Giant spoon worms pumped out of their deep burrows: First collection of the main bodies of *Ikeda taenioides* (Annelida: Thalassematidae: Bonelliinae) in 88 years

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Received 11 May 2020; Accepted 27 November 2020 Responsible Editor: Shigeaki Kojima

doi: 10.3800/pbr.16.155

**Abstract:** *Ikeda taenioides* (Ikeda, 1904) (Annelida: Thalassematidae: Bonelliinae) is the world’s longest spoon worm species, which possesses an extremely long tape-like proboscis with a striped color pattern and a large brownish red trunk. This species is endemic to the Japanese Islands and inhabits a deep vertical burrow in intertidal and subtidal sand flats. Their proboscis, which extends from its small burrow opening, has been frequently observed around Japanese coasts. However, sampling of the main body (i.e., trunk) has been extremely rare because it always stays within a deep part of the burrow. Here, we report the success of the sampling of two specimens of *I. taenioides* with trunks in two different localities of the Seto Inland Sea (i.e., Ohmishima and Hachi), Japan, in 2019 and 2020 using a yabby pump. This is the first sampling of the trunk of *I. taenioides* in 88 years after its last collection in Onomichi Bay in 1931. We described the trunk color and morphological characteristics of the two specimens, including the internal anatomy. The trunks of the two specimens showed different colors, that is, pale brown (Ohmishima) and deep brownish red (Hachi). However, they were not distinguished to the species level by the comparison of partial COI sequences, suggesting that *I. taenioides* has an intraspecific variation in trunk color. Despite the difference in the sampling seasons (Ohmishima: June, Hachi: February), both specimens included numerous ripe eggs. According to previous studies, those collected in November and December also included numerous ripe eggs. Taken together, *I. taenioides* may be reproductive throughout the year or have multiple reproductive seasons per year.

**Key words:** dwarf male, Echiura, reproduction, ventral chaetae, yabby pump

**Introduction**

Echiurans or spoon worms are a group of annelids that have a cylinder-shaped trunk and a spoon-shaped proboscis. They were previously treated as a separate phylum, class, or subclass in Annelida (Newby 1940, Ruggiero et al. 2015, Goto et al. 2018). However, to reflect their phylogenetic placement in Annelida as a sister group of Capitellidae (Weigert et al. 2014, Andrade et al. 2015, Struck et al. 2015), they are currently treated as the family Thalassematidae (Goto et al. 2020). This family contains about 190 described species (WoRMS 2020) and comprises two sub-families, Thalassematinae (with two tribes Thalassematini and Echiurini) and Bonelliinae (Goto et al. 2020). They occur from intertidal to ultra-abyssal depths, and most of them live inside burrows in the soft sediment on the seafloor, although some live inside the crevices in the hard substrata (e.g., rocks and dead corals) (Stephen & Edmonds 1972, Goto 2017).

*Ikeda taenioides* (Thalassematidae: Bonelliinae) is a large echiuran endemic to the Japanese Islands (Ikeda 1904, 1907). This species possesses an over 60-cm long trunk and an over 2-m long proboscis and has been considered as the world’s largest spoon worm species (Nishikawa 2012, Goto et al. 2017). Perhaps, it may be more appro-
appropriate to regard it as the longest spoon worm species, as some echiurans species have a thicker trunk and may have more volume (e.g., *Urechis caupo*). *Ikeda taenioides* lives in deep vertical burrows in intertidal or subtidal sand flats and extends its proboscis from a small burrow opening to the sand flat surface in order to collect sediments containing food particles (Ikeda 1901, 1904, Goto et al. 2017). *Ikeda taenioides* has been reported around the Japanese Islands, from the northern end of Honshu Island to the southern end of the Kyushu Island or to the Amami-Oshima Island (see review in Oshiro et al. 2020). However, except for old records from Moroiso (Ikeda 1901, 1904, 1907, Fuchita 1902) and Onomichi Bay (Sato 1934), all of these previously mentioned records are based on the observation or collection of the proboscis that is extended from the burrows. This is because the trunk of *I. taenioides* always stays within a deep part of the burrows and is thus extremely difficult to dig up.

Dr. Iwaji Ikeda collected two specimens with the trunk at Moroiso Bay, near Misaki Marine Station, University of Tokyo, in Kanagawa, at night low tide on November 14, 1901, with his colleagues, which was the first collection of whole *I. taenioides* (Ikeda, 1901). According to Ikeda (1907), he described *I. taenioides* based on six specimens with trunks, which were collected in Moroiso Bay during a stay between October and November in 1901. We assume that these contained two specimens collected on November 14, 1901. Furthermore, Dr. Ikeda collected two more specimens of the full body of *I. taenioides* on December 24, 1901 (Fuchita 1902), one of which is probably the same as the specimen examined in Nishikawa (2002). Taken together, Dr. Ikeda collected at least eight specimens of the (nearly) full body of *I. taenioides* from November to December in 1901. In addition, Sato (1934) reported the occurrence of *I. taenioides* in Onomichi Bay, the Seto Inland Sea, with a photograph of an *I. taenioides* specimen. This specimen contained a proboscis and part of the trunk. Although Sato (1934) did not provide any information on this specimen, it was found in the museum of Tohoku University with the label “Ikeda taenioides (IK), Onomichi, Seto March 22, 1931 H. Okada” by Prof. T. Nishikawa (T. Nishikawa, personal communication). We interpret that this label means that the specimen was collected by H. Okada in Onomichi Bay, the Seto Inland Sea, on March 22, 1931. To the best of our knowledge, these are all records of the collection of *I. taenioides* specimens with their trunks. However, most of the specimens were lost. Only two specimens of *I. taenioides* have been located at the present: one was deposited at the University of Tokyo, corresponding to the one collected by Dr. Ikeda on December 24, 1901, and examined in Nishikawa (2002), and the other was deposited at Tohoku University, which was photographed in Sato (1934). To understand the biology and morphology of this enigmatic worm species, further examination of new specimens with the trunk is required.

In this study, we succeeded in collecting two new specimens of *I. taenioides* with the trunk using a yabby pump in the intertidal sand flats in the Seto Inland Sea, Japan. This is the first sampling of the main bodies of *I. taenioides* in 88 years after the last one in Onomichi Bay. We assessed the body color and morphological characteristics of the specimens.

**Materials and Methods**

**Sampling**

*Ikeda taenioides* was collected from the tidal flat in
Fig. 2. Living individuals of *Ikeda taenioides* and its habitat. (A) An intertidal flat of Ohmishima Island and field gear (a yabby pump and sieve). (B) A proboscis and trunk of the specimen of *I. taenioides* collected at Ohmishima Island (specimen ID: #1). (C, D) Close-up of the trunk and the proximal part of the proboscis (#1). (E) A trunk of the specimen collected at Hachi (specimen ID: #2). (F) Gonducts exposed to outside of the trunk (#2). (G) Posterior end of the trunk (#2). (H) A fecal pellet expelled from specimen #1. Scale bars: 5 cm (B), 3 cm (C, E), 5 mm (D, F, G), 1 mm (H).
western Ohmishima Island (hereafter referred to as Ohmishima; 34°13'30"N, 132°50'22"E; Figs. 1A, 2A), Imabari, Ehime Prefecture on June 16, 2019, and from the Hachi tidal flat located at the mouth of the Kamo River (hereafter referred to as Hachi; 34°19'31"N, 132°54'40"E; Fig. 1B), Takehara, Hiroshima Prefecture on February 12, 2020. We used a bait pump which was 5 cm in diameter and 75 cm in length (Poseidon 750 mm yabby pump; see Fig. 2A), a commercial suction device to collect bait shrimp, to obtain I. taenioides specimens from the burrow. The pump was pushed onto the sediment with a burrow hole, and the plunger was withdrawn rapidly to pull out the water and sediment from the inside of the burrow. The water and sediment from the burrows were placed on a 1-mm mesh sieve. The pump was then re-inserted into the same burrow hole, and the water and sediment from the deeper burrow were pulled out. We repeated this pumping process five to ten times to be able to work the pump down to a depth of about 75 cm. Such repeated pumping has been used to collect large-sized shrimps living in deep burrows (Hailstone & Stephenson 1961, Dworschak 2015). The collected specimens were photographed with a scale and brought to the laboratory at Kochi University. The approximate length and width of the trunk and proboscis of living I. taenioides individuals were measured from photographs using ImageJ 1.50i (Rasband 2006). They were anesthetized with menthol and fixed in a neutralized 10% formalin solution. A small fraction of the proboscis was fixed in 99% ethanol and sequenced by Eurofins Genomics using PCR primers. The obtained sequences were deposited in the DDBJ/EMBL/GenBank database with the accession numbers (Table 1).

Genomic DNA was extracted from a small piece of proboscis tissue from each specimen using the DNeasy Blood & Tissue Kit (Qiagen). We sequenced fragments of the cytochrome c oxidase subunit I (COI) gene. Polymerase chain reactions (PCRs) were used to amplify the COI gene. Amplification was performed in 25.23-µL reaction mixes containing 0.3 µL of forward and reverse primers [COI490 and HCO2198 (Folmer et al. 1994); 10 µM each], 2.5 µL of 10x Taq Buffer, 2.0 µL of dNTP Mixture, 0.13 µL of TaKaRa ExTaq polymerase (TaKaRa, Otsu, Japan), 2.5 µL of template DNA and 17.5 µL of distilled water. Thermal cycling was performed with an initial denaturation for 3 min at 94°C followed by 30 cycles of 30 s at 94°C, 30 s at 42°C, and 2 min at 72°C, with a final 3 min extension at 72°C. All PCR products were purified by Exo-SAP-IT (Thermo Fisher Scientific, Tokyo, Japan) and then sequenced by Eurofins Genomics using PCR primers. The obtained sequences were deposited in the DDBJ/EMBL/GenBank database with the accession numbers (Table 1).

Table 1. Information on specimens used for a molecular analysis in this study. Asterisks indicate the sequences obtained in this study.

| Species          | Accession number | Location and depth          | Region              | References        |
|------------------|------------------|------------------------------|---------------------|-------------------|
| I. taenioides    | LC126262         | Intertidal: Kure, Hiroshima, Japan | Seto Inland Sea     | Goto et al. 2017  |
|                  | LC126263         | Intertidal: Kure, Hiroshima, Japan | Seto Inland Sea     | Goto et al. 2017  |
|                  | LC126264         | Intertidal: Kure, Hiroshima, Japan | Seto Inland Sea     | Goto et al. 2017  |
|                  | LC126265         | Intertidal: Kure, Hiroshima, Japan | Seto Inland Sea     | Goto et al. 2017  |
|                  | LC126266         | Intertidal: Kure, Hiroshima, Japan | Seto Inland Sea     | Goto et al. 2017  |
|                  | AB771499         | Intertidal: Hakatajima, Ehime, Japan | Seto Inland Sea     | Goto et al. 2013  |
|                  | LC126267         | Subtidal: Otuchi Bay, Iwate, Japan | Pacific (Tohoku)    | Goto et al. 2017  |
|                  | LC126268         | Subtidal: Funakoshi Bay, Iwate, Japan | Pacific (Tohoku)    | Goto et al. 2017  |
|                  | LC500040         | Intertidal: Tanabe Bay, Wakayama, Japan | Pacific (Kii Peninsula) | Oshiro et al. 2020 |
|                  | LC500041         | Subtidal: Maizuru Bay, Kyoto, Japan | Sea of Japan        | Oshiro et al. 2020 |
|                  | LC629178*        | Intertidal: Ohmishima Island, Ehime, Japan | Seto Inland Sea   | This study        |
|                  | LC629179*        | Intertidal: Hachi, Hiroshima, Japan | Seto Inland Sea     | This study        |

In addition to the sequences obtained in this study, we also collected sequence data for I. taenioides previously used for molecular phylogenetic analyses (Goto et al. 2013) and DNA barcoding analyses (Goto et al. 2017, Oshiro et al. 2020). The sequences were aligned with SeaView (Galtier et al. 1996, Gouy et al. 2010) without gaps. A haplotype network was constructed using PopART (Leigh & Bryant 2015) based on the partial COI sequences shown in Table 1.

Results and Discussion

We collected two specimens of I. taenioides with a trunk in the intertidal flats of the Seto Inland Sea, one from Ohmishima and the other from Hachi (hereafter referred to as specimens #1 and #2, respectively) (Fig. 2). The former is the first record of the field collection of the trunk of I. taenioides in 88 years after sampling in Onomichi in 1931 (Sato 1934; see Introduction). In both study sites, we obtained a trunk and a proboscis of I. taenioides at a depth of around 75 cm from the burrow opening, suggesting that the worm stayed at this depth in the burrows. This is congruent with the description in Ikeda (1907) that the depth of the burrows from its entrance is about 70–90 cm. Specimen #1 undulated its long proboscis frequently in the aquaria (Movie S1). Due to damage to the posterior trunk, numerous erythrocytes and eggs were shed into the water from the coelom (Fig. 2C). Specimen #2 intermittently expelled rod-shaped fecal pellets one by
one from the anus in the aquaria (Fig. 2G, H).

Specimen #1 contained only the anterior part of the trunk and the proboscis: the latter was separated into three pieces, one of which was connected to the trunk (Fig. 2B). The remaining anterior trunk (Fig. 2C) was approximately 19.7 cm long and 1.0–1.7 cm wide in a living state. The total length of the three pieces of the unfixed proboscis was approximately 153.5 cm. According to Ikeda (1907), a specimen with a 150-cm-long proboscis possessed a 40-cm-long trunk with a diameter of 2–3 cm. Considering that the proboscis length of our specimen was about 150 cm, the trunk size may be similar to that in Ikeda (1907). If so, specimen #1 may have lacked about half of the trunk. On the other hand, specimen #2 contained a nearly complete trunk (Fig. 2E) and the proboscis was separated into two pieces. The trunk was approximately 53.1 cm in length and 0.5–1.8 cm in width. The total body length, containing the length of the proboscis and trunk, was approximately 131.1 cm.

The surfaces of the trunks of both specimens were papillated (Fig. 2C, D, F). Ikeda (1907) reported that the trunk color of *I. taenioides* was brownish-red over a pale-yellow ground. However, the illustration of the trunk of *I. taenioides* [fig. 3 in Ikeda (1907)] was just brownish red, in which a pale-yellow ground was not evident. In our specimens, a pale brown or pale yellow ground was evident in specimen #1 (Fig. 2C), whereas it was not evident in specimen #2, which was brownish red in color (Fig. 2E), as shown in fig. 3 in Ikeda (1907). The trunk color of our specimens was mostly based on the skin color. Thus, it is less likely that the difference in trunk color was caused by the outflow of the reddish coelomic fluid from the trunk. We compared the fragments of the COI sequences between specimens #1 and #2 to test the possibility of cryptic species with different body colors. We found only two base pair differences between them (Fig. 3). Specimens #1 and #2 belonged to two of the major haplotypes of *I. taenioides* (haplotypes A and B in Fig. 3), respectively, which have been recognized in previous studies (Goto et al. 2017, Oshiro et al. 2020). Considering the results of the genetic assessment, the difference in body color between the specimens was considered to be intra-specific variation. A similar body color variation is also known in the other congeneric species, *Ikeda pirotansis* (Menon & DattaGupta 1962), from the Arabian Sea, which is light to deep red in color (DattaGupta & Menon 1976). It is possible that the body color of *I. taenioides* may change as they grow, although it is difficult to compare the size of the specimens in this study due to the lack of the posterior trunk in specimen #1. Ikeda (1907) mentioned that the brownish-red specimen used for the illustration was the smallest among the six specimens he obtained. Thus, body color may change from brownish red to pale yellow as they grow.

According to previous studies (Ikeda 1904, 1907, Nishikawa 2002), *I. taenioides* has five narrow externally visible longitudinal bands on the trunk, which are caused by the special thickening of the continuous, non-fasciculate sheet of longitudinal muscle (Nishikawa 2002). However, these bands were not observed in our specimens either in the living (Fig. 2C, E) or fixed conditions (Figs. 4A, 5A, B, 7A). Thus, the presence or absence of longitudinal bands may vary within this species. *Ikeda pirotansis*, a smaller congeneric species from the Arabian Sea, also does not have longitudinal bands (Nishikawa 2002). This species possesses less than 30 gonoducts on each side of the trunk (Hughes and Crisp 1976, Nishikawa 2002), whereas our specimens contain several hundreds of gonoducts (Fig. 5A, B), which are identical to those of *I. taenioides*.

*Ikeda taenioides* is characterized by an extremely long proboscis with a striped color pattern. Ikeda (1907) mentioned that the proboscis of the worm on the bottom surface might be easily mistaken for a dead leaf of *Zostera* due to its color pattern. We agree with his argument and presume that such camouflage may help the worm avoid detection from predators, probably birds and fishes, in tidal flats. In addition, Ikeda (1907) described that a striped color pattern is absent in the proximal part of the proboscis. We also observed this characteristic in specimens #1 and #2 (Fig. 2D). The proximal part of the proboscis is always hidden in the burrows and thus it may not need to be camouflaged by a striped color.

Most echiurans, including species of the genus *Ikeda*, possess a pair of chaetae at the anteroventral portion of the trunk (Stephen & Edmonds 1972). Specimen #1 possessed a pair of long, golden-colored chaetae in the anterior ventral portion of the trunk (Fig. 4C), as described by Ikeda (1907), whereas specimen #2 possessed only one right chaeta (Fig. 4A, B). Regarding the latter, the left chaeta was probably lost for some reason before the collection because there were no remaining traces. The tip of these chaetae was sharp, curved, and slightly exposed to the out-

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**Fig. 3.** Haplotype network of *Ikeda taenioides* for the COI marker. Circles indicate independent haplotypes and their different color patterns stand for each sampling region. Each connection represents one inferred base-pair change. Haplotype A and B include the specimen from Ohmishima and Hachi, respectively.
side of the trunk (Fig. 4B, C). The basal part of the chaetae was present inside the trunk, accompanied by radial muscles (Fig. 4D). In addition to these chaetae, we found a short chaeta adjacent to each of the long main chaetae (Fig. 4E). These short chaetae were not exposed to the outside of the trunk. A developing short chaeta adjacent to the main chaeta is known in other echiurans (e.g., *Echiurus* and *Thalassema*) (Tilic et al. 2015). The short chaetae in *Ikeda taenioides* are also likely developing ones. The main chaeta and its adjacent developing chaeta from the right side of specimen #1 (Fig. 4F) were 8.3 and 4.0 mm long, respectively (Fig. 4G).

The anterior part of the trunk in both of our specimens contained numerous gonoducts (Fig. 5A, B), which were tubular in shape, with a gonostome positioned distally (Fig. 5C, D). These observations are congruent with Ikeda’s (1907) description. The living coloration of the gonoducts was yellowish (Fig. 2F). In both specimens #1 and #2,
most of the gonoducts were occupied by ripe and developing eggs (Fig. 5A–D), except for nearly empty gonoducts located in the most anterior part of the trunk in specimen #2 (Fig. 2F). Some ripe eggs floated in the trunk. However, it was uncertain whether they were originally in the gonoducts and shed from them due to damage to the trunk during sampling. The diameter of the ripe eggs was approximately 600 µm (Fig. 5E). Previous studies have reported that *I. taenioides* collected during November–December (fall to winter) contained ripe eggs (Ikeda 1907, Nishikawa 2002). Considering that our specimens, collected in June (early summer) and February (winter to early spring), also contained many ripe eggs, it is likely that *I. taenioides* is reproductive throughout the year or has multiple reproductive seasons per year. Although both of our specimens contained ripe eggs, the gonoducts in specimen #1 tended
Fig. 6. Alimentary canal of *Ikeda taenioides* collected from Ohmishima. The left direction of the figures is the anterior direction of the trunk. (A–C) Pharynx. (A) Pharynx observed from dorsal view. (B) Pharynx dissected to show the contents. (C) The internal surface of the pharynx. (D) The anterior part of the esophagus. (E) A part of the esophagus occupied by fecal pellets. Scale bars: 1 cm (A–C), 5 mm (D, E).

Fig. 7. Anal vesicle of *Ikeda taenioides* collected from Hachi. The left direction is the anterior direction of the trunk. (A) The posterior end of the trunk dissected through the dorsal midline to show the anal vesicles. (B) Close-up of the part of the anal vesicle pointed out by a white arrow in (A). Scale bars: 2 cm (A), 3 mm (B). Abbreviation: AV: anal vesicle.
to contain more and smaller eggs than that in specimen #2 (see Fig. 5C, D). This suggests that they were in slightly different reproductive stages. The gonoducts containing sperm were not observed in either of the specimens, suggesting that they were females. The genus *Ikeda* was recently assigned to the subfamily Bonelliinae (Goto et al. 2020), most of which have tiny dwarf males inhabiting the female bodies. However, dwarf males were not observed in our specimens, as in previous studies (Nishikawa 2002). Goto et al. (2020) suggested that the species of *Ikeda* may perform parthenogenesis considering that they typically produce excessively numerous eggs despite the constant absence of dwarf males.

According to the description in Ikeda (1907), the alimentary canal of *I. taenioides* consists of five parts: the pharynx, esophagus, crop, midgut, and intestine. Owing to the lack of the posterior part of the trunk, specimen #1 (Fig. 2A) contained only the anterior part of the alimentary canal (i.e., the pharynx and the anterior part of the esophagus). The pharynx (Fig. 6A) was connected to the mouth and fixed with the body wall by two mesenteries. It was reddish brown in color in the fixed state and approximately 3.7 cm long and 0.85 cm wide (Fig. 6A). The pharynx was occupied by fine sandy mud particles (Fig. 6B). The inner surface of the pharynx was covered with fine wrinkles (Fig. 6C). The posterior part of the pharynx was connected to the esophagus, which was occupied by rod-shaped fecal pellets (Fig. 6D, E), except for the most anterior part connected to the pharynx. The middle and posterior parts of the esophagus were missing. On the other hand, the alimentary canal of specimen #2 was not well preserved due to poor fixation and was thus difficult to be observed. However, the anal vesicles were preserved and present in a pair in the posterior part of the trunk (Fig. 7A). They were brownish tubes fixed to the body wall and approximately 5 cm in length (Fig. 7A). The anal vesicles were thickly covered by tubules (Fig. 7B).

Yabby pumps have been used mainly for the sampling of burrowing crustaceans (e.g., Hailstone & Stephenson 1961, Dworschak 2015, Komai et al. 2019). The recent application of this field gear to the collection of echiruans has been very successful as it has made it possible to collect species that have been considered extremely rare (e.g., *Ikedosoma elegans*) (Komai 2015, Goto et al. 2018). Our study also shows the efficiency of this field gear for the collection of the trunk of *I. taenioides*, which is one of the most deep-burrowing echiruans. The establishment of a sampling method will advance our understanding of the biology of this enigmatic echiruan. The genus *Ikeda* contains the other described species, *I. pirotansis*, from the Arabian Sea (Menon & DattaGupta 1962, Hughes & Crisp 1976) and several undescribed or uncertain species from southern Japan, the United Arab Emirates, and Australia (Edmonds 1987, Hornby 2005, Goto et al. 2013, Goto 2017). The main bodies of these worms are also often difficult to collect, which prevents the taxonomy of this group (Edmonds 1987, Hornby 2005). Thus, the application of yabby pumps for the collection of these species may also improve the situation.

**Acknowledgements**

We are grateful to Teruaki Nishikawa (National Museum of Nature and Science) for providing information on the specimens of *I. taenioides* deposited in the University Museum, the University of Tokyo, and in the Tohoku University Museum; Masanori Okanishi (the University of Tokyo) for providing the information regarding the sampling records of *I. taenioides* at Misaki Marine Station; and two anonymous reviewers for their comments on the earlier version of this manuscript.

**Supplementary materials**

Supplementary Movie S1. A living specimen of *Ikeda taenioides* collected from Ohnishima (specimen ID: #1).

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