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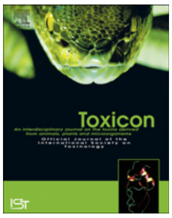

Structural diversity, systematics, and evolution of cnidae

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ABSTRACT

Cnidae are secreted by the Golgi apparatus of all cnidarians and only cnidarians. Of the three categories of cnidae (also called cnidocysts), nematocysts occur in all cnidarians, and are the means by which cnidarians defend themselves and obtain prey; spirocysts and ptychocysts are restricted to a minority of major taxa. A cnida discharges by eversion of its tubule; venom may be associated with the tubule of a nematocyst. About 30 major morphological types of nematocysts are recognized, but no single nomenclature for them is accepted. Function seems not to correlate tightly with morphology—nematocysts of at least some types are used both offensively and defensively. Similarly, it is not clear if morphology correlates with toxicity. Some types of nematocysts are taxonomically diagnostic whereas others are widespread. Nonetheless, an inventory of types of cnidae (the cnidom), with their distribution and size, is an essential component of most taxonomic descriptions. Complicating the taxonomic value of cnidae are the facts that not all members of a species may have the same types of cnidae, even at the same life-cycle stage, and size of nematocysts of a species may vary geographically and with size of individual. The diversity of nematocysts is so great and the features within each major type are so variable that homologies have not been determined. Nematocyst complement, morphology, and size likely reflect both phylogeny and biology; the feedback between the two may confound analysis. Although cnidae are valuable in taxonomy of at least some groups, more understanding of the forces that affect them is needed for their systematic and phylogenetic value to be understood and their potential as indicators of evolution to be realized.

1. Introduction

Nematocysts are the *sine qua non* of phylum Cnidaria—all cnidarians and only cnidarians produce them. At least some types of nematocysts are associated with venom; this is the source of the sting of jellyfish, for example. Nematocysts are the means by which cnidarians protect themselves and capture prey—cnidarians are exclusively carnivorous (e.g. Hand and Fautin, 1988) although some that live in shallow water harbor photo-endosymbionts from which they may derive fixed carbon (e.g. Muscatine, 1961; Muscatine and Cernichiari, 1969). Each microscopic capsule (length range is about 20–200 μm) is secreted by the Golgi apparatus of a cell specialized for this function, termed a nematoblast (Watson and Wood, 1988). Thus, despite common usage to the contrary, a nematocyst is not a “stinging cell”—it is the capsule made by the cell that delivers the sting.

Nematocysts constitute one of three categories of such intracellular secretory products of cnidarians. The others are ptychocysts and spirocysts, capsules that occur in only a limited diversity of cnidarians (see Section 3 below). Bozhenova (1988: 71) expressed a distinctly minority, and somewhat outdated, view in declaring, “The division of cnidae into spirocysts, nematocysts and ptychocysts seems to be groundless.” The collective term for these capsules is

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cnida (plural cnidae), derived from the Greek for nettle (κνιδη) (*knide*). An alternative term for nematocyst is cnidocyst (Weill, 1934a). The cells that make the capsules are cnidoblasts (specific types are nematoblasts, ptychoblasts, and spiroblasts), with the corresponding mature cells cnidocytes (and nematocytes, ptychocytes, and spirocytes) (Watson and Wood, 1988). The word Cnidaria is currently the preferred term for the phylum that some still call Coelenterata, but, as van der Land (2003) has argued, there is no good scientific reason to replace Coelenterata with Cnidaria, so the two are interchangeable in modern usage.

Cnidae are, according to Mariscal (1974: 130), "among the largest and most complex intracellular secretion products known." Upon receipt of an appropriate chemical and/or mechanical stimulus (reviewed by Anderson and Bouchard, 2009), a nematocyst discharges so the tubule that had been coiled and twisted inside the capsule everts, to be emitted from one end of the capsule, which opens as part of the discharge process. This discharge is among the fastest cellular processes (Holstein and Tardent, 1984). It is the discharged nematocyst that gave rise to the name of the structure, literally "thread capsule" (for eversion to occur, clearly the tubule must be hollow, which is why the term thread or filament is unsuitable for it: Watson and Wood, 1988). A spirocyst capsule had been considered single-walled (e.g. Hyman, 1940; Westfall, 1965), but it is actually double-walled like that of a nematocyst, although thinner (Mariscal and McLean, 1976). The nature of the ptychocyst capsule wall was not specified in the publication describing that cnida type (Mariscal et al., 1977). A spirocyst tubule, like that of a nematocyst, is "helically folded with multiple pleats in length, but only three in circumference"; a ptychocyst tubule differs in being "folded accordion-like in circumference into a series of stacked pleats" (Mariscal et al., 1977: 396).

By contrast with the complexity of these secretory products, cnidarians are structurally simple, at the tissue grade of organization, composed of two epithelia, the ectoderm and endoderm. The ectoderm is also referred to as the epidermis and the endoderm as the gastrodermis. Hyman (1940) advocated using epidermis and gastrodermis, reserving the other terms for embryological layers, but she later (Hyman, 1967) repudiated that position, recognizing that the terms ectoderm and endoderm had been coined for adult coelenterates and were applied, in the context of recapitulation, to embryonic layers of "higher" animals (as discussed by Fautin and Mariscal, 1991). Between the epithelia lies the mesoglea, which varies from entirely acellular (as in hydrozoans: e.g. Thomas and Edwards, 1991) to rather rich in cells (e.g. Hyman, 1940). Three-dimensionality is achieved by folding these sheets of cells, which prompted Shick (1991: 3) to quip that "Sea anemones … are at the 'origami' level of construction." *In situ*, a cnida is oriented with the end that opens upon discharge near the free surface of the cell layer, so the tubule is shot into the gastrovascular space (for a cnida in a mesenterial filament, for example) or outside the animal (for a cnida in a tentacle, for example).

Cnidocytes are part of one or both of these epithelia, depending on the taxon. In most cnidarians, most nematocytes are ectodermal, occurring largely in the tentacles: for example, more than 95% of nematocytes of *Hydra attenuata* are in the tentacles, where their number increases from base to tip (Bode and Flick, 1976). In non-skeletalized organisms, such as medusae and sea anemones, nematocysts typically occur elsewhere on the outer surface of the animal. Scyphomedusae have endodermal nematocytes in the gastric cirri (Arai, 1997). Members of Anthozoa also have nematocytes in the endoderm; the mesenteries are edged by filaments containing both gland cells that produce digestive enzymes (summarized by Shick, 1991) and nematocysts that may function in subduing, if not digesting, prey. Spirocysts are typically more abundant than nematocysts in tentacles of sea anemones and their relatives; the amazing number of 43 million "Nesselkapseln" in one tentacle of the common European sea anemone *Anemonia sulcata* reported by Möbius (1866) (who called the animal *Anthea cereus*) is likely to have been mostly spirocysts—which Bedot distinguished as a separate category only in 1890.

Mackie (2002: 1650) called nematocysts "the cnidarians' secret weapon." He continued, "They have enabled the group to achieve enormous success as predators with little of the investment in elaborate sensory and morphological specialization that characterizes most predators. Thus, cnidarians have prevailed despite their exceedingly simple basic body plan." I am unaware of figures for the cost of producing nematocysts, individually or on a per animal basis, but their continual production must be a significant portion of an animal's energy budget: they are complex; an individual possesses large numbers of them [about 30% of the roughly 11,000 cells in a polyp of *Hydra magnipapillata* are nematocytes and nematoblasts (Sugiyama and Fujisawa, 1977), and a large colony of the siphonophore *Nanomia cara* is estimated to have six million nematocysts (Mackie, 1999)]; and each is used but once, with many typically discharging during an offensive or defensive act [Bode and Flick (1976: 31) calculated that nearly 25% of nematocytes—or about 7500 cells—are lost from the tentacles of *H. attenuata* each day].

Because cnidae are so central to both the biology and the concept of cnidarians, papers on them are part of the proceedings of all seven international conferences on coelenterate biology to have been held (Rees, 1966; Tokioka, 1973; Mackie, 1976; Tardent and Tardent, 1980; Williams et al., 1991; den Hartog et al., 1997; Fautin et al., 2004). Other volumes concerned with cnidarians that contain important information on cnidae include *The Biology of Hydra and of Some Other Coelenterates 1961* (Lenhoff and Loomis, 1961), *Coelenterate Biology: Reviews and New Perspectives* (Muscatine and Lenhoff, 1974), *Hydra: Research Methods* (Lenhoff, 1983), *Microscopic Anatomy of Invertebrates, volume 2: Placozoa, Porifera, Cnidaria, and Ctenophora* (Harrison and Westfall, 1991), a dedicated issue of volume 80 of the Canadian Journal of Zoology, and some of the proceedings of hydrozoan workshops such as Bouillon et al. (1987) and Mills et al. (2000). Review articles on cnidae in general or only nematocysts include Hand (1961), Halstead (1965) (who focused on medical aspects of stinging), Picken and Skaer (1966), Mariscal (1974, 1984), and Östman (2000). *The Biology of Nematocysts* (Hessinger and Lenhoff, 1988) comprises the proceedings of an international symposium devoted to these intriguing structures. Some of these sources discuss hypotheses of how nematocysts discharge, which is still unresolved; nematocysts were once considered independent effectors, but it is now clear that the animal can exert control over their discharge (see, e.g., Fautin and Mariscal, 1991; Shick, 1991; Kass-Simon and Scappaticci, 2002; Anderson and Bouchard, 2009) although isolated capsules of most types are capable of discharge (Greenwood et al., 2003).

2. Diversity of cnidae

The most widely-used classification, which recognizes about 30 morphological types of nematocysts, is derived from the work of Weill (1930, 1934a,b) who, in two large volumes, inventoried nematocysts (and spirocysts) from many species, and raised issues of biology and making distinctions that still trouble biologists (Fautin, 1988). Weill's classification of nematocysts, which "has been tinkered with and debated almost since it was proposed" (Fautin, 1988: 489), relies largely on morphology of the tubule [whether one exists at all, whether its tip is open or closed, whether it is of equal diameter throughout its length (an isorhiza), and position of spines on it, if any (basitrichous if the spines are only near the base as in Fig. 1, holotrichous if the spines occur throughout its length)], as viewed with the light microscope. Some research has reduced the number of categories—the supposed atrichous isorhizas are holotrichous ones (H in Fig. 2) in which the spines are very small (Cutress, 1955); but categories have been created as variability in nematocyst morphology has been revealed (e.g. Weill, 1964; Schmidt, 1969), particularly by electron microscopy (e.g. Mackie and Mackie, 1963; Bouillon et al., 1986; Östman, 1988; Carré et al., 1989; Pires, 1997). Östman (2000: 44) redefined some categories of nematocysts in light of such discoveries, retaining the underpinnings originated by Weill; she pronounced the nomenclature created by Schmidt (1969, 1972 1974), which was only for Anthozoa, "rational" but found "it caused confusion by using synonyms for nematocysts already well known." England (1991) discussed nomenclatures of sea anemone nematocysts, proposing names for 12 types in a table that compared his with four other schemas: in no case do more than three of the five agree on the name for a particular type. A single classification schema that accommodates all cnidarians would best serve communication among cnidarian biologists, furthering understanding of the evolutionary history and systematic implications of nematocysts. However, because it seems that no single system will be agreed upon, and the degree of detail relevant to a particular question can affect how a nematocyst is classified, I (Fautin, 1988) have urged that,

Fig. 1. Basitrichous isorhizas ("basitrichs") from a sea anemone. The capsule of a discharged basitrich is at lower right, with the tubule emerging toward the upper left; note the spines along most of what is visible of the tubule. At upper right is an undischarged basitrich, with the tubule visible inside the capsule.

Fig. 2. Undischarged cnidae from sea anemones and corallimorpharians. H: A holotrichous isorhiza ("holotrich") from a corallimorpharian. Note the very spiny tubule packed into the capsule. M: A microbasic *p*-mastigophore from a sea anemone. In the undischarged state, the enlarged basal shaft of this type of cnida has a characteristic notch at its base. S: A spirocyst.

when referring to a particular type of nematocyst, it be illustrated, to improve communication among scientists using different nomenclatural systems.

Nematocysts have also been distinguished on the basis of function, which broadly, but not precisely, correlates with morphology. Based on studies in hydra, Ewer (1947) defined functional categories of nematocysts as prey capture (penetrants), defense (volvents), and adherence to the substratum during locomotion (glutinants), two morphological types effecting feeding, and one each the other two. Summarizing research to that time, including some of his own unpublished studies, in anthozoans as well as hydrozoans, Mariscal (1974) convincingly showed that nematocysts of some types must function in both offense and defense, particularly for sea anemones, in which 60% of the genera have the identical cnida complement (cnidom, sometimes rendered as cnidome) of spirocysts, basitrichous isorhizas, and microbasic *p*-mastigophores (Carlgren, 1945) (Figs. 1 and 2). As Shick (1991: 27) put it, "Our best indication concerning the function of particular nematocysts comes not just from their structure but also from their anatomical location and their use in special situations." For example, in sea anemones, microbasic *p*-mastigophores (M in Fig. 2) are most common in the mesenterial filaments, actinopharynx, and acontia, from which I infer they are likely involved in subduing and perhaps digesting prey; in sea anemones, holotrichous isorhizas characterize tissues used in aggression [such as acrorhagi and fighting (=catch) tentacles] (see Section 3 below). "Whether the various morphological variants of cnidae consistently differ in function, especially for animals having several types, remains unknown" is as true now as when Fautin and Mariscal (1991: 310) wrote those words.

A corollary to this statement is that it is uncertain whether all nematocysts deliver a venom [spirocysts do not (Doumenc, 1971); because ptychocysts function in tube-building, they almost certainly do not], and whether morphologically similar or identical nematocysts have similar or identical venoms in different species or even in different parts of one animal (e.g. Schmidt, 1974). Most nematocysts of siphonophores studied by Purcell (1984) do not penetrate, so it is likely they do not deliver venom.

Although cnidarian venoms are the subject of intensive study (e.g. Smith and Blumenthal, 2007), ascertaining that the venom is from nematocysts can be very difficult (reviewed by Hessinger, 1988; McKay and Anderson, 1988). The review by Honma and Shiomi (2005), for example, mentions nematocysts with the implication that they are the source of the venoms, but precisely how the venom was obtained is seldom sufficiently well described to be certain it was from nematocysts (see, e.g., Shanks and Graham, 1988). Hessinger (1988) pointed out some instances of biologically active compounds erroneously having been attributed to nematocysts. Obvious problems with obtaining only nematocyst venom are that the capsules are small and nematocytes are intermixed with other types of cells, even in areas of high concentration such as nematocyst batteries; isolating nematocysts of a single type from cnidarians with more than one type makes the problem more difficult (e.g. Hessinger, 1988; Underwood and Seymour, 2007). Hessinger (1988) and McKay and Anderson (1988) reviewed techniques that have been used to obtain isolated nematocysts.

How venom delivery has been conceptualized relates to nematocyst structure. Mariscal (1974: 137), for example, stated an "open thread would allow delivery of the toxin," and that, therefore, types of nematocysts in which the tip of the tubule is closed are unlikely to be toxic. Use of the term "inject" (e.g. Kass-Simon and Scappaticci, 2002; Sher and Zlotkin, 2009) to describe venom delivery, although perhaps not intended to, evokes an image of a syringe. This was one of four hypotheses for mode of delivery discussed by Thomason (1991), and the one for which he found support. It seems unlikely, however, because, at the size of a nematocyst, molecular-scale interactions between venom and the inner wall of a tubule are likely to impede or even prohibit flow (see, e.g., Vogel, 1994). The conclusion of Rifkin and Endean (1983) that the venom of the cubozoan *Chironex* (which is capable of killing humans) is the granular material in the undischarged capsule prompted Lesh-Laurie and Suchy (1991: 202) to write "If this hypothesis is true, the distribution of soluble contents throughout the mastigophore would argue for its continuous release as the tubule everts and penetrates its victim." The delivery of venom by the outer wall of the tubule, rather than through its tip, constituted the other three hypotheses of Thomason (1991), which he attributed to Tardent et al. (1985). Lotan et al. (1995, 1996) localized the venom of the scyphomedusa *Rhopilema nomadica* on what becomes the outer surface of the everted tubule; they concluded it is injected by the spines, an idea previously suggested by Hessinger and Ford (1988). This resembles how spirocysts function, spinning microfibrillae from the external surface of the everting tubule (Mariscal, 1974). (A ptychocyst tubule has no spines either; it may have granular material on its external surface: Mariscal et al., 1977.)

As Mariscal (1974) pointed out, not all cnidarian toxins are associated with nematocysts. The best-known one may be palytoxin, "the most deadly nonproteinous [toxin] ever isolated" (Shimizu, 1983: 212). Elucidation of the structure of palytoxin and determination of its stereochemistry, in the precomputer age, which were chronicled by Shimizu (1983), were called "intellectual milestones in the modern history of organic chemistry" (Scheuer 1988: 38). Known to native Hawai'ians (Moore and Scheuer, 1971; Scheuer, 1988), palytoxin is released by some shallow, tropical zoanthids. (Zoanthids resemble sea anemones, and, like anemones, belong to Subclass Hexacorallia of Class Anthozoa. They should not be referred to as soft corals, the term used for them by, e.g. Munday, 2008; soft corals is the common name of some members of anthozoan Subclass Octocorallia). Palytoxin may not even be synthesized by the cnidarian: it has been found in organisms other than cnidarians (Gleibs et al., 1995), may be acquired through the food chain (Usami et al., 1995), and may undergo large concentration changes through the year, sometimes disappearing altogether, and may not occur in all species of the group (summarized by Munday, 2008). Many octocorals contain fundamental (primary) metabolites (such as sterols; e.g. Epifanio et al., 2007) and complementary (secondary) metabolites (such as terpenoids; e.g. Fabricius and Alderslade, 2001) that chemically defend the animal against predators. Some of these compounds may be produced by microbial symbionts.

3. Taxonomic and systematic value of nematocysts

At the highest taxonomic level, the systematic implication of nematocysts is clear. All cnidarians, and only cnidarians, produce them. Few other phyla are diagnosable by a single unambiguous feature such as this (members of Cnidaria share other features that reinforce the monophyly of the group—but none is as diagnostic as nematocysts).

What animals are most closely related evolutionarily to cnidarians is uncertain, but one candidate is ctenophores. Aside from the fact that many are gelatinous zooplankters like most cnidarian medusae, one ctenophore, *Haeckelia rubra*, possesses nematocysts. This had been interpreted as an evolutionary link between Ctenophora and Cnidaria, but we now know the nematocysts are kleptocnidae, obtained through predation on cnidarians (Carré and Carré, 1980); Mills and Miller (1984) were even able to determine the prey species from analysis of nematocysts. That some nudibranch molluscs can acquire nematocysts through predation, store them undischarged, and use them in their own defense has long been known (Conklin and Mariscal, 1977). When a nudibranch feeds on a cnidarian, it appears that mature nematocysts discharge, but immature ones do not, are taken up, and are stored in diverticula of the digestive system where they mature (Greenwood and Mariscal, 1984a,b; Greenwood, 1988); the nudibranch may sequester nematocysts of only some of the types possessed by its prey (e.g. Day and Harris, 1978). Some flatworms—both marine and freshwater—harbor kleptocnidae; some also have autochthonous structures that resemble cnidae (e.g. Kepner and Barker, 1924; Karling, 1966). So possession of nematocysts is not confined to cnidarians—although their production is.

Some classes can be diagnosed by type of nematocysts but others cannot, a pattern that seems to apply at all taxonomic levels within Cnidaria; the biological reality of these groups, as with the phylum, is corroborated by other features. Hydrozoa has the greatest diversity of nematocysts, in part because the greatest number of types is limited to it. Based on the 25 types recognized by Mariscal (1974) and depending on the authority, 22 or 23 occur in Hydrozoa, 17 of them exclusively, and six occur in Anthozoa, two exclusively (e.g. Mariscal, 1974; Kass-Simon and Scappaticci, 2002). Scyphozoa has three types, none exclusive to it, but especially holotrichous isorhizas vary morphologically (Lesh-Laurie and Suchy, 1991). Cubozoa also has three types (e.g. Calder and Peters, 1975; Lesh-Laurie and Suchy, 1991; Avian et al., 1997; Oba et al., 2004), none exclusive to it and one not shared with Scyphozoa; this may explain inventories recording four types for Scyphozoa, of which Cubozoa was previously considered a member. Staurozoa [the group that had constituted Order Stauromedusae of Scyphozoa and that Marques and Collins (2004) have proposed merits class status] has the least diverse cnidom, with two types (e.g. Larson and Fautin, 1989; Collins and Daly, 2005), both of which also occur in Scyphozoa.

The two non-nematocyst cnidae also diagnose groups: spirocysts are confined to anthozoan Subclass Hexacorallia, and ptychocysts are confined to hexacorallian Order Ceriantharia. Octocorals have only one type of nematocyst, called atrichous isorhizas by Mariscal (1974), rhabdoidic heteronemes by Schmidt (1974). Spirocysts are generally asserted to be monomorphic (Hyman, 1940), but gracile and robust forms have been distinguished (e.g. Dunn, 1983), although no taxonomic pattern has been discerned in their occurrence. Size variation in ptychocysts has been documented (Mariscal et al., 1977), but variation in form has not; however, those from few species have been studied, and only 144 valid species of that order are known (Fautin, 2008).

The diagnostic value of nematocysts at lower taxonomic levels is variable, seeming to differ with taxon. For sea anemones, the taxon in which nematocysts seem to be most important taxonomically (Fautin, 1988), a family or genus is characterized—but not necessarily distinguished—by its cnidom. Half the 38 sea anemone families for which Carlgren (1949) provided data have a cnidom of spirocysts, basitrichs, and microbasic *p*-mastigophores; in only two is the cnidom unique (Fautin, 1988). As mentioned above, more than 60% of anemone genera are also characterized by a cnidom of spirocysts, basitrichs, and microbasic *p*-mastigophores (Carlgren, 1945).

The cnidom and the distribution and dimensions of the nematocysts are now considered essential to any taxonomic description or redescription of a cnidarian species of most taxa (Fautin, 1988; Östman, 2000). The diagnostic value of these data may depend on the geographic and taxonomic scope of the comparison, but for no group of cnidarians are nematocyst data consistently informative for taxonomy. Papenfuss (1936) and Peach and Pitt (2005) found nematocyst form and size useful for distinguishing among species of scyphomedusae, but Jensch and Hofmann (1997) found no differences of taxonomic value for two congeneric species. Scyphistomae of three species can be distinguished by morphology and/or size of nematocysts, but Calder (1971) cautioned that nematocysts should not be used to differentiate them from species from other geographic areas—nematocysts of animals from those areas would need to be inventoried to determine how broadly these features are diagnostic. Nematocysts may be diagnostic in at least some hydrozoans (e.g. Mackie and Mackie, 1963; Werner, 1965; Gravier-Bonnet, 1987; Östman, 1988); Östman (1982) could differentiate species of the hydrozoan genus *Obelia* based on nematocyst morphology, and the species recognized by their nematocysts also differed morphologically and ecologically. In sea anemones, nematocyst size is characteristic of a species but does not necessarily differentiate species (Stephenson, 1929; Fautin, 1988; Williams, 1996, 1998), and no species can be identified solely by cnidae (Fautin, 1988). This appears also to be true of zoanthids (Seifert, 1928). Based on a survey of more than 50 species of scleractinians, Pires (1997) concluded nematocyst morphology is potentially of taxonomic importance. Four species of Brazilian scleractinian corals, three belonging to the endemic genus *Mussismilia*, have identical types of nematocysts; size of some nematocysts from some tissues can distinguish the genera but not the congeneric species (Pires and Pitombo, 1992). Hidaka (1992) concluded that two ostensible morphs of one species and two putative species of another genus of scleractinians are distinct species, based on size and form of nematocysts.

Size of some types of nematocysts in some sea anemone species varies clinally with depth and latitude (Zamponi and Acuña, 1994) and in others with size of the animal (e.g. Schmidt, 1972; Acuña et al., 2007). Francis (2004: 126) found larger individuals of several species of sea anemones have larger spirocysts, attributing this to taller epithelial cells, which "should be able to accommodate and support larger cnidae," but did acknowledge this cannot be a general explanation. If it were, all nematocysts in a particular tissue of an individual should be the same size (or have the same size range), but nematocysts of different types in a single tissue commonly differ in length, and more than one size class of a particular type of nematocyst may occur in a tissue (e.g. short and long basitrichs in the mesenterial filaments of *Heteractis malu*: Dunn, 1981). Recognizing that nematocyst size can vary with animal size, Schmidt, (1972: English abstract) stated, "The relation of the medium sizes of several homologous nematocyst types provides a good genus- or species-character."

Even within an individual, size of nematocysts of a particular type from a single tissue varies. For example, length of the stenoteles along the column of hydra increases proximally to distally (Bode and Flick, 1976; Bode et al., 1983), and length of basitrichous isorhizas along the column of the sea anemone *Actinodendron arboreum* varies least in the middle of the column, whereas the pattern of size variability is more complex in the actinopharynx and the tentacles, which are intricately branched (Ardelean and Fautin, 2004).

Using statistics to compare nematocyst size for taxonomic purposes requires considering several factors. The underlying distribution must be known to determine which statistics are appropriate (Fautin, 1988). Williams (2000) found very large numbers must be measured in sea anemones to obtain a statistically valid sample. Acuña et al. (2004, 2007) have proposed statistical treatments to distinguish species of anemones that are indistinguishable with nematocyst data using typical approaches. A practical difficulty with sampling nematocysts is obtaining a representative sample: because nematoblasts arising from a single interstitial cell constitute a clone, measurements of descendents of a single progenitor cell would constitute pseudoreplication.

A problem with taxonomic diagnosis based on nematocysts is that all members of a species may not have the same cnidom. It differs in different stages of the same species of scyphozoan (e.g. Calder, 1983), but may be used to differentiate species the at same stage (Calder, 1977). Holotrichous isorhizas are inducible in structures of anthozoans involved in aggression (Bigger, 1988); thus, for example, individuals having or lacking catch tentacles do not have the same nematocyst complement (Watson and Mariscal, 1983), and individuals in the center of a clone of *Anthopleura elegantissima* have fewer acrorhagi (and so holotrichous isorhizas) than those at the periphery, or even none at all (Francis, 1976).

A practical challenge is accurate identification of some types of nematocysts. Ironically, in an effort to standardize practice and because nematocysts typically do not discharge once a cnidarian is preserved, inventories for taxonomic purposes are from undischarged capsules. Yet nematocyst classification relies largely on tubule attributes. Form of capsule tends to covary with that of tubule, but, for example, a microbasic amastigophore (which has no tubule, or only a very short one, beyond the basal shaft) and a microbasic *p*-mastigophore (which has a long tubule beyond the shaft; M in Fig. 2) may be impossible to distinguish in the undischarged state. Further, classification is based on attributes visible with the light microscope, perhaps a legacy of the time at which the classification was first developed. It is easier to examine the large numbers of capsules necessary for taxonomic purposes by light than by electron microscope. Although detail is superior with the latter, the significance of many sorts of details, such as spination (e.g. Östman, 1982), is unclear—they may have more to do with ecology than with taxonomy or phylogeny (see Section 4).

4. Evolution and cnidae

The distinctiveness of cnidae, the production of which unambiguously diagnoses a cnidarian, also make them unsuitable for determining evolutionary relationships of the phylum—no organism that otherwise seems closely related to cnidarians creates similar structures. The uniqueness of cnidae has led to theories about their restriction to these animals because of symbiosis. Evidence that Shostak (1993) summarized for the "symbiogenetic theory for the origins of Cnidaria" is based on studies in hydra indicating that epithelial and interstitial cells function quite differently. He hypothesized that the latter (which give rise to cnidoblasts) are descended from single-celled organisms that harbored nematocyst-like structures and that formed a symbiosis with the ancestral organism consisting of epithelial cells. The intrinsic genome of plastids and mitochondria allows them to self-replicate; finding different genomes in cells of the two types would bolster the case for symbiosis.

Among candidate symbionts cited by Shostak (1993) are myxosporidians, obligate endoparasites of aquatic vertebrates that had been considered protists, each infective spore of which contains a structure much like a nematocyst. Based on sequences of 18S rRNA, Smothers et al. (1994: 1721) concluded that myxosporidians are closely related to bilateral animals, but equally strongly stated "myxozoans and cnidarians [do not] share a recent, common evolutionary history." By contrast, Siddall et al. (1995) concluded, based on ultrastructure and 18S rDNA, that myxosporidians are cnidarians, which, like parasites of many lineages, have lost morphology typical of their group; the single most diagnostic feature remains the cnidae (in this case atrichous isorhizas), which had been referred to as polar capsules.

The complexity of nematocysts makes them an obvious candidate for inferring evolution within Cnidaria. Ideally, analysis should be based on a single origin, from which all contemporary variation has arisen (Verwoort, 1987). However, the diversity of nematocysts, much less all cnidae, is so great and the features within each major type so variable that homologies have not been determined thus far. Among the few publications containing speculation about evolution of nematocysts themselves are those of Russell (1940), Schmidt (1974), and Bozhenova et al. (1988). That nematocysts are phylogenetically informative was confirmed by Westfall (1966), who found that an operculum closes the distal end of a nematocyst in Hydrozoa and Scyphozoa, whereas three flaps close the distal end of a nematocyst in Anthozoa, from which she inferred that Hydrozoa and Scyphozoa are more closely related to one another than either is to Anthozoa. That conclusion has been confirmed by other data (Bridge et al., 1995; Collins, 2002). Nematocysts of the two major clades of the phylum (Medusozoa and Anthozoa) also differ in how a stimulus for discharge is received (summarized by Mariscal, 1974; Anderson and Bouchard, 2009).

As for taxonomy, evolutionary information and inferences at lower taxonomic levels are still uncertain. For example, Lindner and Migotto (2001) warned against imputing phylogenetic significance to nematocysts until their distribution is better known, having found an ostensibly rare type of nematocyst in an animal not closely related to other hydrozoans in which that nematocyst type had been used as evidence of phylogenetic relatedness of some families. Calder (1977: 17) noted, "Although nematocysts may be useful in solving certain problems of identification in the Scyphozoa, the cnidome is so uniform from one order to another that their overall value in phylogenetic studies within the class appears limited." Schmidt (1972, 1974) considered nematocysts to be useful characters for understanding phylogeny of Anthozoa, but asserted that Weill's classification system impedes such analysis because it obscures significant differences.

It is likely that nematocyst complement and size reflect both phylogeny and biology; the feedback between phylogeny and biology may confound analysis. Type of prey caught has been related to type of nematocysts (e.g. Purcell and Mills, 1988; Peach and Pitt, 2005)—a cnidarian may be constrained to particular types of prey, but perhaps nematocysts can be induced (in the short term), analogous to the way in which holotrichous isorhizas are induced in aggressive structures of anthozoans (see Section 3 above), or evolve (over long periods) in response to prey availability. For the anemonefish anemones, although a size range of particular nematocysts characterizes each species, it cannot be used to distinguish among all of them (Dunn, 1981), possibly because these animals are similar in ecology: evolutionary pressure may tailor nematocyst size (and perhaps even complement) to niche. Purcell (1984) found, in addition to size of prey caught by siphonophores increasing with nematocyst size and number, a second-order phenomenon—morphology of nematocyst batteries may have hydrodynamic implications for how the tentacles are arrayed in the water or function as lures. Thus a variety of evolutionary pressures may affect distribution of nematocysts, and probably also their size, toxicity, and morphology.

Reflecting yet another facet of the fundamental dichotomy between Medusozoa and Anthozoa, hydrozoan and scyphozoan venoms are rather similar to one another, and may differ from those of Anthozoa; certain types of compounds are confined to Anthozoa (Kem, 1988). Venoms could inform studies of cnidarian evolution, as a character separate from or correlated with nematocysts. If venom and nematocyst morphology can evolve separately from each other and from other facets of the organisms that make them, findings about the toxicity of a particular type of cnida in a particular type of cnidarian might not be true of that type of cnida in a different type of cnidarian. Similarities in venoms might indicate, for example, similarities in prey more than evolutionary relatedness of the organisms producing them.

In sum, nematocysts—their morphology, functioning, and distribution both within a single cnidarian and among taxa of Cnidaria—have been demonstrated to be valuable in taxonomy of at least some groups, but more understanding of what morphological aspects are informative and the forces that affect them is needed for their systematic and phylogenetic value to be understood and their potential as reflections of evolution to be realized.

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Conflicts of interest

The author declares no conflicts of interest.

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