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Ingestion of a medusa (*Aegina citrea*) by the nematocyst-containing ctenophore *Haeckelia rubra* (formerly *Euchlora rubra*): phylogenetic implications

C. E. Mills[1] **and R. L. Miller**[2]

[1] **University of Washington, Friday Harbor Laboratories; Friday Harbor, Washington 98250, USA**

[2] **Friday Harbor Laboratories; Friday Harbor, Washington 98250, USA, and Department of Biology, Temple University; Philadelphia, Pennsylvania 19122, USA**

Abstract

The rare ctenophore *Haeckelia rubra* (formerly *Euchlora rubra*) has long been known to have nematocysts rather than colloblasts in its tentacles. Five specimens were collected in the San Juan Archipelago, Washington State, USA in 1980 and 1981, and their feeding behavior was observed in the laboratory. We found that *H. rubra* readily eats the tentacles of a medusa, *Aegina citrea,* whose nematocysts (apotrichous isorhizas) are nearly identical in morphology to the nematocysts of the ctenophore. When *H. rubra* was offered 16 other species of hydromedusae and 1 siphonophore in the laboratory, the ctenophores showed little or no tendency to ingest these potential prey items. In addition to its routinely positive response to *A. citrea,* the ctenophore could be induced by manipulation and starvation to accept and ingest bits of the bodies of 4 additional species of hydromedusae and 1 siphonophore. These results, combined with the histological and rearing experiments of other investigators, leave little doubt that the nematocysts in *H. rubra* are not endogenous, but are "kleptocnidae" similar to those nematocysts retained and subsequently used by some species of nudibranchs that feed on Cnidaria. A close phylogenetic link between the Cnidaria and the Ctenophora is most unlikely.

Introduction

Ever since the discovery (Gegenbauer, 1856) and the identification (Chun, 1880) of nematocysts in the tentacles of one species of ctenophore *Haeckelia rubra* (Kölliker, 1853) (known almost universally by its junior synonym *Euchlora rubra*), the presence of this uniquely Cnidarian feature in a member of the Ctenophora has required special consideration in discussions of phylogenetic origins of lower invertebrates. Komai (1942) and Komai and Tokioka (1942) studied *H. rubra* nematocysts and concluded that they were endogenous to the ctenophore, although Komai (1951, 1963) later became convinced, at the suggestion of L. H. Hyman, that the nematocysts were of foreign origin, probably derived from some medusa eaten by the ctenophore. Hadži (1953) speculated that the nematocysts were probably from the narcomedusa *Cunina* sp. Picard (1955), however, reexamined *H. rubra* and on the basis of morphology and histology reasserted that the nematocysts were endogenous to the ctenophore. Hyman (1959) accepted Picard's evidence and stated that this information supports theories of the origin of ctenophores from a trachyline medusa ancestor. These conclusions have been cited by many current invertebrate zoology textbooks (e.g. Hickman, 1973; Barrington, 1979; Barnes, 1980) as well as by specialists (Hand, 1959; Rees, 1966) in discussions of phylogeny as acceptable, though still inconclusive, evidence of a common ancestor for the Cnidaria and the Ctenophora. Carré and Carré (1980 a, b) have once again examined the nematocysts of this rare ctenophore. They found that young specimens fed plankton (sometimes including medusae) did not gain a population of nematocysts, even though some net growth of the ctenophores was obtained. Older specimens, fed a similar diet, suffered degeneration and eventual loss of their tentacles, after which they had to be fed by hand. These results suggest that the ctenophores, fed a diet sufficient for growth, could not generate their own nematocysts. The rearing studies, combined with electron microscope observations of the incorporation of nematocysts from the digestive canals into the tentacles of *H. rubra,* caused Carré and Carré to conclude that *H. rubra* nematocysts are probably kleptocnidae. On the basis of morphological similarity (Weill, 1934) they agree that the nematocysts probably derive from narcomedusae as originally suggested by Hadži (1953). In the present paper we report observations on the feeding behavior of *H. rubra* and demonstrate its marked preference for tentacles of the narcomedusa *Aegina citrea,* whose nematocyst types closely correspond to those observed in *H. rubra.*

Materials and methods

Five specimens of *Haeckelia rubra* were collected in the San Juan Archipelago, Washington State, USA (Latitude 48°40′N; Longitude 123°0′W) (4 in May 1980 and 1 in May 1981). Two of the ctenophores were obtained in a plankton net towed vertically from 200 m to the surface near Speiden Island, and 3 were obtained at the surface beside a floating dock at the Friday Harbor Laboratories, San Juan Island. These were the only *H. rubra* specimens collected during 7 yr of extensive inspection of plankton for medusae and ctenophores near Friday Harbor (Miller, 1979; Mills, 1981).

The ctenophores were maintained in the laboratory in glass bowls kept at ambient sea temperature in a flow-through sea water table. The water in the bowls was changed every 1 or 2 d.

Haeckelia rubra were offered, over a period of 4 wk (2 wk each in both 1980 and 1981) 17 different species of hydromedusae and one siphonophore as potential food items (Table 1). In the first series of feeding trials, 1 or 2 of the ctenophores were placed together in a bowl (100 ml sea water) with a whole, healthy medusa or siphonophore for several hours; in the second series of feeding trials, small pieces of medusan tissue were held with forceps and placed near the ctenophore's mouth for up to 5 min. The ctenophore responses were similar in both cases, and results of all feeding trials are presented together in Table 1.

Nematocysts in the tentacles of *Haeckelia rubra* were observed and measured on 3 occasions: (1) approximately 24 h after *H. rubra* was collected, and before it was offered any cnidarian material in the laboratory; (2) 24 h after ingesting *Aegina citrea* tentacles in the laboratory; (3) several days after ingesting *A. citrea* tentacles. Nematocysts were also observed and measured in two specimens of *A. citrea.* The nematocysts of both species were measured in unexploded condition using either Nomarski or phase-contrast optics (Figs. 2 and 3).

Results

The specimens of *Haeckelia rubra* were all between 4.2 and 7.2 mm in length and were approximately one-half to two-thirds as wide, depending on their posture (see Fig. 1). The ctenophores usually rested passively, statocyst up, on the bottom of the bowls in which they were kept. Their ctenes beat slowly, but did not usually propel the ctenophores. Tentacles were nearly always contracted into the tentacle sheaths. The ctenophores frequently flexed their tentacle sheaths, causing a brief flexure of much of the body, but otherwise were quiescent.

Whole medusae offered as prey

Healthy *Sarsia tubulosa, Stomotoca atra* and *Phialidium gregarium* medusae in a 100 ml container with one or two *Haeckelia rubra* elicited no observable response from the ctenophores (Table 1). Introduction of wounded *Sarsia tubulosa* or *P. gregarium* (cut across the marginal nerve ring to prevent swimming pulsations) to a dish containing *H. rubra* caused the ctenophores to become temporarily more active, moving around the dish for about 10 min before becoming quiescent again. However, no specific feeding responses such as mouth opening or tentacle extension were observed. Introduction of a wounded *Stomotoca atra* to a bowl containing two *H. rubra* again caused both ctenophores to begin moving slowly around the dish. Both ctenophores opened their mouths several times when close to the medusa. One *H. rubra* attached by its mouth to the apex of the bell of the medusa, which began pulsating weakly until the ctenophore was eventually dislodged. The ctenophores were not left overnight with *S. atra* because *S. atra* is a voracious predator of medusae and presumably also of ctenophores.

On 4 occasions, two *Haeckelia rubra* were placed in a dish along with a healthy *Aegina citrea* medusa. The presence of *A. citrea* elicited a conspicuous feeding response from *H. rubra,* which commenced swimming and tentacle extension. In each case, all 4 *A. citrea* tentacles were removed by the ctenophores within 24 h (see Fig. 1); some tentacles had been ingested and others were lying on the bottom of the bowl. At least once, an *H. rubra* later captured and ingested one of the tentacles lying on the bottom of the dish.

The ingestion of an *Aegina citrea* tentacle was observed 5 times. *Haeckelia rubra* attached with its tentacles to the *A. citrea* tentacle and opened its mouth over the tip of the *A. citrea* tentacle. The medusa tentacle (approximately 15 mm long) was then moved into *H. rubra*'s 3 to 5 mm long pharynx at a rate of about 2 mm min^{-1}, evidently by ciliary movement in the ctenophore's pharynx. When the tip of the *A. citrea* tentacle reached the end of the ctenophore pharynx it became coiled upon itself (Fig. 1), until the entire *A. citrea* tentacle was packed into the somewhat extensible ctenophore pharynx. We never observed the end of this process in which the *A. citrea* tentacle was severed from the medusa. It is not known whether *H. rubra* possesses macrocilia around its mouth like those of the ctenophore *Beroe* spp., which are used to sever portions of other ctenophores on which *Beroe* spp. preys. Autotomy of *A. citrea* tentacles does occur under adverse conditions in the laboratory. Possibly the action of the ctenophore's gut contents serves to trigger this response. Alternatively, digestive enzymes from the ctenophore gut may detach the tentacle. Disintegration of the medusan tentacle tissue was easily observed through the transparent body wall of the ctenophore, and this process usually occurred within 5 h of ingestion. During and after this period, the meridional canals of the ctenophore became very distended and many unfired nematocysts from *A. citrea* could be seen rolling around inside the canals.

On one occasion a *Haeckelia rubra* continued to ingest an entire *Aegina citrea* after initially ingesting a tentacle (the entire process taking 18 h). Another time an *H. rubra*

Table 1. *Haeckelia rubra.* Feeding responses of ctenophores offered a variety of cnidarian potential prey in the laboratory. Number in parentheses indicates number of different medusae of each species tried as prey. + indicates digestion of potential prey. A = Edges of mouth became contracted and firmly shut, no adherence to prey item; B = neutral response, no apparent recognition of prey item; C = mouth opened and either adhered to medusa or partially swallowed piece of tissue, but eventually medusa or tissue piece was dropped without being digested; D = mouth opened and swallowed portion of medusa or piece of tissue and ctenophore subsequently digested it; E = *Cunina* sp. left overnight with two *H. rubra* ate one of the ctenophores

Species offered as prey	Feeding response	Whole medusa	Piece of margin plus tentacle	Piece of bell and mesogloea	Piece of manubrium	Piece of gonad
Anthomedusae						
Bougainvillia principis (2)	–		A	A, C	A	
Catablema nodulosa (2)	–		B, C		C	
Euphysa japonica (2)	–		A, B		C	B
Sarsia sp. A (2)	–		C	A	A	
Sarsia tubulosa (3)	–	B	A	A	A	
Stomotoca atra (4)	–	B, C		C	C	
Leptomedusae						
Aequorea victoria (3)	–		A, C	A		A
Eutonina indicans (1)	–		A		A	
Mitrocoma cellularia (3)	–		A, C	A	A	A
Mitrocomella polydiademata (3)	–		A	B		A
Phialidium gregarium (4)	–	B	A		A	A
Limnomedusae						
Eperetmus typus (5)	–, +		C, D			
Proboscidactyla flavicirrata (1)	–		A		A	
Trachymedusae						
Aglantha digitale (3)	–, +		A	C	A	D
Narcomedusae						
Aegina citrea (9)	+	D	D			
Cunina sp. (1)	–	E				
Solmissus marshalli (4)	–, +	B	C, D			
Siphonophora						
Nanomia cara (1)	+	D				

first attached to the manubrium of an *A. citrea* and ingested a portion of it before being dislodged by pulsations of the medusa.

Haeckelia rubra was offered 2 other species of narcomedusae in alternation with *A. citrea.* One juvenile *Cunina* sp. measuring about 1.5 cm in diameter was left overnight with 2 *H. rubra;* by morning, the medusa had eaten the smaller of the two ctenophores. One *Solmissus marshalli* was later placed in a bowl with 2 *H. rubra.* The ctenophores showed no response at all to the presence of *S. marshalli* over a 1 h period. When the ctenophores were then prodded into contact with the *S. marshalli,* the medusa repeatedly and successfully pulled its tentacles away. The ctenophores were not left overnight with *S. marshalli.*

Pieces of medusae offered as prey

In these experiments (see Table 1), small pieces of various hydromedusae and one siphonophore were offered to *Haeckelia rubra* by gently prodding the ctenophore's lips with a bit of cnidarian tissue held with forceps. The ctenophore was touched repeatedly (about 10 times) on the mouth with each potential food item over a period of 2 min. It was found that acceptable food was usually taken during this time period. Typically, several different tissue types from each species were offered: bell margin including tentacles, bell wall, manubrium and gonad. On most days, 3 to 6 species of medusae were offered before trying a fragment of *Aegina citrea.* This served to confirm at intervals the acceptability of *A. citrea* and that the ctenophore was still healthy enough to be interested in food. Ingestion of portions of *A. citrea* caused the ctenophore to be inaccessible for subsequent feeding trials until after this food was digested, or in the case of a small piece, until it was moved far up into the gut and digestion commenced.

The most frequently observed response of *Haeckelia rubra* to cnidarian material other than *Aegina citrea* was for the ctenophore to contract its lips so that the mouth was tightly shut, so as to reject the potential food parcel. Less frequently, *H. rubra* showed no response whatsoever to being gently prodded with a piece of medusa. Occasionally, a bit of medusa was ingested and remained in the gut for up to several hours before it was rejected and dropped – the likelihood of this behavior increased during the 2 wk of observation and may reflect poor nutritional conditions or some other artifact of the laboratory. *H. rubra* fed on *A. citrea* tentacles on every occasion that they were offered and once ate an entire *A. citrea* having a bell diameter of 4 mm. The same ctenophore also readily ate one of two tentacles of *Solmissus marshalli* early in the series of feeding trials. After 2 wk in captivity, *H. rubra* also successfully retained and digested a small *Nanomia cara*, a bit of gonad from *Aglantha digitale* and 3 separate tentacles of *Eperetmus typus*. In one instance, a piece of the manubrium of *Mitrocoma cellularia* was partially ingested by a ctenophore. After 30 min, this tissue was rejected and dropped, but nematocysts in the medusa's manubrium had by this time caused a substantial wound to the oral region of the ctenophore which required approximately 24 h to heal.

Nematocysts of *Haeckelia rubra* and *Aegina citrea*

A specimen of *Haeckelia rubra* whose tentacles were examined microscopically shortly after it was collected from the field contained two types of nematocysts: most were nearly-spherical apotrichous isorhizas (Mackie and Mackie, 1963), ranging from 3.6 to 13.6 μm in diameter, a few microbasic euryteles (measuring approximately 3.5×14 μm) were also present – morphological details of these nematocysts in their fired condition were difficult to discern. Two weeks after the initial nematocyst observations, an *Aegina citrea* was offered to *H. rubra*. Twenty-four hours after ingesting *A. citrea* tentacles, *H. rubra* tentacles contained apotrichous isorhizas in sizes similar to those measured on the first occasion. No microbasic euryteles were seen at this time. A third examination of *H. rubra* nematocysts several days after the ctenophore had eaten an *A. citrea* tentacle again showed the same sizes of apotrichous isorhizas (Fig. 2). All *H. rubra* nematocyst measurements (from 3 individuals) are plotted to-

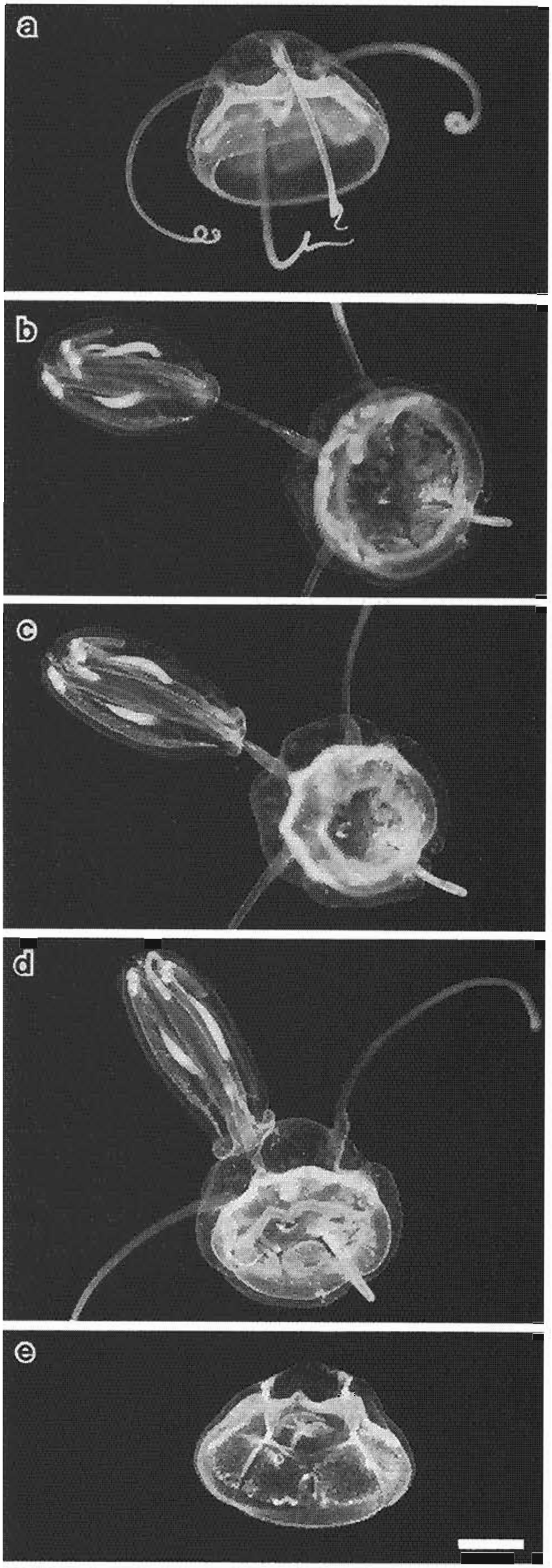

Fig. 1. *Aegina citrea* and *Haeckelia rubra*. (a) Intact specimen of the medusa, *A. citrea*, with all 4 tentacles; (b) specimen of *A. citrea* with tentacle at left being ingested by ctenophore, *H. rubra;* (c) same animals as in (b) photographed 1 min later; (d) same animals as in (c) photographed 2 min later; (e) specimen of *A. citrea* that had all 4 tentacles removed by *H. rubra*. Scale line is 2 mm long and is applicable to (a)–(e)

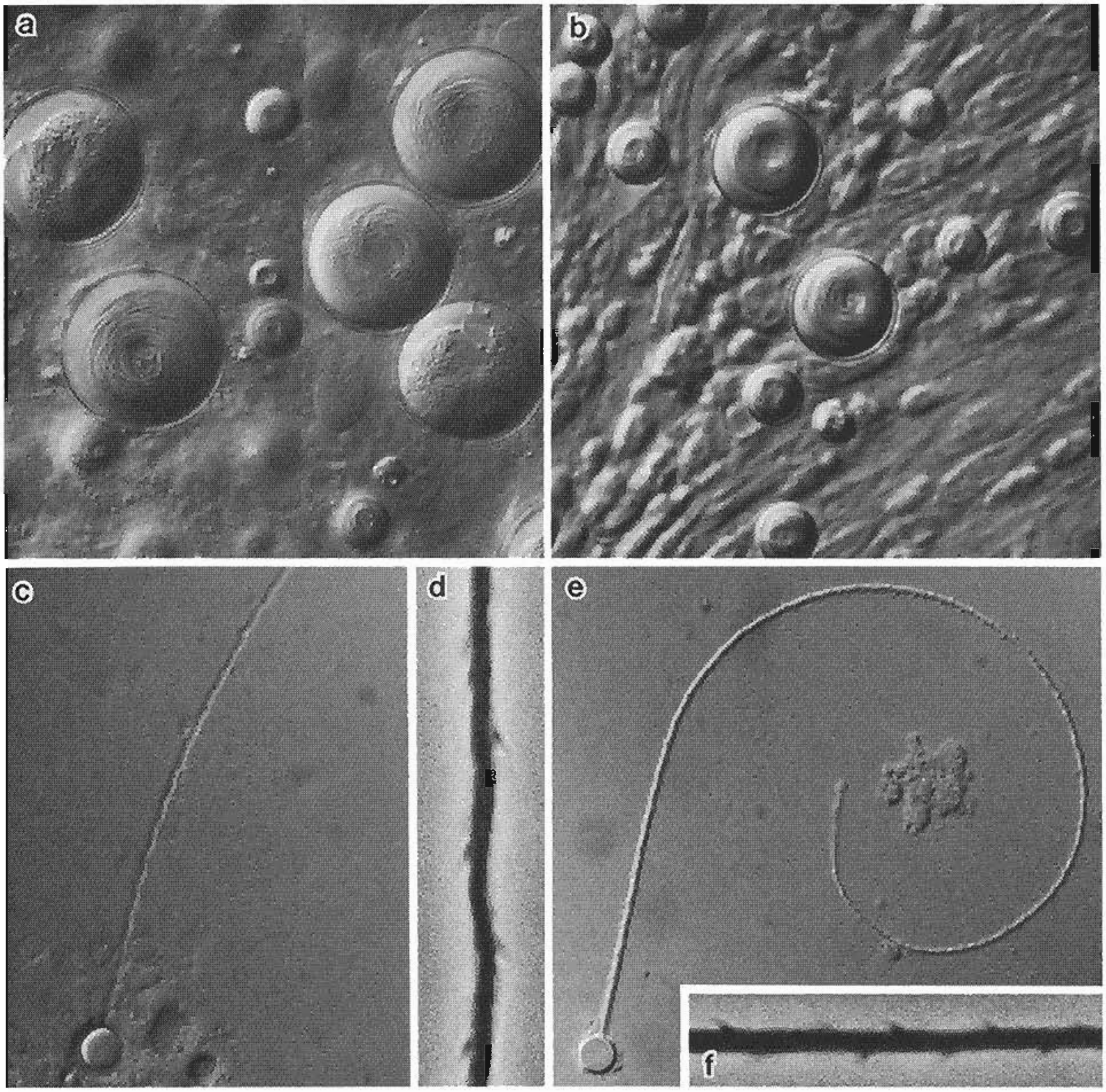

Fig. 2. *Haeckelia rubra* and *Aegina citrea.* (a) Squash preparation of tentacle of the ctenophore, *H. rubra,* including unexploded capsules of large and small nematocysts (apotrichous isorhizas), 1 250×; (b) squash preparation of tentacle of the medusa, *A. citrea,* including unexploded capsules of large and small nematocysts (apotrichous isorhizas), 1 250×; (c) exploded apotrichous isorhiza from tentacle of *H. rubra,* 1 250×; (d) detail of thread of foregoing nematocyst, 3 800×; (e) exploded apotrichous isorhiza from tentacle of *A. citrea,* 1 250×; (f) detail of thread of foregoing nematocyst, 3 800×

gether in Fig. 3. Two size classes are indicated, with means around 6 and 11 µm. Nematocysts in the tentacles of two *A. citrea* medusae were also measured. These were all apotrichous isorhizas in 2 size classes (4.3 to 6.9 µm and 15.0 to 19.2 µm), with mean diameters of 6.0 and 17.4 µm, respectively (Figs. 2 and 3). Evidently, either some shrinkage of medusa nematocysts occurs within the ctenophore tissues or the ctenophore somehow selects only relatively small medusa nematocysts for storage.

Discussion

Our specimens of *Haeckelia rubra* corresponded well to those described by Kölliker (1853), Chun (1880), Komai and Tokioka (1942) and Carré and Carré (1980a). *H. rubra* has now been collected in the Mediterranean Sea near Villefranche-sur-Mer (Picard, 1955; Carré and Carré, 1980a), in the Gulf of Naples (Chun, 1880; Samassa, 1892), and in the Strait of Messina (Kölliker, 1853; Gegenbauer, 1856); and in the Pacific Ocean off south-central Japan near Shirahama (Seto) (Komai and Tokioka, 1942), off the coast of southern China near Xiamen (Chiu, 1980) and in the north-east Pacific in the San Juan Archipelago (Dunlap, 1966; the present paper), in Saanich Inlet, British Columbia (Mills, 1982) and Jervis Inlet, British Columbia (Mills, unpublished observation). In spite of its brightly colored tentacle sheaths, the small size of *H. rubra* makes it difficult to see, thus perhaps contributing to its apparent

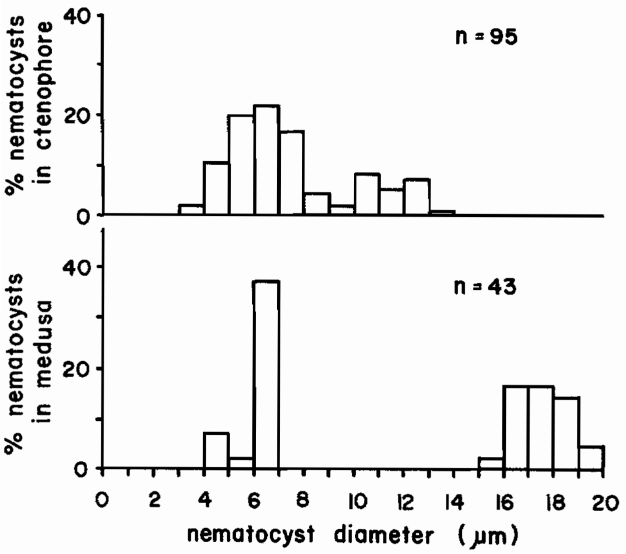

Fig. 3. *Aegina citrea* and *Haeckelia rubra.* Size-frequency histograms of random samples of nematocysts (all apotrichous isorhizas) in squash preparations of living tissue from 2 medusae (*A. citrea,* bottom histogram) and from 3 ctenophores (*H. rubra,* top histogram). A large and a small size class of nematocysts is apparent in both histograms. Presumably, the ctenophore stores nematocysts of ingested medusae, and the evident reduction in size of the stored nematocysts might result from osmotic effects within the tissues of the ctenophore

scarcity. Additionally, it may normally occur in deep water as does *Aegina citrea,* but tidal mixing in the San Juan Archipelago is so great that planktonic animals characteristic of all depths are regularly seen at the surface.

Average diameters of the characteristic apotrichous isorhiza nematocysts in *Haeckelia rubra* are reported by Komai (1942) to be about 2.5 and 6 μm in diameter in Japan; by Carré and Carré (1980a) to be 4.5 and 8 μm in the Mediterranean Sea; and by the present authors (Fig. 3) to be about 6 and 11 μm in the San Juan Archipelago. *Aegina citrea* nematocysts in the San Juan Archipelago (Fig. 3) were about 6 and 17 μm in diameter. The smaller size of *H. rubra* nematocysts may be the result of osmotic shrinkage that might occur in the host ctenophore's tissues, or the ctenophore may select only relatively small nematocysts for storage. *A. citrea* also occurs in Japan near Shirahama (Uchida, 1928: as *A. rosea*) where Komai and Tokioka (1942) collected *H. rubra* and off southern China (Zhang, 1982), so this species of medusa would be a possible source of *H. rubra* nematocysts in Japan and China. *A. citrea* is not found in the region of Villefranche-sur-Mer in the Mediterranean Sea (Goy, 1972) where *H. rubra* has been collected, so at least one of the 7 other species of narcomedusae that occur in this area is apparently also preyed upon by the ctenophore.

Aegina citrea medusae whose tentacles were removed by *Haeckelia rubra* (Fig. 1e) were able to function well without them in the laboratory for several days. Little is known about the field biology of *A. citrea,* or any other narcomedusa, and it is not known whether the tentacles are necessary for feeding, or if they can be regenerated (as is typical of other suborders of Hydrozoa).

The spherical nematocysts typically seen in *Haeckelia rubra* are an unusual cnidarian type found only in narcomedusae. In contrast, the microbasic euryteles seen by the present authors occur commonly among many hydromedusae and scyphomedusae, but do not occur in siphonophores (Werner, 1965). As Table 1 shows, in addition to narcomedusae, starved *H. rubra* may ingest and subsequently digest bits of the limnomedusa *Eperetmus typus,* the trachymedusa *Aglantha digitale* and the siphonophore *Nanomia cara.* Presumably the euryteles observed in *H. rubra* derived from an interaction with a medusa such as one of these. Since the number of euryteles seen was very small, we assume that either very little of the unidentified medusa was ingested, or that this event occurs only infrequently and most euryteles had already been used, expelled, or digested by the ctenophore previous to its capture.

Haeckelia rubra may now be added to the short list of predators on Cnidaria that are able to retain for future use nematocysts that are infested with prey tissues. These "kleptocnidae" are used for either feeding or defense by the new owners. The freshwater turbellarian *Microstoma caudatum* feeds on *Hydra* sp. at the risk of being eaten itself by *Hydra* sp., and uses the stored nematocysts for subsequently capturing other prey organisms (Kepner and Barker, 1924). Some glaucid nudibranchs feed on a variety of floating cnidarian chondrophores and siphonophores, and, in the case of the Portuguese man-of-war *Physalia physalis,* these predators retain only the most virulent nematocyst types for future defensive purposes (Thompson and Bennett, 1969). Some aeolid nudibranchs also retain nematocysts from hydroids and anemone prey for defensive purposes (Edmunds, 1966; Mariscal, 1974; Conklin and Mariscal, 1977). Additionally, one species of pelagic octopus is reported to hold tentacle fragments of *P. physalis* with the suckers on its arms, presumably for use in feeding or defense (Jones, 1963).

Carré and Carré (1980a) found that *Haeckelia rubra* grew well in the laboratory on a diet of mixed plankton, although over the course of 4 mo in captivity on this diet, the ctenophores lost all of their nematocysts and their tentacles degenerated. In the present study, *H. rubra* maintained its size and tentacles, but did not visibly grow on a cnidarian diet, although the ability of the ctenophores to alter their shape makes actual measurement of growth very difficult. It is possible that in nature *H. rubra* feeds on narcomedusae for nematocysts, but in fact gets most of its nutrition by eating crustaceans. The results of Carré and Carré (1980) suggest that an exogenous supply of nematocysts is necessary for maintenance of the tentacles in *H. rubra.* It is possible that ctenophores, like some Cnidaria (Bode and Flick, 1976), slough tissue from the ends of the tentacles during normal growth and that this represents a mode of continuous nematocyst loss in *H. rubra* regardless of the nutritional status of the ctenophores. Without a reliable source of *H. rubra* from the field on which further *in situ* observations can be made, this question will be difficult to answer.

We believe that our results eliminate the possibility that the nematocysts of *Haeckelia rubra* represent an evolutionary link between the Cnidaria and the Ctenophora. Only one further possible evolutionary tie between these two groups remains. The parasitic life stage of the ctenophore *Lampea pancerina* Chun, 1880 (formerly *Gastrodes parasiticum* Korotneff, 1888) begins with a "planula" larva (Komai, 1922) whose existence has been cited as evidence of a phylogenetic relationship to the Cnidaria (Komai, 1922, 1963; Borradaile and Potts, 1959). This larva bores into a host salp to the level of the mantle. Once in this position, it shortens along the anterior-posterior axis, and takes on the characteristics of a ctenophore by developing comb-plates and tentacles. The "planula" larva as shown by Komai (1922) is uniformly ciliated, and presumably penetrates the salp with its anterior end forward. Komai notes that most of the embedded, metamorphosed specimens have their oral ends facing inward. If the larva does not reverse direction by 180° during or prior to penetration, then its anterior end becomes the oral end of the ctenophore. The oral end of metamorphosing cnidarian planulae is always the posterior end. According to Komai (1922), the *L. pancerina* "planula" also carries oocytes. It seems likely that the planuloid form of the *L. pancerina* larva is an adaptation for boring into the tissues of another organism, and is without phylogenetic significance.

After many years of speculation that some intermediate form or character exists which provides a phylogenetic link between the Cnidaria and the Ctenophora, the evidence now appears strong that no such link exists.

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