

## A pandeid hydrozoan, *Amphinema* sp., new and probably introduced to central California: life history, morphology, distribution, and systematics\*

JOHN T. REES

Bay/Delta Shore Institute, California State University, Hayward, Building 7; 751 West Midway,  
Alameda Point, CA 94501 U.S.A. and  
Department of Biological Sciences, California State University, Hayward, CA 94542 U.S.A. E-mail: Johntrees@aol.com

**SUMMARY:** A pandeid hydrozoan new to California, *Amphinema* sp., was collected in 1998 as a hydroid living on the non-indigenous bryozoan, *Watersipora "subtorquata"*, attached to floats in Bodega Harbor 80 km north of San Francisco Bay. The hydroid was cultured in the laboratory and medusae it released were raised to maturity. No species name could be assigned because although the hydroid colony structure and morphology of the polyp most closely resemble descriptions of *Amphinema rugosum*, the immature and adult medusae best resemble *A. dinema*. These two described species are known from widely-spaced locations worldwide including Europe (British Isles and the Mediterranean), New England, the Caribbean, east Africa, India, Japan and China, implying that they may transport easily between sites by man's activities. Such wide-spread distributions of both species, coupled with the notable absence of *Amphinema* sp. from Bodega Harbor during a number of previous field surveys in the 1970's, strongly intimates that *Amphinema* sp. has been introduced from elsewhere into Bodega Harbor during the past 25 years. Two additional species of *Amphinema* medusae present on the west coast of North America are discussed.

*Key words:* *Amphinema rugosum*, *Amphinema dinema*

### INTRODUCTION

The hydrozoan fauna of bays and harbors of the central California coast has been altered through non-indigenous species introductions over the past 50 years or more (Hand and Gwilliam, 1951; Mills and Sommer, 1995; Rees and Gershwin, 2000) and the rate of successful establishment of all non-indigenous species in San Francisco Bay appears to be accelerating in recent decades (Cohen and Carlton, 1998). The present paper describes what is believed to be a recently-introduced species of

*Amphinema*, family Pandeidae, in Bodega Harbor, California, a shallow, sandy harbor located about 80 km north of San Francisco. This is the first formal description of a hydrozoan in the genus *Amphinema* from California, and the first of its type [either *A. dinema* (Péron and Lesueur, 1809) or *A. rugosum* (Mayer, 1900)] to be reported from anywhere on the Pacific coast of the Western Hemisphere.

One pandeid hydroid colony was collected by Ms. Cinzia Gravili on September 25, 1998, from the floating dock at the Coast Guard Station on the south shore of Bodega Harbor, California (during the Fourth Hydrozoan Workshop sponsored by the Hydrozoan Society and held at Bodega Marine Lab-

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oratory September 19–October 3, 1998). The colony was growing on the non-native, bright orange, encrusting bryozoan, *Watersporia* “*subtorquata* (d’Orbigny, 1852)” (see Cohen and Carlton, 1995). The initial generic identification of the hydroid as *Amphinema* was made on the basis of its morphology and a peculiar but specific “flexing” behavior of the polyp, in which disturbed polyps bend over nearly 180° towards the substrate (F. Boero, personal communication). Intriguingly, the *Amphinema* hydroid colony was bright orange-red and nearly invisible on casual inspection of the similarly-colored bryozoan. Without knowledge of the morphology of the adult medusa, a specific identification within the genus *Amphinema* was not possible, so I undertook to culture the hydroid as well as the medusae it was releasing. Medusa buds were present on the field colony, and upon isolation, aeration, and consistent daily feeding, newly-released medusae were reared to sexual maturity in the laboratory.

Taken together, *Amphinema dinema* and *A. rugosum* have a cosmopolitan distribution spanning several different biogeographic provinces. The medusae of *A. dinema* have been reported from northern and western Europe, the Mediterranean, the eastern Atlantic including Rhode Island, the Dry Tortugas, and Brazil, western Africa, and South Asia (Kramp, 1961). *A. rugosum* has been reported from the western Pacific (Japan) by Uchida (1927) as *Stomotoca rugosa* (Kubota, 1998), and in Europe from the British Isles and Italy (Rees and Russell, 1937; Russell, 1953; F. Boero, personal communication). The medusa of *A. rugosum* has also been reported from New England and the Caribbean (Kramp, 1961) and China (Chow and Huang, 1958).

## MATERIALS AND METHODS

To encourage release of medusae, the bryozoan colony on which the hydroid colony was growing was tied onto a glass microscope slide using thread, and the slide placed in a 250 ml plastic rearing cup filled with sea water. The culture was aerated, and the polyps fed daily with *Artemia* nauplii and copepods collected from the sea with a plankton net. Both the hydroid polyps and bryozoan zooids fed avidly on the *Artemia* and copepods. The culture water was changed every other day, and temperature was maintained at about 18° C in the laboratory. Under these conditions both the hydroid and the bryozoan colonies flourished, and many medusae were

released. Newly-released medusae were isolated in separate rearing cups and fed in a manner similar to the polyps. Medusae were maintained in the laboratory for up to 8 weeks, during which they grew and ultimately developed mature male gonads. The colony was maintained in the laboratory for about 6 months, and eventually spread onto the glass slide, where it thrived without the presence of the original host bryozoan, which had long-since perished.

Reference photographs were taken and a photolibrary maintained of all life history stages, including the colony, individual polyps, medusa buds, newly-released and adult medusae, and nematocysts. Photographs were taken with a Nikon 35 mm camera mounted on an American Optical binocular microscope. Nematocysts were examined under high power (500x and 1000x) and photographed. Nematocyst measurements given here are of undischarged capsules.

## RESULTS

### Polyp and Colony (Fig. 1)

The color of the polyps and stolons in the field-procured colony was a deep orange-red. The polyps arose from stolons growing on the surface of the bryozoan colony among the zooids. The hydroid colony was primarily reptant, with occasional upright branches (Fig. 1a). The uprights possessed at most 2 polyps, and protruded 2–3 mm above the surface of the bryozoan. Medusa buds, mounted on short pedicels, developed directly from the stolons as well as on the upright branches. Polyps had 8 to 10 tentacles in two cycles, the top cycle being held upright, nearly parallel to the body of the hydranth, and the bottom cycle held perpendicular to the hydranth wall (Fig. 1a, b). The polyps were mounted on well-defined hydrothecae, at the base of which, adjacent to the stolon, were 2–5 annulations, (Fig. 1c, d). Both field and laboratory colonies possessed more than 100 polyps.

### Medusae (Fig. 2)

Newly-released medusae (Fig. 2a, b) were slightly less than 1.0 mm in height and diameter. The jelly was thin and there was no apical projection. There were two opposite tentacles, each with a broad flat tentacle bulb, and two opposed rudimentary marginal swellings, four broad radial canals, and a total of 1–4

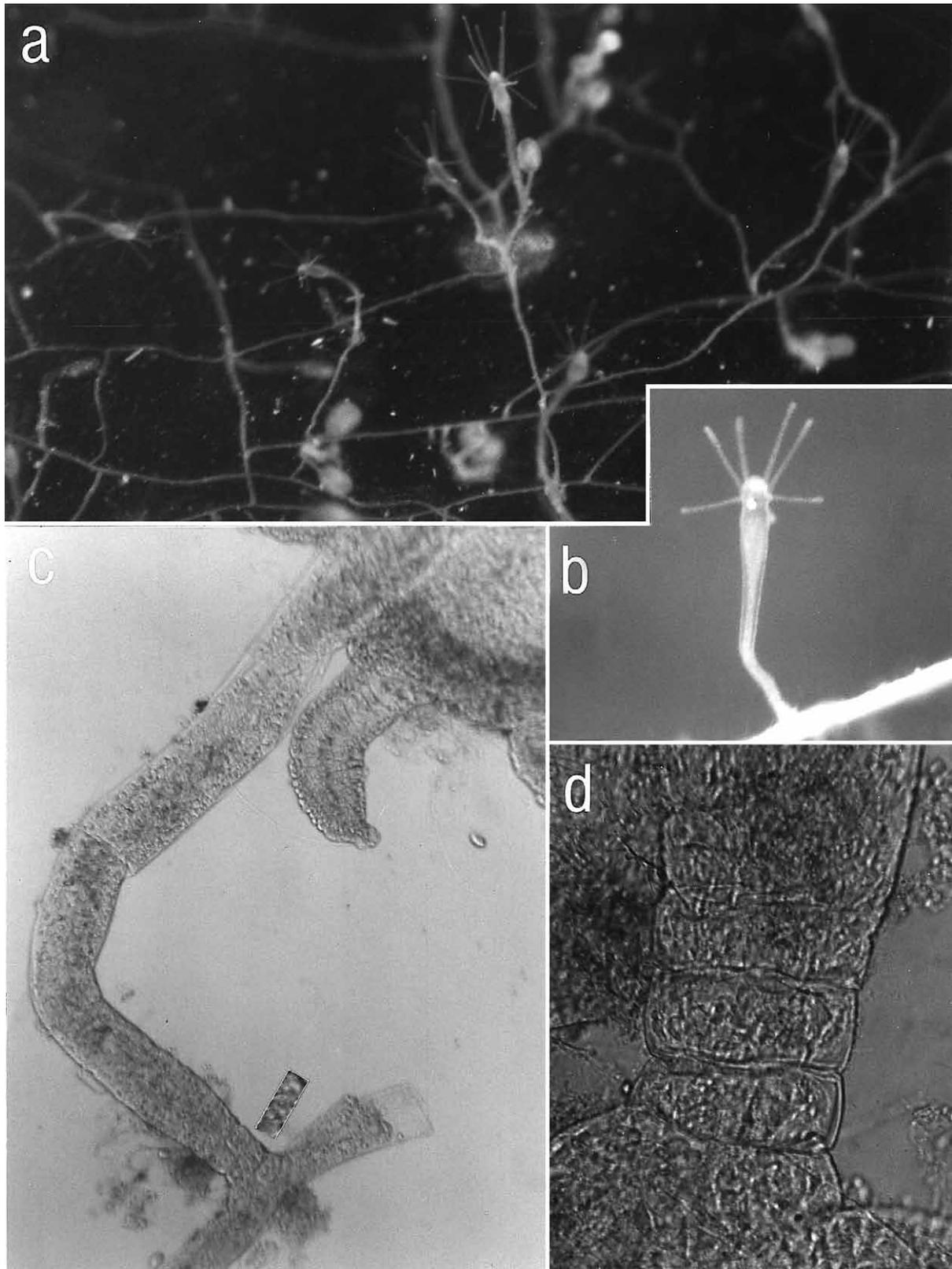


FIG. 1. – *Amphinema* sp. from Bodega Harbor, laboratory-reared specimens. (a) Hydroid colony, showing two polyps and a developing gonophore on an upright branch. (b) Single polyp, showing the two cycles of tentacles, held upward and outward from the body of the hydranth; polyp height, about 1 mm. (c) Photomicrograph of the lower part of a hydranth, showing (from bottom to top) stolon, annulations of the perisarc, perisarc proper, the distinct lip of the perisarc, and the body of the hydranth (one tentacle of the polyp is evident in the photograph). Note the single banana-shaped microbasic eurytele nematocyst on the hydranth; the same nematocysts are scattered over the tentacles. (d) Enlargement of (c), showing annulations of the perisarc at the base of the polyp.

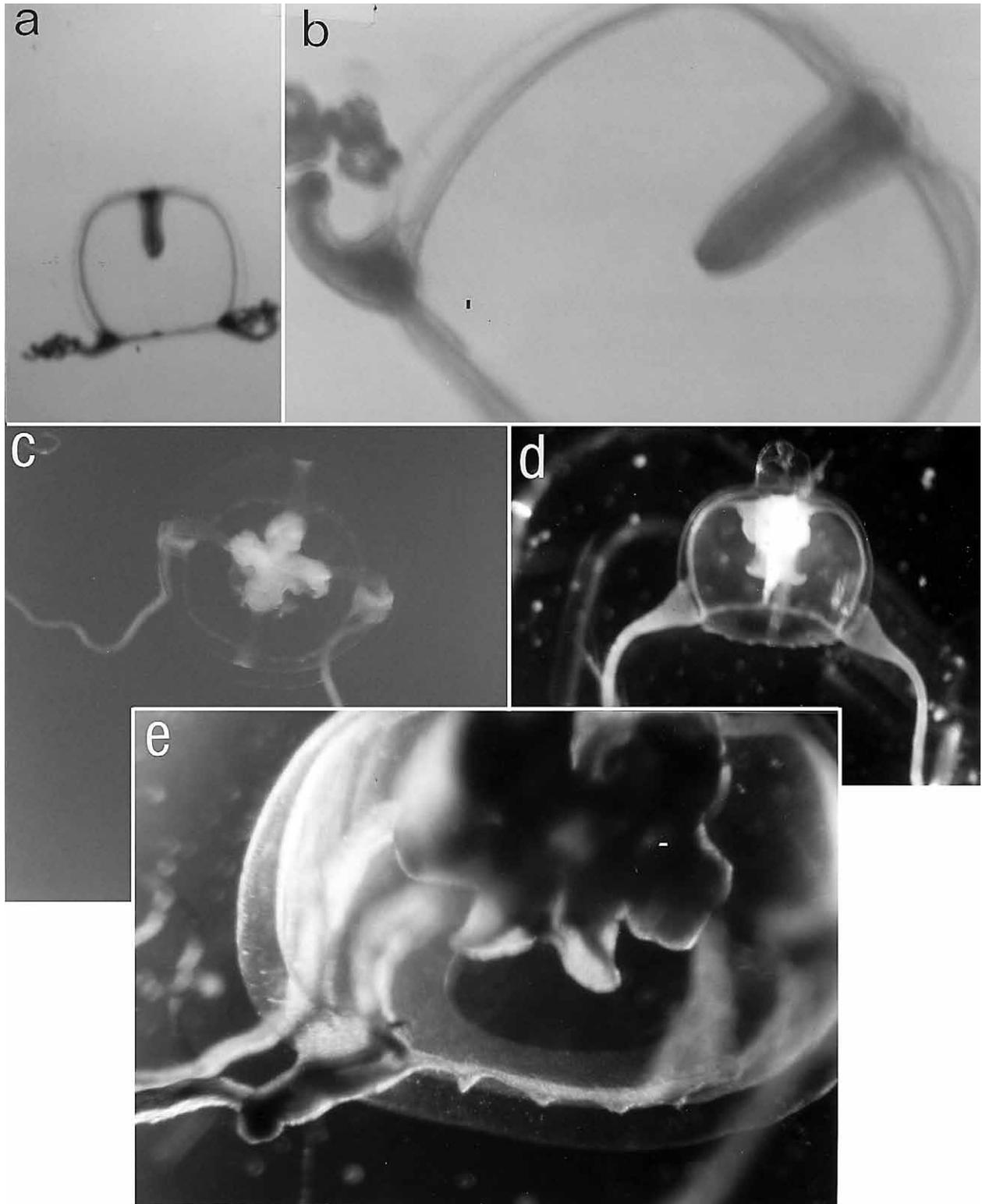


FIG. 2. – *Amphinema* sp. from Bodega Harbor, laboratory-reared specimens. (a and b) Two views of the newly-released medusa, about 0.9 mm wide by 0.7 mm in width. Note the manubrium, which reaches about half-way into the subumbrellar cavity, the two tentacles with large flattened tentacle bulbs, the periradial marginal wart on the rim of the umbrella, and absence of an apical projection. (c) Six week-old medusa, aboral view, 2 mm bell height, 3 mm bell width. Note the cruciform-shaped gonad as seen from above, showing irregularities and convolutions of the gonad structure. Note also the broad radial canals and two extended marginal tentacles. (d) Four week old medusa, side view, 1.5 mm bell height, 1.7 mm bell width. Note the apical projection, very thin jelly of the bell, two prominent tentacle bulbs with tentacles, cruciform manubrium with developing gonad above, and the numerous marginal warts around the base of the bell. (e) Seven-week old senescent medusa, 2.5 mm bell height, 3 mm bell width. The cruciform lips, smooth gonads, and marginal warts are clearly visible. An “abnormal” third tentacle has developed on a previously atentaculate marginal wart.

small interradial warts along the bell margin. The manubrium was simple and extended about 1/2 way into the subumbrellar cavity. The exumbrella was sprinkled with nematocysts. When not extended, the tentacles were held coiled up against the bell (Fig. 2a)

Mature medusae 4–5 weeks old attained a bell height and diameter of about 2.5 mm. The two tentacle bulbs had enlarged and become laterally compressed, extending upwards onto the bell along each corresponding radial canal (Fig. 2d). The extended tentacles were very long, reaching 5 cm or more in length when medusae swam up into the water column. The tentacle bulbs were rose-red in color, which also extended somewhat down the length of each tentacle; the four radial canals were the same rose-red. Three to four marginal warts were present in each interradial sector of the bell margin - none of these warts produced tentacular processes of any kind. The manubrium had four well-developed cruciform lips with a bright greenish tinge. Gonads had formed on the upper half of the manubrium, and consisted of four interradial, somewhat-convoluted areas extending, when viewed from the top, in a cruciform shape out adjacent to the radial canals (Fig. 2c). No oblique, inwardly-pointing, folds on the surface of the gonads, characteristic of many species of *Amphinema*, including *A. rugosum*, were ever observed. No eggs were seen, and all mature medusae observed were assumed to be males; the gonads were whitish and opaque.

The oldest medusae reared, about eight weeks old, attained a bell diameter of about 3.5 mm. Senescence had apparently begun to set in by this stage, and one specimen developed a third tentacle from a previously-atentaculate marginal wart (Fig. 2e); the same tentacle bulb also had a finger-like growth directing inward towards the velum. Russell (1953) noted similar developmental abnormalities in *A. rugosum*, as have Boero *et al.* (1997) in senescent specimens of the pandeid *Codonorchis octaedrus*, which developed multiple manubria and bifurcated tentacles. Whether these senescent morphologies occur in field populations, or are an artifact of laboratory culture, is not known.

Newly-released *Amphinema* sp. medusae were phototactic and swam towards a light source; similar behavior was noted by Boero *et al.* (1997) by the pandeid *Codonorchis octaedrus*. In culture, *Amphinema* sp. medusae usually rested on the bottom of the container and caught brine shrimp nauplii or copepods passively with the lips of the manubrium; the tentacles were never seen to actively capture

or ensnare any provided crustacean food item in the laboratory.

### Cnidom (Fig. 3)

The Bodega Harbor *Amphinema* sp. had two types of nematocysts. Both types were found in the tentacles of the polyp: banana-shaped microbasic euryteles (Fig. 3a, b) were 8–9 x 2–2.5 mm, and very small, almost-round capsules, probably desmonemes, were 2–2.5 mm diameter (Fig. 3c). Only one type of nematocyst, microbasic euryteles 6.5–8.0 x 2.5 mm, were found in the tentacles of the adult medusa (Fig. 3d). The types and sizes of nematocysts seen in the Bodega Harbor animals were virtually identical to those described for both *A. dinema* and *A. rugosum* by Russell (1938).

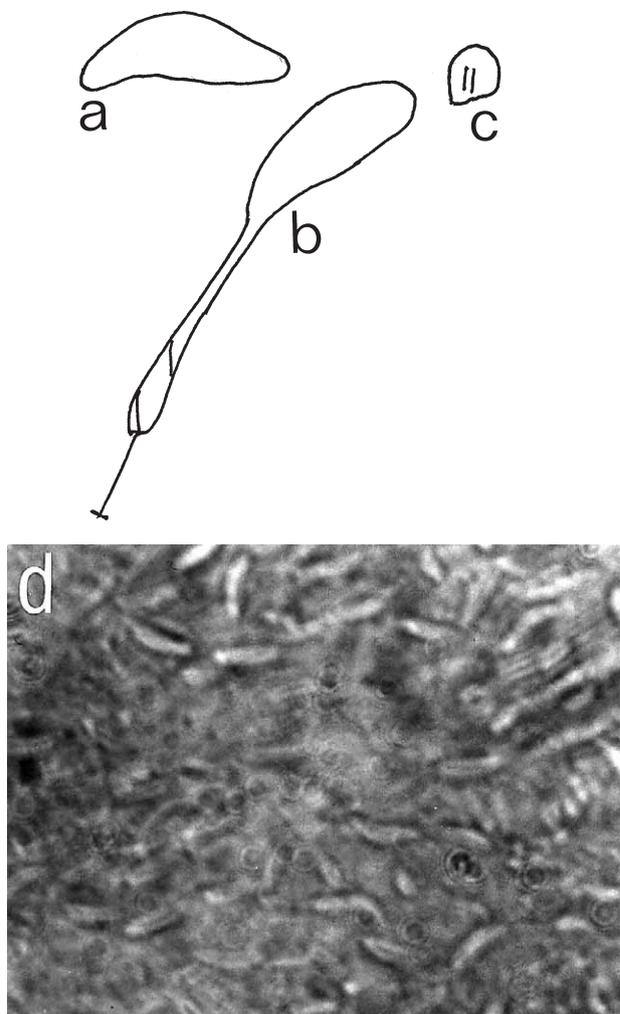


FIG. 3. – Nematocysts of *Amphinema* sp. Sketches of (a) unexploded and (b) exploded euryteles from the tentacles of an adult medusa. (c) Second type of nematocyst, presumably unfired desmoneme, in the tentacles of the polyp. (d) Photomicrograph of a tentacle squash preparation from an adult medusa showing unfired banana-shaped euryteles; the eurytele capsules are all about 10 μm in length.

## DISCUSSION

Differences between *Amphinema dinema* and *A. rugosum* from the British Isles were described in detail by W. J. Rees and Russell (1937) and Russell (1953), for both field and laboratory-reared specimens. Similarities were sufficient to cause Rittenhouse to attempt to cross the two species, but he was unsuccessful (Russell, 1953).

The hydroid of *A. dinema* from Britain, may or may not have annulations at the base of the hydrocaulus and has a membranous, poorly-defined hydrocaulus rim. Medusa buds are borne only on the stolons. The newly-released medusa had no apical projection and the adult medusa has marginal protuberances of the bell that are “mere thickenings of the edge of the umbrella” (W.J. Rees and Russell, 1937, p. 61), also called marginal warts. Mature gonads are “simple adradial plates,” lacking lateral folds.

The British *A. rugosum* hydroid has an annulated base of the hydrocaulus and the distal rim of the hydrocaulus ends abruptly; the hydranth is not seen at all retractile. The newly-released medusa has an apical projection, and the adult medusa has prominent marginal tentaculæ along the umbrellar rim. The gonads of the adult medusa have inwardly-pointing adradial folds.

*Amphinema* sp. from Bodega Harbor shares taxonomic characteristics of both *A. dinema* and *A. rugosum* (see Table 1). The polyp of the Bodega Harbor *Amphinema* possesses an annulated hydrocaulus, and like *A. rugosum*, bears medusa buds on both the reptant stolon and the branched uprights. The Bodega Harbor *Amphinema* medusa, however, matches the description for *A. dinema*, in its absence

of an apical projection in the newly released medusa, lack of oblique folds on the mature gonads, and presence of marginal warts around the margin of the umbrella, rather than the more elongate tentaculæ of *A. rugosum*.

Due to the above inconsistencies in aligning characters in the life cycle of the Bodega Harbor *Amphinema* with either *A. dinema* or *A. rugosa*, it is concluded that a species designation is not possible at this time, although the possibility is certainly indicated that *A. dinema* and *A. rugosum* might be one variable species rather than two separate species. Overlapping specific characters are unfortunately common in hydrozoan systematics. In a group with a limited range of morphologies with which to separate species, this tendency towards character overlap renders identification of many hydrozoan species dubious. Innovative and integrated approaches are needed in hydrozoan systematics, including a “molecular taxonomy” in which species level markers are identified. It is hoped that such markers can be used in association with standard taxonomic characters to more clearly define species in difficult hydrozoan genera such as *Amphinema*. Without new innovative approaches, we continue to be stymied by situations exemplified by the Bodega Harbor *Amphinema*, hobbled by our inability to make field identifications and engaged in fruitless debates over morphological minutiae, which only a specialist who has worked with a particular genus or group of species over a long period of time can interpret.

Both *A. dinema* and *A. rugosum* are apparently widely distributed globally, but neither has been reported from any other location on the Pacific coast of North or South America. It is probably significant

TABLE 1. – Comparison between *Amphinema dinema*, *A. rugosum*, and the *Amphinema* sp. from Bodega Harbor, California. Definitive morphological differences between *A. dinema* and *A. rugosum* are summarized from W.J. Rees and Russell (1937) and Russell (1953).

	<i>Amphinema dinema</i> , (Péron and Lesueur, 1809)	<i>Amphinema rugosum</i> , (Mayer, 1900)	<i>Amphinema</i> sp. Bodega Harbor
<b>Hydroid:</b>			
Base of hydrocaulus	With or without annulations	Annulated	Annulated
Upper end of hydrocaulus	Membranous and delicate	Not membranous	Well-defined, not membranous
Placement of medusa buds	On stolons	On stolons and uprights	On stolons and uprights
Color	Orange-red	Orange-red	Orange-red
<b>Newly released medusa:</b>			
Apical projection	Absent	Present	Absent
Color of stomach	Reddish orange, tinged green	Ochre yellow	Brick-colored; no green
<b>Adult medusa:</b>			
Umbrella rim	Marginal warts	Marginal tentaculæ	Marginal warts
Gonads	Oblique folds absent	Oblique folds present	Oblique folds absent
Color	Tentacle bulbs vivid purple-violet; stomach bright green	Tentacle bulbs and stomach orange to brownish-yellow	Tentacle bulbs light brownish red; stomach yellowish brown with bright green lips

that neither species has previously been reported from either central California, which has been sampled repeatedly by hydroid specialists over the past 100 years (see Fraser, 1937; Rees, 1975), or the Puget Sound/Strait of Georgia region in Washington State and British Columbia, despite relatively intensive sampling there (Foerster, 1923; Arai and Brinckmann-Voss, 1980; Mills, 1981; Mackie, 1985; Wrobel and Mills, 1998). The entire float-fouling fauna in Bodega Harbor has shifted in the past 20 years to a highly disturbed community, dominated by non-indigenous species, not so different from that of San Francisco Bay (C.E. Mills, personal communication). Neither the polyps nor medusae of any *Amphinema* species were collected in Bodega Harbor during intensive surveys of the area 1971–1974 (Rees, 1975), and again in 1980. The host *Watersipora* bryozoan, like many of the other non-indigenous invertebrates now present in Bodega Harbor, was also not present in the 1970s. The only pandeide polyps in the Bodega Harbor region during the 1971–1974 period were thought to be *Leuckartiara octona*, collected on several occasions on the shells of living gastropods, *Olivella biplicata*; *L. octona* medusae were also collected in the plankton during that period (J.T. Rees, unpublished).

There have been two other records of medusae in the genus *Amphinema* from the North Pacific. Arai and Brinckmann-Voss (1983) described a new species, *A. platyhedos*, from British Columbia, collected from depths exceeding 350 m. Wrobel and Mills (1998) show a different *Amphinema* medusa from surface waters in Monterey and Santa Barbara (incorrectly labelled as *A. platyhedos*, but clearly a different species, C.E. Mills, personal communication). *A. platyhedos* can be distinguished from the Bodega Harbor *Amphinema* sp. by its long marginal tentacles and the smooth (unfolded) structure of its gonads. The *A. "platyhedos"* pictured by Wrobel and Mills (1998) is almost certainly a third west coast species. Its gonads show much distinctive lateral folding, a characteristic absent from *A. platyhedos*, and it has numerous marginal warts; it also does not correspond well to the Bodega Harbor specimens described here. A more complete comparison of the medusae of nine species belonging to the genus *Amphinema* is given by Bouillon *et al.* (2000).

The polyp of the Bodega Harbor *Amphinema* sp. seems to be a facultative, rather than obligate, commensal as evidenced by the ability of the colony to grow and thrive under laboratory conditions without the presence of its bryozoan host. Many pandeide

polyps are symbiotic, including *Octotiarra russelli*, also a bryozoan symbiont (Boero and Bouillon, 1989), and *Merga tergestina*, found on sea urchins and polychaetes (Vannucci, 1960). At least one pandeide genus, *Hydrichthys*, is parasitic on fish (Larson, 1982; Boero *et al.*, 1991). A systematic review of symbioses within the Pandeidae would be most enlightening, and might provide insight into the mechanisms by which hydrozoan polyps have evolved from facultative to more obligate forms of symbiosis.

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