

Abyssal sea anemones (Cnidaria: Actiniaria) of the northeast Pacific symbiotic with molluscs: *Anthosactis nomados*, a new species, and *Monactis vestita* (Gravier, 1918)

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Abstract.—We describe *Anthosactis nomados*, new species, which belongs to family Actinostolidae, and redescribe *Monactis vestita* (Gravier, 1918), a species belonging to family Hormathiidae. Anemones of both species live attached to molluscs on the soft-sediment abyssal plain of the northeastern Pacific Ocean. *Anthosactis nomados* is known from 260 specimens, most of which were still attached to scaphopod shells when studied, and the others of which show evidence of having been attached to one. By altering the definition of genus *Anthosactis* to include all tentacles being of equal length, this species can be accommodated in it. The species also differs from the other six species previously ascribed to the genus in the size of its nematocysts. We examined about 600 specimens of *Monactis vestita*, more than 350 of which show evidence of having been attached to a gastropod shell but none of which was still associated with the host when studied. This is the first report of *Monactis vestita* in such a symbiosis and from the Pacific Ocean. We hypothesize that both anemone-mollusc symbioses are mutualistic. In that between *Anthosactis nomados* and the scaphopod, which is the third anemone-scaphopod symbiosis to be documented, the protection provided by the sea anemone may allow the scaphopod to avoid the corrosive environment of sub-surface sediments and to forage at the surface where it can obtain energy and calcium carbonate. For both symbioses, the mollusc may resuspend sediments and carry the actinian to food-rich areas, and the anemone may protect its host from predators.

Specimens of the two species of sea anemones we studied were collected as part of long-term research on the biota of the abyssal northeastern Pacific. Specimens of both *Monactis vestita* (Gravier, 1918) and a new species we describe below were collected by A. G. Carey, Jr. from stations centered around 45°N, 135°W, approximately 1200 km off the coast of Oregon, at 3700–

3900 m (Table 1). Many more specimens of the new species were collected by K. L. Smith, Jr. at a site referred to as Station M by us and Smith (Smith et al. 1994, Lauerman et al. 1996) and as Station N by Reimers et al. (1992), 220 km off the coast of California, at 34°50'N, 123°00'W, and 4100 m (fig. 1 in Lauerman et al. 1996). We examined 161 specimens of the new species

Table 1.—Data for specimens of *Monactis vestita* (*M. v.*) and *Anthosactis nomados*, new species (*A. n.*) collected off the Oregon coast. Shape of *Monactis vestita* specimens are coded as follows: d = dome-shaped, f = flat, co = wrapped around cylindrical object. Shapes are illustrated in Fig. 2. Museum abbreviations are provided in the text.

Catalog number	Station number	Coordinates	Depth	Number of specimens
SBMNH 144459	BMT 233	44°40'48"N, 133°26'18"W	3717 m	8d, 10f, 1co <i>M. v.</i>
SBMNH 144422	BMT 303	45°05'06"N, 133°10'54"W	3700 m	9d, 1f, 1co <i>M. v.</i>
SBMNH 345404	"	"	"	43 <i>A. n.</i>
SBMNH 144424	BMT 305	45°05'12"N, 134°43'24"W	3900 m	20d, 4f, 15co <i>M. v.</i>
SBMNH 144423	BMT 306	45°02'00"N, 134°42'12"W	3900 m	67d, 83f, 3co <i>M. v.</i>
RBCM 999-262-1	"	"	"	2d, 1f <i>M. v.</i>
SBMNH 345405	"	"	"	45 <i>A. n.</i>
SBMNH 144461	BMT 307	45°03'30"N, 134°45'00"W	3900 m	52d, 18f, 1co <i>M. v.</i>
USNM 100314	"	"	"	2d, 2f, 1co <i>M. v.</i>
SBMNH 345406	"	"	"	5 <i>A. n.</i>
SBMNH 144419	BMT 308	45°01'06"N, 135°13'36"W	3932 m	173d, 65f, 10co <i>M. v.</i>
CAS 119154	"	"	"	3d, 2f, 1co <i>M. v.</i>
KUNHM 01210	"	"	"	8d, 1f, 2co <i>M. v.</i>
SBMNH 345407	"	"	"	5 <i>A. n.</i>
SBMNH 144460	BMT 309	45°02'00"N, 135°23'12"W	3990 m	63d, 5f, 6co <i>M. v.</i>
LACM 1972-386.001	"	"	"	2d, 2f, 3co <i>M. v.</i>
SBMNH 345408	"	"	"	1 <i>A. n.</i>

from 36 collections made at Station M from 1989 to 1995. No specimens of *M. vestita* were collected at Station M. At least four specimens from Station M superficially looked like *M. vestita*, but differed significantly in characteristics of their nematocysts.

Each specimen of the new species examined from Station M was attached to the concave surface of a shell of the scaphopod *Fissidentalium actiniophorum* Shimek, 1997. Sixty-two percent of scaphopods we examined carried a sea anemone and another 30% of the shells showed evidence of recent anemone attachment—a brown material secreted by the anemone's pedal disk. This is the third documented sea anemone-scaphopod symbiosis. As part of the redescription of *Hormathia pectinata*, Riemann-Zürneck (1973) mentioned that some specimens collected in 1970–1971 from Stations 251 (53°51'S, 59°54'W, 535 m) and 271 (52°40'S, 60°39'W, 405 m) of the *Walther Herwig* Expedition were attached to a *Dentalium* shell. Shimek & Moreno (1996) reported the symbiosis between *Fissidentalium megathyris* and the species we

describe below. In addition, Zibrowius (1998) reported a symbiosis in the northwestern Pacific between the solitary scleractinian coral *Heterocyathus japonicus* (Verrill, 1866) and the scaphopod *Fissidentalium vernedei* (Sowerby, 1860), and Carlgren (1928b) found the anemone *Paracalliactis stephensoni* Carlgren, 1928b, on a large *Dentalium* shell inhabited by the hermit crab *Parapagurus pilosimanus* Smith, 1879, off the Irish coast.

Specimens of both species we studied from the Oregon sites had been removed from their substrata. However, we were given a photograph (Fig. 1) of a specimen of *M. vestita* attached to the shell of *Buccinum* sp. (probably *B. strigillatum* Dall, 1891; Henry Chaney, Santa Barbara Natural History Museum, pers. comm.). We do not know whether *M. vestita* associates with more than one species of snail, but we infer from variation in concavity of the pedal disk that *M. vestita* attaches to substrata other than snail shells (Fig. 2). For instance, the pedal disk of some specimens had been wrapped around a cylindrical object and a

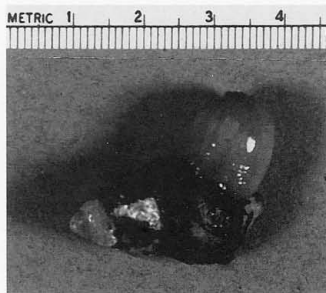


Fig. 1. Rounded specimen of *Monactis vestita* on *Buccinum*, probably *B. strigillatum*.

flat specimen (Fig. 3) was likely attached to a rock.

Paractis vestita Gravier, 1918 was described from 14 specimens collected during the voyages of the *Hirondelle* and the *Princess-Alice* from 1888 to 1913. Twelve specimens were collected in 1895 at Station 749 (38°54'00"N, 21°06'45"W, 5005 m) and two specimens were collected in 1905 at Station 2044 (32°28'00"N, 16°37'30"W, 2286 m). Eleven of the 12 syntypes from Station 749 bear catalog number 13 0022 and the two syntypes from Station 2044 bear catalog number 13 0080 in the Institut Océanographique of Monaco. Gravier's (1918) description was accurate except that he found no acontia. He therefore placed the species in family Paractidae, which is no longer valid. Recognizing acontia in 208 specimens she studied from six stations in the Venezuela deep-sea basin (3476–5060 m) and three stations off the Atlantic coast of Spain (4706–5320 m), Riemann-Zürneck (1986) created the genus *Monactis* for this species, which she placed in family Hormathiidae. The specimens Riemann-Zürneck (1986) studied were poorly preserved, so she could not provide information on internal anatomy or sources of cnidae. In 1992, Zamponi & Acuña described the reproductive structures of three specimens of *M. vestita* collected from 200–250 m near

Mar del Plata, Argentina. Thus, *M. vestita* has been collected from only the Atlantic Ocean; we extend the range of *M. vestita* to the Pacific Ocean.

We infer these symbioses are mutualistic. Both species of sea anemones have increased access to food as they are carried across the sea floor by the mollusc. The scaphopod or snail, when covered by an expanded sea anemone, receives protection from predators. Scaphopods typically live buried within the sediment, but the symbiosis allows the scaphopod to live at the surface, where the sediment contains more calcium carbonate and energy (Smith et al. 1994). We initially hypothesized that the anemone also protects the aragonitic scaphopod shell from dissolution in this high-pressure, low-temperature environment where the water is undersaturated with respect to calcium carbonate (Edmond & Gieskes 1970, Berger 1976, Grottsch et al. 1991), but this hypothesis was not borne out.

Materials and Methods

Immediately after being trawled, some specimens of the new species from California and their host scaphopods were fixed in 10% buffered formalin and were later transferred to 70% EtOH; others were preserved immediately in 70% EtOH. Specimens of *M. vestita* were fixed at sea in buffered 10% formalin and later transferred to 70% EtOH.

Histological study was done of 41 specimens of the new species from California and 13 from Oregon. Five were embedded whole; the others were cut in half longitudinally through the center of the body, and the half on the larger-diameter (anterior) end of the scaphopod shell was removed for histology. Histological study was done of 16 specimens of *M. vestita*. Tissue was 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). Egg dimensions are reported as the average of the

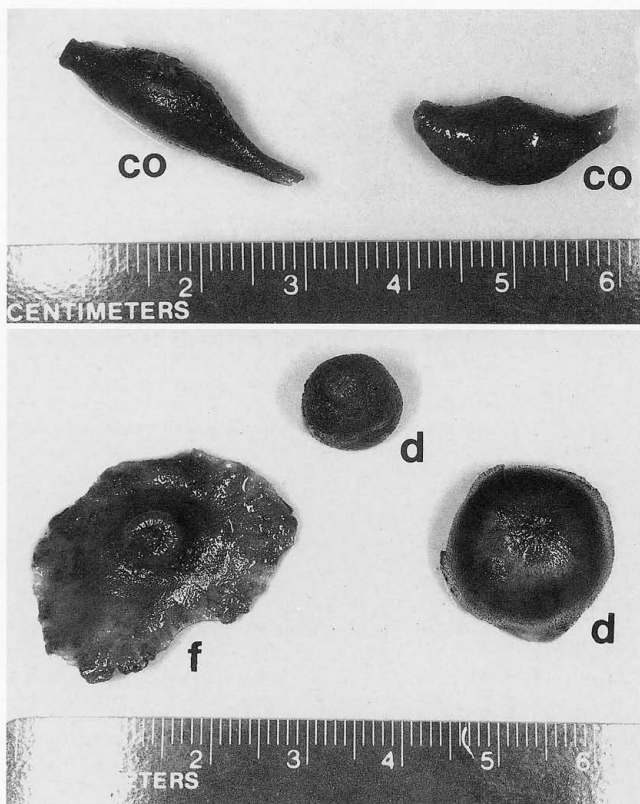


Fig. 2. Specimens of *Monactis vestita* (voucher: KUNHM 01210) demonstrating variety of shapes. (d) Dome-shaped specimens. (f) Flat specimen. (co) Specimens wrapped around cylindrical objects. Note cuticle on smaller specimen labeled d.

maximum diameter and the largest perpendicular diameter in one section of each egg with a visible nucleolus.

Tissue for cnidae squashes was taken from mesenterial filaments, acontia (in *M. vestita*), actinopharynx, tentacle tips, and oral and aboral sides of tentacle bases. Cnidae were studied with differential interference contrast optics; measurements are of

undischarged capsules in squash preparations.

Anthosactis nomados, new species

Figs. 4–8

Column.—Freshly collected and preserved specimens white. All specimens contracted. Column smooth; ectoderm

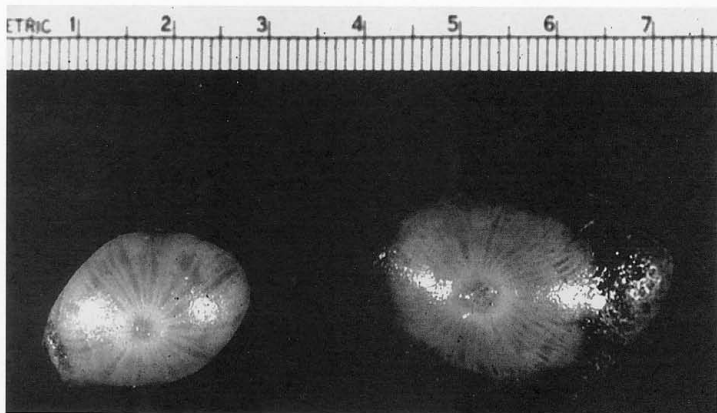


Fig. 3. Contracted specimens of *Monactis vestita* attached to rocks.



Fig. 4. Longitudinal section of *Anthosactis nomados*, new species. s = sphincter muscle, t = tentacle, g = gametes. Note that column ectoderm and pedal disk are absent (holotype: KUNHM 01019).

sloughed off in collected specimens (Fig. 4), a common condition in sea anemones collected from the deep sea (Carlgren 1928a, 1956; Fautin & Hessler 1989; Riemann-Zürneck 1993, 1994).

Sphincter.—Mesogleal. Thick at margin, without external evidence of projecting wall. Typically long: tapered at proximal end (Fig. 5A) but truncated in some (Fig. 5B). Commonly centered in mesoglea but typically closer to the endodermal side at proximal end; closer to ectodermal side in rare specimens. Muscle bundles dense and arranged transversely in most, scattered in others; reticulate in nature along endodermal side of some. Variability in appearance may be related to state of contraction or angle of section.

Pedal disk.—Broad; well-developed; so tightly adherent to shell of scaphopod *Fissidentalium actiniophorum* (Fig. 6) that it typically remains attached to shell when sea anemone is removed (Fig. 4). Maximum diameter never greater than length of scaphopod shell, ranging from 5 to 65 mm; median 44 mm. Midway along scaphopod shell, pedal disk typically covers 75% circumference of shell; coverage increases at

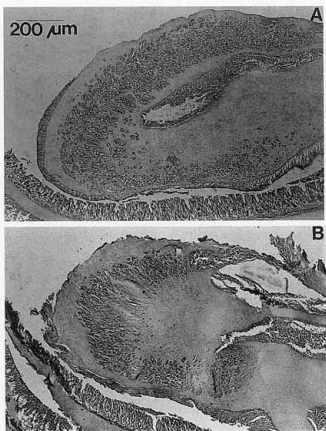


Fig. 5. Cross sections through mesogleal sphincter muscle of *Anthosactis nomados*, new species. Both figures are oriented so external side of sphincter is upward. (A) voucher: KUNHM 01020; (B) holotype: KUNHM 01019.

posterior end of shell, decreases at anterior 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 (Fig. 7). Tentacles taper to a point; 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, ranging from 0.5:1 to 1:1, mean 0.7:1. Tentacles of preserved animals brittle and easily damaged or detached, which may explain variation in tentacle:mesentery ratio. Due to contracted state and morphology, number of siphonoglyphs and arrangement of tentacles could not be determined.

Mesenteries and internal anatomy.—Mesenteries hexamerously arrayed, in 3 cycles; first 2 cycles, including directives, complete, fertile, and filament-bearing; mesenteries in third cycle weak, sterile. Di-

rective mesenteries aligned with long axis of scaphopod. Gametogenic tissue easily damaged or detached so pattern of fertile mesenteries difficult to determine. 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; due to morphology, structure of parietobasilar muscles could not be determined.

Sexes separate; 6 males, 1 female observed among sectioned specimens. Range of minimum and maximum diameter of sperm packets ($n = 45$) $34 \times 36 \mu\text{m}$ – $132 \times 175 \mu\text{m}$. In large packets, cells in various stages of spermatogenesis layered, with spermatozoa central. Diameter of three eggs 51 – $73 \mu\text{m}$.

Cnidom.—Spirocysts, basitrichs, microbasic *p*-mastigophores, and microbasic *b*-mastigophores. Sizes and distribution of cnidae given in Table 2; cnidae illustrated in Fig. 8. No difference in cnidae on oral and aboral sides of tentacle base. All individuals have basitrichs of two size classes in tentacle tips; most have two size classes in tentacle bases. Robust spirocysts differentiated from typical ones by their thick and spiny tubules.

Etymology.—The specific epithet *nomados* is a Greek word for roving (Brown 1956), and was inspired by the nickname “crawling white anemone” bestowed on this sea anemone by Lynn M. L. Lauerman, then a graduate student at Scripps Institution of Oceanography. Its gender is feminine.

Specimens

Holotype.—University of Kansas Natural History Museum (KUNHM), Division of Invertebrate Zoology 01019, half a male intact on scaphopod shell and longitudinal histological sections of the other half (5 slides); collected 7 Nov 1993. Type locality $34^{\circ}42'N$, $123^{\circ}08'W$, 4100 m.

Paratypes.—United States National Mu-



Fig. 6. Contracted specimen of *Anthosactis nomados*, new species, attached to scaphopod shell. The oral disk of the sea anemone is approximately centered on the concave surface of the scaphopod shell. In a minority of the collected specimens, the pedal disk of the anemone is not wrapped tightly around the scaphopod shell but is bunched as shown in Shimek (1997: fig. 1).

seum of Natural History (USNM), Department of Invertebrate Zoology 96574, half a male intact on scaphopod shell and longitudinal histological sections of the other half (5 slides); collected 10 Feb 1994 from 34°41'N, 123°11'W at 4100 m. California

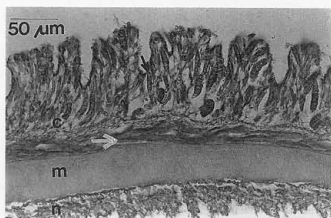


Fig. 7. Longitudinal section through tentacle of *Anthosactis nomados*, new species (voucher: KUNHM 01020). White arrow indicates ectodermal longitudinal muscle. A spirocyst is indicated by the black arrow. c = ectoderm, m = mesoglea, n = endoderm.

Academy of Sciences (CAS), Department of Invertebrate Zoology and Geology 106264, half a male on scaphopod shell and longitudinal histological sections of the other half (5 slides); collected 17 Oct 1992 from 34°46'N, 123°08'W at 4100 m. Royal British Columbia Museum (RCBM), Department of Invertebrate Zoology 996-24-1, half a female removed from its scaphopod host and longitudinal histological sections of the other half (5 slides); collected 19 Jul 1993 from 34°43'N, 123°06'W at 4100 m. RBCM 996-25-1, one specimen intact on scaphopod shell; collected 1 May 1995 from 34°40'N, 123°03'W at 4100 m. Santa Barbara Museum of Natural History (SBMNH), Department of Invertebrate Zoology 143214, half a specimen intact on scaphopod shell and longitudinal histological sections of the other half (5 slides); collected 24 Feb 1993 from 34°45'N, 123°02'W at 4100 m. Los Angeles County

Table 2.—Size and distribution of cnidae of *Anthosactis nomados*, new species (letters refer to Fig. 8). “*n*” is the number of capsules measured and “*#*” is the proportion of animals examined in which that type of cnida was present. A single capsule that fell considerably outside the range of the others is distinguished by parentheses, following the convention of Dunn (1982).

Tissue/Cnida type	<i>n</i>	<i>#</i>	Capsule length (μm)	Capsule 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
Microbasic <i>b</i> -mastigophores (F)	43	7/12	18.1–31.2	4.6–6.8
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 <i>p</i> -mastigophores (E)	102	10/10	(30.2) 35.8–50.3	3.4–6.7
MESENTERIAL FILAMENTS				
Microbasic <i>p</i> -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)

Museum of Natural History (LACM), Department of Malacology and Invertebrate Paleontology 92-113.1, half a specimen removed from its scaphopod host and longitudinal histological sections of the other half (5 slides); collected 17 Oct 1992 from 34°46'N, 123°08'W at 4100 m.

Other material examined.—Sea anemones and scaphopods collected from August 1989 to October 1991 were borrowed from LACM. Scaphopods collected during 1992, from February 1993 to February 1994, during August 1994, and during February 1995 are housed at LACM; sea anemones from these collections are deposited in KUNHM. Scaphopods and sea anemones collected during July, September, and October of 1994, and May and June of 1995, are deposited in KUNHM.

Taxonomic Issues

Family Actinostolidae currently includes 22 genera (Fautin & Hessler 1989). The new species conformed in most respects to the definition of genus *Anthosactis*. To accommodate this species, we amend Carl-

gren's (1949) definition of *Anthosactis* slightly (change underlined):

Actinostolidae with well developed pedal disc. Column smooth, rather low, often longitudinally sulcated in the contracted state. Sphincter strong, mesogloal. Tentacles short, rather few, conical, robust, hexamerously or octamerously arranged, the outer only a little shorter than the inner ones or all tentacles of equal length. Outer tentacles on their aboral sides at the base provided with a stinging battery of microbasic *b*-mastigophors, which are sometimes distributed along the whole aboral side of the tentacle, though more numerous at the base. Longitudinal muscles of tentacles ectodermal, strongest on the oral side. Radial muscles of oral disc ectodermal to ecto-mesogloal. Actinopharynx short with two well developed siphonoglyphs. Pairs of perfect mesenteries 6, 6+2 single, 8, or 12. 2 pairs of directives. Retractors rather weak, parietobasilar muscles fairly well developed. At least the younger mesenteries growing from the basal disc upwards. All stronger mesenteries fertile. Cnidom: spirocysts, basitrichs, microbasic *b*- and *p*-mastigophors.

See Table 3 for the differences between *A. nomados* and five of the six species listed by Carlgren (1949); a description of *A. georgiana* has never been published so is a nomen nudum.

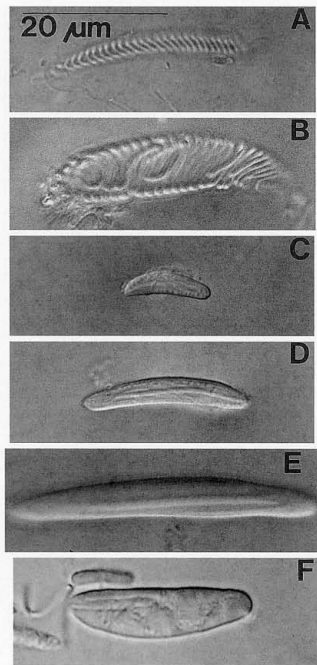


Fig. 8. Ctenidiae of *Anthosactis nomados*, new species. A and B are spirocysts; C and D are basitrichs; E is a microbasic *p*-mastigophore; F is a microbasic *b*-mastigophore. Size and distribution of ctenidiae are shown in Table 2.

Monactis vestita (Gravier, 1918)

Figs. 1-3, 9-11

Column.—Preserved specimens brown; most contracted. Scapus and scapulus distinct in extended specimens. Height of specimens 1.5 mm to 10 mm. Column covered in grainy cuticular material that flakes off (as reported also by Riemann-Zürneck 1986). Column of some specimens not entirely covered with cuticular material; may have been sloughed off during collection [as is common in sea anemones collected from the deep sea (Carlgren 1928a, 1956;

Table 3.—Major taxonomic attributes of *Anthosactis nomados* and the five congeners listed by Carlgren (1949).

Species	Describer (Redescriber)	Basitrichs of tentacles	Mesenteries	Tentacles
<i>Anthosactis nomados</i>	new species	11-18 × 2-4 μm	hexamerous; 12 perfect; first 2 cycles fertile and with filaments	all equal length; not thickened at base
<i>Anthosactis jan mayeni</i> (type species)	Danielssen 1890 (Carlgren 1921)	19-31 × 3-5 μm	octamerous; 8 pairs perfect	inner thicker and longer than outer; outer thickened at base
<i>Antholoba epizoica</i>	Pax 1922 (Carlgren 1928a)	74-93 × 12-13 μm	hexamerous; 12? (6) pairs perfect	all same length
<i>Anthosactis ingolfi</i>	Carlgren 1921	64-118 × 10-11 μm	hexamerous; 6 pairs perfect; all fertile and with filaments	inner thicker and longer than outer
<i>Paractis excavata</i>	Hertwig 1882	53-75 × 11-13 μm	hexamerous; 12 pairs perfect; all fertile	inner shorter than outer; outer thickened at base
<i>Anthosactis capensis</i>	Carlgren 1938	19-24 × 3-3.5 μm	octamerous; 8 pairs perfect; first and second cycles fertile	no data

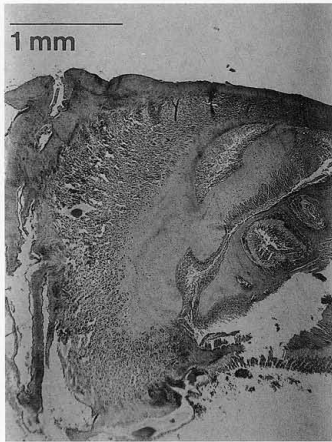


Fig. 9. Cross section through mesogleal sphincter of *Monactis vestita* oriented so external side of sphincter is upward (voucher: SBMNH 144423).

Fautin & Hessler 1989; Riemann-Zürneck 1993, 1994)]. Foraminiferans attached to pedal disk of few specimens; Gravier (1918) reported foraminiferans covering the column.

Sphincter.—Strong, mesogleal (Fig. 9). Centered in mesoglea; proximal end tapered and closer to endodermal side. Alveoli uniform in size.

Pedal disk.—Well-developed; so tightly adherent it usually remains attached to substratum when anemone is removed. Broad or narrow depending on substratum. Width (measured across surface of specimen) of flatter anemones 14.5 mm to 33 mm; 15 mm to 42 mm in anemones with concave pedal disks.

Oral disk and tentacles.—Oral disk not visible due to contracted state. Tentacles conical; base broad, tapering to pointed tip. One expanded specimen with 32 tentacles: 16 large inner tentacles and 16 small outer tentacles.

Mesenteries and internal anatomy.—Mesenteries hexamerously arranged in 4

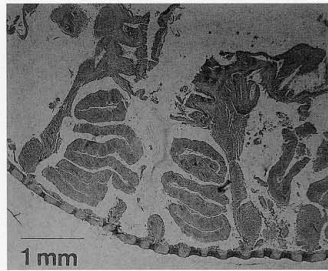


Fig. 10. Cross section of *Monactis vestita* (voucher: SBMNH 144460).

cycles; only those of primary cycle complete. Two distinct siphonoglyphs moderately deep. More mesenteries proximally than distally. Retractor muscles diffuse, strong (Fig. 10). Acontia on primary mesenteries (as reported by Riemann-Zürneck 1986), inconspicuous; lighter in color than mesenterial filaments.

Sexes separate; 4 males, 8 females among those on which histology was done. Diameter of 25 eggs with visible nucleolus 53–107 μ m.

Cnidom.—Spirocysts, basitrichs, and microbasic *p*-mastigophores. Sizes and distribution of cnidae given in Table 4; cnidae illustrated in Fig. 11.

Specimens

For repositories of voucher specimens, see Table 1.

Taxonomic Issues

Because Gravier (1918) did not find acontia in the specimens he studied, he identified them as *Paractis*; the new species differed from known species in number of complete mesenteries. In 1986, Riemann-Zürneck found acontia and established a new genus for the species now termed *Monactis vestita*. Carlgren (1949) listed 15 genera in family Hormathiidae; *Monactis* brings the number to sixteen.

Table 4.—Size and distribution of cnidae of *Monactis vestita* (letters refer to Fig. 11). "n" is the number of capsules measured and "#" is the proportion of animals examined in which that type of cnida was present.

Tissue/Cnida type	n	#	Capsule length (μm)	Capsule width (μm)
TENTACLE TIPS				
Spirocysts (A)	105	9/9	21.4–75.7	3.2–8.8
Robust spirocysts (B)	109	9/9	21.8–69.3	3.2–11.9
Basitrichs (C)	80	8/9	7.6–21.1	1.4–3.5
Basitrichs (D)	92	9/9	18.6–41.2	2.3–4.4
TENTACLE BASES				
Spirocysts (A)	71	7/7	23.8–62.3	3.4–8.8
Robust spirocysts (B)	81	7/7	24.1–53.1	4.1–12.6
Basitrichs (C)	62	7/7	9.8–17.7	1.4–3.3
Basitrichs (D)	71	7/7	19.3–32.7	2.5–4.4
Microbasic <i>p</i> -mastigophores (E)	67	7/7	16.7–23.4	3.0–5.4
ACTINOPHARYNX				
Basitrichs (D)	55	6/6	23.4–34.9	2.6–3.9
Microbasic <i>p</i> -mastigophores (E)	44	4/4	15.4–25.4	3.2–5.0
Microbasic <i>p</i> -mastigophores (F)	36	4/4	27.2–32.8	4.3–7.7
MESENTERIAL FILAMENTS				
Microbasic <i>p</i> -mastigophores (E)	66	7/7	19.8–25.6	3.4–5.1
Basitrichs (C)	68	7/7	10.6–19.3	2.0–3.1
ACONTIA				
Basitrichs (C)	40	4/4	10.9–20.9	1.8–3.2
Basitrichs (D)	40	4/4	27.6–37.7	3.1–4.6

The pedal disk was missing from most specimens we examined; presumably it was torn off when they were removed from their substrata. Acontia were found only in specimens with pedal disks that were intact or present at least at the margins. Gravier's (1918) not having found acontia may be explained if the specimens he studied had torn pedal disks.

Riemann-Zürneck (1986) could not determine the source tissue of cnidae except for acontia in the 208 poorly-preserved specimens of *M. vestita* she studied. Of more than 600 specimens we examined, many were in fine condition, so we could ascertain the cnidom of each tissue. Our data differ in two particulars from those of Riemann-Zürneck (1986): we found gracile spirocysts (in the tentacles) as well as the robust type found by Riemann-Zürneck, and the basitrichs we found fell into two size classes rather than three.

Discussion

Sea anemones of both species and their molluscan hosts from Oregon were separated by the time we obtained the specimens. We were therefore unable to ascertain which species of scaphopod hosted the specimens of *Anthosactis nomados* collected there. Likewise, we could not determine if *Buccinum strigillatum* is the only species of snail that hosts *Monactis vestita*. Gravier (1918) and Riemann-Zürneck (1986) studied specimens of *M. vestita* that were attached to objects such as stones. We are the first to document specimens of *M. vestita* attached to a snail as well as the first to record specimens from the Pacific Ocean. Perhaps only individuals from the northeast Pacific Ocean are symbiotic with molluscs. Despite the existence of other hard surfaces at Station M and off the Oregon coast, such as brachiopods, Mn nodules, snails, and sponge spicules, individuals of the sea

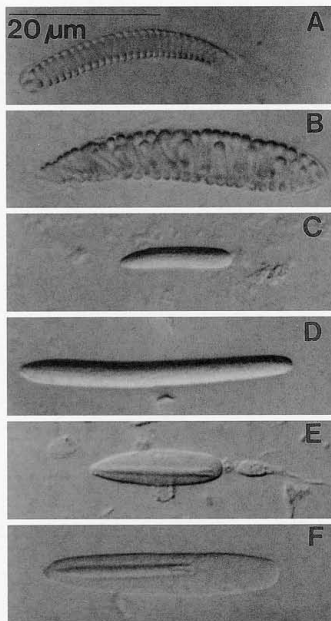


Fig. 11. Cnidiae of *Monactis vestita*. A and B are spirocysts; C and D are basitrichs; E and F are microbasic *p*-mastigophores. Size and distribution of cnidiae are shown in Table 4.

anemone *A. nomados* were found only on the shells of *Fissidentalium actiniophorum*.

We infer from the specificity of *A. nomados* that the scaphopod offers the anemone a benefit in addition to the hard substratum for attachment. By contrast, we infer that individuals of *M. vestita* attach to a variety of substrata. We hypothesize that *A. nomados* and *M. vestita* gain access to food by attaching to a mobile animal: food particles may be resuspended as the mollusc host moves through the sediment; if the sea anemone can pick prey off of the sea floor, it has access to a larger area than it would if it were stationary; and the mollusc host presumably can detect and move to food.

Such benefits have been proposed for other sea anemones that are carried by hermit crabs or snails (Ross 1971, Dunn et al. 1980, Chintiroglou & Koukouras 1991, Riemann-Zürneck 1994).

We infer that the scaphopod and the snail are protected from predators by their actinian symbionts (e.g., Ross 1971, Brooks 1988) and thus that the symbioses are mutualistic. We further hypothesize that this protection provided by *A. nomados* enables its scaphopod host to forage in the upper layers of sediment that are rich in energy relative to sediments at depths in which such scaphopods typically live. The sediment at the surface has three times more ATP (an indicator of microbial activity) than that at a depth of 35 mm (Smith et al. 1994).

Living at the surface may also be favorable to formation and maintenance of the scaphopod's aragonitic shell. Scaphopods prey on foraminiferans (e.g., Shimek 1990, Langer et al. 1995). There are $1-18 \times 10^3 \text{ m}^{-2}$ calcareous foraminiferans in the surface sediments of Station M (Smith et al. 1994). Foraminiferans may be a source of calcium carbonate, as well as energy and nutrients, for the scaphopods (Shimek, pers. comm.). Very little carbonate carbon occurs in surface sediments of Station M (Reimers et al. 1992); absolute values of CaCO_3 in the upper 10 mm of sediment range from 5.14 to 16.36 $\text{mg (g dry weight)}^{-1}$ (Smith et al. 1994). The difficulty of producing and/or maintaining a calcareous shell at this site is reflected by a dearth of shelled organisms such as gastropods, bivalves, and brachiopods (Lauerman et al. 1996). The anoxic sediments below 2.5 to 3 cm (Reimers et al. 1992), the depth at which a scaphopod of this size might typically live, may be expected to be more corrosive to calcareous organisms than the surface sediments.

We had hypothesized the sea anemone might insulate the aragonitic shell of a surface-dwelling scaphopod from the surrounding sea water that is undersaturated

with respect to CaCO_3 . Geological thin-sections were made to compare shell thickness of host scaphopods in areas that had been covered by a specimen of *A. nomados* with areas that had not been covered. Fifteen scaphopod shells, 12 that had been partially covered by a sea anemone and three that showed no evidence of sea anemone attachment, were vacuum-embedded in clear epoxy resin. A 30 μm thin-section was made at one-third of the total shell length from the anterior end of each shell (one shell was sectioned at one-fourth of the total shell length) by Spectrum Petrographics, Inc. (Winston, Oregon). Two shells were thin-sectioned at two-thirds as well as one-third of the way along the shell. We compared cross-sectional area of the shell thin-section that had underlain the anemone with the portion that had been exposed. As a proxy for area, we used weight of the enlarged image of the thin-section traced onto matte board. Tracings of shells that had been bare or completely covered by a sea anemone were also divided into two parts, a portion that extended 270° around the shell, and a 90° portion. We normalized the weights to the length of the inner perimeter of the shell at that position. The ratios of normalized weights of the covered and exposed portions of each shell tracing were analyzed with the Sign Test (Samuels 1989).

Shell thickness in the areas covered and not covered by the anemone did not differ significantly (Sign Test, $p > 0.20$). The shells of *F. actiniophorum* are, however, unusually thin for a scaphopod, ranging in thickness from 189 μm to 479 μm (mean 309 μm ; $n = 15$), which is a third to half as thick as the shells of *F. erosum* collected at 3000–3300 m (Shimek & Moreno 1996). [Shimek (1997:185) stated the thickness of the *F. actiniophorum* shell to be "about 150 μm "; he did not specify in which part of the shell his measurements were made. In one shell from which we had two sections, the anterior end was slightly thicker, and in the other shell there was no difference.]

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