



Acquisition and use of nematocysts by cnidarian predators

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ABSTRACT

Although toxic, physically destructive, and produced solely by cnidarians, nematocysts are acquired, stored, and used by some predators of cnidarians. Despite knowledge of this phenomenon for well over a century, little empirical evidence details the mechanisms of how (and even why) these organisms use organelles of cnidarians. However, in the past 20 years a number of published experimental investigations address two of the fundamental questions of nematocyst acquisition and use by cnidarian predators: (1) how are cnidarian predators protected from nematocyst discharge during feeding; and (2) how are the nematocysts used by the predator?

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1. Introduction

Nematocysts, cnidocysts used to inject venom, offer a formidable defense from predators, but despite this weaponry numerous animals from many phyla prey on cnidarians (Salvini-Plawen, 1972; Ates, 1989, 1991; Arai, 2005). Some of these predators acquire unfired nematocysts from their prey and store them in functional form within their own cells; the acquired nematocysts are referred to as kleptocnidae. While aeolid nudibranchs are known for sequestering nematocysts from their prey (reviewed in Greenwood, 1988), one ctenophore species, *Haeckelia rubra*, preys upon narcomedusae and incorporates nematocysts into its own tentacles (Carré and Carré, 1980; Mills and Miller, 1984; Carré et al., 1989). Some turbellarian flatworms also acquire nematocysts from their prey and store them in cells on their dorsal surface (reviewed by Karling, 1966). Because virtually no additional work (since that already cited) has been published on the use of nematocysts by ctenophores or flatworms, this review focuses on the acquisition and use of nematocysts by aeolid nudibranchs. Excellent reviews by Harris (1973) and Todd (1981) detail many aspects of nudibranch ecology

including the use of kleptocnidae; this review concentrates on research published since the last review of nudibranch nematocysts (Greenwood, 1988). Because this *Toxicon* issue focuses on cnidarian toxins and venoms, this review goes into most depth on how nudibranchs protect themselves from the discharging nematocysts of their prey and how the nudibranchs use acquired nematocysts, or kleptocnidae.

2. Defensive effectiveness of cnidarian nematocysts

Nematocysts are defensive weapons but, as Mariscal (1974) points out, it is difficult to separate experimentally the defensive effects of nematocysts from the defensive effects of other cnidarian chemicals. In an attempt to discern specific effects of nematocysts, Stachowicz and Lindquist (2000) investigated the relative importance of hydroid nematocysts as defense against predators. They found that pinfish did not consume hydroid species with penetrating nematocysts (basitrichous isorhizas and stenoteles), but pinfish readily consumed individual hydroids of those same species whose nematocysts had been discharged chemically. Hydroid species without penetrating nematocysts used chemical defenses that prevented pinfish predation whether functional nematocysts were present or not (Stachowicz and Lindquist, 2000). Some sea anemone

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species possess acontia, which are generally considered defensive (Harris, 1986; Shick, 1991), and the nematocysts found in the acontia are usually the largest (by a factor of two or three) in the species' cnidome (Kramer and Francis, 2004). Harris (1973, 1986) and Conklin and Mariscal (1977) reported that sea anemones could grow large enough to be protected effectively from their nudibranch predators. Larger nematocysts, especially in acontiate sea anemones, might be better defensive weapons, making the larger anemones a more difficult meal.

Given that cnidocysts can effectively deter predation, nudibranchs must employ a number of protective mechanisms to be successful predators. For example, behaviors that limit contact with the prey (Grosvenor, 1903; Todd, 1981) could protect the nudibranch predator from nematocyst discharge. In addition, cuticular gut linings (Edmunds, 1966; Martin et al., 2007a), protective epithelia (Graham, 1938; Martin and Walther, 2003; Martin et al., 2007b), and mucus secretions (Mauch and Elliott, 1997; Greenwood et al., 2004) all serve to protect nudibranchs while feeding.

3. Physical protection from nematocyst discharge

Many aeolids have a hard cuticle covering the epithelium of the buccal cavity and the esophagus (Edmunds, 1966). The cuticle prevents damage from nematocyst discharge during feeding because nematocysts do not penetrate it. Recent work confirms that this cuticle is chitin (Martin et al., 2007a).

Most cells of the skin and stomach epithelia of aeolid nudibranchs contain intracellular ovoid discs called spindles (Fig. 1) (Henneguy, 1925; Graham, 1938), but the protective function of these spindles was not elucidated until recently (Martin and Walther, 2002, 2003; Martin et al., 2007a,b). Chemical analysis reveals that the spindles are composed of intracellular "granular" chitin (Martin et al., 2007a) and form a physical barrier to discharging nematocysts. Martin and Walther (2002, 2003) examined the effects of nematocyst discharge from the hydroid *Eudendrium racemosum* on the cerata of the aeolid

nudibranchs *Cratena peregrina* and *Flabellina affinis*. Little damage resulted from small tentacular nematocysts, but large holotrich nematocysts elicited significant damage to the ceratal epithelium. Although the external ceratal epithelial surface was obliterated in some cases, there was never any damage below the basal lamina of the epithelial sheet. In cases when the epithelial cells were damaged, the spindles were released and apparently became entangled with the tubules of the discharged nematocysts. Even when tentacular nematocysts contacted the ceratal surface, the ceratal epithelium released spindles; the authors speculated that spindle release in this case was simply a secretory mechanism (Martin and Walther, 2003). Following contact with the discharged nematocysts, the epithelial layer of the nudibranch is repaired rapidly (Martin and Walther, 2003). Spindles are also released into the stomach lumen, and may be found throughout the digestive tract, including the digestive diverticulae of cerata (Martin and Walther, 2003), and in the lumen of the ciliated canal between the digestive diverticula and the cnidosac in the nudibranch *Spurilla neapolitana* (Greenwood and Mariscal, 1984a). Martin and Walther (2002, 2003) conclude that the spindle-containing epithelial cells act as biological "sandbags," which absorb the impact of the discharging nematocysts and serve to keep the nematocyst toxins at a safe distance from the underlying basal lamina and muscle layers of the nudibranch. Just as a thin layer of panty hose is enough to protect a human from discharging *Chironex* nematocysts (Fenner et al., 1996), a thickened epithelial layer of chitinous spindles might also be an effective defense for a nudibranch!

Spindles are most abundant in nudibranchs that feed upon cnidarians, but spindles are also found in other nudibranchs (Martin et al., 2007b). Nudibranchs that browse on sponges or bryozoans might frequently come into contact with hydroids that are found in the same habitats; for these slugs, those parts of the body most likely to come into contact with cnidarians contain spindles. For example, the stomach linings of hydrozoan-feeding aeolid nudibranchs contain spindle cells, as does the stomach lining of the hydrozoan-feeding dendronotid, *Doto acuta*. In contrast, the arminacean *Janolus cristatus*, which feeds on bryozoans, has no spindles in the cells lining the stomach, and the dorid nudibranch *Chromodoris krohni* has a greatly reduced number of spindle-containing cells, compared to the hydrozoan feeders. Interestingly *J. cristatus* has spindle-containing cells lining the surface of the cerata and on the most exposed parts of the rhinophores. The dorid nudibranchs examined (Martin et al., 2007b) feed on sponges or bryozoans and all have many more glandular cells on their epithelial surfaces than spindle-containing cells. One dorid species, *Aegires punctilucens*, has virtually no spindle-containing cells on the dorsal surface. The surface epithelium of other non-carnivorous opisthobranchs (several sacoglossan species, a cephalaspidean, and the anaspidean *Aplysia parvula*) consists of only a very thin layer of epithelial cells with no intracellular spindles (Martin et al., 2007b).

4. Mucus protection from nematocyst discharge

A mucus layer provides a physical layer of protection (Boutan, 1898; Grosvenor, 1903; Graham, 1938;

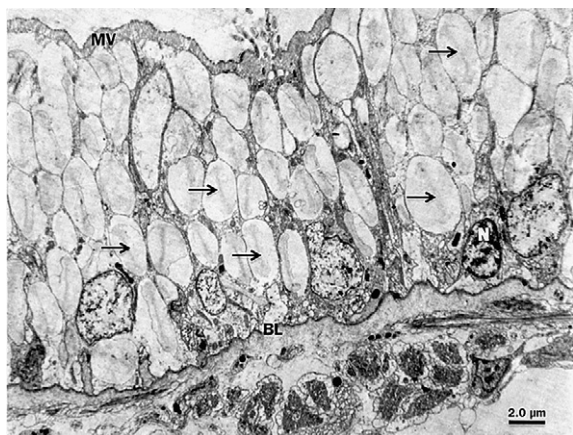


Fig. 1. TEM of ceratal epithelium from the aeolid nudibranch *Spurilla neapolitana*. Chitinous spindles (arrows) are crowded into each epithelial cell. Numerous microvilli (MV) cover the ceratal surface, and a distinct basal lamina (BL) lies below the epithelial cells. A basal nucleus of one epithelial cell is indicated (N).

Salvini-Plawen, 1972; Martin and Walther, 2003), and several authors suggest the possibility of some sort of acclimation to the prey's discharging nematocysts that aids the mucus defense (Grosvenor, 1903; Conklin and Mariscal, 1977). Mauch and Elliott (1997) provided the first direct evidence that the mucus from a cnidarian predator protects it from the prey's nematocyst discharge. Mauch and Elliott (1997) used coverslips coated with mucus from four species of gastropods (the prosobranch snail *Lithopoma gibberosum*, and the nudibranchs *Aeolidia papillosa*, *Phidiana crassicornis*, and *Cadlina luteomarginata*) to elicit nematocyst discharge from the sea anemone *Anthopleura elegantissima*. Nematocysts that adhered to the mucus-coated coverslips were counted and statistically compared among species and to a clean coverslip control. Mucus from all four species caused nematocyst discharge, but the mucus from the nudibranch *Aeolidia papillosa* (the only predator of *A. elegantissima* of the four species tested) caused the fewest nematocysts to discharge (Mauch and Elliott, 1997). Mauch and Elliott (1997) did not determine if *A. papillosa* is innately protected from nematocyst discharge by its mucus, or if the nudibranch must undergo an acclimation process to become protected.

Additional work on mucus protection has been done in my laboratory. We used mucus-coated gelatin probes to quantify nematocyst discharge from several potential sea anemone prey species (*Metridium senile*, *Aulactinia stella*, *Urticina felina*, and *Anthopleura elegantissima*) in response to mucus from the nudibranch *Aeolidia papillosa* (Greenwood et al., 2004). Mucus from *A. papillosa* inhibited nematocyst discharge from the nudibranch's prey species, but did not inhibit discharge from non-prey species. Furthermore, when we switched the prey species, the nudibranch mucus began to inhibit nematocyst discharge from the "new" prey species but no longer inhibited discharge from the "old" prey species. Over the course of the experiments, mucus from *A. papillosa* reduced nematocyst discharge from all prey species by about 60% below control levels, whereas the mucus caused an 11% increase in nematocyst discharge over control levels for the non-prey species (Greenwood et al., 2004). Control experiments established that the nudibranchs did not simply become covered in the prey's mucus. It remains unclear if the nudibranch alters its own mucus or acquires some compounds from the prey during the feeding process (Greenwood et al., 2004). Interestingly, *A. papillosa* cannot switch prey species every time. For example, we obtained a dozen nudibranchs that had been collected from the west coast of the United States feeding on *A. elegantissima* and attempted to feed them individuals of *M. senile* from the east coast; in this instance the nudibranchs were never able to prey successfully on *M. senile* (unpublished observations).

It seems likely that different nudibranch species protect themselves from nematocyst discharge by multiple means. Regardless of the methods employed by an aeolid nudibranch to protect itself from its prey's nematocysts, nematocysts do discharge during feeding, and many nematocysts (both discharged and undischarged) are found routinely in the stomachs and feces of aeolid nudibranchs (Martin, 2003). Because many aeolid nudibranchs acquire

undischarged nematocysts from the prey and store them in cnidosacs at the tips of their cerata, those protective mechanisms that help to inhibit discharge could augment the acquisition process.

5. Acquisition and storage of kleptocnidae

For those aeolid nudibranchs that store nematocysts in their own cells, unfired nematocysts pass through the digestive diverticula and are engulfed by cnidophage cells within the slugs' cnidosacs near the tips of the dorsal cerata (Fig. 2). Several factors may contribute to preventing nematocyst discharge during transit through the nudibranch's gut. As mentioned above, nudibranch mucus may inhibit discharge, either chemically (as suggested by Greenwood et al., 2004), or by physically insulating the nudibranch from the receptor apparatus of the cnidarian's nematocysts (Yarnall, 1972). In the nudibranch *Spurilla neapolitana*, immature nematocysts, which are incapable of discharge, are incorporated into cnidosacs where they complete their maturation (Greenwood and Mariscal, 1984b).

Nematocysts arrive within the proximal lumen of the cnidosacs within 2–3 h after feeding (Greenwood and Mariscal, 1984b; Martin, 2003), and then are engulfed by the cnidophages throughout the cnidosac. The kleptocnidae remain within the cnidosacs for a period of days or weeks and may receive metabolic support from the nudibranch (Greenwood et al., 1989). Greenwood and Mariscal (1984b) reported that the kleptocnidae in the cnidophages of *Spurilla neapolitana* had a membrane closely apposed to the nematocyst capsule and we suggested that the membrane might be the original nematocyst membrane. Subsequent work by Martin (2003) on the nudibranch *Cratena peregrina* and by Ohkawa and Yamasu (1993) on the nudibranch *Cratena lineata* confirmed a single

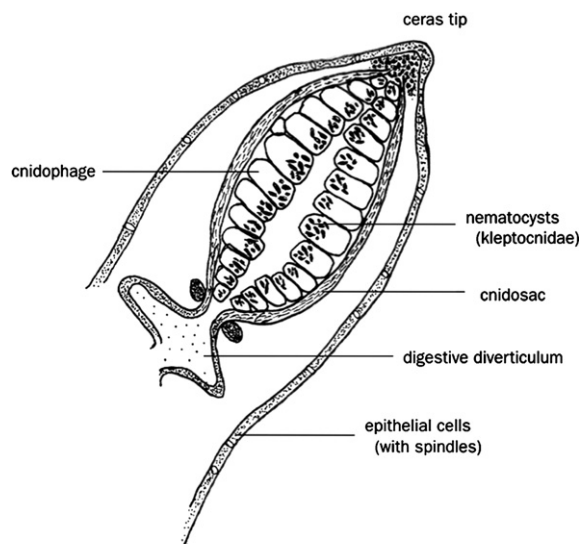


Fig. 2. Illustration of a cerata tip from the nudibranch *Spurilla neapolitana* in longitudinal section. Although ceratal sizes and shapes differ among nudibranch species, the general features of the cnidosac are similar. Cnidophages of *S. neapolitana* average about 70 μ m in length.

membrane surrounding the kleptocnidae, but these authors speculated that the membrane is a phagosome. These studies plus our own ultrastructural research (Greenwood, 1987 and unpublished observations) on several additional aeolid species, lead me to conclude that the kleptocnidae membrane is indeed the phagosome membrane. Digestion of kleptocnidae does not occur quickly within the cnidosacs (Ohkawa and Yamasu, 1993), nor within the cells of the digestive diverticulae (Martin, 2003), but secondary lysosomes containing degraded nematocysts can be found in cnidophages (Greenwood and Mariscal, 1984a; Greenwood, 1987). Therefore, the acquired nematocysts do not escape the phagosome to avoid digestion; the phagosome simply appears to take some time to fuse with a lysosome.

To be useful to a nudibranch, kleptocnidae must discharge when released. Kleptocnidae discharge when squeezed out of the cerata tip (Yarnall, 1972; Conklin and Mariscal, 1977), but few studies have investigated the control of this process. Greenwood and Garrity (1991) isolated kleptocnidae from three different aeolid nudibranch species and found that kleptocnidae discharged in significantly lower numbers than nematocysts isolated from the cnidarian prey. These data indicate that the nudibranchs have more control over kleptocnidae discharge than simply expelling them randomly from the cnidosac. Other experiments used cyclic GMP and cyclic AMP analogs, calcium channel blockers, calcium channel agonists, calcium ionophores, and electrical stimulation on isolated cnidophages, but none of these treatments elicited kleptocnidae discharge (presented in abstract form in Sisson and Greenwood, 1995). We do not know how the kleptocnidae discharge in large numbers when released from the nudibranch.

6. Kleptocnidae function

While kleptocnidae in aeolid nudibranchs are generally considered defensive, there may be other functions. Two published observations showed nudibranch kleptocnidae were used to attack cnidarian prey during feeding (Bergh, 1862; Tardy, 1964). Several researchers discussed the possibility that kleptocnidae are stored in cnidosacs as a means of sequestering these potentially dangerous products of the nudibranch's prey (Grosvenor, 1903; Graham, 1938; Streble, 1968), and this idea has resurfaced recently (Miller and Byrne, 2000; Ohkawa, 1990). However, Megina et al. (2007) found that the aeolid nudibranch *Hermisenda crassicornis* (a generalist carnivore) prefers to prey on the tunicate *Aplidium solidum* rather than on available cnidarian prey. These authors suggest that the nudibranchs consume hydroids specifically for the acquisition of nematocysts, "to maintain the cnidosacs charged" (Megina et al., 2007). This observation implies some benefit of the kleptocnidae to the nudibranch. As Martin (2003) points out, the different possible functions of kleptocnidae need not be mutually exclusive.

To investigate the defensive effectiveness of kleptocnidae, Ohkawa and Yamasu (1993), removed all the cerata from individuals of the nudibranch *Aeolidiella indica*, and then compared predation on those "naked" slugs with predation on individuals of *A. indica* who retained their

cerata ("intact" slugs). Of the 13 fish predators tested, only four consumed intact *A. indica*, and all but one of those fish species ate "naked" individuals at a faster rate (Ohkawa and Yamasu, 1993). Individuals from seven of the remaining fish species ate "naked" nudibranchs and the remaining two fish species did not feed on the nudibranchs at all. The one shrimp species tested (*Palaemon pacificus*) ate naked nudibranchs, but not intact ones (Ohkawa and Yamasu, 1993). This study supports the notion that the cerata have some defensive value to the nudibranchs, but cerata also house defensive secretory cells in addition to the kleptocnidae (Edmunds, 1966). Just as it is difficult to experimentally separate unpalatable components of cnidarians, it is difficult to separate the potential defensive effects of kleptocnidae from the defensive effects of the glandular secretions of nudibranchs (Edmunds, 1966; Greenwood, 1988). In the Ohkawa and Yamasu (1993) research, fluids may also have leaked from wounded nudibranchs and served to attract predators if sufficient healing had not occurred after ceratal removal.

Miller and Byrne (2000) examined ceratal autotomy and regeneration in the nudibranch *Phidiana crassicornis*. These authors found that virtually every nudibranch they collected from two field sites had regenerating cerata, indicating significant predation pressure on these two populations. In laboratory trials only one of the potential predators tested, the kelp crab *Pugettia producta*, preyed on *P. crassicornis*, but the crabs only ate cerata or nudibranch mucus; the nudibranch escaped the encounter each trial (Miller and Byrne, 2000). Miller and Byrne (2000) also placed the arms of two species of asteroids directly onto the dorsal surface of *P. crassicornis* individuals, and examined the asteroid tube feet microscopically to assess damage from kleptocnidae. In two of five encounters, they found discharged kleptocnidae in the tube feet of *Crossaster papposus*. No discharged kleptocnidae were observed in the tube feet of *Pycnopodia helianthoides* following similar encounters (Miller and Byrne, 2000). Miller and Byrne (2000) concluded that ceratal autotomy is an important defensive weapon for *P. crassicornis*, but that the acquired nematocysts do not contribute much defensive value (at least to the predators tested).

Aguado and Marin (2007) used an interesting system of different colored models to investigate the defensive value of kleptocnidae and warning coloration in the aeolid *Cratena peregrina*. The models were mixtures of cuttlefish (as chemoattractant) and carrageenan formed into several shapes and dyed to resemble *C. peregrina* or dyed other colors to serve as controls. For some trials, models were bathed in a slurry of nematocysts extracted from *Eudendrium* hydroids. Individuals of the wrasse *Thalassoma pavo* were offered various colored models with and without nematocysts, and the fish learned quickly to avoid models with nematocysts and those models with the same color pattern as the nematocyst-containing models (Aguado and Marin, 2007). Fish in the field also learned to avoid models with nematocysts after only a few encounters (Aguado and Marin, 2007). It is still necessary to assess the purity and effectiveness of the nematocyst slurry that was applied to the models to determine whether it is just nematocysts that make the models unpalatable or if other components from

the hydroids might be involved. For example, the discharge status of the nematocysts on the models was not assessed.

The most convincing evidence supporting a defensive function of nudibranch kleptocnidae emerged from recent research by Kinsey Frick (2003, 2005). Many aeolid nudibranchs retain only a subset of the available nematocyst types from their cnidarian prey (reviewed in Greenwood, 1988), although at least some species may incorporate nematocysts randomly (Martin, 2003). Kepner (1943) and Edmunds (1966) suggested that aeolid nudibranchs might retain those nematocysts most effective in deterring predators. To test this idea, Frick investigated how the presence of predators affected the nematocyst complements of the nudibranch *Flabellina verrucosa* (Frick, 2003). Frick catalogued the kleptocnidae complement in the cnidosacs of individuals of *F. verrucosa*, and then offered the nudibranchs two types of hydroid prey (*Obelia geniculata* and *Tubularia* spp.). The nudibranchs and their prey were housed in flow-through containers in a larger tank that also contained one of three species of potential predator (the sea star *Crossaster papposus*, the wrasse *Tautoglabrus adspersus*, and the crab *Carcinus maenas*). Nudibranchs housed in the presence of *C. papposus* and *T. adspersus* had a significantly different nematocyst complement than control nudibranchs maintained without the potential predator. In particular, the storage of microbasic mastigophores (a penetrant nematocyst) was favored in both cases (Frick, 2003). A later study by Frick (2005) confirmed that the kleptocnidae complement in several species of the genus *Flabellina* is highly dependent upon the nudibranchs' prey species, although the proportion of kleptocnida types in the nudibranch may vary from the proportions of nematocyst types in the prey. These results suggest that the nudibranchs respond to the presence of a potential predator either by altering their feeding, which changes their kleptocnidae complement, or by retaining particular nematocysts from their prey (Frick, 2003). Both situations support a defensive role of the kleptocnidae.

7. The future

Several fundamental questions of nematocyst toxinology include: (1) how is nematocyst discharge controlled; (2) how can nematocyst discharge be inhibited; and (3) what are some effective defenses from discharging nematocysts? Research over the last two decades (and before) has shown that aeolid nudibranchs and their cnidarian prey can serve as useful model systems to investigate each of these questions. Continued work on how these predators steal and use nematocysts should continue to contribute much to our basic understanding of cnidocyst biology.

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Conflict of interest

None declared.

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