BEAUFORTIA

INSTITUTE FOR SYSTEMATICS AND POPULATION BIOLOGY (ZOOLOGICAL MUSEUM) UNIVERSITY OF AMSTERDAM

Vol. 46, no. 5 October 31, 1996

A REDESCRIPTION OF THE INDO-WEST PACIFIC SPIROBRANCHUS CORRUGATUS STRAUGHAN, 1967 (SERPULIDAE, POLYCHAETA), AND AN ALTERNATIVE HYPOTHESIS ON THE NATURE OF A GROUP OF MIDDLE MIOCENE MICROFOSSILS FROM POLAND.

HARRY A. TEN HOVE* & EIJIROH NISHI**

*Zoological Museum, University of Amsterdam, P.O.B. 94766, 1090 GT Amsterdam, the Netherlands

**Natural History Museum and Institute, Chiba Aoba-cho 955-2, Chuo-ku, Chiba 260, Japan

Key words: Polychaeta, Serpulidae, Indo-Pacific, Miocene, Poland.

ABSTRACT

Spirobranchus corrugatus, a little known species, is redescribed based on ample material from Australia, Indonesia, Japan and the Seychelles. The species is characterized by a seemingly porous tube, sunk into the substrate. Characteristically, the opercular plate shows a number of radial ridges on its distal surface, resembling Middle Miocene microfossils from Poland. The ventral rim of the opercular bulb of Sp. corrugatus bears numerous ocelli, with single lenses. A comparison with similar species is given.

INTRODUCTION

Representatives of the genus Spirobranchus occur commonly in subtropical and tropical waters, but their taxonomy is confused due to the variability of the opercular morphology. For instance, opercula with a conical distal plate may occur instead of the usual flat plate ornamented with horns in at least two taxa, Sp. polycerus (Schmarda, 1861) and the Sp. tetraceros-complex (ten Hove, 1970), making identification of single

specimens hazardous. The tropical Christmastree worms (Spirobranchus giganteus- and Sp. corniculatus-complex), and to a lesser extent Sp. polycerus, have brilliantly coloured branchial crowns, well known to scuba-divers and coral reef researchers. These species usually occur in living corals, and the relation between these organisms has been studied intensively (e.g., Marsden, 1992, 1993; Nishi, 1995: Nishi and Nishihira, 1996). On the other hand, Spirobranchus corrugatus is more cryptic, sunk into the undersides of

corals. It has been diagnosed rather cursorily by Straughan (1967) from Heron Island. Ten Hove (1993, 1994) mentioned the species from the Seychelles, without a description, and placed *Sp. dennisdevaneyi* Bailey-Brock, 1985, from Fiji into its synonymy. A redescription is needed to elucidate characters not given by Straughan, and for a further justification of the above mentioned synonymy.

METHODS

Drawings were made using a camera-lucida and screened paper. Most observations on chaetae and uncini were done on glycerin mounts, a small part of a thorax and abdomen was cut and air-dried for scanning electron microscopy. Description and terminology conform with ten Hove & Jansen-Jacobs (1984). Full details of localities sampled by the Snellius-II Expedition to Indonesia can be found in van der Land & Sukarno (1986); those of the Seychelles Expedition in van der Land (1993).

The following abbreviations have been used in the text:

AIMS: Australian Institute of Marine Science,

Cape Ferguson, Queensland;

AM: Australian Museum, Sydney, N.S.W.;

BMNH: collection numbers of NHM;

CBM: collection numbers of the Natural History Museum and Institute, Chiba,

Japan;

NMNH: National Museum Natural History, Washington, D.C.; formerly United

States National Museum of Natural History (USNM);

NHM: the Natural History Museum, London, U.K.; formerly British Museum (Natural History) (BMNH);

NNM: Nationaal Natuurhistorisch Museum, Leiden, the Netherlands; formerly Rijksmuseum van Natuurlijke Historie

(RMNH);

NTM: Northern Territory Museum of Arts and Sciences, Darwin, N.T., Australia;

QM: Queensland Museum, Brisbane,

Queensland, Australia;

RMNH: collection numbers of NNM; USNM: collection numbers of NMNH; V. Pol: collection numbers of ZMA;

W: short for collection number AM W;ZMA: Zoölogisch Museum, Instituut voor

Systematiek en Populatiebiologie, Amsterdam, the Netherlands;

ZMK: Zoologisk Museum, København,

Denmark.

SYSTEMATIC DESCRIPTION

Genus Spirobranchus Blainville, 1818 Type species: Serpula gigantea Pallas, 1766; by original designation.

Original diagnosis: Corps médiocrement allongé; branchies formées par un axe autour duquel s'enroule en spirale la bandelette branchiale; les tentacules formés, ou mieux très-probablement recouverts par une petite coquille servant d'opercule; tête fort mince, calcaire, entièrement caché.

Emended diagnosis: Tube typically (sub)triangular in cross-section, with medial keel, rarely (sub)circular. More keels may be present, as well as longitudinal series of pits (especially in juveniles). Tubes may be white, blue, pink or salmon, inside and/or outside. Seven thoracic chaetigers. Branchial crown in two lobes; radioles typically arranged in two spires, rarely in two circles. Radioles connected by interradiolar (palmate) membrane. Branchial eyes may be present; stylodes absent. Tonguelets between collar and thoracic membranes present, latter forming apron (i.e. joined ventrally past chaetiger 7). Operculum with calcareous distal plate; with or without groups of spines, or radial ridges. Operculum rarely lacking. Opercular peduncle winged. Pseudoperculum absent. Collar chaetae of two types: simple, narrowly hooded ("capillaries"), and bayonet-like with numerous hair-like teeth in the basal boss ("Spirobranchus-chaetae"). Thoracic chaetae simple, broadly hooded ("limbate") and "capillaries", Apomatus-chaetae absent. Abdominal chaetae trumpet-shaped, i.e. distally with two rows of denticles separated by a hollow groove and forming an extended, pointed tip. Thoracic uncini trapezoid, with gouged fang and single row of teeth (9-25); abdominal uncini similar, but smaller. Ventral ends of thoracic uncinigerous tori widely separated anteriorly,

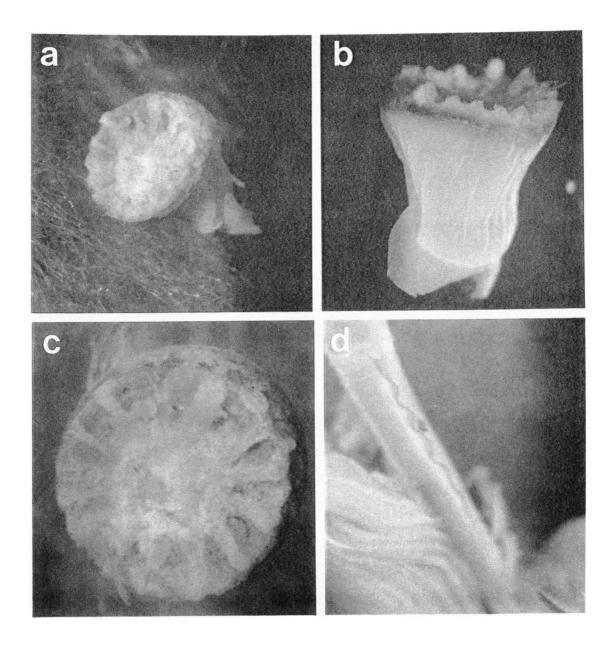


Figure 1. Operculum and opercular peduncle of *Spirobranchus corrugatus*. a, latero-frontal view; b, lateral view; c, upper view; d, opercular peduncle with wing, lateral view. Amakusa, Japan. For size compare Fig. 2a-c.

gradually approaching one another towards the end of the thorax, thus leaving a triangular depression. Posterior abdominal glandular pad absent.

Remarks: The differences between the nominal genera Pomatoceros, Pomatoleios and Spirobranchus are very small (if indeed existing), mainly lying in the collar chaetae. Absent in Pomatoleios, hooded (limbate) in Pomatoceros and bayonet-like with

numerous hair-like teeth in the basal boss in *Spirobranchus*. However, collar chaetae occasionally are absent in *Pomatoceros* and *Spirobranchus*, and present in juvenile *Pomatoleios*. The distinction between hooded chaetae and "*Spirobranchus*-chaetae" sometimes is very hard to make. However, a (needed) revision of the complex of genera falls outside the scope of this paper.

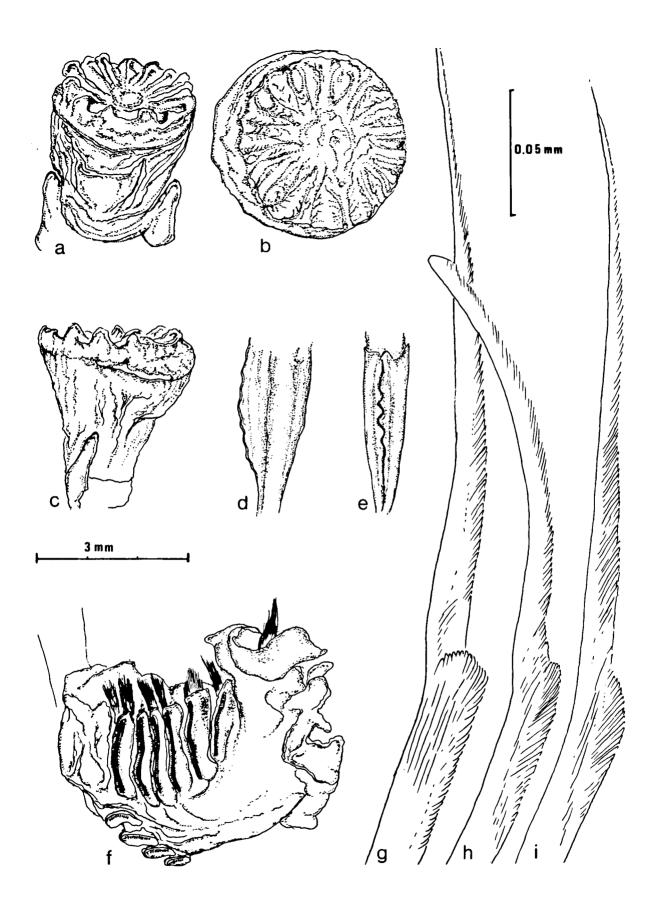


Figure 2. Spirobranchus corrugatus. a, frontal, b, upper, c, lateral view of operculum; d, frontal, e, lateral view of opercular peduncle; f, latero-ventral view of thorax part, showing tori approaching each other posteriorly; all Amakusa, Japan. g-h, collar chaetae. g, off Townsville; h, tip abraded, from Seychelles stn 759; i, from Indonesia stn 4.005. Note variability in development of basal boss.

Spirobranchus corrugatus Straughan, 1967 (Figs. 1-5)

Spirobranchus corrugatus Straughan, 1967, p.39-41, fig.5a-e [Heron Island, material studied] Spirobranchus sp. Vine & Bailey-Brock, 1984, p.146, fig.5b-g [Sudan, mat.stud.] Spirobranchus dennisdevaneyi Bailey-Brock, 1985, p.207-208, fig.9a-e [Fiji, description]; 1987, p.283 [Tonga, name only] Spirobranchus corrugatus: ten Hove, 1993, p.83 [Seychelles, name only]; 1994, p.112 [Seychelles and Amirantes Islands, synonymy].

MATERIAL

Australia--Queensland, Lizard Island, several localities from intertidal down to 20 m, leg. H.A. ten Hove et al., 17.VI.1983 (1 spec., QM213270); 20.VI.1983 (2 spec., USNM); 22.VI.1983 (3 spec., NTM); stn 16, 1.III.1986 (5 juveniles, CBM-ZW-205); stn 17, 1.III.1986 (1 spec., AM); stn 18, 3/4.III.1986 (1 spec., ZMA V.Pol. 4002); stn 20, 5.III.1986 (1 spec., CBM-ZW-202); stn 21, 6.III.1986 (15 spec., V.Pol. 4000, AM W 21678).-Off Townsville, leg. R.A. Birtles & P. Arnold, 7A stn 669 ex.poly 15, 8A stn 673 ex poly 7, 7-8-77 stn 95 ex poly 34 (3 spec., AIMS, V.Pol. 3570, AM W 200492);-Cape Ferguson, 50 km S of Townsville, rocky headland near jetty of AIMS, 1-3 m deep at low tide, from living corals and cobbles in mud, leg. H.A. ten Hove & D. Johnson, stn 23, 8.III.1986 (1 spec., QM213272);-off N. Keppel Island, 51 m, leg. T. Nielsen, VIII.1970 (2 spec., AM);-Heron Island, leg. B. Dew 1956 (HOLOTYPE, AM 4071); between "Coral Gardens", "Staghorn Bank", and Wistari Reef, 7-20 m, leg. H.A. ten Hove, stn 27A, 28, 14.III. 1986 (1 juvenile, AM; 1 spec., V.Pol. 4001).--Western Australia, Abrolhos, W. side of channel of Sandy I., coral rubble, leg. P.

Hutchings 25.VIII.1981 (2 opercula, 1 spec., AM).

Indonesia, Indonesian-Dutch Snellius II Expedition -Ambon, N, stn 4.005 (1 spec. and 17 juveniles, V.Pol. 4004); near Tawiri, stn 4.010 (1 spec., AM).-Tukang Besi Islands, Kaledupa reef, stn 4.016; Binongko W, stn 4.030 (2 spec., RMNH 18299, 18357).-Komodo, E, stn 4.079 (8 spec., RMNH 18365); NE, stn 4.096 (1 spec., V.Pol. 4008).-Sumbawa, N, stn 4.124 (4 spec., RMNH 18366).-Taka Bone Rate, stn 4.139, 4.145B, 4.147A (4 spec., 3 juveniles, BMNH 1996.878-884; 1 spec., CBM-ZW-203; 1 spec., RMNH 18267).-Salayer, 4.152 (1 spec., USNM).

Japan -Uchibuka, Amakusa, West Kyushu, coral rubble, about 10 m depth, on oyster shell, 19.XI.1993, leg. E. Nishi (2 spec., CBM-ZW-80, ZW-178).

Seychelles, Oceanic Reefs Expedition -Mahé, NW coast, Vista do Mar and Beau Vallon, stn 609, 619 (2 spec., V. Pol. 4009, BMNH 1996.877).-St. Joseph Atoll, stn 759 (1 spec., V. Pol. 4010).-Desroches Atoll, submerged W rim, stn 772 (2 spec., RMNH 18368).-Poivre atoll, W rim, stn 780 (1 spec., USNM).-St. François Atoll, W rim, stn 792 (1 spec., CBM-ZW-204).

Red Sea, Sudan -Fringing reef and Wingate barrier reef, under coral from 60 m, leg. P.J. Vine (1 spec.).

DESCRIPTION

Tube: white (but see notes on colour), about 8 (up to 13) mm wide, with lumen of about 1.8 (max. 2.3) mm, and up to 7 cm long. Tube wall very thin at substrate-side, from 0.3-2.1 mm at opposite side; laterally thickness may reach 3.1 mm (median 1.5 mm). Tube extremely variable, yet characteristic. Generally wider than high, broadly encroaching (Fig. 3g) and/or sunk into the substrate. Not infrequently almost triangular in cross-section; rarely almost circular. Medial keel absent, developed as line only or thick and serrated, often flanked at both sides by more or less regular row of (sub)circular holes. Generally with triangular tooth over entrance of tube, latter with two latero-anterior scoops (Fig. 3g). Sides of tube often with thick transverse ridges ("tori" in fossil terminology), smooth in juveniles, but with many dots and pits (as usual for rest of tube) in larger

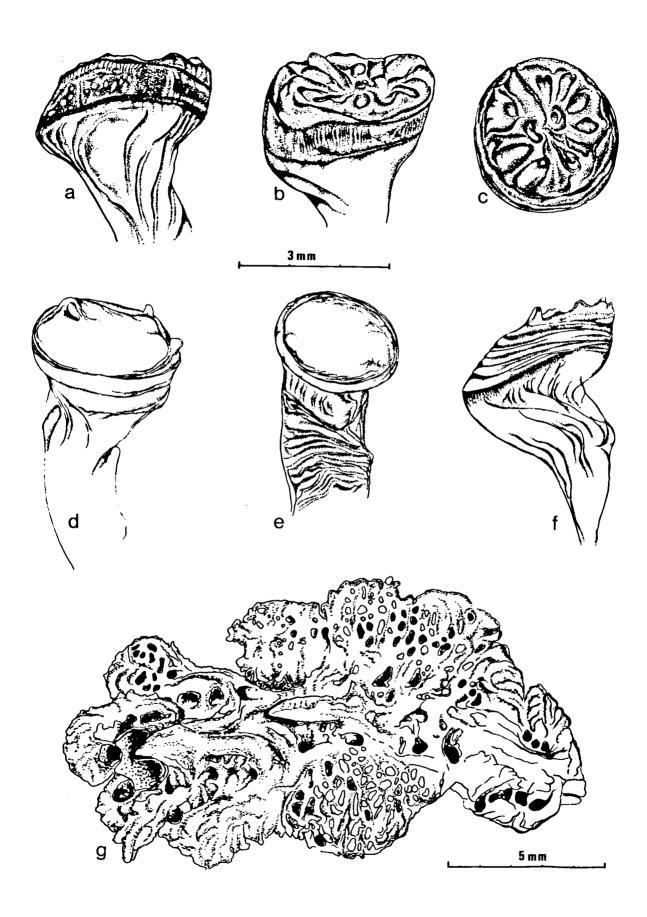


Figure 3. Spirobranchus corrugatus. a-c, operculum from Amakusa, dorso-lateral, ventro-lateral and distal views. d-f, opercula from Indonesia stn 4.145B, Seychelles stn 792, and Lizard Island stn 20. g, tube (without any substrate) from Lizard Island stn 20.

specimens; transverse ridges rarely absent, notably in the Seychelles material. Medial keel in Red Sea specimen consisting of large, rugged teeth; transverse ridges expanding to lateral wings. Substrate-side of lumen marked by two parallel series of holes (each 0.09-0.15 mm wide), connecting lumen with narrow channels in wall. Tube-wall characteristically with very porous structure, except for thin compact layer around lumen. Surface of tube granular, showing innumerable foramina (in addition to the -not always present- regular series flanking medial keel or line, Fig. 3g); surface rough, appearing as if etched with acid. A single specimen, covered by sponge, with almost smooth tube-surface, with faint growth-lines only. Posterior tube parts may be partitioned off by tabulae, calcified septa perforated by 5-12 pairs of lateral transverse slits.

Branchial crown: each lobe with (12) 21-38 radioles (x = 26.3, SD = 4.1, n = 23), arranged in two perfect ovals in small specimens, in two shallow spires of 1 1/2 whorl in large specimens. Radioles connected by interradiolar membrane for about 2/5th (1/5-1/2) of their length. Membrane with smooth edge between radioles, no frills or lappets present. Terminal filament variable in length but usually about twice as long as distal pinnules, and twice as thick. Branchial eyes not found (but see operculum). Stylodes absent. Pinnules increasing in length towards distal 2/3rds of radiole, then decreasing again. Section of radiole U-shaped. External surface of radioles wrinkled. Mouth-structures hard to observe owing to relatively small size of specimens. Long palps associated with dorsal lips, and none with ventral lips observed in 7 specimens. Pair of prostomial ocellar clusters not found.

Peduncle: smooth, subtriangular in cross section, inserted just left of median line. Pair of lateral wings developed along almost entire length, proximally without notch, tapering into base of peduncle (Fig. 2d). Clear constriction just below opercular bulb (Fig. 2a, c). Triangular tip of wing with scalloped inner margin (Fig. 2a; exception-

ally smooth at one or both sides), wing otherwise with smooth edge, which may be wavy (Figs.1d, 2d-e), but not crenulate.

Operculum: diameter of operculum and anterior tube almost equal, operculum very closely fitting. Opercular bulb (ampulla) an inverted fleshy cone, almost as wide as high, with slanting, flat to subconical, calcareous distal plate. Typically showing 10-20 (4-22) ridges radiating from centre of flat or slightly cupped distal plate and ending in as many marginal teeth (Figs. 1a-c, 2a-c, 3b-c, f). Some subconical distal plates crowned by "an off-center ring of ten triangular spines" (Bailey-Brock, 1985: 207) or radiating ridges (Fig. 3f). Distal plates in other specimens -adult as well- almost flat and circular, with raised dorsal edge (Fig. 3d-e), sometimes with (raised) dorsal disc in addition. Flat, conical and ridged plates possible within one population, however, only flat plates (so far?) in Seychelles material. Colour of plates white or - especially near edge- pink. Most characteristic for operculum: band of single lensed ocelli in ventral edge of ampulla, thinning out towards dorsal side (shaded area in Fig. 3f). Ocelli in preserved material only visible by careful illumination, especially hard to discern in Seychelles specimens.

Collar and thoracic membranes: collar high, up to length of radioles, with entire to laciniate edge ventrally; continuous with thoracic membranes, wide anteriorly and tapering to narrow apron across anterior abdominal chaetigers. Tonguelets between ventral and latero-dorsal collar parts consisting of large outer and small, bilobed inner lappet. Pockets on the inner side of the thoracic membrane, like in Floriprotis Uchida, 1978, absent. Pairs of small, wartlike protuberances of collar chaetiger visible proximal from junction of ventral and latero-dorsal collar parts, in large specimens only.

Thorax: with collar chaetiger, and 6 uncinigerous chaetigers. Collar chaetae of two types: simple, narrowly hooded (capillaries), and bayonet-like with numerous hair-like teeth in basal boss (Spirobranchus-chaetae, Figs. 2g-i, 4b). Thoracic chaetae simple, broadly hooded (limbate) and "capillaries" (Fig. 4a, e), Apomatus-chaetae absent. Uncini along entire thorax saw-shaped, with 12-17 curved teeth, with gouged, apparently bifurcated fang (Fig. 4c-d). They are 80 to 100 µm in

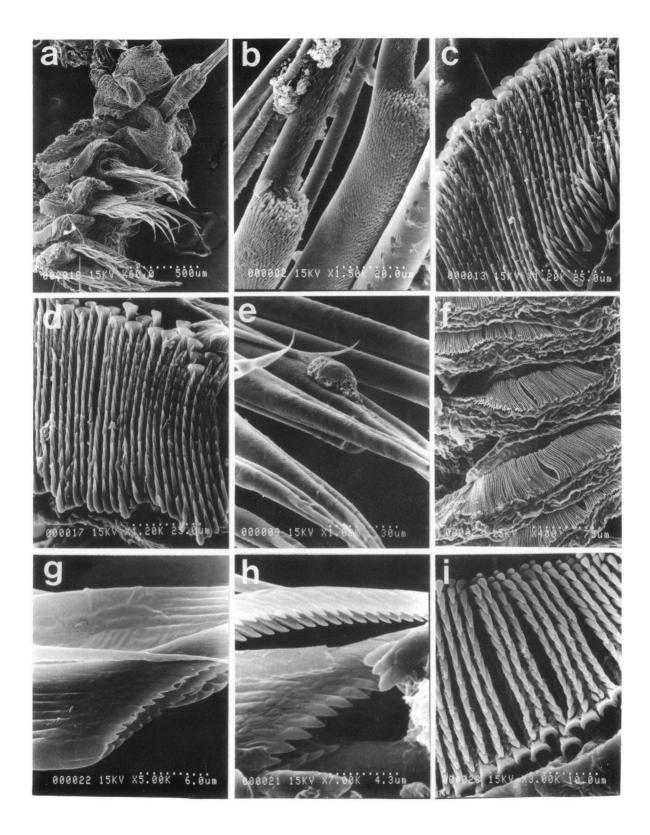


Figure 4. Scanning electron micrographs of Spirobranchus corrugatus. a, anterior part of thorax; b, bayonet-shaped chaetae of collar segment; c,d, thoracic uncini; e, thoracic chaetae; f, abdominal uncinigerous tori; g,h, abdominal chaetae; i, anterior abdominal uncini. Amakusa, Japan.

size, subtriangular. Thoracic tori decreasing in length posteriorly till 2/3 of anterior ones. Uncinigerous tori of thorax widely separated in front, gradually approaching one another posteriorly, thus leaving a triangular depression (Fig. 2f). Thoracic glands observed near basis of collar chaetae in most (but not all) samples from Lizard Island; however, only rarely found in Seychelles and not in Indonesian material.

Abdomen: abdominal chaetigers 58-96 (x = 68.8, SD=9.5, n=21). Uncini saw-shaped anteriorly, with fang and 11-13 teeth (Fig.4f, i); rasp-shaped with 5-6 (?) rows of teeth posteriorly. Chaetae compressed trumpet-shaped, distally with two rows of denticles separated by a hollow groove and forming an extended, pointed tip (Fig.4g-h). Chaetae becoming increasingly longer posteriorly, capillaries absent. Pygidium minute, almost straight, hardly bilobed. Posterior glandular pad absent.

Size: length up to 27 mm, generally about 16 mm. Width of thorax 1-3 mm (x = 1.7, SD=0.4, n=23). Branchiae and operculum accounting for 1/2 (juveniles) to 1/5th of entire length.

For a comparison of some measurements of various populations see Table 1. There are no significant differences between the populations.

Colour

Field-notes could not always be taken, nor are

they consistent. Nevertheless, it is evident that colour is very variable, and not useful for taxonomic purposes.

Lizard Island, 17.VI.1983: Opercular disc purplish-red with orange centre, ocelli in rim bright red. Radioles and peduncle green, banded white. Collar transparently green, tonguelets white. Tube greenish-pink, like its environment. Stn 18: Operculum with orange cap, probably sponge. Marginal teeth white. Opercular bulb and branchial lobes predominantly red, radioles banded white. Collar, thoracic membranes and thorax transparently orange. Abdomen and tube greenish.

Indonesia, stn 4.079B: Operculum yellowish; rim white with dark red ocelli. Radioles transparent, banded white and brown. Thorax transparently brown, abdomen hyaline with dark intestine. Stn 4.096: Radioles banded deep and pale red. Thorax brownish-red, collar and thoracic membranes transparently brown. Abdomen bright red with eggs.

Seychelles, stn 759: Opercular disc bright orange; rim white, with red ocelli. Stn 772: collar and thorax orange. Branchiae mottled white, orange, red and purplish brown; base wine-red.

ECOLOGY

The species has been found from 1-60 m deep, and is fairly common underneath corals and coral rubble in muddy and sandy environments on reef-flat and fore-reef. It also was collected from the ceiling of caves. It is easily overlooked, occurring cryptically, moreover with the tube sunk into the limestone or coral. The way in which the animal achieves this is unknown. One

Table 1. Measurements of adult specimens (being defined as having a thoracic width of at least half the maximum measured). Given are minimum-mean-maximum Standard Deviation (number) for separate populations, and the addition sums (all A I S). The holotype evidently is a juvenile specimen.

	length animal	thoracic width	max. # radioles	abdominal chaetigers	length operculum
Holotype	4.5	0.9	13	35	0.9
Australia	13.0-16.6-27 4.9 (9)	1.5-1.9-3.0 0.49 (9)	25-28.3-38 4.1 (9)	60-66.8-80 6.9 (8)	1.7-2.07-2.3 0.19 (9)
Indonesia	12.0-16.7-20 2.4 (10)	1.5-1.7-2.2 0.21 (10)	23-25.8-36 4.1 (10)	63-73.0-96 10.7 (10)	1.6-1.93-2.5 0.24 (10)
Seychelles	11.5-14.3-16 2.5 (3)	1.0-1.3-1.5 0.22 (4)	21-23.3-26 2.2 (4)	58-60.0-62 2.2 (3)	1.1-1.58-2.0 0.37 (4)
all A I S	11.5-16.5-27 5.9 (22)	1.0-1.7-3.0 0.41 (23)	21-26.3-38 4.1 (23)	58-68.8-96 9.5 (21)	1.1-1.92-2.5 0.29 (23)
Japan	?-24	1.8-2.3	25-31	?-71	2.1-2.5

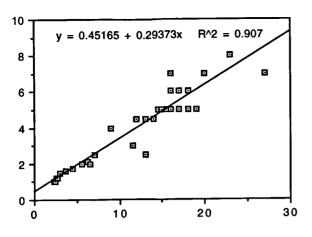


Figure 5. Simple regression of the length of the body (horizontal axis) versus length of radioles. R = 0.95, standard error = 0.0438. Based on all 23 specimens from Table 1, and 15 juveniles.

specimen was observed growing from underneath the coral *Pachyseris* over the edge into the living coral tissue.

In two Indonesian samples, 4.004 and 4.139, we observed two distinct size-classes. In stn 4.139 two adult tubes were overgrown not only by specimens of *Spiraserpula snellii* Pillai & ten Hove, 1994, but also by 3 juvenile congeners. This is suggestive of either preferential selection of conspecific tubes for settlement (cf. ten Hove & van den Hurk, 1993: 32), or, less likely, brood-care (not very common in serpulids nor known for the genus, cf. Ben-Eliahu & ten Hove, 1989: 394; Nishi, 1993). The specimen from Lizard Island (stn 18) started spawning when the tube was opened (4.III.1986).

We had the impression that the length of the crown was proportionally shorter in larger individuals, as mentioned for a sabellid by Giangrande (1991). Her figure indicates that she used a polynomial regression. A simple regression of length of radioles versus entire body length is given in Fig. 5, fifteen juveniles not used for the descriptions are included in these data as well. Data are significant, and indicative of allometric growth.

REMARKS

Comparing the measurements of the holotype

with those of various populations (Table 1), it is evident that Straughan had a juvenile specimen before her. All values of the holotype are much lower than those displayed by adult series. Added to the opercular variability as documented in this paper, it demonstrates the dangers of describing species based upon single specimens.

Spirobranchus sinensis Wu & Chen, 1981 shows a superficial resemblance with those Sp. corrugatus, where only a flat distal plate is present. However, the tube of Sp. sinensis is pink in colour and is distinctly triangular in cross-section, with 3 longitudinal ridges (not depicted in Fig. 1 of Wu & Chen, but according to the text). The proximal insertion of the peduncular wing is set off by a notch from the peduncle proper, a character-state often found in the Sp. latiscapus-complex (including Sp.maldivensis Pixell, 1913) but so far not in Sp. corrugatus, where the wing is gradually merging into the peduncle. Chitinous spines deposited by hydrozoan epibionts are not uncommon in the Sp. tetraceros-complex (see Bouillon, 1974; ten Hove, 1994), Sp. latiscapuscomplex (Philippines, off Jolo, ZMK and from various localities off Australia, AM; ten Hove, unpublished) and occur in Sp. corrugatus as well (e.g. Indonesia stn 4.145B, this study). In our opinion the chitinous spines on the two-tiered operculum of Sp. sinensis belong to the same category and are of no value as "distinguishing character" versus Sp. latiscapus (Marenzeller, 1885) as stipulated by Wu & Chen (1981). They pointed out that Sp. sinensis was closely related to Sp. latiscapus, however, we are inclined to regard it as a synonym of Sp. maldivensis.

Two more nominal Spirobranchus species with a flat distal plate have been mentioned from tropical Indo-Pacific waters: Sp. ceylonensis Pillai, 1960 and Sp. lima (Grube, 1862). When studied by ten Hove (1970: 5), the holotype (and sole specimen) of Sp. ceylonensis was in poor condition. He tentatively synonymised the species with Sp. tetraceros. In retrospection, the red tube with three keels, convex opercular plate and long peduncular wings mentioned and figured by Pillai (1960: 20-21, fig. 7H) rather point to a synonymy with Sp. maldivensis. Spirobranchus lima is a Mediterranean species, not likely to occur in the Indo-Pacific. Amoureux et al.'s (1978) material of "Sp. lima" from the Red Sea was checked by the

senior author and it proved to be a specimen of the Sp. latiscapus-complex. Meng et al.'s (1993, 1994) record of Sp. lima from Hainan regards a small specimen. Its clearly crenulated peduncular wings, with a length of only half the peduncle (Meng et al., Fig. 2, 1), and pink tube rather point to the Sp. tetraceros-complex than to Sp. corrugatus or maldivensis.

The calcareous plate of the operculum of Sp. corrugatus, strengthened by a number of distal radial ridges, is similar to the distal side of the operculum of Sclerostyla Mörch, 1863 (see ten Hove, 1973, pls. 3-4), as well as to that of Vermiliopsis labiata (O.G. Costa, 1861) (see Bianchi, 1981, fig. 27). In Sclerostyla, however, the operculum is more strongly calcified: the opercular plate is continuous with a long calcareous stalk or "talon" proximally, embedded into the peduncle. The opercular cap of V. labiata on the other hand is flat proximally, due to the underlying chitin-like end-plate of the opercular bulb. In all three species the operculum is extremely well fitting into the tube, closing it off hermetically. These well-fitting, ridged opercular plates are a clear case of convergent evolution. The convergence between Sp. corrugatus and Sclerostyla species even goes further. Tubes of Sc. ctenactis Mörch, 1863 in general are embedded into the substrate too; tubes of Sc. semiannulata ten Hove, 1973, show transverse ridges, not unlike those occurring in Sp. corrugatus, maybe making up for the otherwise porous structure of the tube wall.

Most characteristic for Spirobranchus corrugatus is the occurrence of ocelli in the ventral rim of the operculum. The character eye-spots, however, is under-exploited in serpulid taxonomy, the most complete survey so far (of about 50 nominal taxa) was given by Smith (1985: 177-179). He reported a red ocellus at the base of the opercular ampulla in Semivermilia pomatostegoides (Zibrowius, 1969), numerous red eye-spots on ventral rim of operculum in Pomatostegus stellatus (Abildgaard, 1789), and Sp. corrugatus (as Spirobranchus spec.), and possibly non-pigmented eye-spots in the ventral rim of the operculum of Sp. gardineri Pixell, 1913. Series of compound eyes occur in the opercula of Hydroides cf. mongeslopezi Rioja, 1957, and Sclerostyla ctenactis (both ten Hove, unpublished). Presence of ocelli in the ventral rim of the operculum thus is a character-

state shared by Sp. corrugatus, P. stellatus and maybe Sp. gardineri. Although not all species of the genus Spirobranchus have been checked for ocelli (difficult to find in preserved material anyhow), it appears that all have ocellar clusters at the base of the prostomium (Smith, 1985). Representatives with spiral branchiae [Sp. giganteus-complex, Sp. corniculatus-complex, Sp. gardineri, Sp. polycerus, and Sp. nigranucha (Fischli, 1900)) all have large compound eyes at the base of the first left and right dorsal radiole. Representatives of the Sp. tetraceros-complex may show paired rows of ocelli on the first left and right dorsal radiole, numerous red ocelli along the radioles, or no radiolar eyes at all (Smith, 1985; ten Hove, unpubl.). It remains to be seen whether or not the character-states are species-specific within this complex. Small Spirobranchus species (e.g. Sp. polytrema (Philippi, 1844)) may have prostomial ocellar clusters only.

All tubes of Sp. corrugatus consciously checked, from Australia, Indonesia, Japan, and the Seychelles, show two series of small pits in the substrate-side of the lumen, as if the lumen were in open connection with a series of chambers in the lateral bases of the tube-wall. The authors are not aware of any other serpulid species showing this character, but in descriptions the inside of tubes has been disregarded even more than the outside. A check (not exhaustive) of tubes of species with series of chambers in the lateral bases of the tube-wall, failed to find such series of pits: Spirobranchus latiscapus, Sp. coronatus Straughan 1967 (material of both taxa from the Seychelles), Pomatoceros triqueter (Linnaeus, 1758), P. lamarckii (Quatrefages, 1865) (both cast ashore in the Netherlands). Finally it could be observed (by stereo-microscope) in two broken tubes that each pit is the entrance to a thin channel into the tube-wall, and not to a series of lateral chambers, which are poorly developed if not absent in Sp. corrugatus.

AN ALTERNATIVE HYPOTHESIS ON THE NATURE OF A GROUP OF MIDDLE MIOCENE MICROFOSSILS FROM POLAND.

Radwanska (1994b) described a group of microfossils from Middle Miocene origin, from the Korytnica Basin, Central Poland. She considered them to be opercular caps of the serpulid genus *Vermiliopsis* Saint-Joseph, 1894. The calcareous plates or caps, 1-2 mm in size, have the form of a cone, sometimes crowned by a cross of 3-6 ridges, others may be flat and circular. Cone-shaped caps have a hollow (under?)side, and if a cross is present, its ridges are shown as grooves underneath.

As stated above, the calcareous cap of *V. labiata* is flat proximally, due to the opercular endplate of chitin-like material. There is no such chitin-like end-plate in *Sp. corrugatus* (nor in any other species of the genera *Spirobranchus* or *Pomatoceros*), and the fleshy bulb of the operculum is following the contours of the distal calcareous cap or plate. When the latter is ridged, its base shows corresponding grooves. The similarity of the operculum of *Sp. corrugatus* with the microfossils from Poland (as figured by Radwanska, 1994b, pl.4) is much more striking, than with that of the flat based *V. labiata*.

When the opercular cap of Sp. corrugatus is conical, its base or underside is hollow. Such conical opercula, however, are fairly widely spread in the genera Spirobranchus and Pomatoceros. They may occur e.g. in Sp. tetraceros, Sp. polytrema, P. triqueter and P. americanus (Day, 1973). Flat, circular end-plates are common too, occurring e.g. in Sp. corrugatus, Sp. eitzeni Augener, 1918, Sp. lima, Sp. maldivensis, Sp. polycerus, P. lamarckii. The caps and plates generally are rather thick, abruptly tapering towards the edge. If (rarely) the essentially chitin-like cap (or plate) of a Vermiliopsis species is reinforced with calcareous matter on its outside, this calcareous layer gradually peters out towards the edge.

In all thirty years of the senior author's experience, samples with loose opercular caps of Vermiliopsis were extremely rare (if present at all). On the other hand, loose opercula of the genera Spirobranchus and Pomatoceros are not uncommon, as evidenced also by the fact that they have been described as early as 1819. The presumed gastropod Patella tricornis Turton, 1819 (: 139) already has been recognized as an operculum of Pomatoceros triqueter by Harvey & Glossop (1835: 621-622), while Patella extinctorium Turton, 1819 (: 138) too is an operculum of the same serpulid (Zibrowius, pers. comm.). An other supposed gastropod, Hipponyx inexpectata Mestayer (1929:

249, figs 16-17) was thought to be part of a serpulid tube by Dell (1956: 72); however, it most probably is the operculum of *Sp. latiscapus* (ten Hove, unpublished).

Unfortunately for our hypothesis, (sub)triangular tubes, wide spread in the genera Spirobranchus and Pomatoceros, have not been found in the Polish fossils, nor opercula found in situ. On the other hand, Vermiliopsis-like tubes with about 5 longitudinal ridges and peristomes are present (e.g. Radwanska, 1994a, pl.5). Nevertheless, the entire range of opercula as described by Radwanska (1994b), is more easily attributed to the genera Spirobranchus and/or Pomatoceros, than to Vermiliopsis.

ACKNOWLEDGEMENTS

We particularly want to thank R. Smith (at that time AIMS) for renewing senior author's interest in the genus, and stimulating discussions. We thank the following colleagues for sharing ideas, research notes and translations of Chinese texts: J.H. Bailey-Brock (Univ. Hawaii), D. Fiege (Naturmuseum Senckenberg), T.G. Pillai (c/o NHM), H. Zibrowius (Station Marine d'Endoume). For the loan of material we thank M.N. Ben-Eliahu (Hebrew Univ., Jerusalem), P. Hutchings (AM) and P. Vine. Thanks are further due to the Foundations and Institutions which funded the senior author's collecting-trips: The Netherlands Marine Science Foundation (Indonesian-Dutch Snellius II Expedition and Seychelles Expedition) and the Trustees of the Australian Museum, Sydney. Finally but certainly not least we thank T. Komai (Natural History Museum and Institute, Chiba) and an unknown reviewer for useful suggestions on the manuscript-draft.

REFERENCES

AMOUREUX, L., & F. RULLIER & L. FISHELSON, 1978.- Systématique et écologie d'annélides polychètes de la presqu'il du Sinai. Isr. J. Zool. 27: 57-163, 16 figs., 1 map.

BAILEY-BROCK, J.H., 1985.- Polychaetes from Fijian coral reefs. Pacific Sci. 39: 195-220, 19 figs.

BAILEY-BROCK, J.H., 1987.- The polychaetes of Fanga'uta lagoon and the coral reefs of Tongatapu, Tonga,

- with discussion of the Serpulidae and Spiror-bidae. Bull. Biol. Soc. Wash.7: 280-294, 6 figs., 1 tab.
- BEN-ELIAHU, M.N., & H.A. TEN HOVE, 1989.-Redescription of *Rhodopsis pusilla* Bush, a little known but widely distributed species of Serpulidae (Polychaeta). Zool. Scripta 18, 3: 381-395, 11 figs., 2 tabs.
- BIANCHI, C.N., 1981.- Policheti serpuloidei. Guide per il riconoscimento delle specie animali delle acque lagunari e costiere italiane. AQ/1/96, 5: 1-187, 66 figs., 2 pls.
- BOUILLON, J., 1974.- Description de Teissiera milleporoides, nouveau genre et nouvelle espèce de Zancleidae des Seychelles (Hydrozoaires; Athécates-Anthoméduses), avec une révision des Hydroïdes "Pteronematoidea". Cah. Biol. Mar. 15, 1: 113-154, 14 figs., 6 pls., 5 tabs.
- DELL, R.K., 1956.- The archibenthal Mollusca of New Zealand. Dominion Mus. Bull. Wellington 18: 1-235, 6 figs., 27 pls.
- GIANGRANDE, A., 1991.- Behaviour, irrigation and respiration in *Eudistylia vancouveri* (Polychaeta: Sabellidae).
 J. mar. biol. Ass. U.K. 71: 27-35, 5 figs., 2 tabs.
- HARVEY, J.B., [& GLOSSOP, F.H.N.], 1835.- On the opercula of Serpula tubularia and Vermilia triquetra, regarded by Turton as species of Patella. Proc. Zool. Soc. London 3: 128.
- HOVE, H. A. TEN, 1970.- Serpulidae (Polychaeta) from the Caribbean: I. The genus *Spirobranchus*. Stud. Fauna Curação Carib. Isl. 32: 1-57, 124 figs., 5 pls.
- HOVE, H.A. TEN, 1973.- Serpulinae (Polychaeta) from the Caribbean: II. The genus *Sclerostyla*. Stud. Fauna Curação Carib. Isl. **43**: 1-21, 37 figs., 4 pls.
- HOVE, H.A. TEN, 1993.- Chapter 13. Serpulidae. p.83, in: J. VAN DER LAND (ed.) 1993.
- HOVE, H.A. TEN, 1994.- Serpulidae (Annelida: Polychaeta) from the Seychelles and Amirante Islands. In: Oceanic Reefs of the Seychelles. Cruise Reports Neth. Indian Ocean Program, II (ed. J. VAN DER LAND), Nat. Nat. Mus. Leiden, p.107-116, 1 table.
- HOVE, H.A. TEN, & P. VAN DEN HURK, 1993.- A review of Recent and fossil serpulid "reefs"; actuopaleontology and the 'Upper Malm' serpulid limestones in NW Germany. Geol. Mijnbouw 72: 23-67, 12 figs., 5 tabs.
- HOVE, H.A. TEN, & M.J. JANSEN-JACOBS, 1984.- A revision of the genus *Crucigera* (Polychaeta, Serpulidae); a proposed methodical approach to serpulids, with special reference to variation in *Serpula* and *Hydroides*. Proc. First Int. Polychaete Conf., Sydney, P.A.HUTCH-INGS (ed.), 1984: 143-180, 12 figs.
- LAND, J. VAN DER (ed.), 1993.- Shipboard report Seychelles Expedition 'Oceanic reefs'. Netherlands Indian Ocean Expedition, Leg E. Mombasa, 11th December 1992 to Victoria, 9th January 1993. Nat. Mus.Nat.Hist., Leiden, 2nd ed., 117 pp.

- LAND, J. VAN DER, & SUKARNO, 1986.- The Snellius-II Expedition Progress Report. Theme IV, Coral reefs. Part one, R.V. Tyro and K.M. Samudera, September-November 1984. R. Neth. Ac. Arts & Sciences, 76 pp., excl. 4 appendages
- MARSDEN, J.R., 1992.- Reproductive isolation in two forms of the serpulid polychaete, *Spirobranchus polycerus* (Schmarda) in Barbados. Bull. Mar. Sci. **51**: 14-18, 3 tabs.
- MARSDEN, J. R., 1993.- Factors influencing the abundance of the seven-spined morphotype of *Spirobranchus polycerus* (Schmarda), (Serpulidae), on upright blades of the hydrozoan coral, *Millepora complanata*. Mar. Biol. **115**: 123-132, 3 figs., 10 tabs.
- MENG, F., & X. HONG & B. WU, 1993.- Studies on Polychaeta of the Hainan Island waters. I. J. Oceanogr. Huanghai & Bohai Seas 11, 4: 46-63, 4 figs. [in Chinese with English summary]
- MENG, F., & X. HONG & B. WU, 1994.- Studies on Polychaeta of the Hainan Island waters. II. J. Oceanogr. Huanghai & Bohai Seas 12, 1: 11-51, 5 figs. [in Chinese]
- MESTAYER, M.K., 1929.- Notes on New Zealand Mollusca. 4. Trans. N. Z. Inst. 60: 247-250, 6 pls.
- NISHI, E., 1993.- Notes on reproductive biology of some serpulid polychaetes at Sesoko Island, Okinawa, with brief accounts of setal morphology of these species of *Salmacina* and *Filograna implexa*. Marine Fouling 10, 1: 11-16, 2 figs.
- NISHI, E., 1995.- The tropical Christmas tree worm *Spiro-branchus* from Japan. IOP Diving News 8: 3-7 [in Japanese]
- NISHI, E., & M. NISHIHIRA, 1996.- Age-estimation of the Christmas tree worm *Spirobranchus giganteus* (Polychaeta, Serpulidae) living buried in the coral skeleton from the coral-growth band of the host coral. Fish. Sci. **62**, 3: 400-403, 3 figs.
- PILLAI, T.G., 1960.- Some marine and brackish-water serpulid Polychaeta from Ceylon, including new genera and species. Ceylon J. Sci. (biol. Sci.) 3, 1: 1-40, 2 pls., 15 figs.
- RADWANSKA, U., 1994a.- Tube-dwelling polychaetes from the Korytnica Basin (Middle Miocene; Holy Cross Mountains, central Poland). Acta Geol. Polonica 44, 1-2: 35-83, 26 figs., 10 pls.
- RADWANSKA, U., 1994b.- A new group of microfossils: Middle Miocene (Badenian) opercular caps (calottae) of the tube-dwelling polychaetes Vermiliopsis Saint-Joseph, 1894. Acta Geol. Polonica 44, 1-2: 84-96, 4 figs., 7 pls.
- SMITH, R., 1985.- Photoreceptors of serpulid polychaetes. Thesis, James Cook Univ. N. Queensland, 3 vols., xv + iii + 539 pp., 114 pls. [mimeogr.]
- STRAUGHAN, D., 1967.- Some Serpulidae (Annelida: Polychaeta) from Heron Island, Queensland. Univ.

- Queensl. Papers 1, 2: 27-45, 5 figs.
- TURTON, W., 1819.- A conchological dictionary of the British Islands. Booth, London, 1819, xxvii + 272 pp., 28 pls.
- VINE, P.J., & J.H. BAILEY-BROCK, 1984.- Taxonomy and ecology of coral reef tube worms (Serpulidae, Spirorbidae) in the Sudanese Red Sea. Zool. J. Linn. Soc. 80: 135-156, 8 figs.
- WU, B., & M. CHEN, 1981a.- Two new species of the family Serpulidae from the South China Sea. Acta Zootaxonomica Sinica 6, 3: 247-249, 2 figs. [in Chinese with English summary]

Received: September 8, 1996.