately the epicenter of its presently known distribution along NE Pacific shorelines and the location of some of the most-dense populations.

Habitat. On living eelgrass and surfgrass, *Zostera marina* and *Phyllospadix scouleri*, or on various species of red, green, and brown algae in the low intertidal to shallow subtidal, to at least 10 m deep in areas of moderate wave activity.

Distribution. Along the Pacific coast of North America at least from eastern Aleutians to just north of Point Conception in central California (Fig. 12; Table S1). It seems not to occur south of Point Conception, as this species is not listed in the Southern California Association of Invertebrate Taxonomists species list for the Southern California Bight (Cadien *et al*. 2018), nor has it been seen by naturalist diver-photographers Kevin Lee, Merry Passage and Phil Garner in about 4,500 dives near Los Angeles (personal communication to C.E.M.).

On San Juan Island, Washington, the type locality (Fig. 12), very small *H. sanjuanensis* stauromedusae can be found beginning in approximately mid-April, and the last specimens persist into late November. No recognizable life history stages have been found from late fall until mid-spring.

Gene sequences. GenBank accession numbers: LSU (28S): KU308593, AY920782; SSU (18S): AF358102, KU308562, MN329739; SSU-ITS1-5.8S-ITS2-LSU: FJ874776, HM022143, HM022144, HM022145, MN329741; 16S: AY845339, HM022149, HM022150, HM022151, MN329738; COI: KU257477, MH242772, MN329740; Transcribed RNA sequences: HAHB01000001-HAHB01134305; Partial genome: JN700944.

Remarks. *Haliclystus* is a genus comprised of species with four interradial longitudinal muscles in the stalk (=peduncle) (Figs 5, 6, 7), a shared character of the suborder Myostaurida (see Miranda *et al*. 2016a). Within this suborder, *Haliclystus* is placed in the family Haliclystidae, characterized by the presence of perradial and interradial anchors (=rhopalioids, adhesive and sensorial structures derived from primary tentacles, located between adjacent pair of arms) (Figs 1–3) (Miranda *et al*. 2016a; Miranda & Collins 2019). The family Haliclystidae is also represented by species of the genera *Depastromorpha* Carlgren, 1935, *Depastrum* Gosse, 1858; *Halimocyathus* James-Clark, 1863 and *Manania* James-Clark, 1863. However, differently from all these genera, *Haliclystus* does not have claustrum, a tissue composed of a thin layer of mesoglea surrounded by a double layer of gastrodermis (Miranda *et al*. 2016a, 2017). In addition, species of *Haliclystus* generally have four perradial chambers in the stalk (although this character is variable during development) (Figs 5, 6) (Miranda *et al*. 2016a, b) and the coronal muscle at the subumbrellar margin can be divided or entire (Miranda *et al*. 2016a). The genus has shown as monophyletic in all phylogenetic analyses for the class (Collins & Daly 2005; Miranda *et al*. 2010, 2016a; Holst & Laakmann 2019; Holst *et al*. 2019). However, in spite of recent efforts (e.g., Hirano 1997; Miranda *et al.* 2009, 2016a; Kahn *et al*. 2010), the taxonomy of the genus is still a challenge, as characters generally mentioned in the description of the species, such as number of tentacles and number of chambers in the stalk are known to show intraspecific variation (Uchida 1929; Hirano 1986; Miranda *et al.* 2009; Kahn *et al*. 2010).

Haliclystus sanjuanensis, discussed as a *nomen nudum* in different articles (see above), is herein properly described. *Haliclystus sanjuanensis* is unique among other species of *Haliclystus* because of the arrangement of the bright-white nematocyst spots in perradii only, forming a conspicuous line along the perradial edges of gonads and rarely also a few near the perradial calyx margin (Figs 1, 4; see also Table S2; Hirano 1997). *Haliclystus antarcticus* and *H. auricula*, the species phylogenetically most closely related to *H. sanjuanensis* (Miranda *et al*. 2010, 2016a; Holst et al. 2019), do not have these white nematocyst spots (see Hirano 1997; Miranda *et al*. 2009, 2013). *Haliclystus borealis* Uchida, 1933, *Haliclystus californiensis* Kahn *et al*., 2010, *Haliclystus inabai* (Kishinouye, 1893), *Haliclystus monstrosus* (Naumov, 1961), *Haliclystus sinensis* Ling, 1937, *Haliclystus tenuis* Kishinouye, 1910, *H. salpinx*, and *H. octoradiatus* have white nematocysts spots in both perradii and interradii (see also additional differences in Table S2). There is no information concerning white spots for *Haliclystus kerguelensis* Vanhöffen, 1908. However, *H. sanjuanensis* can be distinguished from *H. kerguelensis* based on the proportion between calyx and stalk and on the dark stripes (Table S2). Nevertheless, it is important to highlight that *H. kerguelensis* was described in 1908, based on a drawing and not specimens; Kramp (1957) reports three additional specimens collected in 1929–1930, but he does not include figures, so the validity of this species has never been tested.

The only *Haliclystus* species left for comparison is *H. stejnegeri*, which is morphologically very similar to *H. sanjuanensis* (Table S2). However, although both species have white nematocyst spots found in perradii only, in *H. sanjuanensis* the white spots are relatively abundant along the perradial edges of the gonads, running from near the margin to considerably deep into the subumbrella (Figs 1, 4), whereas in *H. stejnegeri* the white spots are relatively sparse and mainly found along the edge of gonads near the calyx margin (Fig. 13; Table S2). One additional difference is the pattern of pigmentation in the calyx (exumbrella). In *H. sanjuanensis*, eight dark stripes may be present, running halfway up the calyx along the interradial edges of gonads, which join as four stripes in the perradii running the length of the stalk; dark stripes may also be present near calyx margin running along both edges of gonads (Fig. 2; Table S2). On the other hand, *H. stejnegeri* is characterized by its exclusive pattern with eight adradial pairs of dark stripes running the length of the calyx, and each two pairs united at the perradii of calyx base continuing as four dark stripes running down the stalk; the calyx margin is also tinted in the same color (Kishinouye 1899; Fig. 13; Table S2). Unfortunately, preserved stauromedusae frequently lose their live coloration, so this character can be difficult to assess in preserved specimens.

Although some morphological characters used to differentiate species of *Haliclystus* are tricky, the current valid species have good support based on molecular evidence. Nine out of 13 described species of *Haliclystus* have been phylogenetically placed (Miranda *et al*. 2016a; Holst & Laakmann 2019; Holst *et al*. 2019), including *H. sanjuanensis*. Interestingly, although morphologically similar, *H. sanjuanensis* and *H. stejnegeri* did not come out as closely related species (Miranda *et al*. 2016a; Holst & Laakmann 2019; Holst *et al*. 2019). *Haliclystus sanjuanensis* proved to be molecularly very similar to *H. antarcticus* and *H. auricula* (Miranda *et al*. 2010; Kayal et al. 2018; Holst *et al*. 2019), despite the huge geographical gap between the known distributions of these species: Western United States and Canada for *H. sanjuanensis* (Fig. 12); Southern Chile and Argentina and the Antarctic~~a~~ Peninsula for *H. antarcticus* (Miranda *et al*. 2018); and Eastern United States and Europe for *H. auricula* (Miranda *et al*. 2018).

The geographic distribution of *H. sanjuanensis* in the North Pacific Ocean begins at about 34.5° N in central California and extends up at least to Southeast Alaska (about 58.2° N) and also west into the Aleutian Islands (to at least 166.7° W) (Fig. 12). It may or may not overlap *H. stejnegeri* at the upper end of its range in the NE Pacific, but then *H. stejnegeri* appears to swing across and down the NW Pacific to the Kurile Islands and to northern Japan (Miranda *et al*. 2018). *Haliclystus californiensis* is a very distinctive orangey-red species that is sympatric with *H. sanjuanensis*, occurring from southern California to at least central British Columbia (Kahn *et al*. 2010; our studies, see also Table S2). Four more described species of *Haliclystus*, easily separated from *H. sanjuanensis* because of the pattern of white nematocyst spots and the number of secondary tentacles on each arm in adult stauromedusae (see Table S2), are found in NW Pacific waters of China, Far East Russia, Japan, and Korea (*H. sinensis, H. borealis, H. tenuis*, and *H. inabai*) (see Miranda *et al*. 2018).

At least one more undescribed species of *Haliclystus* (Gellermann 1926) picks up about the midpoint of the south to north distribution of *H. sanjuanensis*, from the San Juan Islands and southern Vancouver Island to at least SE Alaska and possibly all the way to the Kuriles, northern Japan, and mainland far-east Russia, where a look-alike has been described as *H. monstrosus* (Naumov 1961; Sheiko & Stepanyants 1990). This undescribed species of *Haliclystus* is also similar to *H. salpinx*, a species found in the North Atlantic (James-Clark 1863; Berrill 1962; but see also Sheiko & Stepanyants 1990), raising the hypothesis that all records of *H. salpinx* in Washington State (Otto 1976, 1978; Mills 1987; Strathmann 1987; Wrobel & Mills 1998, 2003; Mills & Larson 2007) are misidentifications, but we need to complete further work to be sure. We are in the process of collecting more material for DNA and morphological comparisons to determine how many other *Haliclystus* species we are dealing with in the boreal North Pacific.

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REFERENCES

Abbott, D.P. (1987) *Observing Marine Invertebrates: Drawings from the Laboratory*. Hilgard, G.H. (Ed.). Stanford University Press, Stanford, California, 380 pp.

Adriansyah, A.S., Astri, A., Hirano, Y., Collins, A.G., Deshaies, M.-L., Putra, D., Sekiguchi, S., Ikeda, S., Okuizumi, K., Chikuchishin, M., Aoki., M. & Ames, C.L. (2022) Analyses of stalked jellyfish in Kitsunezaki, Japan: *Calvadosia nagatensis*, and two lineages of *Haliclystus inabai* with early life stages observed in an aquarium in Canada. *Hydrobiology*, 1, 252–277. DOI: 10.3390/hydrobiology1030019

Anonymous (1958) Key to the medusae found in the San Juan waters. *In:* Various authors, *Marine Fauna of the San Juan Archipelago (March, 1969)*. Unpublished, but copies were handed out to students at the Friday Harbor Laboratories 1960s–1980s. 2 pp.

Anonymous and undated, but probably about 2001, Docket No. 72-26. Diablo Canyon: Independent Spent Fuel Storage Installation, Environmental Report, 202 pp. Available at https://www.nrc.gov/docs/ML0201/ML020180196.pdf.

Austin, W.C. (1985) *An Annotated Checklist of Marine Invertebrates in the Cold Temperate Northeast Pacific. Volume 1*. Khoyatan Marine Laboratory, Cowichan Bay, British Columbia, Canada, 218 pp.

Barr, L. & Barr, N. (1983) *Under Alaskan Seas: The Shallow Water Marine Invertebrates*. Alaska Northwest Publishing Company, Anchorage, 208 pp.

Berrill, M. (1962) The biology of three New England stauromedusae, with a description of a new species. *Canadian Journal of Zoology*, 40(7), 1262–1249. DOI: 10.1139/z62-101

Bigelow, H.B. (1920) *Report of the Canadian Arctic Expedition 1913–18, Vol. 8, Part H: Medusae and Ctenophora*. Thomas Mulvey, Printer to the King's Most Excellent Majesty, Ottawa, 22 pp., 2 pls.

Brewer, R., Chenelot, H., Harper, S. & Jewett, S. (2011) *Sea Life of the Aleutians: An Underwater Exploration*. Alaska Sea Grant College Program, University of Alaska, Fairbanks, 146 pp.

Brusca, G.J. & Brusca, R.C. (1978) *A Naturalist's Seashore Guide: Common Marine Life of the Northern California Coast and Adjacent Shores*. Mad River Press, Eureka, California, 205 pp.

Cadien, D.B, Lovell, L.L., Barwick, K.L, & Haggin, B.M. (Ed.) (2018) *A Taxonomic Listing of Benthic Macro- and Megainvertebrates from Infaunal and Epifaunal Monitoring and Research Programs in the Southern California Bight. Edition 12*. Prepared by the Southern California Association of Marine Invertebrate Taxonomists, Natural History Museum of Los

Angeles County, Research & Collections, 900 Exposition Boulevard, Los Angeles, California, 167 pp.

Caine, E.A. (1980) Ecology of two littoral species of caprellid amphipods (Crustacea) from Washington, USA. *Marine Biology*, 56, 327–335.

Cairns, S.D., Calder, D.R., Brinckmann-Voss, A., Castro, C.B., Pugh, P.R., Cutress, C.E., Jaap, W.C., Fautin, D.G., Larson, R.J., Harbison, G.R., Arai, M.N. & Opresko, D.M. (1991) *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Cnidaria and Ctenophora*. American Fisheries Society, Special Publication 22, Bethesda, Maryland, 80 pp.

Cairns, S.D., Calder, D.R., Brinckmann-Voss, A., Castro, C.B., Fautin, D.G., Pugh, P.R., Mills, C.E., Jaap, W.C., Arai, M.N., Haddock, S.H.D. & Opresko, D.M. (2002) *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Cnidaria and Ctenophora. Second Edition*. American Fisheries Society, Special Publication 28, Bethesda, Maryland, 115 pp.

Collins, A.G. (2000) Towards understanding the phylogenetic history of Hydrozoa: hypothesis testing with 18S gene sequence data. *Scientia Marina*, 64 (Supplement 1), 5–22.

Collins, A.G. (2002) Phylogeny of Medusozoa and the evolution of cnidarian life cycles. *Journal of Evolutionary Biology*, 15, 418–432.

Collins, A.G., Bentlage, B., Matsumoto, G.I., Haddock, S.H.D., Osborn, K.J. & Schierwater, B. (2006a) Solution to the phylogenetic enigma of *Tetraplatia*, a worm-shaped cnidarian. *Biology Letters*, 2, 120–124. DOI: 10.1098/rsbl.2005.0372

Collins, A.G. & Daly, M. (2005) A new deepwater species of Stauromedusae, *Lucernaria janetae* (Cnidaria, Staurozoa, Lucernariidae), and a preliminary investigation of stauromedusan phylogeny based on nuclear and mitochondrial rDNA data. *Biological Bulletin*, 208, 221–230. DOI: 10.2307/3593154

Collins, A.G., Schuchert, P., Marques, A.C., Jankowski, T., Medina, M. & Schierwater, B. (2006b) Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. *Systematic Biology*, 55, 97–115. DOI: 10.1080/10635150500433615

Eckelbarger, K.J. (1994) Oocytic nutrition in the lower Metazoa: the Scyphozoa. *In:* Wilson, W.H. Jr., Stricker, S.A. & Shinn, G.L. (Ed.) *Reproduction and Development of Marine Invertebrates*, The Johns Hopkins University Press, Baltimore, pp. 15–28.

Eckelbarger, K.J. & Larson, R.J. (1993) Ultrastructural study of the ovary of the sessile scyphozoan, *Haliclystus octoradiatus* (Cnidaria: Stauromedusae). *Journal of Morphology*, 218, 225–236.

Flora, C.J. & Fairbanks, E. (1977) The Sound and the Sea: A Guide to Northwestern Neritic Invertebrate Zoology. The Washington State Department of Printing, Olympia, Washington, 476 pp.

Gellermann, M.P. (1926) *Medusae of the San Juan Archipelago*. M.S. Thesis, University of Washington, Seattle, 100 pp. and 37 plates.

Gornik, S.G., Bergheim, B.G., Morel, B., Stamatakis, A., Foulkes, N.S. & Guse, A. (2021) Photoreceptor diversification accompanies the evolution of Anthozoa. *Molecular Biology and Evolution*, 38 (5), 1744–1760. DOI: 10.1093/molbev/msaa304

Guberlet, M.L. (1936) *Animals of the Seashore*. Metropolitan Press, Portland, Oregon, 410 pp.

Guberlet, M.L. (1949) *Animals of the Seashore (revised)*. Binfords & Mort, Publishers, Portland, Oregon, 410 pp.

Gwilliam, G.F. Jr. (1956) *Studies on Western North American Stauromedusae*. Ph.D. Dissertation, University of California, Berkeley, 192 pp.

Gwilliam, G.F. (1960) Neuromuscular physiology of a sessile scyphozoan. *Biological Bulletin*, 119, 454–473.

Hartigan, A., Jaimes-Becerra, A., Okamura, B., Doonan, L.B., Ward, M., Marques, A.C. & Long, P.F. (2021) Recruitment of toxin-like proteins with ancestral venom function supports endoparasitic lifestyles of Myxozoa. *PeerJ*, 9, e11208. DOI: 10.7717/peerj.11208

Heeger, T. (1998) *Quallen: Gefährliche Schönheiten*. Wissenschaftliche Verlagsgesellschaft mbH, Stuttgart, 358 pp.

Hirano, Y.M. (1986) Species of stauromedusae from Hokkaido, with notes on their metamorphosis. *Journal of the Faculty of Science, Hokkaido University, Series VI, Zoology*, 24, 182–201.

Hirano, Y.M. (1997) A review of a supposedly circumboreal species of stauromedusa, *Haliclystus auricula* (Rathke, 1806). *Proceedings of the 6th International Conference on Coelenterate Biology, 1995*, pp. 247–252.

Holst, S., Heins, A. & Laakmann, S. (2019) Morphological and molecular diagnostic species characters of Staurozoa (Cnidaria) collected on the coast of Helgoland (German Bight, North Sea). *Marine Biodiversity*, 49, 1775–1797. DOI: 10.1007/s12526-019-00943-1

Holst, S. & Laakmann, S. (2019) First record of the stalked jellyfish *Haliclystus tenuis* Kishinouye, 1910 (Cnidaria: Staurozoa) in Atlantic waters. *Marine Biodiversity*, 49, 1061–1066. DOI: 10.1007/s12526-018-0888-3

Holst, S., Miranda, L.S., Meyer, P., Michalik, P. & Sötje, I. (2021) Morphological analyses of the adult and juvenile stages of the stalked jellyfish *Craterolophus convolvulus* (Johnston,

1835) (Cnidaria: Staurozoa: Stauromedusae: Craterolophidae) using micro-CT. *Zoologischer Anzeiger*, 292, 240–260. DOI: 10.1016/j.jcz.2021.04.005

Hyman, L.H. (1940a) *The Invertebrates: Protozoa through Ctenophora*. *Vol. I*. McGraw-Hill Book Company, New York & London, 726 pp.

Hyman, L.H. (1940b) Observations and experiments on the physiology of medusae. *Biological Bulletin*, 79, 282–296.

International Commission on Zoological Nomenclature (1999) *International Code of Zoological Nomenclature, Fourth edition.* International Trust for Zoological Nomenclature, London, xxix + 306 pp.

James-Clark, H. (1863) Prodromus of the history, structure, and physiology of the order Lucernariae. *Journal of the Boston Society of Natural History*, 7, 531–567.

Jensen, G.C., Gotshall, D.W. & Flores Miller, R.E. (2018) *Beneath Pacific Tides: Subtidal Invertebrates of the West Coast.* MolaMarine, Bremerton, 296 pp.

Kahn, A.S., Matsumoto, G.I., Hirano, Y.M. & Collins, A.G. (2010) *Haliclystus californiensis*, a "new" species of stauromedusa (Cnidaria: Staurozoa) from the northeast Pacific, with a key to the species of *Haliclystus*. *Zootaxa*, 2518, 49–59. DOI: 10.11646/zootaxa.2518.1.3

Kayal, E., Bentlage, B., Collins, A.G., Kayal, M., Pirro, S., & Lavrov, D.V. (2012) Evolution of linear mitochondrial genomes in medusozoan cnidarians. *Genome Biology and Evolution*, 4, 1–12. DOI: 10.1093/gbe/evr123

Kayal, E., Bentlage, B., Pankey, M.S., Ohdera, A.H., Medina, M., Plachetzki, D.C., Collins, A.G. & Ryan, J.F. (2018) Phylogenomics provides a robust topology of the major cnidarian lineages and insights on the origins of key organismal traits. *BMC Evolutionary Biology*, 18, 68. DOI: 10.1186/s12862-018-1142-0

Kayal, E., Roure, B., Phillippe, H., Collins, A.G. & Lavrov, D.V. (2013) Cnidarian phylogenetic relationships as revealed by mitogenomics. *BMC Evolutionary Biology*, 13, 5. DOI: 10.1186/1471-2148-13-5

Kishinouye, K. (1899) Contributions to the natural history of the Commander Islands. XIII. A new species of stalked medusae, *Haliclystus stejnegeri*. *Proceedings of the United States National Museum* [No. 1188], 22, 125–129.

Knapp, S.K. (1950) *Checklist of the Animals for the Coos Bay Area*. Student report, Summer, 1950, Oregon Institute of Marine Biology, Charleston, Oregon, 17 pp. On file at the University of Oregon Institute of Marine Biology Library (accessed July 2019).

Koch, T.L. & Grimmelikhuijzen, C.J.P. (2019) Global neuropeptide annotations from the genomes and transcriptomes of Cubozoa, Scyphozoa, Staurozoa (Cnidaria: Medusozoa), and Octocorallia (Cnidaria: Anthozoa). *Frontiers in Endocrinology*, 10, 831. DOI:10.3389/fendo.2019.00831

Kozloff, E.N. (1973) *Seashore Life of Puget Sound, the Strait of Georgia, and the San Juan Archipelago*. University of Washington Press, Seattle and London, 282 pp. and 28 plates.

Kozloff, E.N. (1974) *Keys to the Marine Invertebrates of Puget Sound, the San Juan Archipelago, and Adjacent Regions*. University of Washington Press, Seattle and London, 226 pp.

Kozloff, E.N. (1996) *Seashore Life of the Northern Pacific Coast: An Illustrated Guide to Northern California, Oregon, Washington, and British Columbia*. University of Washington Press, Seattle and London, 370 pp.

Kramp, P.L. (1957) Medusae. *B.A.N.Z. Antarctic Research Expedition, 1929–31, Series B, Volume 6, Part 8*, 151–164.

Kramp, P.L. (1961) Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom*, 40, 1–469.

Lamb, A. & Hanby, B.P. (2005 & 2015) *Marine Life of the Pacific Northwest: A Photographic Encyclopedia of Invertebrates, Seaweeds and Selected Fishes*. Harbour Publishing, Madeira Park, British Columbia, 398 pp.

Larson, R.J. (1990) Scyphomedusae and cubomedusae from the eastern Pacific. *Bulletin of Marine Science*, 47, 546–556.

Lewandowska, M., Hazan, Y. & Moran, Y. (2020) Initial virome characterization of the common cnidarian lab model *Nematostella vectensis*. *Viruses*, 12, 218. DOI: 10.3390/v12020218

Li, H.-H., Sung, P.-J. & Ho, H.-C. (2016) The complete mitochondrial genome of the Antarctic stalked jellyfish, *Haliclystus antarcticus* Pfeffer, 1889 (Staurozoa: Stauromedusae). *Genomics Data*, 8, 113–114. DOI: 10.1016/j.gdata.2016.04.012

MacGinitie, G.E. & MacGinitie, N. (1949) *Natural History of Marine Animals*. McGraw-Hill Book Company, Inc., New York, 473 pp.

MacGinitie, G.E. & MacGinitie, N. (1968) *Natural History of Marine Animals. Second Edition.* McGraw-Hill Book Company, Inc., New York, 523 pp.

McLean, J.H. (1962) Sublittoral ecology of kelp beds of the open coast area near Carmel, California. *Biological Bulletin*, 122, 95–114.

Mejía-Sánchez, N. & Marques, A.C. (2013) Getting information from ethanol preserved nematocysts of the venomous cubomedusa *Chiropsalmus quadrumanus*: a simple technique to facilitate the study of nematocysts. *Latin American Journal of Aquatic Research*, 41, 166–169. DOI: 10.3856/vol41-issue1-fulltext-14

Mills, C.E. (1987) Key to the Class Scyphozoa, Orders Semaeostomeae and Stauromedusae. *In:* Kozloff, E.N. & Price, L.H. (Ed.) *Marine Invertebrates of the Pacific Northwest*. University of Washington Press, Seattle, pp. 65–67.

Mills, C.E. (1996) Key to the Class Scyphozoa, Orders Semaeostomeae and Stauromedusae and New key to Order Stauromedusae. *In:* Kozloff, E.N. & Price, L.H. (Ed.) *Marine Invertebrates of the Pacific Northwest*, *with Additions and Corrections*, University of Washington Press, Seattle. pp. 65–67, 489.

Mills, C.E. (1999–present) Stauromedusae: list of all valid species names. Friday Harbor Laboratories, Friday Harbor, Washington. Available from http://faculty.washington.edu/cemills/Staurolist.html (accessed March 2023).

Mills, C.E. & Hirano, Y.M. (2007) Stauromedusae. *In:* Denny, M.W. & Gaines, S.D. (Ed.) *Encyclopedia of Tidepools and Rocky Shores*. University of California Press, Berkeley, pp. 539–541.

Mills, C.E. & Larson, R.J. (2007) Scyphozoa: Scyphomedusae, Stauromedusae, and Cubomedusae. *In:* Carlton, J.T. (Ed.) *The Light and Smith Manual: Intertidal Invertebrates from Central California to Oregon. Fourth Edition.* University of California Press, Berkeley, pp. 168–173.

Miranda, L.S. & Collins, A.G. (2019) Eyes in Staurozoa: a review. *PeerJ*, 7, e6693, 13 pp. DOI: 10.7717/peerj.6693

Miranda, L.S., Collins, A.G., Hirano, Y.M., Mills, C.E. & Marques, A.C. (2016b) Comparative internal anatomy of Staurozoa (Cnidaria) with functional and evolutionary inferences. *PeerJ*, 4, e2594, 83 pp. DOI: 10.7717/peerj.2594

Miranda, L.S., Collins, A.G. & Marques, A.C. (2010) Molecules clarify a cnidarian life cycle – the "hydrozoan" *Microhydrula limopsicola* is an early life stage of the staurozoan *Haliclystus antarcticus*. *PLoS One*, 5, e10182, 9 pp. DOI: 10.1371/journal.pone.0010182

Miranda, L.S., Collins, A.G. & Marques, A.C. (2013) Internal anatomy of *Haliclystus antarcticus* (Cnidaria, Staurozoa) with a discussion on histological features used in staurozoan taxonomy. *Journal of Morphology*, 274, 1365–1383. DOI: 10.1002/jmor.20185

Miranda, L.S., García-Rodriguez, J., Collins, A.G., Morandini, A.C. & Marques, A.C. (2017) Evolution of claustrum in Cnidaria: comparative anatomy reveals that it is exclusive to some species of Staurozoa and absent in Cubozoa. *Organisms Diversity & Evolution*, 17, 753–766. DOI: 10.1007/s13127-017-0342-6

Miranda, L.S., Hirano, Y.M., Mills, C.E., Falconer, A., Fenwick, D., Marques, A.C. & Collins, A.G. (2016a) Systematics of stalked jellyfishes (Cnidaria: Staurozoa). *PeerJ*, 4, e1951, 48 pp. DOI: 10.7717/peerj.1951

Miranda, L.S., Mills, C.E., Hirano, Y.M., Collins, A.G. & Marques, A.C. (2018) A review of the global diversity and natural history of stalked jellyfishes (Cnidaria, Staurozoa). *Marine Biodiversity*, 48, 1695–1714. DOI: 10.1007/s12526-017-0721-4

Miranda, L.S., Morandini, A.C. & Marques, A.C. (2009) Taxonomic review of *Haliclystus antarcticus* Pfeffer, 1889 (Stauromedusae, Staurozoa, Cnidaria), with remarks on the genus *Haliclystus* Clark, 1863. *Polar Biology*, 32, 1507–1519. DOI: 10.1007/s00300-009-0648-8

Naumov, D.V. (1961) Stsifoidnye meduzy morei SSSR (Scyphomedusae of the seas of the USSR). *Akademiya Nauk SSSR, Opredeliteli po Faune SSSR*, 75, 1–98.

Nicosia, A., Bennici, C., Biondo, G., Costa, S., Di Natale, M., Masullo, T., Monastero, C., Ragusa, M.A., Tagliavia, M. & Cuttitta A. (2018) Characterization of translationally controlled tumour protein from the sea anemone *Anemonia viridis* and transcriptome wide identification of cnidarian homologues. *Genes*, 9(1), 30. DOI: 10.3390/genes9010030

O'Clair, R.M. & O'Clair, C.E. (1998) *Southeast Alaska's Rocky Shores*: *Animals*. Plant Press, Auke Bay, Alaska, 562 pp.

Östman, C. (2000) A guideline to nematocyst nomenclature and classification, and some notes on the systematic value of nematocysts. *Scientia Marina*, 64 (Supplement 1), 31–46.

Otto, J.J. (1976) Early development and planula movement in *Haliclystus* (Scyphozoa: Stauromedusae). *In:* Mackie, G.O. (Ed.) *Coelenterate Ecology and Behavior*. Plenum Press, New York and London, pp. 319–329.

Otto, J.J. (1978) The settlement of *Haliclystus* planulae. *In:* Chia, F.-S. & Rice, M.E. (Ed.) *Settlement and Metamorphosis of Marine Invertebrate Larvae*. Elsevier, New York, pp. 13–22.

Phillips, R.C. (1984) *The Ecology of Eelgrass Meadows in the Pacific Northwest: A Community Profile*. United States Fish and Wildlife Service, FWS/OBS-84/24, 85 pp.

Ricketts, E.F. (1929) *Preserved Zoological Specimens and Mounted Museum Specimens*. Pacific Biological Laboratories, Pacific Grove, California, 27 pp.

Ricketts, E.F. & Calvin, J. (1939) *Between Pacific Tides* [First Edition]. Stanford University Press, Stanford, xxii + 320 pp.

Ricketts, E.F. & Calvin, J. (1948) *Between Pacific Tides. Revised (Second) Edition*. Stanford University Press, Stanford, xxvii +365 pp.

Ricketts, E.F., Calvin, J. & Hedgpeth, J.W. (1952) *Between Pacific Tides. Third Edition*. Stanford University Press, Stanford, xiii + 502 pp.

Ricketts, E.F., Calvin, J. & Hedgpeth, J.W. (1962) *Between Pacific Tides. Revised Third Edition*. Stanford University Press, Stanford, xiii + 516 pp.

Ricketts, E.F., Calvin, J. & Hedgpeth, J.W. (1968) *Between Pacific Tides. Fourth Edition*. Stanford University Press, Stanford, xiv + 614 pp.

Ricketts, E.F., Calvin, J., Hedgpeth, J.W. & Phillips, D.W. (1985) *Between Pacific Tides. Fifth Edition*. Stanford University Press, Stanford, xxvi + 652 pp.

Rodger, K.A. (Ed.) (2006) *Breaking Through: Essays, Journals, and Travelogues of Edward F. Ricketts*. University of California Press, Berkley, 348 pp.

Santander, M.D., Maronna, M.M., Ryan, J.F. & Andrade, S.C.S. (2022) The state of Medusozoa genomics: current evidence and future challenges. *GigaScience*, 11, 1–14. DOI: 10.1093/gigascience/giac036

Sheiko, O. & Stepanyants, S. 1990. Far East representatives of stauromedusae of the family Eleutherocarpida. *In*: Gulbin, V.V. (Ed.) *Systematic and Ecology of the Hydrobionts of the Far-East Marine Reserve*. Far East Branch of the USSR Academy of Sciences, Vladivostok, pp. 30–43.

Singla, C.L. (1976) Ultrastructure and attachment of the basal disk of *Haliclystus*. *In:* Mackie, G.O. (Ed.) *Coelenterate Ecology and Behavior*. Plenum Press, New York and London, pp. 533–540.

Smith, L.S. (1976) *Living Shores of the Pacific Northwest*. Pacific Search Press, Seattle, 160 pp.

Smith, R.I. (1955) *Field notebook #3*, in the possession of James T. Carlton in early 2020, and to be deposited in the Cadet Hand Library of the Bodega Marine Laboratory, University of California, Davis.

Smith, R.I. (1970) Class Scyphozoa. *In:* Light, S.F., Smith, R.I., Pitelka, F.A., Abbott, D.P. & Weesner F.M. (Ed.) *Light's Manual: Intertidal Invertebrates of the Central California Coast. Second Edition*. University of California Press, Berkeley and Los Angeles, pp. 40–41.

Smith, R.I. (1975) Class Scyphozoa. *In:* Smith, R.I. & Carlton, J.T (Ed.) *Light's Manual: Intertidal Invertebrates of the Central California Coast. Third Edition*. University of California Press, Berkeley, Los Angeles and London, pp. 94–97.

Smith, R.I., Pitelka, F.A., Abbott, D.P. & Weesner, F.M., with the assistance of many other contributors (1954) *Intertidal Invertebrates of the Central California Coast*. University of California Press, Berkeley and Los Angeles, 446 pp.

Snively. G. (1978) *Exploring the Seashore in British Columbia, Washington and Oregon: A Guide to Shorebirds and Intertidal Plants and Animals*. Gordon Soules Book Publishers Ltd., Vancouver/London and Pacific Search Press, Seattle, 240 pp.

Steinbeck, J., Ricketts, E. & Hedgpeth, J.W (Ed.) (1978) *The Outer Shores, Part I: Ed Ricketts and John Steinbeck Explore the Pacific Coast*. Mad River Press, Eureka, California, 128 pp.

Steinworth, B.M., Martindale, M.Q. & Ryan, J.F. (2023) Gene loss may have shaped the cnidarian and bilaterian Hox and ParaHox complement. *Genome Biology and Evolution*, 15(1), evac172. DOI: 10.1093/gbe/evac172

Strathmann, M.F. (1987) Phylum Cnidaria, Class Scyphozoa. *In:* Strathmann, M.F. (Ed.) *Reproduction and Development of Marine Invertebrates of the Northern Pacific Coast.* University of Washington Press, Seattle and London, pp. 72–82.

Uchida, T. (1929) Studies on the Stauromedusae and Cubomedusae, with special reference to their metamorphosis. *Japanese Journal of Zoology*, 2, 103–193.

Vöcking, O., Macias-Muñoz, A., Jaeger, S.J. & Oakley, T.H. (2022) Deep diversity: extensive variation in the components of complex visual systems across animals. *Cells*, 11, 3966. DOI: 10.3390/cells11243966

Westfall, J.A. (1968) Electron microscopy of adhesive organs of the stalked jellyfish *Haliclystus*. *American Zoologist*, 8, 803–804 (Abstract).

Westfall, J.A. (1973) Ultrastructural evidence for neuromuscular systems in coelenterates. *American Zoologist*, 13, 236–246.

Westfall, J.A. (1987) Ultrastructure of invertebrate synapses. *In:* Ali, M.A. (Ed.) *Nervous Systems in Invertebrates*. Plenum Press, New York, pp. 3–28.

Westfall, J.A., Yamataka, S. & Enos, P.D. (1970) An ultrastructural survey of synapses in tentacles of coelenterates. *American Zoologist*, 10, 545 (Abstract).

Westlake, H. (2015) *A comparative immunohistochemical study of the neuromuscular organization of Haliclystus 'sanjuanensis' and Manania handi (Cnidaria: Staurozoa)*. M.S. Thesis, University of Victoria, British Columbia, Canada, 185 pp.

Westlake, H.E. & Page, L.R. (2017) Muscle and nerve net organization in stalked jellyfish (Medusozoa: Staurozoa). *Journal of Morphology*, 278, 29–49. DOI: 10.1002/jmor.20617

Wrobel, D. & Mills, C. (1998 & 2003) *Pacific Coast Pelagic Invertebrates: A Guide to the Common Gelatinous Animals*. Sea Challengers and the Monterey Bay Aquarium, Monterey, California, iv plus 108 pages.

Zagal, C.J. (2004) Diet of the stauromedusa *Haliclystus auricula* from southern Chile. *Journal of the Marine Biological Association of the United Kingdom*, 84, 337–340. DOI: 10.1017/S0025315404009245h

Zapata, F., Goetz, F.E., Smith, S.A., Howison, M., Siebert, S., Church, S.H., Sanders, S.M., Ames, C.L., McFadden, C.S., France, S.C., Daly, M., Collins, A.G., Haddock, S.H.D., Dunn, C. & Cartwright, P. (2015) Phylogenomic analyses support traditional relationships within Cnidaria. *PLoS ONE*,10(10):e139068. DOI: 10.1371/journal.pone.0139068

Zhang, X. & Jacobs, D. 2022. A broad survey of gene body and repeat methylation in Cnidaria reveals a complex evolutionary history. *Genome Biology and Evolution*, 14(2), evab284. DOI: 10.1093/gbe/evab284

FIGURES

Figure 1. *Haliclystus sanjuanensis* in the field. A, D, E) oral view; B, C) lateral view. A, B) images courtesy of Gustav Paulay, collected from Cattle Point, San Juan Island (type locality); C–E) images courtesy of Ron Larson from (C) Saxe Point, Victoria, British Columbia; (D) and (E) Seal Rock, Oregon. Abbreviations: am, arm; an, anchor; AR, adradii; cl, calyx; gd, gonad; IR, interradii; mn, manubrium; PR, perradii; sk, stalk; tc, secondary tentacles; ws, white nematocyst spot.

Figure 2. Dark stripes pattern in *Haliclystus sanjuanensis* (see also Table S2). A–D, F) lateral view; E) aboral view. A) Beresford Island, B.C., image courtesy of Neil McDaniel; B–D) Calvert Island, B.C., images courtesy of Gustav Paulay; E, F) Seal Rock, Oregon, images courtesy of Ron Larson. Abbreviations: am, arm; an, anchor; AR, adradii; cl, calyx; ds, dark stripes; gd, gonad; IR, interradii; PR, perradii; sk, stalk; tc, secondary tentacles.

Figure 3. Calyx of *Haliclystus sanjuanensis*, with anchors, gastric filaments, and secondary tentacles. A) Lateral view of a juvenile stauromedusa, with anchors with a remnant of primary tentacle; B–D) lateral view of adult stauromedusae, with more developed anchors with smaller remnant of primary tentacles; E) connection of anchor with calyx; F–G) gastric filaments inside gastrovascular cavity; H–J) secondary tentacles at arms tips. Abbreviations: an, anchor; gd, gonad; gf, gastric filaments; tc, secondary tentacles; ws, white nematocyst spot.

Figure 4. Calyx of *Haliclystus sanjuanensis* with manubrium and white nematocyst spots. A–B) general oral view; C–D) detail of manubrium, with perradial muscular fibers; E–G) general view of the pattern of distribution of white nematocyst spots; H) detail of white nematocyst spots. Abbreviation: gd, gonad; IR, interradii; mf, muscular fibers; mn, manubrium; PR, perradii; tc, secondary tentacles; ws, white nematocyst spot.

Figure 5. Stalk of *Haliclystus sanjuanensis*. A) Lateral view of stalk-calyx connection; B) lateral view of stalk, with pedal disc; C) basal view of pedal disc; D) lateral view of stalk, with four interradial longitudinal muscles and four perradial chambers; E–F) detail of lateral view of stalk, with four interradial longitudinal muscles and with four perradial chambers. Abbreviations: cl, calyx; mu, interradial longitudinal muscle; pc, perradial chamber; pd, pedal disc; sk, stalk.

Figure 6. Internal anatomy of stalk and calyx of a juvenile (immature) *Haliclystus sanjuanensis*. A) stalk, with four perradial chambers and four interradial longitudinal muscles; B) stalk-calyx connection, with fused gastric chambers into one main gastrovascular cavity; C–E) base

of manubrium region, with delimitation of four perradial gastric pockets; F) manubrium region, with central manubrium and four perradial gastric pockets delimited; G) detail of manubrium, with four corners; H) anchor of a juvenile specimen, with remnant of primary tentacle. A–G: cross-sections; H: longitudinal section. Abbreviations: ep, epidermis; gf, gastric filament; gp, perradial gastric pocket; gt, gastrodermis; gv, gastrovascular cavity; in, infundibulum; mn, manubrium; ms, mesoglea; mu, interradial longitudinal muscle; pc, perradial gastric chamber; rm, remnant of primary tentacle; sp, septum.

Figure 7. Interradial longitudinal muscle and infundibula of a juvenile (immature) *Haliclystus sanjuanensis*. A) Interradial longitudinal muscle in stalk; B) Interradial longitudinal muscle at the stalk-calyx connection; C) Interradial longitudinal muscle and infundibulum at calyx base, with a "group" of nematoblasts; D) wider infundibulum and compressed longitudinal muscle; E) even wider infundibulum and more compressed longitudinal muscle, at base of manubrium region, with two "groups" of nematoblasts. A–E) cross-sections. Abbreviations: ep, epidermis; gf, gastric filament; gt, gastrodermis; gv, gastrovascular cavity; in, infundibulum; ms, mesoglea; mu, interradial longitudinal muscle; nmb, nematoblasts; sp, septum.

Figure 8. Internal anatomy of arms tips, secondary tentacles, and white nematocyst spots of a juvenile (immature) *Haliclystus sanjuanensis*. A) Tip of arm, showing intertentacular lobules and secondary tentacles; B, C) detail of intertentacular lobules; D, E) stem of secondary tentacles, with longitudinal muscle; F) stem of secondary tentacles; G, H) knob of secondary tentacle; I) white nematocyst spot. A, B, D, E, G, I) longitudinal sections; C, F, H) cross-sections. Abbreviations: am,

arms; ep, epidermis; gt, gastrodermis; il, intertentacular lobules; ms, mesoglea; mu, longitudinal muscle; nmb, nematoblasts; st, stem; tc, secondary tentacles.

Figure 9. Nematocysts of *Haliclystus sanjuanensis*. A) Knob of a secondary tentacle, with nematocysts covering the capitate tip; B) stem of a secondary tentacle, with migrating nematocysts; C) general view of nematocysts of secondary tentacles; D) isorhizas of secondary tentacles; E) eurytele of secondary tentacles; F) discharged eurytele of secondary tentacles; G) general view of nematocysts of the white spots; H) birhopaloid of white spots; I) discharged birhopaloid of white spots, with two dilatations (black arrows) close together; J, K) nematocysts in the gastric filaments; L, M) nematocysts on exumbrellar surface.

Figure 10. Periderm of *Haliclystus sanjuanensis*. Periderm (A and B), in the form of a thin transparent cup (white arrows) that encases the pedal disc, that has been left behind after the stauromedusa *Haliclystus sanjuanensis* moved.

Figure 11. *Haliclystus sanjuanensis* spawning. A, B) Eggs release through month opening; C) gonadal vesicles, with many eggs; D) isolated egg. Abbreviations: eg, eggs; ve, gonadal vesicles; mn, manubrium.

Figure 12. Map of the geographic distribution of *Haliclystus sanjuanensis*. Star represents type locality.

Figure 13. General morphology of *Haliclystus stejnegeri*. A) Lateral view, with dark stripes pattern (see Table S2); B) oral view, with few white nematocyst spots at perradii. Abbreviations: ds, dark stripes; ws, white nematocyst spot. Images courtesy of Karen Sanamyan and Nadya Sanamyan (locality: Kamchatka, SE Kamchatka, Avacha Bay).

TABLE

Table 1. Holotype, paratypes, and additional material used in this study.

SUPPLEMENTAL TABLES

Table S1. Records of *Haliclystus sanjuanensis* based on this study, literature, photographs, specimens deposited in public and particular collections, and personal communications.

Table S2. Comparison of the thirteen described species of *Haliclystus*.

Table 1(on next page)

Holotype, paratypes, and additional material used in this study.

1 **Table 1.** Holotype, paratypes, and additional material used in this study.

Institution	Catalog number	Data
Smithsonian Institution, National Museum of Natural History	USNM 1522349	1 Holotype in 10% formalin, collected July 15, 2019
Smithsonian Institution, National Museum of Natural History	USNM 1522350	3 Paratypes in 10% formalin, collected July 15, 2019
Smithsonian Institution, National Museum of Natural History	USNM 1522351	5 specimens in 95% ethanol, collected July 15, 2019
Smithsonian Institution, National Museum of Natural History	USNM 1522352	11 specimens in 10% formalin, collected July 3, 2019
Smithsonian Institution, National Museum of Natural History	USNM 1522353	3 specimens in 10% formalin, collected July 29, 2019
Florida Museum at the University of Florida	UF Cnidaria 15456	3 Paratypes in 10% formalin, collected July 15, 2019
Florida Museum at the University of Florida	UF Cnidaria 15457	11 specimens in 10% formalin, collected July 3, 2019
Florida Museum at the University of Florida	UF Cnidaria 15458	5 specimens in 95% ethanol, collected July 15, 2019
California Academy of Sciences	CASIZ 236463	3 Paratypes in 10% formalin, collected July 15, 2019
California Academy of Sciences	CASIZ 236464	11 specimens in 10% formalin, collected July 3, 2019
California Academy of Sciences	CASIZ 236465	2 specimens in 10% formalin, collected July 29, 2019
California Academy of Sciences	CASIZ 236466	5 specimens in 95% ethanol, collected July 15, 2019
Royal British Columbia Museum	022-00040-001	3 Paratypes in 10% formalin, collected July 15,

		2019
Royal British Columbia Museum	022-00040-002	5 specimens in 95% ethanol, collected July 15, 2019
Royal British Columbia Museum	022-00041-001	11 specimens in 10% formalin, collected July 3, 2019
Royal British Columbia Museum	022-00042-001	3 specimens in 10% formalin, collected July 29, 2019
Friday Harbor Labs Synoptic collection	#3140	11 specimens in 10% formalin, collected July 3, 2019
Friday Harbor Labs Synoptic collection	#3141	5 specimens in 95% ethanol, collected July 15, 2019
Taxonomic Collections Center of the Federal University of Minas Gerais	UFMG-INV 2000003, Slides LABEC 001	1 specimen in 10% formalin, collected May 18–19, 2015

2

Figure 1

Haliclystus sanjuanensis in the field.

A, D, E) oral view; B, C) lateral view. A, B) images courtesy of Gustav Paulay, collected from Cattle Point, San Juan Island (type locality); C–E) images courtesy of Ron Larson from (C) Saxe Point, Victoria, British Columbia; (D) and (E) Seal Rock, Oregon. Abbreviations: am, arm; an, anchor; AR, adradii; cl, calyx; gd, gonad; IR, interradii; mn, manubrium; PR, perradii; sk, stalk; tc, secondary tentacles; ws, white nematocyst spot.

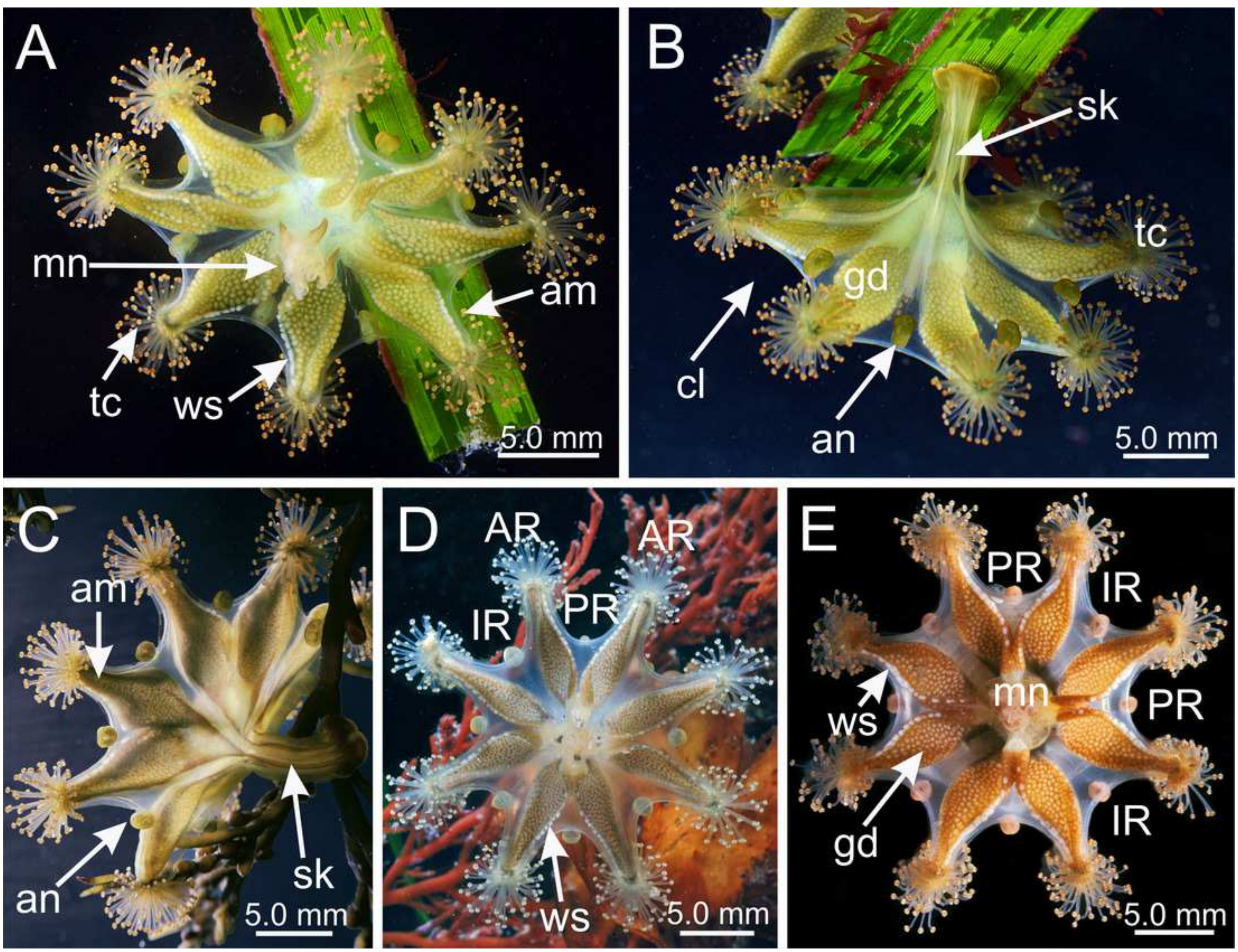

Figure 2

Dark stripes pattern in *Haliclystus sanjuanensis* (see also Table S2).

A–D, F) lateral view; E) aboral view. A) Beresford Island, B.C., image courtesy of Neil McDaniel; B–D) Calvert Island, B.C., images courtesy of Gustav Paulay; E, F) Seal Rock, Oregon, images courtesy of Ron Larson. Abbreviations: am, arm; an, anchor; AR, adradii; cl, calyx; ds, dark stripes; gd, gonad; IR, interradii; PR, perradii; sk, stalk; tc, secondary tentacles.

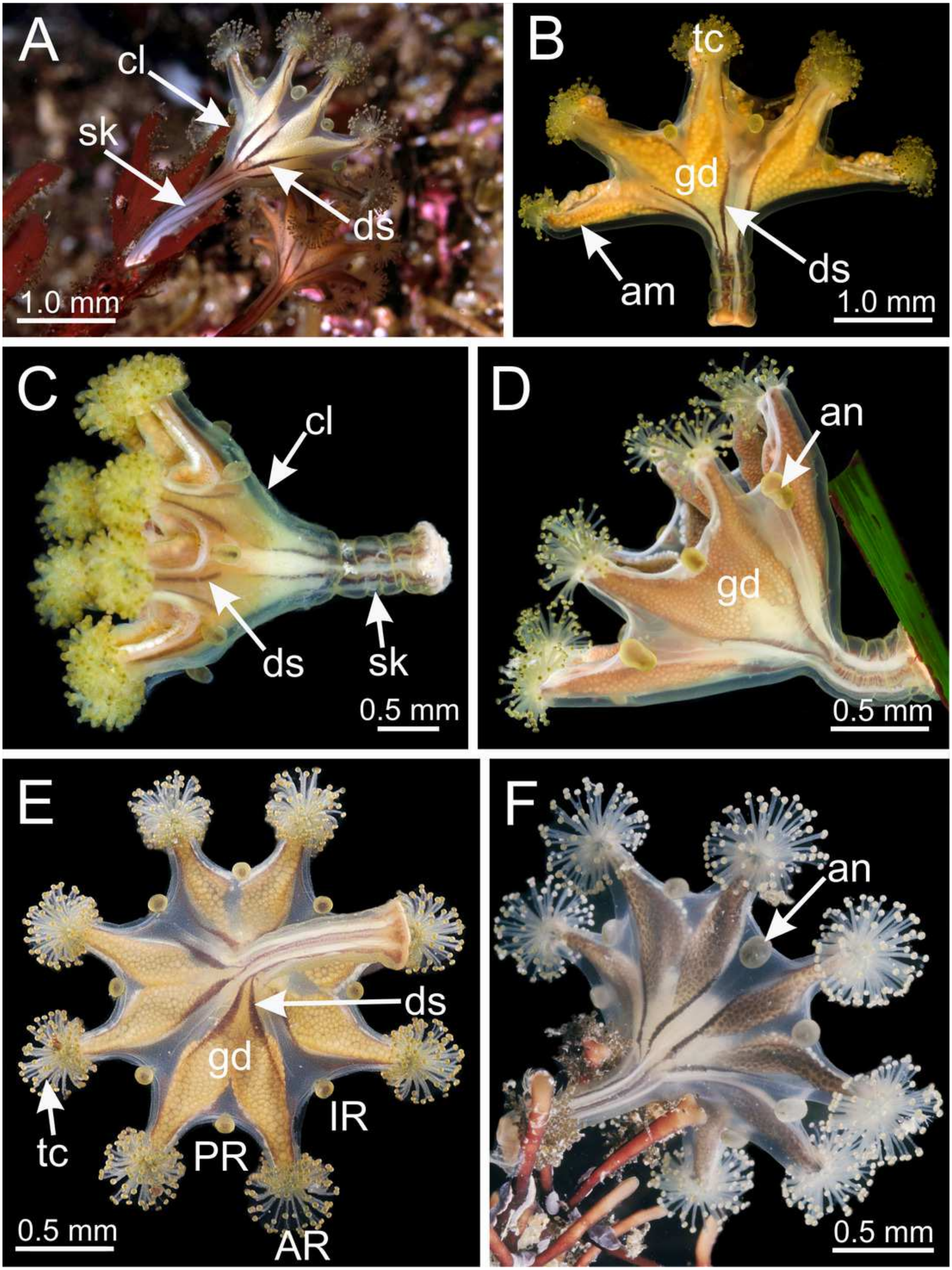
A
cl
sk
ds
1.0 mm
B
tc
gd
ds
am
1.0 mm
C
cl
ds
sk
0.5 mm
D
an
gd
0.5 mm
E
ds
gd
tc
IR
PR
AR
0.5 mm
F
an
0.5 mm

Figure 3

Calyx of *Haliclystus sanjuanensis*, with anchors, gastric filaments, and secondary tentacles.

A) Lateral view of a juvenile stauromedusa, with anchors with a remnant of primary tentacle; B–D) lateral view of adult stauromedusae, with more developed anchors with smaller remnant of primary tentacles; E) connection of anchor with calyx; F–G) gastric filaments inside gastrovascular cavity; H–J) secondary tentacles at arms tips. Abbreviations: an, anchor; gd, gonad; gf, gastric filaments; tc, secondary tentacles; ws, white nematocyst spot.

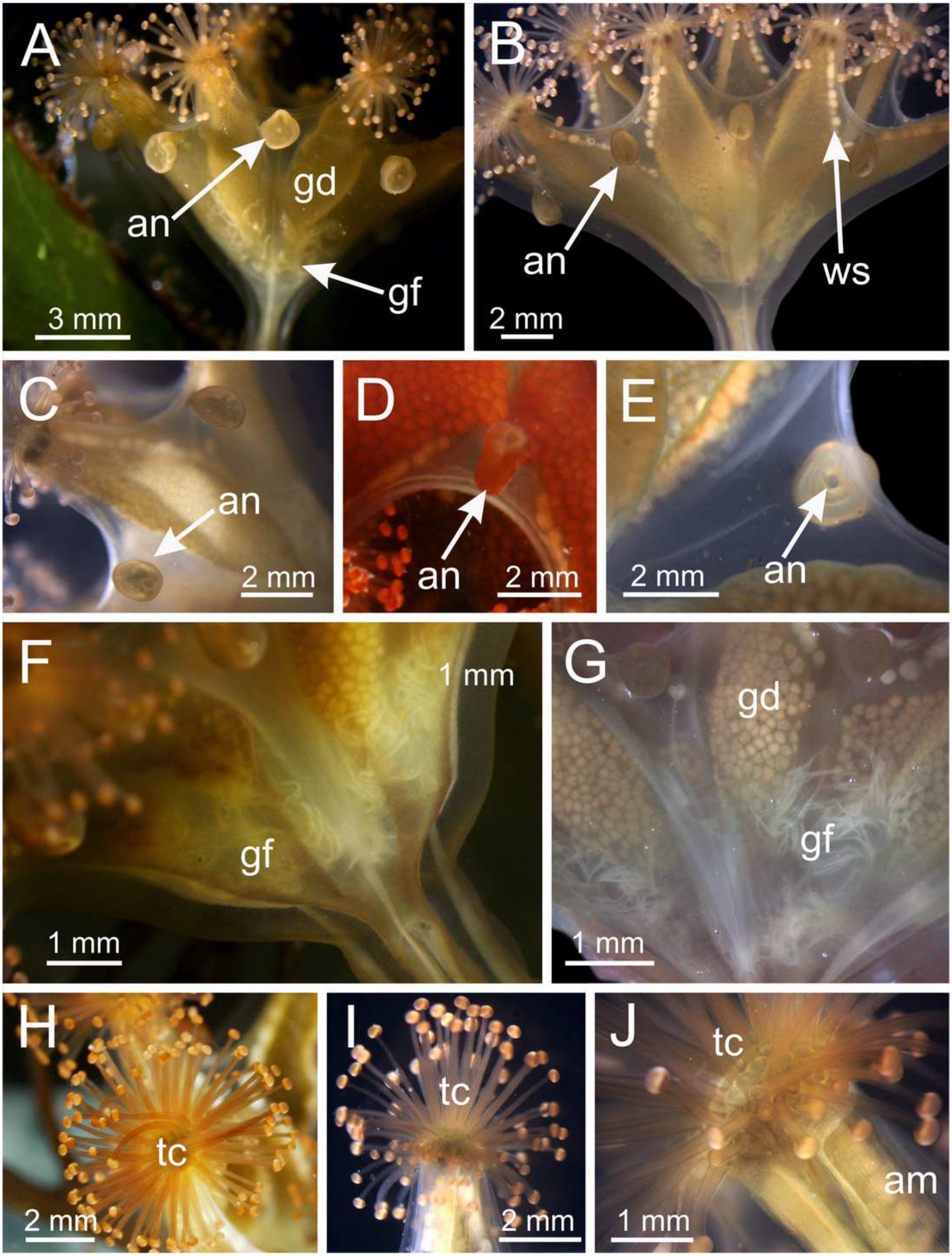
A
an
gd
gf
3 mm
B
an
ws
2 mm
C
an
2 mm
D
an
2 mm
E
2 mm
an
F
1 mm
gf
1 mm
G
gd
gf
1 mm
H
tc
2 mm
I
tc
2 mm
J
tc
am
1 mm

Figure 4

Calyx of *Haliclystus sanjuanensis* with manubrium and white nematocyst spots.

A–B) general oral view; C–D) detail of manubrium, with perradial muscular fibers; E–G) general view of the pattern of distribution of white nematocyst spots; H) detail of white nematocyst spots. Abbreviation: gd, gonad; IR, interradii; mf, muscular fibers; mn, manubrium; PR, perradii; tc, secondary tentacles; ws, white nematocyst spot.

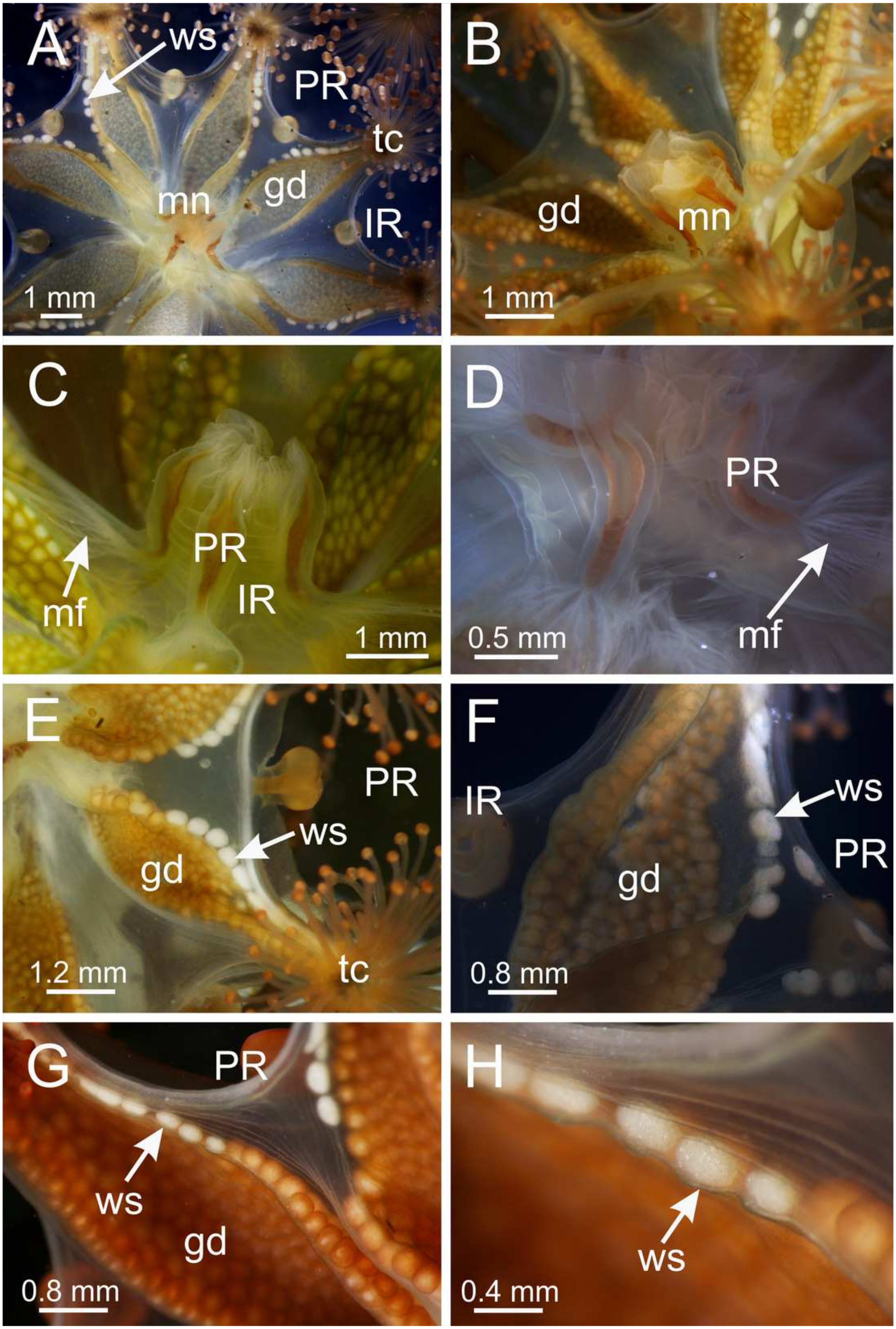
A
ws
PR
tc
gd
mn
IR
1 mm
B
gd
mn
1 mm
C
mf
PR
IR
1 mm
D
PR
mf
0.5 mm
E
PR
ws
gd
tc
1.2 mm
F
IR
ws
PR
gd
0.8 mm
G
PR
ws
gd
0.8 mm
H
ws
0.4 mm

Figure 5

Stalk of *Haliclystus sanjuanensis*.

A) Lateral view of stalk-calyx connection; B) lateral view of stalk, with pedal disc; C) basal view of pedal disc; D) lateral view of stalk, with four interradial longitudinal muscles and four perradial chambers; E–F) detail of lateral view of stalk, with four interradial longitudinal muscles and with four perradial chambers. Abbreviations: cl, calyx; mu, interradial longitudinal muscle; pc, perradial chamber; pd, pedal disc; sk, stalk.

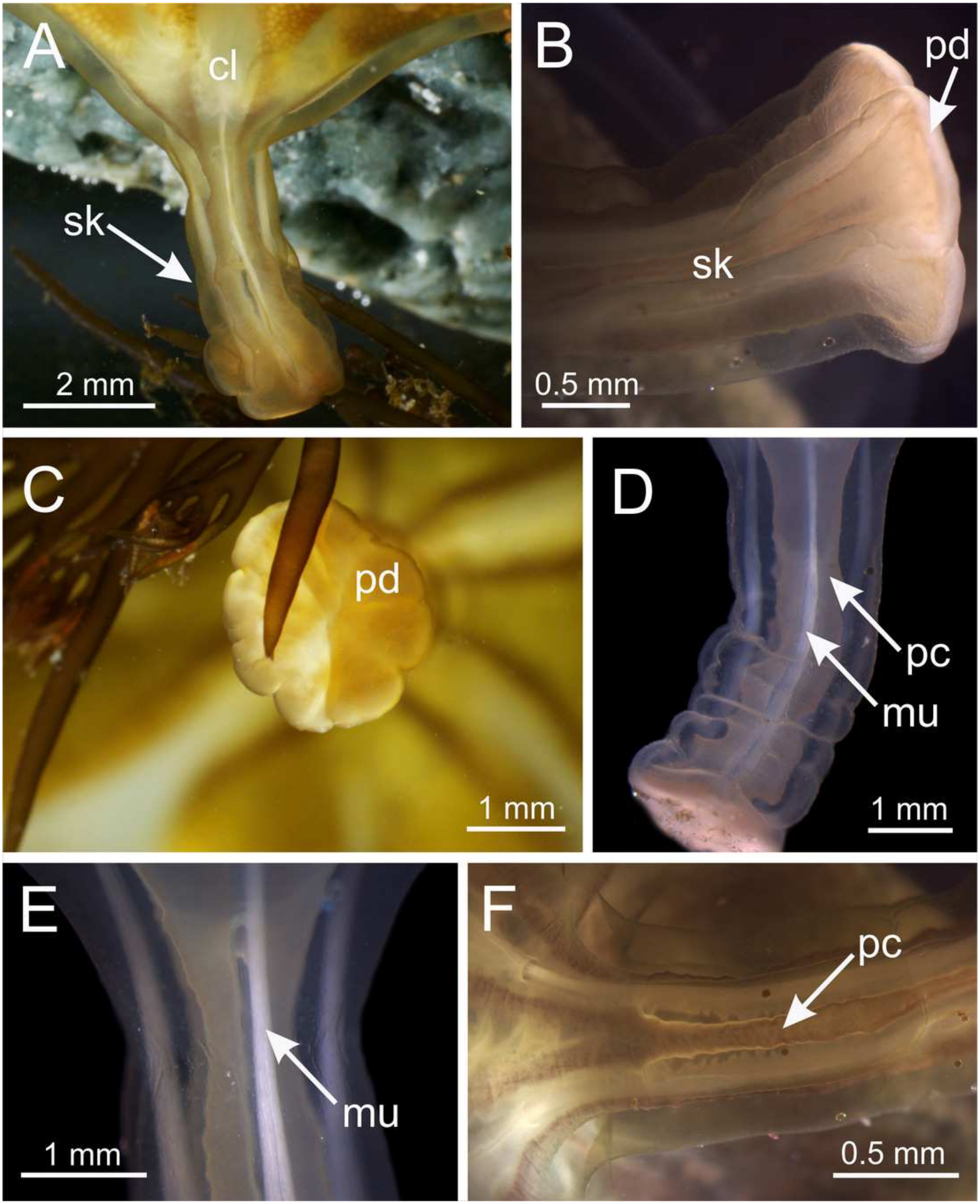
A
cl
sk
2 mm
B
pd
sk
0.5 mm
C
pd
1 mm
D
pc
mu
1 mm
E
mu
1 mm
F
pc
0.5 mm

Figure 6

Internal anatomy of stalk and calyx of a juvenile (immature) *Haliclystus sanjuanensis*.

A) stalk, with four perradial chambers and four interradial longitudinal muscles; B) stalk-calyx connection, with fused gastric chambers into one main gastrovascular cavity; C–E) base of manubrium region, with delimitation of four perradial gastric pockets; F) manubrium region, with central manubrium and four perradial gastric pockets delimited; G) detail of manubrium, with four corners; H) anchor of a juvenile specimen, with remnant of primary tentacle. A–G: cross-sections; H: longitudinal section. Abbreviations: ep, epidermis; gf, gastric filament; gp, perradial gastric pocket; gt, gastrodermis; gv, gastrovascular cavity; in, infundibulum; mn, manubrium; ms, mesoglea; mu, interradial longitudinal muscle; pc, perradial gastric chamber; rm, remnant of primary tentacle; sp, septum.

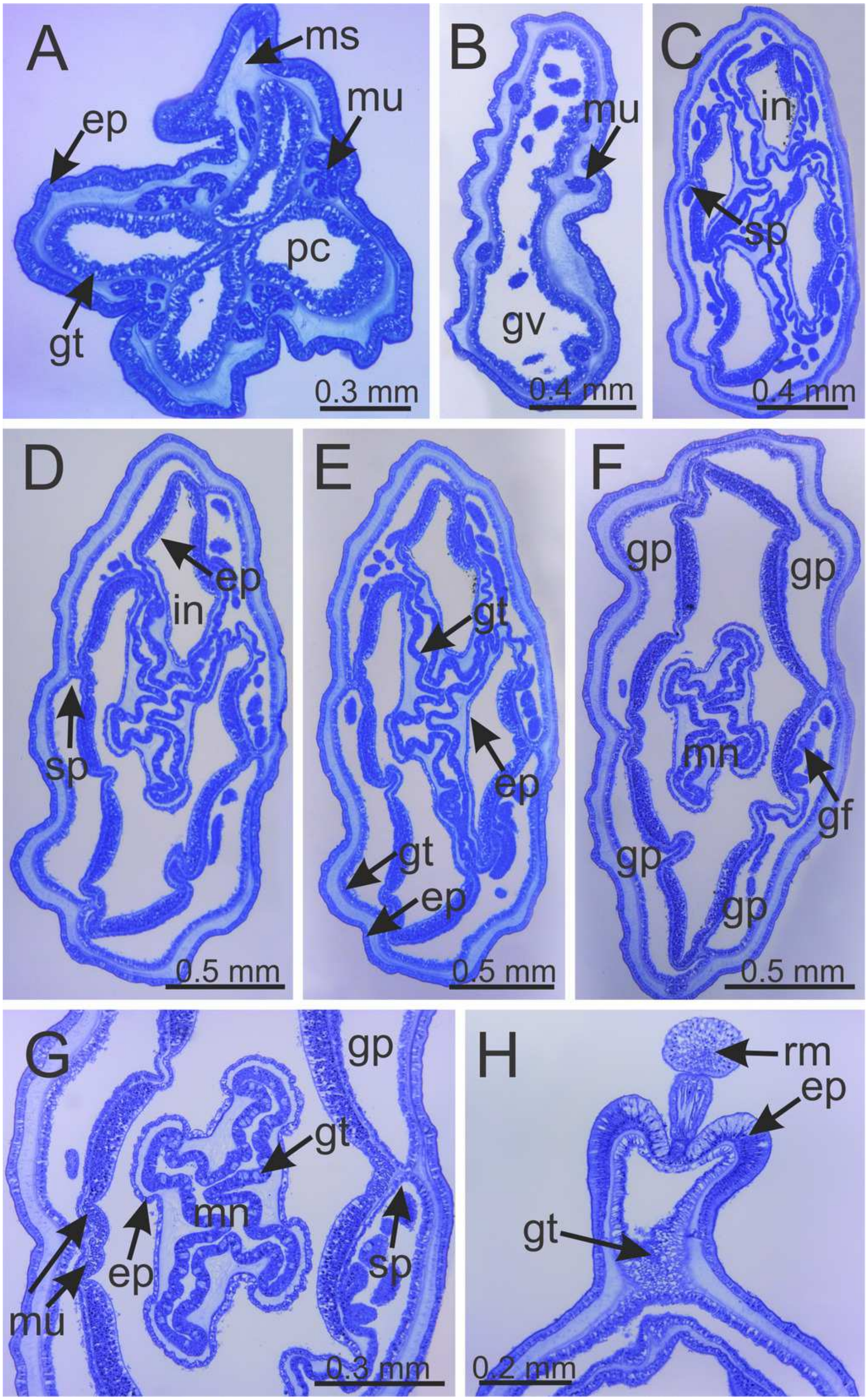
A
ms
mu
ep
pc
gt
0.3 mm
B
mu
gv
0.4 mm
C
in
sp
0.4 mm
D
ep
in
sp
0.5 mm
E
gt
ep
gt
ep
0.5 mm
F
gp
gp
mn
gf
gp
gp
0.5 mm
G
gp
gt
mn
ep
mu
sp
0.3 mm
H
rm
ep
gt
0.2 mm

Figure 7

Interradial longitudinal muscle and infundibula of a juvenile (immature) *Haliclystus sanjuanensis*.

A) Interradial longitudinal muscle in stalk; B) Interradial longitudinal muscle at the stalk-calyx connection; C) Interradial longitudinal muscle and infundibulum at calyx base, with a “group” of nematoblasts; D) wider infundibulum and compressed longitudinal muscle; E) even wider infundibulum and more compressed longitudinal muscle, at base of manubrium region, with two “groups” of nematoblasts. A–E) cross-sections. Abbreviations: ep, epidermis; gf, gastric filament; gt, gastrodermis; gv, gastrovascular cavity; in, infundibulum; ms, mesoglea; mu, interradial longitudinal muscle; nmb, nematoblasts; sp, septum.

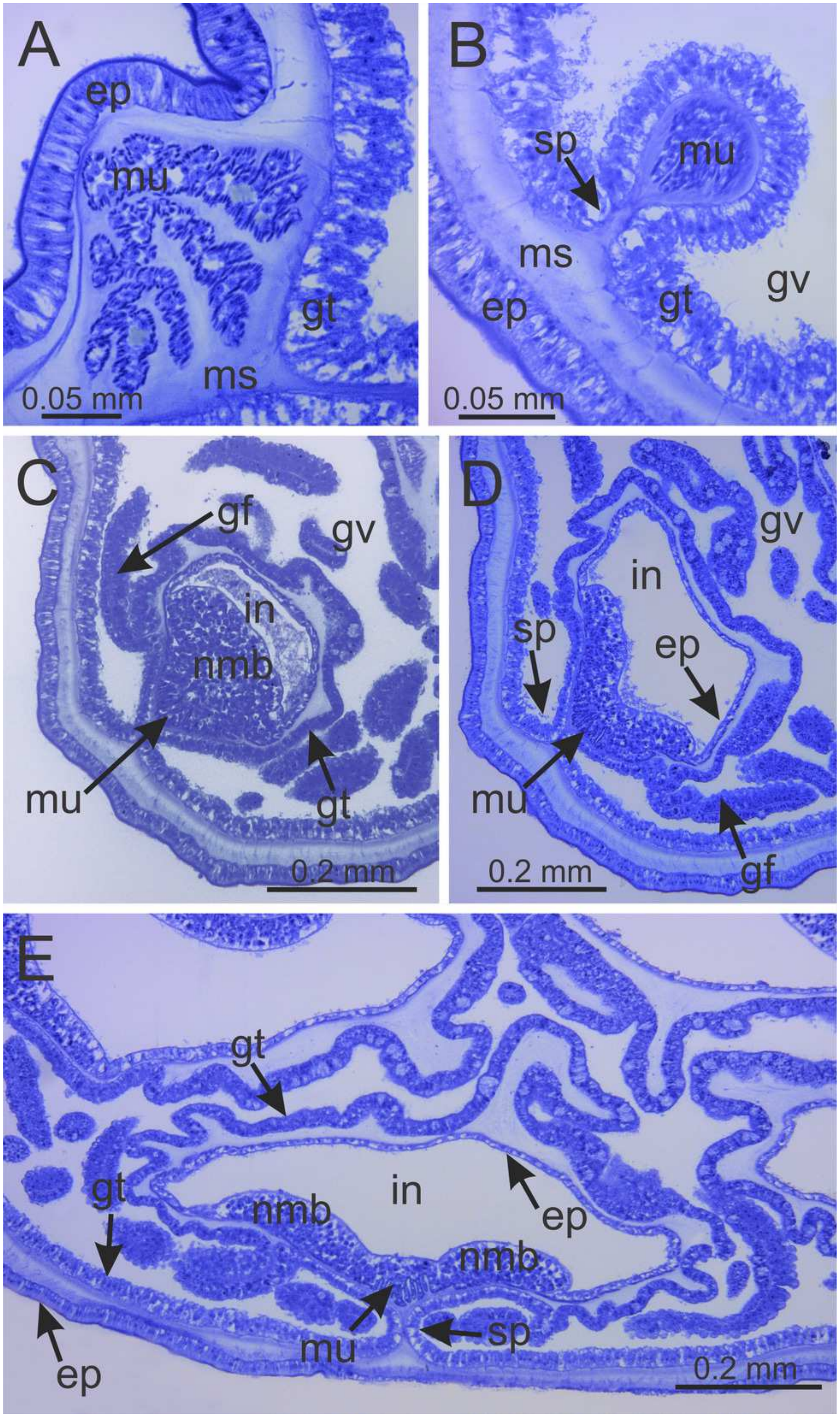
A
ep
mu
gt
ms
0.05 mm
B
sp
mu
ms
ep
gt
gv
0.05 mm
C
gf
gv
in
nmb
mu
gt
0.2 mm
D
gv
in
sp
ep
mu
gf
0.2 mm
E
gt
in
ep
nmb
nmb
mu
sp
ep
0.2 mm

Figure 8

Internal anatomy of arms tips, secondary tentacles, and white nematocyst spots of a juvenile (immature) *Haliclystus sanjuanensis*.

A) Tip of arm, showing intertentacular lobules and secondary tentacles; B, C) detail of intertentacular lobules; D, E) stem of secondary tentacles, with longitudinal muscle; F) stem of secondary tentacles; G, H) knob of secondary tentacle; I) white nematocyst spot. A, B, D, E, G, I) longitudinal sections; C, F, H) cross-sections. Abbreviations: am, arms; ep, epidermis; gt, gastrodermis; il, intertentacular lobules; ms, mesoglea; mu, longitudinal muscle; nmb, nematoblasts; st, stem; tc, secondary tentacles.

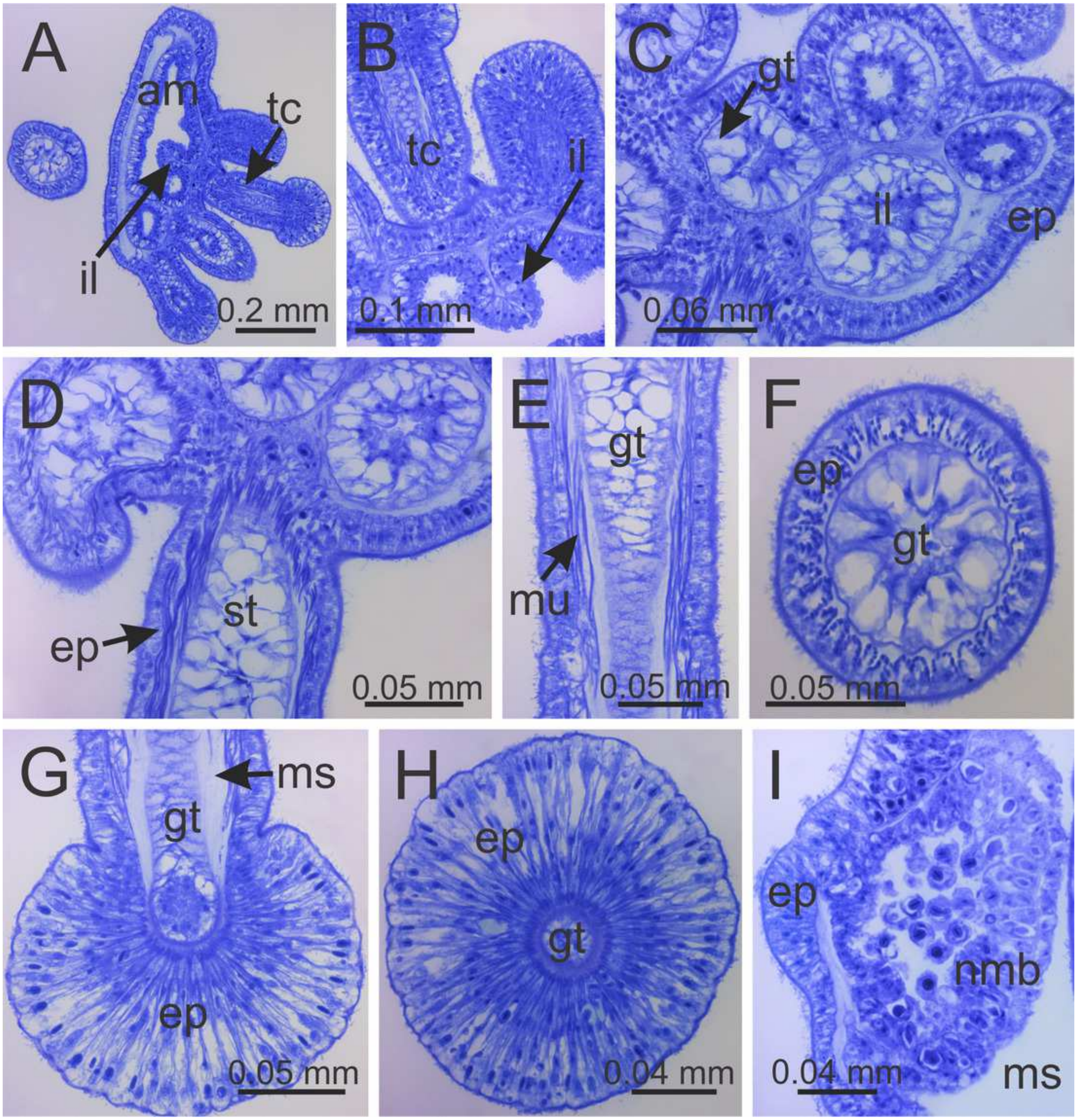
A
am
tc
il
0.2 mm
B
tc
il
0.1 mm
C
gt
il
ep
0.06 mm
D
ep
st
0.05 mm
E
gt
mu
0.05 mm
F
ep
gt
0.05 mm
G
ms
gt
ep
0.05 mm
H
ep
gt
0.04 mm
I
ep
nmb
0.04 mm
ms

Figure 9

Nematocysts of *Haliclystus sanjuanensis*.

A) Knob of a secondary tentacle, with nematocysts covering the capitate tip; B) stem of a secondary tentacle, with migrating nematocysts; C) general view of nematocysts of secondary tentacles; D) isorhizas of secondary tentacles; E) eurytele of secondary tentacles; F) discharged eurytele of secondary tentacles; G) general view of nematocysts of the white spots; H) birhopaloid of white spots; I) discharged birhopaloid of white spots, with two dilatations (black arrows) close together; J, K) nematocysts in the gastric filaments; L, M) nematocysts on exumbrellar surface.

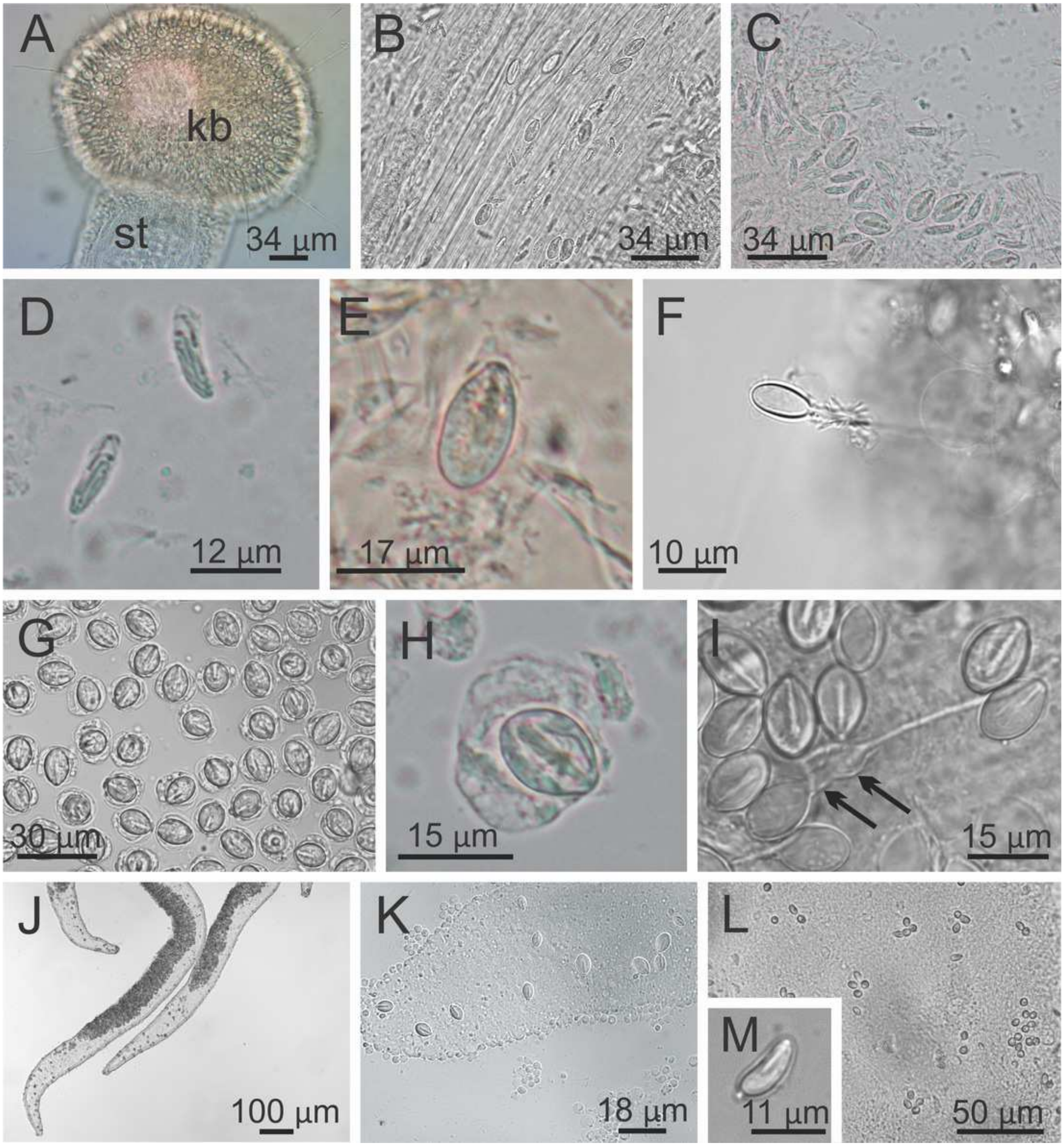
A
kb
st
34 µm
B
34 µm
C
34 µm
D
12 µm
E
17 µm
F
10 µm
G
30 µm
H
15 µm
I
15 µm
J
100 µm
K
18 µm
L
M
11 µm
50 µm

Figure 10

Periderm of *Haliclystus sanjuanensis*.

Periderm (A and B), in the form of a thin transparent cup (white arrows) that encases the pedal disc, that has been left behind after the stauromedusa *Haliclystus sanjuanensis* moved.

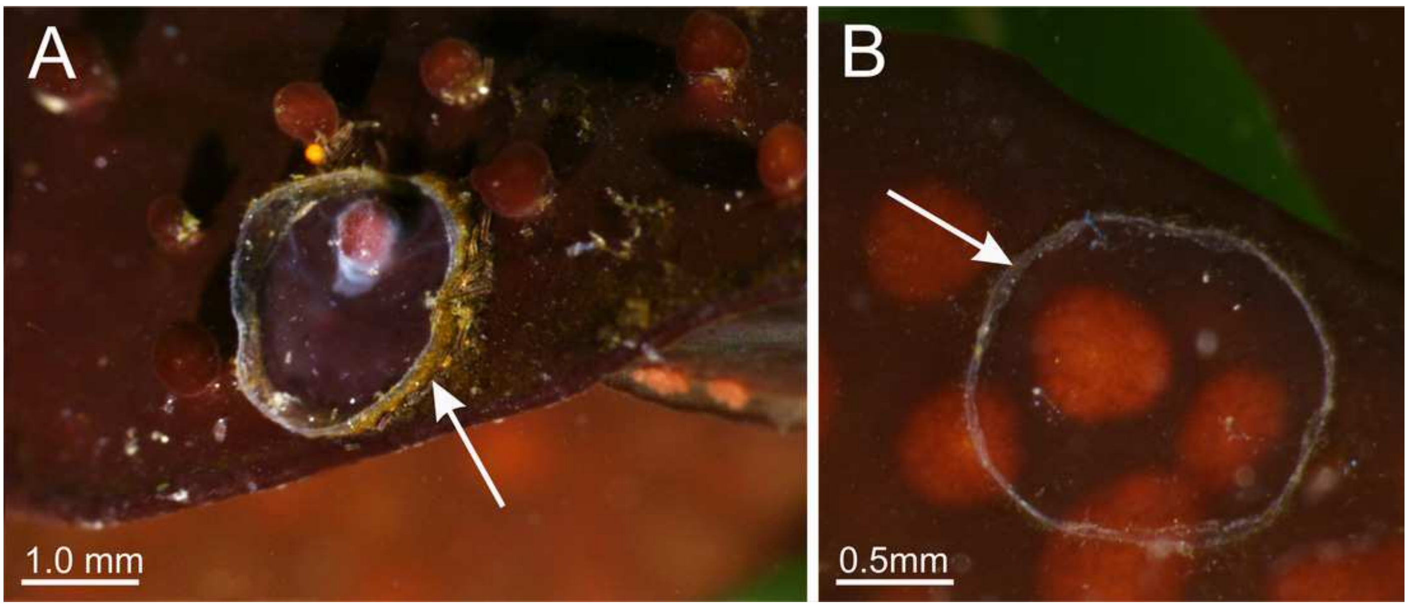

Figure 11

Haliclystus sanjuanensis spawning.

A, B) Eggs release through month opening; C) gonadal vesicles, with many eggs; D) isolated egg. Abbreviations: eg, eggs; ve, gonadal vesicles; mn, manubrium.

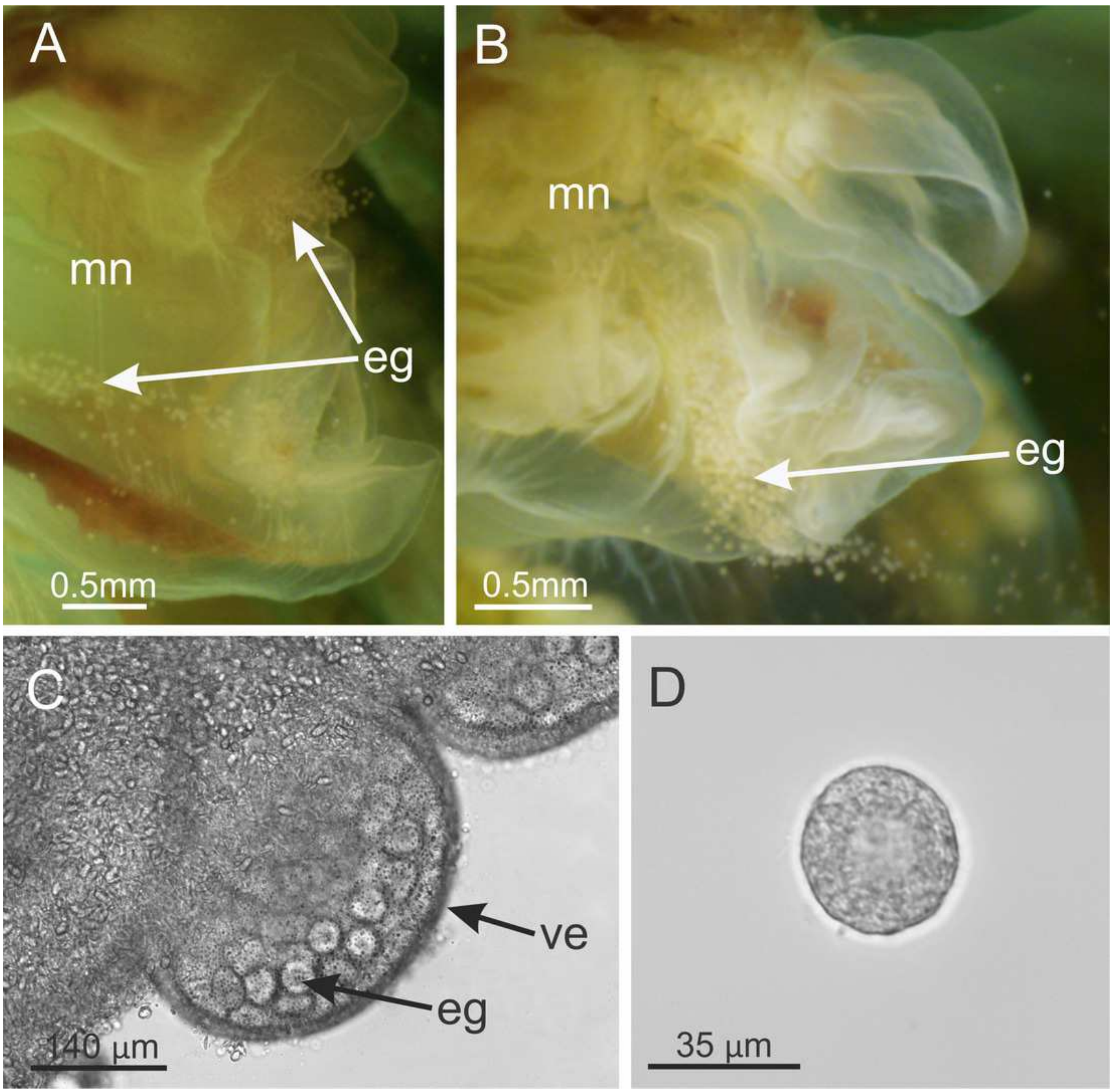

Figure 12

Map of the geographic distribution of *Haliclystus sanjuanensis*.

Star represents type locality.

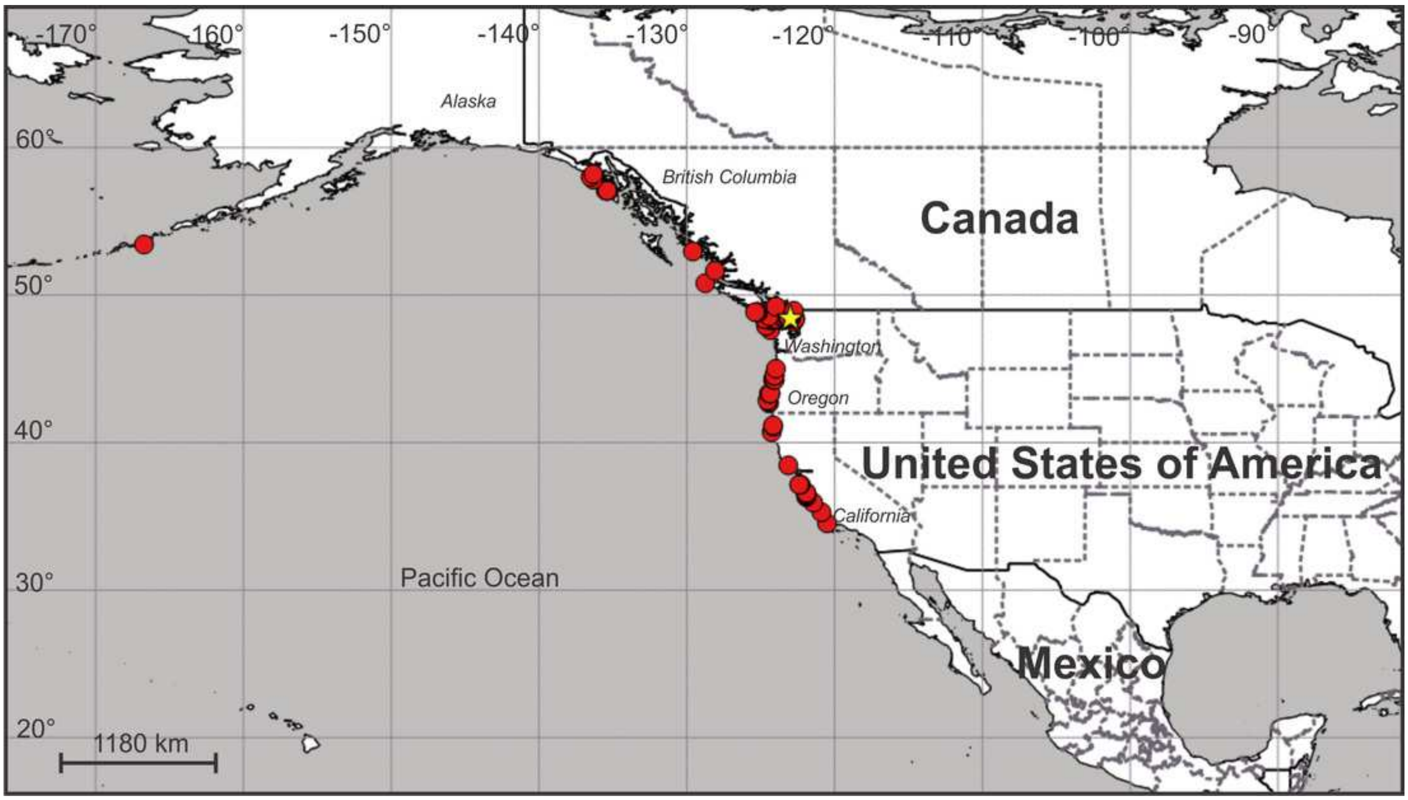

Figure 13

General morphology of *Haliclystus stejnegeri*.

A) Lateral view, with dark stripes pattern (see Table S2); B) oral view, with few white nematocyst spots at perradii. Abbreviations: ds, dark stripes; ws, white nematocyst spot. Images courtesy of Karen Sanamyan and Nadya Sanamyan (locality: Kamchatka, SE Kamchatka, Avacha Bay).