Vesicomyicola trifurcatus, a new genus and species of commensal polychaete (Annelida: Polychaeta: Nautiliniellidae) found in deep-sea clams from the Blake Ridge cold seep

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Abstract.—A new genus and species of deep-sea polychaete belonging to the family Nautiliniellidae is described from the Blake Ridge cold seep off the coast of South Carolina at a depth of 2155 m. This species is commensal within the mantle cavity of ~60% of the vesicomyid clams collected at the seep site. Vesicomyicola trifurcatus is distinguished from previously described nautiliniellid genera and species by the presence of two pairs of tentacular cirri and up to seven trifurcate hooked chaetae on the posterior parapodia. The new species resembles Iheyomytilidicola tridentatus in having trifurcate hooks, but the arrangement and number of chaetae differs. Only two types of chaetae are present in V. trifurcatus: four to seven stout, simple hooks anteriorly to midbody, and up to seven trifurcate hooks posteriorly. In contrast, there are three types of chaetae in I. tridentatus: up to five stout hooks per parapodium, each with a minute projection on cutting edge of the main fang, 10–20 simple, slender tridenate chaetae, and numerous minute mucronate chaetae. A key to species of Nautiliniellidae is included.

The Nautiliniellidae is a small group of deep-sea polychaetes that live in the mantle cavity of a clam or mussel host. Nautiliniellids have been collected from chemosynthetically based deep-sea habitats, including cold seeps and hydrothermal vents. Since nautiliniellids were first reported by Miura & Laubier (1989), 10 genera and 14 species have been described (Table 1). Two undescribed species have also been reported, one from a cold seep at Barbados Trench (4960 m; Olu et al. 1996) and one off the Pacific coast of Mexico (3221 m; Olu, pers. comm.).

An additional genus, *Santelma*, has been assigned to the family Nautiliniellidae (Blake 1993, Glasby 1993), but its affiliation with the Nautiliniellidae remains questionable. The only known species, *Santelma*

miraseta (Fauchald, 1972), was first placed in the family Pilargidae and the genus *Pilargis*. Blake (1993) redescribed the species and assigned it to *Santelma*, a new nautiliniellid genus, based on chaetal similarities. Unlike nautiliniellids, *S. miraseta* has extruded neuroaciculae, a median antenna (or its trace), and it lacks neuropodial hooks and parapodial cirri. Based on these features, *S. miraseta* fits better within the original family Pilargidae (Salazar-Vallejo, pers. comm.). We follow the precedent of Miura & Hashimoto (1996) and exclude *S. miraseta* from the Nautiliniellidae.

Nautiliniellids have reduced and simplified body structures that are associated with a commensal or parasitic life. These modifications include a less developed anterior region, the presence of only simple hooked

Table 1.—Family Nautiliniellidae: list of genera and species, host bivalve genus and family, collection depth of type specimen, location where type specimen was collected and author reference.

Genus and species	Host bivalve Genus (Family)	Depth (m)	Location	Reference
1 Flascarpia alvinae	Unknown	3303	Florida Escarpment	Blake (1993)
2 Iheyomytilidicola tridentatus	Bathymodiolus (Mytilidae)	1395	Okinawa Trough	Miura & Hashimoto (1996)
3 Laubierus mucronatus	(Mytilidae)	3243	Florida Escarpment	Blake (1993)
4 Miura spinosa	Unknown	595	Santa Maria Basin	Blake (1993)
5 Mytilidiphila enseiensis	near Adula (Mytilidae)	625	Okinawa Trough	Miura & Hashimoto (1993)
6 Mytilidiphila okinawaensis	Bathymodiolus (Mytilidae)	701	Okinawa Trough	Miura & Hashimoto (1993)
7 Natsushima bifurcata	Solemya (Solemyidae)	1114	Sagami Bay	Miura & Laubier (1990)
8 Natsushima graciliceps	Solemya (Solemyidae)	86	Kagoshima Bay	Miura & Hashimoto (1996)
9 Nautiliniella calyptogenicola	Calyptogena (Vesicomyidae)	5650	Japan Trench	Miura & Laubier (1989)
10 Petrecca thyasira	Thyasira (Thyasiridae)	3700	Laurentian Fan	Blake (1990)
11 Shinkai longipedata	Calyptogena (Vesicomyidae)	1400	Okinawa Trough	Miura & Ohta (1991)
12 Shinkai sagamiensis	Calyptogena (Vesicomyidae)	1170	Sagami Bay	Miura & Laubier (1990)
13 Shinkai semilonga	Calyptogena (Vesicomyidae)	625	Okinawa Trough	Miura & Hashimoto (1996)
14 Thyasiridicola branchiatus	Conchocele (Thyasiridae)	1160	Sagami Bay	Miura & Hashimoto (1996)
15 Vesicomyicola trifurcatus	Vesicomya (Vesicomyidae)	2155	Blake Ridge Diapir	Present study

chaetae modified to grasp host tissue, and the absence of anal cirri on the pygidium. Diagnostic characters of the family include the number of prostomial appendages, number of tentacular cirri, and chaetal morphology and number. These characters are specific to each genus but are useful for species identifications since seven of the ten nautiliniellid genera are monospecific. Based on these morphological characters, we determined that the specimens collected from the Blake Ridge cold seep belong to a new genus and species described herein.

Material and Methods

Biological samples were collected at the Blake Ridge Diapir site (ODP Site 996; 32°30′N, 76°11′W; 2155 m) on 25 to 28 Sep 2001, using the DSV *Alvin*. A description of the study site can be found in Van Dover et al. (2003). Although geological and chemical properties of this site have been explored during the past decade, the *Alvin* 2001 samples represent the first collections of megafauna and macrofauna from this area.

Host clams were collected using a suction sampler. The clams were identified as a new genus and species in the Family Vesicomyidae, based on morphological characters, molecular differences in comparison to described species, and geographic and bathymetric location (E. Kryolora, pers. comm.). Clams were dissected and nautiliniellids were removed and placed into either 10% buffered formalin or 3% glutaraldehyde and 0.1 M phosphate buffer with 0.25 M sucrose (pH 7.4). After 24 hours, formalin-fixed nautiliniellids were rinsed and stored in 70% ethanol.

Photographs of the external morphology were taken with a compound light microscope (LM) and a scanning electron microscope (SEM). Specimens for LM were mounted in glycerol and ethanol and observed with a Zeiss Axioskop 2 binocular compound microscope. Specimens for SEM were dehydrated through a graded series of

ethanol, terminating with 100% ethanol. Samples were then critical-point dried, gold sputter coated (20 nm thick), and observed with an Amray SEM 1810. Images were captured using a Spot camera (Diagnostic Instruments) or a DP11 digital camera (Olympus). Line illustrations were prepared using a camera lucida attached to a Wild Heerbrugg compound microscope.

Systematics

Family Nautiliniellidae Miura & Laubier, 1989

Vesicomyicola, new genus

Type species.—Vesicomyicola trifurcatus, new species, by present designation.

Diagnosis.—Body with strong dorsal arch, ventrally flattened. Prostomium with one pair of palps, without eyes. Tentacular segment fused with prostomium, with dorsal and ventral cirri, neuroacicula, and neuropodial hooked chaetae. Parapodia sub-biramous, with dorsal and ventral cirri. Notoand neuropodia each with one embedded acicula. Chaetae absent on notopodia. Two types of chaetae present on neuropodia: simple hooked chaetae on anterior segments (some with single subapical tooth present on anterior to mid-body segments), and tricurcate hooked chaetae on posterior segments. Pygidium cylindrical, without anal cirri.

Gender.—Masculine.

Etymology.—The generic name is derived from the name of the host vesicomyid clams these polychaetes inhabit.

Vesicomyicola trifurcatus, new species (Figs. 1–4)

Type material.—Holotype (ODP Site 996; 32°30′N, 76°11′W; 2155 m, 28 Sep 2001, Alvin Dive 3712; USNM 1016220) and five paratypes (USNM 1016221) from same dive and date were deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, District of Columbia. An ad-

ditional five paratypes, each from the same dive and date, were deposited in the Museum National d'Histoire Naturelle, Paris (MNHN POLY TYPE 1405) and the National Science Museum, Tokyo (NSMT—Pol P 458).

Additional material.—Voucher specimens were retained in the collection of CLVD in the Department of Biology at The College of William and Mary.

Description.—Holotype female, ovigerous, measuring 8.4 mm long, 1.3 mm wide, including parapodia, with 37 segments. Paratypes ranging from 4.4–12.7 mm long, 0.8–1.6 mm wide, including parapodia, and with 28–41 segments. Body flattened ventrally, arched dorsally. Some live specimens with green pigment in parapodia, others with pale pink color; preserved specimens in alcohol pink to white in color. Some preserved females pale green; internal oocytes evident through transparent parapodial epidermis. Preserved holotye and paratypes curled (Fig. 1A).

Prostomium rounded, with palps (Fig. 2A–C). Eyes absent. Tentacular segment fused with prostomium, with one pair of dorsal and ventral cirri, neuroacicula, and neuropodial hooked chaetae (Fig. 2C). Foregut with well-developed muscular region (Fig. 2A–C). Pygidium rounded, without anal cirri (Fig. 2D).

Parapodia subbiramous, with dorsal and ventral cirri. Dorsal cirri with inflated base and tapering tip, twice as long as ventral cirri. Notopodia with single embedded acicula, lacking chaetae (Fig. 3A). Neuropodia with a single bent acicula and hooked chaetae (Fig. 3B).

Neuropodial hooks of two types. Anterior neuropodia with simple stout hooks with recurved tips, four to seven on each parapodium (Fig. 4A, B), some anterior to mid-body chaetae with single small apical tooth near tip, appearing slightly bifid (Fig. 4C). Posterior neuropodia with thinner, simple hooks with trifurcate tips, up to seven per neuropodium (Fig. 4D, E).

Etymology.—The specific name comes

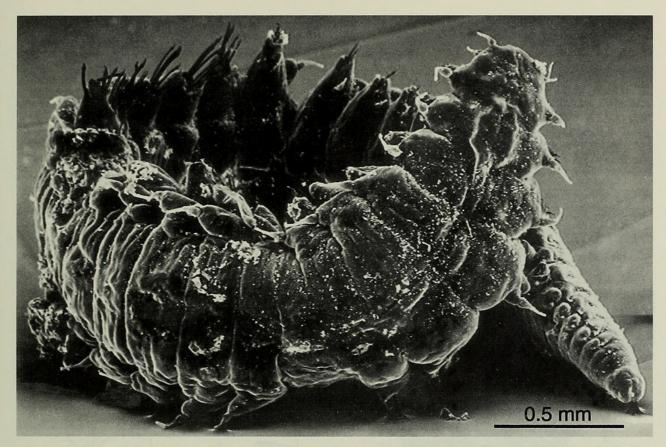


Fig. 1. Vesicomyicola trifurcatus new genus, new species. Scanning electron micrograph (SEM) of whole body.

from tri = three times, + furcatus = forked, in reference to the trifurcate chaetae present on the posterior segments.

Biology.—The mantle cavities of ~60% of the Blake Ridge clams sampled contained one to five nautiliniellid polychaetes. Carbon and nitrogen stable isotope compositions of worm and clam tissues were consistent with a parasitic life-style for the worm, but the sulfur isotope composition of the worms was so distinct from that of the clams that an alternative diet must be inferred (Van Dover et al. 2003). Van Dover et al. (2003) proposed a feeding strategy whereby ciliary activity of the clam gills moves sufficient volumes of seawater to allow the polychaetes to collect and consume suspended organic particles either from gill mucus or from a worm-generated mucus net.

Discussion

Vesicomyicola trifurcatus resembles species in the genera Nautiliniella, Natsushi-

ma, Shinkai, and Thyasiridicola, based on shared characters of the tentacular segment, which in these four genera includes dorsal and ventral cirri and neurochaetae (with the exception of the genus Thyasiridicola, which lacks neurochaetae). The genus Vesicomyicola differs from these four genera in the number and morphology of the neuropodial chaetae.

Vesicomyicola trifurcatus resembles Iheyomytilidicola tridentatus Miura & Hashimoto, 1996 based on the trifurcate chaetal morphology, but the arrangement and number of chaetae on the parapodia differs. There are only two types of chaetae present in V. trifurcatus: stout, simple hooks (four to seven; sometimes bifid) on the anterior to mid-body parapodia, and trifurcate hooks (up to seven) on the posterior parapodia. In contrast, there are three types of chaetae in I. tridentatus: stout hooks (up to five), each with a minute projection on the cutting edge of the main fang; simple,

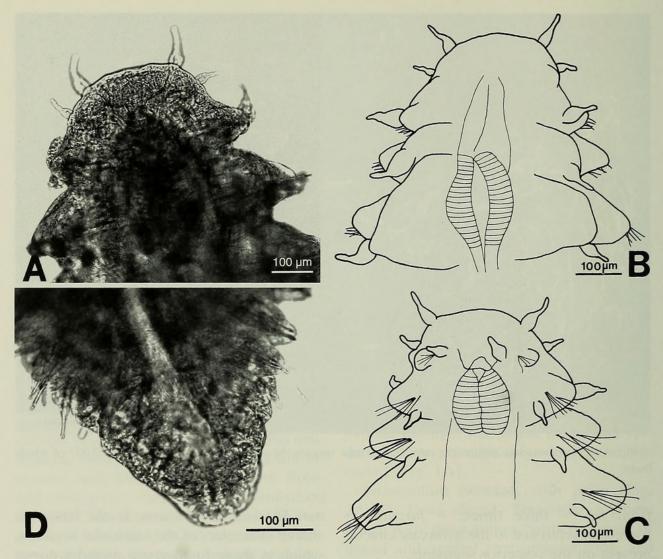


Fig. 2. Vesicomyicola trifurcatus new genus, new species. A. Light micrograph (LM) of anterior end, dorsal view. B. Drawing of anterior end, dorsal view. C. Drawing of anterior end, ventral view. D. LM of pygidium, dorsal view.

slender tridentate chaetae (10–20); and numerous minute chaetae with mucronate tips (Miura & Hashimoto 1996).

Based on its unique set of morphological characters, we consider *V. trifurcatus* to be a new genus and species. A key to nautiliniellid species is provided to aid in identification; most species are location and host specific.

The terminology and interpretation of prostomial appendages in this family is the subject of some debate (Blake 1993, Miura & Hashimoto 1996), suggesting the need for a re-evaluation and revision of this family and its genera once a consistent diagnosis of prostomial appendages can be applied.

Color dimorphism was a distinctive character of live V. trifurcatus, but on preservation the color variation was lost. Polychaetes with green parapodia in new collections (2003) were all gravid females. In other nautiliniellid species, color dimorphism corresponds to sexual dimorphism (Miura & Hashimoto 1996, Miura 1998). We have yet to confirm that the pale colored specimens are males. With the discovery of each new species in the Nautiliniellidae, we learn more about the ecology of these worms and their relationship with their host bivalves; we still know little about the internal anatomy, reproductive biology and larval characteristics, or the trophic ecology of this polychaete family.

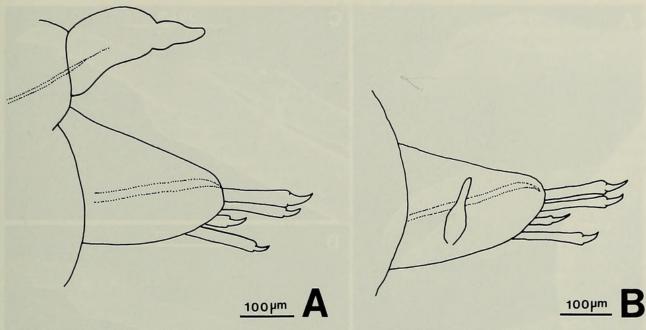


Fig. 3. Vesicomyicola trifurcatus new genus, new species. A. Drawing of mid-body parapodium with embedded aciculum and dorsal cirrus; lateral view. B. Drawing of mid-body neuropodium and ventral cirrus; ventral view.

Key to the species of Nautiliniellidae	One to two large, stout hooks and 15–
 1a. Prostomial appendages (palps or antennae) absent	20 small, mucronate tipped chaetae (in crows of 2) Laubierus mucronatus Blake, 1993 5c. Three types of neurochaetae present: ≤five stout hooks with minute projection on cutting fang, 10–20 tridentate
2a. Tentacular segment with only one pair ofcirri	chaetae, and numerous minute, slen- der chaetae with single mucronate spin Iheyomytilidicola tridentatus
dorsal and ventral cirri	Miura & Hashimoto, 1996 6a. Maximum of one to two stout hooks per parapodium Petrecca thyasira
3b. Tentacular segment without neuro-chaetae; some neuropodial hooks stout	Blake, 1990 6b. Maximum of seven to eight stout hooks per parapodium
4a. Neurochaetae ≥20 (up to 35) per parapodium; neurochaetae with inflated, subdistal stems and slightly	7a. One type of neurochaetae present 8 7b. Two types of neurochaetae present 9
curved, pointed distal ends Mytilidiphila enseiensis Miura & Hashimoto, 1993	8a. One large, stout hook per parapodium Nautiliniella calyptogenicola Miura & Laubier, 1989
4b. Neurochaetae ≤20 per parapodium; neurochaetae with rounded tips and slightly curved, distal ends	8b. Maximum of four stout hooks per parapodium, and branchiae-like notopodial projections present
Miura & Hashimoto, 1993 5a. Only one type of neurochaeta present:	Thyasiridicola branchiatus Miura & Hashimoto, 1996 8c. Number of anterior stout hooks vari-
large, stout hooks	able (2–25) and notopodial branchiae- like projections absent 10

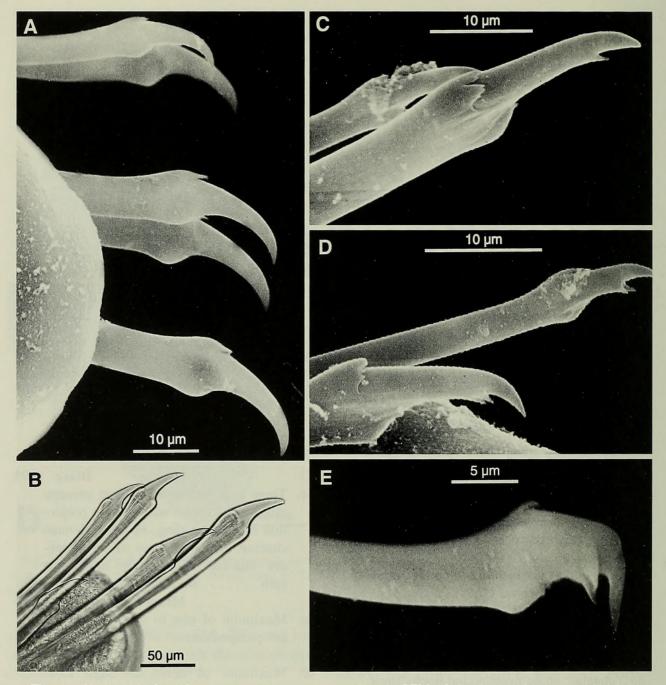


Fig. 4. *Vesicomyicola trifurcatus* new genus, new species. A. SEM of simple anterior neuropodial hooks. B. LM of anterior neuropodial hooks. C. SEM of mid-body chaetae with small apical tooth near tip, appearing slightly bifid. D, E. SEM of posterior trifurcate chaetae.

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- 9b. Neurochaetae with four to seven stout hooks per parapodium present anteriorly and five to seven trifurcate hooks posteriorly . . . *Vesicomyicola trifurcatus*, new genus and species
- 10a. Notopodia in middle regions especially elongate; middle to posterior

- neuropodia with a single hook with strongly curved distal fang Shinkai longipedata Miura & Ohta, 1991

Miura & Laubier, 1990

10c. Notopodia in middle regions slightly

- elongated; middle to posterior neuropodia with ≥five, slightly curved hooks Shinkai semilonga
 Miura & Hashimoto, 1996
- 11a. Short, conical notopodia on middle segments Natsushima bifurcata

 Miura & Laubier, 1990
- 11b. Elongate notopodia on middle segments Natsushima graciliceps Miura & Hashimoto, 1996

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