

Symbiotic association between *Solanderia secunda* (Cnidaria, Hydrozoa, Solanderiidae) and *Medioantenna variopinta* sp. nov. (Annelida, Polychaeta, Polynoidae) from North Sulawesi (Indonesia)

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Abstract. A mimic scale-worm was found associated with the athecate hydroid *Solanderia secunda*, commonly found on reefs of the NW coast of North Sulawesi, Indonesia. The species resembled *Medioantenna clavata* Imajima, 1997, which was originally described without any reference to a symbiotic mode of life and later reported to be living on a solanderiid hydroid both in Japanese waters. A detailed morphological analysis led us to consider the Indonesian specimens as a new species, namely *Medioantenna variopinta* sp. nov., which is con-generic with the Japanese species. The new species differs from the type material of *M. clavata* as it has elytra with one prominent finger-like papilla and all neurochaetae with unidentate tip, instead of an elytral lump and both unidentate and bidentate neurochaetae on segment two. In turn, the Japanese worms associated to *Solanderia* are here referred to our new species. Two morphological features in *M. variopinta* sp. nov. are rather unusual among scale-worms. One of them is its extremely high level of bilateral asymmetry and antero-posterior variability in elytral distribution and the other one is its elongated, upwards directed nephridial papillae. The morphology and geographical distribution of the host together with the known characteristics of the symbiotic association have also been highlighted.

Keywords. Polychaetes · New species · Hydroids · Symbiosis · Camouflage · Indonesia

Introduction

The Class Hydrozoa includes a large variety of life forms that are often involved in symbiotic relationships with other invertebrates (Boero & Bouillon 2005; Gili & Hughes 1995; Puce *et al.* 2008). Their rather rich symbiotic fauna including polychaetes (Genzano & San Martín 2002; Lagardère & Tardy 1980) and some species of *Teissiera* or *Hydractinia* tend to be specifically associated with polychaetes (Bouillon & Boero 1987; Bouillon 1994; Galea *et al.* 2007).

Most polychaetes associated to hydrozoans belong to the families Polynoidae and Syllidae, but a few occur among the Lumbrineridae, Spionidae and Serpulidae (Martin & Britayev 1998). The symbiotic syllids show many different relationships with their hydrozoan hosts, from temporal feeding visitors (*i.e.* predators) to permanent, specific symbionts (Britayev & San Martín 2001; Gidholm 1966; Nygren 2004). In turn, the polynoids (or scale-worms) associated to hydrozoans are in general more diversely and closely related with their hosts. Scale-worms are predominately found in association with stylasterid or antipatharian corals (Martin & Britayev 1998). They can modify the host colony growth causing the formation of galls with open tunnels (*i.e.* the so called “worm runs”) that facilitate movement of the worms (Britayev 1981; Cairns 1987; Hanley & Burke 1991; Molodtsova & Budaeva 2007; Pettibone 1989; Pettibone 1991).

In turn, the associations between scale-worms and other hydrozoans such as the hydroidomedusae seem to be scarce, with only two known records: *Lagisca zibrowii* Hartmann-Schröder, 1992, associated to *Pseudosolanderia* sp. in relatively deep waters off New Caledonia (Hartmann-Schröder 1992), and *Medioantenna clavata* Imajima 1997, found on a solanderiid colony in the shallow waters off Ogasawara Islands (Japan) (Nishi & Tachikawa 1999). In the latter, however, the hydroid identification looked doubtful. It was reported as “*Solanderia misakiensis*”, a misspelling of *S. misakinensis* (Inaba, 1892), in the abstract and then referred to as *S. secunda* (Inaba, 1892) within the polychaete description. Regardless of these name problems, that paper represents the first reference to a symbiotic mode of life for *Medioantenna*. Originally, the genus (and its single species known to date, *M. clavata*) was described from Sagami Bay without any reference to its mode of life (Imajima 1997).

As such, our report on the specimens from North Sulawesi (Indonesia) is the third for the genus. These worms fit well with Nishi & Tachikawa (1999)’s description. However, they

clearly differ from the original description of *Medioantenna clavata* by Imajima (1997), as confirmed by checking an available paratype. Therefore, here we are describing them as a new species within the genus, namely *M. variopinta* sp. nov., which includes specimens from Indonesia and from Ogasawara Islands. We have also highlighted the morphological characteristics and geographical distribution of the host, together with the known characteristics of the symbiotic association.

Materials and methods

The presence of a symbiotic polychaete exhibiting well-defined color mimicry was observed on colonies of the Anthomedusan hydroid *Solanderia secunda* from North Sulawesi (Indonesia), an area which is considered to be a hot spot of marine biodiversity together with the Philippines and Papua New Guinea (Hoeksema 2007).

The taxonomy and ecology of the hydroids of this area have been studied since 2002, when several colonies of the two solanderiid species – *Solanderia secunda* and *S. procumbens* – were analyzed both underwater and in the laboratory. However, the first symbiotic polychaetes were obtained between 2005 and 2008, after randomly sampling the solanderiid colonies by SCUBA diving at different sites of the Bunaken Marine Park and at Mapia House Reef, at a depth ranging between 10 and 30 m (Fig. 1). The scale worms were always found on *S. secunda* colonies and never on *S. procumbens*.

During February and July 2008, additional diving surveys were conducted to check the infestation of *S. secunda* colonies at Siladen Onong and Bunaken Timur. At these sites, horizontal transects of about 100 m length were carried out at three depths (10, 15 and 30 m). The occurrence and number of worms in each colony was noted (Table 1). Any attempts to collect the symbionts *in situ* resulted either in an escape behavior (as the worms tried to hide themselves within the basal portion of the colony) or autotomising. To obtain entire specimens, fragments of the host hydroid were cut with surgical scissors and kept in plastic bags together with the worms. In the laboratory, the hydroid branches hosting polychaetes were observed *in vivo* under a stereomicroscope to understand the peculiarities of the behavior of the symbiont. Later, some polychaete specimens were carefully separated from the host and preserved either in 4% neutralized formaldehyde or in 95% ethanol.

Both the symbiotic polychaetes and host colonies were examined by Scanning Electron Microscopy (SEM). The target fragments were carefully rinsed with distilled water,

dehydrated in a graded ethanol series, Critical Point dried and coated with gold-palladium in a Balzer Union evaporator. They were observed under a Philips XL20 microscope.

Relevant morphological features were drawn with the help of a *camera lucida*, then drawings were scanned and digitized with a Wacom tablet. Body length (L) was measured from the anterior prostomial margin to the posterior border of the last segment. Body width was measured at the level of the widest segment, parapodia excluded (WW) or included but excluding (WP) or non-excluding chaetae (WC). In the “Material examined” and “Measurements” sections, ‘cs’ means complete specimens and ‘mf’ refers to mid-body fragments. The types of the new species are deposited in the “Museo Nacional de Ciencias Naturales” (MNCN) of Madrid (Spain). The types of *Medioantenna clavata* were loaned by the National Science Museum of Tokyo (NSMT).

Results

Phylum ANNELIDA

Class POLYCHAETA

Family POLYNOIDAE Kinberg, 1856

Medioantenna Imajima, 1997, emended

Type species. Medioantenna clavata, Imajima, 1997

Diagnosis

Body dorso-ventrally flattened, long, with up to 83 chaetigers and up to 38 pairs of elytra. Elytra on segments 2, 4, 5, 7, 9, 11, 13, 15, 17, 19, 21, 23, 26, 29, 32, 35 and thereafter with attachment varying between specimens and between left and right side of the same specimen, to end of body, with lump or large finger-like papillae on rear margin. Dorsum more or less covered by elytra. Body with dorsal tubercles on cirriferous segments. Prostomium bilobed, with small cephalic peaks and three antennae. Lateral antennae small, inserted ventrally to median antenna. Median antenna with large ceratophore and style, inserted antero-dorsally on prostomium. Two pairs of eyes and two palps present. Tentaculophores achaetous. Proboscis with nine pairs of papillae and two pairs of jaws. Parapodia relatively long, biramous; both noto- and neuropodia with elongate acicular lobes; notopodia, small, conical, located at antero-dorsal side of neuropodia; neuropodia with a supra-acicular process; tips of noto- and

neuroacicula penetrating epidermis. Notochaetae slightly stouter than neurochaetae, straight to falcate with slight serrations and unidentate tips. Neurochaetae more numerous, with strong serration and unidentate or bidentate tips. Median antenna, tentacular and dorsal cirri with subdistally inflated styles and filiform, pointed tips.

Remarks

Imajima (1997) placed *Medioantenna* in the Arctonoinae. However, the position and size of median antenna and the very small spur-like lateral antennae of the genus are very unusual features for this subfamily. Moreover, neither Imajima (1997) nor Nishi & Tachikawa (1999) mentioned the presence of dorsal tubercles which occur on the tentacular segments in *M. variopinta* sp. nov. and are clearly visible in Imajima's drawings (Imajima, 1997, Fig. 8b, 8c). The presence of dorsal tubercles also disagrees with the subfamily diagnosis. As the separation of Arctonoinae from Polynoinae is still not clear enough, we agree with Barnich & Fiege (2001, 2003) that a revision of the genera should be included within the former. Therefore, we prefer to avoid the inclusion of the genus in any subfamily of polynoids.

Medioantenna was established by Imajima (1997) for *Medioantenna clavata* Imajima, 1997 and has been considered as monotypic to date. Our findings confirmed the existence of a second species of the genus, *M. variopinta* sp. nov., which is found on tropical hydroids in the coastal waters of Japan and North Sulawesi and which is fully described here below.

***Medioantenna clavata* Imajima 1997**

Not *Medioantenna clavata* – *sensu* Nishi and Tachikawa (1999).

Examined material

Paratype: NSMT-Pol R74, two fragments. Kannonzुकadashi, Amadaiba, 80 m deep, March 20, 1951 according to Imajima (1997) (label written in Japanese).

Remarks

The morphological characteristics of the paratype fully agree with the original description by Imajima (1997). However, the following details were not previously mentioned, and as such have been reported here to complete the description of the species. In the observed paratype, the number of notochaetae per bundle ranged from 13 to 16 (on chaetigers 2, 12, 23 and 39). The nephridial papillae become elongated, directed upward between parapodia to reach one

third of the parapodial height from chaetiger 3 to posterior end. The paratype was, thus, a female measuring L: 25 mm (20 mm + 5 mm), WW: 2.9 mm, WP: 6 mm, WC: 10.2 mm, 35 (30 + 5) segments.

***Medioantenna variopinta* sp. nov.** (Figs. 2–9)

Medioantenna clavata – Nishi and Tachikawa (1999): 107 – 110, Fig. 1A-J

Examined material

Holotype: female, cs in two fragments MNCN 16.01/13202, on a colony of *Solanderia secunda*, Celebes Sea, North Sulawesi, Mapia, 1°37'36.28"N; 124°48'8.46"E, 25 m deep, July 7, 2008. Paratype 1: female, cs with pharynx cut off for examination MNCN 16.01/13203, on the same host colony as the holotype, Celebes Sea, North Sulawesi, Mapia, 1°37'36.28"N; 124°48'8.46"E, 25 m deep, July 7, 2008. Paratype 2: juvenile, cs MNCN 16.01/13204, on *S. secunda*; Celebes Sea, North Sulawesi, Siladen Onong, 1°27'31.16"N; 124°45'59.53"E, 23.2 m deep, July 27, 2008. Additional material: mf with regenerated pygidial segments MNCN 16.01/13205, on *S. secunda*; Celebes Sea, North Sulawesi, Siladen Onong, 1°27'31.16"N; 124°45'59.53"E, 23.2 m deep, July 27, 2008.

Diagnosis

Long worm with 78 chaetigerous segments, and 34 to 38 pairs of elytra, markedly irregular in outline, with large fold on external margin, large finger-like papilla on posterior edge, and a few micropapillae irregularly distributed on dorsal surface. Neurochaetae all unidentate. Body orange, with prominent dark violet pigmentation on prostomium, and a combination of dark violet (at basis) and whitish (at tips) pigmentation in cephalic and body appendages and parapodial lobes, visible also in preserved specimens.

Description (based on holotype)

Prostomium, bilobed, wider than longer, with small cephalic peaks. Two pairs of large dark brown eyes, ovate or round in shape; anterior pair larger than posterior one, lateral in position, on widest part of prostomium; posterior pair smaller than anterior one, near posterior margin of prostomium, dorsally orientated (Figs. 2A, 2B, 3A). Median antenna with large ceratophore, inserted antero-dorsally on prostomium; style long, smooth, cylindrical, distally slightly inflated, ending in short terminal filiform tip, with an internal axis (visible by

transparency). Lateral antennae including ceratophores about six times shorter than median antenna, inserted termino-ventrally on distal prostomial end; styles about eight times shorter, basally inflated, smooth, with filiform tips. Palps smooth, stout, conical, gradually tapering to filiform tips, slightly shorter than median antenna (Figs. 2A, 2B, 3A, 3B). Facial tubercle prominent; mouth surrounded by two lateral lips, one dorsal with five lobes, the ventral lip large, lobular, with 10-12 poorly distinct lobes (Fig. 3B). Pharynx not everted, with four light brown jaws, all similar in shape and size (Paratype MNCN 16.01/13203). First segment not visible dorsally; tentaculophores moderately long, achaetous, with two pairs of tentacular cirri, similar in shape to median antenna, dorsal cirrus 1.5 longer than median antenna and twice as long as ventral cirrus (Figs. 2A, 2B, 3A), both with a few small papillae. Second segment with a semi-lunar nuchal lobe, carrying first pair of elytra dorsally (Figs. 2A, 2B); parapodia biramous; ventral cirri with style twice longer as in following segments, similar in shape to antennae and dorsal tentacular ones, with a few minute papillae (Figs. 4A); second and third ventral cirri similar in shape to first one, slightly decreasing in length, with only traces of violet pigmentation; successive ones abruptly becoming more than three times shorter, neither distally swollen nor pigmented, with papillae more numerous than on first one (Figs. 3H, 3I, 5A, 5B).

Elytra numbering 35 (right side) and 34 (left side), on chaetigers 2, 4, 5, 7 and alternating through chaetigers 23, 26, 29, 32, 35, 36, 38, 39, 42; thereafter asymmetrically arranged on 43, 46, 50, 53, 54, 57, 60, 63, 65, 67, 68, 69, 71, 74, 77 (right side) and 46, 47, 50, 53, 54, 57, 60, 61, 63, 65, 69, 71, 74, 76 (left side); reaching posterior end, overlapping antero-posteriorly, leaving mid-dorsum uncovered (Fig. 2A, 2B, 3C). All elytra basically oval, markedly irregular in outline, with a large fold on external margin, a very large finger-like papilla on posterior edge, and delicate transparent micropapillae scattered on dorsal surface; elytra basically transparent, with a few, small white spots, more abundant near edges; elytral nerves visible as ramifying whitish structures (Figs. 3F, 3G, 6A-6C). Cirrigerous segments with dorsal tubercles (Figs. 6A, 6D). Dorsal cirri on postero-dorsal side of parapodia with cylindrical, relatively long cirrophores; styles smooth, cylindrical, with inflated subterminal ends, short filiform tips and few scattered small papillae, more distinct basally than distally (Figs. 3D, 3E). All segments with two prominent, transverse, dorsal ciliary bands, joining at basis of elytraphores or dorsal tubercles (Figs. 2A, 6A, 6D, 6E). Basal part of parapodia with numerous, prominent papillae bearing tufts of cilia on tips (Figs. 3H, 3I, 5C, 6D, 6F).

Parapodia relatively long, biramous (Figs. 4A-4C, 3H); notopodia small, conical. Neuropodia with long anterodorsal acicular lobe (Fig. 5E); neuropodia deeply incised dorsally and ventrally, with long sub-triangular prechaetal lobe and digitiform supra-acicular process; postchaetal lobe half as long as prechaetal one, distally rounded; tips of noto- and neuroacicula protruding (Figs. 4A-4C). Notochaetae as stout as or stouter as neurochaeta, arranged in a tuft (Figs. 2B, 3H), 6-8 per bundle, straight, with entire tips and slight serrations (Figs. 5C, 7A, 7D, 8D, 8E). All neurochaetae of same type, falcate, with distinct rows of spines, with distally bent, unidentate tips; 18-20 per bundle (Fig. 5D, 7B, 7C, 7E-7G, 8A-8C).

Nephridial papillae from segment 6 to posterior end, becoming elongated, upwardly directed, nearly reaching upper side of notopodia in segments 16-18 (Fig. 5G). Pygidium with terminal anus; two ventral cirri below anus, relatively long, as long as and similar in shape to posterior-most dorsal cirri.

Measurements and variability

Holotype (cs), MNCN 16.01/13202. L: 44 mm, WW: 1.5 mm, WP: 4.1 mm, 78 segments. Paratypes: MNCN 16.01/13203 (cs), L: 34 mm, WW: 1.6 mm, WP: 3.3 mm, 77 segments; MNCN 16.01/13204 (cs, juvenile), L: 11 mm, WW: 0.7 mm, WP: 1.9 mm, 43 segments. Additional material: MNCN 16.01/13205 (mf, with regenerated posterior segments), L: 6 mm, WW: 1.8 mm, WP: 4.0 mm, 8 segments.

Number of elytra varying both between left and right sides and between worms. The juvenile paratype MNCN 16.01/13204 has 18 regularly distributed pairs (Table 2). The adult elytral distribution is regular up to segment 42 (Holotype) and 35 (Paratype MNCN 16.01/13203), and the total number of elytra on left and right sides also differed: 35/34 (holotype) and 36/29 (Paratype MNCN 16.01/13203) (Table 2). The number of notochaetae per bundle do not vary significantly in animals of different size (6 – 8 in holotype and juvenile), while the neurochaetae are less numerous in large specimens (holotype 11- 13, juvenile 18 – 20). The juvenile has both eye pairs nearly equal in size, instead of the anterior pair larger than posterior one typical of adults. In addition, the holotype and the mid-body fragment have elongated nephridial papillae, which were much shorter in the other paratypes.

Coloration

Body bright orange on living worms, with a bright violet pigmentation on prostomium, parapodia, cirrophores and basal parts of antennae, palps, dorsal cirri and first 2-3 pairs of ventral cirri. Distal ends on cephalic appendages and dorsal cirri bright whitish. The orange

body mimics the large orange *Solanderia* eumedusoids of the host colony, while the white pigmentation on the cephalic appendages and on dorsal cirri and the finger-like macropapillae of the elytra mimic the coloring of the host polyps (Figs. 9A-9E). Elytra with whitish spots near the margin, whitish pigmentation on distal part of the finger-like papilla, and a pale-white ring surrounding the area of attachment to the elytriphore, extending to the nearby surface (Figs. 3F, 3G). Mimicry of worms on fertile hydroid colonies (Fig. 9D & E) is more efficient than on unfertile colonies (Fig. 9A & B).

Body of alcohol preserved worms becoming whitish in background, with prominent dark violet pigmentation on prostomium, parapodia, cirrophores and basal parts of antennae, palps, dorsal cirri and first 2-3 pairs of ventral cirri (Figs. 3A-3D).

Etymology

The specific epithet *variopinta* refers to one of the most distinctive features of the species, which is its spectacular bright orange, whitish and violet color pattern that perfectly mimics the fertile colonies of its host hydroid.

Taxonomic remarks

The morphology of the new species fits well with the diagnosis of *Medioantenna*, as proposed by Imajima (1997) for *M. clavata*. Both species have an enlarged ceratophore on the median antenna, arising antero-dorsally from the prostomium, and lateral antennae with small ceratophores. The elytral distribution coincided from segments 2 to 35, and became irregular on posterior-most segments (Table 2). However, *M. variopinta* sp. nov. has a very large finger-like papilla on the rear region of elytra, clearly separated from the margin instead of a soft lump on the rear margin of the elytra in *M. clavata* (Imajima 1997, Figs. 7e, 7d). Furthermore, the strongly serrated neurochaetae are similar in the two species, but all of them have unidentate tips in *M. variopinta* sp. nov., instead of bidentate tips in segment two in *M. clavata* (Imajima 1997, Figs. 9g, 9h). The notochaetae are 6–8 per bundle in the new species and are more numerous in *M. clavata*. Although the exact number was not reported in the original description, they ranged from 11 to 16 per bundle according to the illustrations (Imajima 1997, Figs. 7d, 8a, 8b) and from 13 to 16 per bundle in observed paratype. Additionally, *M. variopinta* sp. nov. is slender and has more segments than *M. clavata*. The holotypes of both species have nearly the same length (i.e., 44 mm and 45 mm, respectively), but *M. variopinta* sp. nov. is substantially more slender: 4.1 mm WP vs. ca. 6.0 mm WP in *M. clavata* (based on paratype measurements). In addition, the chaetigers are more numerous in

the former (up to 77-83) than in the latter (up to 59) (Table 2). Additional minor differences are: the presence of micropapillae on the elytral surface in *M. variopinta* sp. nov., which are absent in *M. clavata*, and the prominent dark violet pigmentation on the prostomium and basal parts of prostomial and body appendages visible in *M. variopinta* sp. nov. even in preserved specimens, which is absent in *M. clavata*.

The specimens from Ogasawara Islands, described by Nishi and Tachikawa (1999) as belonging to *M. clavata*, deserve special attention. Their morphology and coloring agree with *M. variopinta* sp. nov. but there seem to be several differences. The tentacular segment bears chaetae, the prostomium lacks cephalic peaks, the second segment lacks nuchal fold, the anal cirri are absent, the elytra lack micropapillae, and the dorsal ciliary bands are absent.

Among them, the first one is the most intriguing feature, as chaetae are absent from the tentacular segment in both in Imajima (1997) and our Indonesian worms, and also because having achaetous tentaculophores is one of the diagnostic features of the Arctonoinae (Hanley 1989; Wehe 2006). Cephalic peaks are not prominent in our specimens, and were described as “rudimentary” in the *Medioantenna* generic diagnosis (Imajima, 1997). As the shape of cephalic peaks might be affected by fixation and may even vary among species of the same genus (e.g. in *Hololepidella*) or among specimens of the same species (e.g. in *Hololepidella laingensis*, Britayev et al. 1999), we consider that its absence may not have a great significance for the identification of species within this genus. In turn, the absence of the nuchal fold and anal cirri in the specimens described by Nishi & Tachikawa (1999) could be a consequence of either an intra-specific variation or a fixation bias (nuchal fold), and of a loss during sample handling (anal cirri). Finally, the presence of the two dorsal ciliary bands, clearly visible in our specimens, have been reported neither by Imajima (1997), nor by Nishi & Tachikawa (1999). Despite this, the position of the inter-segmentary lines on Figs. 1A and 1B in Nishi & Tachikawa (1999) perfectly agrees with that of the ciliary bands, therefore being present (but not reported) in the worms from Ogasawara Islands.

Since the above-mentioned differences might be caused by sample handling or observation biases, they are not sufficient to consider both the Japanese and Indonesian specimens as different species. Keeping this in mind, and taking into account that we did not have the opportunity to check the specimens from Ogasawara Islands, both populations appear to coincide in virtually all diagnostic characteristics (including appendage and elytral morphology, color pattern, mode of life and likely host species), leading us to consider that both belong to *Medioantenna variopinta* sp. nov.

Biology

Medioantenna variopinta sp. nov. was found living on colonies of *Solanderia secunda* at 12 – 25 m deep (Figs. 9A-9E). The symbionts were not present on every checked colony, but their occurrence could have been underestimated due to their ability to quickly hide themselves among the intricate basal branches when the colonies are disturbed. The number of infested hydroid colonies rarely exceeded 3-5%, but exceptionally reached 50% (Table 1). The intensity of infestation varied from 1 to 3 worms per colony. Four of five infested colonies harbored 2 or 3 worms each (Table 1), possibly indicating pair formation.

Damaged and regenerating elytra and dorsal cirri were found on all specimens (for instance: holotype – 2, 4, 7, 9, 11, 13, 15 chaetigers right side, 4, 5, 7, 9, 13 chaetigers left side; Paratype MNCN 16.01/13203 – 7 chaetiger left side, Paratype MNCN 16.01/13204 – 32 both sides, 35, 38, 39 – right side, Fig. 6D), which may indicate the possibility of intra-specific aggressive interactions. In the specimen MNCN 16.01/13205 specimen (fragment), the few posterior-most segments, pygidium and anal cirri were clearly regenerating, which may indicate the presence of predator attacks, as demonstrated in other scale-worms (Britayev 1991; Britayev & Zamyshliak 1996).

The holotype and the fragment with regenerating posterior end were females and had elongated nephridial papillae, while paratype 1 (found on the same hydroid colony as holotype) seemed to be a male and had short nephridial papillae. The single juvenile found also had short papillae.

Distribution

Siladen (Type Locality), Bunaken and Mapia from North Sulawesi, Indonesia; Ogasawara Islands, Japan.

Phylum CNIDARIA

Class HYDROZOA

Family SOLANDERIIDAE Marshall, 1892

Genus *Solanderia* Duchassaing & Michelin, 1846 = *Chitina* Carter, 1873

***Solanderia secunda* (Inaba, 1892)** (Figs. 5, 10)

Dendrocoryne secunda Inaba, 1892:98, figs. 111-113

Solanderia secunda – Bouillon, Wouters & Boero 1992: 12, pls 5–6, 10–12, synonymy

Material examined

Celebes Sea, North Sulawesi, Indonesia: about thirty colonies on the fringing reef of Bunaken Timur, 1°36'34.20"N; 124°46'57.96"E, 10-30 m deep, August 1, 2007 and 10 October 2008; two colonies on the patch reef of Mapia, 1°37'36.28"N; 124°48'8.46"E, 25 m deep, October 7, 2008; two colonies on the fringing reef of Negeri, 1°36'57.11"N; 124°42'15.63"E, 10 m deep, July 24, 2008; about twenty colonies on the fringing reef of Siladen Jeti, 1°37'39.10"N; 124°48'0.26"E, 10-30 m deep, February 11, 2008 and November 27, 2008; about twenty colonies on the fringing reef of Siladen Onong, 1°27'31.16"N; 124°45'59.53"E, 10-30 m deep, July 27, 2008 and February 26, 2005; one colony on the fringing reef of Tanjung Pisok, 1°33'59.00"N; 124°47'55.61"E, November 20, 2006.

Diagnosis

Very large colonies, up to 30 cm high and 50 to 500 cm² in surface, erect, fan-shaped, with one to several fascicled stems; branch thickness decreasing towards distal extremities (Figs. 9A,10A). Ramifications always on a plane. Skeleton permeated, covered by living tissue (coenosarc). Surface of basal part of stems almost smooth, lacking hydrophores (triangular skeletal structures at basis of hydranths). Central and peripheral portions of colonies with thinner branches bearing prominent hydrophores; branches rounded or flattened, ribbon-like.

Hydranths pin-shaped, flanked by hydrophores, with an oral whorl of 4-5 capitate tentacles and 13-15 scattered aboral capitate tentacles. Sphaerolous and refringent cells grouped in a dense cluster at middle of polyp (Fig. 10D). Nematocysts as stenoteles with two sizes (11,5-14 x 15-18 µm and 5-7 x 7-9 µm); inside capitula. Living polyps white, able to curve after mechanical stimulation.

Gonophores are eumedusoids with four radial canals, a circular canal and spadix; spherical or oval, supported by a short pedicel; gonophores mostly concentrated in central part of colonies, on secondary branches.

Coloration

Exoskeleton varying from dark red (on thicker parts) to brilliant red (on thinner branches); hydranths white and gonophores bright orange; canals and spadix reddish (Figs. 9A-9D; 10C).

Biology

Solanderia secunda were found on coral reefs at Bunaken Marine Park, as well as on scattered corals in the sandy slope at Mapia House Reef. The colonies were most abundant along the vertical coral walls. The highest colony density was found at Siladen Jeti, Siladen Onong and Bunaken Timur, where the colonies are under the constant influence of strong, bi-directional tidal currents. Colonies were rare in sites with high sedimentation rates, such as Tanjung Pisok where high turbidity discourages solanderiid development despite the strong currents. Colonies were generally oriented perpendicularly to the reef wall, at 10-35 m deep, being most common at a depth between 10-20 m. The species is fertile all over the year, except July.

Distribution

Widely distributed in the tropical Indo-West Pacific (Bouillon *et al.* 1992; Di Camillo *et al.* 2008; Kirkendale & Calder 2003; Millard 1975; Schuchert 2003; Vervoort 1966; Watson 1999).

Characteristics of the association between *Medioantenna variopinta* sp. nov. and *Solanderia secunda*

Despite the presence of two *Solanderia* species in the study area, *S. procumbens* and *S. secunda*, *Medioantenna variopinta* sp. nov. was only observed in association with the latter. The polychaetes were found on colonies living at a depth between 12 to 25 m, either on the large fan-shaped portion or hidden in the basal portion, where branches formed an irregular bundle (Figs. 9A-9E). The number of polychaete specimens present on the same colony ranged from one to a maximum of three (Table 1).

The color pattern of the symbiotic scale-worm closely mimicked that of the fertile specimens of *S. secunda*. Dorsal cirri resembled the hydranths both in shape and color. The basal part of each cirri had a V-shaped, dark violet pigmentation resembling that of hydrophores, while the apical portion resembled the hydranths, with its pin-shape and numerous white spots (Figs. 9D-9E). Even though cirri lack structure similar to the hydroid tentacles, the scattered white spots mimicked their irregular distribution, a camouflage mimicry that is reinforced by the white spots scattered on the transparent elytrae. The white finger-like macropapillae on elytra resemble the hydranth's hypostome, the dark violet color of parapodia matched that of hydroid's skeleton, and the bright orange body resembled the

gonophores (Figs. 9D-9E). The camouflage turns out to be most effective on fertile colonies bearing the large orange eumedusoids, while the worm's orange body seems to be more distinguishable from the background when the hydroid is infertile (Figs. 9A-9C). Although *S. secunda* is fertile almost all year round (Di Camillo *et al.*, 2008), during the very short periods that the hydroid lacks gonophores, *M. variopinta* sp. nov. stands out on the host, probably becoming more vulnerable to predator attacks (Figs. 9A & B). However, it must be taken into account that we described (and figured) the worm and host coloring under artificial conditions (i.e. in the laboratory or under bright lighting). In the native underwater conditions, the apparently evident differences in color between the symbiont and the host might not be perceived and the pattern resulting from the contrasts in pigmentation intensity (i.e. cirri and elytra vs. body in the symbiont, hydrants and gonophores vs. exoskeleton in the host) become even more relevant than the colors themselves. This gives rise to an effective camouflage and the two partners appear as a unique organism, particularly in ripe hydroid colonies (even under artificial lighting).

In natural conditions, scale-worms crawl slowly among the hydrozoan branches. When disturbed, they quickly run down to the basal part of the colony, sheltering among the sessile epibionts that can be found in this region. When detached from the host, the scale-worms may autotomise. When this happens, their anterior ends quickly swim towards the host. Chemical cues released by hosts to attract the symbionts (i.e. the so called host factor) have been previously reported or suggested for highly specific associations (see Martin and Britayev 1998 and references herein). In the case of *M. variopinta* sp. nov., the behavior of the autotomised fragments also suggests the presence of such a host factor. Moreover, entire worms were also always able to find the fragments of hydroid colonies placed in the same container, particularly if the host was the same individual that had harbored the specimen. However, we did not perform real choice experiments. Thus, although we strongly suspect the presence of a chemical cue causing the response, we could not distinguish whether the observed behavior corresponded to a host-factor response or simply to a random encountering or sheltering.

On the other hand, *Medioantenna variopinta* sp. nov. has never been seen feeding on polyps or gonophores of its host. So we suspect that scale-worms may prey on other vagile animals living on the same colonies, such as amphipods, copepods or ophiuroids. It is interesting to note that, on the colonies, scale-worms are often seen rubbing the chaetae of adjacent parapodia. However, we cannot assess whether this results from a self-cleaning

behavior (either triggered by any host-released substance or by a natural accumulation of debris on chaetae) or from a host-cleaning behavior.

Discussion

From a morphological point of view, *Medioantenna variopinta* sp. nov. is well characterized by its elytra which have a large finger-like papilla on their posterior edge, their unidentate neurochaetae and their peculiar color pattern. However, a couple of features of the species seem to be quite rare among scale-worms: the extremely high variability in elytral distribution (along the body in different specimens and between the sides in a given specimen) and the elongated, upwardly directed nephridial papillae (found only in females). The variability in elytral distribution characterizes both *M. clavata* and the Japanese and Indonesian specimens of *M. variopinta* sp. nov. (Table 2). This variability is rare among scale-worms, and has only been reported for other long-bodied species within *Arctonoe* or *Gastrolepidia*, where the irregularity and asymmetry of elytra starts on chaetiger 33-36 or later (Hanley 1989; Uschakov 1982), or within *Enipo* and *Neohololepidella* (Muir, 1982). *Gorekia*, *Scalissetosus* and *Leucia* are not so long and thin, but all have non-standard elytral arrangements (Muir, 1982). In *M. variopinta* sp. nov., the distribution was regular up to chaetiger 35 (our specimens) or 22 (Japanese specimens) (Table 2).

As for the nephridial papillae, they are usually relatively small and ventro-laterally directed among scale-worms (Uschakov 1982). Elongated and dorsally directed papillae have only been reported once, in ripe *Harmothoe imbricata* females, where this peculiar position between parapodia was adopted to deliver eggs in a dorsal position, to be then brooded beneath elytra (Daly 1972). After breeding, the papillae regressed to a near-juvenile (or male) condition (Daly 1972). Therefore, our finding suggests a pre-reproductive or reproductive status for the females of *M. variopinta* sp. nov. Indirectly, this also supports the existence of a regular distribution with pair formation which was also reported for *H. imbricata* (Daly 1972). Eventually, our findings suggest the possibility of brooding in *M. variopinta* sp. nov., although it has not been possible to confirm this hypothesis.

The host *Solanderia secunda*, in turn, is the largest anthomedusan hydroid in Bunaken among those forming a thick, anastomosed perisarcal skeleton. However, the colonies do not harbor many organisms. The vagile (*i.e.*, copepods, amphipods, ophiuroids and gastropods)

and sessile (*i.e.*, pteroid bivalves on the fan, barnacles and bryozoans at the basal region) associated faunas are very poor, the latter likely because larvae are not able to settle on the living coenosarc covering the skeleton. In addition, several natural products (*i.e.* solandelactones) have been isolated from *S. secunda*, that have an antifouling activity preventing larval settlement (Seo *et al.* 1996). *Medioantenna variopinta* sp. nov. is probably immune to these natural products so its larvae can settle, and adults can spend their whole life, on the hydroid surface. In addition to help in removing debris from chaetae, the observed rubbing behavior could also be induced by an accumulation of mucus from the host. This accumulation occurring in the locomotive appendages (*i.e.* the parapods) could certainly limit the moving ability of the symbiont, which may feel the necessity to eliminate the excess of mucus. However, it is also possible that the worm could take advantage of a thin layer of mucus being deposited on its body. This layer may contain some of the hydroid's natural products that may play a deterrent role helping the worm to avoid predation. Although this is an interesting behavioral consequence of the association, further studies are required to obtain additional evidence. In addition to this possible benefit for the symbiont, the regular presence of *M. variopinta* sp. nov. on the colonies suggests by itself an intimate relationship with the host hydroid which is additionally enhanced by the cryptic coloring and mimicry of the scale-worm.

Nishi & Tachikawa (1999) found the Ogasawara specimens on a solanderiid, reported as *Solanderia misakiensis* in the abstract and then referred to as *S. secunda* in the text. The most relevant difference between the two species is the absence of hydrophores in the former, but Nishi & Tachikawa (1999) did not supply a description for the hydroid so that its classification is, at least, doubtful. In case the hydroid from Ogasawara was indeed *S. misakinensis*, that would mean *Medioantenna variopinta* sp. nov. is able to live on two similar solanderiid species. Both hydroids have dark colonies and probably produce similar chemicals, which could not discourage the presence of the symbiont. However, it is more likely that the Japanese hydroid also belongs to *S. secunda*. In fact, this species has often been reported from Japanese waters (Bouillon *et al.*, 1992), and even its original description by Inaba (1892) has Misaki (Japan) as type locality. Thus, it seems more feasible to consider the association as species-specific. In turn, this specificity is now confirmed by the fact that, in Bunaken, *M. variopinta* sp. nov. were never observed on the yellow colonies of *S. procumbens*, which lived exactly in the same area and habitat as the infested colonies of *S. secunda*. Nevertheless, we have not been able to precise the real nature of the relationship between the new species of scale-worm and its hydroid host.

More than 300 polychaete species are known to be involved in different types of symbiotic relationships with other marine invertebrates which consequently developing morphological, behavioral, physiological or reproductive adaptations to their particular modes of life (Martin & Britayev, 1998; Martin *et al.*, 2002). In monoxenous species, it often happens that the shape of some symbiont appendages perfectly mimics a relevant morphological characteristic of the host. For instance, the swollen dorsal cirri of the scale-worm *Asterophyllia carlae* mimic the ambulacral feet of its host starfishes (Hanley, 1989; Martin & Britayev, 1998). Also, the whole body may display camouflage colorings exactly matching the host color such as those of the syllids *Haplosyllis chamaeleon* and *H. villogorgicola* and their respective gorgonian hosts (Laubier, 1960, 1968; Martin *et al.*, 2002), or *Alcyonosyllis phili* and its alcyonacean host (Glasby & Watson 2001). In particular, it must be pointed out that *A. phili* has a color pattern which closely resembles that of *M. variopinta* sp. nov. In turn, polyxenous species may change their color in relation to that of the hosts, such as in the case of the syllid *Branchiosyllis oculata*, associated to sponges, or the scale-worm *Gastrolepidia clavigera*, associated to holothuroids (Pawlik 1983; Britayev & Lyskin 2002). Some sponge-associated syllids feed on host tissues showing different colors that mimic their particular host (Pawlik 1983; Magnino & Gaino 1998). Among gorgonian-associated syllids, in turn, either feeding on the same food as the host, kleptoparasitism (i.e., stealing food from the gastral cavities of the host polyps) and/or co-evolution seems to be the reason for that mimicry (Martin *et al.* 2002). However, syllids and scale-worms differ in their feeding behavior, the former suck food by means of their pharynx and their muscular proventricle, while the latter bite their prey with the help of their four powerful parrot's beak-like jaws. Curiously enough, among the few cases when feeding of symbiotic scale-worms was studied (e.g., *Arctonoe vittata*, *Gastrolepidia clavigera*) a wide spectrum of strategies, from host-cleaning, stealing food, foraging on free-living organisms to feeding on host tissues, were demonstrated (Wagner *et al.* 1979; Britayev *et al.* 1989; Britayev & Lyskin 2002).

The study of feeding strategies also revealed complementary behavioral trends. For instance, in addition to their prey, both *A. vittata* and *G. clavigera* had chaetae of conspecifics inside the gut whose presence was associated to that of traumas (i.e., on parapodia, head, elytra and body appendages) exactly as those found in *M. variopinta* sp. nov. These findings have been considered as a demonstration of aggressive territorial in behavior symbiotic (Britayev 1991; Britayev & Lyskin 2002) as well as in free-living (e.g. Plyuscheva *et al.*

2010) scale-worms, often leading to regular distributions in the former (Martin & Britayev 1998), and our new species seems to agree in both distribution pattern and behavior.

The few well-known host-symbiont relationships appear to be more complex than it was initially thought, with the associations often resulting to be mutualistic rather than simple parasitic or commensalistic. In most cases, the misinterpretation was caused by both an initial lack of knowledge and our usual antropogenic way of interpreting what we are looking at. For instance, the histriobdellid *Histriobdella homari* was reported as an ectoparasite of the branchial chambers of crustaceans (e.g. in Paris, 1955 or Clark, 1956), mostly because of its leech-like shape which was later confirmed as a host-cleaning mutualist (Jennings & Gelder 1976). Also, *Eunice norvergica*, a gall-forming eunicid (an *a priori* parasitic behavior), enhanced the growth of their cold-water corals hosts by favoring the joining of colonies and the development of reef patches in deep waters (Roberts 2005). Among scale-worms, *Arctonoe vittata* was considered to be a commensal of their limpet or starfish hosts, and later re-considered as a mutualist, which is able to defend the former from the attacks of predatory starfishes (Dimock & Dimock 1969; Williams 2009) or to keep the latter clean by replacing the normal function of the pedicellaria, lacking in their starfish hosts (Wagner *et al.* 1979). This last partnership was also confirmed as mutualism from a chemical point of view, as both the symbiont and the host were attracted by cues coming from the host and the symbiont, respectively (Wagner *et al.* 1979).

Despite the numerous examples of symbiotic polychaetes reported to date, their behavioral and reproductive strategies, as well as the origin of their food and the nature of their cryptic coloring are still open questions in most relationships involving polychaetes, including scale-worms (Martin & Britayev, 1998). The main reasons are probably the rarity of the most known associations, but also the difficulties of either observing the partnership in native conditions or keeping them in experimental tanks for long periods, as it happens with our new species. Therefore, all observed details on any given association may be relevant and must be clearly reported, even if it initially leads to wrong conclusions, such as the report of the Ogasawara Islands specimens as *Medioantenna clavata* by Nishi & Tachikawa (1999). Further studies will certainly help to understand the real nature of either the associates or their associations, as well as to assess the complex relationships between symbiotic polychaetes and their hosts, and again *Medioantenna variopinta* sp. nov. is not an exception.

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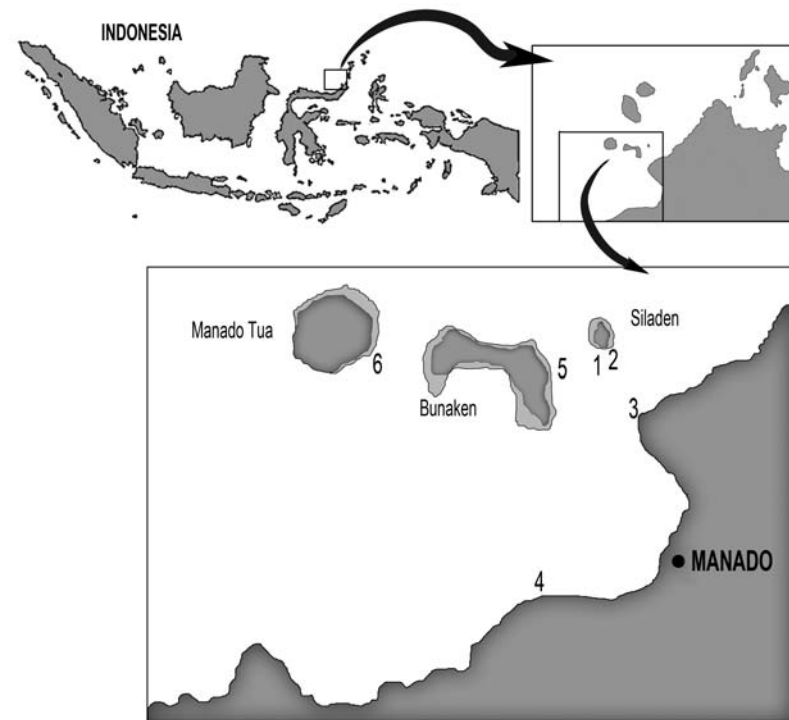


Fig. 1 Map of the studied area in the Indonesian archipelago. Sampling sites: 1. Siladen Onong; 2. Siladen Jeti; 3. Tanjung Pisok; 4. Mapia House Reef; 5. Bunaken Timur; 6. Negeri. Map source: <http://www.gebco.net/>.

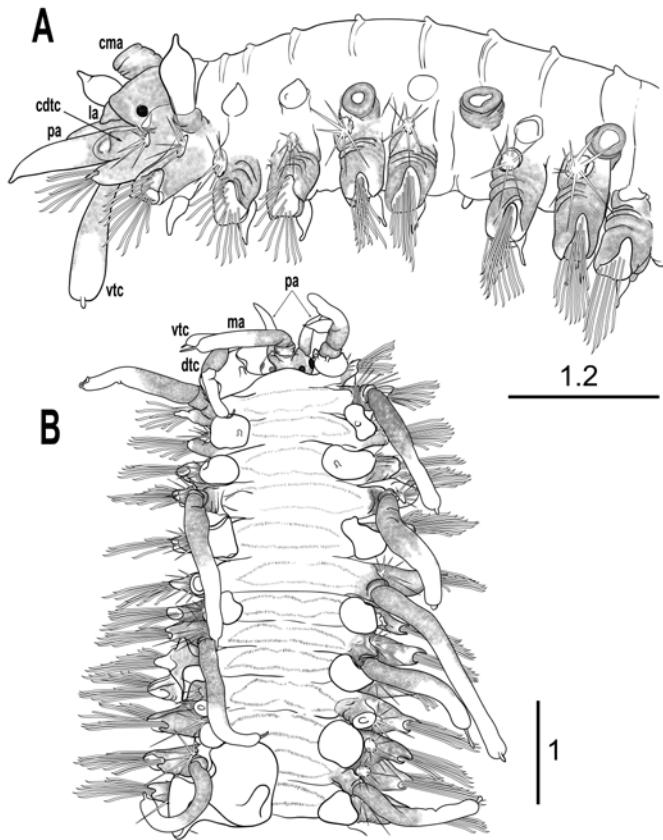


Fig. 2 *Medioantenna variopinta* sp. nov. Holotype. A. Anterior end, lateral view. B. Anterior end, dorsal view; ma – median antenna, cma – ceratophore of median antenna, cdte – cirrophore of dorsal tentacular cirrus, dtc – dorsal tentacular cirrus, vtc – ventral tentacular cirrus, la – lateral antenna, pa – palp. Scale bars are in mm.

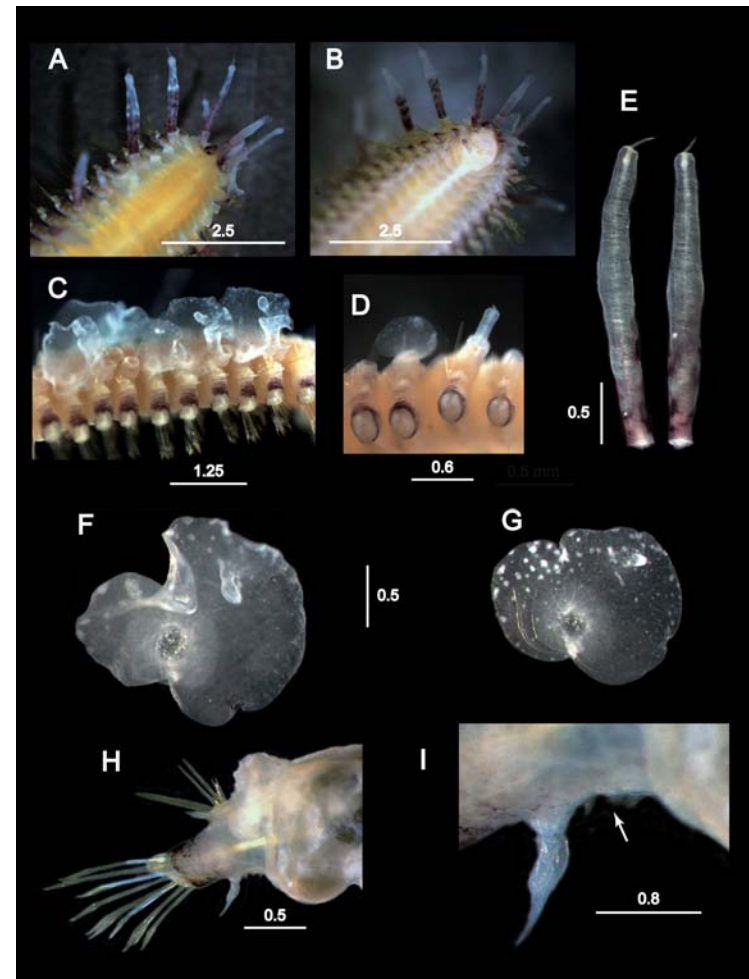


Fig. 3 *Medioantenna variopinta* sp. nov. Preserved specimen. A. Anterior end, dorsal view. B. Anterior end, ventral view. C. Mid-anterior region with elytra attached (anterior end towards the left). D. Mid-posterior region with one regenerating elytron and dorsal cirri (anterior end towards the left). E. Detached dorsal cirri from mid-body. F. Mid-anterior elytron. G. Mid-posterior elytron. H. Mid-body elytrophorous parapodium in postero-anterior view. I. Detail of the ventral side of the same parapodium, showing the ciliated papillae (white arrow). Scale bars are in mm.

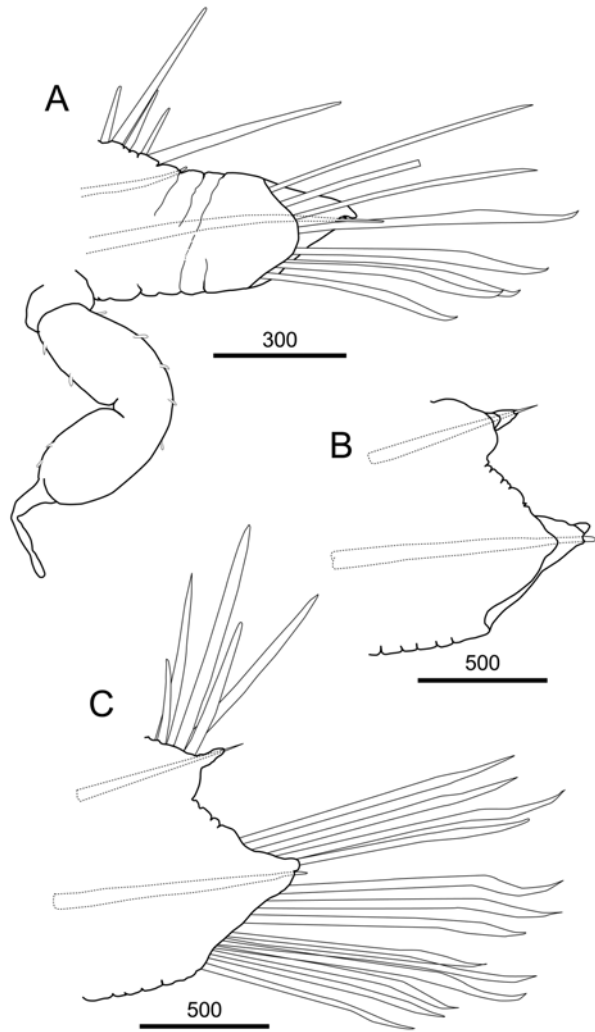


Fig. 4 *Medioantenna variopinta* sp. nov. Holotype. A. Parapodium from the second segment, antero-posterior view, showing the long ventral cirrus. B. Parapodium from mid-body (39 segment), antero-posterior view. C. Same as B, postero-anterior view. Scale bars are in μm .

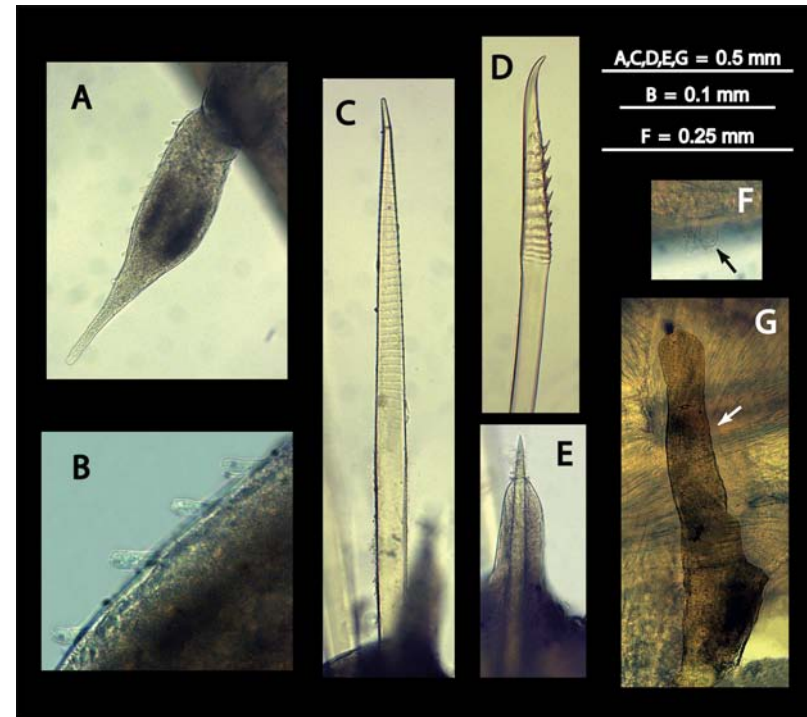


Fig. 5 *Medioantenna variopinta* sp. nov. Preserved specimen. A. Ventral cirrus. B. Detail of the papillae from the same. C. Notochaeta. D. Neurochaeta. E. Notoacicula and notoacicular lobe. F. Cilia from the ventral ciliated mounds (black arrow). G. Nephridial papilla (white arrow).

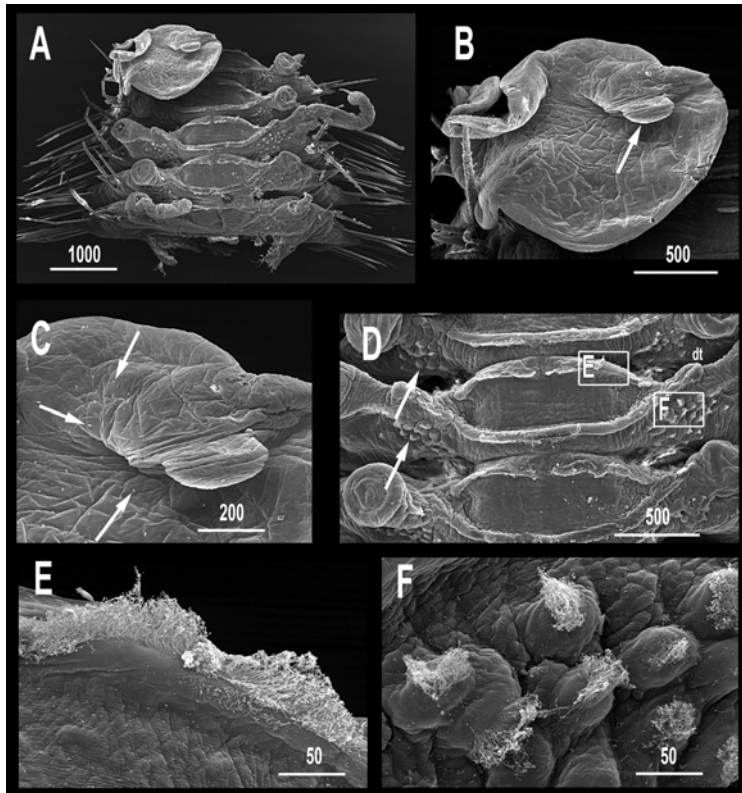


Fig. 6 *Medioantenna variopinta* sp. nov. SEM micrographs. A. Mid-body segments, dorsal view. B. Whole view of elytron; arrow points to finger-like macropapilla. C. Detail of elytral surface around finger-like macropapilla; arrows point on micropapillae. D. Close view of body dorsum; arrows point to ciliated parapodial papillae; dt: dorsal tubercles from mid-body cirriferous segment; squares mark the position of Figs. 6E and 6F. E. Detail of dorsal ciliated crests. F. Detail of ciliated parapodial papillae. Scale bars are in μm .

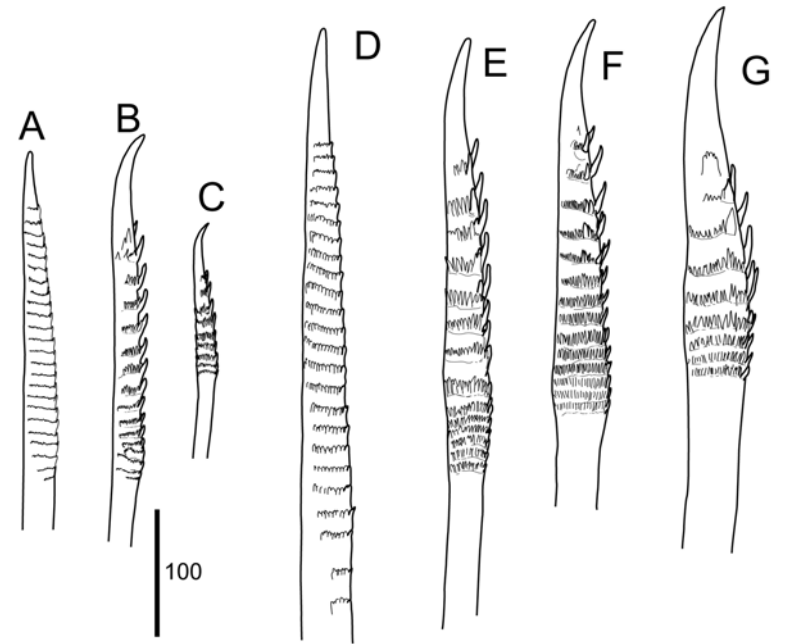


Fig. 7 *Medioantenna variopinta* sp. nov. Holotype. A. Notochaeta from chaetiger 2. B. Dorsal-most neurochaeta from chaetiger 2. C. Ventral-most neurochaeta from chaetiger 2. D. Notochaeta from chaetiger 39. E. Dorsal-most neurochaeta from chaetiger 39. F. Mid-dorsal neurochaeta from chaetiger 39. G. Ventral-most neurochaeta from chaetiger 39. Scale bar is in μm .

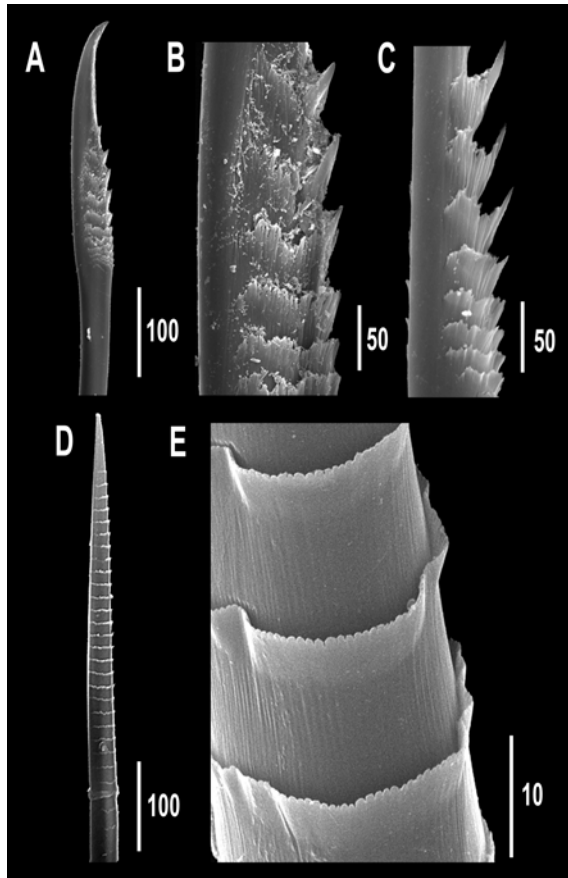


Fig. 8 *Medioantenna variopinta* sp. nov. SEM micrographs. A. Mid-dorsal neurochaeta from mid-body. B. Detail of serration from the same mid-dorsal neurochaeta. C. Detail of serration of a ventral neurochaeta from mid-body. D. Neurochaeta from mid-body. E. Detail of the serration of same neurochaeta. Scale bars are in μm .

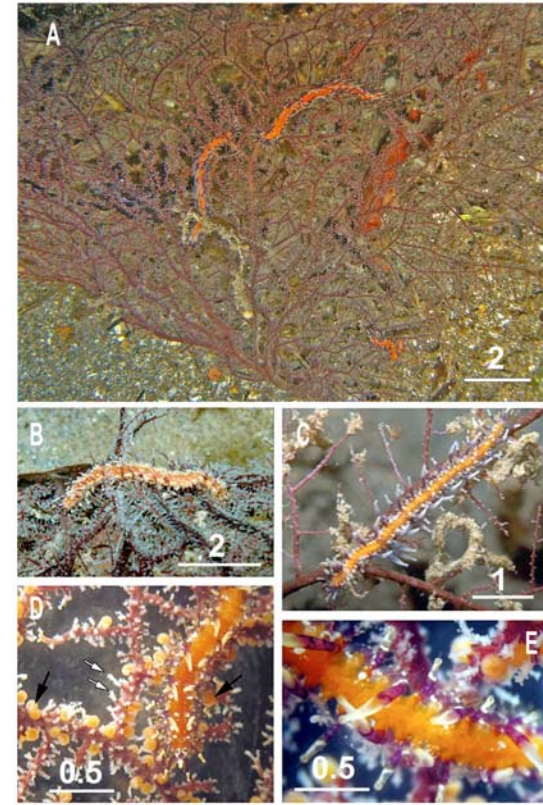


Fig. 9 *Medioantenna variopinta* sp. nov. A-C. Underwater photographs of *M. variopinta* sp. nov. on unfertile *S. secunda* colonies (Photo Massimo Boyer); the polychaete is more evident when hydroid lacks the orange gonophores (A-B) or the hydranths (C). D, E. Stereomicroscope pictures of fertile specimens of *S. secunda* hosting *M. variopinta*, the worm livery perfectly mimics the host colors. White arrows: hydranths; black arrows: gonophores. Scale bars are in cm.

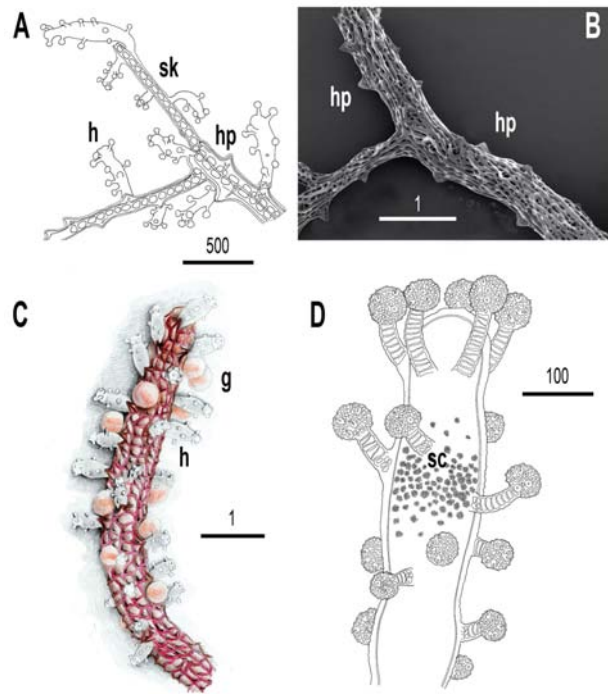


Fig. 10 *Solanderia secunda*. A. Drawing of a colony portion showing hydranths (h) and hydrophores (hp). The inner skeleton is fenestrated (sk). B. SEM picture of the skeleton of *S. secunda*. Hydrophores (hp) and skeletal meshes are clearly visible. C. Portion of a branch showing hydranths (h) and gonophores (g). D. Particular of a hydranth with capitulate tentacles and endocysts inside capitula (c); at middle of polyp sphaerulous and refringent cells are visible (sc). Scale bars of A and D are μm ; scale bars of B, C are in mm.

Table 1 Occurrence of *Medioantenna variopinta* sp. nov. in the studied area.

Diving sites	Date	Coordinates	Depth (m)	Polychaete numb.
1 Siladen Onong	27/07/2008	1°27'31.16"N; 124°45'59.53"E	23.2	2
	26/02/2005	1°27'31.16"N; 124°45'59.53"E	25	1
2 Siladen Jeti	11/02/2008	1°37'39.10"N; 124°48'0.26"E	12	2
	27/11/2008	1°37'39.10"N; 124°48'0.26"E	13	0
3 Tanjung Pisok	20/11/2006	1°33'59.00"N; 124°47'55.61"E	15	0
4 Mapia	07/10/2008	1°37'36.28"N; 124°48'8.46"E	25	3
5 Bunaken Timur	09/10/2008	1°36'34.20"N; 124°46'57.96"E	21	3
	01/08/2007	1°36'34.20"N; 124°46'57.96"E	30, 15, 10	0
6 Negeri	24/07/2008	1°36'57.11"N; 124°42'15.63"E	10	0

Table 2 Variation of elytra distribution pattern and sizes in *Medioantenna variopinta* sp. nov. and *M. clavata*. Width as without/with parapodia. Asymmetrical and irregular elytral positions are marked in italics. MNCN - Museo Nacional de Ciencias Naturales, Madrid; CBM-ZW - Natural History Museum and Institute, Chiba (code, ZW) ; NSMT – National Science Museum, Tokyo (code R).

<i>Medioantenna variopinta</i> sp. nov.	Length (mm)	Width (mm)	Chaetiger numb.	Elytra numb.	Distribution of elytra
Holotype MNCN 01/*	44	1.5/4.1	78	R: 35	2 4 5 7 9 11 13 15 17 19 21 23 26 29 32 35 36 38 39 42 43 46 50 53 54 57 60 63 65 67 68 69 <i>71 74 77</i>
				L: 34	2 4 5 7 9 11 13 15 17 19 21 23 26 29 32 35 36 38 39 42 46 47 50 53 54 57 60 61 63 65 69 71 <i>74 76</i>
Paratype MNCN 02/*	34	1.6/3.3	77	R: 36	2 4 5 7 9 11 13 15 17 19 21 23 26 29 32 35 36 38 44 46 51 53 54 56 58 59 60 62 64 66 68 69 <i>71 72 74</i>
				L: 29	2 4 5 7 9 11 13 15 17 19 21 23 26 29 32 35 37 <i>38 42 43 51 58 60 62 63 66 69 72 76</i>
Paratype MNCN 03/*	11	0.7/1.9	43	R&L: 18	2 4 5 7 9 11 13 15 17 19 21 23 26 29 32 35 38 39
Fragment MNCN 04/*	6	1.8/4.0	8	R: 5	1 4 5 6 7
CBM-ZW-890	40	4*	83	L: 4	1 4 5 8
				R: 37	2 4 5 7 9 11 13 15 11 19 21 23 25 28 31 34 37 38 41 42 44 45 46 48 49 52 55 57 59 62 64 66 <i>68 70 73 75 78</i>
				L: 38	2 4 5 7 9 11 13 15 11 19 21 23 25 28 31 34 37 38 41 42 44 45 48 51 52 55 57 59 60 62 64 66 <i>68 70 72 73 75 79</i>
CBM-ZW-891/**	48	4*	81	R: 38	2 4 5 7 9 11 13 15 11 19 21 23 26 29 32 35 36 39 40 43 46 47 49 52 53 55 56 58 60 61 63 64 <i>67 70 72 73 75 77</i>
				L: 38	2 4 5 7 9 11 13 15 11 19 21 23 26 29 32 35 36 39 40 43 46 47 49 52 53 55 56 58 60 61 62 65 <i>67 70 72 73 75 77 73 75 77</i>
CBM-ZW-892/**	42	4*	75	R: 38	2 4 5 7 9 11 13 15 11 19 21 22 25 28 31 34 35 36 37 40 41 42 46 48 50 52 55 59 60 63 64 67 <i>68 70 71 73 74 75</i>
				L: 35	2 4 5 7 9 11 13 15 11 19 21 23 26 29 32 35 36 37 39 41 43 47 49 51 55 56 60 63 66 68 69 70 <i>72 74</i>
<i>Medioantenna clavata</i>					
Holotype R:114	45	9**	59	R: 32	2 4 5 7 9 11 13 15 17 19 21 23 26 29 32 35 36 37 38 39 40 41 42 44 45 47 48 50 52 54 56 58
				L: 31	2 4 5 7 9 11 13 15 17 19 21 23 26 29 32 35 36 37 38 40 41 42 44 45 47 48 50 52 54 56 58
Paratype R:74	25	2.9/6.2	35	R&L: 16	2 4 5 7 9 11 13 15 17 19 21 23 26 29 32 35

* Type of body width measurement non-reported

** Body width as with parapodia and chaetae (WC)