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## Nematocysts

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### I. INTRODUCTION

Although the literature on nematocysts has recently been reviewed by Werner (1965), Halstead (1965), and Picken and Skaer (1966), an overview of the subject seems appropriate at the present time because of the appearance of much new work, especially concerning the toxicology and

pharmacology of nematocysts. Weill's (1934) classic study on nematocysts remains the best review of the earlier literature and only selected papers from that period will be discussed here. The papers by Carlgren (1940, 1945, 1949) are an extremely valuable source of information on the structure and distribution of nematocysts in the Anthozoa while those of Russell (1938, 1939, 1940), Luc (1961), Werner (1965), Papenfuss (1936), and Calder (1971, 1972) deal with this subject in Hydrozoa and Scyphozoa. Cutress (1955), Hand (1961), and Werner (1965) have provided us with further information on the form and distribution of cnidarian nematocysts. Mariscal (1966) has discussed the possible role and functioning of nematocysts in cnidarian symbioses.

Nematocysts are among the largest and most complex intracellular secretion products known, with some reaching 100  $\mu\text{m}$  in length. They are best known for their stinging properties and many resemble a miniature hypodermic device which, on receipt of the proper combination of stimuli, discharge by eversion to bore their way into prey or an unwary bather and release a drop of toxin.

Not all nematocysts, however, are venomous, nor are all of the penetrating kind. The threads of some may adhere to, or wrap around, portions of the prey. Among cnidarian adhesive organelles is the enigmatic spirocyst. Although spirocysts are also intracellular secretion products and discharge by eversion, they are not considered nematocysts because of their unique physical and chemical properties. Both nematocysts and spirocysts may be used only once. Following use, they are lost from the surrounding cell.

## II. THE MORPHOLOGY OF NEMATOCYSTS

### A. General Structure

The nematocyst consists of a capsule containing a tightly coiled and folded thread (Figs. 1 and 2). Upon the receipt of appropriate stimuli, the nematocyst discharges with the thread evertting (Fig. 3).

Undischarged nematocyst capsules are generally either spherical or rod-like (Fig. 4). They vary greatly in size (from about 3  $\mu\text{m}$  to over 100  $\mu\text{m}$  in length), both intra- and interphyletically (Hand, 1954, 1955a,b; Bonnenfant, 1960). Several distinct size classes of the same type of nematocyst may be found in the tissues of a single species, although the functional significance of this is not yet clear.

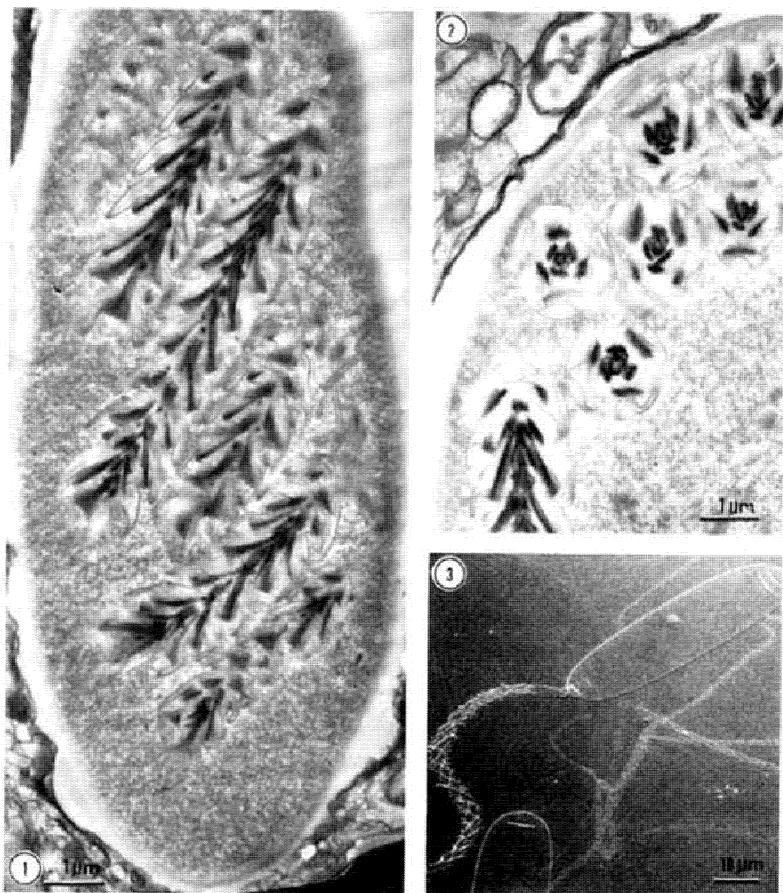


Fig. 1. Longitudinal section of a holotrichous isorhiza capsule from the sea anemone, *Corynactis californica*, showing the folded thread in its undischarged state.

Fig. 2. Cross-sections and a partial longitudinal section (lower left) of the undischarged thread of a holotrichous isorhiza nematocyst of the sea anemone, *Corynactis californica*.

Fig. 3. Scanning electron micrograph of the discharged holotrichous isorhiza nematocyst of the sea anemone, *Corynactis californica*.

The discharged thread is of varying length, diameter, and structure. It commonly bears a formidable array of spines (Figs. 4 and 5). Several distinctly different types of spines may be present on the thread of a single nematocyst type and their size and arrangement are important in nematocyst identification (Figs. 4, 6, and 7).

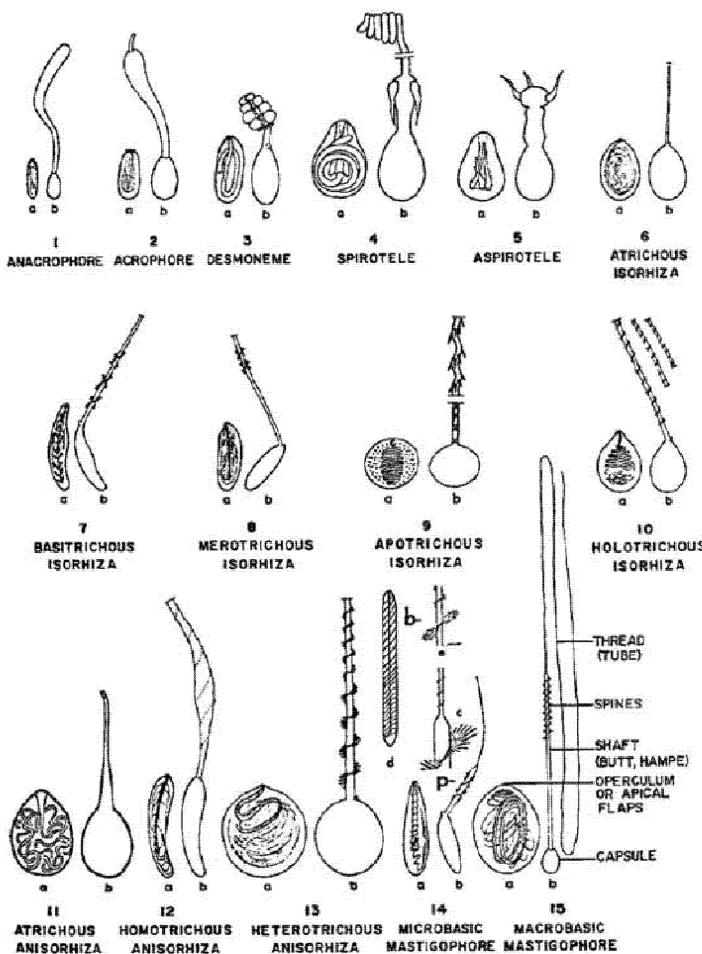


Fig. 4. Illustrations of the various nematocysts and spirocysts described to date. See Table I for a description and classification of the various types of nematocysts. (After Weill, 1934, 1964; Carlgren, 1940; Cutress, 1955; Hand, 1961; Mackie and Mackie, 1963; Werner, 1965; Deroux, 1966; Lacassagne, 1968a,b; Mariscal, 1972a.)

In addition, many nematocyst threads commonly possess a basally enlarged portion known as a butt or shaft (Figs. 4 and 8). The shaft, in turn, may bear spines of considerably different size and configuration from the remainder of the thread (Figs. 4 and 8-10). The functional significance of the great differences in size, shape, and spination of nematocyst capsules, threads, and shafts is not well understood.

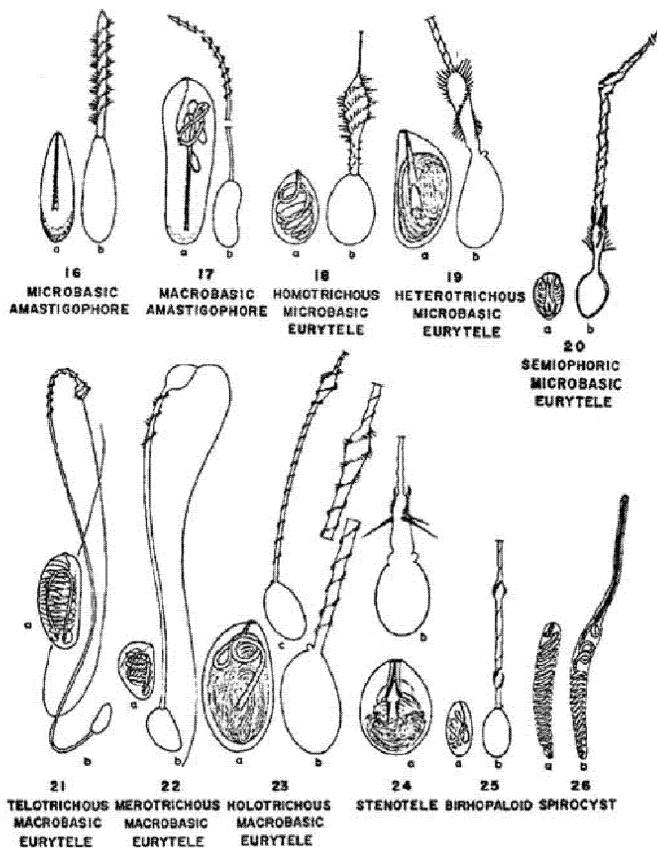


Fig. 4. (Continued)

The discharging nematocyst thread everts through a portion of the capsule whose ultrastructure appears to vary depending on the class of coelenterate involved. In the classes Hydrozoa and Scyphozoa, this region is sealed with a small trapdoor-like operculum (Fig. 4), while the anthozoan nematocysts thus far investigated possess a tripartite series of apical flaps (Figs. 6 and 11) (Westfall and Hand, 1962; Westfall, 1965).

#### B. Classification

Although several limited classification schemes (dealing largely with hydra nematocysts) have been in use over the years, it was not until the monumental work of Weill (1930, 1934) that any semblance of order or uniformity of nematocyst classification was introduced. Weill's elaborate,

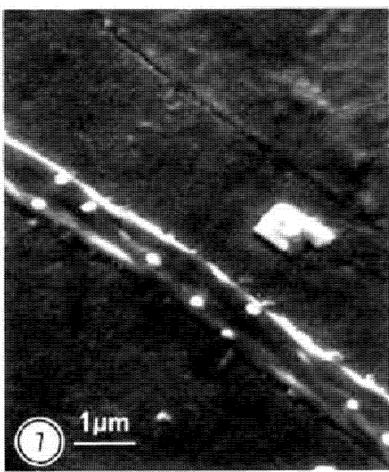
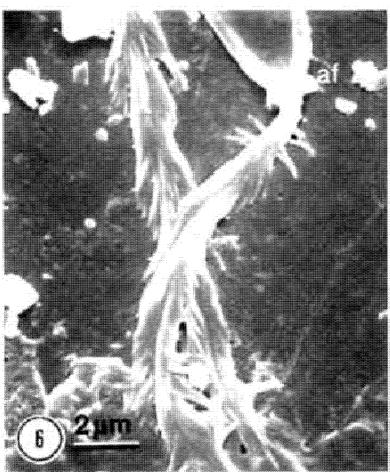
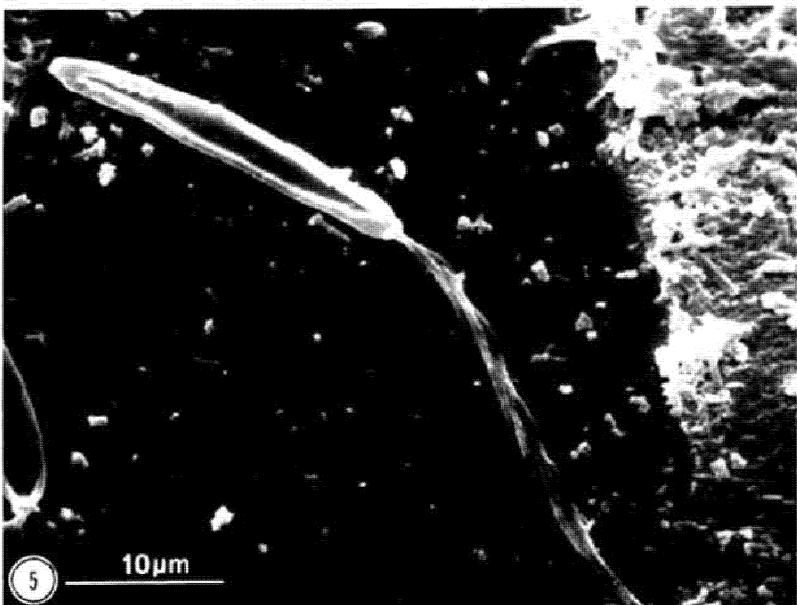


Fig. 5. Scanning electron micrograph of the basitrichous isorhiza nematocyst of the sea anemone, *Calliactis tricolor*.

Fig. 6. Scanning electron micrograph of the larger spines at the proximal portion of the thread of the basitrichous isorhiza nematocyst of the sea anemone, *Calliactis tricolor*. Note also the tripartite apical flaps (af) at the tip of the discharged nematocyst capsule at right.

Fig. 7. Scanning electron micrograph of the tiny, almost vestigial, spines on the distal-most portion of the thread of the basitrichous isorhiza of the sea anemone, *Calliactis tricolor*.

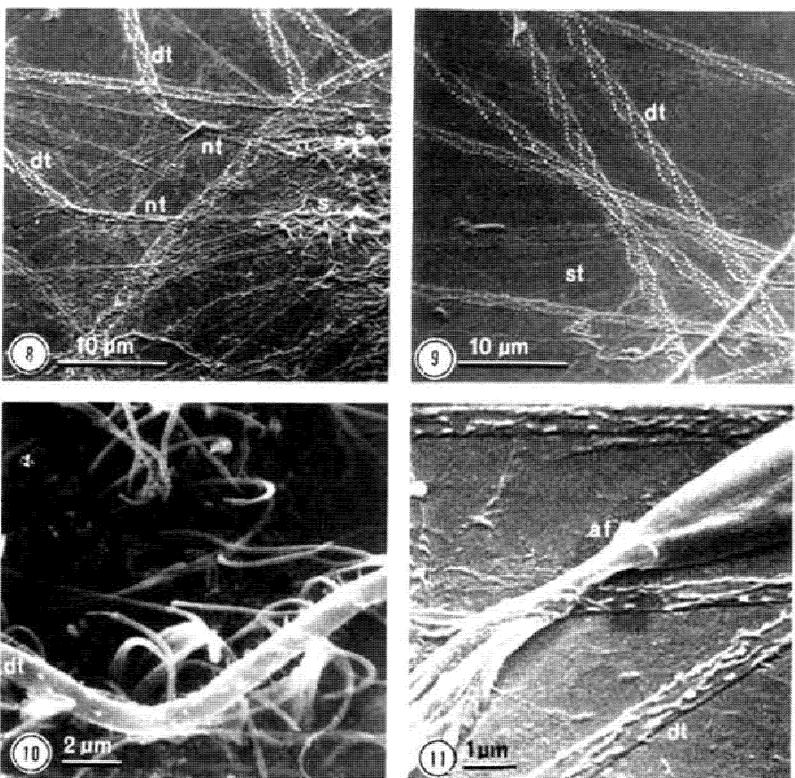


Fig. 8. Scanning electron micrograph of the shafts (s) and threads of the microbasic p-mastigophores of the sea anemone, *Corynactis californica*. Note that the thread appears to be unarmed and narrower just above the shaft (nt) while past this point, the distal-most portion of the thread (dt) appears to be of uniform spination and diameter (cf. Fig. 9).

Fig. 9. Scanning electron micrograph of the distal portions of discharged microbasic mastigophore threads (dt) of the sea anemone, *Corynactis californica*. In the lower left center of the micrograph, note the unspined, and almost indistinguishable, discharged threads of the *Corynactis* spirocyst (st). A number of other very thin, discharged spirocyst threads may be seen criss-crossing the lower half of the micrograph.

Fig. 10. Scanning electron micrograph of the "inflated" distal portion of the thread (dt) of a microbasic mastigophore lying across the surface of the tentacle of *Corynactis californica*.

Fig. 11. Scanning electron micrograph of the basitrichous isorhiza nematocyst of the sea anemone *Epiactis prolifera*, showing the apical flaps (af) at the tip of the capsule and the distal portions of the thread (dt). Note that the distal portion of the thread (dt) of this basitrich nematocyst also possesses tiny spines along its length similar to the basitrich of *Calliactis tricolor* (cf. Fig. 7).

**TABLE I**  
**Classification of Coelenterate Nematocysts\***

- I. ASTOMOCNIDAE—thread closed at the tip
  - A. RHOPALONEMES—thread club-shaped and much greater in volume than the capsule
    - 1. Anacrophores—thread without an apical projection (1)
    - 2. Acrophores—thread with an apical projection (2)
  - B. SPIRONEMES—thread not club-shaped, generally forming a spiral coil distally
    - 1. Haplonemes—thread without a well-defined shaft
      - a. Desmonemes—thread forming a corkscrew-like coil (3)
    - 2. Heteronemes—thread with a well-defined shaft
      - a. Rhopaloides—shaft of unequal diameter
        - (1) Euryteles—shaft dilated distally
          - (a) Microbasic—shaft short, less than three times capsule length
          - (i) Spiroteles—thread forms a spiral coil distally, three spines especially strongly developed
          - (ii) Aspiroteles—no thread beyond the shaft, 3 spines especially strongly developed
- II. STOMOCNIDAE—thread open at the tip
  - A. HAPLONEMES—thread without a well-defined shaft
    - 1. Isorhizas—thread of the same diameter throughout (glutinants)
      - a. Atrichous—thread without well-developed spines (small glutinant) (6)
      - b. Basitrichous—thread with well-developed spines only at base (7)
      - c. Merotrichous—thread with well-developed spines on the intermediate portion only (8)
      - d. Apotrichous—thread with well-developed spines on the distal portion only (9)
      - e. Holotrichous—thread with well-developed spines along whole length (large glutinant) (10)
    - 2. Anisorhizas—thread slightly dilated toward base
      - a. Atrichous—thread without well-developed spines (11)
      - b. Homotrichous—thread spiny throughout, spines all of equal size (12)
      - c. Heterotrichous—thread spiny throughout, spines larger at base of thread (13)
  - B. HETERONEMES—thread with a well-defined shaft
    - 1. Rhabdoïdes—shaft cylindrical, of the same diameter throughout
      - a. Mastigophores—thread continues beyond the shaft
        - (1) Microbasic—shaft short, less than three times capsule length (14)
          - (a) Microbasic b-mastigophore—shaft tapers gradually into thread
          - (b) Microbasic p-mastigophore—shaft tapers abruptly into thread, V-shaped notch prominent at base of unfired shaft
        - (2) Macrobasic—shaft long, more than four times capsule length (15)
      - b. Amastigophores—no thread beyond the shaft
        - (1) Microbasic—shaft short, less than three times capsule length (16)
        - (2) Macrobasic—shaft long, more than four times capsule length (17)
    - 2. Rhopaloides—shaft of unequal diameter
      - a. Euryteles—shaft dilated distally
        - (1) Microbasic—shaft short, less than three times capsule length
          - (a) Homotrichous—spines of shaft all of same size (18)

TABLE I (Continued)

- (b) Heterotrichous—spines of shaft of unequal size (19)
- (c) Semiphore—thread bent whiplike, with large flat spine medially (20)
- (2) Macrobasic—shaft long, more than four times capsule length
  - (a) Telotrichous—spines on distal portion of shaft only (21)
  - (b) Merotrichous—spines not distal, found only on shaft area of uniform diameter proximal to terminal swelling (22)
  - (e) Holotrichous—shaft spiny along whole length (23)
- b. Stenoteles—shaft dilated at base, three spines especially strongly developed (penetrants) (24)
- 3. Birhopaloides—shaft of unequal diameter at distal and proximal ends (25)

III. SPIROCYSTS—thin, single-walled capsule containing a long, spirally coiled, dense-appearing thread of uniform diameter in the undischarged or partially discharged state; no shaft or spines distinguishable. When completely everted, both capsule and thread become extremely transparent (26)

<sup>a</sup> Based on Weill, 1934, 1964; Carlgren, 1940; Cutress, 1955; Hand, 1961; Mackie and Mackie, 1963; Werner, 1965; Deroux, 1966; Lacassagne, 1968a,b; Mariscal, 1972a. Figure 4-15 shows the basic nematocyst terminology. The numbers in parentheses following each description refer to the different nematocyst types in Fig. 4.

but extremely useful, system of nomenclature is based on the morphological characteristics of the discharged thread and/or shaft (Table I, Fig. 4). Weill's system recognized two major types of cnidae: nematocysts proper and spirocysts.

#### 1. NEMATOCYSTS

Nematocysts possess a thick, double-walled capsule, are basophilic, and enclose a thread of varying construction and armature. They may be divided into the Astomocnidae or Stomocnidae depending on whether or not the thread is open or closed at the tip. Among those with a closed thread (Astomocnidae) are included such nematocysts as the desmonemes and spiroteles which probably function by wrapping around projections or limbs of prey.

Stomocnidae are presumably penetrating nematocysts since the open thread would allow delivery of the toxin. Most described nematocysts appear to belong to this category.

One modification of Weill's scheme made necessary by the advent of the electron microscope applies to the isorhizas. Owing to the limits of resolution of the light microscope, the tiny spines on the threads of these nematocysts have not always been visible. For example, contrary to their classic characterization, the author has found that the basitrichous isorhizas of the sea anemones *Calliactis* and *Epiactis* possess tiny spines

along the distal portion of the thread, in addition to the large spines found proximal to the capsule (Mariscal, 1972a). Since it is rather impractical to base nematocyst identification on ultrastructural characteristics, and since Weill's present system of classification is in widespread use, the author has used the presence or absence of "well-developed" spines (i.e., those visible with a light microscope) as the definitive characteristic for the various kinds of isorhizas (Mariscal, 1971a).

Since Weill's original classification of nematocysts was first published, some eight new types of nematocysts have been discovered, bringing the present total of cnidae known to 26 (27 counting both microbasic b- and p-mastigophores) (Table I, Fig. 4).

In addition, three more types of nematocysts have been described about which we still lack enough information to determine if indeed they are new types. Cutress (1955) has described a peculiar type of microbasic mastigophore, the microbasic q-mastigophore possessing a "dart" which is detachable from the thread itself after discharge. Hand (1961) believes that the q-mastigophores are simply p-mastigophores whose shaft spines have failed to separate completely. He finds that this condition can be induced artificially by various chemical means (personal communication). Cutress (1955) has also described the new category of macrobasic p-mastigophore, but their status remains unclear until investigated in more detail with the electron microscope.

Spangenberg (1964) has reported a new type of nematocyst for *Aurelia*, the atrichous polypspira, based on the "numerous coils" of the undischarged thread. However, based on Weill's (1934) criteria, this does not appear to be sufficient justification for the erection of a new category. The atrichous polypspira appears to be another type of atrichous isorhiza, and Calder (1971) has since come to the same conclusion.

## 2. SPIROCYSTS

Spirocysts are limited to the zoantharian anthozoans, whereas all cnidarians possess one or more types of nematocysts. Spirocysts are characterized by a thin, single-walled capsule which is acidophilic and contains a long, spirally coiled, unarmed thread of uniform diameter (Figs. 4 and 13). The electron microscope has revealed that the inner side of the spirocyst capsule has a serrated appearance, although the functional significance of this serration is not clear (Fig. 12).

The electron microscope has also shown that the uneveted spirocyst thread contains a series of closely packed, electron dense rodlets rather than spines (Fig. 12), which appear to spin out to form a meshwork of fine fibrillae (Figs. 14 and 15).

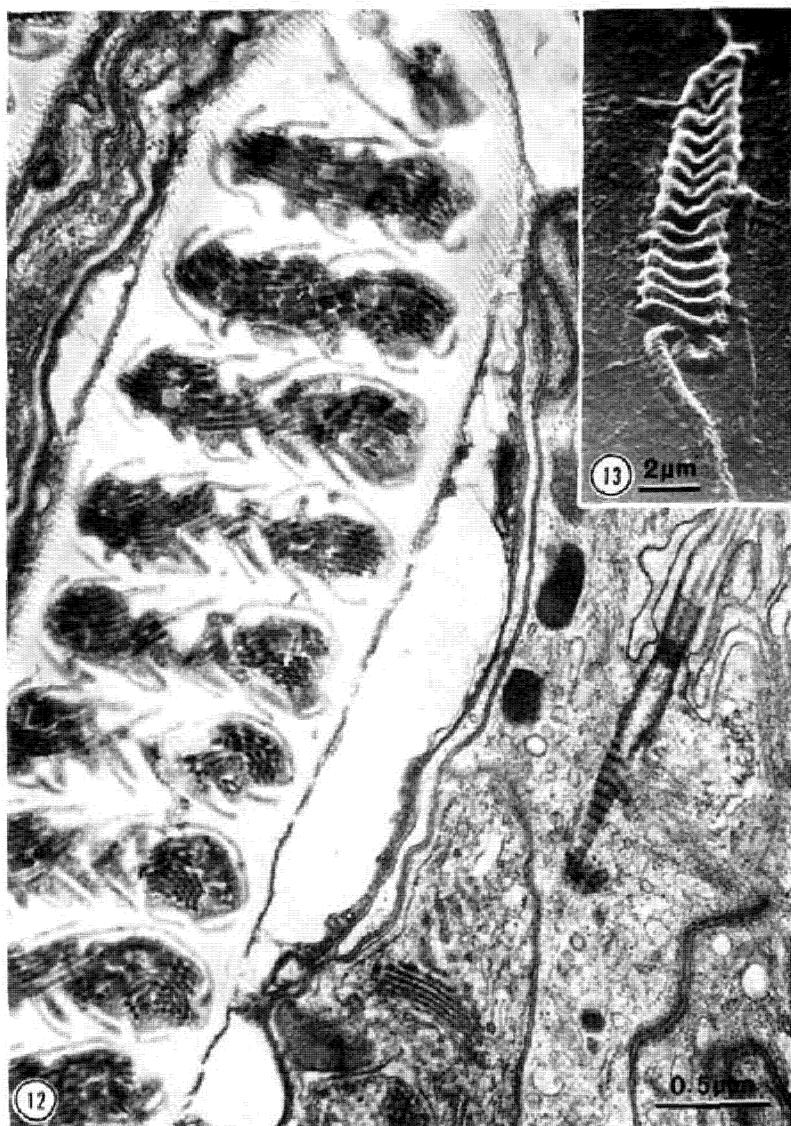
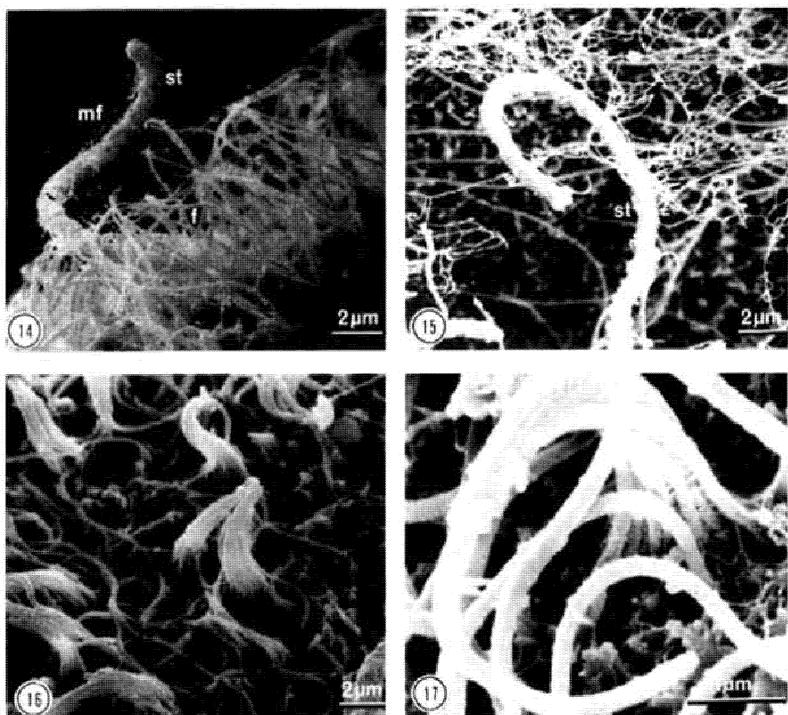


Fig. 12. Longitudinal section of the capsule of an undischarged spirocyst of the sea anemone, *Calliactis tricolor*. Note the ridged appearance of the inner portion of the capsule wall. (Micrograph by R. McLean.)

Fig. 13. Scanning electron micrograph of a partially discharged spirocyst of the sea anemone, *Corynactis californica*.



**Fig. 14.** Scanning electron micrograph of the tip of a discharged spirocyst thread (st) extending away from the edge of the tentacle of the sea anemone, *Corynactis californica*. Note the fine weblike microfibrillae (mf) attached to the tips of the spirocyst thread and extending over the numerous flagella (f) present on the tentacle surface.

**Fig. 15.** Scanning electron micrograph of the tip of a discharged spirocyst thread (st) showing numerous microfibrillae (mf) attached to it.

**Fig. 16.** Scanning electron micrograph of several ciliary tufts, probably sensory in nature, which cover the surface of the nematocyst-bearing portions of the tentacles of the sea anemone, *Corynactis californica*. Each tuft is composed of a single long flagellum surrounded by a clump of shorter cilia (cf. Fig. 17). Other single flagella, perhaps cleansing in function, also are present on the surface of the tentacle.

**Fig. 17.** Scanning electron micrograph of a single ciliary tuft on the surface of the tentacle of the sea anemone, *Corynactis californica*. The single long flagellum surrounded by the shorter cilia is clearly visible here.

### C. Distribution of Nematocysts and Spirocysts

The distribution of the various kinds of nematocysts among the different cnidarian classes has been analyzed by Weill (1934), Russell (1938,

TABLE II

Distribution of the Various Types of Nematocysts and Spirocysts among the Three Classes of Coelenterates<sup>a,b</sup>

Nematocyst type	Class Hydrozoa	Class Scyphozoa	Class Anthozoa
1. Anacrophore	*	—	—
2. Acrophore	*	—	—
3. Desmoneme	*	—	—
4. Spirotele	*	—	—
5. Aspirotele	*	—	—
6. Atrichous isorhiza	+	+	+
7. Basitrichous isorhiza	+	—	+
8. Merotrichous isorhiza	*	—	—
9. Apotrichous isorhiza	*	—	—
10. Holotrichous isorhiza	+	+	+
11. Atrichous anisorrhiza	*	—	—
12. Homotrichous anisorrhiza	*	—	—
13. Heterotrichous anisorrhiza	*	—	—
14. Microbasic mastigophore	+	—	+
15. Macrobasic mastigophore	*	—	—
16. Microbasic amastigophore	—	—	*
17. Macrobasic amastigophore	—	—	*
18. Homotrichous microbasic eurytele	+	+	—
19. Heterotrichous microbasic eurytele	+	+	—
20. Semiophoric microbasic eurytele	*	—	—
21. Telotrichous macrobasic eurytele	*	—	—
22. Merotrichous macrobasic eurytele	*	—	—
23. Holotrichous macrobasic eurytele	*	—	—
24. Stenotele	*	—	—
25. Birhopaloid	*	—	—
26. Spirocyst	—	—	*

<sup>a</sup> Modified after Werner (1965).

<sup>b</sup> Key: —, absent; +, present; \*, found only in this class.

1939, 1940), Carlgren (1940, 1945), Papenfuss (1936), and Werner (1965), among others. Table II, which summarizes the distribution data for the nematocysts described to date, shows that Hydrozoa contains the largest number of different nematocyst types. Some 23 of the 25 described types of nematocysts are found in various hydrozoans with 17 being unique to this class. Only two unique types of nematocysts (three counting the spirocyst) are found among members of Anthozoa whereas none is unique to Scyphozoa.

Carlgren (1940, 1945) has provided us with an important analysis of the distribution of cnidae among Anthozoa. Spirocysts are found throughout Zoantharia (Hexacorallia), but appear to be lacking in Alcyonaria

(Octocorallia). Interestingly, only one type of nematocyst, the atrichous isorhiza, has been reported for any of the alcyonarians. Although eight categories of cnidae are present in the order Actiniaria (the sea anemones), the most common cnidom, occurring in more than 60% of the examined genera, is one composed of only three cnidae; spirocysts, basitrichous isorhizas, and microbasic p-mastigophores (Carlgren, 1945).

### III. THE FUNCTIONING OF NEMATOCYSTS

#### A. Introduction

Wagner (1905) was among the first to investigate the nature of the stimuli involved in nematocyst discharge. He found three factors important in producing a feeding reaction in hydra: (1) a chemical stimulus, (2) a mechanical stimulus, and (3) the length of time the hydra had been starved.

Pantin (1942a,b), using the sea anemone *Anemonia sulcata*, further clarified the importance of both chemical and mechanical stimuli in the discharge process. For example, Pantin found that (1) mechanical stimulation with a clean glass rod generally caused no discharge, (2) immersion of the animal in a food solution generally caused no discharge, and (3) a combination of both the above stimuli caused a strong discharge. Pantin concluded that chemical stimulation (i.e., food substances) "sensitized" the cnidocytes and/or nematocysts to mechanical stimuli. Jones (1947) came to the same conclusion for hydra nematocysts.

#### B. The Chemical Stimuli for Nematocyst Discharge

Glaser and Sparrow (1909) were perhaps the first to notice that possibly two distinct processes were involved in the discharge of some nematocysts. The first step, in response to the appropriate stimuli, involved the extrusion of the tip of the nematocyst above the epithelial surface containing it. This preliminary process, which might be considered as a sort of "priming" mechanism, was then followed by the actual discharge by eversion, possibly as the result of exposure to other and perhaps different stimuli. However, it was not until the studies by Yanagita and his co-worker that identification of the specific chemical factors involved in both extrusion and discharge was attempted (Yanagita, 1943, 1951, 1959a,b,c, 1960a,b,c; Yanagita and Wada, 1953, 1954, 1959).

### 1. EXTRUSION

Using the microbasic p-mastigophore nematocyst from the acontia of the sea anemone *Haliplanella* (= *Diadumene*) *luciae*, Yanagita found that extrusion was caused by various cations ( $K^+$ ,  $NH_4^+$ ), electric shock, certain surface-active agents, and lipoïd solvents, as well as by the mechanical contact of various solid food materials. During this process, the extrusion-inducing factors had to overcome the influence of extrusion-suppressing agents which included certain anions ( $Cl^-$ ,  $Br^-$ ,  $NO_3^-$ ) as well as anesthetic-like substances (e.g.,  $Mg^{2+}$ ) which may be present in the external medium. However, once the extrusion-suppressing influence is overcome and the tips of the nematocysts are exposed, these same extrusion-suppressing substances (e.g., the anions) now act to trip the exposed apical flaps or operculum to discharge the nematocyst.

Blanquet (1966, 1970), working with the acontial microbasic mastigophore nematocysts of the sea anemone *Aiptasia pallida*, found that both the  $SO_4^{2-}$  and  $NO_3^-$  anions and sodium citrate had an extrusion-inducing capability. However, both Blanquet and Yanagita have in some cases used "extrusion" to refer to the complete *expulsion* of nematocysts from the surrounding tissues, as has Pantin (1942b). Since nematocyst expulsion from the cnidocyte is not a component of the normal discharge process, the significance of the extrusion phenomenon in nematocyst discharge is not yet clear.

### 2. DISCHARGE

Yanagita (1959b,c) has reported that various anions such as  $Cl^-$  are effective in causing the actual discharge of nematocysts. Blanquet (1966, 1968), on the other hand, found that relatively little nematocyst discharge was elicited by high chloride concentrations in his material.

Lenhoff and Bovaird (1959) and Lenhoff (1968) mention that the presence of calcium in the medium is necessary for nematocyst discharge in *Hydra littoralis*. In the case of isolated acontial microbasic mastigophore nematocysts of the sea anemone *Aiptasia*, Blanquet (1966, 1970), however, found that calcium (and magnesium) inhibited discharge.

Blanquet (1970), in testing the effect of the dilutions of various salt solutions on the discharge of isolated acontial nematocysts, found the following order of effectiveness: (1) The highest percentage of discharge was elicited by solutions of a univalent cation and a divalent anion (e.g., sodium and potassium in conjunction with sulfate); (2) next in effectiveness were solutions of a univalent cation and a univalent anion (e.g.,  $NaCl$ ,  $KCl$ ); and (3) least effective were solutions of divalent cations and univalent anions [e.g.,  $MgCl_2$ ,  $CaCl_2$ ,  $Ca(NO_3)_2$ ].

From these and other data, Blanquet (1966, 1970) has tentatively concluded that the opercular or apical flap material contains a protein whose conformation is stabilized by association with divalent cations. Any chemical substance which either disrupts this protein directly (such as an enzyme) or somehow causes the chelation or removal of the divalent cations might affect the conformation of the protein, thus leading to a weakening of the capsule in this region and eventual discharge.

Blanquet (1966, 1970) has also studied the effect of pH on the discharge of both isolated and *in situ* acontial nematocysts. Between pH 4 to 11, the isolated nematocysts were relatively stable, but the percentage of discharge increased markedly outside this range. In addition, the isolated nematocysts were much less sensitive to pH changes than were the *in situ* nematocysts.

These findings highlight a major problem in both studying and analyzing the effects of various stimuli on nematocyst discharge. As Blanquet (1970) points out, many stimuli may cause a massive discharge of nematocysts *in situ*, but have relatively little effect on the same nematocysts isolated from their surrounding cnidocytes. This discrepancy has also been noted by a number of other workers including Glaser and Sparrow (1909), Parker and Van Alstyne (1932), Weill (1934), Pantin (1942b), and Yanagita (1959c, 1960a,b,c). Their observations would suggest that (a) some component of the cnidocyte may be acting as an intermediary in the discharge process and/or (2) that the cells or tissues surrounding the cnidocyte may somehow be involved in either raising or lowering the threshold for discharge. Either or both of these possibilities suggest that perhaps nematocysts may not be acting as true independent effectors. The significance of this analysis will be discussed in a later section.

### 3. POSSIBLE RECEPTOR SITES INVOLVED IN NEMATOCYST DISCHARGE

Two different but related kinds of structures, the cnidocil apparatus in the Hydrozoa and Scyphozoa and the ciliary cones in Anthozoa, have been described or considered to be involved in stimulus reception for nematocyst discharge (e.g., Weill, 1934; Pantin, 1942b; Bouillon *et al.*, 1958; Chapman and Tilney, 1959a,b; Chapman, 1961; Slatterback, 1961, 1963, 1967; Mergner, 1964; Mattern *et al.*, 1965; Bouillon and Levi, 1967; Westfall, 1966a,b, 1970b).

a. **The Cnidocil Apparatus.** The focal point of the cnidocil apparatus is the long, modified flagellum surrounded by a circlet of stereocilia of varying length and number (about 36 in *Gonionemus*—Westfall, 1970b; generally 21 in *Hydra*—Slatterback, 1967). Just medial to the ring of

stereocilia is a circlet of structures which, along with the stereocilia, were called "stiff rods" by the early light microscopists (e.g., see Hyman, 1940). These structures are called "supportive rods" by Westfall (1970b) and "rootlets" by Slauterback (1967), the latter term referring to their resemblance to ciliary rootlets (see D. Chapman, Chapter I). These extend down from the surface of the cnidocyte to enclose the nematocyst capsule itself. Apparently similar structures have been seen adhering to the excised nematocysts of *Physalia* (e.g., Parker and Van Alstyne, 1932; Mackie, 1960). All the above components of the cnidocil apparatus, including the central flagellum, stereocilia, and supportive rods or rootlets, are cross-linked together by other fine filaments, this linkage perhaps having significance in the discharge process.

**b. The Ciliary Cones.** Although Westfall (1966a,b, 1970b) distinguishes between the presence of a "cnidocil" in Hydrozoa and Scyphozoa and a flagellum-ciliary cone apparatus in anthozoans, it is clear from her work as well as others (e.g., Chapman, 1961; Slauterback, 1967) that the cnidocil is itself a modified ciliary derivative and basically is not structurally different from other ciliary-flagellar entities.

Some workers have attempted to distinguish functionally between the two structures in that the cnidocil is considered to be rigid whereas the anthozoan flagellum is capable of beating. However, there is no good direct evidence at present to support either contention. Pantin (1942b) states that the anthozoan "ciliary cones, particularly those carrying a stiff cilium, are easily seen." He later mentions that "these cilia may be intermittently active or apparently permanently at rest in the upright position."

The author has recently been able to examine the tentacle epidermis and the associated ciliary cones for several sea anemones and corals using the Freon-critical point method of Cohen *et al.* (1968). The sea anemones *Epiactis prolifera*, *Metridium senile*, and *Corynactis californica* were investigated, as were the corals *Balanophyllia elegans* and *Paracyathus stearnsii*. Small tufts or cones of cilia are scattered over the tentacle surface or the nematocyst batteries. These cones consist of a longer central flagellum surrounded by a circlet of shorter stereocilia, numbering about 20 (Figs. 16 and 17). In gross morphology, these anthozoan ciliary cones do not appear significantly different from those reported for hydrozoans (Slauterback, 1967; Westfall, 1970b; Westfall *et al.*, 1971b). This resemblance perhaps is not too surprising when one considers the remarkable similarity of the anthozoan ciliary cones to the sensory receptors or "hair cells" in the macula utriculi and lateral line organs of fishes or the vestibular apparatus of such diverse vertebrates as

guinea pigs, frogs, pigeons, chinchillas, and man (e.g., Flock and Wersäll, 1962; Flock, 1964, 1965a,b; Flock and Duvall, 1965; Wersäll *et al.*, 1965; Lim and Lane, 1969; Hillman and Lewis, 1971).

Although direct evidence is not yet available, it is possible that both the cnidocil and ciliary cone systems are the primary structures involved in mechanoreception (and perhaps chemoreception) for nematocyst discharge. Tardent and Stoessel (1971), Stoessel and Tardent (1971), and Tardent and Schmid (1972), however, have recently described on the tentacles of several hydroids a separate mechanoreceptor involved in prey detection. The general structure of this mechanoreceptor is similar to the cnidocil apparatus, but its structural and functional relationship to the cnidocyte proper is not yet clear. Bilbaut and Pavans de Cecatty (1971a,b) have observed similar ciliary sensory receptors in the octocoral *Veretillum* and have discussed the possible phylogenetic significance of the presence of these receptors among several diverse phyla. It is hoped that future work in this area, especially using electrophysiological techniques, will be able to give us a better idea of the functioning of the above structures and their relationship to nematocyst discharge.

### C. Hypotheses on the Mechanism of Nematocyst Discharge

In addition to studies on the nature of the stimuli involved in the initiation of discharge, there is a considerable body of literature dealing with the mechanism of discharge itself; i.e., how does the thread get outside the capsule once the operculum or apical flaps are released? Although some rather imaginative theories have been proposed to account for the means by which the thread leaves the capsule, there is no longer any doubt that both nematocysts and spirocysts discharge by eversion, or the turning inside out, of the thread.

As the penetrating nematocyst thread everts, the closely packed spines of the thread and shaft emerge in a rotary motion, flipping up and out to lie perpendicular to the long axis of the thread (Picken, 1953). The triple helix of spines thus tends to bore in and firmly anchor the thread and shaft in the prey as eversion progresses. In addition, some nematocyst threads bear numerous small, rounded spines which appear to be effective in the adhesion to various substrates and perhaps prey (Mariscal, 1972a, and Fig. 7).

In the case of spirocysts, there has been some controversy among cnidarian biologists concerning whether spirocysts actually evert or not (e.g., Cutress, 1955). My recent phase-contrast and scanning electron microscope observations (unpublished) leave no doubt that the thread

of a discharging spirocyst passes up through the already fired portion of the thread, thus demonstrating that eversion is involved in spirocyst discharge. As previously mentioned, the spirocyst thread is considered to be adhesive in nature as a result of the numerous fine rodlets which appear to "spin out" to form a meshwork of fine fibrillae (Figs. 14 and 15).

Weill (1934), Hyman (1940, 1959), Picken (1953), Skaer and Picken (1965), Westfall (1965), and Picken and Skaer (1966) discuss the many hypotheses which have been proposed to account for the physiological and morphological processes involved in getting the thread out of the capsule during eversion, and this topic will only be reviewed briefly here.

One striking feature which has been noted in the discharge of nematocysts is the great apparent increase in the length and diameter of the thread following discharge. This feature is especially noticeable in the case of the large holotrichous isorhizas from the sea anemone *Corynactis* and prompted Picken (1953, 1957) to suggest what might be called the "swelling hypothesis" of discharge. Based on the work of Robson (1953) as well as on his own studies, Picken suggested that an anisometric swelling mechanism at the point of eversion of the thread could account for its increase in length and diameter, as well as providing for a possible propulsive force during discharge. Later studies with the electron microscope by the author, as well as others, revealed that the increase in length and diameter could be accounted for by a simple, accordionlike unfolding of the thread in both length and diameter (Figs. 1 and 2) (Hand, 1961; Westfall and Hand, 1962; Skaer and Picken, 1965, 1966; Westfall, 1965; Picken and Skaer, 1966). These studies, however, have still not determined what energy source is involved in carrying through and completing discharge, once initiated. The variety of hypotheses which have been put forward to account for this can generally be included under either of two major headings: (1) the osmotic hypothesis and (2) the contraction hypothesis.

#### 1. THE OSMOTIC HYPOTHESIS

Most of the hypotheses dealing with nematocyst discharge have attempted to explain how the intracapsular pressure is increased just before, or at the moment of, discharge. According to proponents of the osmotic hypothesis, the intracapsular pressure increases by a rapid swelling due to the sudden uptake of water, or perhaps ions (e.g., Grosvenor, 1903; Glaser and Sparrow, 1909; Weill, 1934; Picken, 1953, 1957; Robson, 1953; Slatterback, 1963; Picken and Skaer, 1966).

Coincidental to this hypothesis has been the observation that some nematocyst capsules are larger after discharge, thus implying a swelling

or stretching phenomenon associated with discharge. The uptake of water or other substances at the time of discharge could be due to either an altered permeability of the capsule wall itself or perhaps the entry of water at the junction of the capsule wall and thread, once the operculum or apical flaps have been triggered.

## 2. THE CONTRACTION HYPOTHESIS

This hypothesis suggests that the increase in intracapsular pressure is due to a contractile mechanism either in or around the nematocyst capsule (Russell, 1940; Yanagita, 1943; Mueller, 1950; Yanagita, and Wada, 1954, 1959; Chapman and Tilney, 1959a,b; Mattern *et al.*, 1965; Westfall, 1965, 1970b). Either the capsule wall material itself contracts in response to the appropriate stimuli, or contractile filaments or fibers, perhaps associated with the stereocilia-flagellar complex, are present in the cnidocyte in close proximity to the capsule. These fibers may form a sphincterlike constriction near the apical end of the capsule and/or may completely invest the capsule. Parker and Van Alstyne (1932) and Jones (1947) have developed mechanisms for discharge which borrow from both of the above hypotheses.

Another possibility, of course, is that nematocyst capsules are under a constant intracapsular pressure and that it is only necessary to trip the operculum or apical flaps chemically, as discussed by Yanagita (1959c) or Blanquet (1970), in order for eversion to proceed to completion. However, there have been no extensive experimental studies in recent years to test any of the above hypotheses and the whole question of just how nematocyst discharge is initiated and carried through to completion remains a problem of great interest.

## D. The Control of Nematocyst Discharge

Nematocysts have classically been considered to be independent effectors, a situation in which the nematocyst and/or its cnidocyte are thought to act both as a sensory receptor and effector without the intervention of the nervous system or another conducting pathway (e.g., Wagner, 1905; Parker, 1919; Parker and Van Alstyne, 1932; Pantin, 1942a,b; Pantin and Pantin, 1943; Ewer, 1947; Jones, 1947; Burnett *et al.*, 1960; Bullock and Horridge, 1965; Picken and Skaer, 1966; Lentz, 1966, 1968; see also D. Chapman, Chapter I).

However, there seem to be two schools of thought concerning the definition of an independent effector. One school more or less holds to

the classic position stated above, even going so far as to deny that "modification" of the threshold for nematocyst discharge by the animal itself contradicts the independent effector hypothesis (e.g., Burnett *et al.*, 1960; Lentz, 1966, 1968; Picken and Skaer, 1966).

A second school of thought holds that if the animal itself is capable of influencing or modifying its nematocyst discharge in any way at all, then one should examine more critically the possibility that these nematocysts may *not* be acting independently and in fact may be under some form of control by the cnidarian itself. For example, Davenport *et al.* (1961), Ross and Sutton (1964), and Ellis *et al.* (1969) have demonstrated that the nematocyst discharge of certain sea anemones may be altered depending on whether or not the pedal disk or tentacles are contacting a substrate and in some cases a specific type of substrate.

Other studies involving cnidarian feeding behavior also suggest that the discharge of some nematocysts, at least, is influenced by the physiological state of the animal. For example, a number of workers over the years have commented that well-fed cnidarians often appear unresponsive to, and may rapidly reject, food placed among their tentacles (e.g., Wagner, 1905; Parker, 1917; Pantin, 1942b; Pantin and Pantin, 1943). Some workers have presented evidence that nematocyst discharge and prey capture in hydra appears to be reduced after heavy feeding (e.g., Burnett *et al.*, 1960; Bouchet, 1961).

Such observations led Sandberg *et al.* (1971) and Mariscal (1973) to develop a means by which nematocyst discharge in feeding sea anemones could be quantified directly. Their experiments showed that the numbers of both spirocysts and especially nematocysts that discharged decreased markedly with increased feeding, and that this decrease was not due to simple depletion of the nematocyst supply. This decrease would be of obvious adaptive significance to the animal in that it prevents a satiated cnidarian from wasting its limited nematocyst supply on food which it is unable to ingest or otherwise use.

If we accept the possibility that at least some nematocysts may not be behaving as "true" independent effectors, then we should perhaps examine the possible means by which a cnidarian might influence the discharge of its nematocysts.

One obvious possibility, of course, is the nervous system. In fact, a great many light microscopists have observed what were considered to be nerves running up to and ending in close proximity to cnidocytes (e.g., Spangenberg and Ham, 1960; Burnett and Diehl, 1964; Jha, 1965; Jha and Mackie, 1967; Noda, 1969). Such observations have since been confirmed by studies with the electron microscope (e.g., Lentz and Barrnett, 1965; Slautterback, 1967; Westfall, 1969, 1970a,b).

Other evidence has suggested the possible role of neurotransmitter substances in the control of nematocyst discharge (e.g., Dahl *et al.*, 1963; Lentz and Barrnett, 1961, 1962; Lentz and Wood, 1964; Wood and Lentz, 1964; Lentz, 1966, 1968). Westfall (1970a,b), and Westfall *et al.* (1971a), using the electron microscope, have observed cnidocyte-neurite synapses in *Gonionemus* and hydra. The appearance of the synaptic vesicles suggested the role of a catecholamine as the neurotransmitter substance.

Another intriguing possibility as a control mechanism for nematocyst discharge is the epithelial, or non-nervous, conducting system known to occur in cnidarians (e.g., Mackie, 1970; see Josephson, Chapter VI). In Hydrozoa thus far investigated at least, both neuroid conduction in simple epithelia and myoid conduction in myoepithelia occur. The electrical impulses transmitted by such epithelia strongly resemble nerve impulses, and although there is little evidence at present, it is possible that epithelial conduction may prove to be important in the mediation of the discharge of some nematocysts.

#### IV. THE FUNCTIONS OF NEMATOCYSTS AND SPIROCYSTS

##### A. Nematocysts

Only one study has been published to date specifically directed at understanding the functions of nematocysts (Ewer, 1947). Ewer's study on the four types of nematocysts found in hydra concluded that (1) the stenoteles were used for prey capture by penetration, (2) the desmonemes were involved in prey capture by adhesion, (3) the atrichous isorhizas were used to adhere to the substrate during locomotion, and (4) the holotrichous isorhizas served a defensive function.

We have recently conducted studies (unpublished) on the functions of sea anemone and coral nematocysts and have found that the holotrichous isorhiza of the California corals *Balanophyllia elegans* and *Paracyathus stearnsii* and the corallimorpharian sea anemone *Corynactis californica* also has a defensive function. The microbasic p-mastigophore nematocyst of the above three forms was found to be the primary prey-capture nematocyst by penetration, similar to the stenotele of hydra, but also had a defensive function as well. The spirocyst was involved in prey capture by adhesion, similar again to the role of the desmoneme in hydra.

However, most sea anemones, at least, possess a cnidom consisting of only spirocysts, basitrichs, and microbasic p-mastigophores, this array being found in more than 60% of the examined genera (Carlgren, 1945). The basitrichs of *Calliactis tricolor* have been found to be involved in both prey capture and shell adhesion (Sandberg *et al.*, 1971; Mariscal, 1972a). The basitrichs of the sea anemones *Epiactis prolifera*, *Anthopleura elegantissima*, *Anthopleura xanthogrammica*, and *Cnidopus ritteri* have been found to be involved in both prey capture by penetration and defense (unpublished).

Ellis *et al.* (1969) have found the pedal disk microbasic p-mastigophores of the swimming sea anemone *Stomphia coccinea* to be involved in substrate adhesion during settling.

Spaulding (1972) reports that the parasitic sea anemone *Peachia quinquecapitata* attaches to its host, the hydromedusan *Phialidium gregarium*, by means of tentacle nematocysts, but does not identify the type. *Peachia* has the usual cnidom consisting of only spirocysts, basitrichs, and microbasic p-mastigophores (Carlgren, 1949), and based on his photomicrographs, it would appear that the basitrichs are the ones involved.

The role of the acrorhagi (located at the base of the tentacles) and their contained atrichous isorhiza nematocysts in "aggression" between various sea anemones has been described by Abel (1954), Bonnin (1964), Doumenc (1972), and Francis (1973a,b). On tentacle contact with another member of the same species (presumably a nonclone mate) or a different species, the acrorhagi may swell markedly until contact is made, whereupon large numbers of atrichs are discharged, resulting in damage and/or withdrawal of the intruding individual.

Lang (1971) has observed a similar situation between several species of solitary corals in which the mesenterial filaments of one species protrude through the body wall to digest the tissues of the other species. Although Lang (1971) and Wells (1971) consider this reaction to be significant in the taxonomic separation of two species of the genus *Scolymia*, it is clear from the above studies with sea anemones that such "non-self recognition" can also occur between members of the same species as well. Although these responses have been labeled "aggression" by most of the above authors, perhaps they are better thought of as a form of territorial "defense" which presumably tends to prevent overcrowding. Many examples of intraspecific territorial defense are, of course, well known among fishes and other vertebrates (e.g., Mariscal, 1970b, 1972b).

Theodor (1970) and Ivker (1967, 1972) have discussed a perhaps analogous "tissue incompatibility" in the overgrowth or contact reactions of colonial marine coelenterates, although nematocysts are probably not involved in these cases.

## B. Spirocysts

The spirocysts of the zoantharian anthozoans have long been enigmatic, both from a morphological and a functional point of view. Based on my phase-contrast, transmission, and scanning electron microscope observations, as well as the observations of Stephenson (1929), Skaer and Picken (1965), and Picken and Skaer (1966), it appears that as the spirocyst thread everts, the electron-dense, tightly packed rodlets (Figs. 12-15) spin out into long microfibrillae. These appear to form a fine meshwork on contact and would appear admirably suited for an adhesive function. Both Pantin (1942b) and myself (unpublished) have observed that food stimuli are effective in causing a massive discharge of spirocysts. It is possible that the spirocysts may discharge to hold prey organisms while the penetrating nematocysts discharge and inject a drop of toxin. My personal light and electron microscope observations of the tentacles of many sea anemones suggest that the nematocysts are much less abundant in the tentacles than are the spirocysts. It is thus somewhat surprising that more attention has not been paid to the role of spirocysts in the biology of the zoantharians.

It is also likely that spirocysts may be involved in adhesion to nonprey objects, since even clean coverslips are capable of eliciting a heavy discharge (unpublished). However, spirocysts did not seem to be as strongly involved as one would expect in the adhesion of the tentacles of the symbiotic sea anemone *Calliactis tricolor* to gastropod shells (Mariscal, 1972a).

## V. THE CHEMISTRY OF NEMATOCYSTS

This topic has been reviewed by Welsh (1964), Russell (1965, 1967), Halstead (1965, 1971), Picken and Skaer (1966), Lane (1968a,b), and Baslow (1971), therefore generally only those papers not cited above will be considered here.

### A. Chemistry of the Capsule, Thread, and Spines

#### 1. NEMATOCYSTS

Studies by Lenhoff *et al.* (1957), Blanquet and Lenhoff (1966), Fishman and Levy (1967), Mariscal and Lenhoff (1969), Stone *et al.* (1970),

and Mariscal (1971a) have revealed that the nematocyst capsule is composed primarily of a collagenlike protein linked together by disulfide bonds. Unlike vertebrate collagens, nematocyst capsules are autoclave insoluble, but are affected by the disulfide reducing agent dithioerythritol (DTE) (Blanquet and Lenhoff, 1966; Mariscal and Lenhoff, 1969). Dithiocrythritol generally dissolved discharged nematocyst capsules in a few minutes, but the fired thread required a longer exposure time and a higher pH in order to be affected in the same way. The spines appeared to be unaffected by the DTE, suggesting that the spines and perhaps the thread may not be of the same chemical composition as the capsule (Blanquet and Lenhoff, 1966).

With one exception, undischarged or partially discharged nematocyst capsules, threads, and spines were not affected by the DTE, suggesting perhaps that it was necessary for the DTE to pass into the lumen of the capsule for it to exert its solubilizing effect (Blanquet and Lenhoff, 1966; Mariscal and Lenhoff, 1969).

## 2. SPIROCYSTS

Spirocysts are well known to differ both chemically and morphologically from nematocysts (e.g., Hyman, 1940; Westfall, 1965) (also Figs. 12 and 13). None of the spirocysts tested thus far with DTE appeared to be affected by it, providing possible evidence for a chemical difference between nematocysts and spirocysts (Mariscal and Lenhoff, 1969).

## B. Chemistry and Physiological Effects of Nematocyst Toxins

The chemistry and physiological effects of cnidarian and nematocyst toxins from a variety of organisms has been of great research interest in recent years. However, knowledge of cnidarian toxin biochemistry, pharmacology, and toxicology still lags far behind that available for other types of toxins such as snake venoms (e.g., Jiménez-Porras, 1970).

In order to summarize briefly the recent developments in cnidarian toxin research in such a way that major gaps in our knowledge may be more apparent, Table III has been prepared. Table III lists all the studies on cnidarian toxins which have appeared between 1960 and 1972, with emphasis on those since about 1965. Several things have become apparent during the review of the literature in the preparation of this table which perhaps should be emphasized here.

(1) It appears that a number of cnidarians possess an inherent tissue toxicity which is not necessarily associated with the presence of nematocysts. Thus, future studies should concentrate on isolating the

**TABLE III**  
**Comparison of the Biochemical, Toxicological, and Pharmacological Properties of the Various Coelenterate Toxins Known**  
**(Generally only Studies from 1960 to 1972 Are Tabulated Here)<sup>a</sup>**

Class and species	Locality	Source of toxic fraction(s)	Number of toxic fractions	Molecular weight(s)	Chemical identification of toxin	Nature of toxin	Physiological effects	References
I. CLASS ANTHOZOA:								
A. Subclass Zoantharia								
1. <i>Rhodactis howesii</i>	Samoa	Whole anemone homogenates and extracts	>1	NG	Protein	Contains an anticoagulant and both a hemolytic factor and a lethal, possibly neurotoxic, effect	1. Ingestion of anemone causes pulmonary edema and death in man 2. Injection of homogenate causes death in salamanders, toads, mice, rats, and rabbits 3. Toxin is antigenic and an effective antitoxin can be prepared	Martin (1960, 1966a,b, 1967); Farber and Lerke (1963)
2. a. <i>Aiptasia pallida</i>	Florida, N. Carolina	Isolated acontial microbasic mastigophore nematocysts mainly	2(?)	a. 132,000 b. 31,000 (nontoxic)	Acidic protein: 80% of total protein is glutamic acid	Neurotoxin (?)	1. Causes leg autotomy and death in fiddler crabs	Blanquet (1968)
b. <i>Aiptasia pallida</i>	Florida	Isolated acontial microbasic mastigophore nematocysts mainly	2	a. >60,000 b. 10–15,000	Protein Phospholipase A activity	Neurotoxin. Also has hemolytic effect on red blood cells	1. Causes leg autotomy and death in fiddler crabs 2. Affects ionic conductance in crayfish giant nerve fibers	Hessinger <i>et al.</i> (1973); Hessinger and Lenhoff (1973a,b, 1974a,b)
3. <i>Condylactis gigantea</i>	Bermuda	Whole tentacle extracts	1	10,000–15,000	Basic protein possibly containing enzymatic activity	Neurotoxin	1. Causes rigid paralysis and death in crayfish 2. Affects firing of all classes of lobster and crayfish	Shapiro (1968a,b); Shapiro and Lilleheil (1969); Lilleheil and Shapiro (1969); Narashashi <i>et al.</i> (1969)
4. <i>Calliactis polypus</i> (probably <i>Calliactis tricolor</i> )	Mississippi Sound	Whole tentacle extracts	NG	NG	NG	Neurotoxin-myotoxin	axons apparently due to the toxin interacting with nerve membrane ionic conductance 1. High doses reduced motor activity and caused respiratory distress and occasionally death in mice 2. Reduced blood pressure, affected smooth muscles, and heart action of various mammals	Huang and Mir (1972)
5. <i>Anemonia sulcata</i>	Mediterranean	Whole tentacle and whole column extracts	2	5000–10,000	Basic polypeptides	Neurotoxin	Causes paralysis and death in crabs, rabbits, and mice	Béress and Béress (1971)
6. <i>Metridium senile</i>	New Brunswick, Canada	Isolated acontial nematocysts	2	<540 for dialyzable fraction	Proteinaceous undialyzable fraction plus a dialyzable fraction containing 1–2 aromatic amines	Neurotoxin (?)	Causes paralysis and death in crayfish, but did not affect fiddler crabs	Goodwin and Telford (1971)
7. <i>Palythoa</i> sp.	Hawaii	Whole animal extracts	1	3400	Amine (?)	NG	1. Caused reduced motor activity,	Moore and Scheuer (1971)

(Continued)

TABLE III (Continued)

Class and species	Locality	Source of toxic fraction(s)	Number of toxic fractions	Molecular weight(s)	Chemical identification of toxin	Nature of toxin	Physiological effects	References
8. <i>Palythoa tuberculosa</i>	Okinawa	Whole animal extracts	NG	NG	NG	NG	paralysis, convulsions, respiratory distress, and death in mice	1. Level of toxicity appeared directly related to the presence of eggs in a polyp; those polyps with the most eggs appeared to be the most toxic Kimura <i>et al.</i> (1972)
B. Subclass Aleyonaria								
1. <i>Renilla mulleri</i>	Mississippi Sound	Whole animal extracts	NG	NG	NG	Neurotoxin-myotoxin	1. Caused reduced motor activity, respiratory distress and death in mice. 2. Reduced blood pressure and affected heart action and smooth muscles of various mammals Huang and Mir (1971)	
C. Class Hydrozoa								
1. <i>Physalia physalis</i>	Florida	Homogenized tentacle nematoecysts, primarily holotrichous isorhizas	Several	NG	Protein containing large amounts of glutamic acid and phospholipase A	Neurotoxin. Also contains a vertebrate RBC hemolytic factor. Possibly a	1. Causes paralysis and death of fiddler crabs, frogs, fish, mice and dogs. Can cause moderate to severe	Parrish (1959); Lane and Dodge (1958); Lane (1960, 1961, 1967a,b, 1968a); Lane <i>et al.</i> (1961); Wangersky and
2. <i>Millepora alcicornis</i>	Florida	Phosphate buffer extracts of whole colony	1(?)	~100,000	Protein	and phospholipase B activity plus other compounds	direct myotoxic effect also	Lane (1960); Lane and Larsen (1965); Larsen and Lane (1966, 1970a,b); Hastings <i>et al.</i> (1967); Garriott and Lane (1969); Stillway and Lane (1971); Russell (1966); Halstead (1965)
3. <i>Millepora tenera</i> (originally identified as <i>M. dichotoma</i> )	Eniwetok	Phosphate buffer extracts of whole colony	1(?)	NG	Protein	Probably a neurotoxin. Also contains a vertebrate RBC hemolytic factor	1. Causes convulsions, respiratory distress, and rapid death in mice 2. Injection of a single sublethal dose prolonged survival of mice subsequently given a lethal dose of toxin Wittle <i>et al.</i> (1971)	
							1. Causes convulsions, respiratory distress, and rapid death in mice 2. Prior injection of a single sublethal dose did not prolong survival of	Middlebrook <i>et al.</i> (1971)

(Continued)

TABLE III (Continued)

Class and species	Locality	Source of toxic fraction(s)	Number of toxic fractions	Molecular weight(s)	Chemical identification of toxin	Nature of toxin	Physiological effects	References	
4. <i>Hydra littoralis</i>	Culture	Solution surrounding electrically shocked hydra	1	50,000	Protein. Possessed a succinoxidase inhibitor and a 5-hydroxyindoleamine	NG. Appears to be a neu-rotoxin based on other studies	subsequently injected mice	1. Demonstrated presence of a powerful succinoxidase inhibitor in water surrounding electrically shocked hydra, possibly due to discharge of tentacle nematocysts 2. Inhibitor produced toxic effects in mice and fiddler crabs	Kline and Waravdekar (1959, 1960); Kline (1961)
D. Class Scyphozoa									
1. <i>Stomolophus meleagris</i>	Mississippi Sound	Heterotrichous microbasic euryteles isolated from oral region	NG	NG	Protein. Possessed protease, leucine aminopeptidase, acid phosphatase, alkaline phosphatase, phosphodiesterase, 5-nucleotidase, and hyaluronidase activities	NG	1. Toxic to mice	Toom and Chan (1972a,b)	
2. <i>Cyanea capillata</i>	Chesapeake Bay	Homogenized tentacle nematocysts;	1	NG	Protein	NG	1. No to slight effects on contact with human skin	Rice and Powell (1972); Burnett (1971a)	
3. a. <i>Chrysaora quinquecirrha</i>	Chesapeake Bay	mostly heterotrichous microbasic euryteles and holotrichous isorhizas a. Homogenized tentacle nematocysts (four types) and whole tentacle extracts	2	1. 100,000-400,000 2. 5,000-70,000	Protein. Contained some nonspecific esterase activity	Neurotoxin. Possessed hemolytic, dermonecrotic, cardio-toxic, and lethal properties. Possibly has a direct myotoxic effect also	2. Injection of toxin fatal to mice 1. Moderate to severe cutaneous lesions and pain in man 2. Affected heart, lung, and kidneys of mice 3. Caused cardiac conduction abnormalities and death in rats 4. Blocks action potentials of rat peripheral nerves and skeletal muscles and contractions of smooth muscle possibly by affecting membrane ionic conductance 5. Toxin antigenic in rabbits with prior injections affording subsequent protection against the lethal hemolytic and dermonecrotic factors	Cargo and Schultz (1966, 1967); Schultz and Cargo (1971); Burnett et al. (1968a,b); Burnett and Goldner (1969, 1970a,b, 1971); Burnett and Sutton (1969); Sutton and Burnett (1969); Goldner et al. (1969); Stone et al. (1970); Burnett (1971b); Gould and Burnett (1971); Burnett and Gould (1971); Rice and Powell (1970)	

(Continued)

TABLE III (Continued)

Class and species	Locality	Source of toxic fraction(s)	Number of toxic fractions	Molecular weight(s)	Chemical identification of toxin	Nature of toxin	Physiological effects	References
b. <i>Chrysaora quinquecirrha</i>	Chesapeake Bay	b. Homogenized isolated tentacle nematocysts (four types)	2	>100,000	Protein containing large amounts of glutamic and aspartic acids	Neurotoxin(?)	1. Caused tetany of leg muscles, paralysis and death in fiddler crabs	Blanquet (1972)
4. a. <i>Chironex fleckeri</i>	Australia	a. Whole tentacle extracts, homogenized tentacle nematocysts (5 types), and isolated ("milked") nematocyst toxin	2	70,000, 150,000	Protein. (Carbohydrate, cystine compounds, and 3-indolyl derivatives also detected histochemically)	Appears to be primarily a myotoxin. Possessed hemolytic, dermonecrotic, cardio-toxic, and lethal properties	1. Can cause rapid death in man and other vertebrates due to convulsions, paralysis, respiratory arrest, and cardiovascular malfunction 2. Antigenic in rabbits and mice with at least partial immunity to some properties of the toxin being produced 3. Causes strong contraction of barnacle striated and vertebrate smooth, respiratory, skeletal, and cardiac muscles possibly by affecting membrane ionic conduction 4. Toxin did not affect nerve conduction or action	Cleland and Southcott (1965); Freeman and Turner (1969, 1971, 1972); Turner and Freeman (1969); Keen and Crone (1969a,b); Crone and Keen (1969, 1971); Baxter et al. (1968); Baxter and Marr (1969); Endean (1969); Endean and Henderson (1969); Keen (1970, 1971, 1972); Barnes (1967); Endean and Noble (1971); Marr and Baxter (1971); Baxter et al. (1972)
b. <i>Chironex fleckeri</i>	Australia	b. Nematocyst-free tentacle tissue	NG	NG	NG	Neurotoxin. Possessed hemolytic and lethal activity but negligible dermonecrotic activity	potentials in toad sciatic nerve 1. Does not affect barnacle striated or rat smooth, respiratory or skeletal muscle 2. Toxin caused atrioventricular block and cardiovascular malfunction 3. Blocked conduction and action potentials in the sciatic nerve of rats and toads	Endean and Noble (1971)
5. <i>Chiropsalmus quadrigatus</i>	Australia	Whole tentacle extracts	2	70,000, 150,000	Probably a protein	Appears to be primarily a myotoxin. Possessed hemolytic, dermonecrotic, and lethal properties similar to <i>Chironex</i>	1. Caused cardiovascular failure and respiratory arrest in mammals, similar to the effects reported for <i>Chironex</i> above 2. Hemolytic component appeared to differ from that found in <i>Chironex</i> 3. Antigenic in rabbits for all three properties of toxin (hemolytic, lethal, and dermonecrotic). No cross-immunity between <i>Chiropsalmus</i> and <i>Chironex</i> toxins detected	Freeman and Turner (1972); Keen (1971)

\* Key: NG = not given.

nematocysts from the surrounding tissue so that the possible toxic factors contained in both fractions can be analyzed independently and without danger of cross-contamination.

(2) Since many isolated nematocyst preparations commonly contain more than one (and perhaps five or more) different types of nematocysts, techniques should be developed for isolating the toxin from each type independently, whenever possible.

(3) Rather than simply injecting a toxin preparation into any available animal for bioassay purposes and then cataloguing the effects, attempts should be made to develop standard bioassay procedures which could be used by different workers in different parts of the world. This would allow for a more practical comparative evaluation of each type of toxin.

(4) Experiments should be designed so that the site of action of the various toxins could be more readily determined. For example, although many appear to be neurotoxic, others appear to be what the author has called "myotoxic" in that they appear to affect muscle directly, perhaps by affecting ionic conductance across the membrane. Other studies, however, suggest that although membrane ionic conductance is involved, it is the nerve membrane which is directly affected. Other toxins appear to be neuromuscular junction-blocking agents and so on.

(5) More work is needed to determine even the approximate chemical structure of the various described toxins. For example, do they appear to be primarily proteins, enzymes, saponins, histamines, etc., or a combination of compounds? Information on the possible synergistic effects of such compounds would also be of great interest.

Although no attempt will be made here to summarize or reconcile the variety of data on the nature of cnidarian toxins, it does seem likely that (a) the toxin(s) in nematocysts are different from those in the nematocyst-free tissues, (b) not all nematocyst toxins are the same, and (c) different types of nematocysts or the same type in different cnidarians may contain different chemical compounds (Table III).

## VI. UTILIZATION OF NEMATOCYSTS BY NONCNIDARIANS

### A. Mollusca

Although many workers have commented on the acquisition, storage, and release of nematocysts obtained by aeolid nudibranchs from their prey (reviewed by Edmunds, 1966), Hyman (1967) points out that no one to date has actually observed nudibranchs discharging nematocysts against enemies or prey.

Recent observations in my laboratory (unpublished) have shown that the basitrichous isorhiza nematocysts acquired from the sea anemone *Epiactis prolifera* by the nudibranch *Aeolidia papillosa* in California are completely functional and capable of being extruded from the cerata and massively discharged on contact with the surrounding medium. Others (e.g., Grosvenor, 1903) have reported similar findings. Other experiments in which glass coverslips were applied to the cerata of the nudibranch *Hermisenda crassicornis* revealed that both atrichous isorhiza nematocysts and stenoteles were discharged to coverslips on contact (unpublished).

Thompson and Bennett (1969, 1970) have reported that although the glaucid nudibranches *Glaucus* and *Glaucilla* feed on the harmless (to man) hydrozoans *Porpita* and *Velella*, the nematocysts of these species were relatively rare in the cnidosacs of these nudibranchs. Instead they selectively accumulated the largest and most potent nematocysts from the tentacles of *Physalia*, on which they also preyed. Interestingly enough, this was discovered only because of the painful stings received by Australian bathers who chanced to contact the nudibranchs possessing the *Physalia* nematocysts.

Although the above observations do not tell us anything about the ecological role of these nematocysts, it seems highly unlikely that the complex morphological, behavioral, and physiological process of nematocyst acquisition and storage by nudibranchs would have evolved had there not been some adaptive benefit to the organisms involved. It is expected that careful future studies will provide us with information in this regard.

Jones (1963) discusses the possible use of fragments of *Physalia* tentacle contained on the dorsal arm suckers of the pelagic octopus *Tremoctopus violaceus* as offensive and defensive weapons.

## B. Crustacea

Ross (1971) finds that Mediterranean *Calliactis* anemones borne by hemit crabs are important in deterring predation on the hermit crab by an octopus. McLean and Mariscal (1973) similarly have found that *Calliactis tricolor* anemones are very effective in protecting various species of Florida hermit crabs from predation by the large carnivorous crab, *Calappa flammea*.

Wright (1973) reports that the symbiotic hydroids *Podocoryne* and *Hydractinia*, which commonly cover gastropod shells carried by *Pagurus* hermit crabs, tend to prevent the utilization of these shells by a larger and more aggressive hermit crab of the genus *Clibinarius*. Although

*Clibinarius* was stung by the nematocysts of these hydroids, the *Pagurus hermit* crabs were apparently unaffected. Thus, interspecific competition for the extremely important hermit crab resource of gastropod shells may be effectively reduced by the presence of the hydroids on the shells.

### C. Vertebrata

Although some workers have considered the association of various fishes with sea anemones to be made possible due to the sea anemone somehow controlling its nematocyst discharge in response to stimuli received from the fish (reviewed by Mariscal, 1966, 1971b), recent studies have not been able to verify this. Experimental studies by Mariscal (1965, 1969, 1970a, 1971b) and Schlichter (1967, 1968, 1970, 1972) have all shown that the anemone fish is protected from being stung by its anemone host by altering its mucous coat during acclimation to the anemone. This mucus appears to "mask" the fish's normal stimuli for nematocyst discharge in such a way that the fish is no longer recognized as a prey object. Although the fish do not "use" the host's nematocysts directly, they are well protected from predators due to their retreat into and intimate nestling among the anemone's tentacles (Mariscal, 1970c). No evidence has been found by these authors that the anemone was somehow controlling or inhibiting its nematocyst discharge in response to its symbiotic fish.

Although there have been a few observations of the association of fishes with scyphozoans (e.g., Mansueti, 1963; Maul, 1964; Nagabhusanam, 1965; Rees, 1966; Phillips *et al.*, 1969), there have been no recent controlled experimental studies concerning the role of the nematocysts in these associations.

## VII. PUBLIC HEALTH ASPECTS OF NEMATOCYSTS

This topic has been thoroughly reviewed by Southcott (1963), Halstead (1965), Cleland and Southcott (1965), Barnes (1966, 1967), and Lane (1968a). There is no doubt that coelenterate stings may be a serious public health problem in certain parts of the world where *Physalia*, various Hydromedusae, and extremely potent Cubomedusae such as *Chironex* and *Chiropsalmus* are common (e.g., Cleland and Southcott, 1965; Pigulevsky and Michaleff, 1969). Such areas would include Australia and parts of Asia. This is also true, but to a lesser degree,

in areas such as Florida and the Gulf of Mexico where both *Physalia* and Cubomedusae are present (Halstead, 1965; Russell, 1966; Phillips and Burke, 1970) and the northeastern Atlantic coast of the United States where *Chrysaora* is found (Cargo and Schultz, 1966, 1967; Burnett *et al.*, 1968a; Schultz and Cargo, 1971).

Maguire (1968) reports on an additional, nearly fatal, case of a *Chironex* stinging and Southcott (1967) discusses a new carybdeid cubomedusan which is responsible for the so-called "Irukandji Syndrome" (e.g., Barnes, 1964). This syndrome is characterized by a general lack of discomfort at the time of stinging, but after an interval of about 25 minutes may result in complete incapacitation of an adult for a period of several days.

Phillips and Burke (1970) have recently reported cases of coelenterate stings on the Texas and Mississippi Gulf Coasts which were severe enough to warrant medical attention and attribute these to the presence of at least two Cubomedusae, one of them being a member of the genus *Chiropsalmus*.

Although there is at present no effective antidote to treat cases of severe stings by coelenterates, Southcott (1963), Halstead (1965), Cleland and Southcott (1965), Barnes (1966), and Cargo and Schultz (1967) discuss the various treatments for jellyfish stings, none of which have been experimentally studied.

Wasuwat (1970) has reported that an extract of a plant (*Ipomoea pes-caprae*) used by Thai fishermen as an antidote to jellyfish stings contains an antihistamine compound. Two antihistamine drugs, diphenhydramine hydrochloride ("Benadryl") and antazoline methanesulfonate ("Antistine"), as well as the extract from the plant, were found to have an antagonistic effect on toxin from the jellyfish, *Catostylus* sp.

Finally, although only the physiological and clinical problems associated with the various coelenterate toxins studied to date have been discussed up to this point, it should be emphasized that many marine toxins as well as other natural products are currently being investigated as a source of new biomedical materials (e.g., Nigrelli *et al.*, 1967; Freudenthal, 1968; Halstead, 1969; Youngken, 1969; Weinheimer and Spraggins, 1970). It is entirely possible that rather than being only a source of discomfort and injury to man the toxins of coelenterate nematocysts may prove useful as a source of new drugs or other biomedical compounds in the future. Although it has not been demonstrated that the nematocyst components were involved, the interesting recent discovery by Tabrah *et al.* (1972) of an antitumor agent in the extracts of four cnidarian species might be a case in point.

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