

Haliclystus californiensis, a “new” species of stauromedusa (Cnidaria: Staurozoa) from the northeast Pacific, with a key to the species of *Haliclystus*

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Abstract

We describe *Haliclystus californiensis*, a new species of stauromedusa from the northeast Pacific. *Haliclystus californiensis* differs from other species within the genus primarily by its horseshoe-shaped anchors, but also by the presence of prominent glandular pads at the base of its outermost secondary tentacles and by geographic range. It has been found from southern to northern California in coastal waters, 10 to 30 m depth. A single specimen of the species was originally described in an unpublished dissertation; nine additional specimens have been found since that time. We provide an annotated key to the known species of *Haliclystus*.

Key words: *Haliclystus*, Staurozoa, stauromedusa, Cnidaria, *H. auricula*, *H. octoradiatus*, *H. californiensis*, *H. tenuis*, *H. stejnegeri*, *H. borealis*

Introduction

Stauromedusae are stalked, benthic medusozoan cnidarians distributed mostly in shallow, temperate and polar waters. They may be locally common but are often highly cryptic. Only about 50 species have been described worldwide (Mills 1999; Daly *et al.* 2007). Until recently, Stauromedusae was considered part of class Scyphozoa, but phylogenetic analyses based on genetic and morphological data suggest that the group represents the earliest diverging clade of extant medusozoan cnidarians (Collins & Daly 2005; Collins *et al.* 2006; Van Iten *et al.* 2006). The establishment of Staurozoa as a new class highlights the importance of the systematics of stauromedusae. Its basal position within Medusozoa offers insights into the early evolution of Cnidaria (Collins 2002; Collins & Daly 2005; Collins *et al.* 2006).

Within class Staurozoa, the genus *Haliclystus* Clark, 1863 has the greatest number of species—10 described—with the most recent addition in 1961 (*H. monstrosus* (Naumov, 1961)). An additional species widely known under the *nomen nudum* *H. sanjuanensis* exists within the genus as well. A survey of stauromedusa species in the eastern north Pacific revealed an additional species of *Haliclystus*. This species was described in detail in a Ph.D. thesis (Gwilliam 1956) as *H. californiensis*, but the account was never published. In spite of the lack of a formal description, references to this species have been made in the literature as *H. californiensis* (Hirano 1997; Mills & Larson 2007; Miranda *et al.* 2009). Another species described by Gwilliam, *Stenoscyphopsis vermiformis*, has not been found during any later surveys.

Stauromedusae within the genus *Haliclystus* have four longitudinal planes of symmetry. Individuals have eight adradial arms tipped with clusters of secondary tentacles, and eight interradial and perradial marginal anchors. The muscle lining the rim of the calyx is not continuous; it is broken into eight parts by the arms (Kramp 1961). Species within the genus vary primarily in the shape of eight large pads called anchors located on the interradia and perradia, but also by geographic range and location of white nematocyst clusters. Miranda *et al.* (2009) reviewed the different species of the genus in their recent redescription of *H. antarcticus*. Members of the genus have been found in the Pacific, Atlantic, Indian, Arctic, and Southern ocean basins, with most species found along the coasts of the northern Pacific Ocean. Here we describe a beautiful and uncommon new species from the northeastern Pacific, known from southern to northern California.

Methods

Stauromedusae were either collected by hand while scuba diving or found on recovered settlement brushes. Subsamples from the arms of the holotype (USNM 1106657) and from one paratype (USNM 1106654) were stored directly in ethanol for molecular analysis, while live specimens were photographed, relaxed in isotonic MgCl₂, then fixed in buffered 10% formalin. Smash slides were prepared for cnida measurements from preserved specimens. Cnidae were photographed under 1000x magnification and measured using ImageJ software (Rasband 1997).

A thorough series of permanent transverse- and longitudinal-sections of *H. californiensis* was prepared by G.F. Gwilliam in 1956 using half of one of the paratypes (CAS#98108). Serial longitudinal-sections along the calyx, transverse sections through the calyx, and transverse sections through the stalk were studied for internal structures, and are stored at the California Academy of Sciences. Generally, 10-micron sections were prepared from tissue mounted in paraffin, bulk stained in Grenacher's borax carmine, then stained with picro-indigo-carmine. Alum hematoxylin and eosin stains were used on sections where greater resolution was needed (Gwilliam 1956). Terminology largely follows that of Hirano (1997).

Results

Haliclystus californiensis, new species

Haliclystus californiensis: Gwilliam, 1956, p. 57; Hirano, 1997, p. 251; Mills & Larson, 2007, p. 173; Miranda *et al.*, 2009, p. 1515 [*nomen nudum*].

Holotype. Smithsonian Institution, National Museum of Natural History (USNM) 1106657, northeast Pacific, off Pacific Grove, CA (Otter Point), 36°38'4"N, 121°55'13"W, 12 m depth, on a blade of red alga attached to rock, July 2006, coll. A. Kahn.

Other material examined. Paratypes: USNM 1106654, Monterey, CA, near Monterey Bay Aquarium, depth unknown, July 2006, coll. J. Mariottini and C. Widmer. California Academy of Sciences (CAS 98108), off Christy Cove, Santa Cruz Island, Channel Islands, CA, 29 m depth, 7 March, 1950, coll. P. Silva. USNM 1139484 Point Piños, Pacific Grove, Monterey Bay, CA, ca. 15 m depth, July 1987, coll. during a marine biology field course (Hopkins Marine Station). USNM 1139485 six specimens—one adult and five juveniles—Horseshoe Cove, Bodega Bay, CA, September 1990, coll. on settling brushes by Laura Rogers-Bennett.

Diagnosis. *Haliclystus* with conical calyx, slightly longer than wide. Calyx tapering towards stalk, becoming nearly tubular; overall shape resembling a martini glass. Gonads extending from base of calyx to tips of each of eight arms (Fig. 1); 40 to 50 gonadal sacs comprising each gonad, with three or four abreast at the widest. Each arm tipped with a cluster of 60 to 80 capitate secondary tentacles (Fig. 2B); with up to five basal tentacles on exumbrellar side possessing a prominent swollen glandular pad (Fig. 2B and 2D). Eight primary tentacles lining coronal margin on interradial and perradial axes, alternating with the eight adradial

arms (Fig. 2A and 2C). Large, horseshoe-shaped anchors, roughly as wide as tall, wrapping around each primary tentacle with open side up (Fig. 2A and 2C). Perradial marginal notches between arms about twice as wide and deep as interradial notches (Fig. 1). White nematocyst clusters lining subumbrellar margin (Fig. 1). Exumbrellar surface grainy with nematocysts (Fig. 2A and 2E); subumbrellar surface smooth. Pigment stripes along calyx absent. Stalk 1/4 length of calyx in adults.

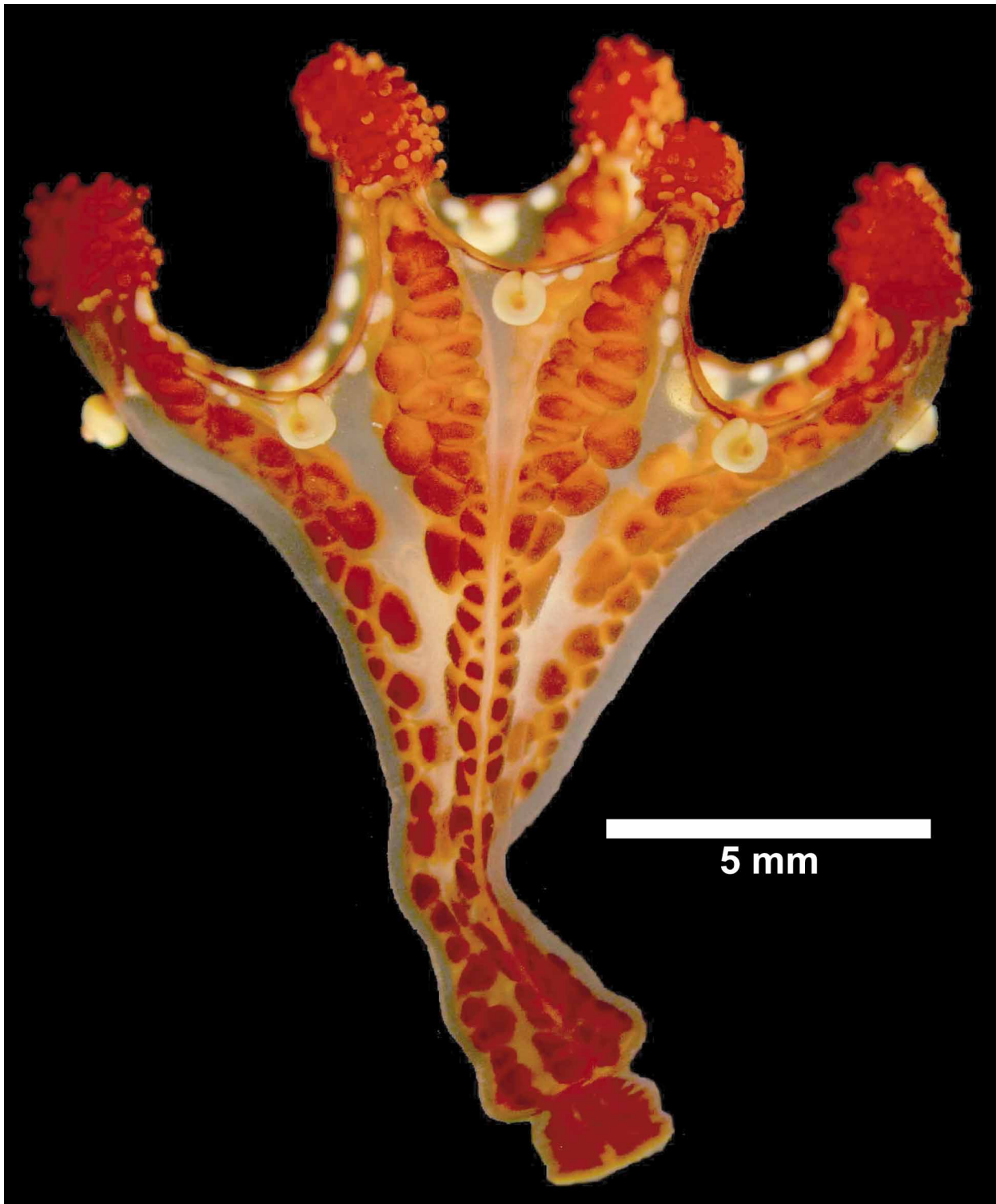


FIGURE 1. *Haliclystus californiensis*, a new species of stauromedusa from the northeast Pacific, photographed alive. Visible features include large, horseshoe-shaped anchors, white nematocyst clusters lining the subumbrellar margin, large reddish-brown gonadal sacs, interradial notches about one half as deep and wide as perradial notches, and the nearly transparent ground color of the calyx and stalk. The stalk is contracted to about half its relaxed length in this photo of the holotype – see Fig. 2G for relaxed stalk. Scale bar: 5 mm.

Description of holotype. Height 21 mm; calyx 17 mm tall, 15.5 mm wide; stalk 4 mm tall, 2.0 mm diameter. Arms united in interradial pairs, with perradial marginal notches twice as wide and deep as interradial ones (Fig. 1). Stalk narrow and short—about 1/4 length of calyx—but well-developed with four chambers and four longitudinal muscle bands extending from base through mesoglea (Fig. 2F, 2G, Gwilliam 1956). Four muscle bands continuing through calyx along interradia, then bifurcating in upper third of calyx and extending to base of secondary tentacles (Fig. 1). Before splitting, each muscle band lying exterior to gonads; in upper 1/3 of calyx, bifurcated muscle bands lining interradial margins of gonads and extending up to bases of clusters of secondary tentacles.

TABLE 1. Dimensions of cnidae found in the gastric filaments and secondary tentacles of *Haliclystus californiensis*. Measurements provide the minimum, mean (in bold), and maximum length of each type of cnida sampled. The number of cnidae measured corresponds with the number found in prepared squash slides; some were more abundant than others.

Cnidae	Length	Width	n
<i>Euryteles</i> (ovoid)	26.86- 30.58 -34.74 μ m	15.00- 16.85 -19.35 μ m	11
<i>Euryteles</i> (round)	8.30- 13.22 -19.68	8.80- 10.32 -13.11	40
Isorhizas	15.21- 23.71 -29.13	4.98- 6.61 -9.26	50

TABLE 2. Comparison of *Haliclystus* species. References for *H. tenuis* followed by * indicate those that discuss the species as *H. auricula*.

	Geographic range	Gonadal sacs	2° Tentacles	Stalk:calyx length	Anchor shape	Reference
<i>H. antarcticus</i>	Southern Ocean: Antarctica, S Argentina, S Chile	50–150	6–224	1/2 to 2/3 length	Biscuit-shaped	Pfeffer (1889), Kramp (1961), Miranda <i>et al.</i> (2009)
<i>H. auricula</i>	N Atlantic, N Pacific	30–200	Usually 100 or more, but as few as 30	Equal length	Coffee bean-shaped	Rathke (1806), Mayer (1910), Hirano (1997)
<i>H. borealis</i>	N Pacific	50, ranging from 30 to 100	20–30	<1/3 length	Large, round, with longitudinal furrow	Uchida (1933), Ling (1937), Kramp (1961), Hirano (1986)
<i>H. californiensis</i>	NE Pacific	40–50	60–80	1/4 length	Horseshoe-shaped	This paper
<i>H. kerguelensis</i>	S Indian	?	50	Twice as long	Small, oval, with tentacular knob	Vanhöffen (1908), Kramp (1961)
<i>H. monstrosus</i>	NW Pacific	Unknown; 4–8 rows at widest	About 100	1/2 length	Large, flattened, margins incurved	Naumov (1961)
<i>H. octoradiatus</i>	N Atlantic	10–70	30–120	Equal length	Large, round	Lamarck (1816), Hirano (1997), Miranda <i>et al.</i> (2009)
<i>H. salpinx</i>	NE Atlantic, N Pacific	40–120	60–70, may be up to 250	Much longer	Large, trumpet-shaped	Clark (1863), Kramp (1961), Mills & Larson (2007)
<i>H. "sanjuanensis"</i>	NE Pacific	200–300, but as few as 150	100–150	2/3 length	Coffee bean-shaped	Gellermann (1926), Hirano (1997), Mills & Larson (2007), pers. obs.
<i>H. sinensis</i>	NW Pacific (China)	17–20	20–25	1/2 length	Globular, slightly wider than tall	Ling (1937)
<i>H. stejnegeri</i>	N Pacific (Alaska to Japan)	100–150, but as many as 250	70–100, but as many as 200	1/2 length	Egg-shaped, taller than wide	Kishinouye (1899), Uchida (1929), Ling (1937, 1939), Kramp (1961), Hirano (1986), Miranda <i>et al.</i> (2009)
<i>H. tenuis</i>	NW Pacific	30–50	20–60	1/2 length	Globular, wider than tall	Kishinouye (1910), Uchida (1929*), Ling (1937*, 1939*), Hirano (1986*, 1997)

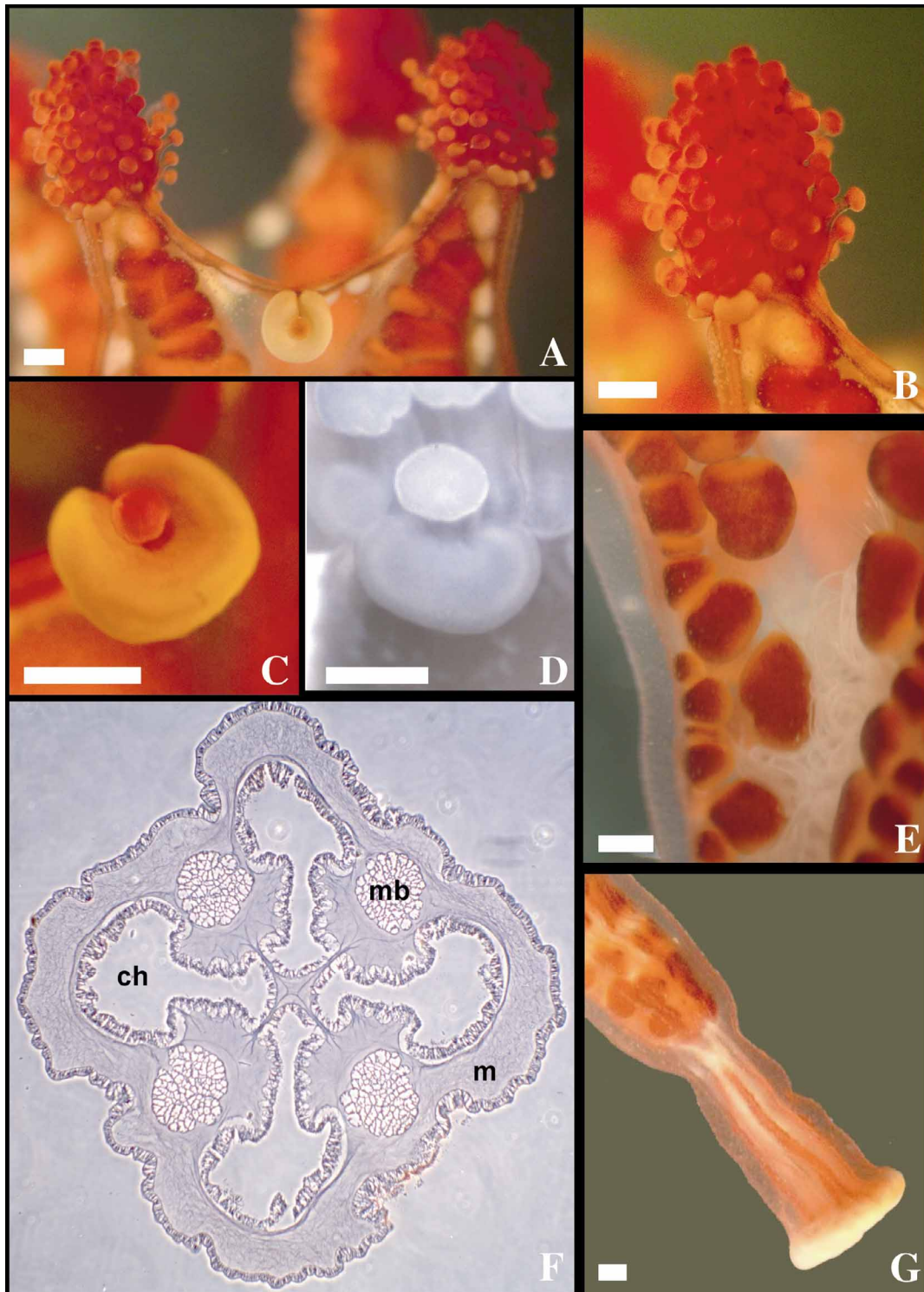


FIGURE 2. All images of the live holotype unless noted otherwise. A. Interradial margin. B. Clump of secondary tentacles on one arm, with enlarged glandular pad visible on aboral side of the outermost tentacle. C. Large, horseshoe-shaped anchor surrounding a well-developed primary tentacle. D. Close-up of outermost tentacle of a tentacle cluster, showing an enlarged glandular pad at the base. Photo from preserved holotype. E. Gastric filaments visible through outer calyx wall in live specimen. F. Transverse-section through the stalk of CAS#98108. m – mesoglea, mb – muscle band, ch – chamber, from a collection of permanent slides prepared by Gwilliam (1956). G. Close up of stalk. Scale bars: 0.5 mm, except for that shown on D, which represents 0.2 mm.

Gonads comprising gonadal sacs, beginning at base of calyx and extending to base of secondary tentacles (Fig. 2A). Gonads paired in lower 2/3 of calyx, but pairing ends at same point that muscle bands bifurcate

(Fig. 1). Each gonad with 40 to 50 reddish-brown gonadal sacs (Fig. 2E). Gonadal sacs ovoid, relatively large (up to 1 mm along longest axis) compared to many other members of the genus (*H. auricula*, *H. octoradiatus*, *H. sanjuanensis*; Hirano 1997, personal observation). At the widest, just above bifurcation of muscle bands, three to four gonadal sacs lie abreast.

Exumbrella finely granulated with small nematocyst clusters (Fig. 2A and 2E); subumbrellar surface smooth. Five to 10 white nematocyst clusters, each with a diameter of about 0.5 mm, lining subumbrellar margin between each arm (Fig. 1). Cnidae examined from gastric filaments and secondary tentacles composed of two size classes of microbasic euryteles and one size class of isorhizas (holotrichous or atrichous; Table 1). Tentacles with ovoid euryteles and isorhizas; gastric filaments with smaller, rounder euryteles.

Tip of each arm with 60 to 80 tightly clustered secondary tentacles (Fig. 2A and 2B). All tentacles short, capitate. In each cluster, up to five of outermost tentacles with swollen glandular pads at base of tentacular stalk (Fig. 2B and 2D).

Eight primary tentacles and anchors lining subumbrellar margin, one between each arm in the interradii and perradii (Fig. 1). Part of primary tentacle retained and well-developed in adult; the anchor surrounding it comprising a large yellow pad with a cleft on upper radius, forming a horseshoe around the tentacle (Fig. 2C). Anchors approximately same diameter as largest gonadal sacs of this species.

Color in life red, cryptically matching color of its algal substrate. The alga, presumably a rhodophyte, was not identified. Gonads reddish-brown; nematocyst clusters along subumbrellar margin vivid white; tentacles red. Muscles in stalk and along subumbrellar margin red, but colorless in calyx.

Description of additional material. Adult specimen (USNM 1139484) from Pt. Piños 15 mm in height; calyx 12 mm tall; stalk 3 mm tall, 2.3 mm diameter (alive). Arms, stalk, muscle bands, and nematocyst clusters as in holotype. Secondary tentacles 40 to 50, clustered; in each cluster, up to three of outermost tentacles with swollen glandular cushions at base of tentacular stalk. Tentacular stalk varying in length, and may be rather long near subumbrellar side of arm. Anchors similar to those of holotype, although one anchor of this specimen was smaller than the others and without the primary tentacle. This may be due to a developmental defect, since all other anchors were similar to each other and to the holotype. Gonads as in holotype, but differing in number of gonadal sacs or follicles. Each gonad with 20 to 30 gonadal sacs. Largest sac about 0.5 mm along longest axis. At the widest, two gonadal sacs lie abreast. Color similar to holotype although ground color of both calyx and stalk almost transparent with slight red tint. Pad of anchor whitish-yellow.

The original adult specimen described by Gwilliam (1956), found off of Christy Cove on Santa Cruz Island, is stored at the California Academy of Sciences (CAS#98108). Half of the specimen was prepared into thin sections, and the remaining tissue has degraded. Still, two intact anchors and the swollen glandular pads of the outermost secondary tentacles were visible on portions of the specimen, allowing us to verify its identity.

The young adult specimen (USNM 1106654) from Monterey Bay, 8 mm in height, is similar in body shape to the adults. Gonads are partially developed, with distinct gonadal sacs occurring only in the upper 1/3 of the calyx. Anchors are of a similar shape as those in the adult, but the primary tentacle appears a bit larger in proportion as compared to the surrounding anchor.

Six additional specimens (USNM 1139485), including five juveniles, were collected from Bodega Bay. The juvenile specimens cannot be definitively identified as *H. californiensis*. We infer them to be the same species because of the co-occurrence of a young adult specimen that can be diagnosed as *H. californiensis*, but some caution is warranted. In juveniles, approximately 1.8–2.5 mm in height (preserved), the stalk is almost 1/2 the length of the calyx height. Outermost tentacles of these specimens were without obvious pads. The anchors were only poorly developed so that the primary tentacles were proportionately longer than in adults. The number of tentacles for each cluster was 4 to 5 (1.8 mm specimen in total height), 5 (1.9 mm specimen), 5 to 6 (2.5 mm specimen), 7 to 8 (2.0 mm specimen). A larger juvenile specimen (4.9 mm in total height) appeared to have more than 10 tentacles for each cluster, however, this specimen was too heavily damaged for more detailed observation. This large juvenile may have glandular pads on outermost tentacles, but that part was also too damaged to see this character. A single specimen (USNM 1139485) from Bodega Bay was mature, measuring 8.5 mm in total height; calyx 5.9 mm tall; stalk 2.6 mm tall in preserved condition. This

mature specimen was with about 30 tentacles for each cluster, of which the outermost three were with glandular pads. It was difficult to locate white nematocyst spots for sure in small preserved specimens, but one small specimen in good condition appeared to have them.

Comparisons. *Haliclystus californiensis*, sp. nov., joins 10 other species in the genus *Haliclystus*: *H. antarcticus* Pfeffer, 1889, *H. auricula* (Rathke, 1806), *H. borealis* Uchida, 1933, *H. kerguelensis* Vanhöffen, 1908, *H. monstrosus* (Naumov, 1961), *H. octoradiatus* (Lamarck, 1816), *H. salpinx* Clark, 1863, *H. sinensis* Ling, 1937, *H. stejnegeri* Kishinouye, 1899, and *H. tenuis* Kishinouye, 1910 (Table 2). Original species descriptions were used for the following comparisons unless specifically noted otherwise.

One distinctive feature of *H. californiensis* is the presence of prominent glandular pads on up to five of its outermost secondary tentacles. Glandular pad swellings are encountered in other *Haliclystus* species, including *H. auricula* and *H. "sanjuanensis"*, but they are much slighter than those observed in *H. californiensis* and are variable in occurrence (Gwilliam 1956; Hirano pers. obs.). Outside *Haliclystus*, glandular pads associated with secondary tentacles are fairly widespread, occurring for example in species of *Depastromorpha* (Carlgren, 1935), *Kyopoda* (Larson, 1988), *Manania* (Hirano, 1986).

The most distinctive character of *Haliclystus californiensis* is the unique shape of the marginal anchors. The anchor forms a large, yellow horseshoe around the primary tentacle, with the cleft pointing up (Fig. 2C). Morphologically, the anchors of this species most closely resemble those of *H. auricula*, *H. borealis*, and *H. tenuis* (Clark 1878; Hirano 1997). As in *H. californiensis*, many specimens of *H. auricula* have anchors that surround a rudimentary primary tentacle (Clark 1878; Hirano pers. obs.). Although the anchors of both *H. auricula* and *H. californiensis* curve and are open at the top, the anchors of *H. californiensis* nearly complete a circuit around the primary tentacle and are approximately as wide as long. The coffee bean-shaped anchors of *H. auricula* curve gently, wrapping only about halfway into a circle, and are distinctly longer than wide. Unlike *H. californiensis*, the marginal anchors of *H. borealis* and *H. tenuis* are round and without a cleft. In addition, the remnant of the primary tentacle is not retained in adults of either of these two species. The geographic range differs as well; *H. borealis* and *H. tenuis* are found in the northwest Pacific, whereas *H. californiensis* is thus far known only from the coast of California. The gonadal sacs of *H. californiensis* are ovoid and relatively large (up to 1 mm along the longest axis) compared to many other members of the genus (*H. auricula*, *H. octoradiatus*, *H. "sanjuanensis"*; Hirano 1997, personal observation). The number of secondary tentacles, gonads, and other differences are summarized in Table 2.

Other species within the genus differ in both morphology and geographic distribution (see Miranda *et al.* 2009 for further discussion of ranges of the species of *Haliclystus*). Two species are found only in the southern hemisphere: *H. antarcticus* from Antarctica, and probably southern Chile and Argentina (Miranda *et al.* 2009), and *H. kerguelensis* from the southern Indian Ocean. *Haliclystus sinensis* has been found only off the coast of China, and *H. monstrosus* is only known near Russia. *Haliclystus octoradiatus* has been reported from the northeastern Atlantic, near Iceland and Europe. *Haliclystus stejnegeri*, restricted to the boreal Pacific (Miranda *et al.* 2009), differs from *H. californiensis* in the number of gonadal sacs, with 90 to 240 versus 40 to 50 (Hirano 1986). The anchors of *H. stejnegeri* are egg-shaped rather than round, and have a cleft only when there is still a remnant of the primary tentacle. *Haliclystus auricula* is found in the north Pacific and north Atlantic Ocean. *Haliclystus salpinx* has a somewhat surprising distribution, with specimens reported from the north Pacific [in bays near the San Juan Islands and southern Vancouver Island (Mills & Larson 2007), and in Alaska and the Russian coast of the Japan Sea (Mills 2001)] and north Atlantic (Mills & Larson 2007, Miranda *et al.* 2009). It differs from *H. californiensis* by having a long stalk—longer than the height of the calyx—and trumpet-shaped anchors (Kramp 1961).

Etymology. The specific name refers to the state of California, the first and thus far only region where the species has been found.

Distribution. Specimens have been found in shallow (10-30 m), wave-exposed kelp forests along the California coast from the Channel Islands in the south to Bodega Bay in the north.

Gene sequences. Mitochondrial 16S rDNA and COI were amplified and sequenced from the holotype and young adult specimen (USNM 1106654; GenBank accession numbers GU201828-GU201831).

Discussion

Haliclystus is presently assigned to family Lucernariidae Johnston, 1847 and suborder Eleutherocarpida Clark, 1863, but available data suggest that both taxa are polyphyletic (Collins & Daly 2005; Daly *et al.* 2007). More detailed systematic study of Staurozoa is necessary to establish a stable classification that mirrors evolutionary history.

Haliclystus californiensis, discussed as a *nomen nudum* in numerous works (Gwilliam 1956; Hirano 1997), is herewith formally described and named. That it took nearly 50 years to find 10 specimens reflects the rarity of this species; its addition brings the number of species in the genus *Haliclystus* to 11 in four ocean basins (plus one *nomen nudum*: *H. "sanjuanensis"*). A current dichotomous key to species of the genus is given below. Note, however, that in their redescription of *H. antarcticus*, Miranda *et al.* (2009) documented considerable variability in many features of that species, and stressed that variation of *Haliclystus* features, several of which we employ in the key, need better documentation in most species. We include annotations in the key, highlighting issues of ambiguity that need further attention.

Annotated key to known species of *Haliclystus*

1. Found in southern hemisphere 2^I
 - Found in northern hemisphere 3
2. Stalk 1/2 to 2/3 length of calyx. Anchors figure "8"-shaped, with longitudinal furrow and wrinkled surface; tentacular knob present in adults (L. Miranda *pers. comm.*). Each tentacle cluster with up to roughly 200 secondary tentacles. 50–150 circular to hexagonal gonadal sacs in each gonad. Antarctica, S Chile, S. Argentina
 - *Haliclystus antarcticus*
 - Stalk twice as long as calyx. Anchors small ovals, tentacular knob present in adults. Each tentacle cluster with up to 50 secondary tentacles. An undocumented number of gonadal sacs in lancet-shaped, widely-separated gonads. Kerguelen Islands in the S Indian Ocean *Haliclystus kerguelensis*
3. Perradial marginal notches deeper and wider than interradian 4^{II}
 - Perradial marginal notches equally as wide and deep as interradian 7
4. Stalk length considerably less than one half of calyx length 5
 - Stalk length approximately one half of calyx length 6
5. Anchors large, cushion-like disks, each with a longitudinal furrow and no vestige of primary tentacle. With 20–30 secondary tentacles in each tentacle cluster. Usually about 50 gonadal sacs (ranging from 30 to 100) in each gonad. Often with white stripes or white flecks in the interradian along calyx. White nematocyst clusters line bell margin;

I. The genus has an anti-tropical distribution and no species have thus far been found in both the northern and southern hemispheres. The specimen of *H. californiensis* from Santa Cruz Island in southern California appears to be among the closest thus far known to the equator ("off Christy Cove", 34° 1.5' N, 119° 52.7' W, approximated using Google Earth). A record of *H. tenuis* from Gogoshima, Seto Inland Sea (Uchida 1929) appears to be a bit farther south (33°55'N, 132°40'W).

II. This character appears to be variable in *H. auricula*, which has arms that are usually arranged rather equidistantly. However, Mayer (1910) described the arms of *H. auricula* from New England as "United as pairs. Interradial clefts, only half or two-thirds as wide as perradial" (description and table on p. 532). The figure (after Clark 1878) on the next page shows the opposite pattern of pairing. The oral view of the top, right of the figure shows a pattern where interradian clefts are smaller than perradial ones, while the one of the bottom, right, shows the opposite (perradial clefts are smaller than interradian ones). Although a figure given in Clark (1878) (Plate II, Fig. 22) shows the pattern of pairing that Mayer (1910) gave in the description and the table (and Clark himself mentioned it was the most frequent pattern in the paper), Clark wrote "Viewed from the front, it presents an octolateral outline, with eight strongly projecting corners. Of these eight sides four alternate ones are usually shorter than the others, and they are those which lie directly opposite the four flanks of the proboscis. Frequently, however, the proportions are reversed and the longer four become the shorter ones, or they are all alike. The first case, though, is the one which is most generally met with..." Clark (1863) did not give details of the arrangement of arms, but mentioned, "The disc shallow umbellaeform, strongly octangular; the arms as broad as long..." The figures by Rathke (1809) do not show clear pairing of arms. There may be a slight difference between perradial clefts and interradian clefts of *H. auricula*, but the difference is probably not obvious enough to diagnose this species.

- inner subumbrella smooth. NW Pacific *Haliclystus borealis*
- Anchors horseshoe-shaped, each surrounding a primary tentacle. With 60–80 secondary tentacles in each tentacle cluster; outermost tentacles with a prominent glandular pad at their bases. With 40–50 gonadal sacs in each gonad. Stalk about 1/4 length of calyx. Large white nematocyst clusters line bell margin (Fig. 2A). NE Pacific, California ..
..... *Haliclystus californiensis*
6. With 17–20 gonadal sacs in each gonad, arranged in single file. Calyx equally as tall as wide, or slightly taller than wide. Anchors ovoid, slightly wider than tall. Each tentacle cluster with 20–25 secondary tentacles. Stalk half the length of calyx. White nematocyst clusters few in number along subumbrellar surface near margin. Coast of China near Tsingtao *Haliclystus sinensis*^{III}
- With 30–50 gonadal sacs in each gonad, arranged in 2 rows. Calyx slightly taller than wide. Anchors ovoid, wider than tall. Each tentacle cluster with 20–60 secondary tentacles. Stalk half the length of calyx. White nematocyst clusters scattered on the subumbrella. NW Pacific on coasts of Japan and China (Shandong province)
..... *Haliclystus tenuis*
7. Intertentacular lobules (see Hirano 1997, Miranda *et al.* 2009) absent 8^{IV}
- Intertentacular lobules present 9
8. Stalk about as long or longer than calyx. Anchors very large, trumpet-shaped to flattened with incurved margins. Commonly 60–70 secondary tentacles in each tentacle cluster, but up to 250. 40–120 gonadal sacs in each gonad, with 6–8 abreast at the widest. N Atlantic and in isolated bays in N Pacific (San Juan Islands and S Vancouver Island, Alaska, Russian coast of Japan Sea) *Haliclystus salpinx*
- Stalk 1/2 length of calyx. Anchors large, flattened, with incurved margins surrounding a diminutive primary tentacle. 100 secondary tentacles in each tentacle cluster. Gonadal sacs arranged 4 to 8 abreast. NW Pacific, Kurile Islands *Haliclystus monstrosus*
9. Stalk length approximately equal to calyx length. White nematocyst clusters either present in both perradii and interradii or completely absent 10
- Stalk length less (1/2 to 2/3) than calyx length, white nematocyst clusters only in perradii 11
10. Lacking white nematocyst clusters. With 30–200 gonadal sacs in each gonad. Anchors coffee bean-shaped, longer than wide. Usually more than 100 secondary tentacles, but as little as 30, in each tentacle cluster. N Atlantic and N Pacific *Haliclystus auricula*
- White nematocyst clusters in both perradii and interradii. With 10–70 gonadal sacs in each gonad. Anchors large, globular knobs. With 30–120 secondary tentacles in each tentacle cluster. N Atlantic, mainly near N Europe and Iceland *Haliclystus octoradiatus*
11. Anchors egg-shaped, taller than wide, without longitudinal furrow. Commonly with 70–100 (possibly up to 200) secondary tentacles in each tentacle cluster. With 100–150 (possibly up to 250) gonadal sacs in each gonad. Only a few white nematocyst clusters in the perradial sinuses near calyx margin. N Pacific *Haliclystus stejnegeri*
- Anchors coffee bean-shaped, taller than wide, with longitudinal furrow. With 100–150 secondary tentacles in each tentacle cluster. With 200–300 (but perhaps as few as 150) gonadal sacs, 10–20 abreast at widest. Gonadal margin in the perradial sinuses fringed with a number of white nematocyst clusters. NE Pacific, from central California, N Washington (San Juan Islands) to British Columbia... *Haliclystus* sp. (often referred to as *H. "sanjuanensis"*)

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III. *H. sinensis* may be conspecific with *H. tenuis*. Ling (1937) described *H. sinensis* based on four specimens collected from a single tide pool. Even in this small sample, the single row of gonadal sacs reported for the species showed variation with occasionally two gonadal sacs lying next to each other (Ling, 1937; Figs. 4 and 5). Ling (1937) also described the white spots (nematocyst clusters) as sparse for *H. sinensis* while they are prominent for *H. tenuis*. However, differences in the abundance and size of white spots appear to be slight [compare Fig. 3 for *H. tenuis* (as *H. auricula*) and Fig. 5 for *H. sinensis* in Ling (1937)]. The number may be smaller in *H. sinensis*, but this could be because the studied individuals had narrower calices than typical *H. tenuis*.

IV. This character is as yet unobserved for *H. monstrosus*, but inferred to be absent. Based on the distinctive and similar shapes of the anchors of *H. monstrosus* and *H. salpinx*, one can hypothesize that the two species are very closely related if not indistinct. The major difference between the two appears to be the proportion of the stalk length to calyx length, but these two characters may be quite variable.

specimen that became the holotype to the attention of AGC and allowing him to observe and photograph the animal alive in their basement. Thanks are due to C. Widmer and J. Mariottini of the Monterey Bay Aquarium for collecting a specimen of *H. californiensis* and graciously allowing us to study it. L. Ivanov provided a crucial Russian translation, without which the dichotomous key would have been incomplete. N.T. Pierce, L. Scheimer, T.S. Burrow, F. Sommer, J. Watanabe, K.W. Demes, T. Suskiewicz, and A. Alifano provided scuba diving and collection assistance. We are grateful to L. Miranda for providing very helpful feedback on an earlier draft. L. Miranda and C. Mills provided valuable feedback that improved an earlier draft. Finally, we thank the Monterey Bay Aquarium Research Institute and Moss Landing Marine Laboratories for use of facilities and resources. AGC acknowledges support from the US National Science Foundation Assembling the Tree of Life grant 0531779 (to AGC, P. Cartwright, and D. Fautin).

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