

The life cycle of *Halimedusa typus*, with discussion of other species closely related to the family Halimedusidae (Hydrozoa, Capitata, Anthomedusae)*

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SUMMARY: The little-known Anthomedusa *Halimedusa typus* has been collected from several locations in California, Oregon, and British Columbia on the Pacific coast of the United States. The adult medusa is redescribed based on new observations of living material and is found to have capitate tentacles. Polyps of *H. typus* were raised several times after spawning field-collected medusae in the laboratory; the cultures on one occasion lived for more than a year. The capitate polyp is solitary and very tiny, emerging from a basal perisarc measuring 200–300 μm in diameter. One cultured polyp produced a medusa, which is described. The taxonomic positions of several other morphologically-similar Anthomedusae in the Capitata are compared and discussed here. *Tiaricodon coeruleus* and *Urashimea globosa* are moved from the Polyorchidae to the Halimedusidae, and the similarity of *Boeromedusa auricogonia* (Boeromedusidae) to all of these medusae and to the genera *Polyorchis*, *Scrippisia* and *Spirocodon* of the family Polyorchidae is considered. The group of species under consideration is basically restricted to the Pacific Ocean, except for *T. coeruleus* and *U. globosa*, which have also been collected in the south Atlantic and south Atlantic/Antarctic. It is noted that medusae of the Halimedusidae are typically found quiescent near the surface, whereas those of the Polyorchidae either rest on the bottom or must continue pulsating to stay up in the water column, indicating a basic underlying difference in buoyancy and resultant behavior between the medusae in these two families.

Key words: *Halimedusa*, *Tiaricodon*, *Urashimea*, *Boeromedusa*, *Polyorchis*, *Spirocodon*, *Scrippisia*.

INTRODUCTION

Halimedusa typus Bigelow, 1916 is a little-known species whose medusa has only infrequently been collected and whose polyp has not been described. Its taxonomic position has been uncertain because so few live medusae had been observed. Until recently (Wrobel and Mills, 1998), the only images available in the literature (Bigelow, 1916, reproduced in Kramp, 1968; Arai and Brinckmann-Voss, 1980) were drawings of highly contracted,

preserved specimens that were of limited value in recognizing live medusae or for understanding the taxonomic placement of the species. This paper derives from observations of live material collected in central and northern California; polyps were grown several times in the laboratory from field-collected medusae and one time produced a medusa.

The monotypic northeast Pacific genus *Halimedusa* was originally placed, with some trepidation, in the family Pandeidae by Bigelow (1916), and remained in this catch-all family (Kramp, 1961, 1968) until it was removed and assigned its own family in the suborder Filifera by Arai and Brinck-

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mann-Voss (1980; Brinckmann-Voss and Arai, 1998). It has been mentioned only occasionally in the literature since its original description except in summary lists, with only a little new information (McCormick, 1969 as “moerisiid”; Rees, 1975; Arai, 1987). *Halimedusa* and the Halimedusidae are here moved to the suborder Capitata, within the Anthomedusae, based on new information about morphologies of both the medusa and polyp phases of its life cycle and the cnidom.

Also considered here is the southern Atlantic and Pacific *Tiaricodon coeruleus* Browne, 1902. This monotypic genus was originally placed in the Anthomedusae, family Tiaridae (Browne, 1902), was then moved to the Anthomedusae, Codonidae (Mayer, 1910), and later to the Limnomedusae, Moerisiidae (Browne and Kramp, 1939; Kramp, 1959, 1961; Zhang, 1982). *Tiaricodon* has most recently been moved to the Polyorchidae (Petersen, 1990; followed by Schuchert, 1996). In the present paper, *Tiaricodon* is moved once more, to the family Halimedusidae, based on similar characters of the medusae.

Urashimea globosa Kishinouye, 1910, another monotypic Pacific genus, apparently endemic to Japan, is also moved here into the Halimedusidae. This genus was originally placed in the Anthomedusae, Cladonemidae (Kishinouye, 1910), but was eventually moved into the catch-all Pandeidae by Uchida and Nagao (1961). *Urashimea* remained for many authors in the Pandeidae within the Filifera (e.g. Kubota, 1998), but has also been subjected to other taxonomic relocation several times, most recently having joined *Tiaricodon* and others in the family Polyorchidae (Bouillon, 1995 - which gives the full history).

The relationships of all of the above species to the Polyorchidae (which will henceforth contain only *Polyorchis*, *Scrippisia* and *Spirocodon*) are discussed.

MATERIALS AND METHODS

Medusae of *Halimedusa typus* were collected in Bodega Bay and Bodega Harbor, California, and in Yaquina Bay, Oregon in the 1970s, and in Humboldt Bay, California in 1991. In Bodega Harbor, *H. typus* medusae were collected at both Mason's Marina and at the Coast Guard Station floating docks. In Humboldt Bay, they were collected off the floating docks of the Woodley Island Marina, Eureka, California.

The medusae were individually hand-collected using glass bowls or beakers, or were taken in short plankton tows.

The *H. typus* medusae were transported back to the laboratory and were set up in bowls of fresh seawater for spawning, incubated at ambient seawater temperature of about 11°C. Medusae were removed from the bowls after spawning, and planulae were allowed to settle either directly onto the surface of the glass bowls or on glass slides placed on the bottom of the bowls. Polyps that developed from the settled planulae were maintained in these bowls, incubated in a running seawater table at ambient temperature (9-12°C), and offered a variety of potential prey.

Nematocysts were examined in squash preparations of live material, with measurements taken of undischarged capsules at 1000 times magnification.

RESULTS

Systematic account

Class HYDROZOA

Order ANTHOMEDUSAE-ATHECATA

Suborder Capitata Kühn, 1913

Family HALIMEDUSIDAE Arai and
Brinckmann-Voss, 1980

Halimedusa typus Bigelow, 1916

Description of the adult medusa (Fig. 1A). Up to 16 mm tall and 13 mm wide, jelly thick, especially at the apex. Manubrium suspended from a broad, low peduncle; cruciform and extending along each radial canal until the point where the radial canals turn down the subumbrellar wall; typically hanging about half-way down the subumbrellar cavity. Mouth small and quadrate, studded with a row of tightly-packed round nematocyst batteries around its rim. Gonads cover the entire surface of the manubrium, with flat, not folded, surface, typically whitish in color, with a dark brown horizontal stripe, which parallels the base a bit down from the top, sometimes coalescing into a nearly black spot at the intersection of each radial canal. With 4 straight, smooth-sided, narrow, radial canals and four characteristic interradial “peaks” in the jelly between radial canals, rising up above the level of the radial canals. With 4 hollow perradial tentacles and 4 interradial groups of up to 10–11 smaller hollow tentacles, all

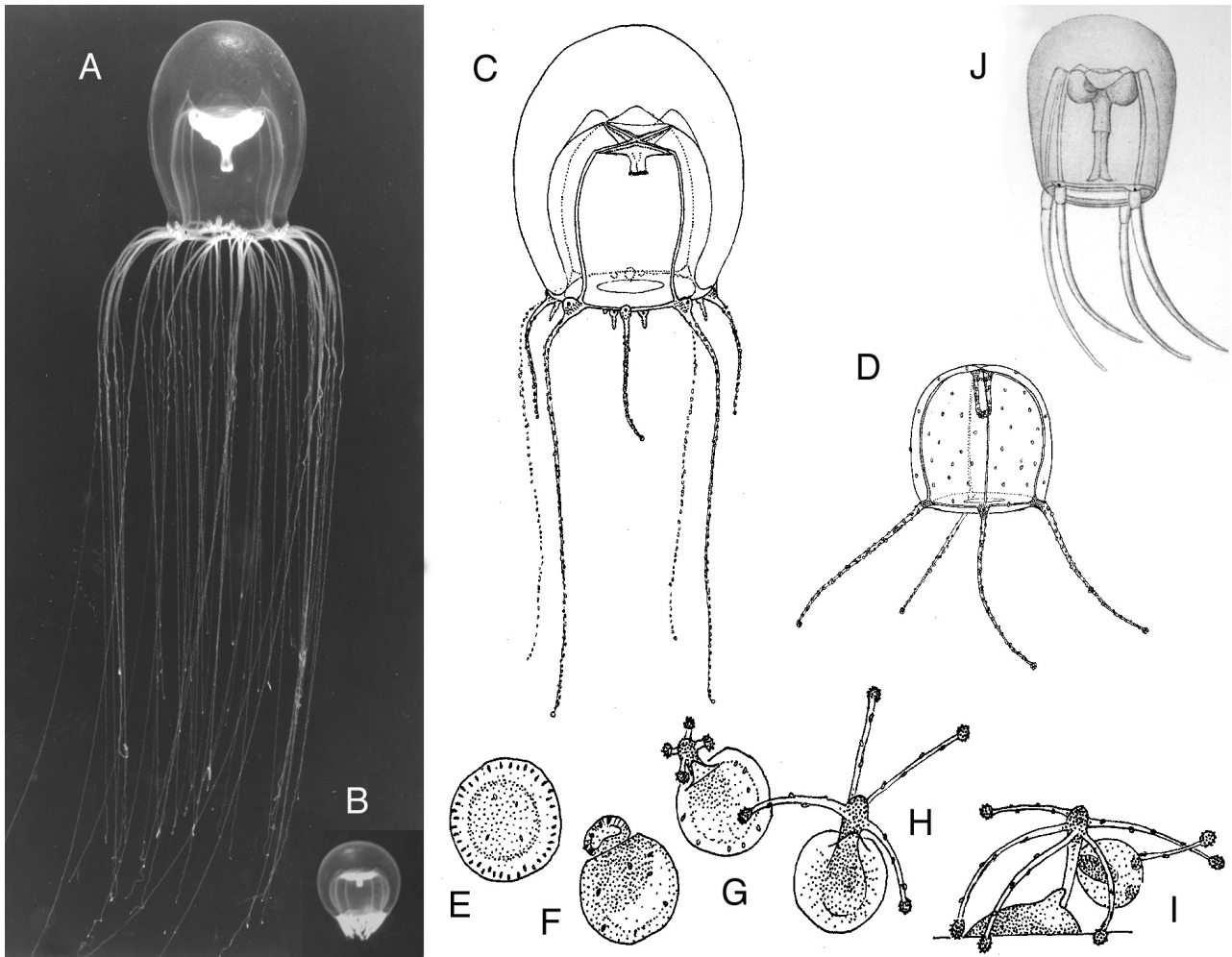


FIG. 1. – A-I *Halimedes typus*. J *Tiaricodon coeruleus* (reproduced from Browne and Kramp, 1939, with the permission of Cambridge University Press). A, mature medusa; B-C, developing medusa stages; D, newly-released medusa; E, settled planula; F and G, primary polyps; H and I, mature polyps; I, polyp with developing medusa bud; sizes given in text.

with red-orange to purple-black ocelli on the outer, abaxial side of their basal bulb, but without the additional splash of red pigment typical of the bulbs of the Polyorchidae; the core of each tentacle bulb is blackish-brown. Tentacles are covered with scattered nematocyst batteries which begin a short distance below the bulb and terminate in a small round cluster that is only evident when the tentacles are relaxed. Bell very transparent in life.

Nematocysts of the medusa (Fig. 2A–C). Desmonemes, stenoteles, and microbasic mastigophores were observed in the tentacles of four adult medusae measuring 8–13 mm in bell height. Nematocysts on the tentacles are arranged in spherical batteries that are scattered unevenly over the length of the tentacles. Desmonemes (Fig. 2B), the most common nematocysts, measured undischarged 7.6–10.5 μm

tall x 3.8–5.0 μm wide (n=15); stenoteles (Fig. 2A) were uncommon and measured undischarged 12.0–14.5 μm tall x 9.0–11.4 μm wide (n=15); microbasic mastigophores (Fig. 2C) were uncommon and measured undischarged 9.0–12.3 μm tall x 7.0–9.9 μm wide (n=15). The tentacle bulbs contained primarily stenoteles (not measured), with a few desmonemes and microbasic mastigophores. Lips of the manubrium were lined by a row of spherical nematocyst batteries, which contained only stenoteles that measured undischarged 10.4–12.4 μm tall x 8.6–9.5 μm wide (n=10) in a medusa that was 13 mm tall. Stenoteles were also scattered in the tissue of the manubrium itself.

Remarks. This report differs in several important respects to Bigelow's original description (1916), which was reiterated by Kramp (1961, 1968).

Bigelow's preserved specimens had contorted so as to fold and twist the manubrium and gonad region, and Bigelow noted the irregularity of these folds; in fact all living specimens had smooth, unfolded gonads. The tentacles of Bigelow's preserved specimens were highly contracted, so that he was unable to see the nematocyst clusters throughout the tentacle length and the small terminal nematocyst cluster, visible only on very relaxed tentacles (Fig. 1A,C,D).

Distribution and behavior of medusae. Known from the Queen Charlotte Islands and the west coast of Vancouver Island in British Columbia, and bays on the outer coast of Oregon and northern to central California, in the summer and autumn. In all cases, the medusae were collected near the surface, where they are typically quiescent, bell upright, with tentacles outstretched in a fishing posture. All known collections are cited below, from north to south on the Pacific coast:

- Masset Inlet, Queen Charlotte Islands, British Columbia
12–19 June 1984, four, surface plankton tow, Arai, 1987.
- Amphitrite Point, west coast of Vancouver Island, British Columbia
12 Sept. 1914, three, at the surface, Bigelow, 1916.
- Yaquina Bay, Oregon
18 August 1967, one (as "moerisiid"), McCormick, 1969
10 July 1968, several (as "moerisiid"), near the surface, McCormick, 1969
25 July 1968, one? (as "moerisiid"), near the surface, McCormick, 1969
Sept.-Nov. 1971, several, near the surface, R.J. Larson, collector
12 July 1973, near the surface, R.J. Larson, collector
July 1974, near the surface, R.J. Larson, collector
- Bodega Bay, California
25 July 1972, one, surface plankton, J.T. Rees, collector
27 July 1973, one, surface plankton, J.T. Rees, collector
- Bodega Harbor, California
11 Oct. 1974, one, at the surface, with *Bythotiarra stilbosa*, C.E. Mills, collector
15 Oct. 1974, one, at the surface, with *Bythotiarra stilbosa*, C.E. Mills, collector
20 Nov. 1978, two, at the surface, with *Polyorchis penicillatus* and *Eutonina indicans*, C.E. Mills, collector
23 Nov. 1978, 22, at the surface, with *Polyorchis penicillatus*, *Aglauropsis aeora* and *Eutonina indicans*, C.E. Mills, collector
- Humboldt Bay, California
25 Oct. 1991, ~ 50 at the surface, with *Polyorchis penicillatus* C.E. Mills, collector

Development. Female medusae spawned 1–3 hours after dark, producing about 500–700 eggs per female. The eggs were 110–120 μm in diameter and colorless. The eggs and planulae initially floated high near the water surface, but eventually the planulae sank (many hours later). The planulae were elongate, about 225–250 x 100–120 μm , and completely ciliated, without nematocysts. Planulae began settling in glass bowls after two days; most settled individually, with little clumping. The flat,

settled planular disks were 200–300 μm in diameter (Fig. 1E). About 50 nematocysts (of the isorhiza/anisorhiza type, below) developed in each settled planular disk, primarily near the edge and oriented in a radiating pattern. Within two days of settlement, the central portion of the settled disk thickened and a slight bulge containing two types of nematocysts became evident on the side of each disk as the primary polyp began to form (Fig. 1F). In all cases, the primary polyp emerged out of the side of the disk; 3–4 small capitate tentacles developed within hours of the emergence of this polyp (Fig. 1G), about 3 days after settlement. A small, blunt thecal spine formed over the base of the polyp. The "footprint" of the fully-formed solitary polyp remained the same as that of the original settled planula.

Description of the polyp (Figs. 1H, 1I). The polyps remained very small and solitary, with a small circular thecal base that had a short, fingerlike, protective perisarc extension, or spine, above the polyp. Most polyps had four capitate tentacles, but occasionally had three, or up to eight tentacles; the tentacles were arranged in a single whorl just below a rounded-cone shaped hypostome. Each tentacle had a capitate tip with terminal nematocyst cluster and also had a few nematocysts scattered along its length. The hydranth was 150–200 μm in length and the most robust specimens had tentacles about twice that length (Fig. 1I). Within the basal perisarc, the central portion contained the opaque base of the polyp, with a transparent outer "rim" area characterized by fine, radiating fiber-like structures.

Nematocysts of the polyp (Figs. 2D–E). Nematocysts were not seen in 17-hour old swimming planulae viewed with a compound microscope, but were first evident around the border of settled planulae several days after fertilization. These elongate nematocysts looked like the isorhiza/anisorhizas found later in the polyps, but were not seen discharged; undischarged they measured 5.7–7.6 μm tall x 1.9–2.8 μm wide (n=10). The polyps contained 2–3 types of nematocysts in their tentacles. Stenoteles (Fig. 2D) were the most common and measured undischarged 6.2–7.6 μm tall x 4.3–5.7 μm wide (n=10). There were also a few elongate nematocysts (Fig. 2E) that were either basitrichous isorhizas or anisorhizas or both; these measured undischarged 6.6–7.6 μm tall x 1.9–2.4 μm wide (n=10) and 4.7–5.7 μm tall x 1.9–2.4 μm wide (n=6).

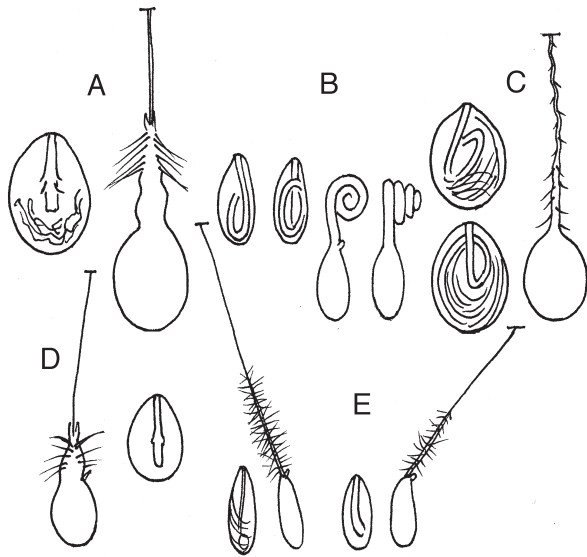


FIG. 2. — Nematocysts of *Halimedusa typus*; A–C, medusa; D–E, polyp. A and D, stenoteles; B, desmonemes; C, microbasic mastigophores; E, basitrichous isorhizas or anisorhizas; drawn to scale, sizes given in text.

Polyp behavior and ecology. The polyps ate small nematodes and rotifers in the culture dishes. They were too small to feed on *Artemia* nauplii or harpacticoid copepods, typical foods for many cultured hydroids; they also did not capture very small (80 μm) sea urchin or polychaete eggs that were offered. When a polyp was disturbed, it contracted slightly, rolling its tentacles inward, but it could not withdraw entirely within the basal perisarc. The longest-lived polyps persisted in the laboratory for more than one year. The polyps are so small and colorless that the possibility of finding them in the field is very slight.

Medusa development. Seven months after settlement, in late June and early July, two polyps each developed a single medusa-bud, attached just below the whorl of tentacles. One of these buds matured, reaching a diameter of about 250 μm (Fig. 1I); the newly-released medusa was 0.55 mm in both bell height and diameter (Fig. 1D). This medusa had scattered nematocysts over its entire bell-surface and had four tentacles, each about as long as the bell height, with scattered nematocysts along the length and a round terminal nematocyst cluster. The manubrium and mouth also had scattered nematocysts on them. The medusa was an active swimmer and had a strong crumple response when disturbed, pulling the tentacles inside its contracted bell. It did not feed and died within 4 days of its release. A small *Halimedusa typus*, 4 mm in bell height with 8

tentacle bulbs, was collected in the plankton in late July; this specimen developed 16 tentacles and was 5 mm tall after 10 days of culture in the laboratory. (Arai [1987] reports very small *H. typus* medusae in early July in British Columbia, and the earliest collections of *H. typus* medusae in Yaquina Bay were also in July [Larson, see above]). A small 16-tentacled medusa that was 5 mm in bell height was collected in November (Fig. 1C), indicating that medusa bud production may take place over a prolonged period in the summer and early fall.

Tiaricodon coeruleus Browne, 1902

Description of the medusa. The abbreviated description of *T. coeruleus* from Kramp (1968, p. 103) reads as follows: “24 mm wide, 25 mm high, jelly thick, bell-shaped; stomach nearly to velar level, four lips distinct, crenulated; radial lobes sac-like, on peduncle only; four perradial tentacles, stout, tapering, nematocysts in proximal part in small, rounded warts, in middle part forming transversal clasps, in distal part rings; an abaxial ocellus. Polyp unknown.” Browne and Kramp (1939, p. 312) add that “The gonads occupy the lobes of the stomach and also extend about half way down the manubrium.” Many more details are given by Browne and Kramp (1939), whose illustration (Fig. 1, Plate XVIII) is reproduced here as Figure 1J. The nematocysts of *T. coeruleus* medusae are reported to be stenoteles, desmonemes and heteronemes (Schuchert, 1996).

Distribution of medusae. This species occurs primarily in the southern hemisphere, having been collected (details follow) in the South Atlantic at the Falkland Islands and the coast of Argentina, in the South Pacific in several locations in South America, China and New Zealand, and in the Weddell Sea in the Southern Ocean; it is also present in at least two NW Pacific locations in China. The collection data imply that it may occur nearly year-round, but is especially abundant in the austral summer (even when collected in northern hemisphere China): Stanley Harbor, Falkland Islands, S Atlantic, November–March, 1898–1902, numerous specimens (Browne, 1902; Browne and Kramp, 1939); Weddell Sea, S Atlantic/Antarctic, 2 February 1902, three specimens (Kramp, 1948); Straits of Magellan, Chile, SE Pacific (Vanhöffen, 1913); Callao, Peru, SE Pacific, September 1883, one specimen (Vanhöffen, 1913); Valparaíso Bay, Chile, SE Pacific, 15

August 1958, one specimen (Kramp, reported by Schuchert, 1996); coast of Argentina, SW Atlantic, no date given (Kramp, 1968); Xiamen Harbour, China, NW Pacific, Dec. 1980–April 1981, numerous specimens (Zhang, 1982; Lin and Zhang, 1990); Shandong Province, Huanghai Sea, China, NW Pacific, no date given (Zhang, 1982); Wellington Harbor, New Zealand, S Pacific, 15 June 1994, 1 specimen (Schuchert, 1996).

Behavior and ecology of medusae. Like *Halimedusa typus*, *T. coeruleus* is typically seen oriented upright, a few inches below the surface, quiescent with tentacles streaming out very far; adult specimens were collected in November, with young stages appearing along with other size classes in January (observations from the Falkland Islands, reported in Browne and Kramp, 1939).

Remarks. I propose to move *Tiaricodon coeruleus* from its most recent resting place in the Polyorchidae (Petersen, 1990; Schuchert, 1996) to the Halimedusidae. The rationale for this move is presented in the Discussion, below. In order to accommodate *Tiaricodon coeruleus* in the Halimedusidae, the description of this family must be modified (see below).

Urashimea globosa Kishinouye, 1910

Description of the medusa. The abbreviated description of *U. globosa* from Kramp (1968, p. 52) reads as follows: “Up to 16 mm high, slightly higher than wide, bell-shaped or globular; exumbrella with numerous (up to about 36) meridional lines of nematocysts; manubrium short, four-sided, four frilled lips with nematocysts; gonads 8–16 sac-like protruberances in walls of stomach; four long tentacles with numerous stalked nematocyst knobs in their entire length; with abaxial ocelli.” Additional details are given by Kishinouye (1910) and Uchida and Nagao (1961), who both collected specimens 17 mm high. The nematocysts of *U. globosa* have not been published.

Distribution of medusae. This species has been collected in many locations from central to northern Japan, including Hokkaido, and on Sakhalin Island (Kishinouye, 1910; Kramp, 1961; Uchida and Nagao, 1961). It was also reported in Amoy, China (Chiu, now Qiu, cited by Kramp 1961), but this location was not confirmed by Zhang (1982). Forty-

five *U. globosa* medusae were collected in plankton samples from in St. Helena Bay, South Africa in 1991 and 1993 (Buecher and Gibbons, 2000). Whether this species is indigenous or recently introduced to South Africa cannot be determined, but the likelihood of an introduction there via shipping or other human-mediated processes is possible, if not probable.

Description of the polyp (from Uchida and Nagao, 1961). Polyp lacking periderm emerges from thin, circular membrane measuring 0.2 mm diameter. Polyp measures 0.2–0.3 mm in height, with cone-shaped hydranth not distinctly demarcated from the hydrocaulus; with 4 or 5 filamentous tentacles, each terminated by a small but distinct nematocyst knob, but without nematocyst rings along the shaft.

Remarks. I propose to move *Urashimea globosa* from the Polyorchidae (Bouillon, 1995) to the Halimedusidae. The rationale for this move is presented in the Discussion, below. In order to accommodate *Urashimea globosa* in the Halimedusidae, the description of this family must be modified (see below).

Family HALIMEDUSIDAE

The family Halimedusidae Arai and Brinckmann-Voss, 1980 (p. 62) was originally described, including only *Halimedusa typus*, as follows: “Anthomedusae with four radial canals; with subumbrella protruding into stomach giving a peduncle-like appearance; mouth cruciform with row nematocysts; with four perradial tentacles and four interradial groups of tentacles, each hollow and lacking adhesive organs; with marginal bulbs with abaxial ocelli.”

The revised family Halimedusidae is now modified in order to also accommodate *Tiaricodon coeruleus* and *Urashimea globosa* and described as follows: Anthomedusae with four radial canals; with low peduncle and with distinct interradial peaks in jelly above base of the manubrium; gonads extending out from the manubrium as lobes below the upper portions of the four radial canals, but without mesenteries; quadratic mouth with lips lined by a row of sessile nematocyst clusters; with four perradial hollow tentacles or with four perradial tentacles and four interradial groups of hollow tentacles; with cylindrical marginal bulbs each with an abaxial ocellus.

DISCUSSION

Bigelow (1916), with some hesitation placed *Halimedusa* in the Pandeidae because of its hollow tentacles with abaxial ocelli. He noted the peculiar row of nematocyst knobs at the margin of the mouth as different from other pandeids, but failed to see the relationship to the Capitata on his distorted and somewhat damaged preserved specimens. Arai and Brinckmann-Voss (1980) removed *Halimedusa* to its own family in order to better define the family Pandeidae, noting the structure of the lips and clustered interradian tentacles of *Halimedusa* as diagnostic to this new family, the Halimedusidae. Its capitate nature was still not evident. Observation in the present study of both polyps and living medusan morphology, as well as the cnidom, reveals that this genus belongs in the Capitata.

Tiaricodon fits much more naturally into the same family with *Halimedusa* than it does with *Polyorchis*, *Scrippisia* and *Spirocodon* (see Table 1). The gonad of *Tiaricodon*, on the peculiar sac-like extensions of the gut out onto the radial canals is very similar to the (unpouched) gonad and manubrium arrangement in *Halimedusa*, but is different from gonads in the Polyorchidae, which are suspended from the peduncle (see below). Similarly, both *Halimedusa* and *Tiaricodon* have a low, gelatinous peduncle with distinctive interradian "peaks" in the adjacent jelly that rise above the level of the radial canals, unlike the very well-defined peduncle and unmarked jelly above the subumbrella characteristic of the Polyorchidae. *Halimedusa* and *Tiaricodon* both have abaxial ocelli, on otherwise unpigmented tentacle bulbs; whereas additional red pigment accompanies the dark abaxial ocelli of all of the Polyorchids. Both *Halimedusa* and *Tiaricodon* have a quadratic manubrium and mouth with four slightly crenulated lips lined with a row of nematocyst clusters; the lips of *Polyorchis* are lined with a band of nematocysts. *Halimedusa* and *Tiaricodon* both have scattered nematocysts on the exumbrella of newly released medusae, whereas newly-released polyorchids have distinctive clusters of nematocysts arranged in eight vertical adradial rows on the exumbrella. Finally, both *Halimedusa* and *Tiaricodon* medusae are typically found fishing quiescently at the surface with tentacles outstretched (Browne and Kramp, 1939; this paper), whereas the polyorchids are primarily benthic in habit, sometimes swimming up and then sinking passively again (Mills, 1981; Arkett, 1984). Polyorchids can not rest

passively at the surface without sinking (Arkett, 1984, 1985). Their distinctly different intrinsic buoyancies lead to very different habitats and behaviors between these two families.

Placement of *Urashimea globosa* into the Halimedusidae is a bit less certain, but I have resisted the temptation to create a separate family for *Urashimea*. With the genus *Urashimea*, some novel characters are added to the Halimedusidae, specifically the presence of numerous meridional nematocyst tracks on the exumbrella, and the unusual tentacles with stalked nematocyst knobs along their lengths. Neither of these characters, however, affect the family diagnosis. Like *Halimedusa* and *Tiaricodon*, *Urashimea* medusae also have characteristic interradian jelly peaks above the radial canals, and the manubrium extends out onto the radial canals carrying saclike swollen gonads (as figured by Hartlaub, 1913, and Uchida and Nagao, 1961) in a manner very similar to *Tiaricodon coeruleus*. The lips of *Urashimea* are a bit more crenulated than those of *Halimedusa* and *Tiaricodon*, but they are also lined by a row of nematocyst knobs. The tentacles have abaxial ocelli. There are no behavior descriptions for *U. globosa* medusae in the literature. The solitary, capitate polyps of *U. globosa*, reared by Uchida and Nagao (1961), look very similar to those described here for *H. typus*, except the *U. globosa* polyps are shown with nematocysts only at the tips of the tentacles and not also scattered along their lengths, as occurs in the polyps of *H. typus*.

The Halimedusidae (*Halimedusa*, *Tiaricodon* and *Urashimea*) and the Polyorchidae both have similar hollow tentacles with large cylindrical bulbs, that are attached to the margin of the umbrella with a narrow base and do not protrude into the substance of the umbrella. But the Polyorchidae are also characterized by unusual tubular gonads that are attached to the radial canals on the peduncle (rather than on the manubrium), large tentacle number, many times branched or diverticulate radial canals, and newly-released medusae bearing highly characteristic adradial rows of nematocyst clusters (newly released *Scrippisia* have never been seen). This suite of characters unites only *Polyorchis*, *Scrippisia* and *Spirocodon* into a fairly solid morphologically-defined family, the Polyorchidae. The cnidom of all of these polyorchids includes stenoteles and desmonemes in the adult medusae (Rees and Mills, in preparation); microbasic mastigophores were also found in the exumbrellar nematocyst clusters of newly released *P. penicillatus* medusae, along with

TABLE 1. — Comparison of some characters of medusae in the capitate genera *Halimedusa*, *Tiaricodon*, *Urashimea*, *Boeromedusa* and the polyorchids *Polyorchis*, *Spirocodon* and *Scrippisia*. Characters that stand out as particularly out of line with the others are noted with an asterisk and set in italics.

Family Genus	Nematocysts	Mouth	Gonads	Radial canals	Tentacles and tentacle bulbs	Interradial jelly "peaks"	Exumbrellar nematocysts new medusae	References
HALIMEDUSIDAE <i>Halimedusa</i>	stenoletes, desmonemes, microbasic, mastigophores, isorhizas <i>or</i> anisorhizas	quadratic with 4 lips, lined by a row of spherical nematocyst knobs	on manubrium with smooth lobes extending out onto radial canals (not folded or pendant sacs)	4 smooth, unbranched	4 periradial hollow tentacles and *4 clusters of <i>interradial tentacles</i> , all with cylindrical bulb with abaxial ocellus, and scattered clusters of nematocysts	4 present in mature specimens	scattered	Bigelow, 1916 This paper
HALIMEDUSIDAE <i>Tiaricodon</i>	stenoletes, desmonemes, heteronemes	quadratic with 4 lips, lined by a row of spherical nematocyst knobs	on manubrium with lobes extending out onto radial canals as swollen pouchlike sacs	4 smooth, unbranched	4 periradial hollow tentacles, each with cylindrical bulb with abaxial ocellus, and scattered clusters of nematocysts	4 present in mature specimens	scattered	Browne, 1902 Browne and Kramp, 1939 Schuchert, 1996
HALIMEDUSIDAE <i>Urashimea</i>		quadratic with 4 lips, lined by a row of spherical nematocyst knobs	on manubrium with lobes extending out onto radial canals, as undulating swollen sacs	4, with * <i>num- erous minute abaxial processes</i> , cylindrical bulb with unbranched abaxial ocellus, and * <i>stalked nematocyst knobs</i>	4 periradial hollow tentacles, each with cylindrical bulb with abaxial ocellus, and * <i>stalked nematocyst knobs</i>	many present in mature specimens	not known	Kishinouye, 1910 Uchida and Nagao, 1961 Bouillon, 1995
BOEROMEDUSIDAE <i>Boeromedusa</i>	stenoletes, desmonemes, * <i>microbasic euryteles</i>	* <i>circular, surrounded by an inconspicuous ring of nematocysts</i>	not on manubrium, but as pendant, flattened, sacs suspended from junction of radial canals and manubrium	4 smooth, unbranched	4 periradial hollow tentacles, each with cylindrical bulb * <i>without ocelli</i> , and scattered clusters of nematocysts	4 present in mature specimens	not known	Bouillon, 1995
POLYORCHIDAE <i>Polyorchis</i> <i>Scrippisia</i> and <i>Spirocodon</i>	stenoletes, desmonemes, microbasic mastigophores, * <i>or microbasic euryteles</i>	quadratic with 4 lips, lined by a distinct marginal band of nematocysts	* <i>as pendant tubes suspended from junction of radial canals and manubrium or from radial canals along peduncle</i>	4 with * <i>many blind branches or diverticulae</i>	numerous hollow tentacles not in clusters, all with cylindrical bulb with abaxial ocellus, and scattered clusters of nematocysts	* <i>not present</i>	* <i>in clusters, in 8 adradial rows</i>	Itô and Inoue, 1962 Kramp, 1968 Mills, 1976 J.T. Rees and C.E. Mills, unpublished

stenoteles and desmonemes (Mills, 1976 and unpublished). The halimedusids *Halimedusa* and *Tiaricodon* have stenoteles, desmonemes, and at least one other type of nematocyst, variously identified as isorhizas, anisorhizas or heteronemes (Table 1).

Boeromedusa auricogonia Bouillon, 1995 is the sole representative of another (south) Pacific monotypic genus placed in its own family in the Capitata, the Boeromedusidae, and shows certain distinctive morphological similarities to the species being considered here (see Table 1). It has been collected only near New Zealand (Bouillon, 1995; Schuchert, 1996). Like *Halimedusa*, *Tiaricodon* and *Urashimea*, *Boeromedusa* has distinctive interradial peaks in its jelly between, but above the 4 radial canals, which are solid rather than hollow extensions of the subumbrella (Schuchert, 1996). Like *Halimedusa* and *Tiaricodon*, *Boeromedusa* has hollow tentacles with scattered clusters of nematocysts along the length, terminating with a nematocyst cluster. Like *Tiaricodon*, it has saclike gonads that develop from extensions of the manubrium out along the tops of the radial canals; but in *Boeromedusa*, as in the polyorchids, the gonadal material is restricted to the region just beyond the manubrium and does not cover the manubrium itself. One might postulate a progression of gonad shape from *Halimedusa* to *Tiaricodon* to *Urashimea* to *Boeromedusa* and the polyorchids. Further differentiating *Boeromedusa*, its tentacle bulbs lack the ocelli found on all other species mentioned here and are of a different shape that those of the Halimedusidae and the Polyorchidae. Its cnidom is also somewhat different, comprising stenoteles, desmonemes and microbasic euryteles (Bouillon, 1995).

All of the species considered here are basically of Pacific distribution, with one species, *Tiaricodon coeruleus*, also occurring in the South Atlantic and Southern Ocean. The recent discovery of *Urashimea globosa* off South Africa seems likely to represent a recent introduction. It seems evident that members of the Halimedusidae (*Halimedusa*, *Tiaricodon* and *Urashimea*), the Boeromedusidae (*Boeromedusa*), and the Polyorchidae (*Polyorchis*, *Scrippsia* and *Spirocodon*) are closely allied within the Capitata, but are still separated by small differences in cnidoms and morphologies. Of all of these medusae, only the polyps of *Halimedusa typus* and *Urashimea globosa* are presently known; complete knowledge of all of the life cycles would be very helpful in better understanding their relationships, as would molecular studies.

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