A New Species of Abyssal Sea Anemone and Its Symbiotic Relationship with a Scaphopod

By

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B.A. University of Kansas, 1993

Submitted to the Department of Systematics and Ecology and the Faculty of the Graduate School of the University of Kansas in partial fulfillment of the requirements for the degree of Master of Arts

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7/8/96
Date thesis accepted

ABSTRACT

In this thesis I report the results of the first study of a symbiosis between an abyssal sea anemone and a scaphopod. I describe the sea anemone as Benthactis nomadas n. g., n. sp.

The sea anemones and scaphopods were collected at a soft-sediment site at 4100 m depth in the northeastern Pacific Ocean. Sea anemones of this species were always attached to a scaphopod shell; thus, I infer that the symbiosis is obligate for the sea anemone. I conclude that the symbiosis is facultative for the scaphopod because 8% of the shells showed no evidence of recent sea anemone attachment.

I infer from sea floor photographs and from the fact that these organisms are trawled that the scaphopods carrying these sea anemones live at or near the surface, an atypical habitat for a scaphopod. I hypothesize that this symbiosis is initiated when a planula larva of Benthactis nomadas, n. g., n. sp. lands on the exposed dorsal tip of a scaphopod shell. The results of a biomechanics experiment I conducted support my hypothesis that as the sea anemone grows, the scaphopod adjusts its position in the sediment because remaining near the surface requires less energy than dragging a sea anemone through the sediment.

Typically, a scaphopod at the sediment surface would be exposed to pelagic and epibenthic predators; I infer that this scaphopod is protected from its predators by the sea anemone. Under the protective shelter of the anemone, the scaphopod can remain at the sediment surface and forage in upper layers of sediment that contain more energy than deeper layers.

The sea anemone also benefits from the symbiosis. It receives an attachment site in an environment where hard substratum is limited, and it may gain increased access to food.

Based on the results of experiments that I conducted and on inferences, I propose that the relationship between the sea anemone and the scaphopod is mutualistic.

ACKNOWLEDGMENTS

I acknowledge the members of my thesis committee for their guidance throughout my years as a graduate student. I thank my major advisor, Dr. Daphne Fautin, for insisting that I meet high standards in every aspect of my project and for exposing a landlubber from Kansas to marine biology. Thanks to Dr. Cynthia Annett for her encouragement and faith in my abilities. I thank Dr. David Alexander for his assistance in designing the biomechanics experiment.

I am greatly indebted to Dr. Kenneth L. Smith, Roberta Baldwin, Lynn Lauerman, and Stace Bealieu of Scripps Institution of Oceanography for collecting the sea anemones and scaphopods that I studied and for generously sharing information about the collection site and the deep sea. Many thanks to Dr. Kenneth L. Smith who gave me the opportunity to visit the deep sea floor in *Alvin* and to Daphne who arranged for me to go on the oceanographic cruise with the Scripps group.

I extend my thanks to Dr. Ron L. Shimek who has shared his knowledge of scaphopod diet, habitat, and lifestyle. I thank Dr. Michael Barfield for his help with data analysis and his patience when he explained statistics to me. Many thanks to the following people for stimulating scientific discussions: David Miles, Steve Swaffar, Marc Branham, Jennifer Hsieh, Jimena Aracena, Dr. William Bell, David Banks, Dr. Mike Tourtellot, and many others.

Many other people have helped me with technical support. Dr. Howard Feldman from the Kansas Geological Survey taught me the art of thin-sectioning. Ken Olson and Bill McGregor in the BioShop fixed the technicon multiple times and provided me with the necessary equipment for the biomechanics experiment. Dr. Kurt Sorensen from the Geography Department provided me with sieves.

The two people who deserve the most gratitude are my husband, Shawn Pagels, and my officemate, Susanne Hauswaldt. Both of them have supported and encouraged me, listened to me rant and rave, and helped me see the humor in the lifestyle of a graduate student. I extend special thanks to Susanne for her countless readings of my thesis and to Shawn for his help with the figures included in this document. Last but not least, I thank my family for instilling in me the love of knowledge and for encouraging me to pursue all of my educational goals.

Financial support of this research was provided by the Panorama Society Small Grant Fund, Natural History Museum, University of Kansas, and the Ida H. Hyde Scholarship, Division of Biological Sciences, University of Kansas.

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CHAPTER 1 - INTRODUCTION

In this thesis I report the results of the first study of a symbiosis between a sea anemone and a scaphopod. Both organisms are new species; the sea anemone Benthactis nomadas n. g., n. sp. is described in this thesis and the scaphopod Fissidentalium n. sp. is being described by R.L. Shimek (pers. comm.).

Sea anemones of many species are involved in symbioses with other animals, such as crustaceans (e.g. Ross, 1971, 1973, 1979; Hand, 1975; Dunn et al., 1980; Brooks, 1988, 1989, 1993; Fautin et al., 1995), fishes (e.g. Fautin, 1986; Fautin and Allen, 1992), and gastropods (e.g. Hand, 1975; Pastorino, 1993; Riemann-Zürneck, 1994). Symbioses between sea anemones and scaphopods are rare; only two sea anemone-scaphopod symbioses have been reported (Riemann-Zürneck, 1973; Shimek and Moreno, 1996). Rarity of such a symbiosis may be because: (1) the infaunal habitat of a typical scaphopod reduces the likelihood of a sea anemone settling on its shell, and (2) the soft-bodied sea anemone would be damaged as the scaphopod burrowed through the sediment.

A sea anemone is a sessile cnidarian that does not possess a hard skeleton and that protects itself from most predators with its nematocysts (i.e. stinging capsules). A scaphopod is a mollusk distinguished by a slightly curved, conical, aragonitic shell that is open at both ends. The broad end of the shell is defined as ventral; the narrow end is dorsal. Typically, scaphopods are positioned with the concave surface of the shell uppermost and the ventral end deeper in the sediment than the dorsal (Dinamani, 1964; Trueman, 1968). Scaphopods can adjust their position in the sediment to locate prey, typically foraminiferans (Gainey, 1972; Taib, 1980; Shimek, 1989), to avoid predators (Shimek, 1989), and to flush their mantle cavities (Yonge, 1937; Shimek, 1989; Shimek and Steiner, in press). When a scaphopod flushes its mantle cavity, its dorsal end protrudes through the sediment (Yonge, 1937; Shimek, 1989, Shimek and Steiner, in press). Broken dorsal tips of collected scaphopods indicate that predation attempts by epibenthic and/or pelagic organisms, such as grenadier fish, occur when shells are partially exposed (Shimek, 1989).

Specimens of *Benthactis nomadas* n. g., n. sp. and scaphopods *Fissidentalium* n. sp. were among benthic organisms collected as part of a study conducted by Dr. Kenneth Smith, Scripps Institution of Oceanography at an abyssal soft-sediment site (designated Station M) in the northeastern Pacific Ocean (Figure 1). Typical of the deep sea, the collection site is a high-pressure, low-temperature, low-energy environment. It is not near hydrothermal vents nor cold seeps where chemosynthesis might occur; therefore, there is no primary production. Food arrival at the sea floor fluctuates spatially and temporally because food sources must originate in the upper layers of the ocean, then sink (Hinga et al., 1979; Smith et al., 1994). Researchers such as Smith and Brown (1983), Wilson and Smith (1984), Grassle (1991), Snelgrove et al. (1992), and Smith et al. (1993, 1994) have found that scarcity and patchy distribution of food influence the diversity, density, and behavior of deep-sea organisms.

1980). Thus, potential attachment sites for sessile organisms are absent at Station M.

During the six-year ecological study at Station M, Smith and colleagues trawled benthic organisms three or four times per year (Table 1) when they assessed physical, chemical, and biological parameters with water samples, sediment cores, and in-situ respirometers (Smith et al., 1993, 1994; Lauerman et al., in press). They also observed the benthic community via camera sled photographs, time-lapse photographs, and a manned submersible.

In photographs, individuals of Benthactis nomadas n. g., n. sp. appear to be making trails in the sea floor sediment (Figure 2). After examining the trawled organisms, I infer that the sea anemone leaving the trail is the one attached to a scaphopod shell. The shell is only occasionally observed in photographs (Lauerman et al., in press). Based on camera-sled photographs from nine transects, the density of these sea anemones ranged from 12 to 250/10^4 m^{-2}, with a mean of 156 (Lauerman et al., in press).

Another factor which may influence the diversity, density, and behavior of deep-sea organisms is water chemistry. Most deep sea water is undersaturated with respect to calcium carbonate ($CaCO_3$) (Berger, 1976; Chen, et al., 1988). In the Pacific Ocean, the lysocline, defined as a depth at which there is a “marked increase in the rate of carbonate dissolution” (Berger et al., 1982, p. 249), is at an average depth of 3000 m (Berger, 1976). This dissolution makes it difficult for deep-sea organisms that secrete calcium carbonate to lay down shells (Nybakken, 1988). This is especially true for organisms like scaphopods, which use aragonite, a crystal form of $CaCO_3$ more soluble than calcite.

Below the lysocline exists the calcium carbonate compensation depth (CCD), a depth at which dissolution of $CaCO_3$ equals its rate of supply (Edmond and Gieskes, 1970; Berger, 1976; Berger et al., 1982). In the Pacific, at the latitude of Station M, the average depth for the CCD is 4100 m (Grotsch et al., 1991). Calcareous shells or skeletons that sink below this depth dissolve as a result of the solubility of $CaCO_3$ (Belyaeva, The total number of scaphopod shells collected in 30 trawls was 257. The number per trawl ranged from 1 to 18, with a mean of 8.6. Sea anemones were attached to 62% of the scaphopod shells, 30% of the scaphopod shells showed evidence of previous sea anemone attachment, and 8% showed no evidence of recent sea anemone attachment (Table 1; Figure 3). I infer that the symbiosis is facultative for the scaphopod because 8% of the scaphopods showed no sign of recent sea anemone attachment. The symbiosis appears to be obligate for Benthactis nomadas n. g., n. sp.; it was never collected alone nor attached to any other substratum.

Each sea anemone is attached by its pedal disk to the concave surface of a scaphopod shell. Unless the sea anemone is small, the pedal disk typically wraps around the shell, covering the entire circumference of the shell at the dorsal end and 270° near the ventral end (Figure 4); this exposes a triangular shaped portion of the shell on the convex surface (Figure 3B). This pattern of coverage can be seen on some scaphopod shells without an attached sea anemone as well because a brown residue (scar) is left by the sea anemone (Figure 3B). The scar may consist of remnants of the pedal disk and/or chitin secreted by the sea anemone. Sea anemones of several species, such as *Adamsia* (Gosse, 1858) and *Stylobates* (Dunn and Liberman, 1983), secrete chitin.

After evaluating several possible advantages and disadvantages, I hypothesize that the symbiosis between the sea anemone *Benthactis nomadas* n. g., n. sp. and the scaphopod *Fissidentalium* n. sp. is mutualistic. The sea anemone benefits by receiving an attachment site in an environment where hard substratum is limited and by gaining increased access to food. In return, under the protective shelter of the sea anemone, the scaphopod can leave its infaunal habitat and forage in upper layers of sediment that contain more energy than deeper layers (Smith et al., 1994).

CHAPTER 2 - TAXONOMY

The abyssal sea anemone collected on the shell of Fissidentalium n. sp. belongs to a new genus and a new species in the family Actinostolidae. I am naming it Benthactis nomadas.

Materials And Methods

Specimens

Collections of epibenthic megafauna were made with an otter trawl (5-m foot rope; 3.8-cm stretch mesh with 1.3-cm mesh cod-end liner) (Smith et al., 1993, 1994; Lauerman et al., in press). Some scaphopods and sea anemones were fixed in 10% buffered formalin immediately after collection and later transferred to 70% EtOH; others were preserved only in 70% EtOH.

I borrowed specimens collected on cruises 1-10 from the Los Angeles County Museum of Natural History (LACM catalog numbers 89-137.8, 89-147.5, 90-162.3, 90-163.2, 90-164.2, 91-40.3, 91-41.2, 91-130.1, 91-131.1, 91-132.1, 91-133.1, and 91-134.1). Scaphopods collected on cruises 11-15 and most of the scaphopods and sea anemones from cruises 16-19, 21, and 24 will be deposited in LACM. Sea anemones collected on cruises 11-15 and selected specimens from cruises 16-19, 21, and 24 will be deposited in The University of Kansas Natural History Museum (KUNHM). All scaphopods and sea anemones collected on cruises 20, 22, 23, 25, and 26 will be deposited in KUNHM.

Histology

Thirty-six sea anemones attached to scaphopod shells (collected on cruises 15 through 21) were cut in half longitudinally through the center of the contracted oral disk. The half on the dorsal end of the scaphopod shell was left attached for use in cnidae measurements and dissection. The half on the ventral end of the scaphopod shell was removed for histology. Five whole anemones (from various cruises) were also used for histology. The pedal disk typically remained attached to the shell when the sea anemone was removed. Sea anemones were embedded in Paraplast® (melting point 56°C); 8 μm longitudinal sections or 10-20 μm cross sections were stained with hematoxylin and eosin (Humason, 1979).

Cnidae

Tissue for cnidae squashes was taken from the mesenterial filaments, actinopharynx, tentacle tips, and oral and aboral sides of the tentacle bases. Specimens lacked column ectoderm, a common condition in sea anemones collected from the deep sea (Carlgren 1928, 1956; Fautin and Hessler, 1989; Riemann-Zürneck, 1993, 1994). Cnidae were studied with differential interference contrast optics; measurements are of undischarged capsules in squash preparations.

Benthactis, new genus

Definition

Actinostolidae with well developed, broad pedal disk. Column smooth. Mesogleal sphincter strong; tentacles can be completely covered when animal contracts. All tentacles of uniform thickness and length, without nematocyst batteries. Longitudinal muscles of tentacles and radial muscles of oral disk ectodermal. Mesenteries not arranged according to Actinostola-rule. More mesenteries proximally than distally; 12 pairs of mesenteries perfect and fertile. Cnidom: spirocysts, basitrichs, microbasic *p*-mastigophores.

Type species: Benthactis nomadas, n. sp.

Etymology

The name Benthactis is a composite of "benthos," which is Greek for depths of the sea (Jaeger, 1931) and refers to the habitat of this sea anemone, and "actis," which is Greek for ray (Jaeger, 1931) and is used in the name of many actinians. Its gender is feminine.

Differential diagnosis

The family Actinostolidae currently includes 22 genera (Fautin and Hessler, 1989). The new genus Benthactis differs from Actinostola, Antholoba, Anthosactis, Antiparactis, Cnidanthea, Cnidanthus, Epiparactis, Hadalanthus, Hormosoma, Isoparactis, Marianactis, Ophiodiscus, Parasicyonis, Paractinostola, Pycnanthus, Sicyonis, Stomphia, Synsicyonis, and

Tealidium in a combination of the following diagnostic characters: mesenteries not arranged according to the Actinostola-rule, longitudinal muscles of the tentacles and radial muscles of the oral disk ectodermal, 12 perfect pairs of mesenteries, no nematocyst batteries or microbasic *p*-mastigophores in the tentacles.

The genera most similar to Benthactis are Bathydactylus, Paranthus, and Pseudoparactis. Benthactis has hexamerously arranged mesenteries; Bathydactylus does not. The column of Paranthus is divided into a scapulus and a capitulum; that of Benthactis is not. Benthactis has more mesenteries proximally than distally; Pseudoparactis has more mesenteries distally than proximally.

Benthactis nomadas, n. sp.

Description:

Column

Freshly collected and preserved specimens white. Column smooth; ectoderm sloughed off in collected specimens (Figure 5).

Sphincter

Mesogleal. Thick at margin, without external evidence of projecting wall. Typically long and tapered at proximal end (Figure 6A, 6B) but truncated in others (Figure 6C); centered in mesoglea although closer to either side in some; muscle bundles dense and arranged transversely in most (Figure 6A, 6C), scattered in others (Figure 6B); variability in appearance may be related to state of contraction or angle of section.

Pedal disk

Broad; well-developed; wrapped around shell of scaphopod Fissidentalium n. sp. (Figure 5). Maximum diameter of pedal disk ranges from 5 to 65 mm, median 44; never greater than length of scaphopod shell. Midway along scaphopod shell, pedal disk typically covers 3/4 circumference of shell; coverage increases at dorsal end of shell, decreases at ventral end. Secretes brown cuticle onto scaphopod shell.

Oral disk and tentacles

Oral disk not visible in specimens examined due to contracted state. Radial musculature of oral disk and longitudinal musculature of tentacles ectodermal (Figure 7). Tentacles conical or flattened depending on condition of animal; not thickened at base. Tentacle length uniform within an individual; range from 2 to 5 mm. Ratio of number of tentacles to number of mesenteries variable; range from 0.5:1 to 1:1, mean 0.7:1.

Mesenteries and internal anatomy

Mesenteries arranged hexamerously in 3 cycles; first 2 cycles, including directives, perfect, fertile, and filament-bearing; mesenteries in third cycle weak, sterile. More mesenteries proximally than distally. Tertiary mesenteries develop asynchronously; either not all pairs of tertiary mesenteries present or not all reach distal portion of animal. Retractor muscles diffuse.

Sexes separate; 6 males, 1 female observed. Range of minimum and maximum diameter of sperm packets (n = 45) 34 x 36 µm-175 x 132 µm. In large packets, cells in various stages of spermatogenesis layered with spermatozoa in center. Maximum and minimum diameters of eggs with visible nucleus (n=3) 85 x 16 µm, 99 x 47 µm, 109 x 28 µm.

Cnidom

Spirocysts, basitrichs, and microbasic *p*-mastigophores (Table 2, Figure 8).

Etymology

The specific epithet nomadas is derived from the Greek word "nomad," meaning wanderer (Jaeger, 1931), and was inspired by the nickname “crawling white anemone” bestowed on this sea anemone by Lynn M. L. Lauerman, graduate student at Scripps Institution of Oceanography. Its gender is feminine.

Type locality and specimens

Holotype : A male cut longitudinally at its margin through the sphincter (KUNHM 01019) with histological sections (5 slides); collected 7 November 1993.

Type locality: 34°42'N, 123°08'W; depth 4100 m.

Paratypes : United States National Museum of Natural History (USNM 96574), one specimen (male) with histological sections (5 slides) collected from 34°41'N, 123°11'W at 4100 m on 10 February 1994.

California Academy of Sciences (CASIZ 106264), one specimen (male) with histological sections (5 slides) collected from 34°46'N, 123°08'W at 4100 m on 17 October 1992.

Royal British Columbia Museum (RBCM996-24-1), one specimen (female) with histological sections (5 slides) collected from 34°43'N, 123°06'W at 4100 m on 19 July 1993 and (RBCM996-25-1) one specimen collected from 34°40'N, 123°03'W at 4100 m on 1 May 1995.

Santa Barbara Museum of Natural History (SBMNH 143214), one specimen with histological sections (5 slides) collected from 34°45'N, 123°02'W at 4100 m on 24 February 1993.

LACM (92-113.1), one specimen with histological sections (5 slides) collected from 34°46'N, 123°08'W at 4100 m on 17 October 1992.

Discussion

Due to the contracted state and the morphology of the sea anemone, I was unable to determine number of siphonoglyphs, arrangement of tentacles, and structure of parietobasilar muscles. Tentacles and gametes are easily damaged or detached, which may explain the variation in number present and variation in their apparent arrangement.

CHAPTER 3 - SYMBIOSIS

INTRODUCTION

Symbiosis literally means "living together," and describes a close association between organisms of two unrelated species without any implication of the nature of the relationship (Henry, 1966; Cheng, 1970, 1991; Toft, 1991). I evaluated several aspects of the symbiosis between Benthactis nomadas and Fissidentalium n. sp. and concluded that it is a mutualistic relationship.

To determine the prevalence of this symbiosis, I needed to establish whether scarred shells and bare shells exist in the deep sea or are a result of the sea anemone being torn off during the trawling process. If scars remain on scaphopod shells for a long time, I could infer from the bare shells collected that scaphopods are able to survive without a sea anemone. I subjected scarred shells to museum conditions or simulated deep sea conditions to determine how long the scars remain on shells. I chose to test museum conditions to determine if the scar was affected by temperature. Because many of the shells had been housed at LACM for several years prior to my study, I wanted to be confident that I had not misclassified shells that originally had scars as bare shells.

I investigated several possible advantages and disadvantages for the anemones and scaphopods. Possible advantages of the symbiosis for Benthactis nomadas are an attachment site and increased access to food. Increased access to food may be achieved by resuspension of food particles as the scaphopod moves through the sediment and/or by the increased area of sea floor from which the sea anemone can collect prey. Such benefits have been proposed for sea anemones that are carried by a hermit crab or snail (Ross, 1971; Dunn et al., 1980; Chintiroglou and Koukouras, 1991; Riemann-Zürneck, 1994).

Possible disadvantages for the sea anemone are that it may be damaged if it is dragged through the sediment. Another disadvantage is that if the symbiosis is obligate, the sea anemone will die when the scaphopod dies.

The symbiosis may benefit the scaphopod in several ways. Cnidarians protect their symbiotic partners from predators (e.g.

Ross, 1971; Brooks, 1988; Fautin and Allen, 1992; Riemann-Zürneck, 1994). The protective presence of the sea anemone may allow the scaphopod to live in the upper layers of the sediment without risk of predation. Living near the sediment surface would be beneficial to the scaphopod because the upper layers of sediment are energy-rich compared to deeper layers (Figure 9) (K.L. Smith, unpubl. data).

Another possible advantage to the scaphopod is protection from shell dissolution. I hypothesized that the sea anemone insulates the shell from the sea water, which is undersaturated with respect to $CaCO_3$. Evidence that organisms have difficulties secreting $CaCO_3$ at this depth are the thin skeletons of the sea urchin Echinocrepis and of the solitary coral Fungicyathus collected at Station M (pers. obs.). If my hypothesis were correct, I predicted that the scaphopods with attached sea anemones would be longer than those without sea anemones and that the portion of shell covered by the sea anemone would be thicker than the exposed portion. To test these hypotheses, I compared the lengths of scaphopod shells that had attached sea anemones, were scarred, and were bare, and I measured shell thickness in thin-sections of scaphopod shells.

A possible disadvantage for the scaphopod is that carrying a sea anemone requires more energy than is otherwise needed for the scaphopod to move. Assuming that energy is proportional to force, I designed an experiment to determine if moving a scaphopod shell with an attached sea anemone model, either contracted or expanded, required more force than moving a bare shell through the sediment. I expected that it requires more energy for a scaphopod to drag a sea anemone through the sediment than to move at the surface of the sediment.

Another aspect of the symbiosis I addressed was how a relationship between these organisms could be initiated. Although scaphopods are typically infaunal, I infer from the collection method and sea floor photographs that those with attached sea anemones live near the surface of the sediment. I hypothesized that a planula larva of Benthactis nomadas lands on the exposed dorsal tip of a scaphopod shell. To test this hypothesis, I determined whether there was a correlation between the maximum diameter of the pedal disk of a sea anemone and its position on a scaphopod shell. I expected to find smaller sea anemones closer to the dorsal end of the scaphopod shell. I predicted that after the sea anemone attaches, the scaphopod adjusts its position in the sediment to avoid the increased energetic demands of dragging the sea anemone through the sediment.

MATERIALS AND METHODS

Measurements

Figure 10 illustrates the measurements I made: the maximum diameter of the pedal disk of a sea anemone (A), the distance from the center of its contracted oral disk to the ventral end of the scaphopod shell (B), shell length (C), and the diameter of ventral end of the shell (D). I compared the length of scaphopod shells (C) among the three categories of shells using a Kruskal-Wallis test (Sokal and Rohlf, 1981).

I tested for a correlation between maximum diameter of sea anemone pedal disk (A) and scaphopod shell length (C) using a product-moment correlation (Sokal and Rohlf, 1981).

I also tested for a correlation between maximum pedal disk diameter (A) and the position of the anemone on a scaphopod shell (Sokal and Rohlf, 1981). To account for size differences of scaphopod shells, the position of the sea anemone on the shell was normalized by dividing the distance from the center of its contracted oral disk to the ventral end of the shell (B) by the length of the scaphopod shell (C).

Scar Duration

To conduct this experiment, I used 15 scarred scaphopod shells and created nine more by peeling off sea anemones. I filled the shells with modeling clay to reduce contact of water and sediment with the inside of the shell and to strengthen the shells.

Sediment collected from Potter's Lake, University of Kansas, was strained through a 6.5 mm^2 mesh and drained. To six of the 12 jars, I added 250 ml of sediment and 200 ml of artificial sea water (Instant Ocean®); to the other six, I added 250 ml of sediment and 200 ml of a 1% formalin/sea water solution to inhibit microbial activity. Three jars containing sea water and formalin and three without formalin were maintained at 8°C to simulate deep sea conditions; the other six jars were maintained at 21°C. Two scaphopod shells, one that had been fixed in formalin and kept in 70% EtOH and one that had been preserved only in 70% EtOH, were placed in each jar. Shells were either placed on top of the sediment, buried in the sediment, or buried and moved through the sediment twice a week, so that each treatment was combined with all possible combinations of sediment type and temperature.

All scaphopod shells were examined and photographed weekly for six weeks, then at 2 months, at 4 months, and at 7 months. Any reduction in scar coverage or darkness was noted.

Thin-sections

Scaphopod shells were vacuum-embedded and 30 μm thin-sections were made by Spectrum Petrographics, Inc. (Winston, OR). Thin-sections were made from undamaged scaphopod shells that were partially covered by a sea anemone or a scar, or that were bare.

I selected eight shells that had an attached sea anemone, four with scars, and three controls that were bare. I removed scaphopod bodies and sea anemones, if any, from each shell and marked with permanent red ink the area of the shell that had been covered by the sea anemone or scar. So that the thin-section included covered and exposed shell and to standardize the position of the thin-section on shells of different sizes, thin-sections were made at one-third of the total shell length from the ventral end (Figure 4). There were two exceptions: (1) one shell was sectioned at a position that had been completely covered by a sea anemone, and (2) one shell was sectioned at one-fourth of the total shell length from the ventral end to ensure a position of partial coverage. Two shells were thin-sectioned at two-thirds as well as one-third of the way along the shell.

Using bright-field microscopy at 20X, I measured shell thickness in the center of the covered portion of the shell (A)

(Figure 4a), the concave surface of the shell that had presumably been covered longest by the sea anemone. I also measured shell thickness at a position diametrically opposite, in the exposed portion, on the convex surface (B). On shells that were bare or had been completely covered with a sea anemone, I measured shell thickness in comparable positions -- at the point of maximum concavity and convexity.

In addition to a single measure of thickness, I compared, by means of a proxy, total amounts of shell underlying the sea anemone and in the exposed portion in the thin-section. I projected an enlarged image of the thin-section onto matte board, traced the shell outline, then cut the covered portion of the shell model from the exposed portion (Figure 4b). On shells that were bare or completely covered by a sea anemone, a 270° portion of the thin-section model, centered at A, was cut for comparison with the covered portion of other shell thin-sections based on the average coverage of a sea anemone or scar on other shells (Figure 4b). I weighed each portion on an electronic balance and normalized the weight by dividing it by the length of the inner perimeter of the shell in that portion. The ratios of normalized weights of the covered and exposed portions of each shell were analyzed with the Sign Test (Samuels, 1989).

Biomechanics Experiment

I used scaphopod shells and silicon models of sea anemones to measure the amount of force required to move a scaphopod with or without an attached model sea anemone through sediment and at the surface of the sediment. Ten scaphopod shells and one plastic model of a shell were filled with modeling clay to simulate the scaphopod body, to increase the strength of the shell, and to prevent the shell from floating. I modeled the sea anemone of silicon sealant because it is approximately the density of a sea anemone. A contracted sea anemone was represented by a small mound of silicon sealant; an expanded sea anemone was represented by a large cylindrical mound of silicon sealant covering the entire length of the scaphopod shell. In both models, I wrapped a thin layer of silicon sealant around the shell to represent the pedal disk of the sea anemone (Figure 11).

Sediment collected from Clinton Lake (Lawrence, KS) was sieved to a particle size less than 0.053 mm to equal that at Station M and placed in a plastic trough. A scaphopod shell was placed on top of the sediment or buried 2.5 cm deep in the sediment and attached with fishing line to a spring scale (Chatillon, 500g or Ohaus, 200g) that was attached to an electric motor (Figure 11). As the motor wound the string at a rate of 3 cm/sec, the spring scale recorded the maximum force required to pull the shell. All shells were tested five times without an attached sea anemone in the sediment and at the surface of the sediment. I added a contracted sea anemone model to all of the shells and repeated the experiment. The experiment was done again after I had replaced the contracted sea anemone model on all shells with an expanded sea anemone model. The forces required for each position and shell status were compared using the following nonparametric statistics (Sokal and Rohlf, 1981): multiple comparisons by STP, Kruskal-Wallis Test, and Mann Whitney *U*-test.

RESULTS

Measurement

Scaphopod shells that were broken or sea anemones with pedal disks bunched at either or both ends of the scaphopod shell were not measured. Depending on the aspect of the symbiosis being studied, sample size varied. A total of 257 scaphopod shells were collected and categorized but only 253 were measured; 161 shells had sea anemones, but only 150 of those shells were measurable.

The mean length of the scaphopod shells with an attached sea anemone, shells with scars, and bare shells (Table 3) does not differ significantly (Kruskal-Wallis, $p = 0.18$).

There is a positive correlation between maximum pedal disk diameter of sea anemone and scaphopod shell length ($n = 150$, $r = 0.66$, $p < 0.01$) (Figure 12). The maximum diameter of the pedal disk of the sea anemone is never greater than the length of the scaphopod shell to which it is attached but they are commonly equal.

A correlation exists between sea anemone size and its position on the shell ($n = 150$, $r = -0.29$, $p < 0.01$) largely due to the fact that when the sea anemone covers the entire length of the scaphopod shell, the oral disk is centered midway along the scaphopod shell (Figure 13). Excluding sea anemones that cover the entire length of the scaphopod shell, no correlation exists between size of sea anemone and its position on the scaphopod shell ($n = 40$, $r = -0.1$, $p > 0.05$) (Figure 13).

Scar duration

Less than 24 h after I filled the jars with sediment and sea water, water and surface sediment turned black and an orange film covered the surface of the water in four jars. I replaced the water in these jars. During the experiment, a similar reaction gradually occurred in three other jars, but I did not replace the water. As a result of this reaction, some of the shells stained black, but the scars were still visible.

The scars in all treatments showed no visible reduction in coverage area or intensity during the 7-month experiment.

Thin-sections

Shell thickness ranged from 189 μm to 479 μm, with a mean of 309 μm. Ratio of shell thickness in covered portion of thin-section to exposed portion is presented in Table 4.

Shell thickness measured at one location in the covered portion of the scaphopod shell (A) is not significantly different from shell thickness in the exposed portion (B), nor is there a significant difference in shell thickness when considering the total amount of shell in the covered and exposed portions (Table 4) (Sign Test, $p > 0.20$).

Biomechanics Experiment

The force required to move a bare shell, a shell with a contracted sea anemone model, and a shell with an expanded sea anemone model through the sediment (Table 5) differed significantly (Kruskal-Wallis, $p < 0.001$). Using the STP test, I found that the force required to move a bare shell is significantly different from that required to move a shell with either a contracted or an expanded sea anemone model ($p < 0.05$). The force required to move a bare shell or a shell with an expanded sea anemone on the sediment surface did not differ statistically (Mann-Whitney, $p > 0.10$), but there was a significant difference between the force required to move a shell with an expanded sea anemone and a shell with a contracted sea anemone (Mann-Whitney, $p < 0.001$). I used two different scales because at low force levels, such as those required to pull a bare shell at the sediment surface, the limit of resolution of the 500 g scale was too high to obtain accurate measurements.

DISCUSSION

I conclude that the symbiosis is obligate for _Benthactis nomadas_ because no individuals of this sea anemone are collected alone nor on other hard substrata. I infer that the symbiosis is facultative for the scaphopod because scaphopods are collected that show no sign of recent sea anemone attachment.

Considering the chemical conditions of deep sea water, I expected that the presence of the sea anemone would insulate the scaphopod shell from sea water undersaturated with respect to

$CaCO_3$. As I hypothesized, the effect of the solubility of $CaCO_3$ at this site is pronounced; shells of individuals of Fissidentalium n. sp. are 2-3 times thinner than the shells of F. erosum, a species collected at 3000-3300 m. However, contrary to my expectations, shells with attached sea anemones are neither longer than those without sea anemones nor thicker in portions covered by a sea anemone.

Because the sea anemones can be seen in sea floor photographs and because the trawl used to collect these organisms bites into the sediment only 2 to 3 cm, I infer that individuals of Fissidentalium n. sp. are living at or near the surface. The energetic demands of dragging a sea anemone may cause the scaphopod carrying a sea anemone to live in the upper layers of the sediment rather than infaunally. As demonstrated by the biomechanics experiment, there is a difference in the amount of force required to drag a bare shell or a shell with an attached sea anemone through the sediment; absolute values may differ from live animals because a scaphopod moves more slowly and may balance itself differently than the model scaphopod.

Although I had a subjective impression that more small sea anemones attach to the dorsal end of a scaphopod shell (Figure 14) than to the ventral end, no correlation exists between size of sea anemone and its position on a scaphopod shell. Observations of living animals would be required to find an explanation for this discrepancy. A planula larva may land on the dorsal end of a scaphopod shell, but rapidly move to the center of the shell for balance. Brooks (1989) found that balance was an important factor for hermit crabs that actively position the sea anemones on their shell.

Limitations to study

Studying deep-sea organisms is challenging. Inferences about the benthic community may be erroneous if based on trawled specimens because the quantity and diversity of organisms collected in this manner is not necessarily representative of the community (Gage and Tyler, 1991; Lauerman et al., in press). Sea floor photographs offer information unobtainable from trawled specimens, but photographs can be hard to interpret (Gage and Tyler, 1991; Smith et al., 1993; Lauerman et al., in press). An example of the discrepancy between the two collecting methods is that the average density of sea anemones attached to a scaphopod shell is $156/10^4$ m^{-2} when based on camera-sled photographs (Lauerman et al., in press) but $34/10^4$ m^{-2} when inferred from number of specimens per estimated area trawled. I suspect that the estimate based on trawled specimens is low because scaphopods may slip through the holes of the net, yet the estimate based on photographs may be high because other organisms may be misidentified as Benthactis nomadas.

The symbiosis of Benthactis nomadas and Fissidentalium n. sp. offers a concrete example of a relationship between two deep-sea organisms. However, I was able to test only some advantages and disadvantages proposed for this symbiosis; some advantages and disadvantages can only be inferred.

In-situ observation of the burrowing behavior of the scaphopod and the feeding behavior of the sea anemone would be necessary to support some of the proposed advantages to each organism involved in this symbiosis. I could also test the protective abilities of the sea anemone against predators of the scaphopod if the animals survived being trawled from the deep sea.

Although the shells are not thicker underneath a sea anemone, it may take less energy for the scaphopod to lay down and maintain the shell when the sea anemone is insulating the shell from the $CaCO_3$ undersaturated sea water. If I had live animals, I could test this hypothesis by measuring the metabolic rates of scaphopods with sea anemones and without sea anemones.

Conclusion

Individuals of the abyssal sea anemone Benthactis nomadas are found only on the shells of scaphopods Fissidentalium n. sp. I propose that a larva of the sea anemone attaches to the exposed portion of a scaphopod shell. As the sea anemone grows, the scaphopod remains in the upper layers of the sediment because it requires less energy than dragging the sea anemone through the sediment. The symbiosis could be classified as commensal or as a parasitism if these were the only two results.

However, I propose that the relationship between these two organisms is mutualistic. In addition to an attachment site, I hypothesize that the sea anemone has increased access to food as a result of its association with a scaphopod.

I infer that these scaphopods are living at or near the surface because they are carrying a sea anemone. I propose that the energetic costs of dragging a sea anemone are minimal when compared to the amount of energy that is available to the scaphopod when they are able to live and forage in the energy-rich upper layers of sediment (Figure 9) because of the protection afforded by the sea anemone.

LITERATURE CITED

Belyaeva, N.V. 1980. Position of foraminiferal lysocline in various zones of the Pacific. Lithology and Mineral Resources (USSR) **15(2)**: 11-17.

Berger, W.H. 1976. Biogenous deep-sea sediments: production, preservation and interpretation. **In**: Riley, J.P. and R. Chester, editors. Chemical Oceanography, Volume 5. 2nd ed. London: Academic Press. p. 265-338.

Berger, W.H., M.C. Bonneau, and F.L. Parker. 1982. Foraminifera on the deep-sea floor: lysocline and dissolution rate. Oceanologica Acta **5(2):** 249-258.

Brooks, R.W. 1988. The influence of the location and abundance of the sea anemone Calliactis tricolor (Le Sueur) in protecting hermit crabs from octopus predators. Journal of Experimental Marine Biology and Ecology **116**: 15-21.

Brooks, R.W. 1989. Hermit crabs alter sea anemone placement patterns for shell balance and reduced predation. Journal of Experimental Marine Biology and Ecology **132**: 109-121.

Brooks, R.W. 1993. Protection of symbiotic cnidarians by their hermit crab hosts: evidence for mutualism. Symbiosis **15**: 1-13.

Carlgren, O. 1928. Actiniaria der Deutschen Tiefsee-Expedition. Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition **12**: 126-266.

Carlgren, O. 1956. Actiniaria from depths exceeding 6000 meters. Galathea Report **2:** 9-16.

Chen, C.T.A., R.A. Feely, and J.F. Gendron. 1988. Lysocline, calcium carbonate compensation depth, and calcareous sediments in the North Pacific Ocean. Pacific Science **42(3/4):** 237-252.

Cheng, T.C. 1970. Symbiosis: Organisms Living Together. New York: Western Publishing Company, Inc. 250 pp.

Cheng, T.C. 1991. Is parasitism symbiosis? **In:** Toft, C.A., A. Aeschelimann, L.Bolis, editors. Parasite-Host Associations; Coexistence or Conflict? New York: Oxford University Press. p. 15-36.

Chintiroglou, C. and A. Koukouras. 1991. Observations on the feedings habits of Calliactis parasitica (Couch, 1842), Anthozoa, Cnidaria. Oceanologica Acta **14(4):** 389-396.

Dinamani, P. 1964. Burrowing behaviour of Dentalium. Biological Bulletin **126:** 28-32.

Dunn, D.F., D.M. Devaney, and B. Roth. 1980. Stylobates: a shell-forming sea anemone (Coelenterata, Anthozoa, Actiniidae). Pacific Science **34(4):** 379-388.

Dunn, D.F. 1982. Paraphelliactis pabista, a new species of hormathiid sea anemone from abyssal northeastern Pacific waters (Coelenterata: Actiniaria). Syesis **15:** 51-56.

Dunn, D.F. and M.H. Liberman. 1983. Chitin in sea anemone shells. Science **221:** 157-159.

Edmond, J.M. and J.M.T.M. Gieskes. 1970. On the calculation of the degree of saturation of sea water with respect to calcium carbonate under in situ conditions. Geochimica et Cosmochimica Acta **34**: 1261-1291.

Fautin, D.G. 1986. Why do anemonefishes inhabit only some host actinians? Environmental Biology of Fishes **15(3):** 171-180.

Fautin, D.G. and R.R. Hessler. 1989. Marianactis bythios, a new genus and species of actinostolid sea anemone (Coelenterata: Actiniaria) from the Mariana vents. Proceedings of the Biological Society of Washington **102(4):** 815-825.

Fautin, D.G. and G.R. Allen. 1992. Field Guide to Anemonefishes and Their Host Sea Anemones. Perth: Western Australian Museum. 157 pp.

Fautin, D.G., C.-C. Guo, and J.-S. Hwang. 1995. Costs and benefits of the symbiosis between the anemoneshrimp Periclimenes brevicarpalis and its host Entacmaea quadricolor. Marine Ecology Progress Series **129:** 77-84.

Gage, J.D. and P.A. Tyler. 1991. Deep-Sea Biology: A Natural History of Organisms at the Deep-Sea Floor. Cambridge: Cambridge University Press. 504 pp.

Gainey, L.F., Jr. 1972. The use of the foot and the captacula in the feeding of Dentalium (Mollusca: Scaphopoda). Veliger **15(1):** 29-34.

Gosse, P.H. 1858. On the nature of the sub-basal membrane of Adamsia palliata. Annals and Magazine of Natural History, Series 3 **2(8):** 107-108.

Grassle, J. F. 1991. Deep-sea benthic biodiversity. BioScience **41(7):** 464-469.

Grotsch, J., G. Wu, and W. H. Berger. 1991. Carbonate cycles in the Pacific: reconstruction of saturation fluctuations. **In:** Goldberg, E. D., editor. The Sea. Berlin: Springer-Verlag. p. 110-125.

Hand, C. 1975. Behaviour of some New Zealand sea anemones and their molluscan and crustacean hosts. New Zealand Journal of Marine and Freshwater Research **9(4):** 509-527.

Henry, S.M. 1966. Symbiosis. Volume 1, Associations of Microorganisms, Plants, and Marine Organisms. New York and London: Academic Press. 478 pp.

Hinga, K.R., J.McN. Sieburth, and G.R. Heath. 1979. The supply and use of organic material at the deep-sea floor. Journal of Marine Research **37:** 557-579.

Humason, G.L. 1979. Animal Tissue Techniques, 4th edition. San Francisco: Freeman and Company. 661 pp.

Jaeger, E.C. 1931. A Dictionary of Greek and Latin Combining Forms Used in Zoological Names Springfield: Charles C. Thomas. 157 pp.

Lauerman, L.M.L, R.S. Kaufmann, and K.L. Smith, Jr. In press. Distribution and abundance of epibenthic megafauna at a long time-series station in the abyssal NE Pacific. Deep Sea Research

Nybakken, J.W. 1988. Marine Biology: An Ecological Approach. New York: Harper Collins. 514 pp.

Pastorino, G. 1993. The association between the gastropod Buccinanops cochlidium (Dilwyn, 1817) and the sea anemone Phlyctenanthus australis Carlgren, 1949 in Patagonian shallow waters. Nautilus **106(4):** 152-154.

Riemann-Zürneck, K. 1973. Actiniaria des Südwestatlantik I. Hormathiidae. *Helgoländer wissenschaftliche Meeresunterschungen* **25:** 273-325.

Riemann-Zürneck, K. 1993. Redescription of the athenarian sea anemone *Halcampoides abyssorum* Danielssen, 1890 (Actiniaria: Halcampoididae). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* **90:** 31-40.

Riemann-Zürneck, K. 1994. Taxonomy and ecological aspects of the subarctic sea anemones *Hormathia digitata*, *Hormathia nodosa*, and *Allantactis parasitica* (Coelenterata, Actiniaria). *Ophelia* **39(3):** 197-224.

Ross, D.M. 1971. Protection of hermit crabs (*Dardanus* spp.) from octopus by commensal sea anemones (*Calliactis* spp.). *Nature* **230 (5293):** 401-402.

Ross, D.M. 1973. Protection of a hermit crab by its symbiotic sea anemone *Calliactis tricolor*. *Experientia* **29:** 128-130.

Ross, D.M. 1979. The association between the pagurid and the actinian Calliactis parasitica. Recovery of activity in "inactive" D. arrosor in the presence of cephalopods. Marine Behavior and Physiology **6:** 175-184.

Samuels, M.L. 1989. Statistics for the Life Sciences. New Jersey: Prentice-Hall, Inc. 597 pp.

Shimek, R.L. 1989. Shell morphometrics and systematics: a revision of the slender, shallow-water Cadulus of the northeastern Pacific (Scaphopoda: Gadilida). Veliger **32:** 233-246.

Shimek, R.L. and G. Moreno. 1996. A new species of eastern Pacific Fissidentalium (Mollusca: Scaphopoda). Veliger **39(1):** 71-82.

Shimek, R.L. and G. Steiner. In press. Scaphopoda. **In:** Harrison, F. and A.J. Kohn, editors. Mollusca. Microscopic Anatomy of Invertebrates. Volume 6. New York and other cities: Wiley-Liss, Inc.

Smith, K.L., Jr. and N.O. Brown. 1983. Oxygen consumption of pelagic juveniles and demersal adults of the deep-sea fish Sebastolobus altivelis, measured at depth. Marine Biology **76:** 325-332.

Smith, K.L., Jr., R.S. Kaufmann, and W.W. Wakefield. 1993. Mobile megafauna activity monitored with a time-lapse camera in the abyssal North Pacific. Deep-Sea Research **40(11/12):** 2307-2324.

Smith, K.L., Jr., R.S. Kaufmann, and R.J. Baldwin. 1994. Coupling of near-bottom pelagic and benthic processes at abyssal depths in the eastern North Pacific Ocean. Limnology and Oceanography **39(5):** 1101-1118.

Snelgrove, P.V.R., J.F. Grassle, and R.F. Petrecca. 1992. The role of food patches in maintaining high deep-sea diversity: field experiments with hydrodynamically unbiased colonization trays. Limnology and Oceanography **37(7):** 1543-1550.

Sokal, R.R. and F.J. Rohlf. 1981. Biometry. 2nd edition. New York: W.H. Freeman and Company. 859 pp.

Taib, N.T. 1980. Some observations on living animals of Dentalium entalis L. Journal of the College of Science, University of Riyadh **11:** 129-144.

Toft, C.A. 1991. An ecological perspective: the population and community consequences of parasitism. **In:** Toft, C.A., A. Aeschelimann, L. Bolis, editors. Parasite-Host Associations; Coexistence or Conflict? New York: Oxford University Press. p. 319-339.

Trueman, E.R. 1968. The burrowing process of Dentalium (Scaphopoda). Journal of Zoology **154:** 19-27.

Wilson, R.R., Jr., and K.L. Smith, Jr. 1984. Effect of near-bottom currents on detection of bait by the abyssal grenadier fishes Coryphaenoides spp., recorded in situ with a video camera on a free vehicle. Marine Biology **84:** 83-91.

Yonge, C.M. 1937. Circulation of water in the mantle cavity of Dentalium entalis. Proceedings of the Malacological Society **22:** 333-337.

Figure 1. Bathymetric chart of collection site. Insert shows location of site (demarcated M) approximately 200 km off the California coastline (adapted with permission from Lauerman et al., in press).

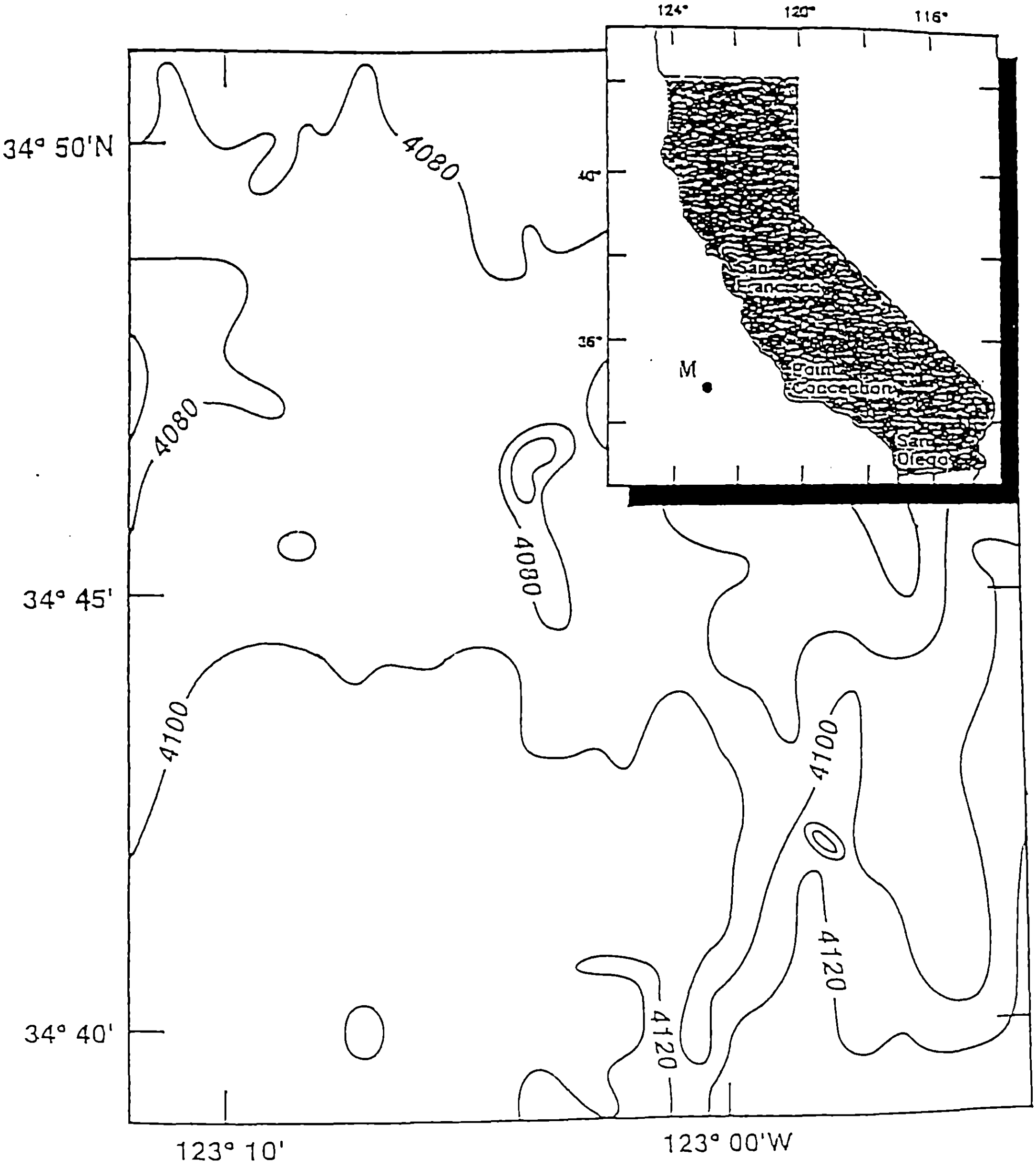

34° 50'N
34° 45'
34° 40'
123° 10'
123° 00'W
4080
4080
4080
4100
4100
4120
4120
124°
120°
116°
40°
36°
M
San Francisco
Point Conception
San Diego

Figure 2. Benthactis nomadas n. g., n. sp. in situ. Black arrows point to the trail that is made as the scaphopod host of the sea anemone moves through surface sediment. Outlined arrow indicates the expanded sea anemone at the end of the trail.

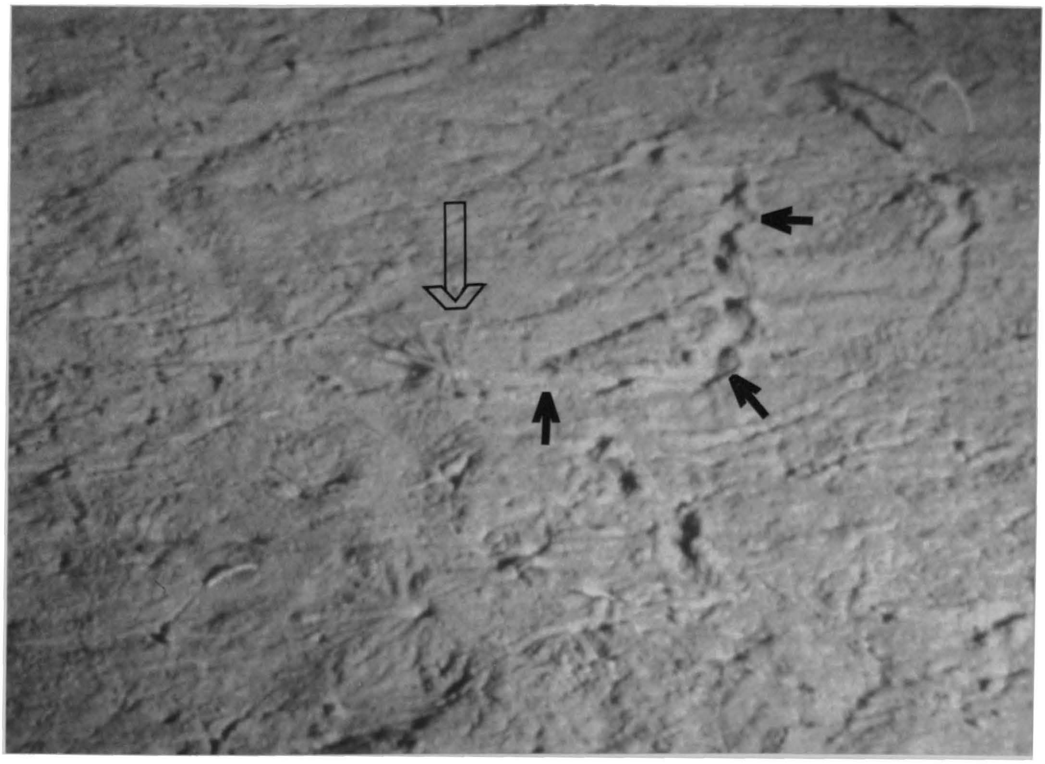
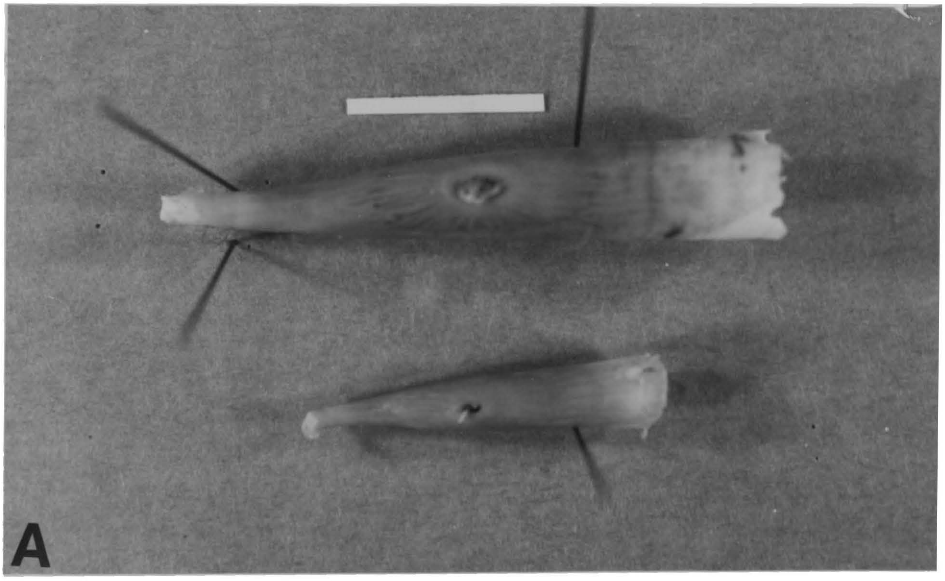
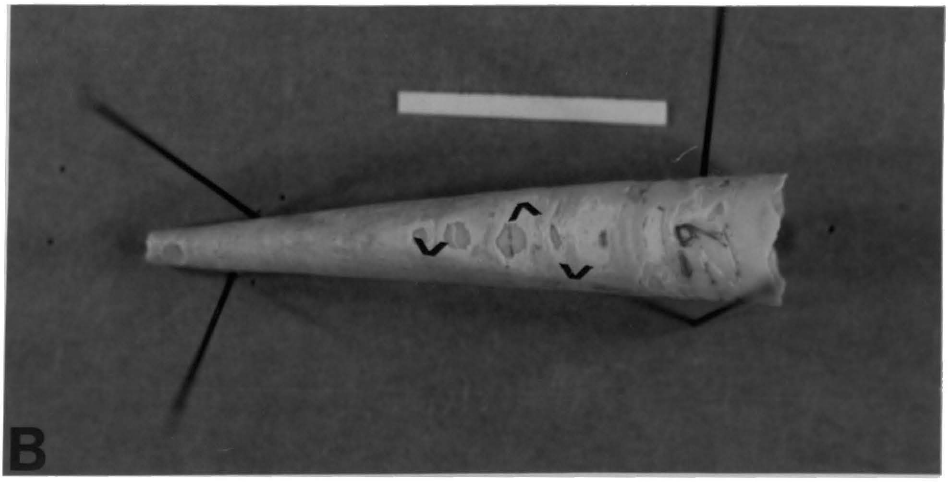


Figure 3. Categories of scaphopod shells. White scale bar equals 20 mm. (A) Concave surface of shell covered by an attached sea anemone; demonstrates range of sizes. Note that the oral disk of the sea anemone is approximately centered on the concave surface of the scaphopod shell (voucher; LACM 90-163.2). (B) Convex surface of a scarred shell; arrow heads point to edge of scar. Note the abrasions on the shell (voucher; LACM 91-41.2). (C) Side view of a bare shell (voucher; LACM 90-162.3).


A


B

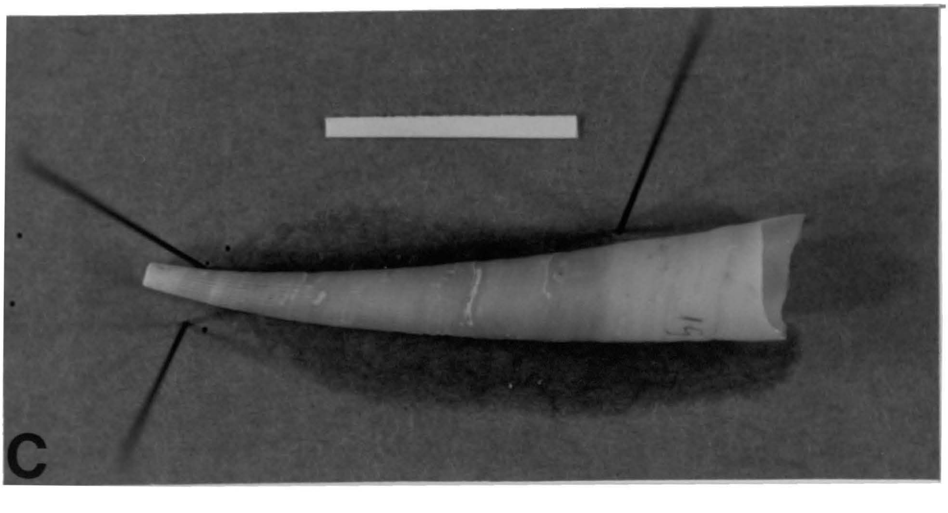
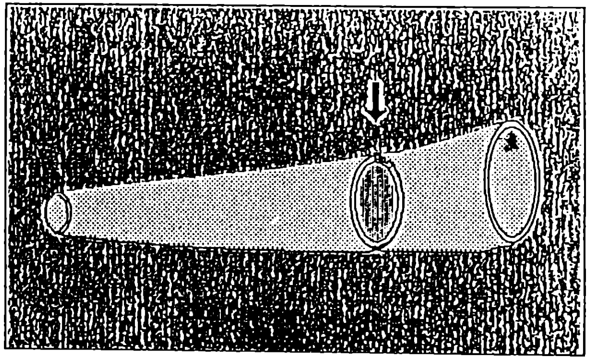

14
C

Figure 4. Schematic diagram of scaphopod shell thin-section (cross section). Three layers correspond to shell ultrastructure; shaded layer represents the portion of the shell surface that was covered by a sea anemone or a scar. (1) Shell thickness was measured at A and B. (2) Normalized weight of covered portion of thin-section model was compared to exposed portion. Insert shows position were shell was thin-sectioned; arrow corresponds to A.



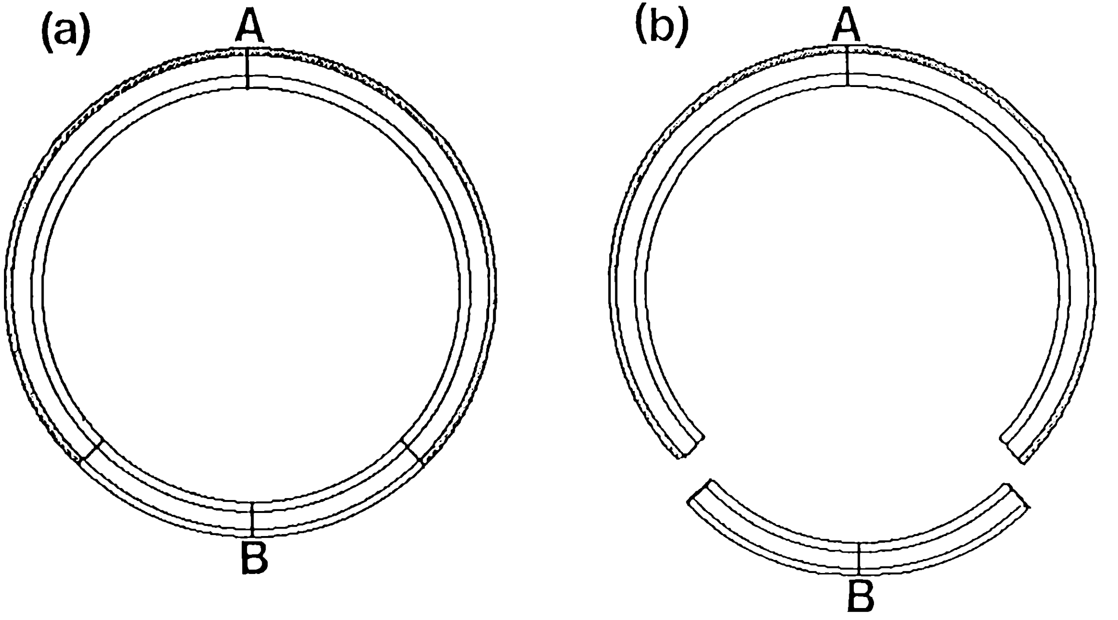

(a)
A
B
(b)
A
B

Figure 5. Longitudinal section of Benthactis nomadas n. g., n. sp. Shows geometry of sea anemone; pedal disk is not present because it remained on shell. s = sphincter muscle, t = tentacle, g = gametes. Note that the column ectoderm is missing (holotype; KUNHM 01019).

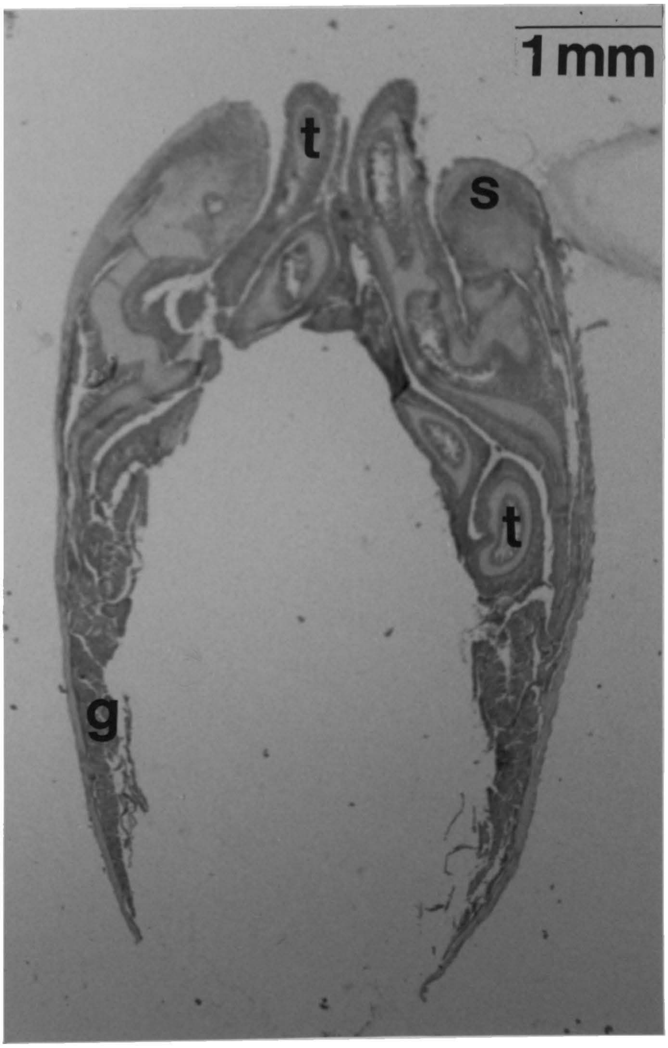
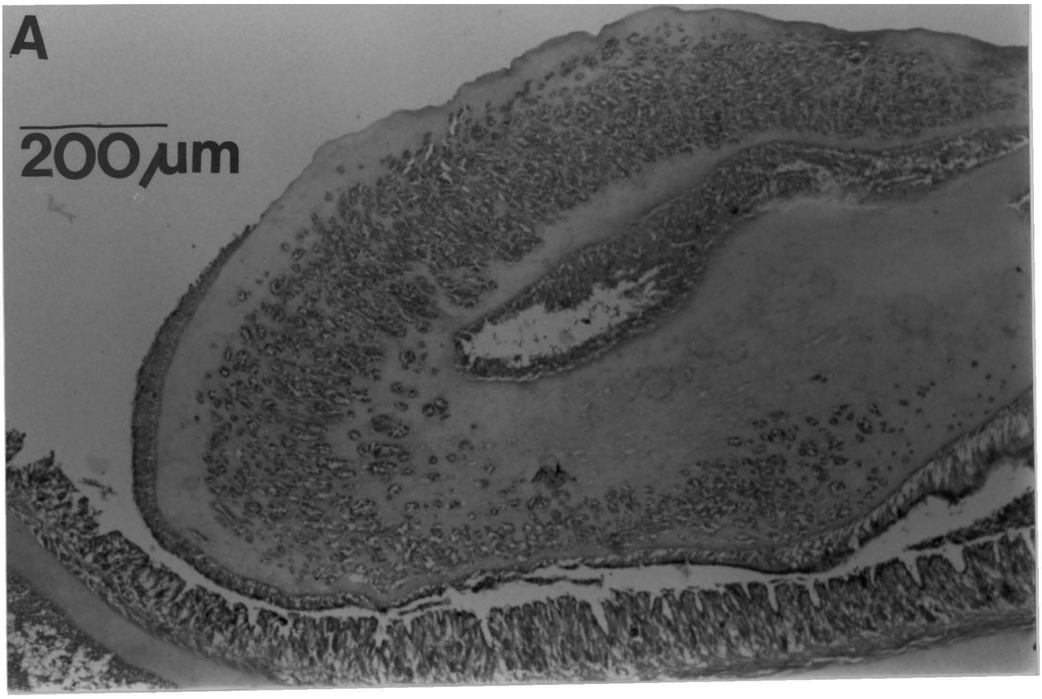
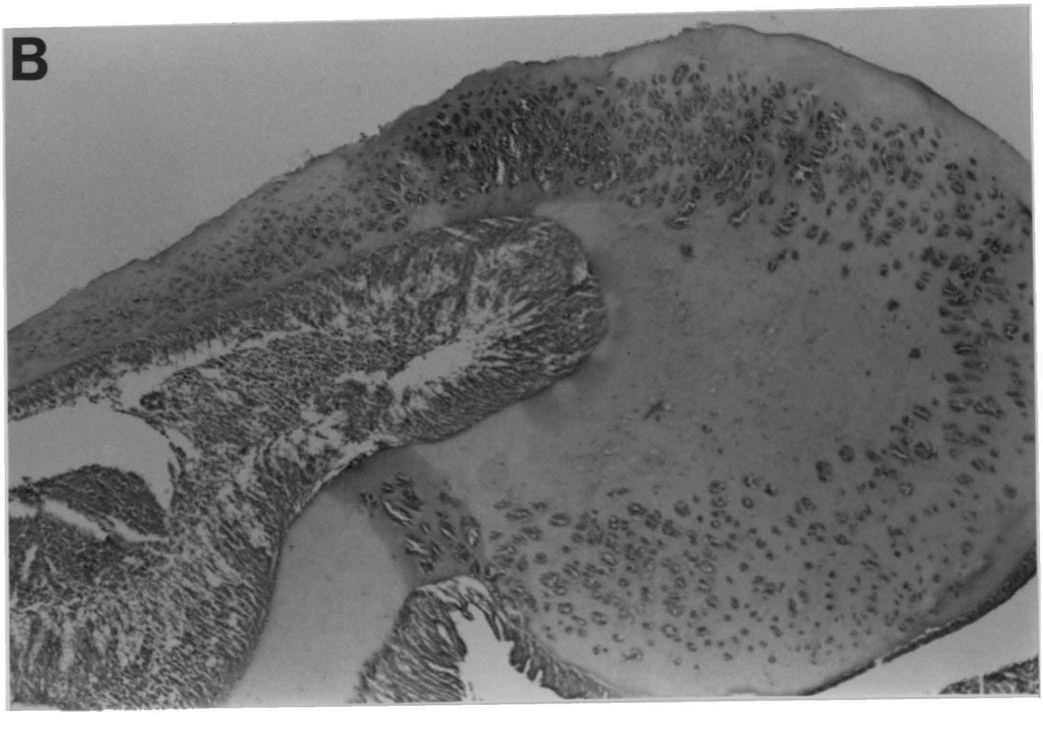

1mm
t
s
t
g

Figure 6. Longitudinal sections through upper column of Benthactis nomadas illustrating variability of mesogleal sphincter muscle. All figures oriented so that column side of sphincter is upward. (A) voucher; KUNHM 01020 (B) voucher; KUNHM 01021 (C) holotype; KUNHM 01019.


A
200 µm


B

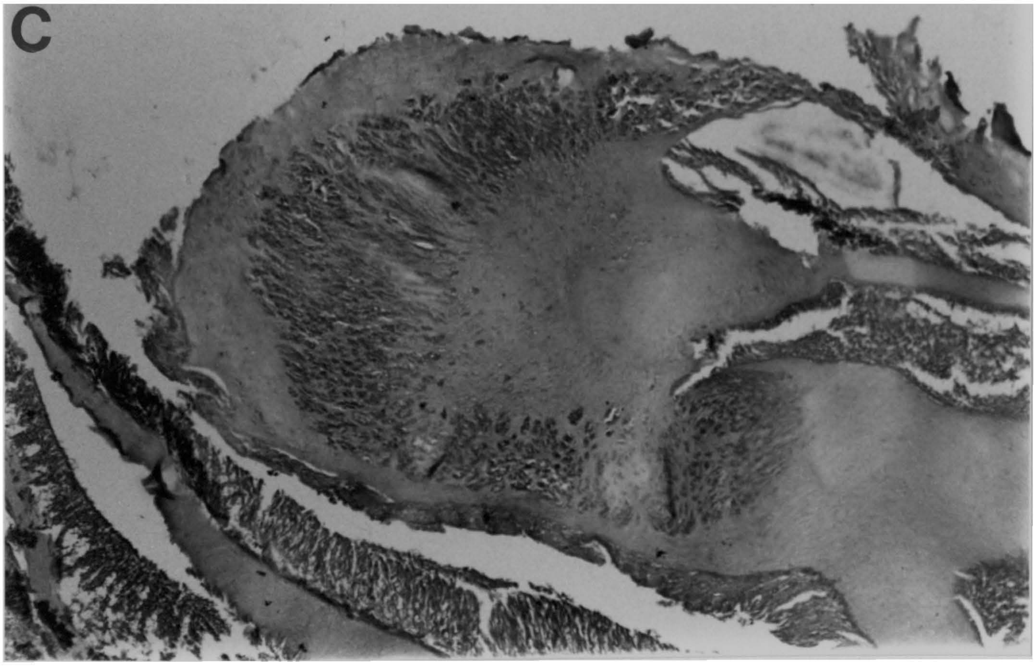

C

Figure 7. Longitudinal section through tentacle of Benthactis nomadas. White arrow indicates ectodermal muscle. A spirocyst is indicated by the black arrow. c = ectoderm, m = mesoglea, n = endoderm (voucher; KUHNM 01020)

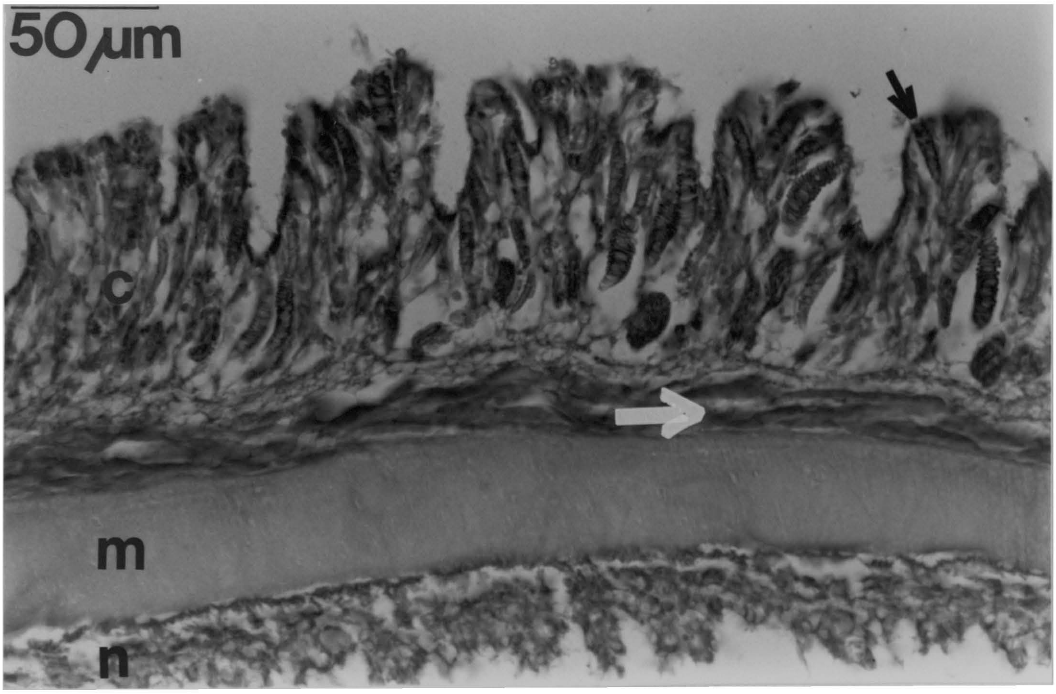

50 μm
c
m
n

Figure 8. Cnidae of _Benthactis_ _nomadas_. See Table 2 for explanation.

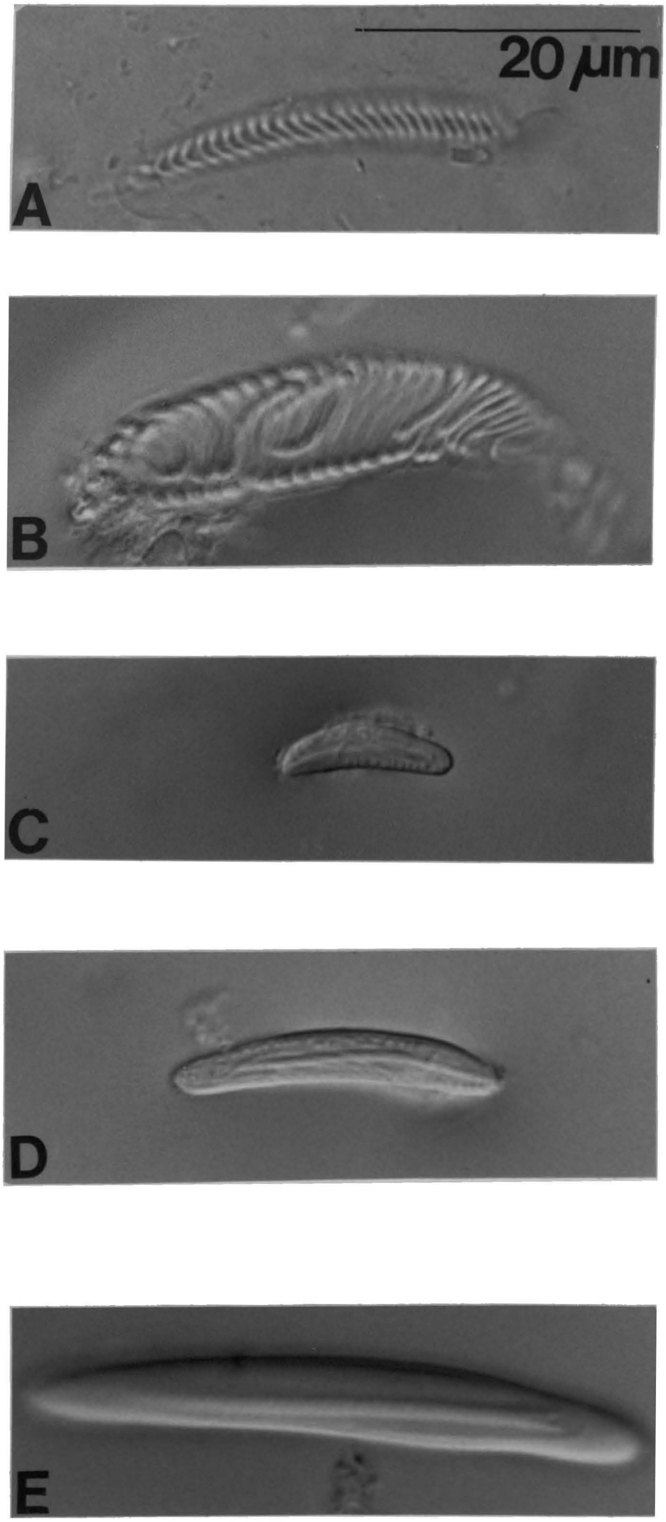
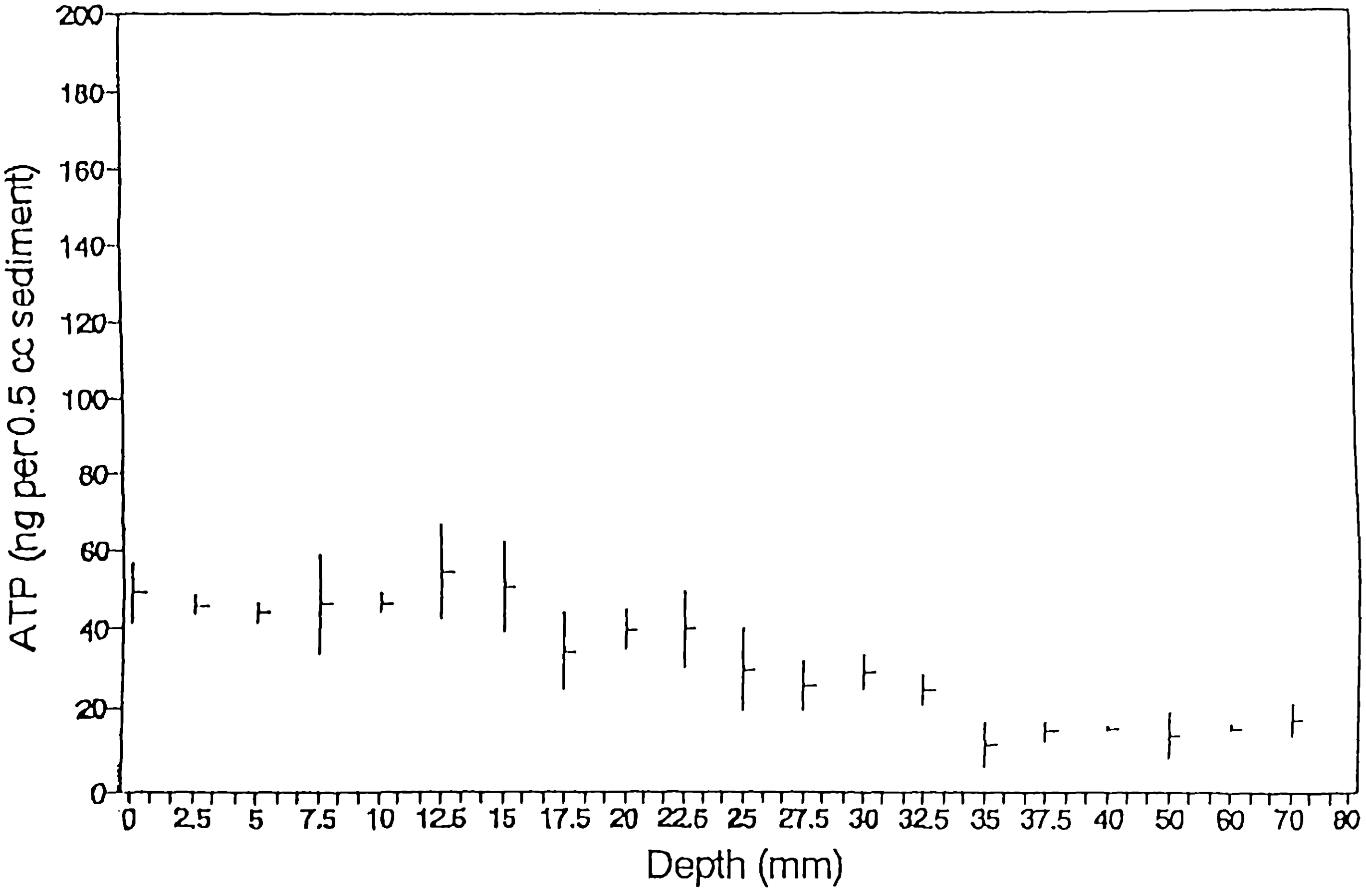

20 µm
A
B
C
D
E

Figure 9. Distribution of ATP in the sediment at Station M. ATP, representative of microbial activity, decreases as a function of sediment depth (data provided by Dr. K.L. Smith).



ATP

Station 1807, FVGR

Figure 10. Measurements of sea anemone and scaphopod shell. (A) maximum diameter of pedal disk of sea anemone; (B) distance from the center of contracted oral disk of sea anemone to the ventral end of the scaphopod shell; (C) shell length; (D) diameter of ventral end of shell.

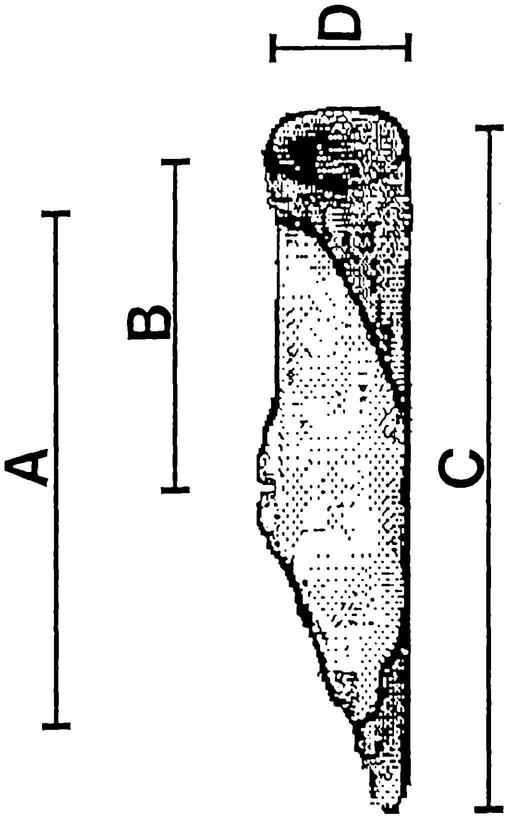

A
B
C
D

Figure 11. Biomechanics experimental set-up. (1) Scaphopod shell buried 2.5 cm in the sediment. (2) Scaphopod shell on surface of the sediment. (A) bare shell; (B) shell with contracted sea anemone model; (C) shell with expanded sea anemone model.

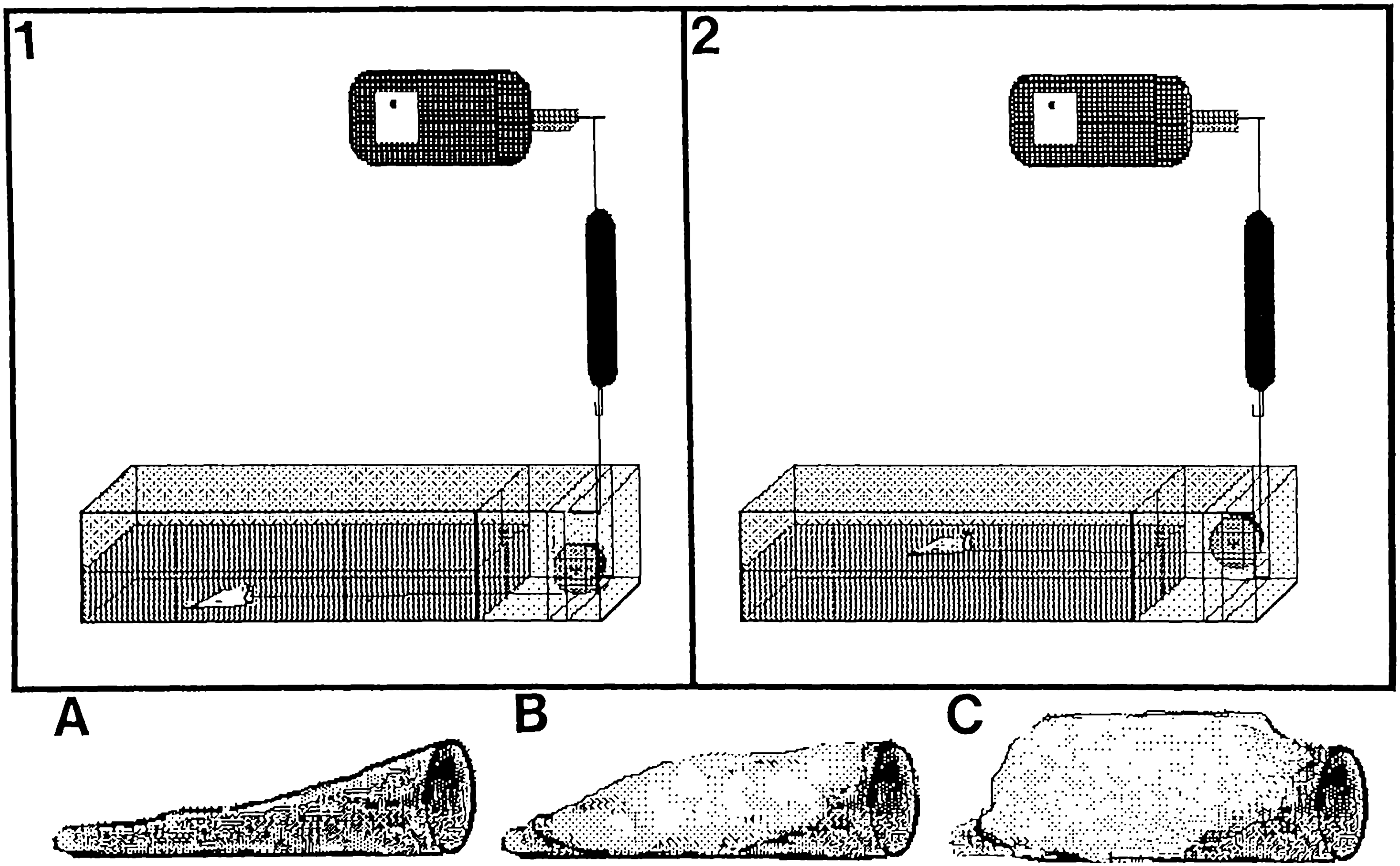

1
2
A
B
C

Figure 12. Scaphopod shell length versus maximum diameter of sea anemone pedal disk.

Relationship between maximum diameter of pedal disk of sea anemone and the position of the sea anemone on the scaphopod shell

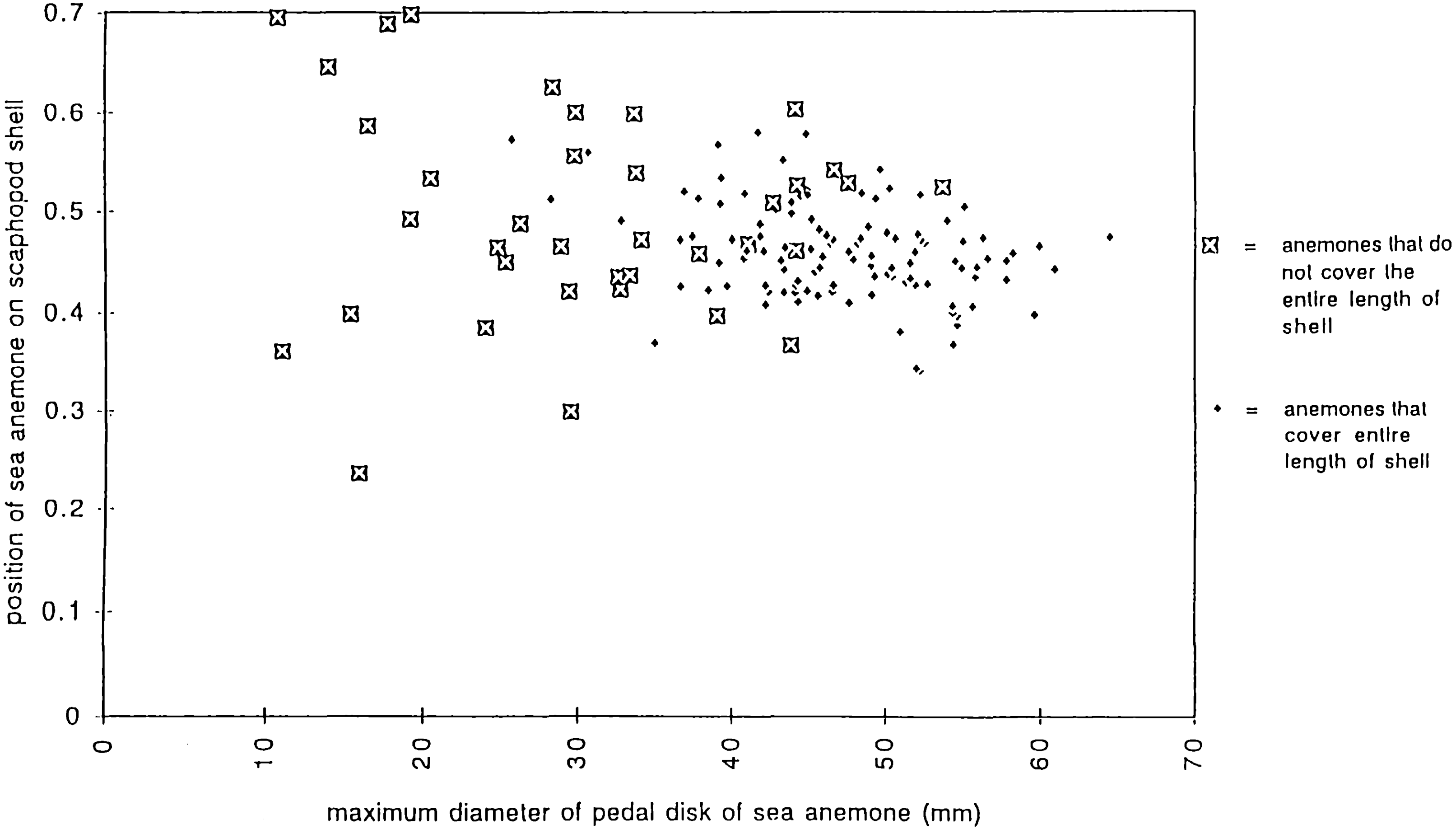


Figure 13. Relationship between maximum diameter of sea anemone pedal disk and position of sea anemone on scaphopod shell.

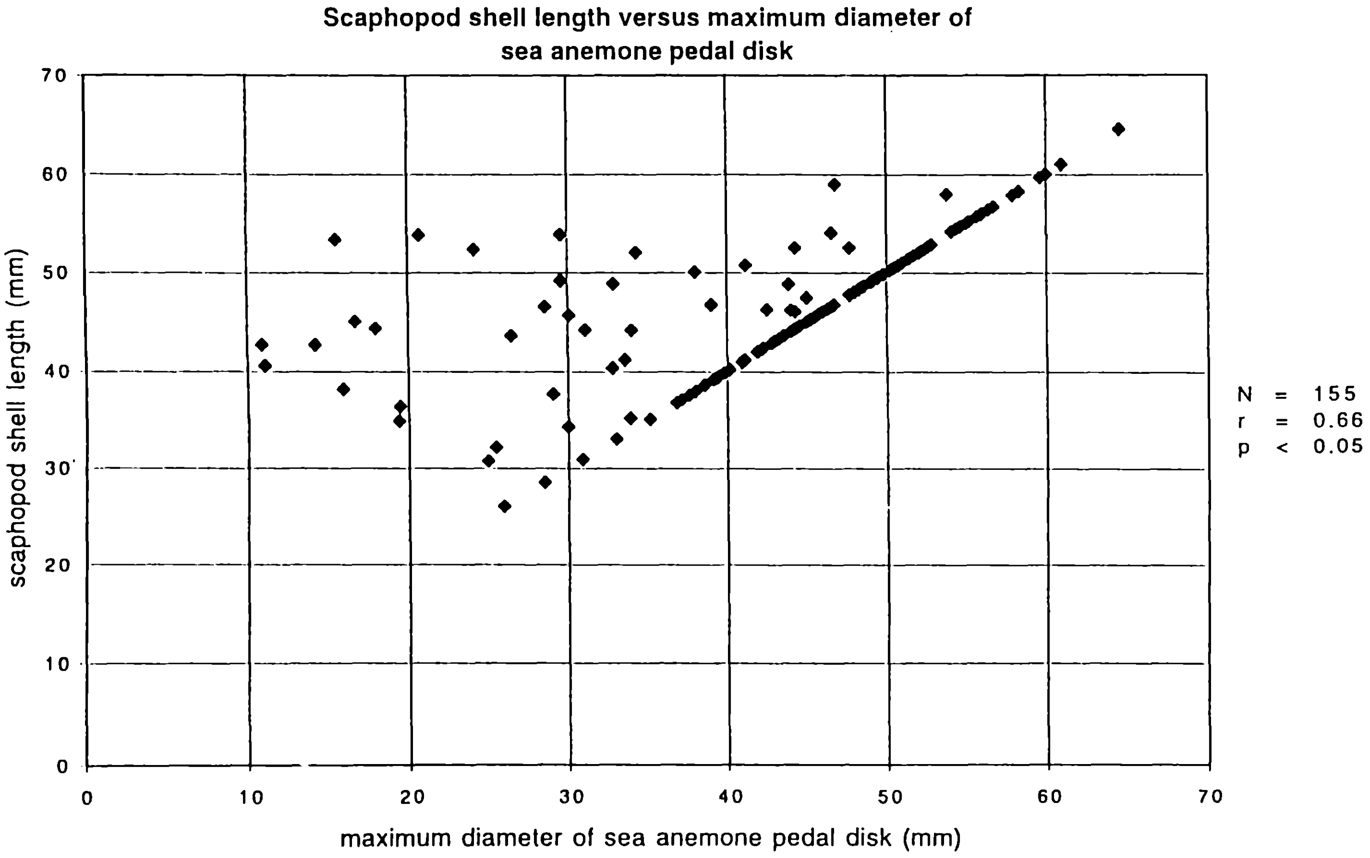

Scaphopod shell length versus maximum diameter of sea anemone pedal disk
scaphopod shell length (mm)
0
10
20
30
40
50
60
70
maximum diameter of sea anemone pedal disk (mm)
0
10
20
30
40
50
60
70
N = 155
r = 0.66
p < 0.05

Figure 14. Scaphopod shell with small sea anemone attached to dorsal end. Sea anemone is indicated by the arrow. White scale bar equals 20 mm.

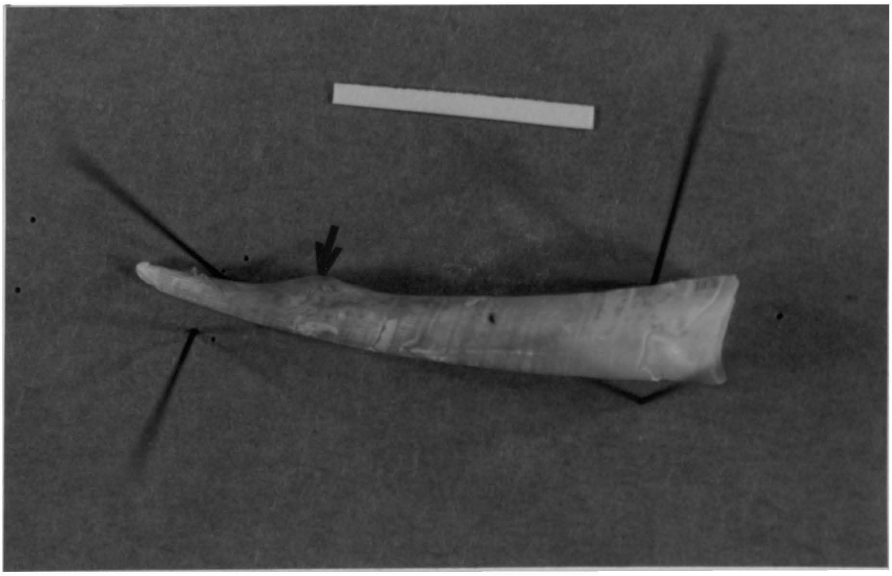


Table 1. Date, site and number of scaphopod shells collected.

Station code used by Smith et al. (1993, 1994) and Lauerman et al. (in press). First digit of 3 digit station number or first two digits of 4 digit station number is cruise number; last two digits represent the location at Station M.

N = number of scaphopod shells collected; also indicated are the numbers (and percentages) of scaphopod shells that had an attached sea anemone (anemone), showed evidence of previous sea anemone attachment (scar), or did not show evidence of recent sea anemone attachment (bare).

Date	Collection Site	Station code	N	anemone	scar	bare
1989						
25 VI	34°49'N, 123°07'W	124M	6	5 (83)	1 (17)	0 (0)
26 X	34°48'N, 123°00'W	216M	13	12 (92)	1 (8)	0 (0)
30 X	34°48'N, 123°08'W	224M	1	0 (0)	0 (0)	1 (100)
1990						
18 II	34°44'N, 123°11'W	314M	16	6 (38)	6 (38)	4 (25)
24 VI	34°44'N, 123°08'W	426M	7	3 (43)	3 (43)	1 (14)
13 X	34°43'N, 123°10'W	505M	9	8 (89)	1 (11)	0 (0)
23 X	34°43'N, 123°10'W	505M	2	2 (100)	0 (0)	0 (0)
1991						
10 II	34°46'N, 123°06'W	606M	14	10 (71)	4 (29)	0 (0)
24 VI	34°45'N, 123°07'W	721M	8	5 (63)	2 (25)	1 (13)
22 VII	34°14'N, 123°07'W	803M	9	5 (56)	3 (33)	1 (11)
1 VIII	34°43'N, 123°07'W	907M	10	9 (90)	1 (10)	0 (0)
2 VIII	34°43'N, 123°06'W	910M	9	4 (44)	4 (44)	1 (11)
21 X	34°45'N, 123°04'W	1007M	7	6 (86)	1 (14)	0 (0)
25 X	34°42'N, 123°03'W	1017M	7	5 (71)	2 (29)	0 (0)
1992						
21 II	34°44'N, 123°08'W	1108M *				
26 II	34°47'N, 123°04'W	1121M	1	0 (0)	1 (100)	0 (0)
21 VI	34°47'N, 123°07'W	1206M *				
25 VI	34°41'N, 123°03'W	1219M *				
2 VII	34°38'N, 123°01'W	1406M *				
17 X	34°46'N, 123°08'W	1506M	8	7 (88)	1 (13)	0 (0)

Date	Collection Site	Station code	N	anemone	scar	bare
20 X	34°43'N, 123°04'W	1516M *				
1993						
24 II	34°45'N, 123°02'W	1625M	10	6 (60)	1 (10)	3 (30)
19 VII	34°43'N, 123°06'W	1716M	19	7 (37)	11 (58)	1 (5)
4 XI	34°44'N, 123°12'W	1809M	6	3 (50)	3 (50)	0 (0)
7 XI	34°42'N, 123°08'W	1820M	9	6 (67)	2 (22)	1 (11)
1994						
5 II	34°41'N, 123°05'W	1906M	4	2 (50)	1 (25)	1 (25)
10 II	34°41'N, 123°11'W	1916M	6	4 (67)	1 (17)	1 (17)
17 VI	34°39'N, 122°58'W	2017M * *				
21 VIII	34°44'N, 123°13'W	2108M	7	1 (14)	5 (71)	1 (14)
22 IX	34°40'N, 123°11'W	2231M	9	7 (78)	2 (22)	0 (0)
22 X	34°42'N, 123°14'W	2304M	15	12 (80)	3 (20)	0 (0)
1995						
14 II	34°42'N, 123°02'W	2404M	12	4 (33)	6 (50)	2 (17)
17 II	34°42'N, 123°05'W	2409M	8	4 (50)	3 (38)	1 (13)
1 V	34°40'N, 123°03'W	2534M	11	6 (55)	5 (45)	0 (0)
3 VI	34°40'N, 123°11'W	2606M	11	9 (82)	2 (18)	0 (0)
9 VI	34°40'N, 123°11'W	2628M	3	3 (100)	0 (0)	0 (0)
Total			257	161 (62)	76 (30)	20 (8)

* Sea anemones collected on cruises 11 through 15 (excepting two trawls) were removed from the scaphopod shells before being sent to me in one container, so I do not know how many were collected in each trawl.

* Due to possible removal of sea anemones from scaphopod shells, I chose not to include specimens from this trawl.

Table 2. Size and distribution of cnidae. (letters refer to photographs in Figure 8).

"n" refers to the number of capsules measured and "N" is the proportion of animals examined in which that type of cnida was present. A single capsule falling considerably outside the range of the others is distinguished by parentheses, following the method of Dunn (1982). Size classes of basitrichs in tentacle tips and bases differed in some individuals; no difference was found between oral and aboral cnidae of the base. Robust spirocysts are differentiated from typical ones by their thick and spiny tubules.

Tissue/Cnidae type	n	N	length (μm)	width (μm)
Tentacle tips				
spirocysts (A)	102	10/10	14.6 - 44.7(51.5)	1.8 - 5.0
robust spirocysts (B)	72	9/10	(16.7)20.3 - 62.9(66.6)	3.4 - 9.1(9.6)
basitrichs (C)	68	10/10	9.7 - 19.4	1.5 - 4.1
basitrichs (D)	91	10/10	17.8 - 31.0(32.8)	2.2 - 5.8
Tentacle bases				
spirocysts (A)	101	10/10	14.8 - 37.8(42.9)	2.3 - 5.7
robust spirocysts (B)	114	10/10	(15.1)18.2 - 45.6	3.0 - 10.9(11.9)
basitrichs (C)	60	7/10	10.6 - 17.9(20.6)	2.3 - 4.1
basitrichs (D)	135	9/10	18.5 - 30.9	2.6 - 5.1
Actinopharynx				
microbasic *p*-mastigophores (E)	102	10/10	(30.2)35.8 - 50.3	3.4 - 6.7
Mesenterial filaments				
microbasic *p*-mastigophores (E)	100	10/10	28.9 - 44.7(50.8)	(2.8)3.3 - 6.6(7.1)
basitrichs (C)	102	10/10	(10.5)11.3 - 15.9(18.8)	2.2 - 5.4(6.1)

Table 3. Scaphopod shell length.

N = sample size; measurements are in mm.

	Sea anemone	Scarred	Bare
N	157	76	20
Range	26-65	26-67	29-54
Average	46.7	45.2	44.0
Median	46.5	46.2	45.9

Table 4. Ratio of shell thickness in covered portion to exposed portion.

Numerals in heading refer to Figure 4. The sign test was based on the ratio generated by the entire thin-section (2). I assigned a plus sign to thin-sections if the covered portion was thicker and a negative sign if exposed portion was thicker. I omitted the ratio of the dorsal section (d) in the two shells in which two thin-sections were made.

Category	Specimen	1. Covered portion : exposed portion (two isolated locations)	2. Covered portion : exposed portion (entire thin-section)
SEA ANEMONE	9-07 (d)	0.51:1	0.65:1
	4-03	0.50:1	0.74:1
	5-06	0.77:1	0.91:1
	10-02	0.73:1	0.94:1
	4-02	0.81:1	1.03:1
	8-04	0.95:1	1.06:1
	9-07	1.12:1	1.07:1
	4-02 (d)	0.82:1	1.08:1
	1-02	1.07:1	1.10:1
	8-03	1.07:1	1.18:1
average		**0.84:1**	**0.98:1**
SCAR	21-07	0.56:1	0.85:1
	17-13	0.80:1	0.97:1
	6-10	1.06:1	0.99:1
	2-01	1.02:1	1.06:1
average		**0.86:1**	**0.97:1**
BARE	3-11	0.77:1	0.93:1
	3-14	0.81:1	0.95:1
	19b-05	0.95:1	1.15:1
average		**0.84:1**	**1.01:1**

Table 5. Force required to pull scaphopod shell.

The force required to pull each bare scaphopod shell, shell with contracted sea anemone, and shell with expanded sea anemone is presented as an average of five trials. Average of all trials is based on average forces required for all shells. Force reported as mN.

In Sediment_

	with 500 g scale		
scaphopod shell	bare	contracted sea anemone	expanded sea anemone
A	151.9	1058.4	637.0
B	156.8	450.8	450.8
C	156.8	323.4	490.0
D	245.0	343.0	784.0
E	-	421.4	676.2
F	186.2	382.2	490.0
G	225.4	499.8	588.0
H	186.2	382.2	735.0
I	98.0	490.0	607.6
J	156.8	529.2	666.4
K	196.0	372.4	646.8
Average of all trials	176.4	480.2	617.4

On Top of Sediment

	with 200 g scale		with 500 g scale	
scaphopod shell	bare	expanded sea anemone	expanded sea anemone	contracted sea anemone
A	15.7	35.3	78.4	78.4
B	23.5	7.8	0	137.2
C	7.8	7.8	0	235.2
D	0	3.9	58.8	215.6
E	-	7.8	68.6	284.2
F	7.8	19.6	49.0	88.2
G	3.9	3.9	39.2	88.2
H	7.8	27.4	29.4	156.8
I	11.8	7.8	58.8	147.0
J	15.7	15.7	49.0	39.2
K	11.8	0	137.2	166.6
Average of all trials	10.8	12.7	51.9	148.9