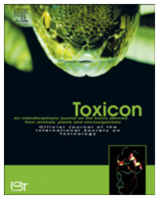
Toxicon 54 (2009) 1148–1161

Contents lists available at ScienceDirect

Toxicon

journal homepage: www.elsevier.com/locate/toxicon



A hydra with many heads: Protein and polypeptide toxins from hydra and their biological roles

Daniel Sher [a,b,*], Eliahu Zlotkin [a,1]

[a] Department of Cell and Animal Biology, Silberman Institute of Life Sciences, Hebrew University, Jerusalem 91904, Israel
[b] Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, MA, USA

ARTICLE INFO

Article history:
Available online 21 March 2009

Keywords:
Hydra
Toxin
Nematocyte
Nematocyst
Pore-forming

ABSTRACT

Hydra have been classical model organisms for over 250 years, yet little is known about the toxins they produce, and how they utilize these toxins to catch prey, protect themselves from predators and fulfill other biological roles necessary for survival. Unlike typical venomous organisms the hydra allomonal system is complex and "holistic", produced by various stinging cells (in the hunting tentacles and body ectoderm) as well as by non-nematocytic tissue. Toxic proteins also fulfill novel, non-allomonal roles in hydra. This review described the toxins produced by hydra within the context of their biology and natural history. Hydra nematocyst venom contains a high-molecular weight (>100 kDa) hemolytic and paralytic protein and a protein of ~30 kDa which induces a long-lasting flaccid paralysis. No low-molecular weight toxicity is observed, suggesting the lack of "classical" 4–7 kDa neurotoxins. The occurrence of a potent phospholipase activity in the venom is supported by the detection of several venom-like phospholipase A2 genes expressed by hydra. Hydra also produce toxins which are not part of the nematocyst venom. In the green hydra, Hydralysins, a novel family of Pore-Forming Proteins, are secreted into the gastrovascular cavity during feeding, probably helping in disintegration of the prey. Other putative non-nematocystic "toxins" may be involved in immunity, development or regulation of behavior. As the first venomous organism for which modern molecular tools are available, hydra provide a useful model to answer many outstanding questions on the way venomous organisms utilize their toxins to survive.

© 2009 Elsevier Ltd. All rights reserved.

> "When the arms of such a polyp are well extended…it [a millipede] need but touch an arm for it to be seized. As soon as the millipede feels itself captured, it struggles vigorously, making great efforts to free itself. Often it sets out to swim…and drags the arm… by which it is caught from one side to the other as a fish caught on a hook drags the line if given slack… in a moment, the millipede ends up entangled in most of these arms." (Trembley, 1744)

These lines, written over 250 years ago by Abraham Trembley, still echo with his surprise when noticing that the small, plant-like creatures he found in the water from a stream near his home in Switzerland, can be such voracious predators. Trembley's studies of hydra ("polyps") are considered by many to have opened the age of experimental biology, revealing the animal nature of cnidarians, as well as describing processes such as phototaxis and regeneration (Lenhoff and Lenhoff, 1988). Since their discovery, hydra have been studied extensively, revealing insights into many important biological phenomena

* Corresponding author at: Department of Civil and Environmental Engineering, Massachusetts Institute of Technology, Cambridge, MA, USA.
E-mail addresses: dsher@mit.edu, dsher@pob.huji.ac.il (D. Sher).

[1] Deceased May 18, 2008. This review is dedicated to Eli's memory; he was a true scientist, a mentor and a friend.

0041-0101/$ – see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.toxicon.2009.02.036

including pattern formation (Hobmayer et al., 2000), regeneration (Bosch, 2007), the cell biology of animal–plant symbiosis (Rahat and Reich, 1986) and many others. However, several of the most intriguing aspects of these organisms remain unclear: how are such morphologically simple, soft organisms able to catch mobile, advanced and well protected prey? How do they survive in an aqueous medium infested with potential predators? How do they avoid colonization by fouling organisms and pathogenic bacteria? It is clear that the answers to these questions involve the use of offensive or defensive toxic allomones.

The main goal of this review is to summarize the current knowledge on protein and polypeptide toxins from hydra. However, we feel that hydra have the potential to be more than just the source of novel toxins: these animals are well characterized model organisms, with an array of experimental tools available unrivaled by any other venomous organism. Thus, they provide a unique model to study many ecological aspects of their toxinology, such as the way different toxins interact within the complex venom, different ecological roles for different venom components, and the possible roles of venom besides prey capture or protection from predators. Our motivation to study hydra toxinology and chemical ecology is our belief that these simple, soft-bodied and static animals compensate for their morphological simplicity and vulnerability by using elaborate and advanced chemistry in order to survive. Therefore, the description of the known protein and polypeptide toxins is best viewed within the larger context of the biology and natural history of the organisms producing them, the hydra.

1. Hydra – a biological resumé

Hydra are freshwater cnidarians, living in lakes, streams and ponds all over the globe (Kanaev, 1952). They usually live in the upper, photic zone where prey is abundant, but can be found down to depths of over 400 m (Link and Keen, 1995). Commonly, these small animals (several millimeters to several centimeters in length) are found attached by their base to a hard substratum such as aquatic plants or rocks. However, they are mobile, and may in fact become planktonic at times (Reisa, 1973; Elliott et al., 1997). Under the magnifying glass, hydra are among the most morphologically simple cnidarians. They have the general shape of a sac surrounding a water-filled gastrovascular cavity (GVC) or coelenteron, with one major opening, the mouth, surrounded by a ring of tentacles (Fig. 1). They have only two cellular layers, the endoderm and the ectoderm, separated by a thin, acellular layer termed mesoglea (Fig. 1E). Hydra have a limited number of cell types (Bosch, 2007), which are derived either from one of the epithelial cell lineages (endodermal or ectodermal) or from the interstitial cell lineage, which gives rise to nematocytes, nerve cells, gland cells and gametes. Hydra have a simple, diffuse nerve network, located mainly around the hypostome (Bode, 1996). The hydra's life cycle includes only a polyp stage (unlike many other cnidarians which also have a pelagic, medusa stage), which can reproduce either asexually (by budding, see Fig. 1B) or sexually. Despite the fact that hydra have a more simple morphology and life cycle than many other cnidarians, they are in fact highly derived, and do not represent the "ancestral" cnidarian, as once thought (Collins et al., 2006; Hemmrich et al., 2006).

In nature, hydra are often found in dense patches (Elliott et al., 1997). With their tentacles hanging down and covering a large volume of water, these hydra patches pose formidable barriers for prey organisms. Hydra feed on a variety of organisms, including crustaceans, annelids and fish larvae, and they can have an important effect on aquatic food webs (Schwartz et al., 1983; Elliott et al., 1997).

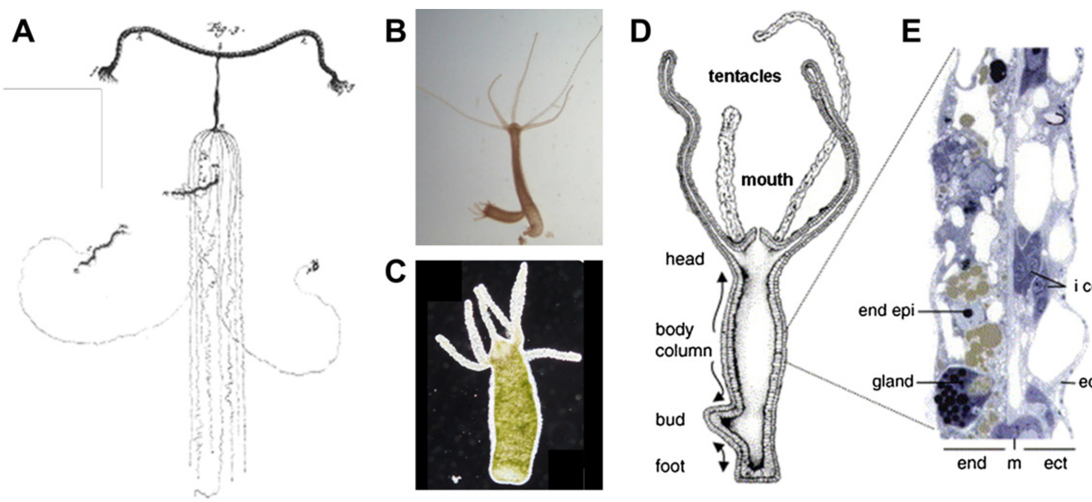


Fig. 1. A general description of hydra anatomy. A) One of the original drawings by Trembley, depicting a "long-armed polyp" (*Hydra oligactis*) catching a "millipede" B) A brown hydra, *H. vulgaris*, with a mature bud. The length of the animal in the picture is about 1 cm. C) A green hydra, *Chlorohydra viridissima* (syn. *Hydra viridis*). The length of the animal is about 5 mm. D) A schematic diagram of the hydra body plan. The arrows depict the direction of cell migration during the development of hydra. E) A section through the body of hydra, showing the two epithelial cell layers, the interstitial cells and the acellular mesoglea. End epi = endodermal epithelial cells, ect epi = ectodermal epithelial cell, m = mesoglea, i-cells = interstitial cells. Panel A was reproduced from Trembley (1744). Panels D and E were reproduced from Bosch (2007), with permission from Elsevier.

Download English Version:

https://daneshyari.com/en/article/2065113

Download Persian Version:

https://daneshyari.com/article/2065113

Daneshyari.com