Bull. Natl. Mus. Nat. Sci., Ser. A, 52(3), pp. 105–119, August 24, 2026
DOI: 10.50826/bnmnszool.52.3_105

Morphology of *Pennella filosa* (Linnaeus, 1758) (Copepoda: Pennellidae) Parasitic on Black Marlin *Istiompax indica* (Cuvier, 1832) (Carangiformes: Istiophoridae) in the Sea of Japan off Central Japan, with Lists of the Known Fish, Cetacean, and Cephalopod Hosts of *P. filosa* (1758–2025)

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(Received 20 April 2026; accepted 24 June 2026)

Abstract Two postmetamorphosis females of the mesoparasitic copepod *Pennella filosa* (Linnaeus, 1758) were collected from black marlin *Istiompax indica* (Cuvier, 1832) in the Sea of Japan off the coast of central Japan. This collection represents the second record from black marlin and the first specimen-based record in the Sea of Japan for *P. filosa*. The parasite is redescribed and characterized by two posterolateral holdfast horns or two posterolateral and one posterodorsal holdfast horn, a truncated anterior cephalothoracic end covered by numerous small papillae, and branching abdominal plumes. Lists of the known fish, cetacean, and cephalopod hosts and collection areas of *P. filosa* are provided based on the literature published between 1758 and 2025. In total, 17 species of teleosts in eight families and three orders, six species of cetaceans in one order and three families, and six species of cephalopods in four orders and four families have been recorded as hosts of this parasite worldwide.

Key words: fish parasite, redescription, new host record, new locality record.

Introduction

Copepods of the pennellid genus *Pennella* Oken, 1815 (Siphonostomatoida) are mesoparasites of ocean-migrating fishes and cetaceans (Kabata, 1979; Hogans, 2017). Due to their large body size and occurrence on commercially important fishes, there are many records of *Pennella* spp. worldwide (Hogans, 2017; Suyama *et al.*, 2021b), and *Pennella* sp. has been suggested to cause mortality in its host, Pacific saury *Cololabis saira* (Brevoort, 1856), in the western North Pacific Ocean (Suyama *et al.*, 2021a).

In Japan, several species of *Pennella*, including unidentified ones, have been reported since 1916 (e.g., Ishii, 1916a, b, c; Leigh-Sharpe, 1928; Yamaguti, 1939; Kamegai, 1963; Nagasawa, 1984; Nagasawa *et al.*, 1988; Uchida and Araki 2000; Ho and Nagasawa, 2001; Momoyama and Tensha, 2006; Nagasawa and Uyeno, 2014; Suyama *et al.*, 2021b; Yumura *et al.*, 2022). However, their distinct morphological variability

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makes identification difficult, and both morphological and molecular analyses are currently employed for species identification (Suyama *et al.*, 2019, 2021b). Furthermore, recent studies have used photographs of body parts to illustrate their morphological features (Suyama *et al.*, 2019, 2020, 2021b), and no paper of *Pennella* spp. with line illustrations has been published in Japan since 1939 (Yamaguti, 1939).

Photographs have also been used to show the body of *Pennella* spp. collected from fishes in other countries, such as Turkey (Tuncer *et al.*, 2010; Tanrikul and Akyol, 2011), Mexico (Hernández-Trujillo *et al.*, 2014; Román-Reyes *et al.*, 2019), India (Surya *et al.*, 2023; Ramkumar *et al.*, 2024), Algeria (Ramdani *et al.*, 2021), and Spain (Ten *et al.*, 2025), and in offshore waters of the Atlantic Ocean (Llarena-Reino *et al.*, 2019). Although such photographs are useful for recognizing the gross morphology of the species in question, they often lack information on important taxonomic characters necessary for species identification, and descriptions accompanied by line illustrations are desirable for better understanding of the morphology of *Pennella* spp.

Recently, we collected two postmetamorphosis females of *Pennella filosa* (Linnaeus, 1758) from black marlin *Istiompax indica* (Cuvier, 1832) in the Sea of Japan off the coast of central Japan. Previously, Kensley and Grindley (1973) found specimens of *P. filosa* (reported as *P. orthagorisci* Wright, 1870) in the collection of the South African Museum, Cape Town, taken from black marlin (as *Makaira indica*), and our collection of this parasite represents its second record from the same fish species. This paper reports on the morphology of the postmetamorphosis females collected and provides lists of the known fish, cetacean, and cephalopod hosts and collection areas of *P. filosa* based on the literature published between 1758 and 2025.

Materials and Methods

Two copepods, referred to as Specimens 1 and 2, each recognized on the skin of two black marlin in the Sea of Japan off the coast of central Japan were collected. The fish were individually captured by fixed-net fishing off Kyoto Prefecture on 17 June 2014 and off Niigata Prefecture on 10 June 2019. Specimen 1 was fixed in 70% ethanol one day after collection, whereas Specimen 2 was fixed in 99% ethanol on the day of collection. Later, at the Aquaparasitology Laboratory in Shizuoka Prefecture, the specimens were examined under an Olympus SZX10 stereo microscope. Antennae taken from Specimen 1 were cleared in lactophenol and examined using the wooden slide procedure (Humes and Gooding, 1964) with an Olympus BX51 phase-contrast compound microscope. All drawings were made with the aid of drawing tubes attached to the microscopes. Morphological terminology follows Hogans (2017). The two specimens of *P. filosa* have been deposited in the Crustacea (Cr) collection at the National Museum of Nature and Science in Tsukuba, Ibaraki Prefecture (NSMT-Cr).

Results

Pennella filosa (Linnaeus, 1758)

[Japanese name: Maguro-hijikimushi, based on Ho and Nagasawa, 2001]

(Figs. 1–3)

Material examined. Two postmetamorphosis females (Specimen 1 collected on 17 June 2014, NSMT-Cr 33347; Specimen 2 collected on 10 June 2019, NSMT-Cr 33348).

Host. Black marlin *Istiompax indica* (Cuvier, 1832) (Carangiformes: Istiophoridae).

Localities. The Sea of Japan off Niizaki (35°41′N, 135°18′E), Ine, Kyoto Prefecture and off Washizaki (38°32′N, 138°52′E), Sado, Niigata Prefecture, central Japan.

Site of infection. The cephalothorax and the anterior part of the neck were embedded in the musculature of the host trunk near the dorsal fin, and the other part of the body protruded externally.

Description of postmetamorphosis female. Cephalothrorax subcylindrical, with bluntly trun-

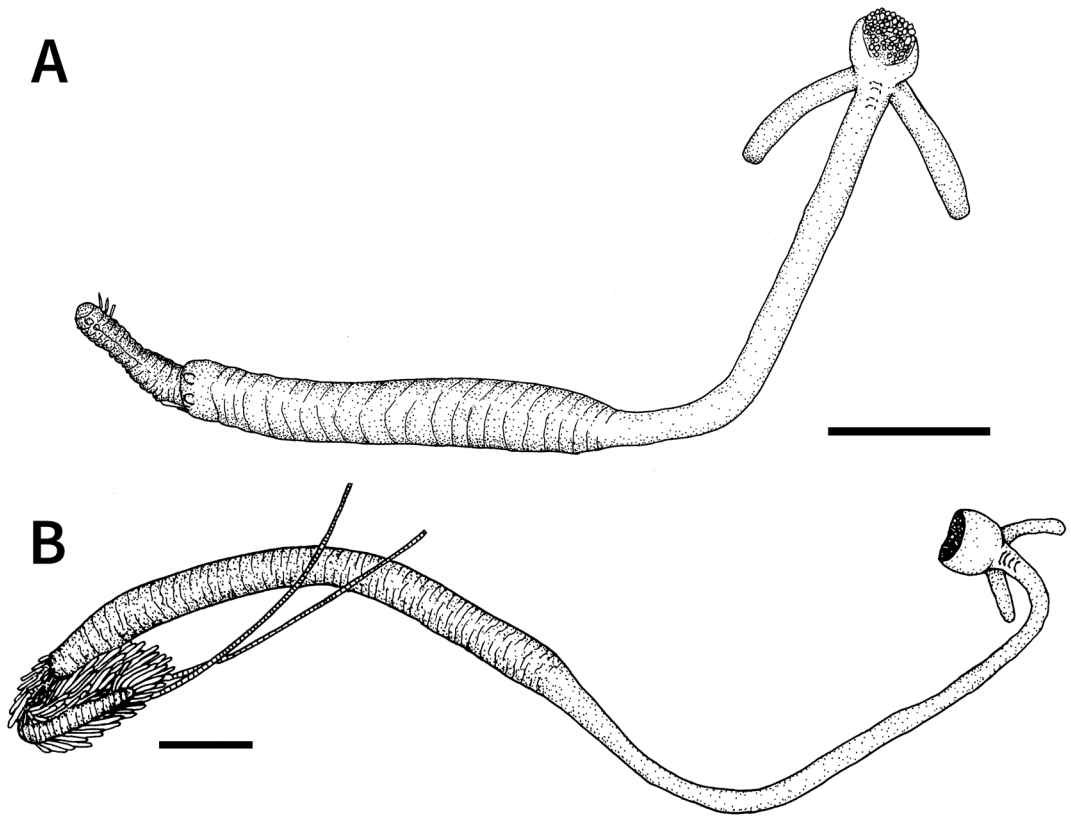

Fig. 1. *Pennella filosa*, postmetamorphosis females (A, Specimen 1, NSMT-Cr 33347; B, Specimen 2, NSMT-Cr 33348), from black marlin *Istiompax indica* in the Sea of Japan off central Japan. A, B, habitus, ventral. Scale bars: 10 mm.

cate anterior end. Numerous small papillae, mostly spherical, on surface of anterior end; papillae found in a group (Fig. 2B, Specimen 1) or in four indistinct groups consisting of two marginal and two central ones (Fig. 2D, Specimen 2). Two posterolateral and one shorter posterodorsal holdfast horn (Figs. 1A, 2A, B, Specimen 1) or two posterolateral holdfast horns (Figs. 1B, 2C, D, Specimen 2); horns immediately posterior to bulbous portion of cephalothorax, cylindrical, directed diagonally, ending in blunt tips. Thoracic neck long, cylindrical. Trunk cylindrical, transversely annulated. Abdomen shorter than trunk, dorsoventrally flattened, transversely annulated, with rounded posterior extremity. Ventral abdominal surface covered by plumes (Figs. 1B, 3A); number of plumes on one side 26; number of branches per plume variable and up to 23 in Specimen 2 (Fig. 3B); abdominal plumes undeveloped in Specimen 1 (Fig. 1A). Egg strings cylindrical, long, each issuing from posteriormost ventral surface of trunk. Eggs uniseriate. Total length 72 and 134 mm in Specimens 1 and 2 (excluding egg strings), respectively.

First antennae missing (due to heavy damage when removed). Second antennae each three-segmented, sclerotized; basal and second segments subquadrangular, unarmed; terminal segment with triangular projection at anteromedial corner and large recurved claw possessing single basal seta (Fig. 2E). Four pairs of foliaceus swimming legs consist of protopods without rami on ventral surface near posterior margin of cephalothrorax; first two pairs set closer together than remaining two pairs; fourth pair smallest (Fig. 2F).

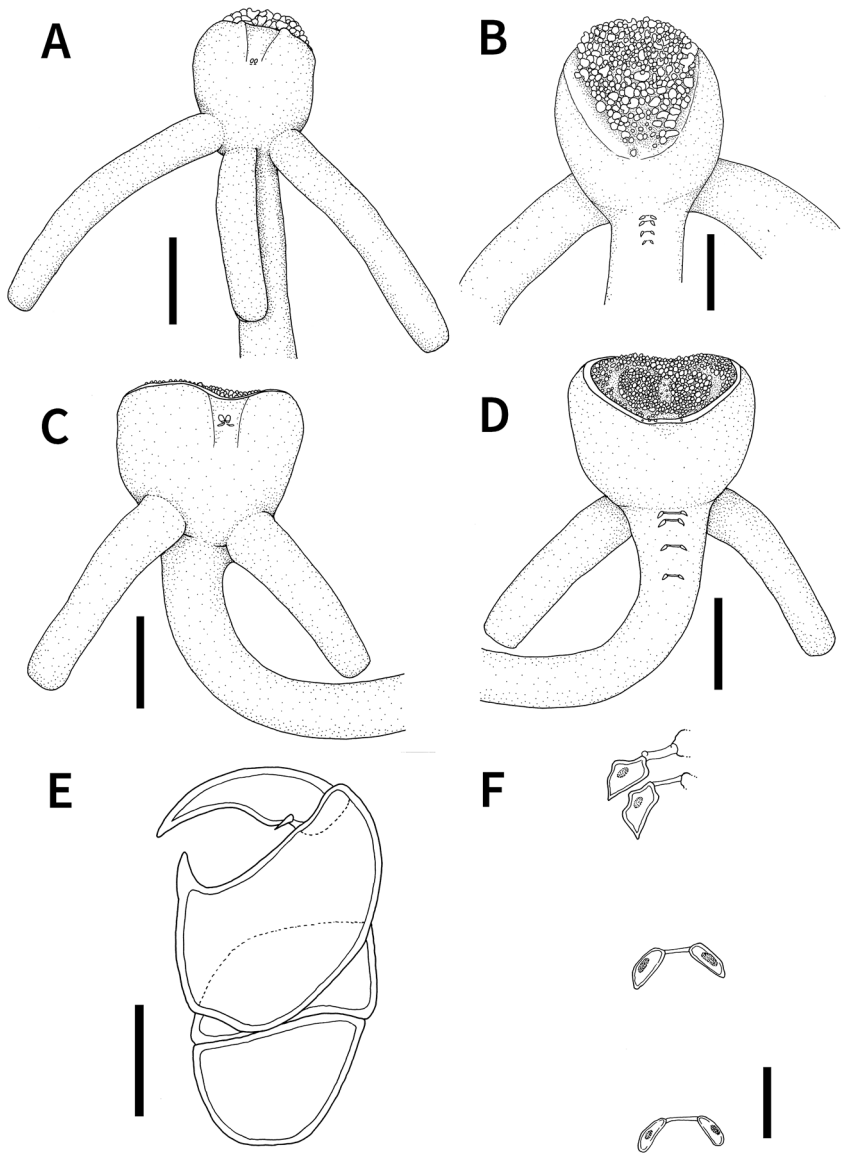

Fig. 2. *Pennella filosa*, postmetamorphosis females (A, B, E, Specimen 1, NSMT-Cr 33347; C, D, F, Specimen 2, NSMT-Cr 33348), from black marlin *Istiompax indica* in the Sea of Japan off central Japan. A, C, cephalothorax and anterior portion of neck, dorsal; B, D, cephalothorax and anterior portion of neck, ventral; E, second antenna, ventral; F, swimming legs, ventral (right swimming legs of first and second pairs were heavily damaged when observed). Scale bars: A, C, D, 3 mm; B, 2 mm; E, 0.1 mm; F, 0.4 mm.

Discussion

The two postmetamorphosis female specimens examined are characterized by two lateral holdfast horns or two lateral and one dorsal holdfast horn, a truncated anterior cephalothoracic end covered by numerous small papillae, and branching abdominal plumes. These morphological characters are essentially identical to those previously reported for *P. filosa* (Kabata, 1979; Hogans, 1987b, 2017; Suyama *et al.*, 2021b). Thus, the specimens are identified as this species. Recently, Suyama *et al.* (2021b) provided brief descriptions of *P. filosa* based on specimens

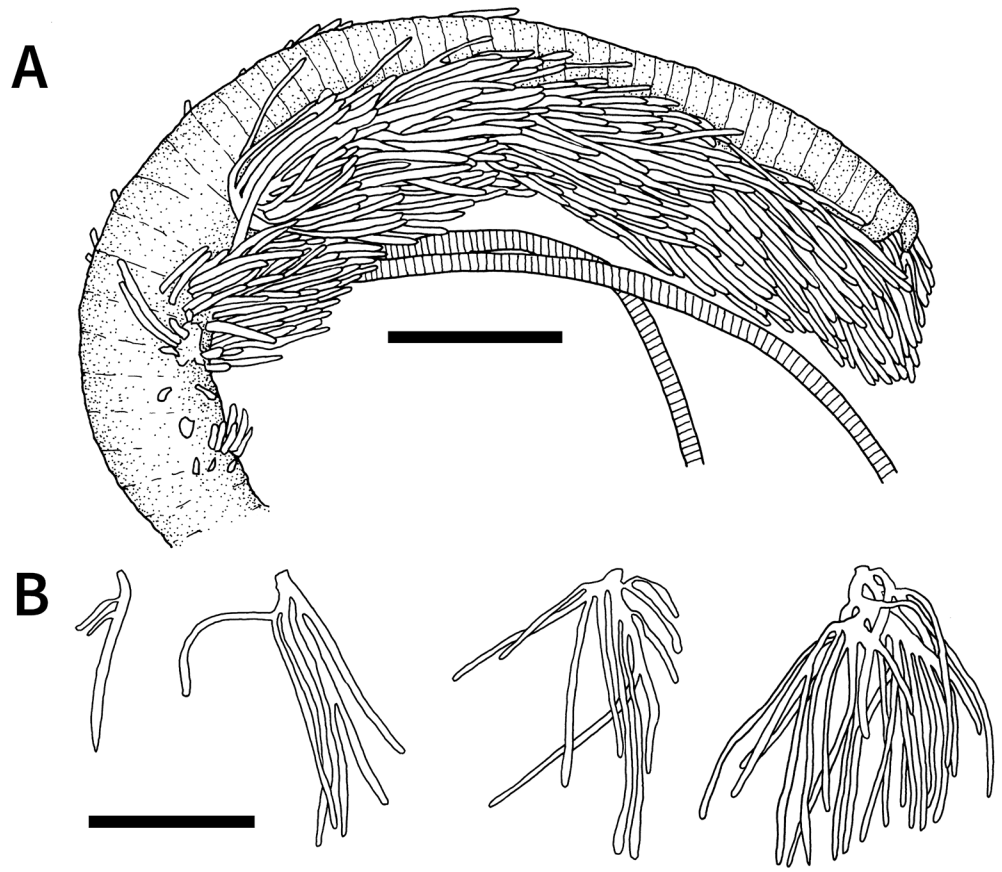

Fig. 3. *Pennella filosa*, postmetamorphosis female (Specimen 2, NSMT-Cr 33348), from black marlin *Istiompax indica* in the Sea of Japan off central Japan. A, posteriormost portion of trunk, and abdomen with plumes and egg strings, lateral; B, abdominal plumes. Scale bars: A, 5 mm; B, 3 mm.

(including tentatively identified individuals of this species) each from six fish species [common dolphinfish *Coryphaena hippurus* Linnaeus, 1758; striped marlin *Kajikia audax* (Philippi, 1887); swordfish *Xiphias gladius* Linnaeus, 1758; escolar *Lepidocybium flavobrunneum* (Smith, 1849); ocean sunfish *Mola mola* (Linnaeus, 1758); and Japanese pufferfish *Takifugu rubripes* (Temminck and Schlegel, 1850)] captured in the North Pacific Ocean including Japanese waters. Their specimens of *P. filosa*, ranging from 61 to over 220 mm total length, exhibited the following morphological characters: two or three holdfast horns; an anterior cephalothoracic end covered by numerous small papillae, which are separated into four groups in several specimens; and 15–36 abdominal plumes. These characters are recognized in the specimens examined in this study.

Hogans (1986a, 2017) noted that a morphologically similar species, *P. instructa* Wilson, 1917 has four distinct groups of papillae on the anterior surface of the cephalothorax, and Specimen 2 examined in this study has similar groups of papillae on the anterior cephalothoracic end (Fig. 2D). However, Suyama *et al.* (2021b) stated that this feature is not specific to *P. instructa* because it is also found in *P. filosa* and, based on molecular data, suggested that both species and two others (*P. balaenoptera* Koren and Danielssen, 1877 and *P. benzi* Hogans, 2017) are all conspecific. Similarly, Fraija-Fernández *et al.* (2018) and Ten

et al. (2025) regarded *P. balaenoptera* as a junior synonym of *P. filosa*. However, as of April 2026, Walter and Boxshall (2026) still treated these two species as valid, and the present paper follows these authors.

Pennella filosa was originally described as *Pennatula flosa* by Linnaeus (1758), and the genus *Pennella* was established by Oken (1815). Currently, this genus comprises 10 valid species, and the following eight species and one subspecies have been regarded as junior synonyms of *P. filosa*: *P. crassicornis* Steenstrup and Lütken, 1861; *P. germonia* Leigh-Sharpe, 1931; *P. germonia fagei* Poisson and Razet, 1953; *P. histiophori* Thomson, 1890; *P. orthagorisci*; *P. pustulosa* Baird, in Angas, 1847; *P. rubra* Brian, 1906; *P. tridentata* Listowsky, 1892; and *P. varians* Steenstrup and Lütken, 1861 (Hogans, 2017; Walter and Boxshall, 2026). Based on the literature published between 1758 and 2025, *P. filosa* and the above synonymized species have been reported as adults from a variety of marine fishes, and 17 species of teleosts belonging to three orders and eight families are known as hosts of this parasite (Table 1). More records of *P. filosa* came from swordfish and ocean sunfish than from other fish species. In addition to the fish hosts, *P. filosa* has also been reported as adults from six species of cetaceans in one order and three families (Table 2) and as juveniles from six species of cephalopods in four orders and four families (Table 3). This information indicates that *P. filosa* uses teleosts and cetaceans as its final hosts and cephalopods as its intermediate hosts to complete its life cycle (for cephalopod hosts of *Pennella*, see also Hochberg, 1990; Pascual *et al.*, 1996, 1997, 2005; Gestal *et al.*, 1999).

Pennellid specimens initially reported as *P. filosa* (Hogans, 1986b) from mink whale *Balaenoptera acutorostrata* Lacépède, 1804 were later reidentified as *P. balaenoptera* (Hogans, 1987b, fig. 2). Thus, the record of *P. filosa* by Hogans (1986b) is not included in Table 2. However, as stated above, recent studies have suggested that *P. balaenoptera* and *P. filosa* are conspecific (Fraija-Fernández *et al.*, 2018; Suyama *et al.*, 2021b; Ten *et al.* (2025), and it may be necessary to revise Table 2 in the future to include the past other records of *P. balaenoptera*. Hogans (2017) listed eight species of mammals as hosts of *P. balaenoptera*, consisting of three species of whales [mink whale; fin whale *B. physalus* (Linnaeus, 1758); sei whale *B. borealis* Lesson, 1828], four species of dolphins and porpoise [Risso's dolphin *Grampus griseus* (Cuvier, 1812); bottlenose dolphin *Tursiops truncatus* (Montagu, 1821); striped dolphin *Stenella coerleoalba* (Meyen, 1833); harbor porpoise *Phocoena phocoena* (Linnaeus, 1758)], and one species of pinniped [northern elephant seal *Mirounga angustriostris* (Gill, 1866)].

To date, *P. filosa* has not been reported from elasmobranchs. However, Benz (2005) reports on a record of a pennellid identifiable as *Pennella* sp., which was originally described as *Penicillus indicus* Kumar and Hameed, 1993 from three species of sharks captured in the Arabian Sea, part of the Indian Ocean (Kumar and Hameed, 1993).

Ten species of *Pennella* have been reported from waters off India (Kirtisinghe, 1932, 1933, 1935, 1964; Gnanamuthu, 1957; Sebastian, 1966; Pillai, 1985), but there is no record of a pennellid that was identified as *P. filosa* in this region. Currently, two of the 10 reported species [*P. diodontis* Oken, 1816 and *P. instructa* (including *P. zeylanica* Kirtisinghe, 1932)] are recognized as valid, while *P. oxyporhamphi* Sebastian, 1966 is regarded as a junior synonym of *P. longicauda* Gnanamuthu, 1957 and six species (*P. longicauda*; *P. biloba* Kirtisinghe, 1933; *P. elegans* Gnanamuthu, 1957; *P. platycephalus* Gnanamuthu, 1957; *P. robusta* Gnanamuthu, 1957; and *P. selaris* Kirtisinghe, 1964) are considered *species inquirendae* (Walter and Boxshall, 2026). Because *P. instructa* and *P. filosa* have been proposed as conspecifics (Suyama *et al.*, 2021b), it is necessary to determine the taxonomic status of these two and other species of *Pennella* from Indian waters.

In Japan, *P. filosa* was initially reported as *P. orthagorisci* (Ishii, 1916a; Kihara, 1960; Kamegai *et al.*, 1961; Kamegai, 1963). However,

Table 1. Known fish hosts and collection areas of *Pennella filosa**. The classification scheme and scientific and common names of fishes are adopted from Froese and Pauly (2026).

Host				Collection area	Reference
Order	Family	Scientifc name	Common name		
Carangiformes	Xiphiidae	*Xiphias gladius*	swordfish	Meditterranean Sea	Linnaeus (1758, as *Pennatula filosa* from *Xiphias*)
				Meditterranean Sea, Adriatic Sea	Valle (1881, as *P. crasscornis*)
				Meditterranean Sea, Italy	Listowsky (1892, as *P. tridentata*)
				North Atlantic Ocean, USA	Thompson (1905)
				Mediterranean Sea, Italy	Brian (1906)
				North Atlantic Ocean, Canada	Wilson (1917, from swordfish)
				North Atlantic Ocean, USA	Wilson (1917, from swordfish)
				North Atlantic Ocean, USA	Wilson (1932, from swordfish)
				North Atlantic Ocean, Canada	Nigrelli (1938)
				Mediterranean Sea	Rose and Vaissière (1953, as *P. filosa* and *P. crassicornis*)
				Mediterranean Sea, France	Delmare Deboutteville and Nunes-Ruvio (1953)
				North Atlantic Ocean, Canada	Tibbo *et al.* (1961, as probably *P. filosa*)
				North Atlantic Ocean, Canada	Hogans *et al.* (1985)
				—**	Hogans (1987b)
				North Atlantic Ocean, Canada	Kabata (1988)
				North Atlantic Ocean, Ireland	Pollock (1994)
				North Atlantic Ocean, Canada	Hogans (1995)
				North Atlantic Ocean, Puerto Rico	Williams and Williams (1996)
				North Atlantic Ocean, Gulf of Guinea	Castro-Pampillón *et al.* (2002)
				Mediterranean Sea, Italy	Merella *et al.* (2003)
				Aegean Sea, Turkey	Tanrikul and Akyol (2011)
				Mediterranean Sea, Spain	Fraija-Fernandez *et al.* (2018)
				North Pacific Ocean, Japan and off Japan	Suyama *et al.* (2021b)
				Mediterranean Sea, Spain	Ten *et al.* (2025)
	Istiophoridae	*Makaira nigricans*	blue marlin	South Pacific Ocean, New Zealand	Thomson (1890, as *P. histiophori* from *Histiophorus herschelii*)
				North Atlantic Ocean, Puerto Rico	Williams and Williams (1996)
		Makaira mazawa	Indo-Pacific blue marlin	North Pacific Ocean, Japan	Ho and Nagasawa (2001)
		Kajikia audax	striped marlin	South Pacific Ocean	Lewis (1967, as *P. histiophori*?)
				—	Hogans (1987b, from *Tetrapterus audax*)
				North Pacific Ocean, Mexico	Benz (2005, fig.1)
				North Pacific Ocean, Mexico	Hernández-Trujillo *et al.* (2014)
				North Pacific Ocean, off Japan	Suyama *et al.* (2021b, based on tentative parasite identification)
		Kajikia albida	Atlantic white marlin	North Atlantic Ocean	Wilson (1917, from *Tetrapturus albidus*)
		Istiompax indica	black marlin	South Atlantic Ocean, South Africa	Kensley and Grindley (1973, as *P. orthagorisci* from *Makaira indica*)
				Sea of Japan, Japan	This paper
		Istiophorus platypterus	Indo-Pacific sailfish	North Pacific Ocean, Mexico	Causey (1960, from *Istiphorus greyi*)
		Tetrapturus angustirostris	shortbill spearfish	North Pacific Ocean, Japan	Ho and Nagasawa (2001)
	Coryphaenidae	*Coryphaena hippurus*	common dolphinfish	North Atlantic Ocean, Puerto Rico	Dyer *et al.* (1997, as *P. varians*)
				Mediterranean Sea, Spain	Carbonell *et al.* (1999)
				Mediterranean Sea, Spain	Martí García *et al.* (2011)
				North Pacific Ocean, Japan	Suyama *et al.* (2021b, based on tentative parasite identification)

Table 1. Continued.

Host				Collection area	Reference
Order	Family	Scientifc name	Common name		
		Coryphaena sp.	unidentified dolphinfish	South Atlantic Ocean	Angas (1847a, b, as *P. pustulosa*)
				Atlantic Ocean	Steenstrup and Lütken (1861, as *P. varians* from dolphinfish)
				South Atlantic Ocean, Australia	Leigh-Sharpe (1928, as *P. pustulosa*)
	Carangidae	*Naucrates ductor*	pilotfish	Meditterranean Sea, Adriatic Sea	Valle (1881, as *P. crasscornis*)
		Seriola dumerili	greater amberjack	Turkish waters	Tuncer *et al.* (2010)
Scombriformes	Scombridae	*Thunnus alalunga*	albacore	North Pacific Ocean, USA	Wilson (1924 as *P. orthagorisci* from *Germo alalunga*)
				North Atlantic Ocean, France	Leigh-Sharpe (1931, as *P. germonia* from *Germo alatunga*)
				North Atlantic Ocean, France	Legendre (1939, from Germon)
				North Atlantic Ocean, France	Poisson and Razet (1953, as *P. germonia fagei* from *Germo alalunga*)
				North Atlantic Ocean, Gulf of Guinea	Baudin Laurencin (1971, as *P. crassicornis*)
				British waters	Kabata (1979)
				North Atlantic Ocean, Ireland	Pollock (1994)
		Thunnus thynnus	Atlantic bluefin tuna	British waters	Kabata (1979)
				Adriatic Sea, Croatia	Žilić and Mladineo (2006)
		Thunnus albacares	yellowfin tuna	North Atlantic Ocean, Puerto Rico	Williams and Williams (1996)
				South Atlantic Ocean, South Africa	Kensley and Grindley (1973, from *Thynnus albacares*)
				North Pacific Ocean, Mexico	Román-Reyes José *et al.* (2019)
	Gempylidae	*Lepidocybium flavobrunneum*	escolar	North Pacific Ocean, Japan	Suyama *et al.* (2021b)
Tetraodontiformes	Molidae	*Mola mola*	ocean sunfish	North Atlantic Ocean, Ireland	Wright (1870, as *P. orthagorisci* from *Orthagoriscus mola*)
				North Atlantic Ocean, USA	Leidy (1890, as *Penella filosa* from *Mola rotunda*)
				North Atlantic Ocean, USA	Rathbun (1905, from sunfish)
				North Atlantic Ocean, UK	Scott (1905, from *Orthagoriscus mola*)
				South Atlantic Ocean, South Africa	Stebbing (1905, as *P. orthagorisci* from *Orthagoriscus mola*)
				North Atlantic Ocean, UK	Norman and Scott (1906, from sunfish)
				Meditterranean Sea, Italy	Brian (1906, as *P. rubra* from *Orthagoriscus mola*)
				North Atlantic Ocean	Brian (1908, as *P. filosa*? from *Orthagoriscus mola*)
				Meditterranean Sea, France	Brian (1908, as *P. crassicornis* from *Orthagoriscus mola*)
				South Atlantic Ocean, South Africa	Stebbing (1910, as *P. orthagorisci* from *Orthagoriscus mola*)
				North Atlantic Ocean	Brian (1912, from *Orthagoriscus mola*)
				North Atlantic Ocean	Brian (1912 as *P. crassicornis*? from *Orthagoriscus mola*)
				North Atlantic Ocean, France	Quidor (1912 as *Penella filosa* from *Orthagoriscus mola*)
				North Atlantic Ocean, USA	Fowler (1912)
				North Atlantic Ocean, USA	Summer *et al.* (1913)
				British waters	Scott and Scott (1913, as *P. orthagorisci* from *Orthagoriscus mola*)
				North Pacific Ocean, Japan	Ishii (1916a, as *P. orthagorisci* from ocean sunfish)

Table 1. Continued.

Host				Collection area	Reference
Order	Family	Scientifc name	Common name		
				North Atlantic Ocean, USA	Wilson (1917, as *P. filosa* from *Mola rotunda* and sunfish and as *P. orthagorisci* from *M. mola)*
				Irish Sea, Isle of Man	Leigh-Sharpe (1928, as *P. orthagorisci* from *Orthagoriscus mola*)
				North Atlantic Ocean, USA	Wilson (1932, as *P. filosa* from sunfish and as *P. orthagorisci* from sunfish)
				South Atlantic Ocean, Brazil	Carvalho (1951)
				Mediterranean Sea	Rose and Vaissière (1953, as *P. filosa* and *P. rubra*)
				Mediterranean Sea, France	Delmare Debouttéville and Nunes-Ruvio (1953)
				Mediterranean Sea, Algeria	Delmare Debouttéville and Nunes-Ruvio (1953)
				Mediterranean Sea	Rose and Vaissiere (1953, from *Orthagoriscus mola*; *P. rubra* from *Orthagoriscus mola*)
				South Atlantic Ocean, South Africa	Barnard (1955, as *P. filosa*; *P. orthagorisci* from *Mola*)
				North Sea, English Channel	Markevich (1956, as *P. orthagorsci*)
				North Atlantic Ocean, North America	Markevich (1956, as *P. orthagorsci*)
				Sea of Japan, Russia	Markevich (1956, as *P. orthagorsci*)
				Japanese waters	Kihara (1960, as *P. orthagorisci*)
				Seto Inland Sea, Japan	Kamegai *et al.* (1961, as *P. orthagorisci* from *Orthagoriscus*)
				Seto Inland Sea, Japan	Kamegai (1963, as *P. orthagorisci* from *Orthagoriscus*)
				South Atlantic Ocean, South Africa	Kensley and Grindley (1973)
				British waters	Kabata (1979)
				North Sea, Netherlands	Huwae (1986)
				North Atlantic Ocean, Canada	Hogans (1987a)
				—	Hogans (1987b)
				North Pacific Ocean, Canada	Kabata (1988)
				British waters	Kabata (1992)
				North Atlantic Ocean, Ireland	Pollock (1994)
				North Atlantic Ocean, Ireland	Hogans (1995)
				South Atlantic Ocean, Brazil	Boxshall and Montú (1997)
				South Atlantic Ocean, Brazil	Luque and Tavares (2007)
				Mediterranean Sea, Spain	Fraija-Fernandez *et al.* (2018)
		Mola alexandrini	bumphead sunfish	South Pacific Ocean, Chile	Atria (1967, as *P.* cf. *filosa* from *Mola ramsayi*)
		Mola sp.		North Pacific Ocean, Japan and off Japan	Suyama *et al.* (2021b)
	Tetraodontidae	*Takifugu rubripes*	Japanese pufferfish	North Pacific Ocean, Japan	Suyama *et al.* (2021b)
—	—	—	—	—	Giard (1889, as *P. orthagorisci*)
—	—	—	—	—	Quidor (1912, as *Penella filosa*)
—	—	—	—	—	Wilson (1917)
—	—	—	—	Mediterranean Sea, Italy	Leigh-Sharpe (1928)

*Included are the records of "*Penella filosa*" (Leidy, 1890; Quidor, 1912), "*Pennella filosa*?" (Brian, 1908), "probably *P. filosa*" (Tibbo *et al.*, 1961), "*P.* cf. *filosa*" (Atria, 1967), "*P. filosa* (tentative identification)" (Suyama *et al.*, 2021b), *P. crassicornis* (Valle, 1881; Brian, 1908; Rose and Vaissière, 1953; Baudin Laurencin, 1971), "*P. crassicornis*?" (Brian, 1912), *P. germonia* (Leigh-Sharpe, 1931), *P. germonia fagei* (Poisson and Razet, 1953), *P. histiophori* (Thomson, 1890), "*P. histiophori*?" (Lewis, 1967), *P. orthagorisci* (Wright, 1870; Giard, 1899; Stebbing, 1905, 1910; Scott and Scott, 1913; Ishii, 1916a; Wilson, 1924; Barnard, 1955; Markevich, 1956; Kihara, 1960; Kamegai *et al.*, 1961; Kamegai, 1963; Kensley and Grindley, 1973), *P. pustulosa* (Angas, 1847a, b), *P. rubra* (Brian, 1906; Rose and Vaissière, 1953), *P. tridentata* (Listowsky, 1892), and *P. varians* (Steenstrup and Lütken, 1861; Dyer *et al.*, 1997).

** Not reported.

Table 2. Known cetacean hosts and collection areas of *Pennella filosa**,**. The classification scheme and scientific names of cetaceans are adopted from WoRMS Editorial Board (2026).

Host				Collection area	Reference
Order	Family	Scientifc name	Common name		
Cetartiodactyla	Ziphiidae	*Hyperoodon ampullatus*	northern bottlenose whale	North Atlantic Ocean, Faroe Islands	Steenstrup and Lütken (1861, as *P. crassicornis* from *Hyperoodon rosratus*)
		Ziphinus cavirostris	goose-beaked whale	North Atlantic Ocean, Mauritania	Delmare Deboutteville and Nunes-Ruvio (1953, as *P. crassicornis*)
				Meditterranean Sea, Italy	Donato and Torchio (1966, as *P. crassicornis*)
	Balaenopteridae	*Balaenoptera acutorostorata*	mink whale	South Atlantic Ocean, South Africa	Barnard (1955, as *P. crassicornis*)
				South Atlantic Ocean, South Africa	Kensley and Grindley (1973, as *P. crassicornis*)
		Balaenoptera physalus	fin whale	Meditterranean Sea, Spain	Ten *et al.* (2025, as *P.* cf. *fillosa*)
		Megaptera novaeangliae	humpback whale	Meditterranean Sea, Spain	Ten *et al.* (2025, as *P.* cf. *fillosa*)
	Delphinidae	*Stenella coeruleoalba*	striped dolphin	Meditterranean Sea, Italy	Brian (1906, as *P. crassicornis* from *Prodelphinus euphrosyne*)

*Included are the records of *Pennella crassicornis* (Steenstrup and Lütken, 1861; Brian, 1908; Delmare Deboutteville and Nunes-Ruvio, 1953; Barnard, 1955; Donato and Torchio, 1966; Kensley and Grindley, 1973) and "*P.* cf. *filosa*" (Ten *et al.*, 2025).
**The records of *Pennella balaenoptera* are not included. See the Discussion.

Table 3. Known cephalopod hosts and collection areas of *Pennella filosa**. The classification scheme and scientific names of cephalopods are adopted from WoRMS Editorial Board (2026).

Host				Collection area	Reference
Order	Family	Scientifc name	Common name		
Sepiida	Sepiidae	*Sepia officinalis*	common cuttlefish	Meditterranean Sea, Italy	Wierzejski (1877, as *P. varians*?)
				Meditterranean Sea, Algeria	Rose and Hamon (1953, as *P. varians*)
				Meditterranean Sea	Rose and Vaissière (1953, as *P. varians*)
		Sepia elegans	elegant cuttlefish	Meditterranean Sea, Algeria	Rose and Hamon (1953, as *P. varians*)
Myopsida	Loliginidae	*Loligo vulgaris*	European squid	Meditterranean Sea, Italy	Wierzejski (1877, as *P. varians*?)
				Meditterranean Sea, Algeria	Rose and Hamon (1953, as *P. varians*)
				Meditterranean Sea	Rose and Vaissière (1953, as *P. varians*)
		Alloteuthis subulata	European common squid	British waters	Hochberg (1990, as *P. varians*)
Oegopsida	Ommastrephidae	*Todaropsis eblanae*	lesser flying squid	Meditterranean Sea, Spain	Stock (1960, as *P. varians*)
Octopoda	Eledonidae	*Eledone moschata*	musky octopus	Meditterranean Sea, Italy	Wierzejski (1877, as *P. varians*?)
		Eledone sp.		Meditterranean Sea	Rose and Vaissière (1953, as *P. varians*)

*Included are the records of "*Pennella varians*?" (Wierzejski, 1877) and *P. varians* (Rose and Hamon, 1953; Rose and Vaissière, 1953; Stock, 1960; Hochberg, 1990).

the latter species has been regarded as a junior synonym of *P. filosa* (Kabata, 1979; Hogans, 2017; Walter and Boxshall, 2026), and this name is currently used in the country (Ho and Nagasawa, 2001; Nagasawa and Uyeno, 2014; Suyama *et al.*, 2021b). The collection of *P. filosa* in the present study represents its second record from black marlin and first specimen-based record from the Sea of Japan. Before this study, there was a record of *P. filosa* (as *P. orthagorisci*) collected from black marlin (as *Makaira indica*) off South Africa (Kensley and Grindley, 1973, p. 127). Moreover, Markevitch (1956) reported this parasite (as *P. orthagorisci*) from ocean sunfish in the Sea of Japan off the Russian Far East.

Copepods of the genus *Pennella* exhibit signifi-

cant morphological variability, which makes them difficult to accurately identify (Kabata, 1979; Hogans, 1987b, 2017; Suyama *et al.*, 2019, 2021b). Heavily damaged or pre-metamorphosis individuals are also difficult to identify because important taxonomic clues are missing or undeveloped. Molecular analyses have been used as powerful identification tools in such cases (Fraija-Fernández *et al.*, 2018; Llarena-Reino *et al.*, 2019; Suyama *et al.*, 2021b; Ten *et al.*, 2025), but it is still difficult to accurately identify species within this genus. Further morphological and molecular studies using materials of various sizes and developmental stages from different fish, cetacean, and cephalopods hosts are necessary.

Acknowledgments

We thank Sachiko Onishi (Miyazu) for providing us with Specimen 1 and Naofumi Tanimoto (Fisheries Technology Department of the Kyoto Prefectural Agriculture, Forestry and Fisheries Technology Center, Miyazu) for his assistance with sample collection. We are also grateful to Shun-ichiro Shibata (Kagoshima University, Kagoshima), Fabiano Paschoal (Rio de Janeiro State University, Rio de Janeiro), and Satoshi Suyama (Hachinohe Field Station, Highly Migratory Resources Division, Fisheries Stock Assessment Center, Fisheries Resources Institute, Japan Fisheries Research and Education Agency, Hachinohe) for their help with the literature and Tomoyuki Kuwahara (JAPAN NUS Co., Ltd., Tokyo) for his collaboration during fish sampling. We acknowledge Geoffrey A. Boxshall (Natural History Museum, London) and an anonymous referee who provided comments to improve the manuscript of the paper. This work was partially funded by the Fisheries Agency of the Japanese Ministry of Agriculture, Forestry and Fisheries.

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