

Two New Species of *Spiochaetopterus* (Polychaeta: Chaetopteridae) from Okinawa, Japan, with Notes on Pacific *Spiochaetopterus*¹

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ABSTRACT: Two new species of *Spiochaetopterus* are described from recently collected material from sandy substrates at Bise Beach and Sesoko Island in northern Okinawa, southern Japan. These two new species, *Spiochaetopterus okinawaensis* and *S. sesokoensis*, are similar in body size but differ with respect to presence or absence of eyes, bilobed or unilobed B1 neuropodia, and morphology of the specialized modified A4 chaeta. In *S. okinawaensis* there are oculate spots on the lateral side of the prostomium, neuropodia of segment B1 are unilobed but those on the other segments are bilobed, and the tube lacks periodic rings. There are no oculate spots in *S. sesokoensis*; all the neuropodia of the B segments are bilobed, including B1; and the ventral gland in the anterior A region lacks a pale white crescent.

NISHI AND ARAI (1996) recently reported four chaetopterid polychaete species from the sandy bottom of Sesoko Island, Okinawa, Japan, one of which was identified as *Spiochaetopterus costarum costarum* Claparède. The morphology of the specialized modified chaeta of A4 (see below for terminology) differs markedly from that of Mediterranean specimens of *S. costarum*. One of us (M.B.) considered this difference to be of specific value. Apart from the systematic aspects, this genus is also of ecological interest because of the dispersal ability of a planktonic larval stage of long duration (Bhaud 1966, Bhaud and Cazaux 1988, Scheltema 1971, 1974). Scheltema (1981, 1986) suggested that larval transport plays an important role in dispersal of contemporary benthic species along both the coastlines of continents and across

great expanses of open ocean. Species with teleplanic or long-distance larvae have the capacity for widespread dispersal and, accordingly, a large geographic range. *Spiochaetopterus* provides an opportunity to test this generalization because the genus is widely distributed and the number of recognized species (about 12 [Fauchald 1977] with the addition of *S. solitarius* (Rioja, 1917) by Bhaud et al. [1994]) is relative small. If larvae really do have a marked ability to disseminate, then it should be possible to obtain samples of the same species at two extreme locations of ocean. This hypothesis has been substantiated by detailed morphological analyses of the specialized chaeta borne by the A4 segment, the fourth segment in the anterior region of species of *Spiochaetopterus*, in an initial survey of species in the Atlantic-Mediterranean biogeographic area where no species were found to be common to both sides of the Atlantic (Bhaud 1998a). This paper represents the first attempt to address the question of utilizing the same test in the Pacific Ocean.

Two subspecies of *Spiochaetopterus costarum* have been reported from Japan, *S. costarum okudai* (Gitay 1969) and the subspecies reported as *S. costarum costarum* by Nishi (1996) and Nishi and Arai (1996), herein described as a new species. Recently

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Nishi et al. (1999) described *S. sagamiensis* from a cold-seep site off Hatsushima in Sagami Bay.

MATERIALS AND METHODS

The material was collected by hand by gently digging in the sand to free tubes from the sediment. Worms were taken alive to the laboratory, sorted, and examined before they were fixed. They were removed from the tubes, placed in 10% neutralized formaldehyde, and after 1 or 2 days transferred to 70% ethanol. Fixed materials were examined with a dissecting microscope and later prepared for scanning electron microscopy (SEM).

Because Bhaud (1998a) has shown for Atlantic species that the morphology of the A4 chaeta may be diagnostic at the species level, a detailed description of this feature is a requirement in any description of a new species. The specialized chaetae are organized such that the body of the chaeta consists of two parts, a shaft and a swollen tip, the boundary lying where the diameter of the cross section of the shaft begins to increase. The swollen tip is divided into two parts at the point of maximum diameter, the upper part (head) and the lower part (collar), which forms the base of the head. The head is obliquely truncated by an upper oblique plane. This plane defines a dorsal and a ventral side, opposite to, and on the same side as, the plane of truncation.

An SEM was used for detailed observation of the A4 modified chaetae. The chaetae were dissected from the tissue, and the shaft was cleaned with KOH, washed in three changes of distilled water, and transferred through a graded ethanol series (70, 80, 90, 95, 99, and 100%), each for 10 to 20 min. Before observation they were transferred to 100% methanol (France) or acetone (Japan), air dried, mounted on a grid with double-sided sticky tape, and coated with gold-palladium on a Hitachi Ion Sputter E-1030. Observations were conducted on an SEM (a Hitachi S-520 in France, University of Perpignan, and a Hitachi S-800 in Japan).

For observation of uncini, temporary mounts of uncini were made. Some parapodia were dissected, rinsed with freshwater, squashed under a cover glass, and drawn with the aid of an Olympus drawing apparatus. Drawings of trunks and tubes were made from alcohol-preserved specimens with the aid of the Olympus drawing apparatus.

Terminology for body regions and parapodia of regions A, B, and C follows Bhaud et al. (1994). The anterior, middle, and posterior body regions are herein designated A, B, and C, respectively; A4, chaetiger 4 in region A; B2, chaetiger 2 in region B, etc. (Bhaud et al. 1994). The type material is deposited in the Natural History Museum and Institute, Chiba (CBM); a few specimens have also been deposited at the Zoological Museum, University of Copenhagen (ZMUC), the Observatoire Océanologique de Banyuls-sur-Mer (OOB), and the Coastal Museum of Natural History (CMNH).

SYSTEMATIC TREATMENT

Family CHAETOPTERIDAE Malmgren, 1867
Genus *Spiochaetopterus* M. Sars, 1853

Small, slender chaetopterids with a pair of palps, lacking a pair of tentacular cirri. A single large, modified cutting chaeta on each parapodium of A4.

Spiochaetopterus okinawaensis Nishi & Bhaud, n. sp.

Figures 1A, B, 2, 3, 4A–C

Spiochaetopterus costarum costarum Nishi, 1996: 37–40, figs. 1–2; Nishi and Arai, 1996: 52–56, 56–60, figs. 1L–K, 5A–J, 6, Table 1 [not Claparède (1870)].

TYPE MATERIAL: Holotype: CBM-ZW302, complete, unstained, without tube, Bise Beach, Motobu, Okinawa Island, sandy bottom, 1–2 m deep, 10 February 1995, collected by E. Nishi.

Paratypes: CBM-ZW303 (2 worms, one complete, and one separated into two parts in the middle region), zw304 (1 worm), zw305 (1 worm), zw306 (1 worm), zw307 (1 worm),

zw308 (2 worms), zw309 (2 worms), zw310 (1 worm), zw311 (1 worm), unstained, without tubes, collection data as for holotype.

DIAGNOSIS: Oculate *Spiochaetopterus* of small size, minute eyes on the outer flanks of prostomium, with specialized modified A4 chaeta cordate in end view, marked dissymmetry of the two lobes of the ventral edge of blade, shaft with groove along its whole length; region A with ventral gland brown on A7 and pale white on A8 to A9; region B with about 15 to 30 segments, neuropodia unilobed on B1, bilobed on remainder. Tube flimsy, soft, tough in parts. Body size: Length 12 to 25 mm (total length 10.8 mm, A + B, 6.8 mm in zw302; 14 mm long in zw303; 16 mm in zw304; 17 mm in zw307), slender and fragile, body width 0.5–1 mm (tube width about 0.5–1 mm; 0.8–0.9 mm width in holotype), complete fixed worms up to 30 mm long, with up to 90 chaetigers (8–9A + 10–25B + 10–65C; $n = 15$; 9A + 15B + 17C in holotype; 9A + 15B + 40C in zw303; 9A + 18B + 40C in zw304; 9A + 20B + 60C in zw307). Color: Anterior and middle regions creamy white, posterior region brown or dark brown, partly greenish brown.

DESCRIPTION: Region A (anterior region) long and narrow, with 9 segments. Peristomium horseshoe shaped (Figure 1A,B), marked within the rim by a brownish band. A pair of minute eyespots on lateral inner side of prostomium, visible in dorsal view when palpi omitted or dorsal side of peristomium retracted. Peristomium much larger than prostomium, shape in fixed materials strongly contracted. Two long, grooved palpi (Figure 1B), yellow line inside bottom of groove, arising dorsally just posterior to eyespots, at junction of lateroposterior border of prostomium and posterior limit of peristomium. No tentacular cirri posterior to palpi. Middorsal ciliate groove beginning between bases of palpi and continuing posteriorly throughout region A, deeper in region B, ending in conspicuous dorsal cupule on B2 through B1 extended notopodia, anterior to notopodia of B3, where all food particles converge, finally ending in pygidium. Ventral

surface of region A with long, slender plastron (ventral glands) (Figure 1A), wider anteriorly and posteriorly, with whitish glandular areas on A8–A9, A7 posteriorly with a brownish gland area. Ventral A1–A7 with conspicuous brown longitudinal strips covering plastron; anterior to A6 creamy white preserved and in life, prominent dark or pale brownish hemispherical area at level of A6–A7, with transverse border of hemisphere at level of A7 chaetae, following pearly white and glandular areas. A1 to A3 with single row of 6 to 10 slender chaetae with bordered margins (Figure 2E,F).

On A4 a single specialized modified chaeta with obliquely cordate, asymmetrical, slightly concave, modified heart-shaped head, yellow or light brown (Figures 2A–D, 4A–C). Notch or sinus of ventral edge of modified chaeta oriented toward middle line and anterior part of body. Two ventral lobes separated by this notch dissimilar. Longer edge of upper triangular tip facing outward, ventral edge of the two lobes always marked; upper plane of the section oblique. Distal part 100 μm long, 120 μm wide; shaft 360 μm long, 50 μm wide in the middle portion. This chaeta accompanied dorsally by 3–5 slender, lanceolate chaetae. A5–A9 with a single row of 10–15 slightly brownish, asymmetrical lanceolate chaetae and 3–5 extended bordered chaetae (Figure 2E); dorsalmost lanceolate chaetae longest and most slender, ventralmost chaetae gradually becoming shorter and wider, lanceolate chaetae folded leaflike, the surface smooth, edges serrated (Figure 2F).

Region B (median region) with 18–25 segments ($n = 15$). Segments elongate, glandular dorsally, B1 and B2 longer than following segments (Figure 2K,L). B1 bearing a pair of biramous notopodia (Figures 1A, 2L), B2 bearing a cupule that disappears in preserved specimens. Parapodia of region B biramous, both rami subdivided; notopodia trilobed, foliaceous, composed of a bilobed Y-shaped inner part, cirriform inner and outer side, and a slightly longer unilobed, cirriform inner lateral side (Figure 2M). Posterior notopodia with smaller lobes, Y-shaped inner lobe and lateral lobe widely separated (Figure 2M). Neuropodia fleshy

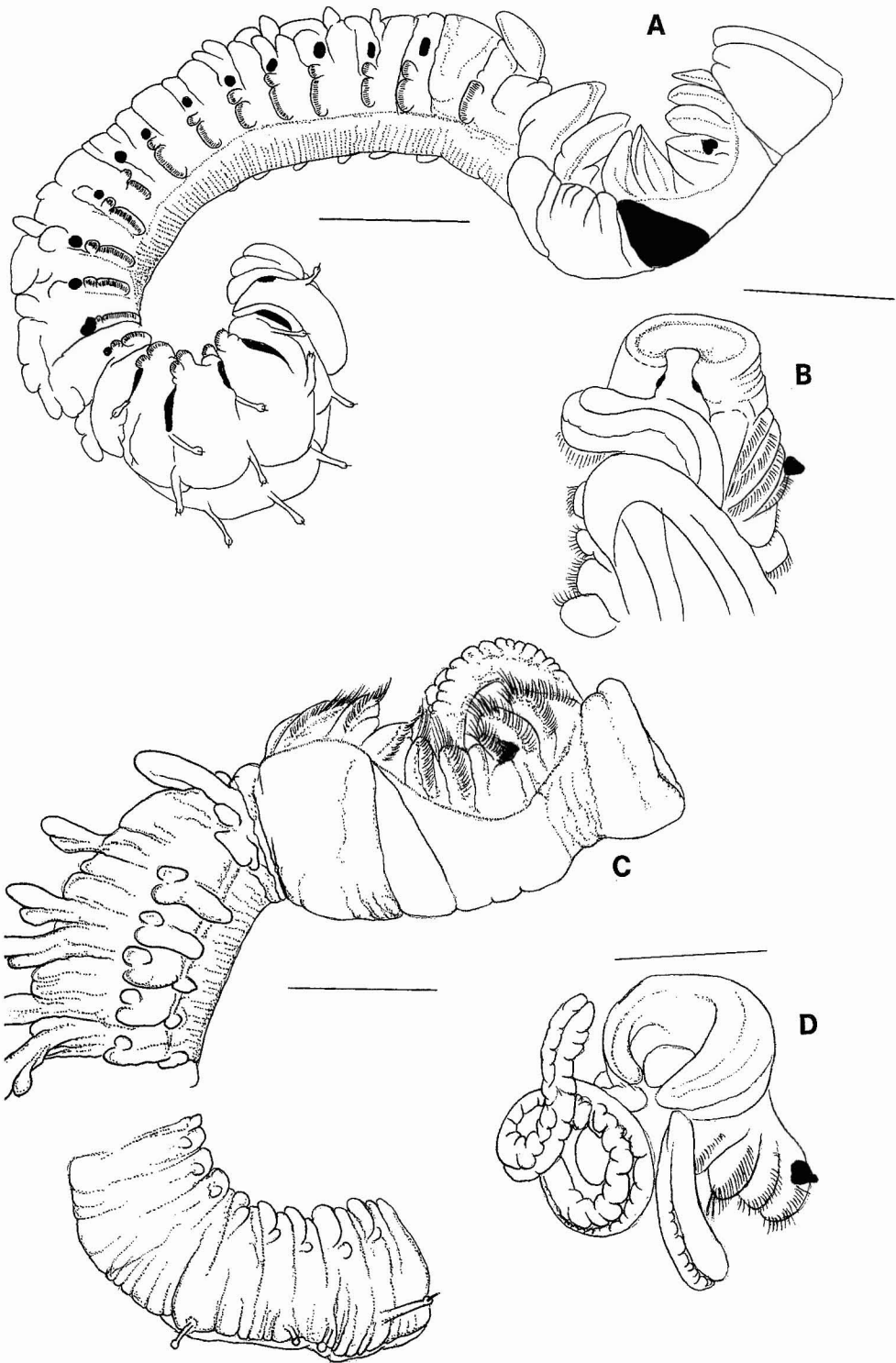


FIGURE 1. Holotype of *Spiochaetopterus okinawaensis* (A,B) and *S. sesokoensis* (C,D). A, Lateral view of whole body; B, dorsal view of anterior region; C, lateral view; D, dorsolateral view of anterior region. Scale lines = 1 mm.

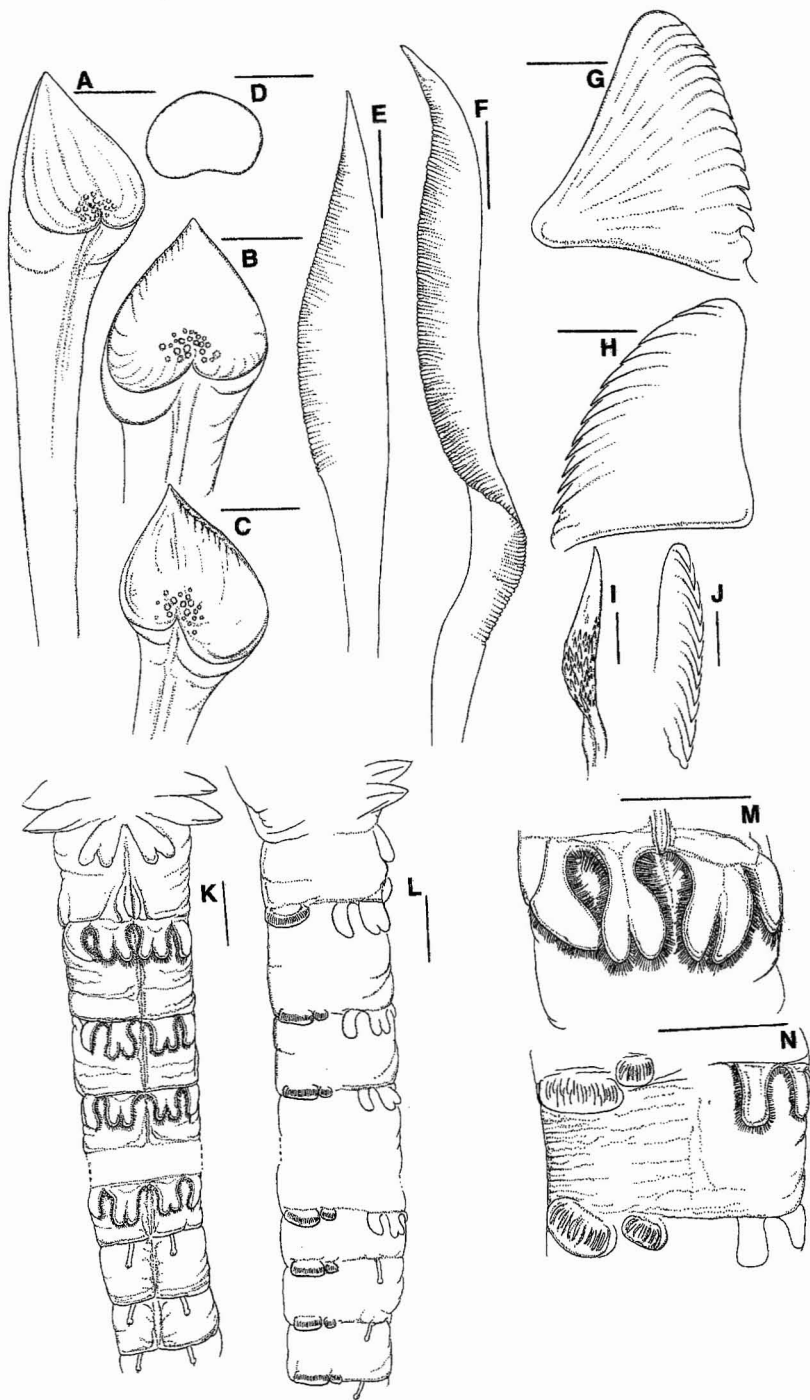


FIGURE 2. *Spiochaetopterus okinawaensis*. Chaetae and uncini (A–J) and B and C regions (K–N). Partly drawn from SEM micrographs. A–D, Specialized modified chaeta (seta) of A4, anterior part (A–C) and cross section of the shaft (D); E and F, A region chaetae; G and H, B region uncini; I, lanceolate chaeta of C notopodia; J, C region uncini; K, dorsal view of posterior A region, B region, and anterior C region; L, lateral (left) side view of K; M, B region neuropodium; N, lateral view of B region. Scale lines are 50 μ m (A–D), 10 μ m (E,F), 5 μ m (G–J), and 0.5 mm (K–N).

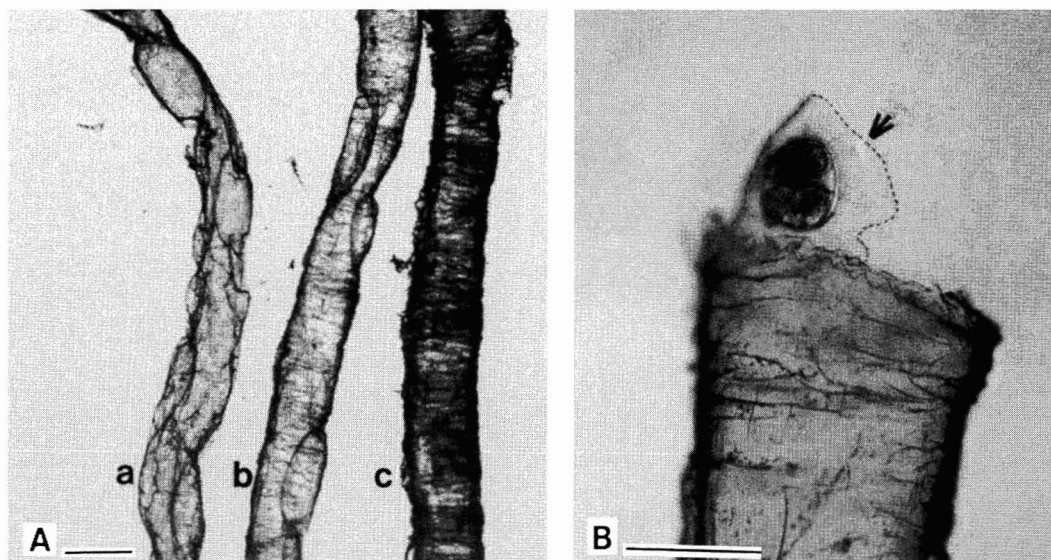


FIGURE 3. *Spiochaetopterus okinawaensis*. A, Tubes in three states, a, flimsy tube; b, soft, with some annulations; c, hard with annulations. B, Serrations on the mouthparts with partition (arrow). Scale lines are 1 mm (A) and 0.5 mm (B).

lobes with uncini (uncinal plate), biramous except for B1, which is uniramous; neuropodia of B1 with lower lobe only, those of B2 and following segments with short, rounded, anteriorly oriented upper lobe and transversely elongate, posteriorly oriented lower lobe.

Uncini deposited in lobe oriented at an angle, each tooth row facing the connected part of lobe (Figure 2L,N). Uncini bluntly triangular, with single row of minute teeth (14–16, $n = 10$) visible only at higher magnification (Figure 2G,H). B1–B3 with 15–20 uncini, B7–B10 with 30–40 uncini (in a specimen with 20 B segments). A pair of brown spots present on lateral side of B2 to B10, position and number of spots varied: on B2–B5 in holotype (zw302), with 15 B segments; on B2–B5 in zw304, with 18 B segments; on only B3 in zw311, with 20 B segments; and brown spots absent in zw307 and zw310.

Region C (posterior region) with 20–70 segments ($n = 15$). Parapodia all biramous; notopodia unilobed, digitiform, distally swollen and with 1–3 slightly enlarged lanceolate

chaetae (Figure 2J); neuropodia subdivided as in region B: each lobe rounded, upper dorsal lobe oriented anteriorly, lower lobe oriented posteriorly. Uncini similar to those of region B, with 13–15 teeth (Figure 2J). Pygidium simple, with slight dorsal notch, anus terminal, surrounded by pygidial lobes.

Tube oriented vertically in the substratum, with opening at uppermost end and greater part of the tube below surface of substratum. Tubes also distributed between bases of *Thalassia* roots and coral rubble. Tubes straight, long, slender, fragile or slightly tough, of three types: A, flimsy, of a restricted number of secreted layers, wall easily distorted, no circular structures visible (Figure 3A, a); B, tube wall consisting of several layers of secretion, wall solid, not distorted, circular fold visible (Figure 3A, b); C, tube with thick wall consisting of a large number of secreted layers, circular folds not located as periodic rings but spread the length of the tube (Figure 3A, c). Many fragments of tube at various stages of growth without periodic rings. Some tubes with serrations at tube opening and internal septa (Figure 3B). Highest den-

sity found about 10–20 individuals per 500 cm² (winter of 1994–1995).

ETYMOLOGY: The name is derived from the type locality, Okinawa Island.

REMARKS: The lack of periodic rings in the tubes in *S. okinawaensis* distinguishes this species from other species and subspecies (where descriptions are available) known from the Pacific. Rings were absent in all observed fragments of tubes of *S. okinawaensis* at various stages of growth (Figure 3), indicating that lack of rings is not characteristic of specific parts of tubes. This lack of rings in *S. okinawaensis* is analogous to the Atlantic situation, where *S. bergensis* has tubes without rings in contrast to the ringed tubes of *S. typicus*, and *S. oculatus* has tubes without rings in contrast to the ringed tubes of *S. costarum* and *S. solitarius*.

Regeneration occurs by the progressive addition of new segments as described by Nishi (1966) rather than by the simultaneous development of new segments as observed in *S. solitarius* in the Mediterranean (Bhaud 1998b).

Spiochaetopterus sesokoensis Nishi & Bhaud, n. sp.

Figures 1C–D, 4D–F

TYPE MATERIAL: Holotype: CBM-ZW70, complete, without stain, without tube (except for a small fragment), beach, Sesoko Island, Motobu, Okinawa Island, sandy bottom, 1–2 m deep, 10 February 1995, collected by hand by E. Nishi.

Paratype: CBM-ZW700 (1 worm), collection data as for holotype.

DIAGNOSIS: Nonoculate *Spiochaetopterus* of small size, with specialized modified A4 chaeta cordate in end view, shaft without longitudinal groove; region A with ventral gland brown on A7 and cream colored on A8 to A9; region B with about 15–30 segments, with all neuropodia biramous. Body size: Holotype length 20 mm, paratype length 25 mm (A + B; holotype 12 mm; paratype 15 mm); slender and fragile; body width 0.8–1.1 mm (tube width about 1 mm), with up to 90 chaetigers (9A + 17–22B + 50–

60C; $n = 2$). Color: Anterior and middle regions creamy white, posterior region brown or dark brown, partly greenish brown.

DESCRIPTION: Region A (anterior region) long and narrow, with 9 segments. Prostomium ovoid (Figure 1C,D). Eyespots absent. Peristomium covering prostomium, nearly same height (Figure 1C), shape in fixed materials strongly contracted. Two long, grooved palpi, without coloration. No tentacular cirri posterior to palpi. Middorsal ciliated groove beginning between bases of palpi and continuing backward along whole length of body. Ventral surface of region A with long, slender plastron (ventral glands) (Figure 1C), widest anteriorly and posteriorly, with extended bulbous areas on A8–A9, with a light brownish glandular area on posterior of A7. Ventral A1–A7 with longitudinal stripes covering plastron; anterior to A6 creamy white preserved and in life, prominent dark or pale brownish hemispherical area at level of A6–A7, following glandular areas. A1 to A3 with single row of bordered or slender leaflike chaetae on each parapodium, A4 with a single dorsally and distally swollen, obliquely cordate, asymmetrical, slightly concave specialized modified chaeta (Figure 4D–F), yellow, with many pits on convex side, shaft without groove and with 3–5 slender, lanceolate chaetae posterior to modified chaeta. A5–A9 with a single row of slightly brownish, asymmetrical lanceolate chaetae and extended bordered chaetae. On the A4 segment, a specialized modified chaeta, obliquely triangular in section, occurs singly. Oblique plane of this distal section heart-shaped, as in *S. okinawaensis*, with notch or sinus facing middle line and anterior part of body. Longer edge of oblique plane external. Distal part 100 μ m long, 120 μ m wide; shaft 450 μ m long, 60 μ m wide in the middle portion.

Region B (median region) with 17–22 segments ($n = 2$). Segments elongate, glandular dorsally, B1 and B2 longer than following segments. Parapodia of region B biramous, both rami subdivided; notopodia trilobed, foliaceous, composed of a bilobed, Y-shaped inner part, cirriform inner and

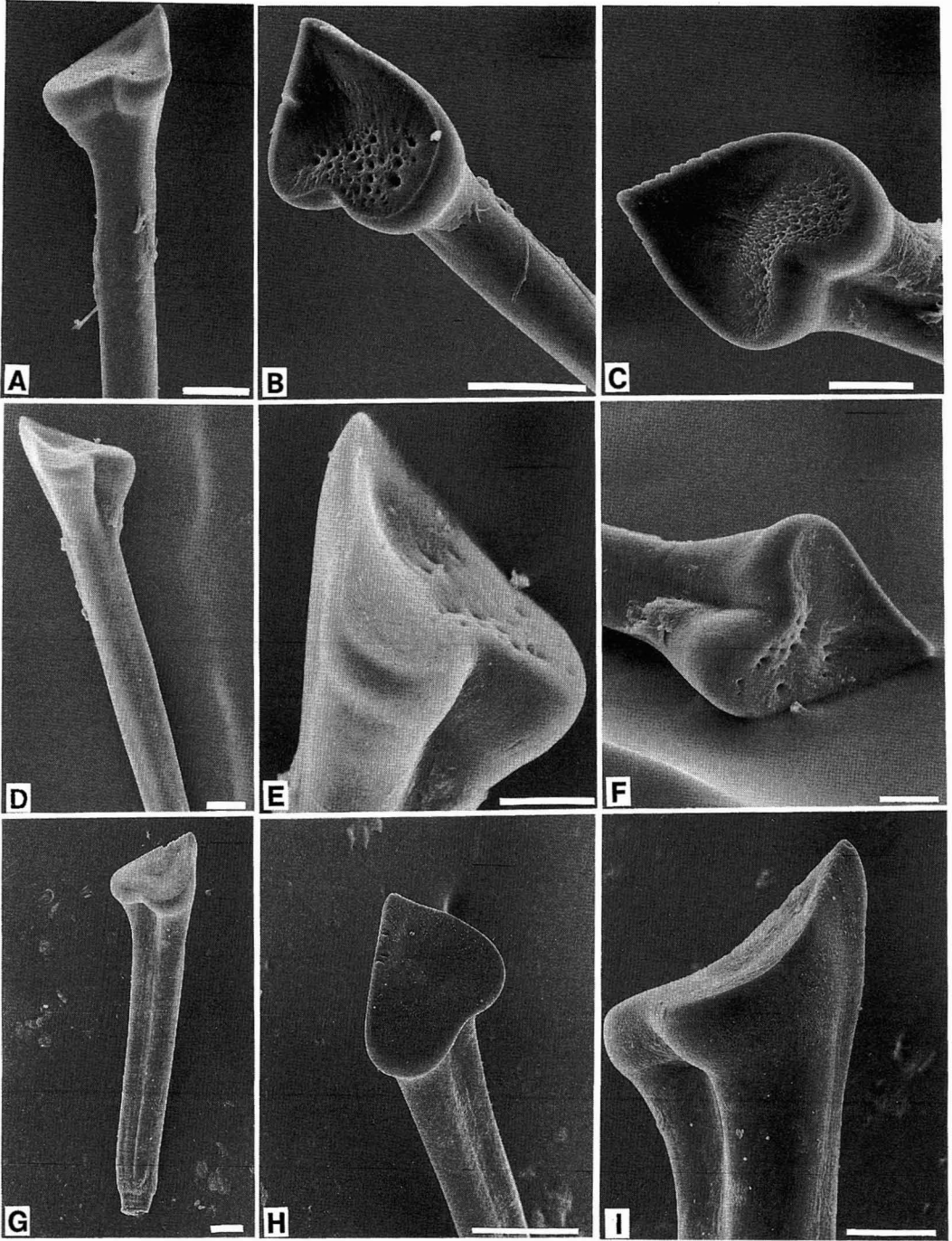


FIGURE 4. *Spiochaetopterus okinawaensis* (upper row, A-C), *S. sesokoensis* (middle row, D-F), and *S. costarum* (lower row, G-I): comparison of A4 chaeta (SEM micrographs). Scale lines are 50 μm (A-F, I) and 100 μm (G, H).

outer side, and a slightly longer unilobed, cirriform inner lateral side. Neuropodia (Figure 1C) fleshy lobes with uncini (uncinal plate), biramous in the B region; upper lobe short, rounded, oriented anteriorly and lower lobe dorsoventrally elongated posteriorly.

Uncini bluntly triangular, with single row of minute teeth (14–15; $n = 20$) visible only at higher magnification. B and C regions lack coloration.

Region C (posterior region) nearly as in *S. okinawaensis* (Figure 1C).

Tubes not known.

ETYMOLOGY: The name *sesokoensis* is derived from the type locality, Sesoko Island, Okinawa Island.

REMARKS: The two new species differ in their morphology and habitat. *Spiochaetopterus okinawaensis* bears oculate spots on the lateral side of the prostomium, unilobed neuropodia on segment B1, the other segments bilobed, and the tube lacks periodic rings. *Spiochaetopterus sesokoensis* has no oculate spots, all the neuropodia of the B segments are bilobed, including B1, but the form of the tube is not known. The morphology of the modified chaeta is also different, both in the shape of the ventral edge of the oblique section and in the angle formed, in lateral view, by the subvertical dorsal plane of the head with the subhorizontal ventral plane or angle between the upper and lower oblique planes as defined by Bhaud (1998a). The oblique plane of the distal section of the A4 modified chaeta is concave in *S. okinawaensis* but tends to swell outward in *S. sesokoensis*. *Spiochaetopterus sesokoensis* was collected on the beach on Sesoko Island in clear white coral sand, 1–2 m deep; *S. okinawaensis* was found in Bise Beach seagrass beds with rubble and seagrass thalli and roots, 1–2 m deep.

DISCUSSION

Distinguishing the Two New Species

The two new species are here differentiated on the basis of original descriptions and preliminary observations of species now

known from Japanese waters, the Pacific, and the Atlantic.

Before this work, only *Spiochaetopterus sagamiensis* (Nishi, Miura & Bhaud, 1999) and two subspecies, *S. costarum okudai* and *S. costarum costarum*, were known from Japan. The last, reported by Nishi (1996) and Nishi and Arai (1996), is described above as *S. okinawaensis*. *Spiochaetopterus costarum okudai* is now being redescribed (unpubl. data) based on type material and recently collected specimens. However, the large body size (width 4–4.5 mm for regions outside the tube, length to 180 mm or more [Okuda 1935, Gitay 1969]) is sufficient to consider *S. c. okudai* as distinct and to distinguish it from the two species described here, specimens of which do not approach the dimensions of *S. c. okudai*. The morphology of the specialized modified chaeta is another differentiating character: in *S. c. okudai* the head in cross section is circular; in the two new species the head in cross section has two unequal protruberances. *Spiochaetopterus c. okudai*, unlike *S. okinawaensis*, lacks eyespots. *Spiochaetopterus sagamiensis* from Sagami Bay (Nishi et al. 1999) is distinguished from the others by the A4 chaeta in which the horizontal edge is regularly circular with no trace of a ventral sinus, and the cross section of the shaft has two dorsolateral grooves resulting in a section with two previously undescribed lateral sinuses.

Two congeneric subspecies were also known from the Pacific (as distinct from Japanese waters), *S. costarum pottsi* Gitay, 1969 (Potts 1914, Berkeley 1927) from Nanaimo District, British Columbia, and *S. costarum monroi* Gitay, 1969 from Gorgona Island in the equatorial eastern Pacific. Specimens of *S. costarum pottsi* differ from those of *S. okinawaensis* and *S. sesokoensis* in large size (480 mm long, 3 mm wide) and unilobed notopodia and neuropodia on the C region. Maximum length in the two new species described here is 50 mm, width is 1 mm, and the C neuropodia are bilobed. The C neuropodia in *S. costarum monroi* are also unilobed, but size was not recorded (Monro 1933). Insufficient diagnostic descriptions of the specimens recorded as *S.*

costarum by Gilbert (1984) and Blake (1995) from the California Basin and the Gulf of Mexico, respectively, do not permit us to recognize either as *S. costarum pottsi* or *S. costarum monroi*.

Last, the Okinawan species are differentiated from congeneric European species of *Spiochaetopterus* by the morphology of the A4 chaeta: the cross section of the head is more rounded, the diameter of the collar is progressively smaller and separated from the shaft by a slight constriction, and the disposition of the oblique plane does not overhang the shaft (Figure 4). The large number of specimens of the Atlantic-Mediterranean species (*S. costarum* and *S. solitarius*) and those in Japanese waters (*S. okinawaensis*) show little variability in the morphology of the A4 specialized chaeta and consistent differences in shape. In *S. okinawaensis* (as *S. costarum costarum*), Nishi (1996) described tubes 40–150 mm in length, 1 mm in diameter, and so fragile and aggregated that complete tubes could not easily be collected. Tri-branched tubes with two worms have also been found. No branched specimens of the closely related (on the basis of size and tubes) Mediterranean species *S. solitarius* have been collected. Regeneration occurs with the simultaneous development of a new segment instead of the progressive addition of each new segment (Nishi 1996), and after about 30 segments have appeared in region B the worm divides and the missing parts of each section are regenerated. In 20 specimens of *S. okinawaensis* (as *S. costarum costarum* [Nishi 1996]), the maximum number of B segments was 43. In 72 specimens of *S. costarum* (Bhaud 1998b), a maximum of 54 segments is recorded in region B.

Species or Subspecies

The problem of species or subspecies is discussed by Bhaud (1998a), commenting on Gitay's (1969) review of the genus *Spiochaetopterus* in which 11 features are used to differentiate among species. The features include morphology of the prostomium, presence or absence of eyes, morphology of the peristomium, size of grown specimens (if

the difference exceeds 100%), number of midregion segments (if difference exceeds 100%), and morphology of neuropodia in regions B and C. Specimens distinguished by at least three of the seven features are considered as representing distinct species; specimens distinguished by any two of the same list inhabiting part of the range of a closely related species are considered to be of sub-specific rank.

Three comments are pertinent: (1) The number of distinguishing features does not affect the validity of an identification, and one characteristic alone may be sufficient to distinguish a species or subspecies. It is, therefore, important to examine each characteristic. (2) The differences in the number of segments in region B means that the Pacific species cannot remain as subspecies of the Atlantic species of *Spiochaetopterus* (Bhaud 1998b). (3) The basis for defining subspecies is not convincing. The biogeographic argument of partial sympatry can rarely be used because the range of most species is not known, nor has local cohabitation or sympatry for two taxa (species or subspecies) been observed. New criteria such as morphology of the A4 chaeta (shape of the head, length:width ratios of cross sections of the shaft), structure of the tube (width, integrity of successive layers of the tube wall, organization of septa), and morphology of the secretory pores on the ventral shield permit a better degree of differentiation among species.

For the reasons given above, we propose the following list of taxa, in which Gitay's (1969) subspecies (*S. costarum pottsi*, *S. costarum monroi*, and *S. costarum okudai*), named for the author who first collected the variant (Potts 1914, Monro 1933, Okuda 1935), are raised to specific rank.

1. *S. monroi* (Monro, 1933) (Synonyms: *Telesavus costarum* Monro, 1933; *Spiochaetopterus costarum monroi* Gitay, 1969)

2. *S. okinawaensis* Nishi & Bhaud, n. sp., this paper

3. *S. okudai* (Okuda, 1935) (Synonyms: *Telesavus costarum* Okuda, 1935; *Spiochaetopterus costarum okudai* Gitay, 1964)

4. *S. pottsi* (E. Berkeley, 1927) [Synonyms:

Telepsavus sp. (Potts 1914); *Leptochaetopterus pottsi* E. Berkeley, 1927; *Telepsavus costarum* E. & C. Berkeley, 1952; *Spiochaetopterus costarum pottsi* (E. Berkeley, 1927)]

5. *S. sagamiensis* Nishi, Miura & Bhaud, 1999

6. *S. sesokoensis* Nishi & Bhaud, n. sp., this paper

The taxa are not always allopatric; that is, they may be sympatric, but they are never cosmopolitan.

Why Have So Many Subspecies of Spiochaetopterus Been Proposed?

In recent years, numerous chaetopterid species have been regarded as cosmopolitan, partly because of the long planktonic larval life (Scheltema 1971, 1974). Gene flow was perhaps interrupted during the long voyage made by larvae, but morphological divergence does not appear to be sufficient to distinguish new species. In this milieu, the "mother" species, described first from the Mediterranean, spread, and genetic flow was presumed to maintain local subspecies. However, just because the first description of the species was from the Mediterranean does not mean that the taxon had a Mediterranean origin: each subspecies named thereafter could be considered the equivalent of the first described species. Therefore we believe it far more useful to give the same status to all the examined forms, recognizing them on the strength of their discriminant features such as the presence or absence of ocular spots and the shape of the specialized chaetae. It has also been demonstrated (Bhaud 1998a) that, despite the ability of larvae to disseminate widely, adults of species in the Atlantic-Mediterranean biogeographic region are restricted in their geographical distribution. Teleplanic larvae may not be so efficient in occupying large areas, as has been generally thought, and what have previously been recognized as two populations of the same species may, in fact, represent two distinct species. Thus thorough morphological examination is essential in distinguishing differences among species of *Spiochaetopterus*.

CONCLUSIONS

Two new species are described from Japanese waters, *S. okinawaensis* and *S. sesokoensis*. Provisionally, species occurring in the Pacific Ocean are distinguished by six characteristic features. Other species now being described will be added to the list of Pacific species, and numerous reports of undetermined species may also be recognized. Despite a long planktonic larval life, neither evolution in this genus nor phyletic ramification is necessarily slow.

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