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## Fauna of whale falls: systematics and ecology of a new polychaete (Annelida: Chrysopetalidae) from the deep Pacific Ocean<sup>☆</sup>

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### Abstract

*Vigtorniella flokati*, a new species of polychaete worm associated with decaying whale remains, is described. Three separate *V. flokati* populations were sampled using submersibles: two associated with implanted gray whale carcasses in the San Diego Trough (1240 m depth) and the Santa Cruz Basin (1670 m) off California, and one from sperm whale and balaeopterid bones implanted on the slope of Oahu, Hawaii at 1000 m. Extraordinarily large numbers of live specimens were observed and videotaped in situ using submersibles in the San Diego Trough and the Santa Cruz Basin. The populations on the carcass implanted for 4 months in San Diego Trough, and on the bones implanted for 2 years off Oahu, were composed only of small sized individuals (including juveniles). *V. flokati* most closely resembles the poorly known *V. zaikai* Kiseleva, 1992, described from the Black Sea. Forty-six morphological characters were used in a phylogenetic analysis of selected nereidiform polychaetes. The resulting most-parsimonious trees indicate sister taxon status between *V. flokati* and *V. zaikai*, and that this clade is sister to the putatively ancient polychaete clade Chrysopetalidae. Whale falls, which are intense point sources of organic enrichment at the deep-sea floor, pass through three successional stages. *V. flokati* appears to colonize the middle, “enrichment opportunist” stage, inhabiting organic-rich bones and sediments ~4–24 months after carcass arrival. *V. flokati* exhibits remarkable behavior, clinging posteriorly to whale bones or nearby sediments to form a writhing carpet at densities exceeding 8000 m<sup>-2</sup>. Its extraordinary abundance on whale falls, and apparent absence from other habitats, suggests it to be a whale-fall specialist. The precise feeding mechanism of the worm remains unknown, but we hypothesize that it may utilize dissolved organic carbon derived from the organic-rich setting of whale falls. The widespread occurrence of *V. flokati*

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on ephemeral, food-rich habitat islands in the Pacific suggests life-history strategies analogous to those for hydrothermal-vent and cold-seep species.

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## 1. Introduction

The discovery of a chemoautotrophic faunal assemblage on a lipid-rich whale skeleton (Smith et al., 1989) has spurred the study of whale falls as intense point sources of organic enrichment at the deep-ocean floor. Recent investigations have examined their significance in both ecological (Bennett et al., 1994; Naganuma et al., 1996; Deming et al., 1997; Smith et al., 1998, 2002; Smith and Baco, 2003) and evolutionary (Goedert et al., 1995; Feldman et al., 1998; Smith and Baco, 1998, 2003; Baco et al., 1999) terms. Ecological research, through experimental implantation, indicates that fresh whale falls pass through a series of successional stages (Smith et al., 2002; Smith and Baco, 2003). Evolutionary research, using both morphological and molecular methods, indicates that whale bones could have acted as sulfide-rich “stepping stones” for the dispersal of sulfide “loving” fauna across the deep ocean basins, and from shallow-water into deep-sea habitats (Smith et al., 1989; Bennett et al., 1994; Baco et al., 1999; Smith and Baco, 2003).

Studies of whale carcasses implanted at bathyal depths off California for less than 1.5 months have revealed largely intact carcasses, with soft tissue predominantly scavenged by hagfish, *Eptatretus deani*, sleeper sharks, *Somniosus pacificus*, and lysianassid amphipods (Smith and Baco, 2003). Carcasses at the seafloor for 4–18 months still attracted hagfish, but (depending on carcass size) were essentially stripped of soft tissue and primarily supported invertebrate opportunists on bones and in organically enriched sediments (Smith et al., 1998, 2003). The bones of carcasses at the seafloor for 4.5 to > 15 years were colonized by chemoautotrophic microbial mats and macrofaunal invertebrates, including some taxa known from vents and seeps, such as vesicomid clams,

bathymodiolin mussels and vestimentiferan polychaetes (Bennett et al., 1994; Baco et al., 1999; Distel et al., 2000; Smith and Baco, 2003). During both the opportunist and chemoautotrophic stages, whale falls also harbor a number of potentially endemic species (Smith and Baco, 2003).

Although the species diversity of these assemblages has been well documented using operational taxonomic units (Ampharetidae sp. A, etc.; Baco and Smith, 2003; Smith and Baco, 2003), much of the whale-fall fauna remains undescribed, inhibiting further research into the autecology and functional significance of the remarkable whale-fall endemics. Here we present both the systematics and ecology of a dominant new species of polychaete from the opportunistic successional stage. Perhaps atypically for a deep-sea polychaete, both in situ observations and fixed samples are available for the description.

Chrysopetalid polychaetes are a diverse group of marine worms inhabiting most seas and substrates, including arctic, temperal and tropical littoral habitats, as well as decaying wood and soft sediments in the deep sea (Dahlgren, 2000; Watson Russell, 2000). Most intertidal and shallow subtidal chrysopetalids possess flattened notochaetae, called paleae, covering the dorsum in a roofing-tile like pattern. Many of the deep-sea forms, however, lack the paleae and instead carry erect spines that are rounded in cross section. Further, close examination of newly collected material of known but poorly described species indicates a wider diversity of chaetal morphology within the group than has been previously suggested (Dahlgren, 1996, 2000, in press; Aguirrezabalaga et al., 1999). Based on structural similarities to Cambrian annelid fossil taxa, it has been argued that chrysopetalids represent a basal group within the Annelida (Butterfield, 1990, 1994; Westheide and

Watson Russell, 1992; Dahlgren, 2000; Rouse and Pleijel, 2001). Chrysopetalidae has traditionally been treated as an aberrant family within the order Phyllodocida (e.g. Pettibone, 1982). Perkins (1985) and Glasby (1993) emphasized the close relationships between the Hesionidae, Nereididae, and Chrysopetalidae within the order Phyllodocida, a hypothesis further supported by cladistic analyses of morphological and molecular data (Pleijel and Dahlgren, 1998; Dahlgren et al., 2000).

The new whale-fall chrysopetalid most closely resembles the poorly known *Vigtorniella zaikai* (Kiseleva, 1992). *V. zaikai* was described from pelagic polychaete larvae that were raised to supposedly adult stage in the laboratory (Kiseleva, 1992). The original name *Victoriella* Kiseleva, 1992 was found to be pre-occupied and subsequently replaced with *Vigtorniella* Kiseleva, 1996. Larvae of this form were first reported from Black Sea plankton tows by Kiseleva (1959), and can occur in large numbers throughout the year (Murina, 1997). The larvae were also described in detail by Murina (1986) who misidentified them as the larvae of *Pelagobia serrata* Southern, 1909 (Phyllodocidae). In 1994, live adults were first recorded from sediments at 117–151 m depths at the oxic-anoxic boundary of the Black Sea floor (Sergeeva et al., 1997, 1999; Zaika, 1999). Unfortunately, these records include only ecological observations and no new data are available on adult morphology. Adult specimens are not available for loan, (V. E. Zaika in litt.) and further morphological and molecular studies of *V. zaikai* are not possible at present.

Although the phylogenetic affinity of *V. zaikai* has never been determined, largely due to lack of adult specimens available for examination (Dahlgren and Pleijel, 1995), *V. zaikai* was placed in the family Chrysopetalidae based on several points of overall morphological similarity (Kiseleva, 1992). Given the apparent sister relationship of the new taxon to *V. zaikai*, a more rigorous phylogenetic analysis of the position of the taxon *Vigtorniella* is now possible.

Museums are referred to by the following abbreviations: Natural History Museum, London (NHM), and Natural History Museum, Stockholm (NRM), Natural History Museum of Los Angeles County, Allan Hancock Foundation Polychaete Collection (LACM-AHF).

## 2. Material and methods

Specimens of *Vigtorniella flokati* sp. n. were collected using manned and remotely operated submersible vehicles from whale-bone habitats at three different locations in the Northern Pacific Ocean. Two of the whale falls are located off the coast of California in the San Diego Trough (SDT) and Santa Cruz Basin (SCrB), and the third is located off Oahu, Hawaii (Fig. 1). Details of collection methods, locations, and depths are provided in Table 1. All specimens for morphological analyses were initially fixed in a 4% formaldehyde solution in seawater and subsequently transferred to 70% ethanol. In addition, four specimens from SCrB were fixed directly in EtOH for subsequent DNA extraction.

### 2.1. Imaging

Formalin-fixed specimens were examined using dissecting and compound light microscopes and digitally imaged. The digital images were converted to halftones and contrast enhanced using Adobe Photoshop 6.0. For size measurements, batches of specimens were placed under the dissecting microscope and digitally photographed. NIH Image 2 was used to measure the length and maximum width of the worms in the digital images. Color video of live specimens from Alvin's camera system was imported digitally into an Apple Macintosh computer and edited using iMovie 2.1.1. Still frame grabs were exported as JPEG files and contrast-enhanced using Adobe Photoshop 6.0. Specimens used for scanning electron microscopy (SEM) were transferred to 100% ethanol, prepared in a critical-point-dryer, mounted on aluminum stubs, sputter-coated with gold, and imaged using a JEOL scanning electron microscope (JSM-840).

### 2.2. Phylogenetic analyses

The phylogenetic position of *V. flokati* sp. n. was tested using a dataset of morphological characters (Table 2). The dataset was based on an earlier analysis of nereidiform annelids that was in part designed to determine the position and

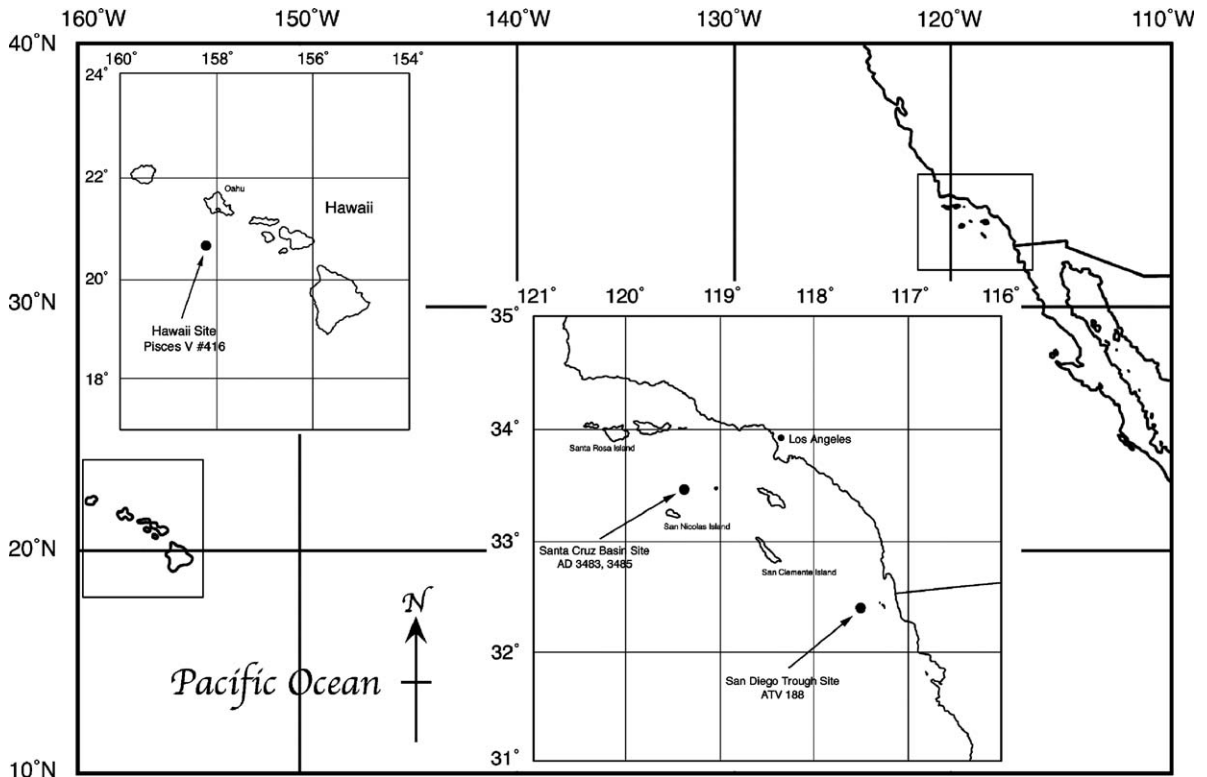


Fig. 1. Distribution map, showing the locations of samples. Box insets provided for Californian and Hawaiian sites.

Table 1

*V. flokati* sp. n. Collection details for each population sample

	San Diego Trough	Oahu slope	Santa Cruz Basin
Position	33°35'N, 117°30'W	21°21'N, 158°13'W	33°27'N, 119°22'W
Depth (m)	1240	1057	1675
Date and dive number	10/23/96, ATV Dive #188	8/31/99, <i>Pisces V</i> Dive #416	10/17/99, DSV <i>Alvin</i> Dive #3485
Water temperature (°C)	3.2	4.2	4.1
Salinity (PSU)	34.4	34.5	34.5
Bottom water oxygen concentration (ml/l)	1.0	1.8	0.8
Substrate	Sediment	Whale bones	Whale bones
Method	Sediment coring	Box wash	Slurpgun, box wash
Carcass details, age	Juvenile grey whale, ~Five ton wet weight (after removal of head), four months since deposition	One balaeanopterid vertebra and two humpback whale vertebrae, two years since implantation	Gray whale, ~35 ton wet weight, 18 months since deposition
Population characteristics	Small bodied individuals only	Five juveniles and one anterior fragment with eggs and large type notoseatae	Large and small bodied individuals (123 of the small individuals were collected on 5 vertebrae)

Table 2  
Summary of the morphological characters used in phylogenetic analysis

1	Eyes
2	Two pairs of eyes
3	Median antenna
4	Anteriorly inserted median antenna
5	Dorsally inserted median antenna
6	Posteriorly inserted median antenna
7	Longitudinal furrows flanking insertion point of median antenna
8	Differentiated paired antennae and palps
9	Biarticulated palps
10	Proboscis terminal ring with papillae
11	Proboscis terminal ring with ten papillae
12	Proboscis terminal ring with 14 papillae
13	One pair of lateral jaws
14	Dorsal tooth
15	Mouth flap
16	Cirrophores of anterior cirri
17	Dorsal tentacular cirri segment 1
18	Dorsal tentacular cirri segment 2
19	Dorsal tentacular cirri segment 3
20	Dorsal tentacular cirri segment 4
21	Dorsal tentacular cirri segment 5
22	Ventral tentacular cirri segment 2
23	Ventral tentacular cirri segment 3
24	Ventral tentacular cirri segment 4
25	Aciculae tentacular cirri segment 1
26	Notochaetae
27	Notochaetae segment 2
28	Notochaetae segment 3
29	Notochaetae segment 4
30	Notochaetae segment 5
31	Notochaetae appearing further back than neurochaetae
32	Neurochaetae segment 2
33	Neurochaetae segment 3
34	Neurochaetae segment 4
35	Multiple notoacaculae median segments
36	Multiple neuroacaculae median segments
37	Cirrophores of dorsal cirri
38	Annulated dorsal cirri
39	Alteration of dorsal cirri
40	Elevated dorsal cirri on segment 6, 7, 9, 11, 13 and 15
41	Elevated dorsal cirri on segment 5, 8, 10, 12, 15 and 17
42	Chambered chaetae
43	Chambered notochaetae
44	Chambered compound neurochaetae
45	Anal plate
46	Median pygidial appendage

All characters are binary with absence and presence scored as 0 and 1, respectively.

delineation of chrysopetalid annelids (Plejdel and Dahlgren, 1998). Taxon sampling and outgroup choice in the analysis of Plejdel and Dahlgren (1998) were directed by an initial analysis of all major members of the order Phyllodocida. Our analysis is based on the same 46 morphological characters (Table 2) used by Plejdel and Dahlgren (1998) coded for *V. flokati* sp. n. and *V. zaikai*, in addition to the 12 nereidiform and outgroup taxa sampled in the original study (Table 3).

MacClade 3.0 (Maddison and Maddison, 1992) was used to construct data matrices (Table 3) and PAUP\* (Phylogenetic Analysis Using Parsimony) (Swofford, 2000) for phylogenetic analyses. Heuristic parsimony searches were performed with 100 replicates of random sequence addition. Factory settings of PAUP\* were used in all other instances. To test for tree stability, we used PAUP\* to calculate bootstrap and jackknife values (1000 replicates each with 10 replicates of random addition of taxa). The jackknife values were calculated using “Jack” emulation and 0.37 removal probability (Farris et al., 1996). Bremer support (Bremer, 1988) was computed with Auto-Decay (Eriksson, 1998).

### 3. Systematics

#### 3.1. Taxon description

*V. flokati* sp. n. (Figs. 2–6).

*Material examined:* East Pacific, Santa Cruz Basin (SCrB), 33°29'N, 119°22'W, 1674 m, holotype (NHM 2003.645), paratype (LACM-AHF POLY 2128), and two specimens preserved in formaldehyde, one of which used for SEM, three specimens preserved in ethanol, one used for DNA extraction, coll. Craig R. Smith Alvin Dive #3485, 10/17/99; East Pacific, San Diego Trough (SDT), 33°35'N, 117°30'W, 1240 m, three paratypes (NRM-5758) and two specimens preserved in formaldehyde, one dissected, one used for SEM, coll. Craig R. Smith ATV 188 SDT TC#11, 10/23/96; Hawaii, 21°21'N, 158°13'W, 1057 m, five juveniles and one anterior fragment with eggs and large type notochaetae preserved in formaldehyde, coll. Amy Baco, Pisces V Dive 416, 8/31/99.

Table 3

Matrix of scores for the 46 morphological characters (Table 2) for the 12 nereidiform and outgroup taxa, and the two species of *Vigtorniella*

	1		2		3		4		12345	67890	12345	67890	12345	6
	12345	67890	12345	67890	12345	67890	12345	67890						
<i>Pisione remota</i>	11000	00001	01000	010?0	01001	00000	00110	10000	00000	0				
<i>Chrysopetalum debile</i>	11101	0001?	??101	10000	0100?	11111	00110	01011	01110	0				
<i>Dysponetus caecus</i>	00101	00111	0?101	10000	01001	11111	00110	01011	01110	1				
<i>Hesionides arenaria</i>	00100	10101	10000	01?00	0?000	10111	00110	10000	00001	0				
<i>Heteropodarke formalis</i>	11110	01111	10000	11110	01101	?0000	??010	01110	10000	0				
<i>Microphthalmus</i> sp.	10100	10101	10000	01110	01100	10001	11010	00000	00001	0				
<i>Neanthes virens</i>	11000	00010	00100	11100	01000	10001	11110	00000	01110	0				
<i>Ophiodromus flexuosus</i>	11110	01110	00000	11111	11101	10000	11011	11110	11110	0				
<i>Leocrates chinensis</i>	11101	00011	00010	11111	11111	10000	11001	11110	11110	0				
<i>Psamathe fusca</i>	11000	00011	00000	11111	11111	00000	00001	11110	11010	0				
<i>Typosyllis armillaris</i>	11101	00001	10010	10000	00000	00000	00110	11110	00000	1				
<i>Sigambra cf. tentaculata</i>	00100	10111	01000	01100	00000	10001	11110	00000	00000	0				
<i>Vigtorniella zaikai</i>	00000	0010?	??000	?1100	0100?	11111	01110	0?000	01110	0				
<i>Vigtorniella flokati</i> sp. n.	00000	0010?	??000	11100	01000	11111	01110	01000	01110	0				

“?” denotes unknown or not applicable state. Character numbers correspond to character list in Table 2.

If not stated otherwise, all specimens are in the collection of Craig R. Smith, at the University of Hawaii.

**Morphology:** Color yellow to red in live specimens. Adult live specimens from SCrB formed a red, moving ‘carpet’ on the surface of whale bones and associated sediments (Fig. 2a, b). In the SDT, specimens formed an undulating carpet on the sediments surrounding the skeleton. Specimens from SCrB faded to yellow-white when preserved. Length up to 40 mm for 91 segments. Body shape elongated with slight tapering at posterior and anterior ends. The long cirri and well developed parapodia give a shaggy and ruffled look (Fig. 2c).

Prostomium reduced, ventrally displaced, not visible dorsally (Fig. 3a). Minute digitiform paired antennae inserted anteroventrally (Fig. 3b). Median antenna, eyes, caruncle, and pronounced nuchal organ absent. Palps small, spherical, inserted ventrally, directly anterior to mouth (Fig. 3a). Elongated ciliary patches present posteriorly and ventrally on prostomium. Retracted proboscis visible through epidermis terminating posteriorly in segment 5–6 (Fig. 2d, e). Feeding apparatus retrieved from segment 5 in dissected small (SDT) specimen only, hyaline, fragile, resembles two stylets attached to each other at

base, length 200 µm, not visible through epidermis (Fig. 4). Feeding apparatus not found in large specimens.

Segment 1 reduced, chaetae and aciculae absent, tentacular cirri dorsal, fusiform, directed forward, partially fused with segment 2 (Fig. 3a). Biramous segments with dorsal and ventral cirri, and dorsal and ventral single aciculae from segment 2 (Fig. 3a, 5a). Parapodial lobes of segment 2 reduced, tentacular cirri directed forward and chaetal fascicles inserted directly on segment. Well developed noto- and neuropodia from segment 3 onwards.

Notopodia with dense ciliary patches on front and back sides. Dorsal cirrus inserted distally, cirrophore weakly developed (Fig. 5a). Notochaetae 10–22 are round spines, inserted distally on notopodia, partly surrounding dorsal cirrus (Fig. 5a, b). Different shaped notochaetae in large and small specimens.

Notochaetae in large specimens: External longitudinal striation, fine frays on convex side of distal half present, serration absent, length <500 µm, width <50 µm (Fig. 6a), internally chambered (Fig. 5b).

Notochaetae in small specimens: External fine longitudinal striation, serration present, denticles



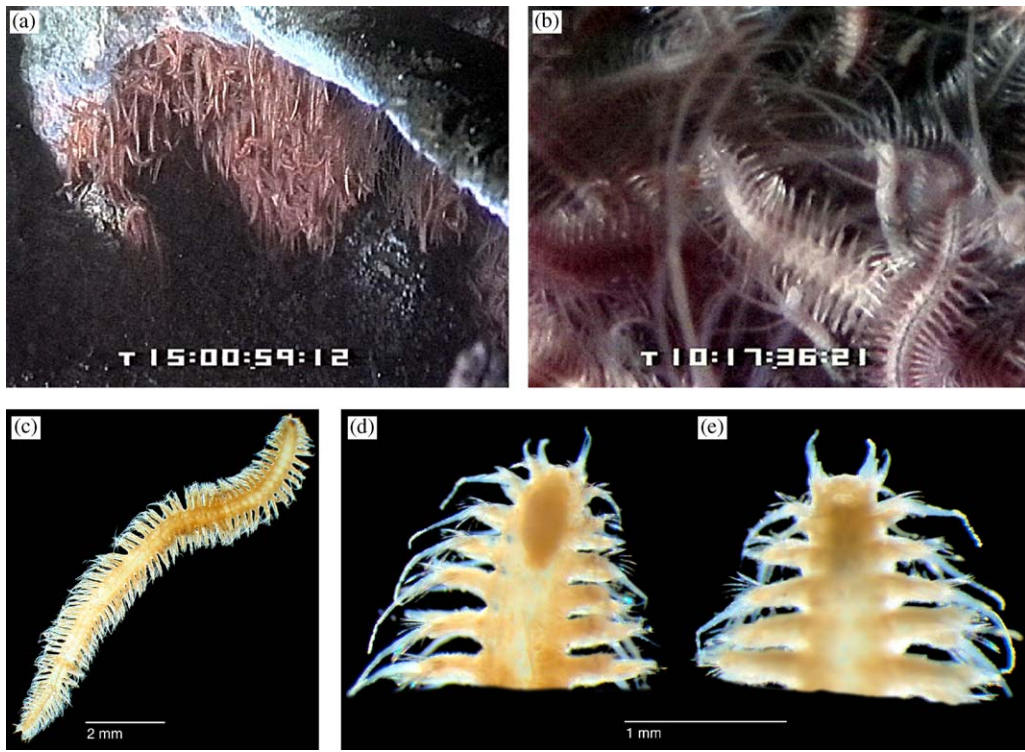


Fig. 2. *Vigtorniella flokati* sp. n., (a) video still from DSV *Alvin* showing colony of worms hanging from the underside of a 35 tonne gray whale vertebrae in the Santa Cruz Basin at 1675 m depth (AD#3485); (b) macro-video detail of above, showing *V. flokati* and an unknown genus and species of ampharetid polychaete; (c) general view of formalin-fixed specimen from Santa Cruz Basin (AD#3485); (d) detail of dorsal surface of head; (e) detail of ventral view of head.

minute, alternating in two directions, length  $<275\ \mu\text{m}$ , width  $<7.5\ \mu\text{m}$  (Fig. 6c), internally chambered.

Neuropodium in mid-body segments slightly longer than notopodium, ventral cirrus inserted basally, posteriorly directed, fusiform with short cirrophore (Fig. 5a). Ciliary patches present but fewer than in notopodium. Single neuroacicula present extending to end of acicular lobe (Fig. 5a). Acicular prechaetal lobe pronounced, pointed (Fig. 5a). Neurochaetae compound unidentate falcigers, bifid heterogomph shafts chambered, inserted distally in two loosely defined groups, upper 3–4 with long slender finely serrated blades (Figs. 5c and 6b, d), lower blades gradually shorter and wider (Fig. 5d).

One transverse row of ciliary patches ventrally on each segment.

Pygidium rounded, reduced, posteriorly flattened, pygidial cirri paired, single pygidial projection absent, anus terminal.

*Distribution:* Only known from depths of  $\sim 1000$ – $1700$  m on northeast Pacific whale falls and experimentally implanted whale bones on the Hawaiian slope.

*Reproduction:* Eggs ( $\varnothing = 50$ – $100\ \mu\text{m}$ ) present in segment 6–9, in large worms only (SCrB). Some of the small specimens from SDT had a bulbous swollen shape and parapodia filled with white matter, possibly spermatids.

*Remarks:* *V. flokati* sp. n. is similar to *V. zaikai* in shape and distribution of lateral antennae, absence of median antennae, appearance of the barrel shaped proboscis, and presence of paired pygidial cirri, but different in cephalisation of anterior segments by the presence of an achaetous

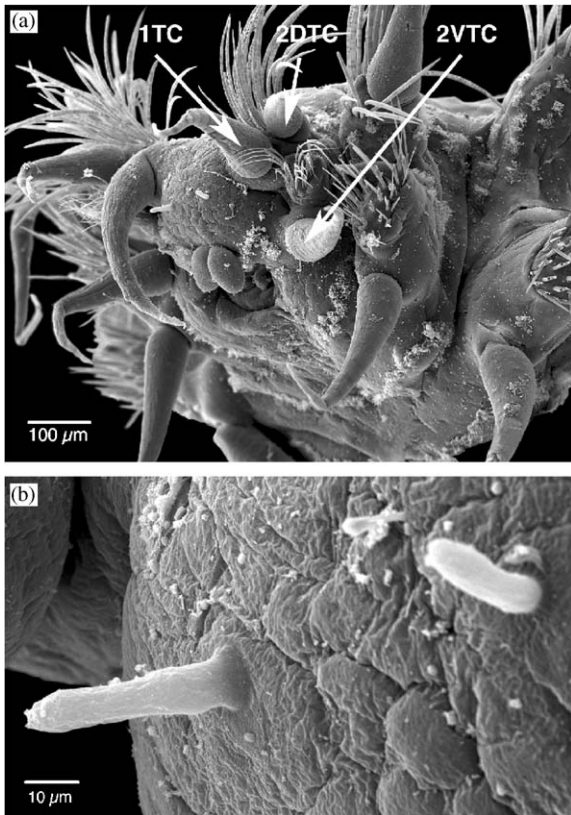


Fig. 3. *V. flokati* sp. n., specimen from Santa Cruz Basin (AD#3485). SEM micrographs of (a) head region and (b) detail of digitiform antennae. Abbreviations: 1TC = tentacular cirri segment 1, 2DTC = dorsal tentacular cirri segment 2, 2VTC = ventral tentacular cirri segment 2.

first segment with dorsal tentacular cirri only, and the absence of plate like jaws. Most known chrysopetalids have a pair of stylet shaped jaws. Small specimens of *V. flokati* sp. n., however, are unique in carrying an articulated apparatus that is small, fragile and probably lost in adults. The whip-like chaetae that are reported from *V. zaikai* are absent in *V. flokati*. This type of chaetae is interpreted as similar to the simple neuropodial chaetae found among the normal compound ones in some chrysopetalids (Dahlgren and Pleijel, 1995).

*V. flokati* sp. n. is further similar to *V. zaikai* in having eggs from segment six onward. Kiseleva (1992) states that the production of gametes takes place in the notopodia beginning at segment six, without giving measurements of the eggs. While the presence of developing and ripe gametes in the parapodia of chrysopetalids has been reported numerous times, detailed information on the distribution of gametes among the segments is often not given. For the chrysopetalid taxon *Strepternos didymopyton*, however, gametes are found in segments 21–51 (Watson Russell, 1997).

*Etymology*: Concentrations of *V. flokati* living on whale bones and on surrounding sediments give the appearance of a Greek ‘flokati’, or shaggy woolen rug.

### 3.2. Phylogeny

The cladistic analysis, based on 46 morphological characters, resulted in three most parsimonious

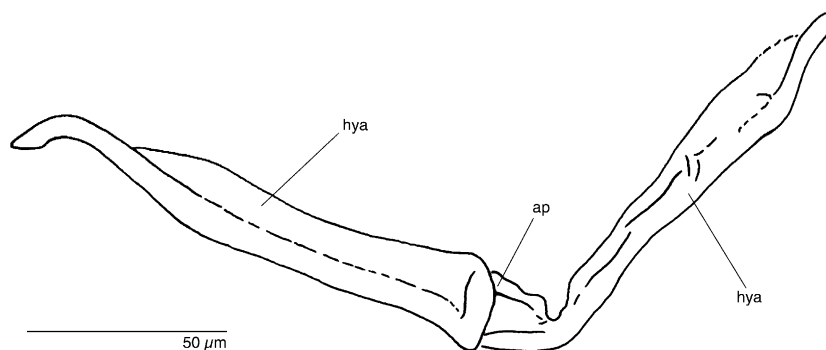


Fig. 4. *V. flokati* sp. n., small specimen from San Diego Trough (ATV 188). Dissected feeding apparatus drawn from compound microscope with aid of camera lucida.



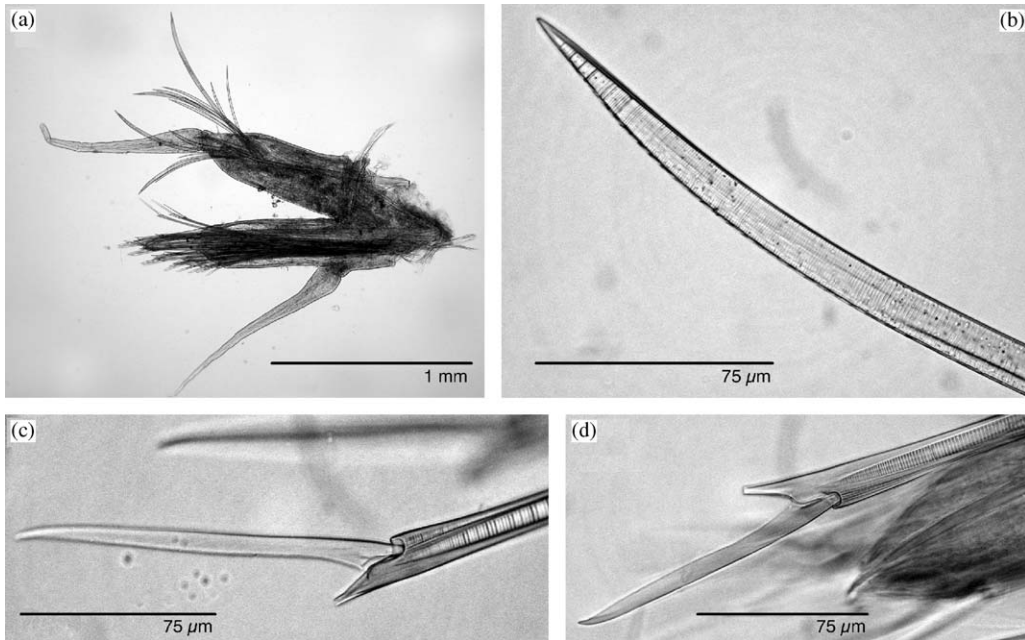


Fig. 5. *V. flokati* sp. n., specimen from Santa Cruz Basin (AD#3485), light micrographs: (a) general view of parapodia from mid-body region; (b) detail of notopodial spine; (c) detail of compound heterogomph neuropodial falsigers from dorsal side of neuropodia; (d) detail of falsigers from ventral side of neuropodia.

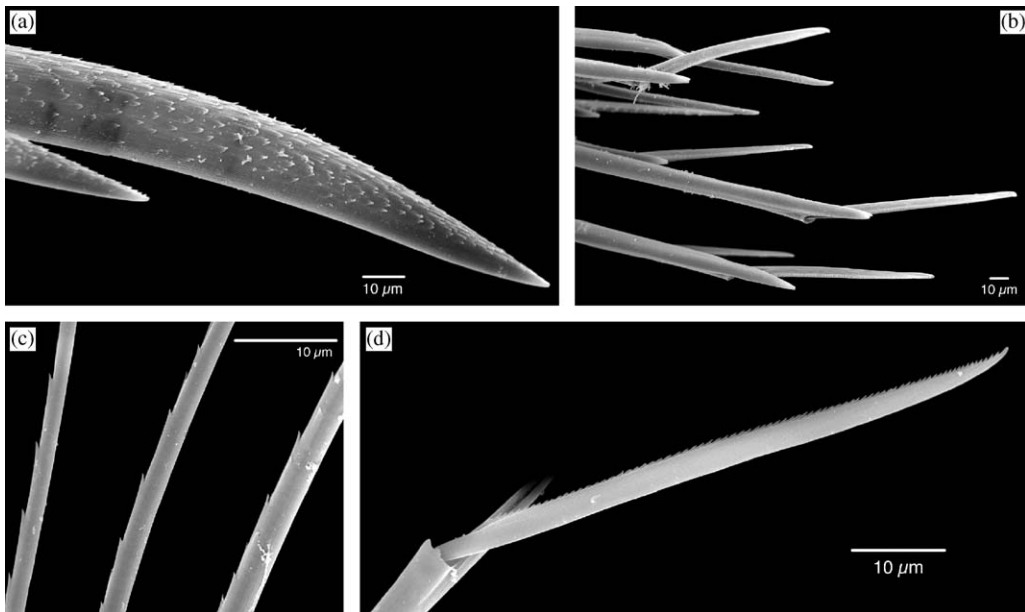


Fig. 6. *V. flokati* sp. n., specimen from Santa Cruz Basin (AD#3485) and San Diego Trough (ATV 188). SEM micrographs of (a) notopodial spine (AD#3485), (b) neuropodial falsiger (AD#3485), (c) notopodial spine (ATV 188), (d) neuropodial falsiger (ATV 188).

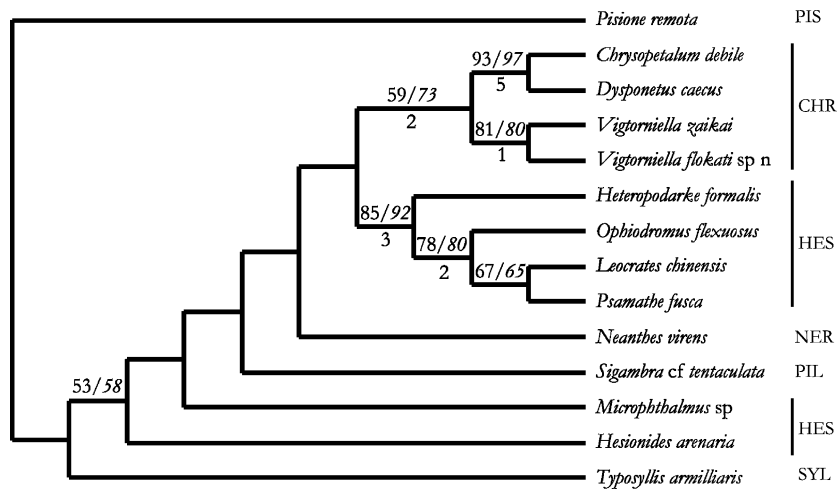


Fig. 7. *V. flokati* sp. n. phylogeny in a cladistic analysis of 13 nereidiform taxa with *Pisone remota* as the outgroup. One of three shortest trees (98 steps, CI = 0.4694, RI = 0.6312). Bootstrap (upright) and jackknife (italic) values are given above branches and Bremer support under branches. Capitalized abbreviations following species names indicate their current family assignment: CHR, Chrysopetalidae; HES, Hesionidae; NER, Nereididae; PIL, Pilargidae; PIS, Pisionidae; SYL, Syllidae.

trees with a length of 98 steps (Fig. 7). In all most parsimonious trees, *V. flokati* sp.n. and *V. zaikai* form a clade that is a sister group to the two included chrysopetalid taxa *Dysponetus caecus* and *Chrysopetalum debile*. The clade consisting of *V. flokati* and *V. zaikai* has bootstrap and jackknife support of 81 and 80, respectively, and a Bremer support of 1. The hypothesis of a clade including *Vigtorniella* and the two chrysopetalids is supported by bootstrap and jackknife values of 59 and 73, respectively. For this clade, the Bremer support is 2. Except for the included hesionid taxa, the rest of the tree has weaker support, in agreement with the analysis of the original dataset (Plejdel and Dahlgren, 1998).

3.3. Growth and size

Forty specimens were measured, and ranged from 0.49 mm in length for 8 chaetigers, to 29 mm length for 80 chaetigers (Fig. 8). (The type specimen is 40 mm for 91 segments.) There were significant differences in size of specimens between geographical populations and sampling devices. The largest specimens came from *Alvin* slurp-gun samples collected in the SCrB (mean length 14.73 mm, n = 17), the next largest came from

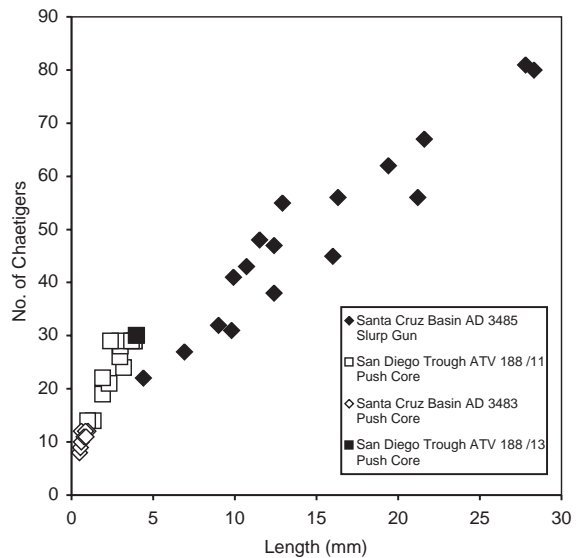


Fig. 8. Relationship between the number of chaetigers and total body length in 40 specimens of *V. flokati* sp. n. in different geographical localities and sampling methods.

push cores collected at the SDT site (mean length of 2.83 mm, n = 15), and the smallest from the push cores in the SCrB (mean length 0.72 mm, n = 8). ANOVA analysis indicates significant differences between these groups (p < 0.01). There

does not appear to be any upper limit to chaetiger number, and specimens from within geographical groups show a near linear relationship between chaetiger number and body length (Fig. 8).

### 3.4. Ecology

We observed *V. flokati* sp. n. living in colonies on the surfaces of whale bones and on adjacent sediments at carcasses that had been on the seafloor for 4–18 months, at water depths between 1057 and 1675 m. In situ observations from remotely operated vehicles and the DSV *Alvin* showed a writhing mass of large, visible, worms on the surface of the bones (SCrB, Fig. 2a), or a carpet of worms undulating in the current on sediments within 1–2 m of the skeleton (SDT). The majority of specimens appeared to adhere to the bones or sediments with their posterior ends. In some colonies, the specimens were hanging from the underside of the whale vertebrae (Fig. 2a). Some specimens appeared to be swimming anterior-end forwards through the colony (Fig. 2b). An undescribed new genus and species of ampharetid polychaete was present in close association with the colonies of *V. flokati* sp. n. on the SCrB skeleton, and dorvilleid polychaetes were mingled with *V. flokati* in sediment samples from the SDT. Small, possibly juvenile, specimens of *V. flokati* sp. n. were present in both the sediments and on the surface of the whale bones. All of the specimens from the implanted Hawaii bones appeared to be juveniles. Although *V. flokati* sp. n. attained extremely high abundances and biomass on the SDT and SCrB whale skeletons, we saw no evidence of predation occurring on these worms at these sites. In Hawaii, however, large numbers of galathaeid crabs covered the surfaces of the implanted bones, potentially preying on the worms.

## 4. Discussion

### 4.1. Taxonomic comparison

The new polychaete taxon described in this paper, *V. flokati*, appears to be the sister taxon to

*V. zaikai* (Fig. 7). The characters that were emphasized by Kiseleva (1992) as justifying the erection of a new chrysopetalid genus are chiefly related to the anterior end. Within Chrysopetalidae, the lack of median antenna, the presence of (noto-) chaetae in segment 1, the presence of simple, whip-like neurochaetae in segment 2, and the plate-like jaws, are all autapomorphic characters (notochaetae of segment 1, however, are also stated as present in *D. bulbosus* Hartmann-Schröder, 1982). Additionally, *Vigtorniella* possesses paired pygidial appendages, present in paleate chrysopetalids and *Acanthopale* San Martin, 1986.

Due to the problems associated with the original description of *V. zaikai* from laboratory-reared larvae only, this taxon was not included in a cladistic analysis of chrysopetalid genera by Dahlgren and Pleijel (1995). Morphology of the adult specimens of *V. zaikai* recently discovered in the Black Sea (see above) is in agreement with the morphological description of reared larvae (*V. E. Zaika* in lit.) which allowed us in this paper to include *V. zaikai* in the Nereidiformia analysis. Since the analysis indicated a clade consisting of the new worm (*V. flokati* sp. n.) and *V. zaikai*, we have at this point no reason to name a new clade (i.e., genus) for *V. flokati* sp. n. Further, our analysis supports the inclusion of *Vigtorniella* within the Chrysopetalidae and we suggest that the revised diagnosis of *Vigtorniella* Kiseleva, 1996 is: Chrysopetalid with spinigerous notosetae, absence of median antenna, barrel shaped proboscis, and paired pygidial cirri.

### 4.2. Growth and size

The apparent size discrepancy between geographical populations (Table 1, Fig. 8), and size-related changes in the ultrastructure of the notopodial spines (Figs. 6a, c), led us to initially conclude that there was more than one species of *Vigtorniella* present on these whale-falls. However, closer examination of the spines from intermediate-size individuals indicates that the morphological changes are most likely ontogenetic in nature. Additionally, the change in size from small specimens to large is in fact continuous, with both small

and large specimens represented at the Santa Cruz Basin site (Fig. 8). The minute specimens from Hawaii are almost certainly juveniles. The specimens from the SDT site, although significantly smaller than the slurp gun material from SCrB, appeared to contain spermatids, although this could not be confirmed. Material preserved for DNA analyses are at present only available from a few large SCrB specimens, preventing a genetic assessment.

These patterns would seem to indicate that the small worms found at SDT constitute a cohort, the first offspring of very few founders. The mixed sizes observed at the older SCrB carcass may be a result of recruitment from more than one local reproduction event. This hypothesis could be confirmed with population genetic analyses and could imply a lecithotrophic larval type with dual dispersal options that can either settle immediately to rapidly populate an existing site or spend a significant time in the plankton for long-distance dispersal (Shilling and Manahan, 1994; Young et al., 1997; Tyler and Young, 1999; Marsh et al., 2001). Other chrysopetalid larvae have been described as “initially lecithotrophic” (Blake, 1975) or simply as lecithotrophic (Cazaux, 1968). Alternative hypotheses that may explain the skewed size distribution pattern include different growth rates due to variation in environmental conditions (e.g., Thiebaut et al., 2002), analogous to differences in growth rates found at a small spatial scale at vent sites (De Bevoise and Taghon, 1988). Accordingly *V. flokati* sp.n. would only grow to full adult size on larger whale carcasses. Small vertebrae and sediments surrounding a carcass may harbor juveniles and/or young adults only. The occurrence of a feeding apparatus only in smaller specimens is consistent with an ontogenetic shift in feeding behavior. The presence of jaws in small specimens may, however, only be a phylogenetic constraint as in *V. zaikai* (Kiseleva, 1992) and of no ecological importance here.

#### 4.3. Ecology

Recent ecological investigations of both natural and implanted whale-carcass communities at bathyal depths off California demonstrate a series of

successional stages (Smith et al., 1998, 2002). Small to moderately sized whale carcasses remaining on the seabed for 4–18 months have been stripped of soft tissue, and support dense assemblages of opportunistic polychaetes and cumaceans. Sediments within one meter of the skeletons exhibited extraordinary macrofaunal abundances (up to 45,000 individuals  $m^{-2}$ ) roughly 20-fold greater than in background sediments, and species richness in the bone epifaunal community and adjacent to the whale falls was strongly reduced (Baco-Taylor, 2002; Smith et al., 2002). High density, low diversity assemblages of opportunistic organisms are characteristic of organically enriched sediments in shallow-water habitats (e.g. Pearson and Rosenberg, 1978) and in the deep sea (e.g., Levin et al., 1994). Abundant taxa around the whale falls during this stage included the dorvilleid *Ophryotrocha* sp., and the species described here, *V. flokati* sp. n. The genus *Ophryotrocha* frequently colonizes organically enriched sediments, but is rare in nutrient-poor sediments at all depths, hence its characterization as an enrichment opportunist (Levin and Smith, 1984; Levin et al., 1994, 2000; Dahlgren et al., 2001). It seems probable that *V. flokati* sp. n. is also an enrichment opportunist and, like other potential whale-fall endemics, is attracted by some cue associated with the lipid-rich cetacean remains (Allison et al., 1991; Smith and Baco, 2003). Preliminary results suggest that specimens morphologically similar to *V. flokati* sp. n. occur in the eutrophic benthos underlying a Norwegian fish farm (Dahlgren, unpublished data) raising the possibility that *V. flokati* sp. n. is widely distributed.

The feeding ecology of *V. flokati* sp. n. remains enigmatic. Chrysopetalids, in general, are omnivorous species with stylet-like jaws and an eversible pharyngeal structure (Dahlgren, 2000), yet the observed behavior of *V. flokati* sp. n. and the apparent absence of jawed structures in the adult specimens suggest an alternative feeding strategy. While many individuals exhibited high activity, none were observed feeding directly on the whale bones or sediments. Eversion of the pharynx was not recorded and guts of collected adult specimens appeared to be empty. Nonetheless, stable isotopic analyses yielded  $\delta^{13}C$  and  $\delta^{15}N$  values consistent with assimilation of whale soft tissue at the SDT

whale fall, and whale bone organics and soft tissue at the SCrB skeleton (Smith and Baco, 2003). The unknown species of ampharetid, observed in close association with *V. flokati* sp. n., were also highly motile, and repeatedly extended and retracted the buccal tentacles, as is observed for many deposit-feeding ampharetids. *V. flokati* sp. n. does not possess these feeding structures. Additionally, it seems unlikely to be preying on the ampharetid, since *V. flokati* sp. n. was in much higher abundance. We hypothesize that *V. flokati* sp. n. is utilizing dissolved organic material emanating from whale soft tissue and bones. Since all known chrysopetalids possess a feeding apparatus, the tiny jaw observed in small specimens may be a vestigial structure without any adaptive value.

Larval ecology and life history traits could be very different for the two *Vigtorniella* taxa. While *V. zaikai* is found in a large and presumably relatively stable environment (the oxic/anoxic boundary in the Black Sea), the opposite is true for *V. flokati* sp. n. The enrichment opportunist stage harboring *V. flokati* sp. n. appears to persist on whale falls for months to few years (Smith et al., 2002; Smith and Baco, 2003) and whale falls are clearly small habitat islands at the deep-sea floor. The dynamics of these ephemeral island habitats resemble those of decaying wood and hydrothermal vents at the deep-sea floor and we hypothesize that the larval ecology of *V. flokati* sp. n. may resemble those of many wood-fall and vent specialists, allowing both broad dispersal across the deep-sea floor as well as effective local recruitment at a new site (Turner, 1973; Tunnicliffe, 1991; Tyler and Young, 1999; Marsh et al., 2001). It is intriguing to note that larvae of *V. zaikai* can survive for very long periods in the laboratory, persisting for more than eight months before metamorphosis when held in complete darkness above oxygen-depleted sediment (Sergeeva et al., 1999). Similar larval longevity would confer very broad dispersal abilities on *V. flokati* sp. n.

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