The Form and Function of the Hypertrophied Tentacle of Deep-Sea Jelly *Atolla* spp.

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ABSTRACT

In situ observations and species collection via remotely operated vehicle, laboratory observations, and structural microscopy were used with the objective to shed light on the form and subsequently the function of the hypertrophied tentacle exhibited by some *Atolla* species. Based upon the density of nematocysts, length, movement, and ultrastructure of the hypertrophied tentacle, the function of the tentacle is likely reproductive, sensory, and/or utilized in food acquisition.

INTRODUCTION

The meso- and bathypelagic habitats are of the largest and least known on the planet. They are extreme environments, characterized by high atmospheric pressure, zero to low light levels, scarcity of food sources, and cold water that is low in oxygen content. Animals that live and even thrive in these habitats exhibit unique characteristics enabling them to survive in such seemingly inhospitable conditions. One such organism, the deep-sea medusa of the genus *Atolla,* trails a singular elongated tentacle, morphologically distinct from the marginal tentacles. This structure, often referred to as a trailing or hypertrophied tentacle, is unique within the cnidarian phylum.

Ernst Haeckel described the first species of this deep pelagic jelly, *Atolla wyvillei,* during the 1872-1876 HMS Challenger Expedition. In the subsequent 135 years, the genus *Atolla* has expanded to several species not yet genetically established, which have been observed in all of the worlds oceans (Russell 1970). Although the general morphology and external anatomy of *Atolla,* has been thoroughly described (Haeckel 1881, Kramp, Russell 1959,1970), very little is known about the form and function of the hypertrophied tentacle. This is due in part to the historical use of midwater trawling techniques employed to collect deep-sea organisms such as *Atolla spp.*

Gelatinous organisms tend to be highly misrepresented when sampling with nets because soft-bodied animals are easily damaged. But with the advent of remotely operated vehicles (ROVs), it is possible to observe and collect *Atolla spp. in situ*, without damaging the individual. One such observation was made by Hunt & Lindsay (1998), who witnessed an *Atolla* with its hypertrophied tentacle entwined with a siphonophore, *Nanomia bijuga*. The subsequent paper suggested that the hypertrophied tentacle is used in prey capture. However, it is unclear from this single observation, which animal was prey and the possibility exists that the two were simply entangled. The Hunt & Lindsay paper remains the only published observation of behavior concerning the hypertrophied tentacle of *Atolla spp.* Thus the purpose of this study was to further investigate the form and potential function of the hypertrophied tentacle of the deep-sea jelly *Atolla.*

Cnidarians are generally thought to be passive predators, feeding on prey that adhere to the tentacles where numerous nematocysts are deployed. Aside from aiding in prey capture, these nematocyst-laden tentacles have a secondary function in defense. Provided that these are typical functions of cnidarian tentacles, the hypertrophied tentacle of *Atolla spp.* may serve a similar function possibly as a lure, for prey specialization, and/or as the mechanism of food transport. Given the extreme habitat of *Atolla spp.* and the uniqueness of the hypertrophied tentacle, it is reasonable to assume it is used in another functional capacity. In an environment where it is difficult to find a mate, the elongated tentacle could serve a reproductive function as an attachment point for potential mates or used in sperm transfer (Chad Widmer 2011 pers.comm.). *Atolla spp.*

are dioecious and can be differentiated by the shape of the gonads and the presence or absence of eggs.

There is yet another hypothesis that is based upon the suggested function of trailing filaments belonging to the squid *Vampyroteuthis infernalis.* Although this deep-sea cephalopod has two trailing structures, they are remarkably similar in appearance and behavior to the hypertrophied tentacle of *Atolla spp.* Young (1967) and Dilly et. al. (2009) have suggested the trailing filaments of *Vampyroteuthis,* function both as feeding and sensory structures. The hypertrophied tentacle analogous to the trailing filaments, could serve a sensory function, detecting chemical cues from a mate or potential prey items. Therefore, we investigated four possible functions of the hypertrophied tentacle of *Atolla spp.*: reproduction, sensory, feeding, and defense.

MATERIALS AND METHODS

ROV COLLECTION

30 *Atolla* specimens, 24 *A. vanhoeffeni*, 5 *A. wyvillei,* and 1 unidentified species, were collected at two deep-water sites off Moss Landing, CA in Monterey Bay during the Midwater Ecology Expedition between Jun 13-19th, 2011. The Midwater 1 (MW-1) and Canyon Axis (3500m depth over axis of Monterey Submarine Canyon) sites are located approximately 12km and 100km offshore respectively. Specimens were collected at depths between 406-2794m via the ROV Doc Ricketts, aboard the R/V *Western Flyer*, with low-impact suction and detritus samplers.

VARS

Behavioral, morphological, and distributional information on *Atolla* species were obtained through MBARI's Video Annotation and Reference System (VARS) database. Behavioral observations, with respect to the marginal and hypertrophied tentacles, consisted of recording movement, orientation, reactions, and interactions within the water column. Morphological observations were based upon the presence and subsequent length of the hypertrophied tentacle. The approximate length of the elongated tentacle was determined using known bell diameter, from collected specimens, and the corresponding video footage. Depth distribution was derived from VARS using observations made between 1989 –June 2011.

LAB OBSERVATIONS

Several types of lab observations were conducted during this study. These observations included both live and preserved organisms. Specimens collected were measured, preserved in 5% formalin-seawater solution, or kept alive for further observation and experimentation. Lab observations were made aboard the R/V *Western Flyer* and, later, in the MBARI wetlab where surviving individuals were placed in three plankton kreisels. Those specimens that survived long enough and in good condition were placed in three separate kreisels. Kreisel I consisted of 3 *Atolla wyvillei* collected between 873-1582m, all female. Kreisel II contained 4 *Atolla vanhoeffeni* sampled from 499-533m, consisting of 3 gravid females and 1 male. Finally, in Kreisel III were 5 *Atolla vanhoeffeni* collected between 445-562m, consisting of 3 juveniles of unknown sex, 1 male, and 1 gravid female. Specimens were ultimately preserved in 5% formalin/ seawater solution.

Daily qualitative observations were made of interactions between male and female *Atolla* both on the research vessel as well as in kreisels II and III in the wetlab. Gonad state was monitored and any reproductive events noted.

A total of 27 live *Atolla spp.* were involved in both passive and invasive feeding experiments. The passive experiments consisted of the addition of potential prey items to the *Atolla* kreisels without further human involvement and included the feeding of frozen krill, live mysid shrimp, *Artemia* nauplii, *Aurelia* ephryrae, *Aegina citrea,* various copepods, unidentified polychaete, doliolids, ctenophores, chaetognaths, *Cyclothone* parts, and a marine snow simulation. Marine snow was obtained from the water collected with the *Atolla* from the ROV, and then dispersed in kreisels I and II. The invasive feeding experiments involved the forced application of each prey organism previously mentioned, via forceps, to both the hypertrophied and marginal tentacles of the *Atolla.*

Gut contents were also investigated to further determine the diet of *Atolla spp.* and were analyzed only from individual specimens that were preserved immediately after collection aboard the *Western Flyer*. Experimentation testing the sensory hypothesis consisted of mixing fluoresceine dye with three solutions: 1:1 *Artemia*-seawater , 1:1

blended krill-seawater, and a seawater control. The solutions were added to the kreisels via pipette and responses were recorded.

HISTOLOGY

Tentacles, both marginal and hypertrophied, were prepared for histological study. A distal, mid, and proximal segment of each tentacle was placed in 5% formalin/distilled seawater solution and sent to the histology lab at the Community Hospital of Monterey Peninsula (CHOMP). At CHOMP they processed the tentacle samples from 5% Formalin solution through graded ethanol series to xylene, and finally paraffin wax. The sample was then embedded in paraffin blocks and oriented for three longitudinal and three cross section cuts of each tentacle segment. Each section was then stained with a standard Hematoxylin and Eosin stain (H&E), and mounted on labeled glass slides. These slides were used to determine the presence or absences of nematocysts, cilia, along with other specialized ultrastructure and cells. Nematocysts densities for the marginal and hypertrophied tentacles were also calculated using the histological slides. The area, mm^2, of each tentacle sample was determined under 10x objective on compound microscope using calibrated Infinity Analyze software. Then unfired nematocysts, that were easily identifiable at 10x magnification, were counted for each tentacle segment and divided by the area of that segment. Nematocyst density was calculated for 3 individuals, 2 marginal and 1 hypertrophied tentacle segment for each individual, which were averaged for both tentacle types.

SEM

Marginal and hypertrophied tentacles were fixed in 2% Glutaraldeyhyde buffered solution and kept at room temperature for two hours. The samples were then post-fixed for one hour in 1% osmium tetroxide. Each sample was then rinsed three times each, for 5 minutues, with DI water. Each sample was then taken up to 100% ethanol through a series of graded steps, in increments of 10% ethanol, from a 10% ethanol/DI solution, remaining in each ethanol step for 15 minutes. After three washes at 100% ethanol for another 15-minute interval, the chemical drying reagent HMDS was added to the ethanol mixture in 3:1 ethanol→ HMDS ratio and taken up to 100% HMDS over one hour. The samples were left for 16hrs under a chemical fume hood, mounted on stubs, grounded with gold spattering, and run through the scanning electron microscope (get model type).

RESULTS

LAB OBSERVATIONS / VARS

The depth distribution for *Atolla spp* in Monterey Bay is 300 – 3000 m. Video footage over 71 dives and individuals, revealed that *Atolla spp.* displayed at least three general postures pertaining to the marginal tentacles: tucked aboral; where the base of the tentacles are tucked against the exumbrellar bell, tucked oral; the tentacles are tucked tightly under the subumbrellar bell, and trailing oral; the tentacles are trailing unfurled behind the body.

The presence of the hypertrophied tentacle was apparent over all video observations made of both *A. vanhoeffeni* and *A. wyvillei* and calculated to be 1.5- 36 times the length of the bell diameter. Video also revealed that the hypertrophied tentacle is capable of retraction, coiling, and autotomy along the length of the tentacle (Fig.2). These movements were later confirmed during lab observations, although it is important to note that it is not conclusive whether the tentacle is autotomizing or just detaching under strain.

Two notable observations were made of female and male interactions. The first was aboard the *Western Flyer* involving one male and one female *A.vanhoeffeni*, with the male attached to the female via hypertrophied tentacle. A whitish substance on the tentacle appeared to move from the male to the female. Unfortunately we were unable to collect the substance. The second observation is really one that included several different days of observation of kreisel II (1 male and 3 females). On more than one occasion the male *A. vanhoeffeni* was connected to a female via hypertrophied tentacle, however there were no observations of female-female connections.

The passive and invasive feeding experiments proved inconclusive for all types of organisms used as prey. As indicated in Fig.3, there were only 4 out of 12 prey items that were successfully adhesive amongst both the passive and invasive feeding methods. *Aegina citrea* and the *Aurelia* ephyrae adhered to the hypertrophied tentacle in the invasive experiment only, but were not consumed and sloughed off at a later point in time. The small, unidentified polychaete adhered to the marginal tentacles only during the invasive feeding, and was again not consumed by the *Atolla*. The marine snow had the highest success in adhesion to both the marginal and hypertrophied tentacles staying attached until removed or until death of the individual. None of the organisms fed to the *Atolla* were observably consumed. As for gut contents, two of the specimens dissected for analysis yielded unidentified organisms, which were too deteriorated to determine.

HISTOLOGY

Nematocysts were found on both the hypertrophied and marginal tentacles of *Atolla.* Although, not yet identified, it is likely that there are at least two or more different types of nematocysts present within *Atolla* tentacles. Marginal tentacles had significantly greater numbers of nematocysts than did hypertrophied tentacles, on average 226 nematocysts/mm^2 and 42 nematocysts/ mm^2 respectively (Fig.5). Unidentified cells were also found within both types of tentacle. A prominent feature found at the base of the hypertrophied tentacle, is a pronounced groove (Fig. 7)

SEM

The difference in ultrastructure between the hypertrophied tentacle and marginal tentacles can be observed in Fig. 6, which shows the distinct presence and absence of particular structures between tentacle types. Spherical structures, likely unfired nematocysts, that are prolific on the marginal tentacle, are sporadic on the hypertrophied tentacle. Conversely the hair-like structures, possible cilia, found covering the hypertrophied tentacle are sparse at best on the marginal tentacle. These structures are yet to be identified. The SEM images of the base of the hypertrophied tentacle confirm the groove-like structure (Fig.7) observed on the histology slides

DISCUSSION

Thorough analyses of both the hypertrophied and marginal tentacles suggest that they are functionally distinct, although it is important to note that they may work in concert toward the same goal. Based upon the calculated nematocyst densities mentioned in

Figure 5, it is likely that the marginal tentacles serve a defensive purpose, as well as aid in prey capture, as they are equipped to immobilize potential predators and prey. The hypertrophied tentacle, on the other hand, is almost certainly not used in a defensive capacity, as the nematocyst density was very low and sporadic. This does not rule out a potential function in feeding, however, as preliminary findings indicate a groove at the base of the tentacle (Fig.7) and hair-like structures (Fig.6), which could aid in the adhesion and transport of food materials to the manubrium. This, in conjunction with the low nematocyst density, optimal placement of the hypertrophied tentacle, near the opening of the manubrium, as well as the ability to coil/retract all suggest a potential for the tentacle to be utilized in food acquisition. Here, we use the term food acquisition instead of prey capture because the evidence suggests that, if used as a feeding structure, the tentacle specializes in the accumulation of prey that are relatively small, non-mobile, or slow-moving. Several video observations revealed that enough current and drag on the hypertrophied tentacle resulted in detachment of the tentacle and thus loss of potential prey items, which as depicted in Figure 2e and 2f., could occur even with very small prey. Therefore, it seems unlikely that *Atolla* would capture larger, highly mobile prey with the more delicate hypertrophied tentacle when it is armed with 17-36 thicker, nematocyst-laden marginal tentacles. If the hypertrophied tentacle is a feeding structure, we suspect that it is a transport mechanism for prey caught and paralyzed by the marginal tentacles as well as reserve food source akin to flypaper. As *Atolla* moves through the water column with it's hypertrophied tentacle extended, it accumulates small organisms and marine snow that adhere to it, providing the jelly with increased surface area and a supplementary diet, useful particularly if larger prey is scarce as is often the case in the deep-sea (Sandrini 1989, Sötje 2007, Robison 2010).

In an immense, dark world where mates are difficult to come by, it may be that the hypertrophied tentacle "fishes" for and adheres to potential mates. Proximity during a spawning event would increase the odds of fertilization; particularly in the mesopelagic realm where *Atolla* live. Microscopy revealed a groove and hair-like structures on the hypertrophied tentacle, which aside from food acquisition, could be utilized in reproduction. The placement of the hypertrophied tentacle is such that it lies not only near the manubrium, but close to the gonads and therefore may serve as a mechanism of sperm transport as purposed by Chad Widmer (2011). The hypertrophied tentacle of a male *Atolla* could potentially attach near the gonads of a female to transfer sperm. Very little is known about the life history of *Atolla*, however scyphomedusae are generally accepted as broadcast spawners, thus making it remarkable if the hypertrophied tentacle is utilized in sperm transport, but that would require further investigation.

There is the least amount of evidence available to support or refute the sensory hypothesis, although the hair-like structures and unidentified cells on the hypertrophied tentacle may serve as a start for further investigation. The hair-like structures could aid in chemical or mechanoreception as suggested for the trailing filaments of *Vampyroteuthis* aforementioned (Young 1969, Dilly 2009). A study conducted on the mesopelagic scyphomedusa, *Mitrocoma cellularia* revealed that these jellies could sense the presence of prey via waterborne chemical signals and even pursue scent trails (Tamburri 2000). It is important to note, however, that the mechanism of chemoreception has not yet been identified. Being that the hypertrophied tentacle can extended over 30 times the length of the bell diameter, it would make an ideal sensory structure with the ability to "taste" waters far from the organism itself in order to assess nearby locales for potential food, mates, or predators.

CONCLUSIONS/RECOMMENDATIONS

It is clear that the hypertrophied tentacle is a unique structure that is morphologically, behaviorally, and anatomically distinct from the marginal tentacles of *Atolla spp.* Where marginal tentacles are primarily for feeding and defense, the hypertrophied tentacle, may have multiple uses. Whether a primary or secondary function, it is likely that the hypertrophied tentacle has some sensory capabilities to aid in either food acquisition or reproduction. Further *in situ*, morphological, behavioral, microscopic, experimental, and gut content analysis is needed. During this investigation more questions were produced than answered. Aside from the mystery surrounding the form and function of the hypertrophied tentacle, there are many interesting questions we have about *Atolla*, such as genetic and morphological differences between species, patterns of bioluminescence, photosensitivity, and details of its life history that remain obscure. Thus, *Atolla* are an optimal study organism for future research. The deep- sea jelly *Atolla* however, remains, as many of their midwater counterparts, highly enigmatic.

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Fig.1. Sample Sites. This figure shows the Midwater 1 and Canyon Axis sites, which were plotted based upon the GPS coordinates from the Midwater Research Expedition of June 2011.

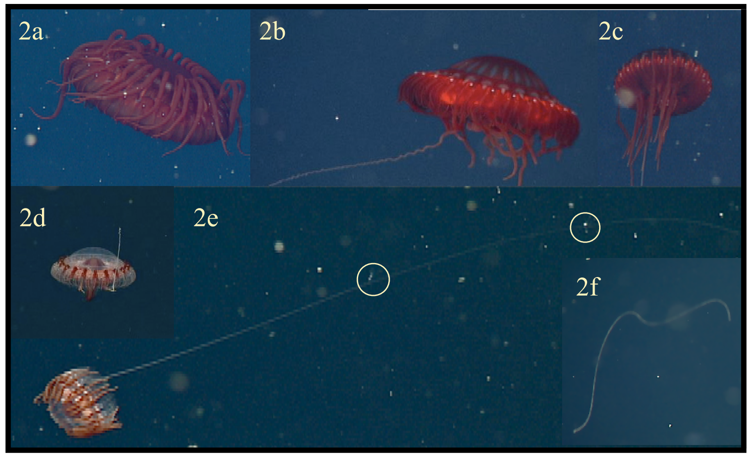
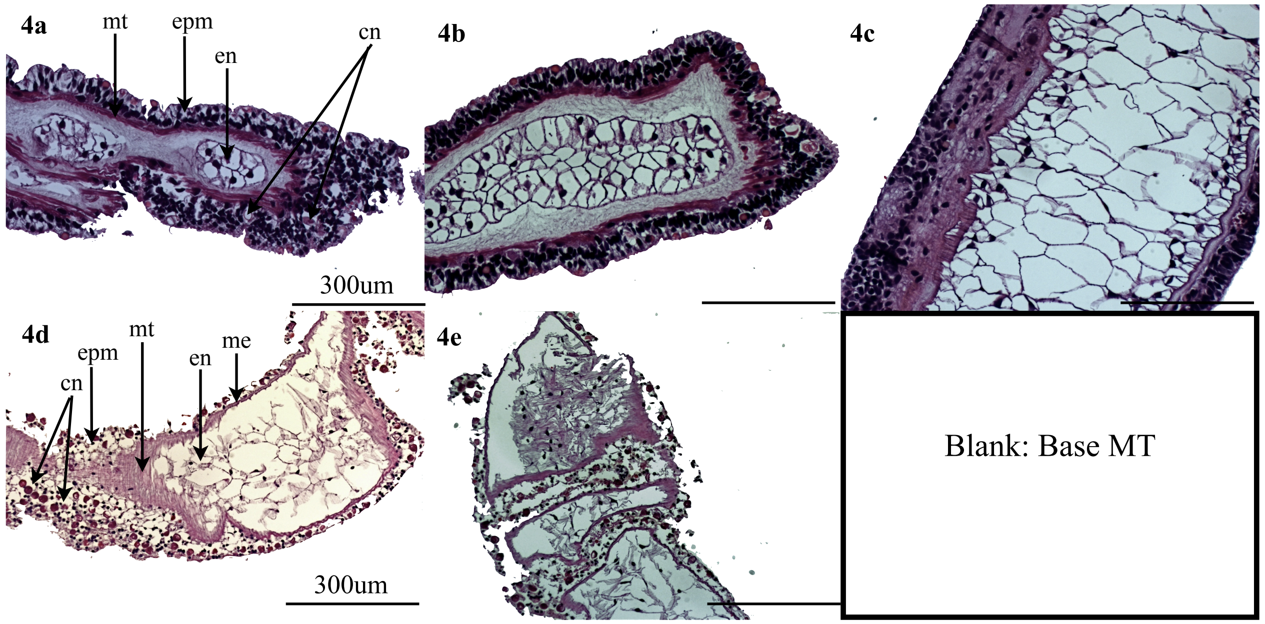


Fig.2. Movements of Marginal and Hypertrophied Tentacles. Analysis of the video footage revealed three general postures with respect to the marginal tentacles: 2a. tucked aboral, 2b. tucked oral, and 2c trailing oral. The ability of the hypertrophied tentacle to coil and retract is depicted by pictures 2b and 2c. Two small organisms, a *Solamaris* medusa and a radiolarian (indicated by the yellow circles), were observed stuck to the hypertrophied tentacle of the *A.vanhoeffeni* in picture 2e. While we were observing the *Atolla* in 2e a current came through and the hypertrophied tentacle detached just above the *Solamaris,* the first organism circled above. The detached segment of the tentacle is pictured in 2f.

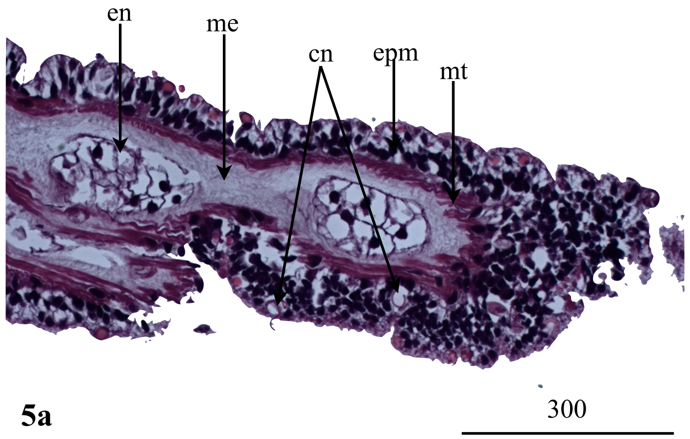
Prey Type (alive/dead)	Passive Feeding Marginal	Passive Feeding Hypertrophied	Invasive Feeding Marginal	Invasive Feeding Hypertrophied
Frozen Krill	0	0	0	0
Mysid Shrimp	0	0	0	0
Copepods	0	0	0	0
Artemia nauplii	/	/	/	/
Aurelia ephyrae	0	0	0	+
Aegina citrea	0	0	0	+
Polychaetes	0	0	+	0
Ctenophores	0	0	0	0
Doliolids	0	0	0	0
Chaetognath	0	0	0	0
Cyclothone	0	0	0	0
Marine Snow	*	*	*	*

Fig.3. Passive and Invasive Feeding Experiments
The table above shows which prey items successfully adhered to the marginal, hypertrophied, or both tentacles; none of the items were observably consumed. The 0 represents organisms that did not adhere to either tentacle type. The / indicates that the adhesiveness or consumption of organism is unknown. In this case the *Artemia* nauplii were too small to determine feeding success or even perform the invasive technique. The + represents organisms that attached to the tentacle but eventually detached without assistance, whereas the * indicated items that adhered and remained on the tentacle until removal or death of the individual.

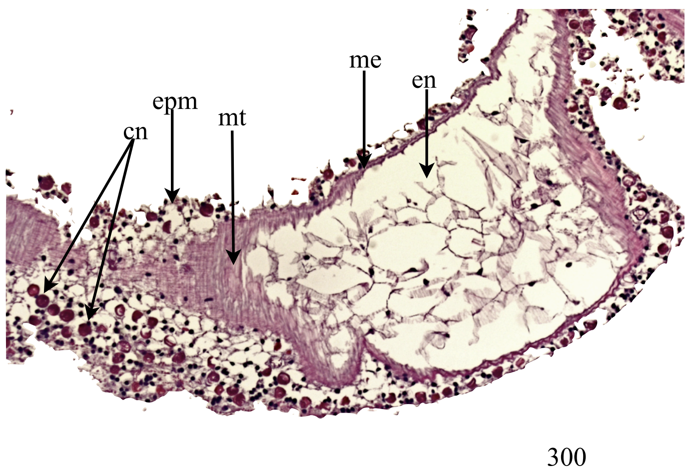


300um

Fig.4. **Basic Mesodermal Anatomies of *Atolla* tentacles.** The figure above is comparing the general anatomies of the hypertrophied, **a-c**, to that of the marginal tentacle, **d-f**. Each column represents the corresponding segment for each tentacle, i.e. **a** and **d** are the distal, **b** and **e** the mid, and **c** and **e** the proximal segments of both the hypertrophied and marginal tentacles from the same individual. The abbreviations are as follows: cn, cnidocytes; epm, epithelial muscular cells; mt, muscle tissue; me, mesoglea; en, endo/gastrodermis.



5a



5b

Tentacle Type	Nematocyst Density
Hypertrophied	42 nem/mm^2
Marginal	226 nem/mm^2

5c

Fig. 5. Comparison of *Atolla* tentacles. The photographs in this figure shows a longitudinal section of a distal segment of the **(a)** hypertrophied and **(b)** marginal tentacles at 20x magnification. Nematocyst densities **(c)** were calculated from similar photographs to be 42 nematocysts/mm^2 for the hypertrophied tentacles and 226 nematocysts/mm^2 for the marginal tentacles. See **Fig.4.** for abbreviations.

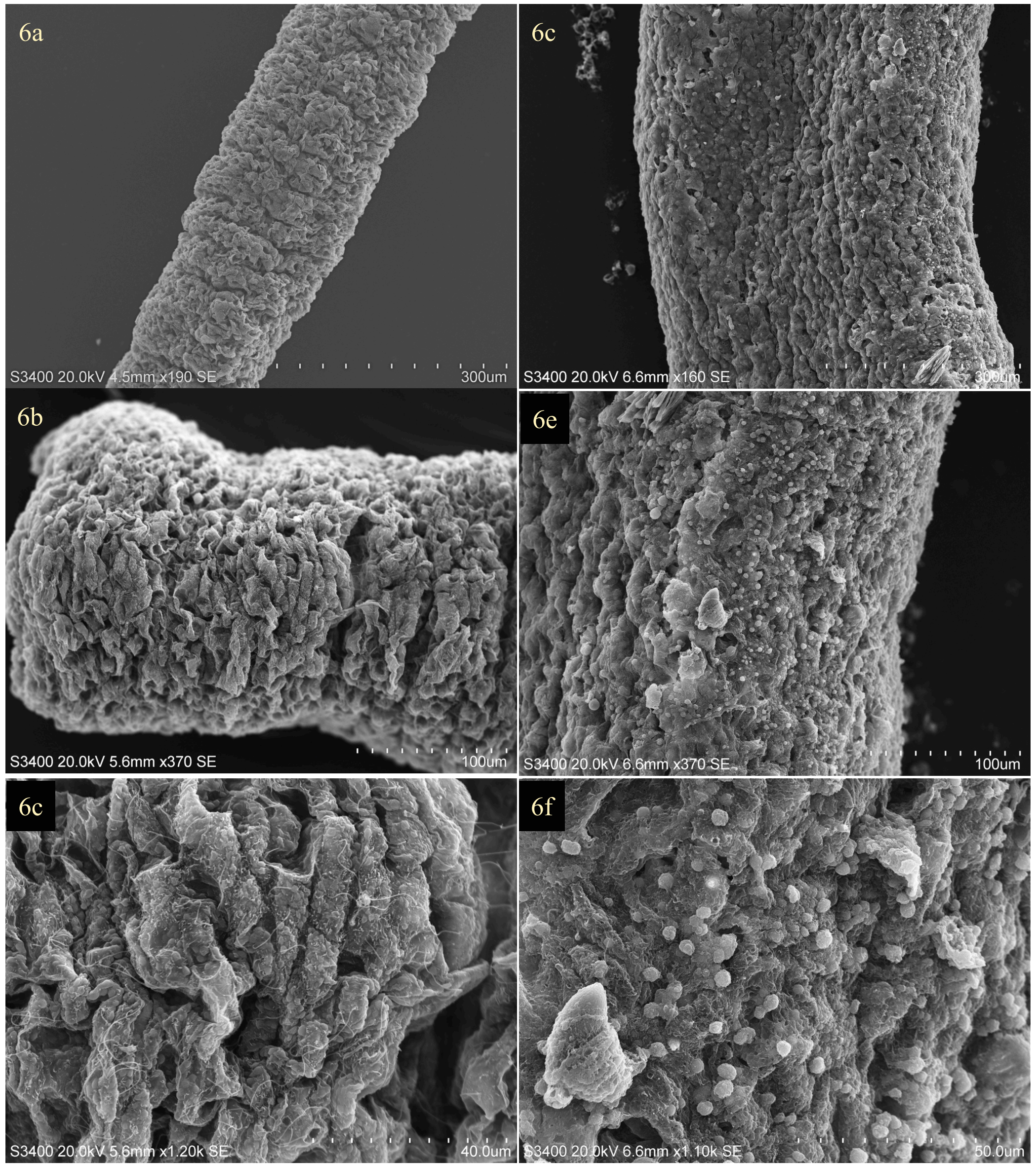


Fig. 6. SEM Ultrastructure of Hypertrophied and Marginal Tentacle. This figure shows both the ultrastructure of the marginal and hypertrophied tentacle, as well as a comparison between similar segments of tentacle types at the same magnification scale. Images 6a-6c are of the hypertrophied tentacle, while images 6d-6f are of the marginal tentacle. The marked differences between the two tentacles are: size, hypertrophied is smaller in width than the marginal, hair-like structures blanketing the hypertrophied, and not the marginal, and the appearance of obtuse spherical structures, likely nematocysts, in abundance on the marginal and not the hypertrophied tentacle.

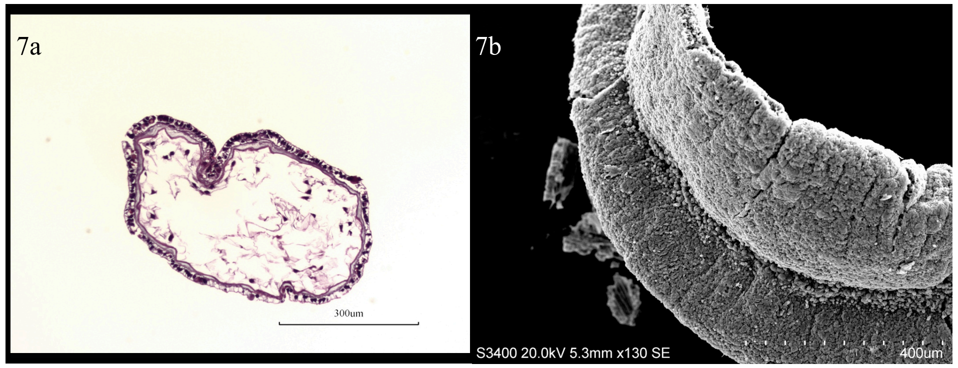


Fig.7. A Groove in the Hypertrophied Tentacle. The cross section basal segment of the hypertrophied tentacle, as shown in image 7a, has a very distinct invagination of the epi- and endodermal tissues, indicating the presence of a groove. This is further supported by the SEM image (7b) of the base of the hypertrophied tentacle on the right.