Zootaxa 2671: 31–39 (2010)
www.mapress.com/zootaxa/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

Voragonema tatsunoko (Trachymedusae: Rhopalonematidae), a new species of benthopelagic medusa, host to the hyperiid amphipod *Mimonectes spandli* (Physosomata: Mimonectidae)

DHUGAL LINDSAY[1,4] & FRANCESC PAGÈS[2,3]

[1]*Marine Biodiversity Research Program, Institute of Biogeosciences, Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15 Natsushima-cho, Yokosuka-shi, Kanagawa Prefecture, Japan. 237-0021. E-mail: dhugal@jamstec.go.jp, FAX: 81-46-867-9525*

[1]*Institut de Ciències del Mar (CSIC), Passeig Marítim de la Barceloneta 37-49. E-08003 Barcelona, Catalonia, Spain*

[3]*deceased*

[4]*Corresponding author*

Abstract

Large numbers of a distinctive trachymedusa were observed at 1967 m depth just above the bottom in Suruga Bay, Japan, during a dive by the crewed submersible *Shinkai 2000* in April 2002. Two individuals were collected and proved to be an undescribed species, herein described as *Voragonema tatsunoko* **sp. nov.** This species is characterised by the number (9) and shape of the centripetal canals. An immature male hyperiid amphipod, *Mimonectes spandli* Stephensen and Pirlot, 1931, was observed attached to the subumbrella of one of the individuals adjacent to a gonad. This is the first record identifying an association between another organism and *M. spandli* and is the first record of this amphipod species outside of the Atlantic Ocean.

Key words: Jellyfish, submersible, *Shinkai 2000*, Cnidaria, trachymedusa, new species, Suruga Bay, Japan, commensal amphipod

Introduction

Benthopelagic zones around the world are largely unstudied due to the difficulties in towing nets close to the sea floor and little is consequently known about the composition and dynamics of benthic boundary layer communities. Recently the benthic boundary layer has been receiving attention for the important role it plays as the site of biogeochemical fluxes and transformations between the benthic and pelagic oceanic compartments (Marcus & Boero 1998; Raffaelli *et al.* 2003, Gili *et al.* 2006). The existence of a rich fauna and a high biomass of pelagic organisms near the deep-sea floor has been illustrated during the last decade, mainly using crewed submersibles and remotely-operated vehicles (*e.g.*, Lindsay *et al.* 1999; Miyake *et al.* 2002; Toyokawa *et al.* 2003; Miyake *et al.* 2004), and although these faunas are well-known in a few selected marine areas (Angel 1990), more remains unknown than known (Bucklin *et al.* 2010). There seems to be a tendency for the deep-sea benthopelagic fauna to be distinct and perhaps more diverse than the overlying bathy- and mesopelagic faunas (Childress *et al.* 1989).

One of the most neglected components of the fauna inhabiting the deep-sea benthic boundary layer appears to be the gelatinous zooplankton. The use of new observation techniques such as submersibles, remotely operated vehicles, and underwater cameras has allowed documentation of the near-bottom gelatinous fauna in a way that was previously impossible (Larson *et al.* 1992; Matsumoto *et al.* 1997). One of the most conspicuous organisms of the deep-sea fauna, the medusae, may develop dense concentrations near the bottom (Smith 1982; Lindsay *et al.* 1999; Miyake *et al.* 2002; Toyokawa *et al.* 2003; Miyake *et al.* 2004) with populations quite different, in comparison with the better-known mesopelagic ones (Mackie 1985). In

Accepted by A. Collins: 14 Oct. 2010; published: 9 Nov. 2010

recent years, a wide variety of gelatinous organisms have been described from the benthopelagic zone both using submersibles (*e.g.*, Hissmann 2005; Lindsay & Miyake 2007), plankton nets mounted in epibenthic sledges or bottom trawls (*e.g.*, Bouillon *et al.* 2001), traditional plankton nets (Hosia & Pagès 2007), and even from sediment traps moored near the sea floor (Gili *et al.* 1998; Gili *et al.* 1999; Bouillon *et al.* 2000). In this paper, we describe the distinctive trachymedusan species *Voragonema tatsunoko* **sp. nov.** that occurred in large numbers at 1967 m depth, just above the bottom in Suruga Bay, Japan, during a dive by the crewed submersible *Shinkai 2000* in April 2002.

Material and methods

Two specimens of the new trachymedusa were collected using a suction sampler (slurp gun) outfitted with six rotatable canister bottles (Hunt *et al*. 1997; Miyake *et al*. 2001; Lindsay 2003) attached to the crewed submersible *Shinkai 2000* during R/V Natsushima cruise NT02-06 (chief scientist: Shuhei Nishida). Environmental parameters (depth, temperature, salinity and dissolved oxygen concentration) were measured using a CTD-DO meter (SEABIRD: SBE-19, SBE-23).

Animals were transferred to a shipboard aquarium for behavioural observations, taxonomic identification, and photographic recording with a Nikon D1H digital still camera equipped with a macro lens (AF Micro Nikkor 105 mm 1:2.8 D) and recorded in JPEG format at an image size of 2000 X 1312 pixels. Observations of the live animals were also made in the ship's laboratory under a Nikon SMZ-U dissecting microscope. Specimens were fixed in buffered 5% formalin–seawater after detailed morphological analysis. Photographs of the slightly shrunken and deformed preserved specimens were taken with a Leica DFC300FX camera under a Leica MZ16 dissecting scope with a Leica KL2500LCD illuminator at full power setting under both transmitted and darkfield light conditions. Line drawings were made by Dr. Aska Yamaki using a camera lucida under the supervision of DL.

Results

Systematics (after Daly *et al.*, 2007).

Phylum Cnidaria Verrill, 1865

Class Hydrozoa Owen, 1843

Subclass Trachylinae Haeckel, 1879

Order Trachymedusae Haeckel, 1866 (1879)

Family Rhopalonematidae Russell, 1953

Genus *Voragonema* Naumov, 1971

***Voragonema tatsunoko* sp. nov.**
(Figs. 1, 2, 3)

Synonymy. "*Voragonema* sp." in Lindsay & Miyake 2009, 2K1337SS6g, 2K1337SS6h.

Type material. Two specimens collected immediately above the sea floor at 1967 m depth (temperature 2.17˚C, salinity 34.58, dissolved oxygen concentration 2.3 ml/L) at 15:18 and 15:24 by a suction sampler outfitted to the crewed submersible *Shinkai 2000* on 7 April 2002 during dive number 1337 at 34˚ 43.21'N, 138˚ 35.06'E. The holotype [2K1337SS6g] has been deposited at the Showa Memorial Institute, National

Science Museum, Tokyo, under registration number NSMT-Co-1533. The paratype is deposited in the JAMSTEC biological sample collection under registration number 2K1337SS6h (048250).

Additional material examined. The holotype of *V. laciniata* Bouillon, Pagès & Gili 2001, deposited in the Zoologisches Institut und Zoologisches Museum der Universität Hamburg (Germany). One individual of *V. laciniata* [NIWA 35989] sampled by the National Institute of Water and Atmospheric Research, New Zealand, in a non-closing Rough-bottom (orange roughy) trawl (ORH) that trawled the seafloor at 916–930 m depth on 12 February 2008 at Ross Sea Station TAN0802/41 (74.7˚S, 167.0˚E) as part of Oceans Survey 2020 for the International Polar Year and the Census of Antarctic Marine Life (CAML).

Etymology. The specific epithet *tatsunoko* (Japanese) means "child of the dragon" and refers to the legendary dragon king, whose palace is at the bottom of the sea.

Generic diagnosis

Genus *Voragonema* Naumov, 1971

Rhopalonematidae with gastric peduncle; 8 radial canals, numerous centripetal expansions of the ring canal; up to 500–2000 marginal tentacles superimposed in several rows; statocysts free, club-shaped.

Species diagnosis

Voragonema tatsunoko sp. nov.

Voragonema with subumbrella rose-orange-coloured, peduncle medium, manubrium vermillion, beige-cream gonads pendant from just above the midpoint of the radial canals, circular canal with nine triangular-based filamentous centripetal expansions in each octant, about 1050 marginal tentacles of 2 types in 6–7 rows.

Species description. Umbrella slightly more conical than hemispherical, not as high (14 mm) as wide (19 mm) (Fig. 1A) [all measurements based on the living holotype which shrunk to approximately 70% of its original size after preservation; paratype umbrellar height was 16 mm]; mesoglea 2.8 mm thick in the apex and tapering towards the umbrella margin; exumbrella transparent with fine meridional ridges, subumbrella pale rose-orange (Fig. 1A, B, C), hemispherical in fresh specimens, with circular and crossed oblique-radial muscles.

Gastric peduncle medium, cylindrical, pale rose-orange, one quarter of subumbrella height, 1.8 mm in diameter and 4 mm in height.

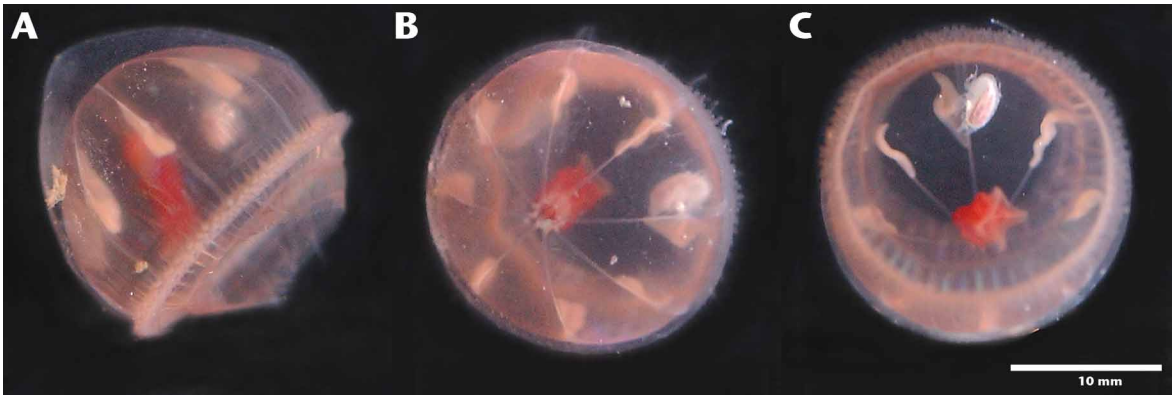

FIGURE 1. Specimen of *Voragonema tatsunoko* with the hyperiid amphipod *Mimonectes spandli* Stephensen and Pirlot, 1931 attached [paratype: 2K1337SS6h]. Specimen collected at 15:24:36 above muddy sediment in Suruga Bay at 1967 m depth on 7 April 2002 and photographed in an aquarium on board ship. *Voragonema tatsunoko*: lateral (A), apico-lateral (B), and oral (C) views; scale: 10 mm.

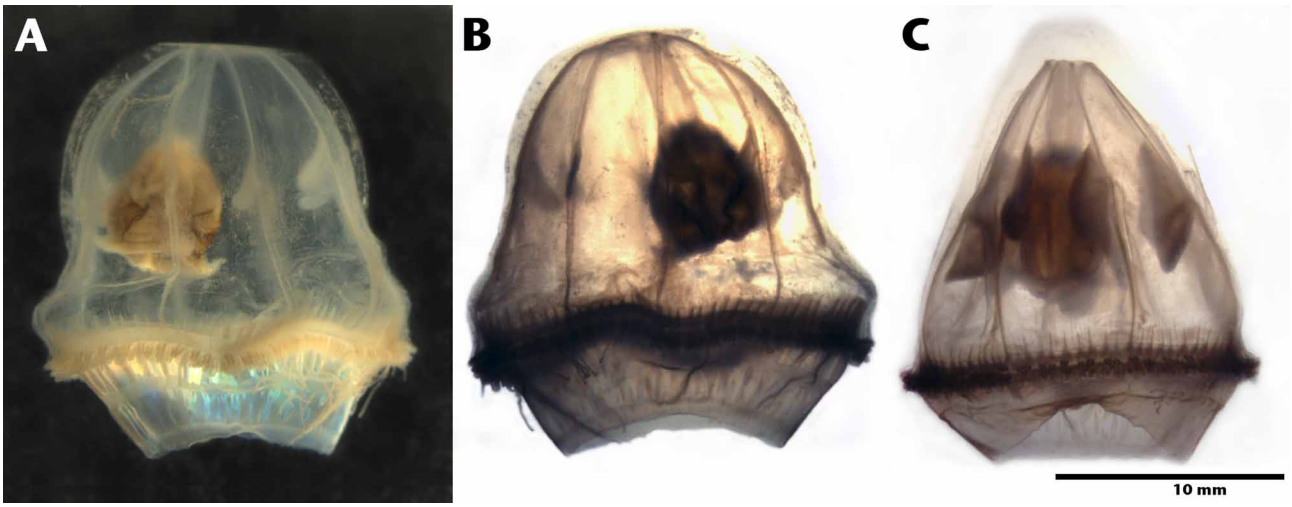

FIGURE 2. Lateral views of the holotype of *Voragonema tatsunoko* [2K1337SS6g], collected at 15:18:15, under darkfield illumination (A) and transmitted light (B), and the paratype [2K1337SS6h] under transmitted light after removal of the parasitoid amphipod (C). Note the striations on the external surface of the exumbrella (A), reminiscent of those in *Crossota rufobrunnea* (Kramp, 1913); scale: 10 mm.

Radial canals 8, whitish, translucent, straight, of uniform width but with perpendicularly striated tissue beneath the distal half causing them to appear broader.

Manubrium long, narrow, square and vermillion in fresh specimens (Fig. 1A, B, C) and brown when preserved (Fig. 2A, B, C), over twice the length of the peduncle; mouth with four flared simple lips; manubrial cavity not divided into gastric pouches; peduncle and manubrium height approximately equal to that of the subumbrella in fresh specimens.

Gonads beige-cream, laterally flattened, with distal margin of attachment at midpoint of radial canals, not extending onto upper one-third, distally pendant.

Ring canal rose-orange, wide, with nine triangular-based filamentous centripetal expansions between each radial canal.

Tentacles rose-orange and translucent, of two types, superimposed in 6–7 rows, following a regular pattern as follows: outermost row of 80 solid tentacles, with adnate bases, situated below each of the centripetal and radial canals, arranged in pairs below the centripetal canals but with the centralmost and those below the radial canals singular, in the pattern 2-2-1-2-2-1 per octant; second outermost row also with 80 solid tentacles, in pairs below each of the singular outermost tentacles; third outermost row with 48 large solid tentacles pointing downwards and situated below the spaces between the tentacles of the two outermost rows; up to 4 rows of thinner, hollow, annulate tentacles of a second type, approximately 108 tentacles per octant. Total tentacle number approximately 1075, with 208 of the larger, solid type and situated in the outer rows (Fig. 3A, B).

Statocysts free, numerous, approximately 20 per octant.

Velum translucent, pale rose-orange, 4.2 mm wide, with two marked muscle bands, the inner twice the width of the outer (Fig. 2A, B; Fig. 3A).

Remarks. An immature male of the rare hyperiid amphipod *Mimonectes spandli* Stephensen and Pirlot, 1931, measuring 6.6 mm from head to telson, was attached to the subumbrella next to a gonad in the paratype specimen (Fig. 1A, B, C). This is only the fourth record of this species in the literature and the first record outside of the Atlantic Ocean, being a significant range extension (Vinogradov *et al.* 1996). Although this is the eleventh example of an association between a hyperiid amphipod of the Infraorder Physosomata and a gelatinous macroplanktonic host, it is only the second within the family Mimonectidae (Bovallius, 1885), with Gasca *et al.* (2006) reporting a congener *Mimonectes sphaericus* Bovallius, 1885 (male) as an associate of the prayid siphonophore *Nectadamas diomedeae* (Bigelow, 1911). Only one previous example of an association

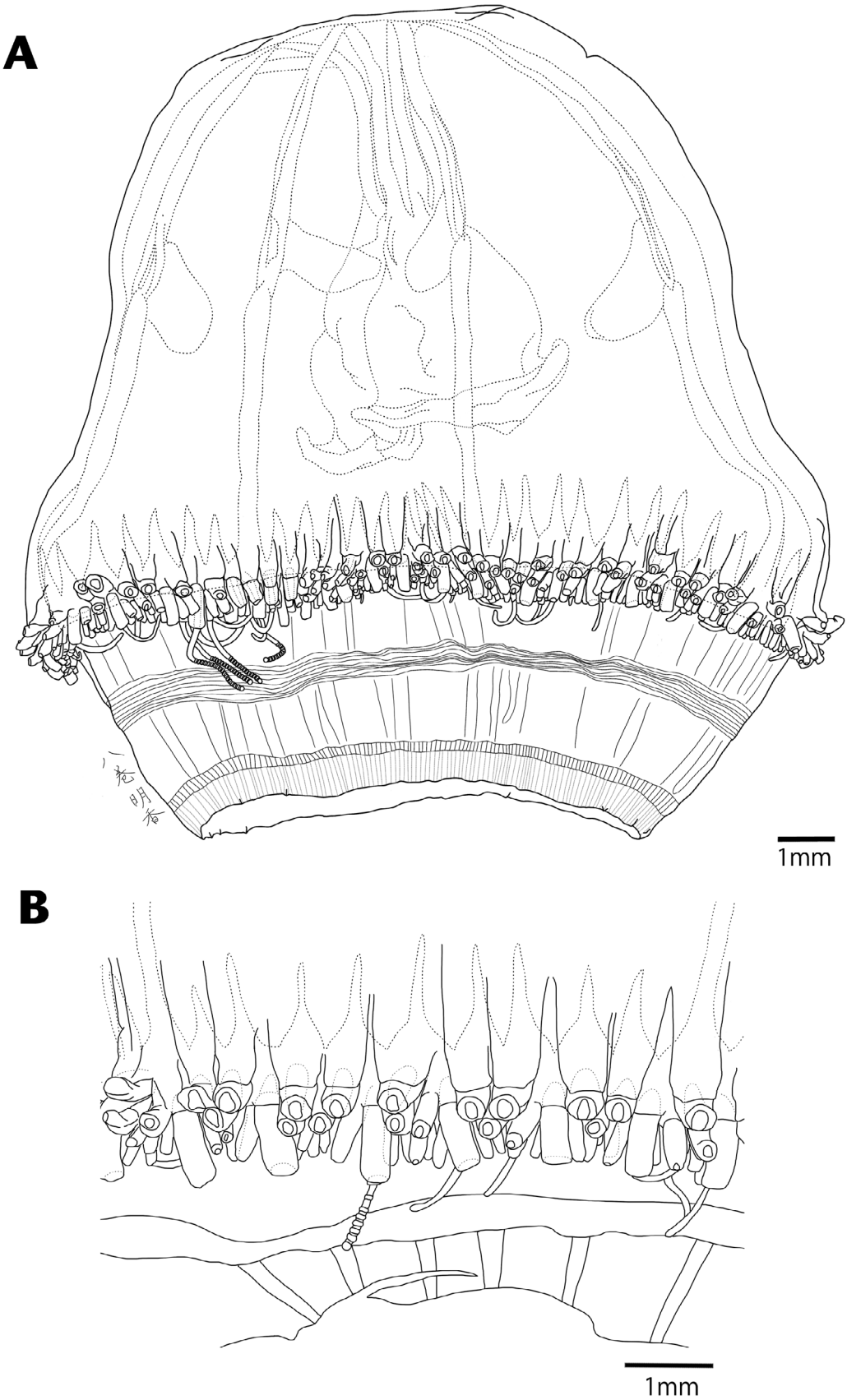

FIGURE 3. (A) Lateral view of the holotype of *Voragonema tatsunoko* [2K1337SS6g], collected at 15:18:15; scale: 1 mm. (B) detail of the bell margin of the paratype [2K1337SS6h], from the external surface showing the proximal part of the autotomized marginal tentacles superimposed in several rows together; scale: 1 mm.

TABLE 1. Main morphological features of the four species of the genus *Voragonema*. Key interspecific differences are in bold typeface.

	Exumbrella	Subumbrella	Radial canals	Peduncle	Manubrium	Mouth	Gonads	Centripetal canals	Tentacles	Statocysts	Velum	Distribution and depth	Main references
V. profundicola Naumov, 1971	10 mm high, 15 mm wide; transparent	**Transparent,** hemispherical	8, slightly undulated along the peduncle, uniformly narrow along the subumbrella	Medium, 1/5 of subumbrellar height, solid, cylindrical in section	Narrow	With 4 simple oral lips	Unknown	**8 per octant, triangle-shape, regular in length and width**	About 500	Unknown	Rather wide	Kurile-Kamchatka Trench, 8700-6800 m	Naumov, 1971
V. pedunculata (Bigelow, 1913)	Up to 31 mm high and 41 mm in diameter; transparent with a little rusty pigment, with many fine meridional furrows	**Dark reddish-brown,** more conical than hemispherical	8, white-cream, proximal half narrow, distal half broader	Short, small	Short, broad, square, dark red, folded gastric pouches	With 4 flared lips	White-cream, thin, proximal half attached along the radial canal, distal half free, pendant	**8 per octant, triangle-shape, regular in length and width**	Superimposed in 4-5 rows; 1000-2000 in number; 2 types: outermost, solid and heavily pigmented; inner, hollow, shorter and thinner	Up to 30 per octant	6.0 mm wide	Northwest U.S.A., 900 m; Bahamas, 830-910 m; Virgin Is. 870-900 m; Monterey Canyon, California, 175-975 m	Bigelow, 1913; Larson *et al*., 1992; Matsumoto *et al*, 1997; Wrobel and Mills, 1998
V. laciniata Bouillon, Pagès and Gili, 2001	Almost as high (30 mm) as wide (35 mm in diameter); transparent with numerous fine meridional ridges	Dark red-brownish, circular and crossed oblique-radial muscles	8, white-cream, proximal half narrow, distal half broader	Medium, 1/5 of subumbrellar height, circular from above and slightly octagonal from below	Short,broad, square, dark red, thick muscular walls; cavity divided by 8 longitudinal and folded gastric pouches	With 4 prominent elongated, perradial lips and with prominent interradial swellings	Whitish, thin, proximal half attached along the radial canal, distal half free, pendant	**11-13, usually 12 per octant, triangle-shape, irregular in length and width**	Superimposed in 5-6 rows, about 1200 in number, 2 types: outermost row, solid, with adnate base; shorter and thinner in the innermost rows	Free, numerous, with a single and large statolith	6.0 mm wide	Weddell Sea, 1583 m	Bouillon *et al*, 2001
V. tatsunoko Lindsay and Pagès 2010	Transparent with many fine meridional furrows, more conical than hemispherical, 14 mm wide and 19 mm wide	**Pale rose-orange** when fresh, slightly brown when preserved, hemispherical	8, whitish translucent, uniform width but with perpendicularly striated tissue under the distal half	Medium, ¼ of subumbrellar height, solid, cylindrical in section	Long, narrow, square, vermillion when fresh, dark brown when preserved	With 4 flared simple lips, without prominent interradial swellings	White-cream, laterally compressed, distal half free, pendant, attached just above midpoint of radial canals	**9 per octant, filamentous with triangular bases, regular in length and width**	Superimposed in 6-7 rows, about 1050 in number, 2 types: (outermost 3 rows, solid, first row with adnate bases; hollow and thinner in the innermost rows)	Around 20 per octant	Wide, 4mm in preserved specimen, with 2 circular muscle bands	Suruga Bay, Japan,1967 m	This study

between a trachymedusa of the genus *Voragonema* and another organism exists in the literature. Larson *et al.* (1991) report an association between *Crossota* (=*Voragonema*) *pedunculata* (Bigelow, 1913) and an unidentified pycnogonid species between 830–910 m in the benthopelagic layer in the Bahamas.

The presence of centripetal expansions arising from the ring canal places this trachymedusan species in the genus *Voragonema* Naumov, 1971. *Voragonema tatsunoko* Lindsay & Pagès, 2010 differs markedly from *V. profundicola* Naumov, 1971 by the markedly greater number of tentacles (1050 vs 500) and from other described species of *Voragonema* by the shape and number (9) of the centripetal canals (Table 1). Preservation in 5% formalin-seawater has lead to shrinkage and distortion in both of the specimens with one becoming more conical (Fig. 2C) while the other now exhibits a somewhat flattened exumbrella (Fig. 2A)—resembling that of *V. profundicola* in the diagram by Naumov (1971). The colour of the manubrium has also changed from vermillion to brown (Fig. 1 vs. Fig. 2A). The determination of whether *V. profundicola* does indeed have a flattened exumbrella or whether the original colour of the manubrium was in fact brown or some other colour will need to await collection of fresh specimens from the type locality of 6800–8700 m in the Kurile-Kamchatka Trench. As the other three species of *Voragonema* are benthopelagic in habitat, it can be inferred that *V. profundicola* may also be so. The loss of the world's deepest diving submersible platform, the ROV *Kaiko*, in May 2003 is therefore unfortunate and procuration of further specimens may only be possible following the development of a new submersible platform with the capability of reaching depths of over 7000 m.

In total, seven specimens of *V. tatsunoko* were observed during 64 minutes over the muddy bottom in the central axis of the Suruga Trough where the current speed was 0.1 knots, current direction 240˚. The specimen without the commensal amphipod pulsed at a rate of 0.7 Hz (11 times in 16.5 seconds), and that with the amphipod also pulsed at 0.7 Hz (7 times in 10 seconds), suggesting that the presence of the amphipod did not affect swimming ability. Other members of the benthopelagic fauna included a species of the lobate ctenophore *Bathocyroe* that had black pigmentation on the inner surfaces of the lobes and auricles as well as dark red-brown pigmentation on the gut, mysids, gammarid amphipods, *Poralia rufescens* Vanhöffen, 1902, munnopsid isopods, oikopleurids and an orange-pigmented chaetognath.

In conclusion, the genus *Voragonema* presently comprises four species: *V. profundicola* Naumov, 1971, *V. pedunculata* (Bigelow, 1913), *V. laciniata* Bouillon et al, 2001, and the species described herein, *V. tatsunoko* Lindsay & Pagès, 2010. The number and shape of the centripetal canals (Table 1) easily identifies this newly-described species.

Acknowledgements

We sincerely thank the captain and crew of the R/V *Natsushima* and the commander, pilots, and operations team of the manned submersible *Shinkai 2000* for their dedicated efforts. Thanks are also due to Dr. Shuhei Nishida, Ocean Research Institute, University of Tokyo, for his efforts as chief scientist during the R/V Natsushima cruise (NT02-06) during which these organisms were collected. Line drawings were kindly sketched by Dr. Aska Yamaki under the supervision of DL. Sadie Mills (NIWA Invertebrate Collection, curatorial technician) organized the loan of the recently-caught specimen of *V. laciniata* [NIWA 35989]. Dr. Wolfgang Zeidler (South Australian Museum, honorary associate) checked the identification of the associate amphipod. This study is a contribution to the Census of Marine Zooplankton (CMarZ), a Census of Marine Life ocean realm field project, and was done under the umbrella of the Japan National Regional Implementation Committee (Japan NRIC).

References

Angel, M.V. (1990) Life in the benthic boundary layer: connections to the mid-water and seafloor. *Philosophical Transactions of the Royal Society of London A*, 331, 15–28.

Bigelow, H.B. (1913) Medusae and Siphonophorae collected by the U.S. Fisheries steamer "Albatross" in the

northwestern Pacific, 1906. *Proceedings of the United States National Museum*, 44(1946), 1–119, plates 1–6.
Bouillon, J., Gravili, C., Pagès, F., Gili, J.-M. & Boero, F. (2006) *An introduction to Hydrozoa*. Mémoires du Muséum national d'Histoire naturelle, Paris, 194, 1–591.
Bouillon, J., Pagès, F. & Gili, J.-M. (2001) New species of benthopelagic hydromedusae from the Weddell Sea. *Polar Biology*, 24, 839–845.
Bouillon, J., Pagès, F., Gili, J.-M., Palanques, A., Puig, P. & Heussner, S. (2000) Deep-water hydromedusae from the Lacaze-Duthiers submarine canyon (Banyuls, northwestern Mediterranean) and description of two new genera, *Guillea* and *Parateclaia*. *Scientia Marina*, 64, 87–95.
Bouillon, J. & Boero, F. (2000) The Hydrozoa: a new classification in the light of old knowledge. *Thalassia Salentina*, 24, 1–45.
Bucklin, A., Nishida, S., Schnack-Schiel, S.B. Wiebe, P.H., Lindsay, D.J., Machida, R. & Copley, N.J. (2010) The Census of Marine Zooplankton (CMarZ). *In:* McIntyre, A. (Ed), *Marine Life: Diversity, Abundance and Distribution.* Wiley-Blackwell, Oxford, 247–265.
Childress, J.J., Gluck, D.L., Carney, R.S. & Gowing, M.M. (1989) Benthopelagic biomass distribution in a deep-sea benthic boundary layer dominated by gelatinous organisms. *Limnology & Oceanography*, 34, 913–930.
Daly, M., Brugler, M.R., Cartwright, P., Collins, A.G., Dawson, M.N., Fautin, D.G., France, S.C., McFadden, C.S., Opresko, D.M., Rodrigues, E., Romano, S.L. & Stake, J.L. (2007) The phylum Cnidaria: a review of phylogenetic patterns and diversity 300 years after Linnaeus. *Zootaxa*, 1668, 127–182.
Gasca, R., Suárez-Morales, E. & Haddock, S.H.D. (2007) Symbiotic associations between crustaceans and gelatinous zooplankton in deep and surface waters off California. *Marine Biology*, 151(1), 233–242.
Gili, J.M., Rossi, S., Pagès, F., Orejas, C., Teixidó, N., López-González, P.J. & Arntz, W.E. (2006) A new trophic link between the pelagic and benthic systems on the Antarctic shelf. *Marine Ecology Progress Series*, 322, 43–49.
Gili, J.-M., Bouillon, J., Pagès, F., Palanques, A., Puig, P. & Heussner, S. (1998) Origin and biogeography of deep-water Mediterranean hydromedusae including the description of two new species collected in submarine canyons of Northwestern Mediterranean. *Scientia Marina*, 62, 113–134.
Gili, J.-M., Bouillon, J., Pagès, F., Palanques, A. & Puig, P. (1999) Submarine canyons as habitats of prolific plankton populations: three new deep-sea Hydromedusae in the western Mediterranean. *Zoological Journal of the Linnean Society*, 125, 313–329.
Hissmann, K. (2005) In situ observations on benthic siphonophores (Physonectae: Rhodaliidae) and descriptions of three new species from Indonesia and South Africa. *Systematics & Biodiversity*, 2(3), 223–249.
Hosia, A. & Pagès, F. (2007) Unexpected new species of deep-water Hydroidomedusae from Korsfjorden, Norway. *Marine Biology*, 151, 177–184.
Hunt, J.C., Hashimoto, J., Fujiwara, Y., Lindsay, D.J., Fujikura, K., Tsuchida, S. & Yamamoto, T. (1997) The development, implementation, and establishment of a mesopelagic and benthopelagic biological survey program using submersibles in the seas around Japan. *JAMSTEC Journal of Deep Sea Research*, 13, 675–685.
Larson, R.J., Matsumoto, G.I., Madin, L.P. & Lewis, L.M. (1992) Deep-sea benthic and benthopelagic medusae, recent observations from submersibles and a remotely operated vehicle. *Bulletin of Marine Science*, 51, 277–286.
Larson, R.J., Mills, C.E. & Harbison, G.R. (1991) Western Atlantic midwater hydrozoan and scyphozoan medusae: *in situ* studies using manned submersibles. *Hydrobiologia*, 216/217, 311–317.
Lindsay, D.J., Hunt, J.C., Hashimoto, J., Fujikura, K., Fujiwara, Y., Tsuchida, S. & Itoh, K. (1999) The benthopelagic community of Sagami Bay. *JAMSTEC Journal of Deep Sea Research*, 14, 493–499.
Lindsay, D.J. & Miyake, H. (2007) A novel benthopelagic ctenophore from 7217m depth in the Ryukyu Trench, Japan, with notes on the taxonomy of deep sea cydippids. *Plankton & Benthos Research*, 2(2), 98–102.
Lindsay, D.J. & Miyake, H. (2009) A checklist of midwater cnidarians and ctenophores from Japanese waters –species sampled during submersible surveys from 1993-2008 with notes on their taxonomy. *Kaiyo Monthly*, 41(8), 417–438.
Lindsay, D.J. (2003) Bioluminescence in the mesopelagic realm. *Kaiyo Monthly*, 35(9), 606–612.
Mackie, G.O. (1985) Midwater macroplankton of British Columbia studied by submersible PISCES IV. *Journal of Plankton Research*, 7, 753–777.
Marcus, N.H. & Boero, F. (1998) Minireview: The importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnology & Oceanography*, 43(5), 763–768.
Matsumoto, G., Baxter, C. & Chen, E.H. (1997) Observations of the deep-sea trachymedusa *Benthocodon pedunculata*. *Invertebrate Biology*, 116, 17–25.
Miyake, H., Lindsay, D.J. & Hunt, J.C. (2001) Submersible-based research on gelatinous plankton. *Kaiyo Monthly*, 27, 216–223.
Miyake, H., Lindsay, D.J., Hunt, J.C. & Hamatsu, T. (2002) Scyphomedusa *Aurelia limbata* (Brandt, 1838) found in deep waters off Kushiro, Hokkaido, Northern Japan. *Plankton Biology and Ecology*, 49(1), 44–46.
Miyake, H., Lindsay, D.J., Kitamura, M. & Nishida, S. (2004) Occurrence of the Scyphomedusa *Parumbrosa polylobata* Kishinouye, 1910 in Suruga Bay, Japan. *Plankton Biology and Ecology*, 52(1), 58–66.
Naumov, D.V. (1971) Gydroidnye i stsifoidnye medusy iz Kurilo-Kamchatskogo zhelova. [Hydromedusae and

scyphomedusae from the Kurile-Kamchatka trench]. *Trudy Institute Okeanologii*, 92, 9–17.
Raffaelli, D., Bell, E., Weithoff, G., Matsumoto, A., Cruz-Motta, J.J., Kershaw, P., Parker, R., Parry, D. & Jones, M. (2003) The ups and downs of benthic ecology: considerations of scale, heterogeneity and surveillance for benthic-pelagic coupling. *Journal of Experimental Marine Biology and Ecology*, 285–286, 191–203.
Smith, K.L. (1982) Zooplankton at a bathyal benthic boundary layer: in situ rates of oxygen consumption and ammonium excretion. *Limnology & Oceanography*, 27, 461–471.
Toyokawa, M., Toda, T., Kikuchi, T., Miyake, H. & Hashimoto, J. (2003) Direct observations of a dense occurrence of *Bolinopsis infundibulum* (Ctenophora) near the seafloor under the Oyashio and notes on their feeding behavior. *Deep-Sea Research I*, 50, 809–813.
Vinogradov, M.E., Volkov, A. & Semenova, T.N. (1996) *Hyperiid amphipods (Amphipoda, Hyperiidea) of the world oceans*. Science Publishers, Lebanon, 632 pp.
Wrobel, D. & Mills, C.E. (1998) *Pacific coast pelagic invertebrates: a guide to the common gelatinous animals*. Sea Challengers and Monterey Bay Aquarium, Monterey, 112 pp.