



Review of *Pennella* Oken, 1816 (Copepoda: Pennellidae) with a description of *Pennella benzi* sp. nov., a parasite of Escolar, *Lepidocybium flavobrunneum* (Pisces) in the northwest Atlantic Ocean

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Abstract

The genus *Pennella* Oken, 1816, mesoparasitic copepods from marine fish and mammals, is reviewed with the objective of determining the validity of members of the genus. Details of the external morphological structures of the adult female are presented. *Pennella* species are differentiated based on a combination of characters: the type of host parasitized, overall length of the parasite, shape, size and configuration of cephalothoracic papillae, segmentation of the first and second antenna, holdfast horn number, shape and configuration, and structure of the abdominal plumes. A new species of *Pennella*, *Pennella benzi* sp. nov., is described from the escolar, *Lepidocybium flavobrunneum* in the northwest Atlantic. *Pennella balaenoptera* Koren & Danielssen, 1877 is reported from the harbor porpoise (*Phocaena phocaena*) in the Bay of Fundy, a new locality record. The validity of 44 species is assessed; nine species (*P. balaenoptera* Koren & Danielssen, 1877, *P. benzi* sp. nov., *P. diodontis* Oken, 1816, *P. exocoeti* (Holten, 1802), *P. filosa* Linnaeus, 1758, *P. hawaiiensis* Kazachenko & Kurochkin, 1974, *P. instructa* Wilson, 1917, *P. makaira* Hogans, 1988 and *P. sagitta* Linnaeus, 1758) are considered substantiated and valid; six species (*P. elegans* Gnanamuthu, 1957, *P. longicauda* Gnanamuthu, 1957, *P. platycephalus* Gnanamuthu, 1957, *P. remorae* Murray, 1856, *P. robusta* Gnanamuthu, 1957, and *P. selaris* Kirtisinghe, 1964) exhibit unique characteristics, but are based on descriptions of single specimens, have not been found since the original reports and are considered as *species inquirendae*; the remaining species are unsubstantiated and invalid based on inadequate or missing original descriptions, or are designated as synonyms of valid species. A key to the valid species of the genus is provided.

Key words: review, parasite, Copepoda, *Pennella*

Introduction

Copepods of the genus *Pennella* are parasites of a wide range of marine fish and mammal hosts. The largest of all copepods, some species (ex: *P. balaenoptera* Koren & Danielssen, 1877) may reach 320mm in length, but the genus also contains very small species (ex: *P. sagitta* Linnaeus, 1758) which measure only 20mm. *Pennella* species are among the most recognized of all parasitic copepods; their size and mesoparasitic habits make them very conspicuous on the external body surfaces of hosts. Specimens of *Pennella* show about one half the total parasite outside the host body (Fig. 1) and the remaining anterior portion is a modified and enlarged cephalothorax with holdfast horns (Figs. 2–4) deeply embedded in host tissues.

Pennella contains many species, at least in terms of the number previously reported or described (44). There are numerous issues concerning the taxonomy of the genus. Many species have been described from the adult mesoparasitic female, but others are based on different stages of the life cycle or metamorphosis of the parasite. *Pennella* changes shape and size significantly as it grows after initial attachment to the definitive host (Thompson 1905; Wilson 1917). The validity of new species based on adult females has been confused due to morphological variation, phenotypic plasticity and age of individual specimens (Kabata 1979; Hogans 1987). Many authors have described new species based on structurally unique specimens (of a probable single species) recovered from the same host species or individual host. In the most serious cases of poor original attempted validation, previous

workers reporting on *Pennella* used only the external portion of the parasite on the host to describe or name a species, unaware that an accurate description and a correct rationale for considering the species as distinct could only be accomplished using the entire animal. To further complicate the taxonomy of the genus, the type specimens (or any specimens) for a particular species are missing and lost to science, the original descriptions are based only on a single specimen, are brief, incomplete and lacking in figures which might otherwise portray the species, and the rationale for why the species was unique and different from its congeners is inadequate, unconvincing or missing altogether. Unfortunately, some previously documented species have all of these features in common.

In terms of taxonomic history, *Pennella* is the oldest of parasitic copepods. The first to publish an account of a *Pennella*, Linnaeus (1758), incorrectly assumed the specimen he encountered to be an alcyonarian coral polyp and named it *Pennatula sagitta*. Oken (1816; this date has been previously and repeatedly documented as 1815; however, the actual publication date for the manuscript was 1816 as indicated in Wilson 1917). Oken (1816) correctly determined that the parasites were crustaceans, not polyps, and placed them in the Lernaeidae. Oken (1816) also identified and named another species in the genus (*P. diodontis* Oken, 1816) as a lernaeid and renamed *Pennatula* as the new genus *Pennella*. Wilson (1917) considered *P. diodontis* to be a synonym of *P. sagitta*. Hogans (1988a) showed that *P. sagitta* and *P. diodontis* were valid and distinct species; *P. sagitta*, the oldest described species of *Pennella*, is the actual type for the genus.

In spite of its long history, there have been relatively few attempts to comprehensively review or revise *Pennella*, most efforts have only listed species. Turner (1905) listed and commented on the extant species; in his opinion, further and more careful scrutiny would likely reduce the number of true species. Wilson (1917) next made a more serious attempt. His careful determinations considered the morphological characters which define the genus and he correctly realized that some species exhibited structural variability between specimens; he also commented on the change in external morphology as the parasite grew in the host, indicating that age influenced its structure. Wilson (1917) reviewed the taxonomic status of 27 species; he dismissed 13 as invalid based on poor original descriptions or insufficient information, described a new species, *P. instructa* Wilson, 1917, and redescribed or commented on 14 others which he included in a key to species of the genus. Leigh-Sharpe (1928) examined specimens of *Pennella* from the British Museum and listed what he considered to be the individual differentiating characters, although he did not attempt to revise *Pennella*. Delamare Deboutteville and Nunes-Ruivo (1951) compared their redescribed *P. remorae* to other similar species; they also listed some other species and considered many as probable synonyms of those which were better documented. Yamaguti (1963) listed all of the known species (or those on which he had information) and commented briefly on the validity of several. Kabata (1979) in his seminal work on parasitic Copepoda from British fishes, discussed the taxonomy of *Pennella*, indicated the morphological features of the parasites potentially useful for differentiating species and commented on species which were synonymous with *P. filosa* Linnaeus, 1758. More recently, Hogans (1987) reviewed *Pennella* previously described from Cetacea and reduced all reported from marine mammals to synonymy with *P. balaenoptera*. In the most recent attempt to revise *Pennella*, Hogans (1988a) discussed the validity of 31 species and considered only seven species to be valid (*P. balaenoptera*, *P. diodontis*, *P. exocoeti* (Holten, 1802), *P. filosa*, *P. instructa*, *P. makaira* Hogans, 1988, *P. sagitta*). However, that revision was provisional in nature and did not include all of the species previously reported or described. The latest listing of previously documented species by Walter and Boxshall (2015) summarizes the taxonomic status of the genus and considered 14 species as potentially valid and having no previous designations of synonymy.

In this present review, information on all species that have been previously documented is discussed and assessed with the objective of further determining the validity of known members of the genus; it reviews *Pennella* based on previous literature, reports on examinations of newly available specimens and provides details of the external morphological structures of the genus. A new species, *Pennella benzi* sp. nov., is described and the structural features which differentiate it from other *Pennella* species are presented.

Materials and methods

For this review of *Pennella*, the author has relied heavily on accounts of species in the available literature, but has also examined new specimens: two *Pennella* recovered from the blubber and sub-cutaneous musculature of a minke whale (*Balaenoptera acutorostrata*) and a single specimen found on a harbor porpoise (*Phocoena*

phocoena) in the lower Bay of Fundy in 1989. The specimens recovered from each cetacean host were initially frozen in saltwater in 500 ml polyethylene jars; the specimens were later thawed and fixed whole in 10% formalin. Other specimens examined were preserved in 70% ethanol: *P. filosa* (two), *P. instructa* (one) (from swordfish, *Xiphias gladius* collected in 1990 off Nova Scotia), *P. filosa* (one) from ocean sunfish, *Mola mola* collected in 1982 near Campobello Island, New Brunswick and *P. exocoeti* (one) from *Cheilopogon melanurus* collected off the Georgia coast, U.S.A. in 1987. A single specimen of *P. benzi* **sp. nov.** was recovered from an escolar (*Lepidocybium flavobrunneum*) caught off coastal North Carolina, U.S.A. in 2009. The specimen was dissected from host tissues and fixed in 10% formalin and later transferred to 70% ethanol.

The first and second antenna of all specimens examined were removed from each parasite and examined separately. Whole transverse sections of the anterior end of the cephalothorax of the cetacean parasites, and specimens of *P. filosa* and *P. instructa* were cleared and mounted in 85% Lactic Acid. Observations and drawings were made using Nomarski Interference Phase Contrast illumination at up to 1200X magnification. Drawings were made with the aid of a camera lucida. Morphological terminology of appendages generally follows Huys and Boxshall (1991), excepting the first and second antenna (antennule and antenna, respectively) and first and second maxilla (maxillule and maxilla, respectively); the previous terminology for these appendages is retained to make clear comparisons to descriptions in the older literature. All measurements listed are in millimeters.

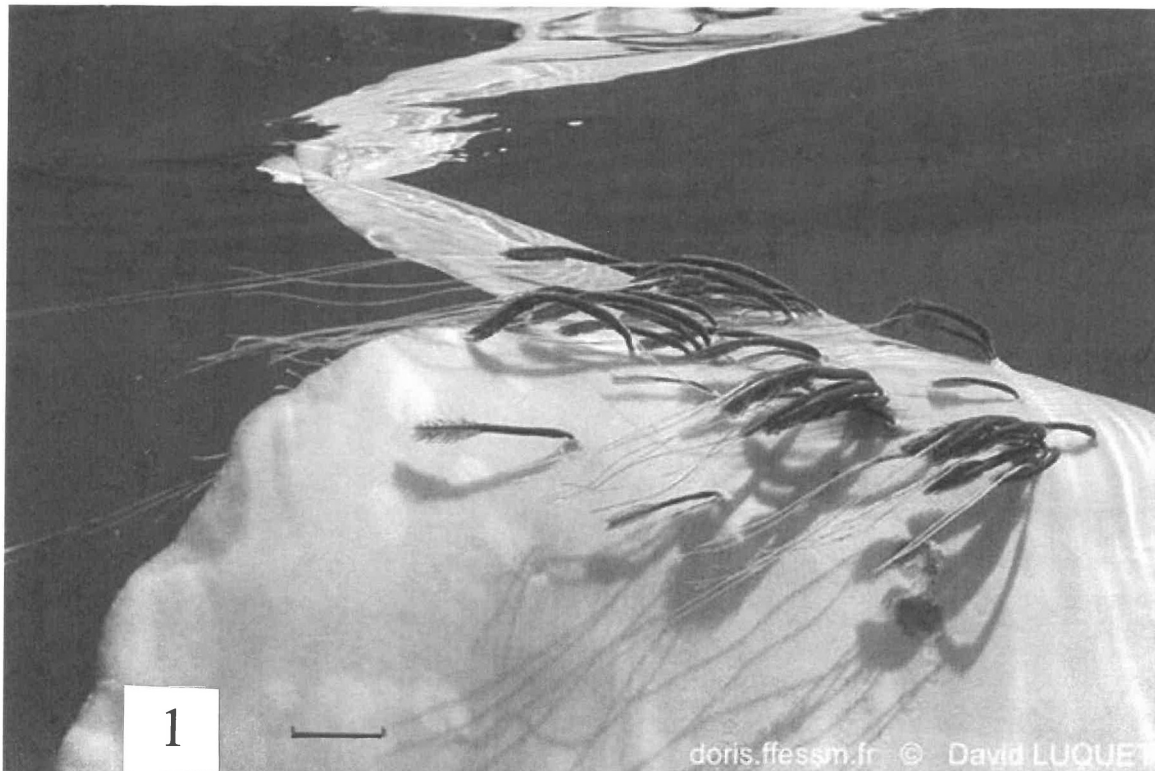


FIGURE 1. Photograph of several *Pennella filosa* parasitizing the dorsolateral flank of an ocean sunfish (*Mola mola*). Reproduced from doris.ffessm.fr. Scale bar = 100 mm.

Results

External morphology of *Pennella*

To propose the use of a particular structural feature to discriminate between species it is necessary to define the external morphology of the adult female. These structures are here described beginning at the anterior end of the parasite; *Pennella* can be roughly divided into five morphological regions: the cephalothorax, holdfast horn region, neck, trunk and abdomen.

The cephalothorax (sometimes referred to as the “head”) of *Pennella* (ex: *P. filosa*, Fig. 2) exhibits a range of

shapes and sizes, dependent on species, parasite age and site of infestation (or a combination of these). The cephalothorax shape can be roughly spherical, or a squat and rounded cylinder depending on the individual and/or species. The apical end of the cephalothorax shows a variety of shapes; it may be flattened and truncate or rounded and concave. The shape is influenced by the arrangement and structure of the cephalothoracic papillae (also referred to as antennary processes; Kabata 1979). The papillae of *Pennella* are characteristic of a particular species based on shape, size, arrangement and number. The shape of individual papillae can be smoothly or roughly spherical, or short clavate or tubiform processes which may exhibit simple branching depending on the specimen and/or species. The papillae are not considered as hold-fast structures per se, but are often densely packed with host tissues. The cephalothoracic papillae fully or partially-cover the end of the cephalothorax randomly (ex: *P. filosa*) or may be found in distinct groups or bands, as in *P. instructa* (Wilson 1917; Hogans 1986) and *P. remorae* Delamare Deboutteville & Nunes-Ruivo, 1951. Hogans (1988a, c) showed that papillae shape and arrangement on the apical end of the cephalothorax was consistent between individuals of a single species <50mm in total length.

Other structures found on the cephalothorax are those appendages which are remnant from the last larval infective stage; some are functional and may be used by the parasite (ex: buccal complex may or may not function actively as the mouth) and others become dwarfed by growth of the parasite and are not used. These would include structures such as the first antennae (sensory in nature and used by the free-swimming infective larva to assist in locating the host), the second antennae and maxillipeds (used only for initial attachment to the host), the maxillae which have limited or no obvious use once the adult female stage is reached and the swimming legs which are not used after initial attachment to the definitive host.

The mouth (buccal complex) of *Pennella* is a typical siphonostome structure located amongst and near the middle of the cephalothoracic papillae at the very anterior end of the cephalothorax. It is difficult to locate in many specimens, where some of the papillae must often be moved aside or removed to see the structure. It is so small in relation to the total size of the parasite that it is difficult to understand how the structure could actively contribute to significant nutrient uptake. The structure of the buccal complex in the adult female *P. balaenoptera* was partially elucidated by Scanning Electron Microscopy (SEM) (Abaunza *et al.* 2001). The complex was observed in *P. balaenoptera* and *P. instructa* in this study under light microscopy, but its structure was not determined in detail. Based on these examinations, the structure of the buccal complex resembles that of other pennellids, such as *Sarcotretes* (Ho *et al.* 2006; Hogans 1988b), *Ophiolernaea* Shiino, 1958 (Ho 1966) and *Metapeniculus* (Castro-Romero & Kuroki 1991). The complex appears as an eversible cone supported by a longitudinal series of chitinous rings (hard cuticle rings telescoping into each other of Abaunza *et al.* 2001) and exhibits a terminal membranous fringe around the periphery of the anterior end. The labrum associated with the buccal complex has not previously been clearly defined in *Pennella* and was not found in any specimens in this present study. Boxshall (1990) in his detailed treatment of the oral cone of siphonostome copepods, suggests that the labrum of pennellid copepods decreases in size during development; this may be the reason why it is not evident in *Pennella*. As the buccal complex is difficult to locate on most specimens of *Pennella* and its structure is uniform between species (Kabata 1976, 1979), it is not presently useful as a discriminating character.

Abaunza *et al.* (2001) found under SEM, a distinct tri-lobed structure in *P. balaenoptera* associated with and close to the buccal cone (the labrum was suggested to perhaps be found at the base of the posterior lobe of this structure). This structure was not found in specimens of *P. balaenoptera* in recent examinations of dissected and cleared buccal complexes under light microscopy. However, this feature may become evident only under the more three-dimensional perspective of SEM; it has not been recorded from other genera in the family. It was suggested that the structure may play a role in assisting in muscular peristalsis of the buccal complex during feeding (Abaunza *et al.* 2001).

The mandible of the female *Pennella* on the definitive host has been described only twice. Wilson (1917) defined the appendage as a “broad lamellate basal joint tipped with a curved spine without teeth”. Castro-Romero and Kuroki (1986) described the mandible of the pre-metamorphosis female as exhibiting ten teeth, and in other pennellid genera teeth are evident on this appendage, as in *Sarcotretes scopeli* (Hogans 1988b). Thompson (1905) could not find the mandible even in recently-attached copepodids or young, developing specimens of *P. filosa* and it was not positively identified in the present study. However, a small process with one apical spine was found just inside the buccal cone of a specimen of *P. instructa*; this structure is reminiscent of that described for the mandible by Wilson (1917).

The first and second maxillae are not easily found on any specimens of adult *Pennella*. When observed they

are located at the base and along the lateral sides of the buccal cone (Abaunza *et al.* 2001 and present study). The structure of the first in the mature parasite is basically the same as that described for other pennellid genera (ex: as in *Ophiolernaea*) (Ho 1966): simple processes with a few apical setae of various sizes on the precoxal endite and palp (Kabata 1979). In this study, the first maxilla was located in specimens of *P. balaenoptera*, but its structure was not clearly defined. The appendage was a raised process with two simple setae (Fig. 5c), no clear endite or palp was evident. Wilson (1917) reported the first maxillae of a young *P. filosa* to be a simple process with two long apical setae; the second maxillae were “long and stout; each consists of a basal joint with two strong, claw-like spines”. In recent examinations the second maxillae was not seen distinctly in any specimens. Abaunza *et al.* (2001) and Kabata (1979) mentioned that the maxillae in *Pennella* may be subject to some regressive metamorphosis and this feature, along with the difficulty in locating these appendages on most specimens, makes them currently unreliable for use as characters to discriminate species.

The first antennae are found on the dorsal surface of the cephalothorax, near the apical end and within a distinct dorsal cleft in some species (ex: *P. filosa*, Fig. 2). Their position is always just posterior to the second antennae (Fig. 5g). The basic structure of the first antenna on the adult female is much like that found on the recently-attached infective larva (as described for *Pennella* sp. by Castro-Romero & Kuroki 1986). Various authors have described and/ or figured the first antenna with or without segmentation, with or without setae on the segments (when observed) and having some particular segment as long as or slimmer than another (Wilson 1917 and references therein; Kabata 1979; Hogans 1987). Hogans (1987) described and figured the first antenna from museum specimens of *P. balaenoptera* from whales and the fish parasite *P. filosa*; he found the appendage on whale parasites to be somewhat more robust and with a shorter second segment than that exhibited by *P. filosa*. Abaunza *et al.* (2001) did not find this to be evident in their specimens of *P. balaenoptera*; however, they did not describe the appendage in detail. Examinations completed in the present study show that in specimens of *P. balaenoptera* the first antenna can exhibit unclear (Fig. 5d) or distinct segmentation (Fig. 5e). In other species of *Pennella*, segmentation of the first antenna is generally clear and consists of three to five segments based on the relatively few good descriptions of this appendage. In some species (ex: *P. instructa* and *P. exocoeti*) a geniculation formed between the first and second segments is often observed, although this may be an artifact of fixation of the material. Setation of the first antenna appears to be variable between specimens and species; probably due mostly to the difficulty in observing these appendages in detail. The apical armature when observed consists of as many as 13 setae, some of which may be as long, or longer than the entire appendage, and some lateral setules on the tips of the longest setae are rarely observed. Setae from the penultimate segments are shorter and more or less numerous depending on the species (and may vary even between specimens of a single species: ex: *P. exocoeti*, see Fig. 9d, g). Occasionally non-apical setae show a plumose condition (ex: *P. sagitta*, Fig. 18c; *P. exocoeti*, Fig. 9d). Other pennellid genera often show an aesthete as part of the apical armature of the first antenna (Castro-Romero & Kuroki 1989), but this feature does not appear to be common in *Pennella*. One specimen of *P. benzi* **sp. nov.** did exhibit a seta that could be considered as an aesthete based on its shape (shorter and marginally wider than other apical seta, with a rounded end and an indistinct pore-like terminus- see Fig. 6e).

The second antennae (ex: Figs. 5f, 6c) are two or three-segmented and prehensile, with a large hook at the apex of the terminal segment which closes on a distal spur. The spur can be small and blunt (ex: *P. benzi* **sp. nov.**, Fig. 6f) or an acute, pointed and larger process (ex: *P. instructa*, Fig. 12e). It is unknown if parasite age or appendage atrophy influences the sharpness and size of this spur; its shape can be vary in specimens of *P. balaenoptera* and *P. instructa*. As in most other pennellid genera (Kabata 1979), there is a small seta or spine near the base of the hook. The second antennae function as part of the initial attachment mechanism, but the female quickly outgrows the need for the appendage as it burrows deeply into host tissues. In the two-segmented second antenna, the shape of the basal segment is variable: triangular, sub-quadrangular, etc. (Abaunza *et al.* 2001; Kabata 1979; Hogans 1987) and there is no real consistent shape of this segment. There are somewhat different shapes of the basal segment even between two second antennae on a single *Pennella* specimen, probably due to fixation artifact or compression resulting from the site of infestation. The triangular basal segment for *P. balaenoptera* in the photomicrograph of this appendage shown by Abaunza *et al.* (2002) was considered by those authors to be the actual shape for that species. In species with a three-segmented second antenna, the basal and second segments are subquadrangular, not triangular (ex: *P. benzi* **sp. nov.**, Fig. 6f).

The maxillipeds have not been found on the adult female *Pennella* (any species); their structure is inconsistent and variable even among specimens of recently-attached and metamorphosing females (Thompson 1905). Wilson

(1917) reported the maxillipeds from an immature *Pennella* (attached to a swordfish) to be reduced to simple spines. Maxillipeds were not evident in any specimens (of any species) examined for the present review, not unexpected as maxillipeds are lacking in all adult female pennellid copepods (G. Boxshall pers. comm.).

The swimming legs of the adult female *Pennella* are found on the ventral surface usually just below the level of the holdfast horns; there are four pairs which are often somewhat atrophied or reduced to sympods only (see Fig. 10e). Cicek *et al.* (2007) described *P. balaenoptera* specimens from whales in Turkish waters as exhibiting five pairs of swimming legs: this is incorrect; in the whole of the family Pennellidae, the fifth swimming leg is represented by a single seta at most (G. Boxshall pers. comm.). When found as relatively complete (i.e. retaining the larval character state with rami intact, (ex: *P. exocoeti*, Fig. 9h; *P. hawaiiensis*, Fig. 11f, g; *P. diodontis*, Fig. 7e), the anterior two pairs are biramous and the posterior two pairs are uniramous. The rami (see Fig. 9h) exhibit familial characteristics: many long, flagelliform setae, often with fine lateral setules (Castro-Romero & Kuroki 1986; Ho *et al.* 2007). The distance between the pairs of swimming legs is not uniform and is probably dependent on the growth of the parasite; the distance may or may not change as the parasite gets longer and larger (Hogans 1987). The swimming legs found on most *Pennella* specimens are incomplete or missing; rarely, the swimming legs of small species are found intact and the armature formulas for two species (*P. makaira* and *P. sagitta*) have been documented and were found to be very similar (Hogans 1988a). The swimming leg structure is thought to be uniform through-out the Pennellidae and these appendages may not necessarily be useful features to discriminate between species of other genera (Castro-Romero & Kuroki 1989).

The holdfast horns are found at the posterior end of the cephalothorax, at the junction with the neck. These horns are one of the salient distinguishing features of *Pennella*. In the two largest species, *P. balaenoptera* (Fig. 4) and *P. filosa* (Fig. 2, 10b), they are variable in number, shape and length (Kabata 1979; Hogans 1987) and this variation has been largely responsible for previous descriptions of new species based on structurally unique specimens. No two specimens of *P. balaenoptera* or *P. filosa* are exactly alike as concerns the shape and configuration of the holdfast horns. There are usually three holdfast horns present on *P. balaenoptera*; *P. filosa* may exhibit two or three horns, the number exhibited by this species is not consistent between specimens. The three holdfast horn state exhibits two long horns extending from the lateral margins, and one shorter horn projecting on the same level from the dorsal margin (*P. filosa*, Fig. 2; *P. balaenoptera*, Fig. 4). The holdfast horn length may be influenced by site of infestation and the type of host tissue infested (Hogans 1987): longer lateral horns are often (but not always) found in soft tissue of the host (*P. balaenoptera* in the blubber layer of cetaceans and *P. filosa* in the soft tissues of ocean sunfish), and shorter horns in dense, hard musculature (*P. filosa* in scombriform fishes, Hogans 1987). In smaller and younger specimens of *P. filosa*, the dorsal horn often appears as a small swelling or protuberance; it elongates as the parasite grows and ages (Thompson 1905). Recently, Hrvoje (2004) reported on a specimen of *P. balaenoptera* from a fin whale in the Adriatic Sea which exhibited four holdfasts: a ventral horn, as well as the two lateral and single dorsal holdfasts, further characterizing the variability in these structures. In small and intermediate size *Pennella* species, the structure and number of holdfasts is much more uniform.

The neck of *Pennella* is derived from the posterior thoracic portion of the larval parasite. In many species, it is elongate, thin and tubular (ex: *P. balaenoptera*, Fig. 5a), its length is partially dependent on the depth of penetration into the host flesh. There is also a relationship between the age of the parasite and the length of the neck; older (and larger) individuals have a neck which is sometimes proportionally longer (relative to total length of the parasite) than in shorter (younger) specimens. However, one large *P. balaenoptera* specimen examined in this study exhibited an uncharacteristically short and thick neck (the specimen was collected from the dense musculature at the base of the caudal fin of the whale host). In those species of *Pennella* <50 mm long, the neck can be short and thick (ex: *P. makaira*, Fig. 14a) or not separate from the trunk as a distinct structure (ex: *P. sagitta* (Fig. 18a). Leigh-Sharpe (1928) considered the ratio of neck length to trunk length (some, usually smaller species with a neck shorter than the trunk; larger species with a neck longer than the trunk) as a useful character to separate species. The feature is evident for a few small species, (ex: *P. diodontis* and *P. makaira*), but is unreliable for most others.

The trunk in all species except *P. sagitta* (Fig. 18a) is obvious and is a distinct structure (ex: *P. benzi* sp. nov., Fig. 6a). It begins anteriorly as a gradual swelling of the posterior portion of the neck and is an elongate cylinder with parallel sides, translucent brown and somewhat pseudo-segmented in young females; smooth, unornamented and black in the largest specimens of *P. balaenoptera*, *P. benzi* sp. nov., *P. filosa* and *P. instructa*. The trunk in all species tapers abruptly at its posterior end to form the abdomen which is one-third to one-half the total length of the trunk in all species. The abdomen is roughly triangular in cross section, the dorsal surface is rounded and the

ventral surface flattened or slightly concave. The dorsal surface of the abdomen often shows some vestige of annulation even in the oldest and largest *Pennella*.

The abdominal plumes arise from and completely cover the ventral flattened surface of the abdomen in most species, although in *P. makaira* the plumes arise randomly from all surfaces of the abdomen (Fig. 14a). These plumes are a unique feature within the Pennellidae, no other genera exhibits structures exactly like those characteristic of *Pennella* (Kabata 1979). Smaller species (ex: *P. sagitta*, *P. makaira*, and *P. diodontis*) exhibit single or double plumes only; even in the oldest and largest specimens the plumes are simple and restricted to one or two elements (*P. sagitta*: Fig. 18a). In the intermediate-sized and largest species of *Pennella*, each individual plume set arises from a single stem and then branches repeatedly to form a mass of digitiform plumules (ex: *P. balaenoptera*, Fig. 5f; *P. instructa*, Fig. 12f). The number and shape of plumules varies considerably between individuals of species. It has long been known (Thompson 1905; Wilson 1917; Kabata 1979; Hogans 1987) that the number and branches of the abdominal plumes which become complexly dendritic increase through metamorphosis with the age and size of the individual parasite. Quidor (1912) attempted to use the number and shape of plumes to differentiate between *Pennella* species found on whales; this method was incorrect.

The genital complex is found at the posterior end of the trunk on the ventral surface (ex: *P. benzi* sp. nov., Fig. 6f; *P. exocoeti*, Fig. 9i). It is a small and simple bi-lobed structure exhibiting the two oviduct orifices as raised circular openings. The two egg strings in gravid females originate from the oviduct orifices; they are long (often much longer than the entire parasite), filiform and the eggs are uniseriate.

Discriminating species of *Pennella*

Adult female *Pennella* exhibit several characteristics which may be used to differentiate species. For morphological characters, it is best to assess these only on mature specimens which have reached the end of metamorphosis and development on the definitive host. One potential end-point of *Pennella* development can be considered as the ovigerous condition in the adult female. A specimen exhibiting egg strings is assumed to be the mature form and should not show further significant change in morphological structures. Knowing the maturity and/ or age of a specimen assists in differentiating species: as an example, *P. makaira* which exhibits egg strings at 28 mm in length and is parasitic on blue marlin, is obviously a different species than *P. filosa* which is mature at 150-200 mm in length based on presence of egg strings, but also occurs on several species of marlins. Williams and Bunkley-Williams (1996) found mature specimens of *P. makaira* interspersed within groups of ovigerous *P. filosa* parasitic on individual blue marlin in the western Atlantic, proving that very different species, with unique size and structural characteristics, can infest an individual host or host species.

For all species, a combination of characters is required to consider specimens as belonging to a particular member of *Pennella*. These characters are as follows:

Host type. As concerns basic separation of species based on the type of host infested, most species of *Pennella* show high host specificity. Only the largest species, *P. balaenoptera*, which is found on several species of marine mammals and *P. filosa*, which infests a wide range of large marine fish species, can be considered as exhibiting low host specificity. All other potentially valid species are reported from only one or two species of hosts. The definitive host type can be used to further corroborate the distinctness of an individual species or exclude others from consideration (ex: *P. balaenoptera* is found only on marine mammals). Some *Pennella* species (ex: *P. sagitta*, *P. diodontis*, *P. makaira*) have been found repeatedly (to date) on only one host species; multiple findings on a single host species help establish the species morphologically, show structural variability between specimens and confirm high host specificity as relates to species distinctness.

Size. In his review Wilson (1917) recognized that there were two groups of species based on total length of the parasite: those <50mm and those >50mm. Hogans (1988c) in validating a new species (*P. makaira*), also used this general grouping to define species taxa. In this present review, there is defined a third intermediate size grouping. These species (*P. hawaiiensis* Kazachenko & Kurochkin, 1974, *P. remorae* and *P. robusta* Gnanamuthu, 1957) comprise a group measuring between 50 and 100mm. For *Pennella*, the parasite and host size are usually proportional. The smaller species of *Pennella* (<50mm) infest small size hosts, whereas the largest species are found on very large-size hosts (ex: *P. balaenoptera* on cetaceans, and *P. filosa* on billfishes, tunas and ocean sunfish). There are few exceptions to this grouping, the only notable case being *P. makaira*, a small species (28mm) found on blue marlin (*Makaira nigricans*), a very large scombriform billfish.

Cephalothoracic papillae. Once the female parasite has completed development and is mature, the shape, size and arrangement of the papillae appear to become fixed on each individual. There is uniformity in papillae shape and arrangement on the cephalothorax between specimens of a particular species. Based on the review of literature and examination of specimens, this feature is most evident in those species which belong to the intermediate and small size groups. The two largest species (*P. balaenoptera* and *P. filosa*) show less uniformity in the number and arrangement of papillae, but the papillae shape is consistent between specimens (roughly spherical, not tubiform, clavate or branched). In those species for which numerous specimens have been available for examination and have been repeatedly documented (ex: *P. exocoeti*, *P. instructa*, *P. makaira*, *P. sagitta*), uniformity in papillae structure and/or arrangement between individuals is clear. For species considered herein as *species inquirendae* which have been reported only once and are described from a single parasite, the variability in papillae structure and arrangement between individuals is unknown. It can only be assumed that the papillae exhibited by the mature parasite of these species will also be relatively consistent if additional material is found.

Holdfast horns. In small and intermediate size species of *Pennella*, the trend in morphological variability is reduced and there is more consistency in structure between specimens of a single species. Holdfast horn shape and number, which can be variable between specimens of the larger species, is much less so in smaller forms (Hogans 1988a). From the perspective of genus review, validity of the smaller species based on holdfasts is more easily asserted. *Pennella* embedded in large-bodied hosts, like *P. balaenoptera* from marine mammals and *P. filosa* from large pelagic scombriform fishes, are subject to significant muscular activities of tissues and great hydrodynamic forces; to deal with these the parasite must be large, robust and adaptable to a particular site of infestation, and much of this adaptation is seen in the structure of the holdfast horns. Small *Pennella* species, found on small hosts with softer tissue and subject to less external forces, may have a lesser requirement to adapt and are consequently more uniform in holdfast horn structure. Life span of the parasite could also contribute to variability within a species: small species may mature at an earlier age and do not exhibit the longevity of the very large species. Consequently, there is less time available to express significant morphological variability in holdfast horn structure between specimens.

First and second antenna. Various authors (Kabata 1979; Hogans 1987; Benz & Hogans 1993 and references therein) have discussed the usefulness of fine structure of the cephalothoracic appendages to further discriminate between species. Generally, the prevailing opinion has been that the appendage structure amongst *Pennella* species is fairly uniform, much like that of other genera in the Pennellidae and of limited usefulness as species discriminators (Kabata 1979; Hogans 1987; Benz & Hogans 1993). However, differences between the segmentation of first and second antenna between *Pennella* species <50 mm have been reported (Hogans 1988a), and this feature has been validated for nearly all of the species in the genus based on the present study. If these appendages can be found on the mature parasite and the number of segments is consistent between specimens of a suspected single species, then this feature may be used as further corroborating evidence of distinctness.

Abdominal plumes. The plumes are characteristic of a particular group (size category) of species based on complexity of the branches. In the plumes of small species, the mature parasite does not exhibit complex branching and the plumes are limited to single or double elements. In the intermediate and large size *Pennella* the plumes become complex and dendritic. For these parasites, the abdominal plume configuration can only be used to differentiate species in the mature parasite; during development/ metamorphosis the plumes are continually changing, becoming more complex as the parasite ages (Kabata 1979; Hogans 1987).

Systematics

Order Siphonostomatoida Thorell, 1859

Family Pennellidae Burmeister, 1835

Review of *Pennella* Oken, 1816

In this review, three basic categories of species validity are proposed: 1) Valid and substantiated. These established nine species have adequate original descriptions or redescriptions based on several specimens. They have been

found and described on more than one occasion, from the same host species or types of hosts. The validity of all but the new species, *P. benzi* **sp. nov.**, has been repeatedly suggested in the literature. 2) *Species inquirendae*. All six species in this category have acceptable (but often brief) original descriptions, with figures that portray the parasite. All show unique features which serve to distinguish them from other members of *Pennella*. However, the original reports are based on a single (adult) specimen and the parasite has not been reported or described since the initial record. Type (or other) specimens are not available or do not exist. 3) Unsubstantiated and invalid. This category contains 29 species for which there are very poor or no original descriptions (*nomen nudum*) and those which have been previously designated as synonyms of established species.

For each of the 15 species designated as valid or *species inquirendae*, the differentiating characters are presented. For size (length) listing for each species, the range is given (unless based on a single specimen) based on previous reports and recent examinations and is from the mature, ovigerous female (anterior end of cephalothorax to posterior end of abdomen). Information on the hosts and localities (where known) are listed. An assessment of the value of the original descriptions and figures, as well as the rationale for considering the species as different from its congeners is discussed.

***Pennella antarctica* (Quidor, 1912)**

Not valid. Adult female originally reported from the Sei whale *Balaenoptera borealis* off Chile. Also on the sei whale, Japan (redescribed by Wilson 1917). Found on the same hosts, in the same localities and falls easily within the morphological variability range of *P. balaenoptera*. Synonym of *P. balaenoptera* (Hogans 1987); accepted as *P. balaenoptera* (Walter & Boxshall 2015).

***Pennella anthonyi* (Quidor, 1912)**

Not valid. Described from fin whales, *Balaenoptera physalus*, Chile. Quidor (1912) used abdominal plume configuration to differentiate this species; this is an unreliable character. A synonym of *P. balaenoptera* (Hogans 1987); accepted as *P. balaenoptera* (Walter & Boxshall 2015).

***Pennella balaenoptera* Koren & Danielssen, 1877**

(Figs. 4, 5)

Synonyms. *P. antarctica* (Quidor, 1912), *P. anthonyi* (Quidor, 1912), *P. cetti* (Quidor, 1912), *P. charchoti* (Quidor, 1912), *P. crassicornis* Steenstrup & Lutken, 1861

Type host and locality. *Balaenoptera acutorostrata*, North Sea.

Morphology. Size: 175–320 mm. Papillae: full or partial coverage, generally spherical, variable in size and shape, not found in organized groups. Holdfasts: usually three, laterals can be very long; dorsal horn shorter. First antenna with three segments, second with two segments. Plumes: dendritic, complex branching.

Remarks. A valid species. *Pennella balaenoptera* is the largest of all copepods and is the only *Pennella* found so far on marine mammals (Hogans 1987) and as such is unique amongst the mesoparasitic Copepoda in parasitizing warm-blooded hosts. *Pennella balaenoptera* is a pan-global parasite of whales (*Balaenoptera acutorostrata*, *B. physalus* and *B. borealis*; Hogans 1987 and references therein) and dolphins and porpoises (Rissos, *Grampus griseus* and bottlenose, *Turisops truncatus*; Vecchione & Aznar 2014; striped dolphin, *Stenella coeruleoalba*, Aznar *et al.*, 2005; harbor porpoise, *Phocaena phocaena*, Danyer *et al.* 2014), but it has also been found on pinnipeds (northern elephant seal, *Mirounga angustirostris*; Dailey *et al.* 2002). Both the original description by Koren and Danielssen (1877) and a redescription by Turner (1905) were very well done; more recent reports on the morphology of *P. balaenoptera*, based on the entire parasite, including some details of the fine structure of the cephalothoracic appendages, have been completed (Hogans 1987; Abaunza *et al.* 2002; Hrvoje 2004).

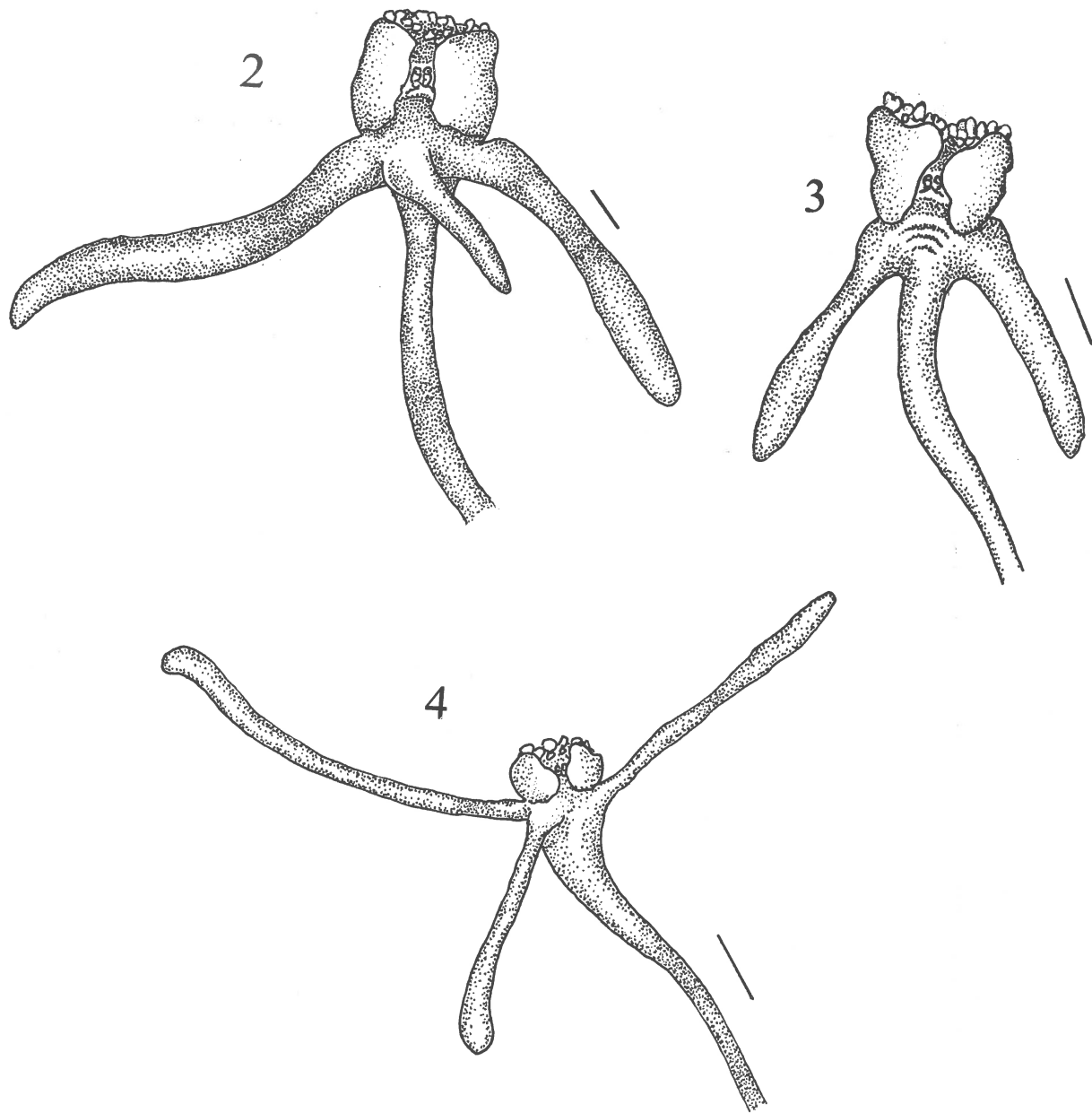


FIGURE 2. Anterior (embedded) end of female *Pennella filosa* from *Mola mola*, dorsal. Scale bar = 1.0 mm.
FIGURE 3. Anterior (embedded) end of female *Pennella exocoeti* from *Cheilopogon melanurus*, dorsal. Scale bar = 0.5 mm.
FIGURE 4. Anterior (embedded) end of female *Pennella balaenoptera* from *Balaenoptera acutorostrata*, ventral. Scale bar = 1.0 mm.

In his review of *Pennella* on cetaceans (Hogans 1987) considered all previously described species from marine mammals to be synonyms of *P. balaenoptera*. Although another species, *P. crassicornis*, had been found on whales earlier (Steenstrup & Lutken 1861), and based on taxonomic priority was technically the oldest *Pennella* from mammals, *P. crassicornis* had also been reported from fish hosts in the same paper. Based on the host designations, *P. balaenoptera* was the oldest species to be found only on mammals and had priority over *P. crassicornis*.

Hogans (1987) reported on the morphological variability of *P. balaenoptera* reported from marine mammals. Based on examinations of the material reported on herein, the plasticity in *P. balaenoptera* has been further substantiated and is most evident in holdfast horn and neck structure.

Although *P. balaenoptera* has been previously reported from harbor porpoises (Aegean Sea; Danyer et al. 2014), it is here reported from this host in the Atlantic Ocean for the first time. To find *P. balaenoptera* on porpoises in a different locality is not unexpected considering the very wide known distribution of this parasite and

the fact that minke whales and harbor porpoises live in close association and are common cetaceans in the lower Bay of Fundy (where the parasites were collected). There were no external morphological differences between the specimens collected from the minke whale and that found on the harbor porpoise reported on in this study. There was only one specimen from the porpoise to examine, however, it was identical in all aspects with the whale parasites except that it was 25mm shorter (178) than the average length (203) of the two specimens from the whale.

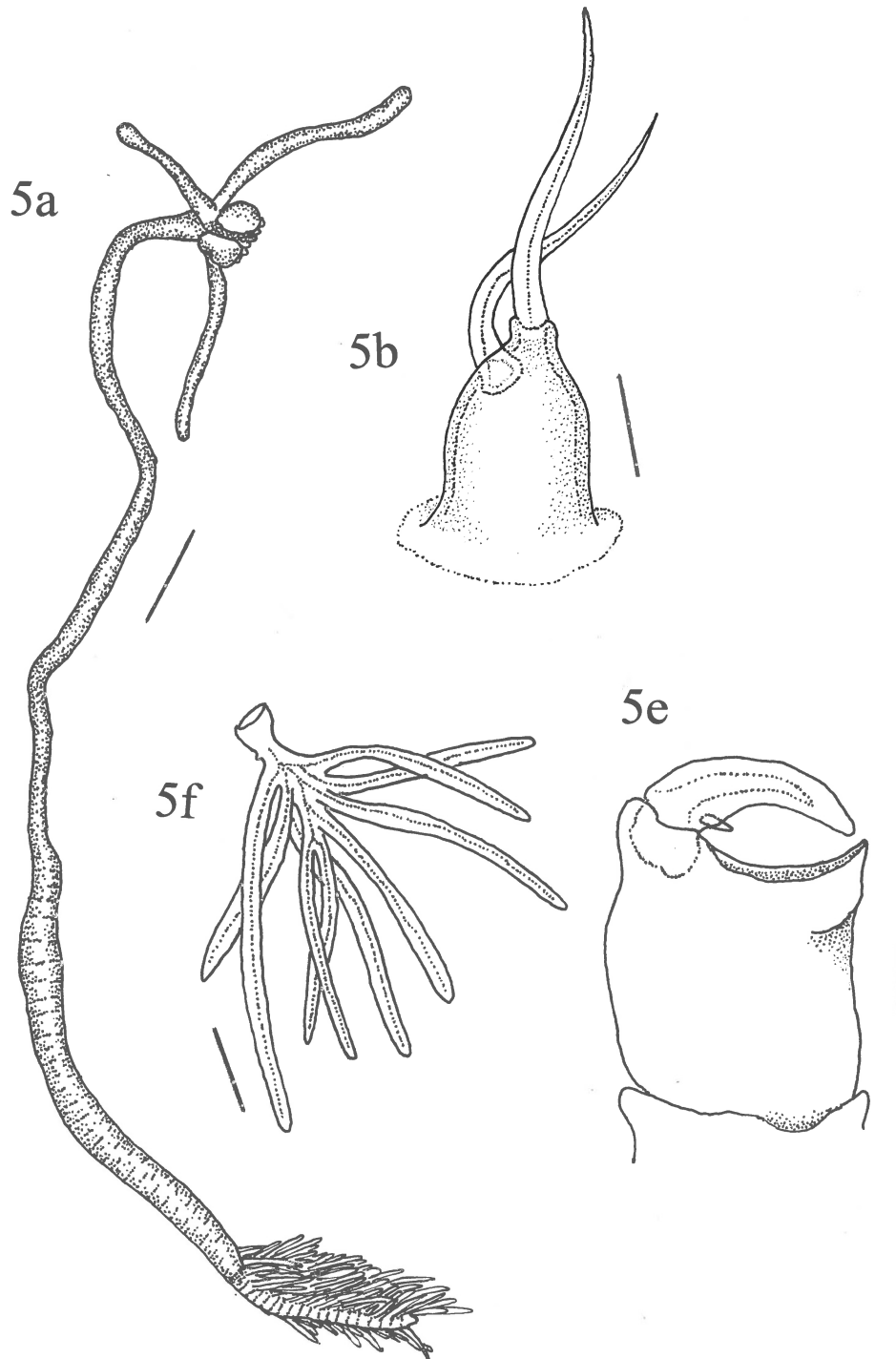


FIGURE 5. *Pennella balaenoptera* a. Habitus, dorsal; b. First maxilla, ventral. e. Terminal segment, second antenna, dorsal. f. Abdominal plumes from specimen shown in 5a. Scale bars: a= 3.0 mm; b= 0.04 mm; e = 0.02 mm; f = 2.0 mm.

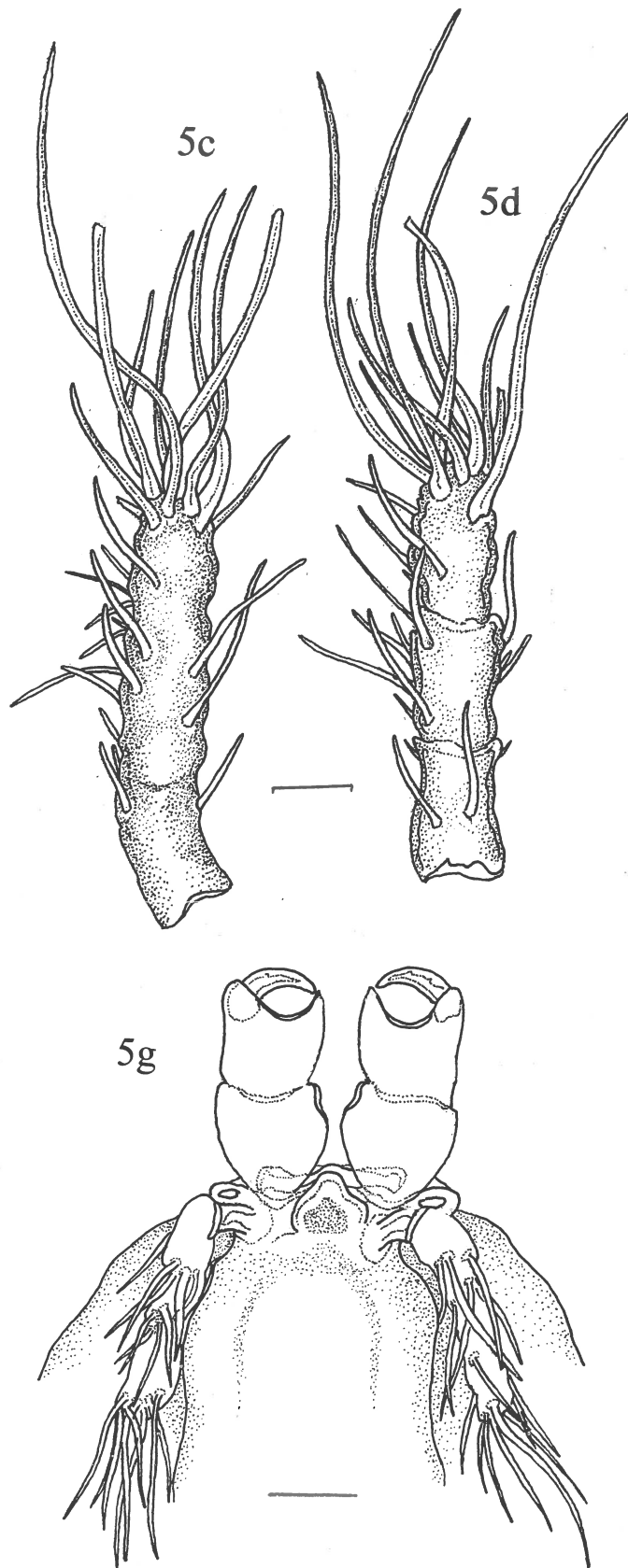


FIGURE 5c. *Pennella balaenoptera*, first antenna, largest specimen, dorsal. Scale bar = 0.02 mm.

FIGURE 5d. *Pennella balaenoptera*, first antenna, smallest specimen, dorsal. Scale bar = 0.02 mm.

FIGURE 5g. *Pennella balaenoptera*, antennary region, dorsal. Scale bar = 0.02 mm.

***Pennella benzi* sp. nov.**

(Fig. 6)

Host. Escolar (*Lepidicybium flavobrunneum* Smith, 1843)

Type Locality. Holotype and paratype 1: Host caught in the northwest Atlantic (no specific locality)

Paratype 2: Host caught off coastal North Carolina, northwest Atlantic

Site of infestation. Embedded in deep musculature, along base of dorsal fin

Etymology. The species is named for Dr. George W. Benz, in honor of his contributions to the study of parasitic Copepoda

Type material. Holotype: United States National Museum (USNM) 180162; Paratype 1: USNM 180163; Paratype 2: Fisheries and Oceans Canada, Atlantic Reference Center (ARC), ARC 29529

Description. Oviparous female (Fig. 6a, b): cephalothorax bulbous, spherical, apical end flattened, armed with numerous roughly spherical cephalothoracic papillae of various sizes (Fig. 6d). Configuration of papillae unorganized and different between all three specimens. Three holdfast horns radiating from below cephalothorax: two lateral, and one shorter dorsal horn bifurcate at tip (Fig. 6c, i). Thoracic neck tubular, elongate, posterior end enlarged to form anterior end of trunk. Trunk one-half length of entire parasite, cylindrical, with parallel sides. Trunk tapering abruptly at its posterior end to form the abdomen. Abdomen about one-half length of trunk, annulated, with rounded dorsal surface and flattened ventral surface. Abdominal plumes arising from ventral surface of abdomen in two rows; individual plume (24–28) sets arise from a single stem and then branch repeatedly to form a mass of digitiform plumules (Fig. 6h). Number of plumules per set variable. Genital complex (Fig. 6g) at posterior end of abdomen, exhibiting two small oviduct orifices on ventral surface. Egg strings paired, filiform, about 1.5x length of each parasite, eggs uniseriate.

First antenna (Fig. 6e), observed clearly on one specimen only (paratype 2), two-segmented. Apical armature of 9 setae of various lengths. Setae of middle portion shorter and more numerous. Second antenna (Fig. 6f), distinctly three-segmented; terminal segment with prehensile large re-curved hook which closes on a blunt, distal spine; small spine at base of hook. Buccal complex (mouth), mandibles, first and second maxillae and maxillipeds not observed on any specimen. Swimming legs (4) reduced to sympods only, rami lost or atrophied and not observable. Total length (anterior end of cephalothorax to posterior end of abdomen) of three specimens: 131, 157, 162.

Remarks. This new species is erected based on a newly collected specimen and on two others previously assigned to *Pennella filosa* also collected from the escolar (oilfish) in the northwest Atlantic (Benz & Hogans 1993). Benz & Hogans (1993) considered their two specimens to be phenotypic variations of *P. filosa*, but finding a new and third specimen on the same species of host shows *P. benzi* sp. nov. to be a different species than *P. filosa* which it closely resembles. *Pennella benzi* sp. nov. has several features which are unique and distinguish it from *P. filosa*: *P. benzi* sp. nov. is a somewhat smaller parasite (150 mm) than *P. filosa* (180mm); a unique host (escolar) which has not previously been recorded as parasitized by any other *Pennella* sp.; dorsal horn configuration: all three known specimens of *P. benzi* sp. nov. have a bifurcate dorsal horn, a feature never previously reported within the genus. *Pennella benzi* sp. nov. possesses a three-segmented second antenna; *P. filosa* exhibits two segments on this appendage. It can be easily distinguished from the other large *Pennella* found on fish, *P. instructa*, based on the cephalothoracic papillae (not arranged in distinct groups) and possessing a dorsal horn (not found in *P. instructa*).

***Pennella biloba* Kirtisinghe, 1932**

Not valid. Described from the Pacific sailfish, *Histiophorous brevirostris* (= *Istiophorus platycephalus*), Indian Ocean. Kirtisinghe's specimen resembles *P. filosa* in overall shape and size, which has been found previously on Pacific sailfish (Causey 1960). The rationale to differentiate *P. biloba* from other *Pennella* found on large billfish is brief and unconvincing. Not reported since the original record. Status of *species inquirendae* (Hogans 1988a). Synonym of *P. filosa*.

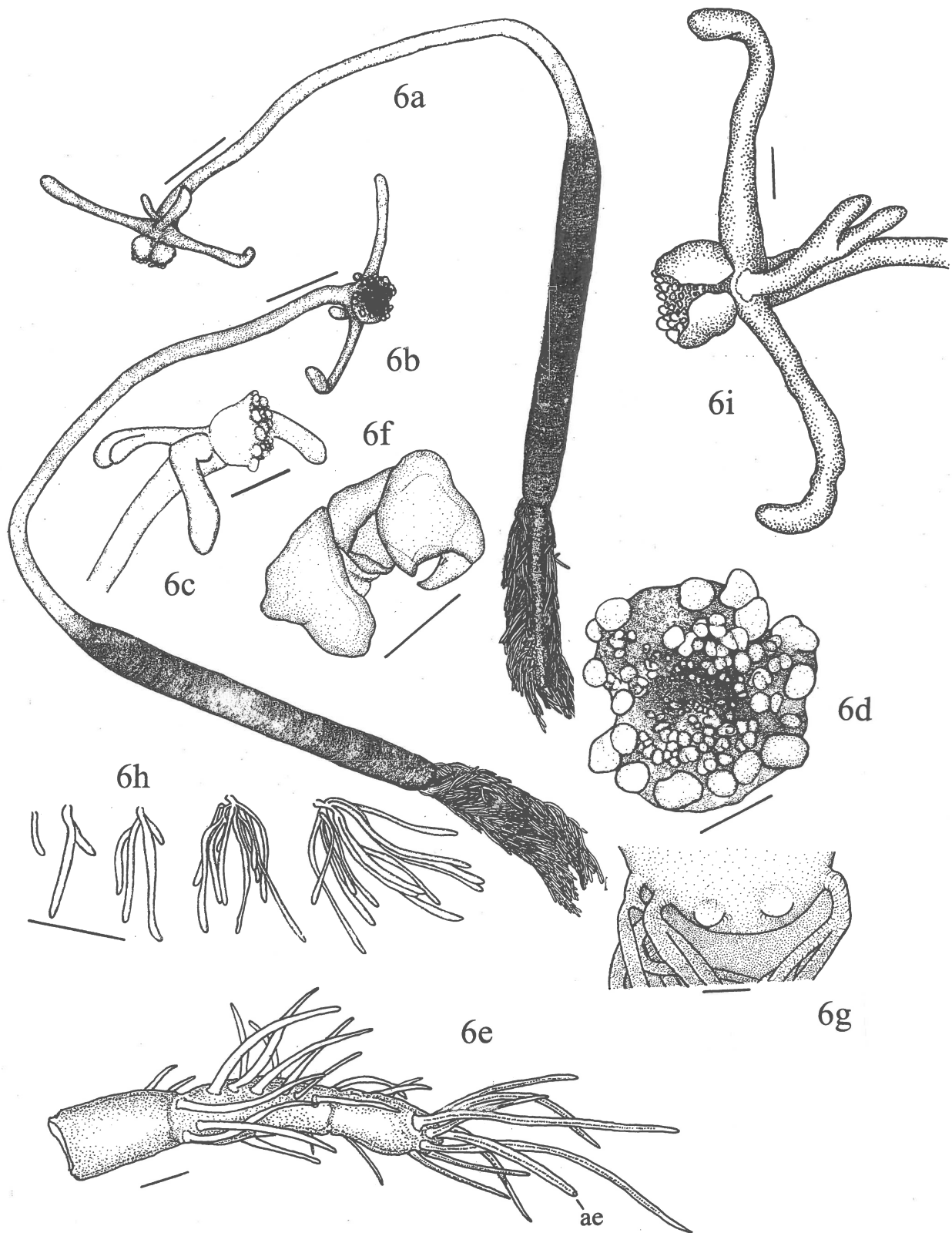


FIGURE 6. *Pennella benzi* sp. nov. a. Habitus, holotype, dorsal (USNM 180162). b. Habitus, holotype, ventral. c. Anterior end showing holdfast horns, lateral. d. Apical end showing cephalothoracic papillae, ventral. e. First antenna, paratype 2 (from ARC 29529), dorsal. (ae = aesthetae), f. Second antenna, dorsal. g. Genital complex, ventral. h. Abdominal plumes of mature female. i. Anterior end of female, paratype 2 (from ARC 29529), dorsal. (a, b, c, d, f, g, h reproduced from Benz and Hogans, 1993). (scale bars = a, b—10.0; c—0.5; d—0.2; e—0.02; f—0.01; g—1.0; h—5.0; i—2.0)

***Pennella blainvillei* (Lesueur, 1824)**

Not valid. Described from flying fish (no specific host species name given) in the Atlantic; probably *Exocoetus* sp. (Yamaguti 1963); incomplete original description; (possibly *P. exocoeti* Leigh-Sharpe 1928); synonym of *P. exocoeti* (Wilson 1917; Hogans 1988a). Accepted as *P. exocoeti* (Walter & Boxshall 2015).

***Pennella bocconii* Lamartiniere, 1798**

Not valid. Documented from a single figure only (Lamartiniere, 1798); no description, no host listed. Probable synonym of *P. sagitta* (Wilson 1917; Walter & Boxshall 2015).

***Pennella brachiata* (Blainville, 1822)**

Not valid. Blainville (1822) established a new genus *Lenaeopenna* (synonym of *Pennella*; Wilson, 1917) based on a single specimen (probably *P. sagitta*; Wilson 1917), which was not actually seen or examined by the author. Accepted as *P. sagitta* (Walter & Boxshall 2015).

***Pennella cervicornis* Heegaard, 1943**

Not valid. Reported from *Diodon* sp. In the Bay of Bengal. The specimens described by Heegaard (1943) are similar to *P. diodontis* from the same host species in size, cephalothorax, neck, trunk and abdominal plume structure. Synonym of *P. diodontis* (Hogans 1988a). Accepted as *P. diodontis* (Walter & Boxshall 2015);

***Pennella cetti* (Quidor, 1912)**

Not valid. Original description (incomplete) from *Balaenoptera* sp. Antarctic. Quidor (1912) used abdominal plume configuration to differentiate this species; an unreliable character. Synonym of *P. balaenoptera* (Hogans 1987); accepted as *P. balaenoptera* (Walter & Boxshall 2015).

***Pennella charchoti* (Quidor, 1912)**

Not valid. Original description (incomplete) from *Balaenoptera* sp. Antarctic. Quidor (1912) used abdominal plume configuration to differentiate this species; an unreliable character. Synonym of *P. balaenoptera* (Hogans 1987); accepted as *P. balaenoptera* (Walter & Boxshall 2015).

***Pennella costai* Richiardi, 1880**

Not valid; No original description, briefly mentioned by Richiardi (1880). Synonym of *P. filosa* (Brian (1906); *nomen nudum* (Walter & Boxshall 2015).

***Pennella crassicornis* Steenstrup & Lutken, 1861**

Not valid. Original report from Bottlenose whales (*Hyperodon ampullatus* and *Xiphias cavirostris*) and pelagic fishes (*Xiphias gladius*, *Mola mola* and *Naucrates ductor*) in the Atlantic and Mediterranean. Original figures and description not detailed enough to separate the species from *P. filosa* or *P. balaenoptera*, both of which it closely

resembles; synonym of *P. filosa* on fishes, of *P. balaenoptera* on mammals (Hogans 1987); accepted as *P. filosa* (Walter & Boxshall 2015).

***Pennella cylindrica* (Brady, 1883)**

Not valid. The original description (Brady, 1883), (brief with insufficient detail) of *Hessella* (syn. of *Pennella* (Wilson 1917) *cylindrica*) was based on a developmental stage of a supposed *Pennella*, host not recorded. There have been no records of *P. cylindrica* since the original report. Considered herein as *nomen nudum*.

***Pennella diodontis* Oken, 1816**

(Fig. 7)

Synonyms. *Pennella cervicornis* Heegaard, 1943, *P. plumosa* (Dekay, 1844)

Type host and locality. *Diodon sexmaculatus*, Philippines.

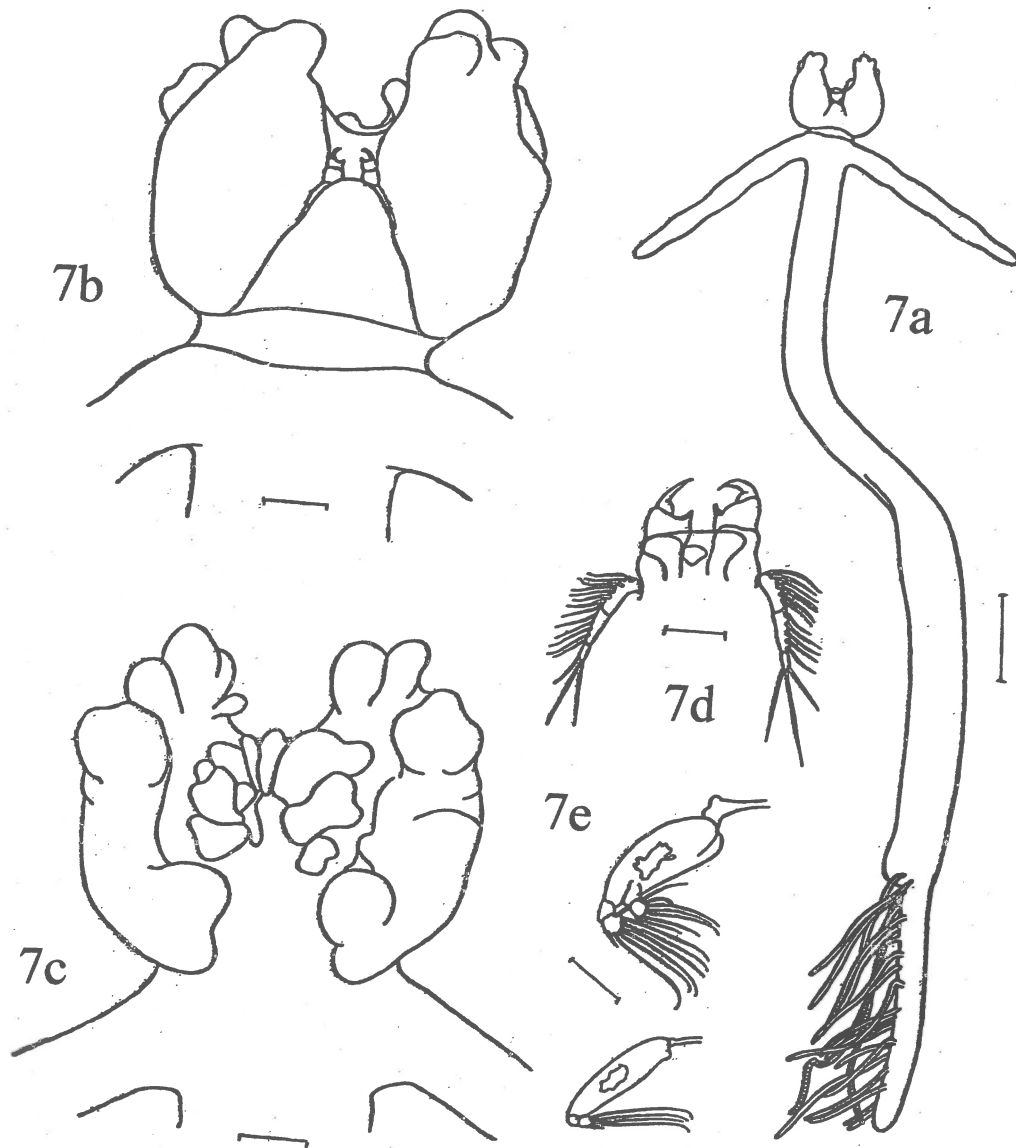


FIGURE 7. *Pennella diodontis*, a. entire parasite; b. cephalothorax, dorsal; c. same, ventral; d. first and second antenna, dorsal; e. second and third swimming legs (redrawn from Kirtisinghe, 1935). Scale bars: a = 2.0 mm; b, c = 0.2 mm; d, e = 0.02 mm.

Morphology. Size: 24–28 mm. Papillae: partial coverage, clavate and club-like, consistent in size and shape, not found in organized groups. Holdfasts: two only, short. First antenna with three segments, second with two segments. Plumes: simple, single.

Remarks. A valid species. Original description from porcupine fish, *Diodon sexmaculatus* (= *D. holacanthus*) (Oken 1816); redescription from the same host species, Ceylon (Kirtisinghe 1932; Fig. 7). Considered incorrectly as infesting two host genera: *Lophius* and *Diodon* (Wilson 1917). The history of *P. diodontis* was often confused with that of *P. sagitta* (Wilson 1917), however, *P. diodontis* reported from *Lophius* was an error of Blainville (1822) based on a poor description and incorrect host identification; *P. diodontis* is in fact a parasite of porcupine fish (Diodontidae: *Diodon*) and *P. sagitta* is found so far only on frogfish (Antennariidae: *Histrio*, possibly *Antennarius*). Lasarus and Sreenivasan (1977) reported *P. diodontis* from the moorish idol (*Zanclus canascens* (= *Z. cornuta*) in the Indian Ocean. The single habitus figure and brief description are not sufficient to confidently place their specimens (eight) in *P. diodontis*. However, the size of the parasite (26mm) and the cephalothoracic papillae (few small at center, and larger branched papillae around the cephalothorax periphery) are reminiscent of the species. As a parasite of *Diodon*, *P. diodontis* is a small species with uniformity in most structures between specimens (Hogans 1988a), however, its cephalothoracic papillae may vary slightly in arrangement and number depending on the individual parasite (Hogans 1988a; Heegard 1943).

***Pennella elegans* Gnanamuthu, 1957**

(Fig. 8)

Synonyms. None

Type host and locality. *Cypselurus* sp., Indian Ocean

Morphology. Size: 35 mm. Papillae: partial coverage, clavate, a few spherical, unorganized arrangement. Holdfasts: two only, short. First antenna (no information), second with three segments. Plumes: simple, single or double.

Remarks. *Species inquirendae*. Hogans (1988a) considered *P. elegans* as *species inquirendae* based on a lack of type material. The original description, though brief, portrays the species as exhibiting a unique cephalothoracic shape and papillae configuration (Fig. 8b). *Pennella elegans* is a small species originally described from a single female without egg strings. The only other record of *P. elegans* (from the same host and locality as the original record) is by Kannapuandi (1976) who described the cuticular adaptations in various structures of the parasite, but did not further elaborate on its morphology.

***Pennella elongata* (Lubbock, 1860)**

Not valid. Briefly documented (but not described) from a planktonic (larval) stage of *Pennella* (?). Incomplete account. Considered herein as *nomen nudum*.

***Pennella exocoeti* (Holten, 1802)**

(Figs. 3, 9)

Synonyms. *Pennella blainvillei* (Lesueur, 1824), *P. holteni* (Desmarest, 1825), *P. liouvillei* Quidor, 1912

Type host and locality. *Exocoetus* sp., Atlantic Ocean.

Morphology. Size: 34–42 mm. Papillae: partial coverage, tubiform and branched, arranged around perimeter of cephalothorax, not found in organized groups. Holdfasts: two only, short. First antenna with four segments, second with two segments. Plumes: simple, single or double.

Remarks. A valid species. Parasitic on flying fishes (Exocoetidae: *Exocoetus*, *Cheilopogon*) in the Atlantic Ocean (Hogans 1988a and references therein). A small species exhibiting uniform morphology between specimens. Redescribed from USNM material by Hogans (1988a).

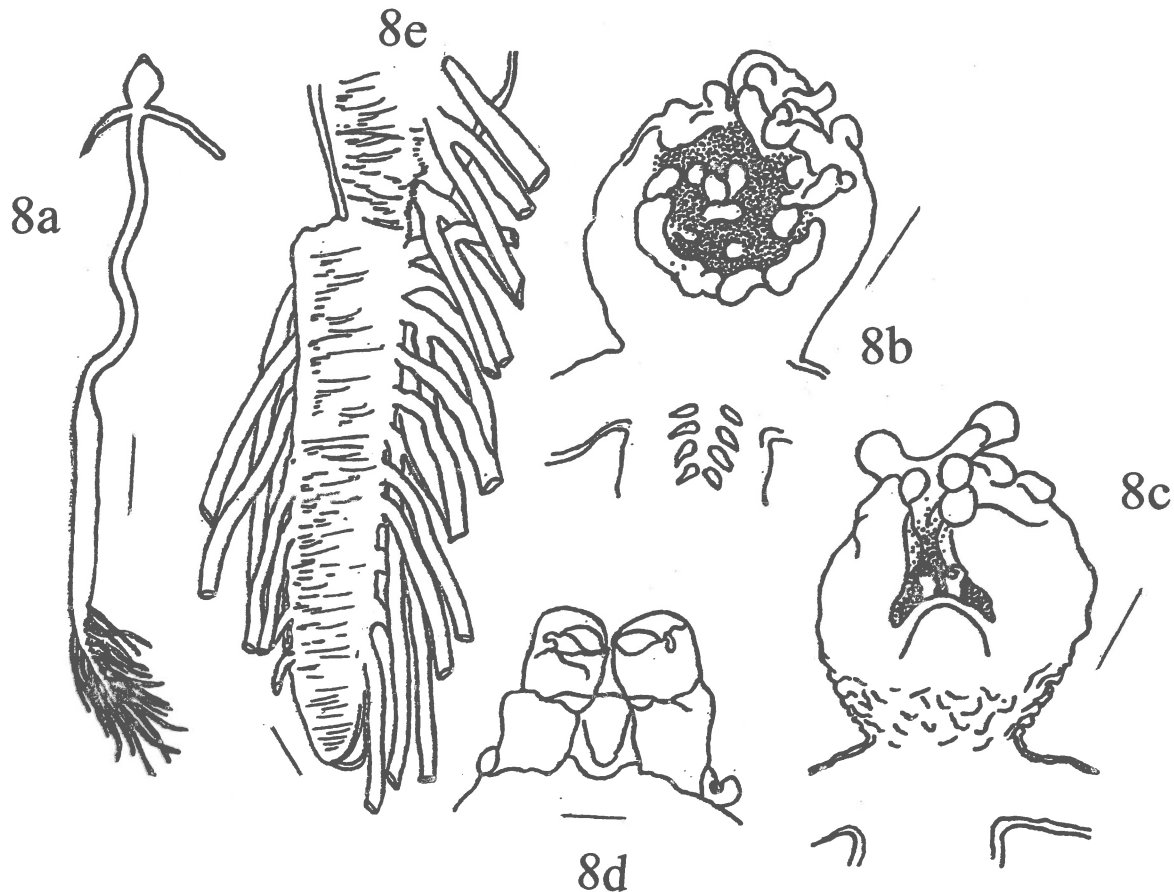


FIGURE 8. *Pennella elegans*, a. entire parasite; b. cephalothorax, ventral; c. cephalothorax, dorsal; d. abdomen and plumes; e. second antennae, dorsal (from Gnanamuthu, 1957). Scale bars: a= 5.0 mm; b, c = 2.0 mm; d = 0.02 mm; e = 0.1 mm.

***Pennella filosa* (Linnaeus, 1758)**

(Figs. 2, 10)

Synonyms. *Pennella biloba* Kirtisinghe, 1932, *P. crassicornis* Steenstrup & Lutken, 1861, *P. germonia* Leigh-Sharpe, 1931, *P. germonia fagei* Poisson & Razet, 1954, *P. histiophori* Thomson, 1889, *P. orthogorisci* Wright, 1877, *P. pustulosa* Baird, 1850, *P. rubra* Brian, 1906, *P. tridentate* Listowsky, 1893, *P. varians* Steenstrup & Lutken, 1861

Type host and locality. *Xiphias gladius*, Atlantic Ocean.

Morphology. Size: 165–205 mm. Papillae: full or partial coverage, generally spherical, variable in size and shape, not found in organized groups. Holdfasts: two or three, laterals can be short or long; dorsal horn, when present, shorter. First antenna with three segments, second with two segments. Plumes: dendritic, complex branching.

Remarks. A valid species. The most frequently documented species of *Pennella*, *P. filosa* is also the most recognized species due to its common occurrence on commercially-important fish hosts. It is a large parasite of low host specificity and variable external morphology (Kabata 1979; Hogans 1987). Reported from many marine fish, but most frequently on large pelagic scombriform fish (swordfish (*Xiphias*), marlins (*Makaira*, *Tetrapterus*), sailfish (*Istiophorus*) and tunas (*Thunnus*)), also on ocean sunfish (*Mola*), and dolphinfish (*Coryphaena*), Atlantic, Mediterranean and Pacific distribution (Wilson 1917; Causey 1960; Kabata 1979, Hogans 1987, 1988a; Benz & Hogans 1993 and references therein; Williams & Bunkley-Williams 1996; Hernández-Trujillo *et al.* 2014). *Pennella filosa* can be distinguished from the other large *Pennella* which occurs on some of the same types of hosts, *P. instructa*, by its slightly larger size, (180 mm for *P. filosa*; 140 mm for *P. instructa*), the variable holdfast

horn shape and number (often three in *P. filosa* all directed laterally, two only in *P. instructa* always directed posteriorly) and the configuration and size of the cephalothoracic papillae (random, unorganized and variable in size in *P. filosa*; uniform size and in distinct bands/ groups in *P. instructa*).

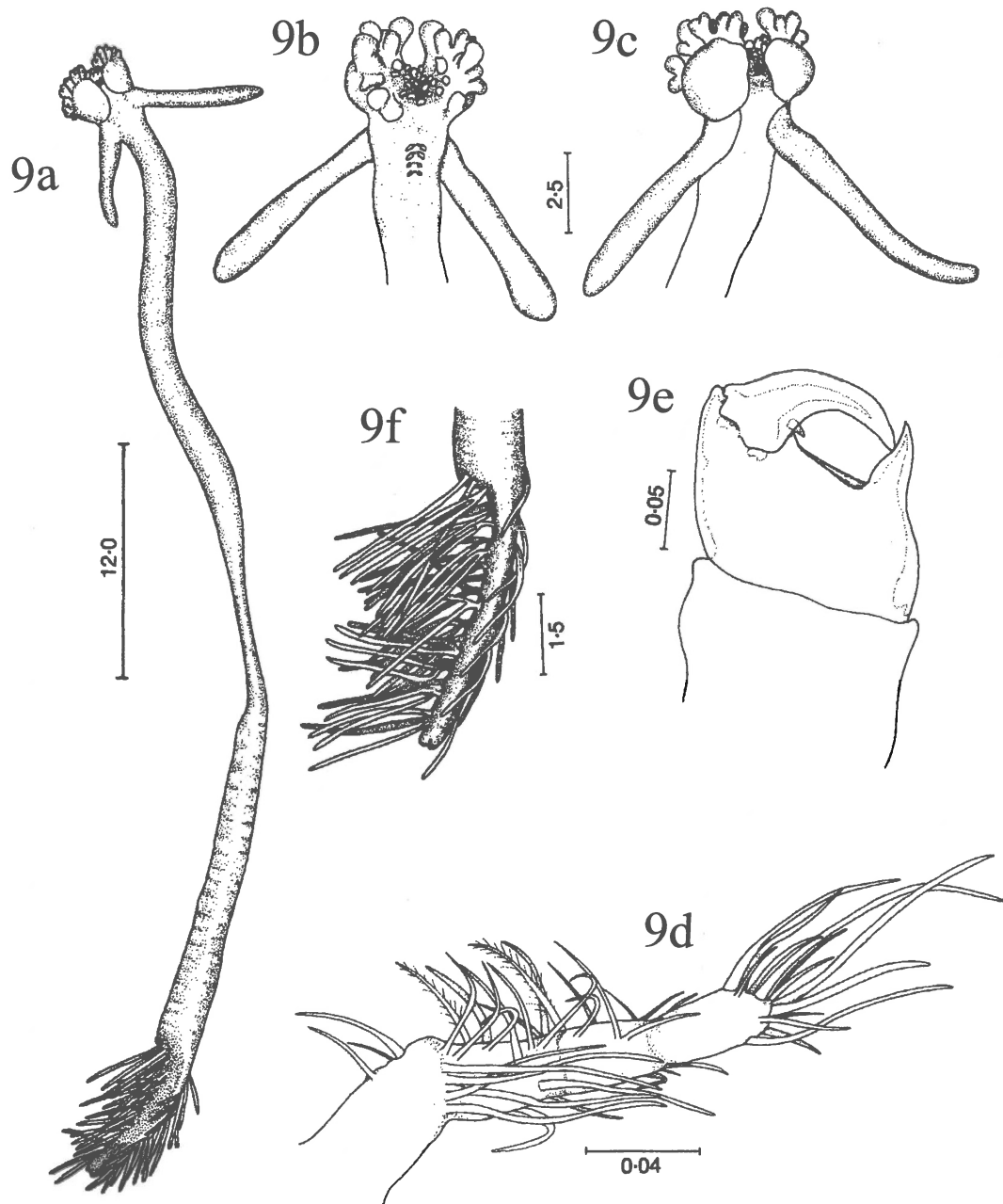


FIGURE 9. *Pennella exocoeti*, a. habitus, dorsal; b. apical end, ventral; c. apical end, dorsal; d. first antenna, dorsal; e. terminal segment, second antenna, dorsal; f. abdomen and abdominal plumes of mature female; g. first antenna, dorsal; h. rami of first swimming leg, ventral; i. genital complex region, ventral. (a–f from USNM 112252; g, h, i from new material). Scale bars: g = 0.02 mm; h = 0.04 mm; i = 0.5 mm. (a–f from Hogans 1988a).

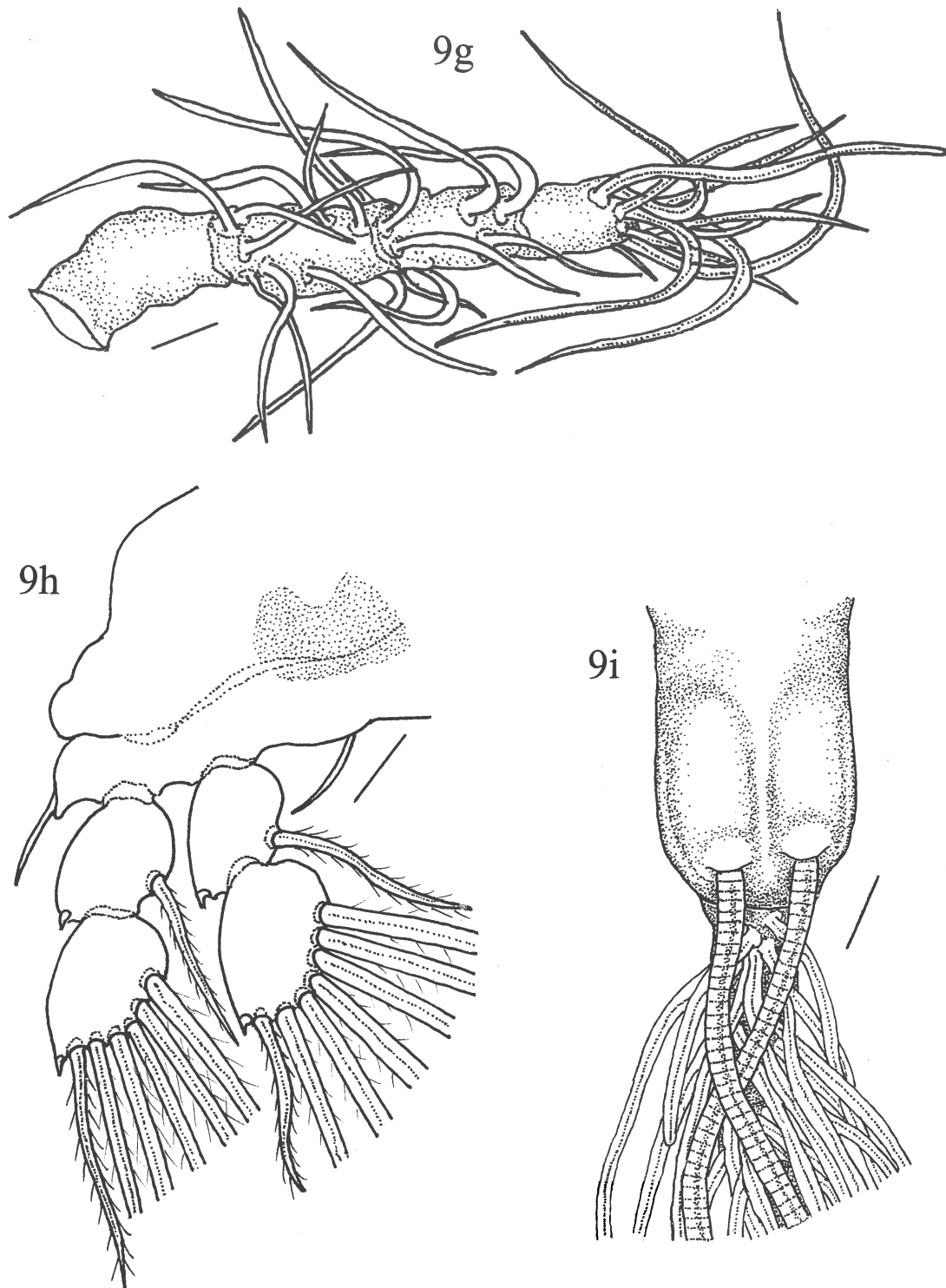


FIGURE 9. continued

***Pennella germonia* Leigh-Sharpe, 1931**

Not valid. Described from tuna, *Germo alalonga* (= *Thunnus alalonga*), Mediterranean. Falls within the length and variability range of *P. filosa* (also found frequently on species of large tunas). There is nothing within the original description, figures and remarks which distinguishes *P. germonia* from *P. filosa*. Synonym of *P. filosa* (Kabata 1979; Hogans 1988a); accepted as *P. filosa* (Walter & Boxshall 2015).

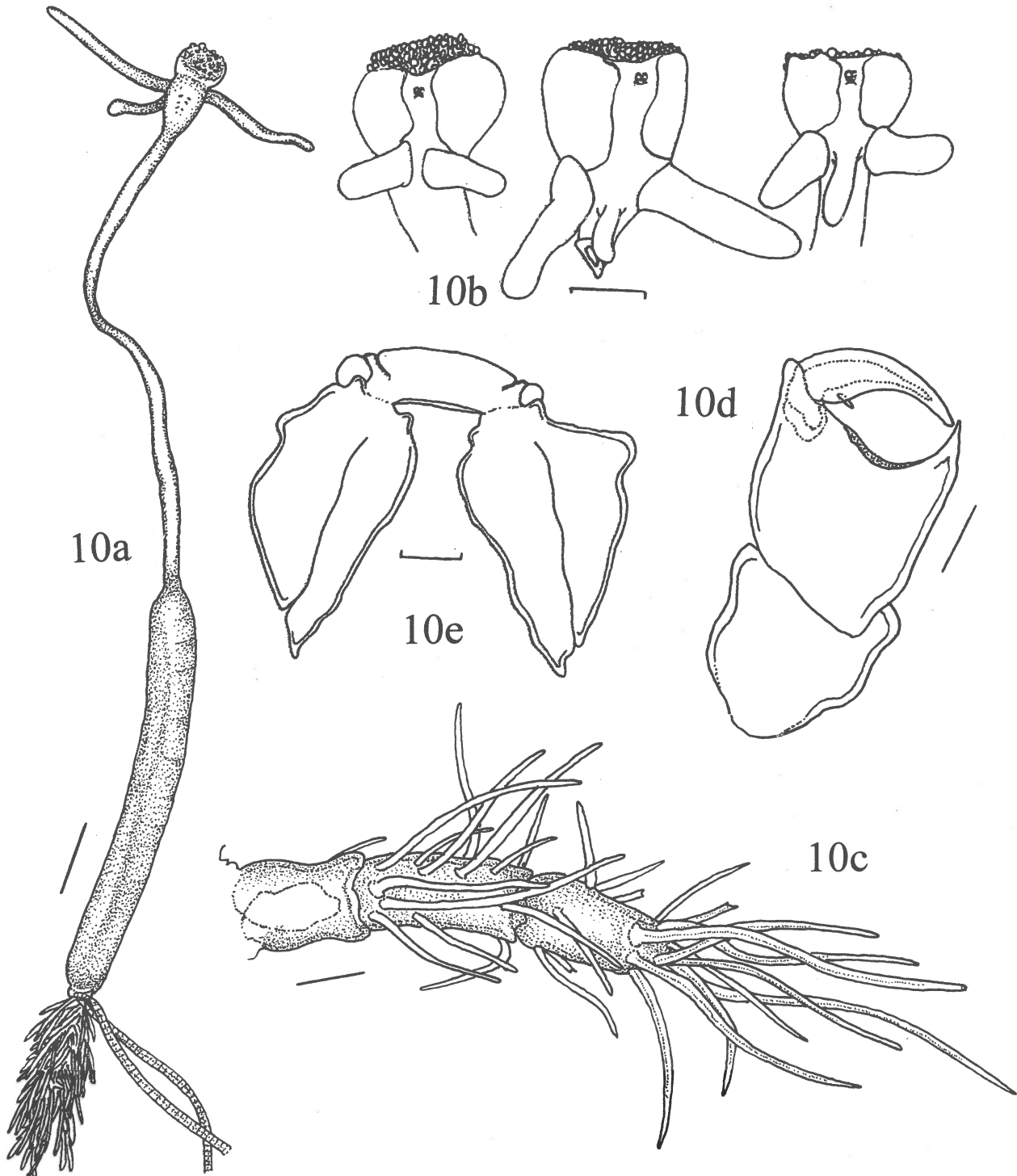


FIGURE 10. *Pennella filosa*, a. habitus, ventral; b. anterior ends of 3 specimens from *Mola mola* (USNM 47821, 54120), all dorsal; c. first antenna, dorsal; d. second antenna, dorsal; e. sympods of first swimming legs. (b, e from Hogans 1987). Scale bars: a= 5.0 mm; b = 2.0 mm; c- e = 0.02 mm.

***Pennella germonia fagei* Poisson & Razet, 1954**

Not valid. Described from *Thunnus alalunga*; no locality, but probably Mediterranean. An apparent sub-species of *P. germonia* (determined to be synonymous with *P. filosa* (Hogans 1988a)). There is nothing within the original description which differentiates this “sub-species” from *P. filosa*. A variable form and synonym of *P. filosa* (Hogans 1988a).

Pennella gracilis (Costa, 1847)

Not valid; reported, but not described or figured. *Nomen nudum* (Walter & Boxshall 2015).

Pennella hawaiiensis Kazachenko & Kurochkin, 1974

(Fig. 11)

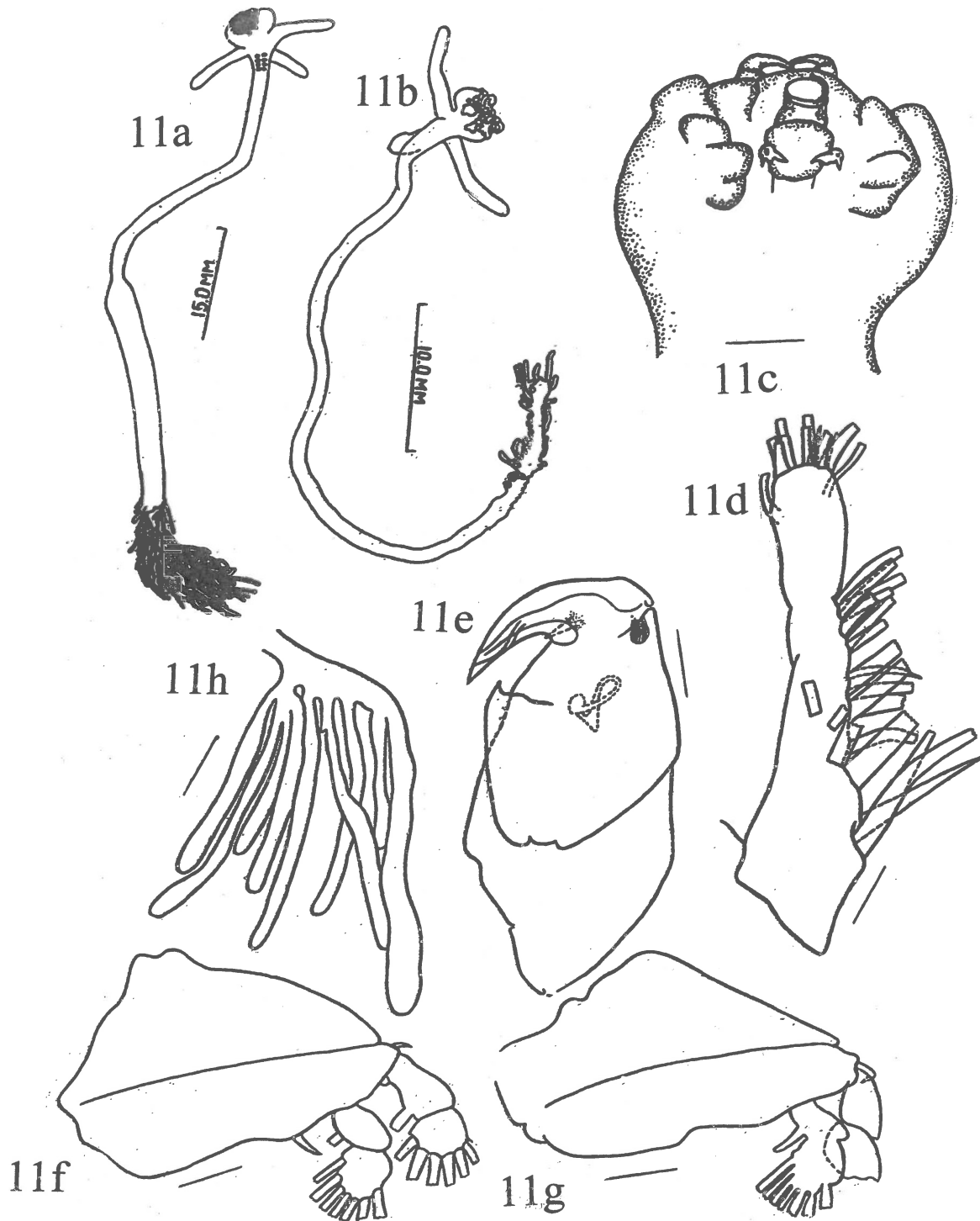


FIGURE 11. *Pennella hawaiiensis*, a. habitus, old female; b. habitus, younger female; c. cephalothorax of young specimen, ventral; d. first antenna; e. second antenna; f. first swimming leg; g. second swimming leg; h. detail of abdominal plume (from Kazachenko & Kurochkin 1974). Scale bars: c = 0.1; d-f = 0.02 mm; g = 0.2 mm.

Synonyms. None.

Type host and locality. *Pentoceros richardsoni*, south Pacific Ocean.

Morphology. Size: 80–90 mm. Papillae: partial coverage, generally spherical, variable in size and shape, not found in organized groups. Holdfasts: three, two laterals short; dorsal horn shorter. First antenna with four segments, second with two segments. Plumes: dendritic, complex branching.

Remarks. A valid species. Well described, figured and discussed in the original report. An intermediate size *Pennella* species parasitic on a unique host, the pelagic armourhead (boarfish), *P. richardsoni*. Kazachenko and Kurochkin (1974) documented several specimens of the adult female and younger pre-adult individuals in metamorphosis. *Pennella hawaiiensis* resembles *P. filosa* but is a smaller parasite; it also superficially resembles and is close in size to *P. remorae*, but has a different cephalothoracic papillae configuration, has one less segment on the first antenna, and parasitizes a much different type of host. *Pennella hawaiiensis* is the only species of *Pennella* other than *P. exocoeti* (a smaller parasite which does not possess a dorsal holdfast horn and is found on flyingfish) which exhibits a four-segmented first antenna.

***Pennella histiophori* Thomson, 1889**

Not valid. The original description is from specimens recovered from the Pacific Sailfish *Histiophorus hescheli* (= *Istiophorus platycephalus*) off New Zealand. The descriptions and figures resemble closely specimens of *P. filosa* also recorded from Pacific Sailfish (ex: off coastal Mexico, Causey 1960). The specimens of *P. histiophori* fall within the length and morphological variability range of most specimens of *P. filosa* from many different species of large pelagic scombriform fishes (Hogans 1987). *Pennella histiophori* is a synonym of *P. filosa* (Hogans 1988a); accepted as *P. filosa* (Walter & Boxshall 2015).

***Pennella holteni* (Desmarest, 1825)**

Not valid. Desmarest (1825) named a new species while transferring the species described by Holten (1802), *P. exocoeti*, from *Lernaea* to *Lernaepenna*, both of which are synonyms of *Pennella*. There was no actual description of a new species in the original report. Accepted as *P. exocoeti* (Walter & Boxshall 2015).

***Pennella incerta* Brian, 1927**

Not valid. Found in a plankton sample, Italian Mediterranean region. Based on a larval (copepodid) stage. Brief and inadequate original description. Not reported since the original description.

***Pennella instructa* Wilson, 1917**

(Fig. 12)

Synonyms. *Pennella zeylanica* Kirtisinghe, 1933

Type host and locality. *Xiphias gladius*, northwest Atlantic Ocean.

Morphology. Size: 122–163 mm. Papillae: full coverage, generally spherical, variable in size and shape, found in distinct bands or groups. Holdfasts: two lateral only. First antenna with five segments, second with two segments. Plumes: dendritic, complex branching

Remarks. A valid species. One of the largest species of *Pennella*. Found on swordfish (*Xiphias*) and sailfish (*Istiophorus*) in the Atlantic, Indian and Pacific Oceans and Mediterranean Sea (Wilson 1917; Kirtisinghe 1932; Devaraj & Bennet 1972; Hogans *et al.* 1985, 1986; Speare 1995; Mattiucci *et al.* 2005). *Pennella instructa* superficially resembles another large *Pennella*, *P. filosa* which is found on the same host species and sometimes found on the same individual host (Hogans *et al.* 1985). Well-executed original description and figures (Wilson, 1917); redescribed by Hogans (1986). This parasite exhibits two lateral holdfast horns only (*P. filosa* may have

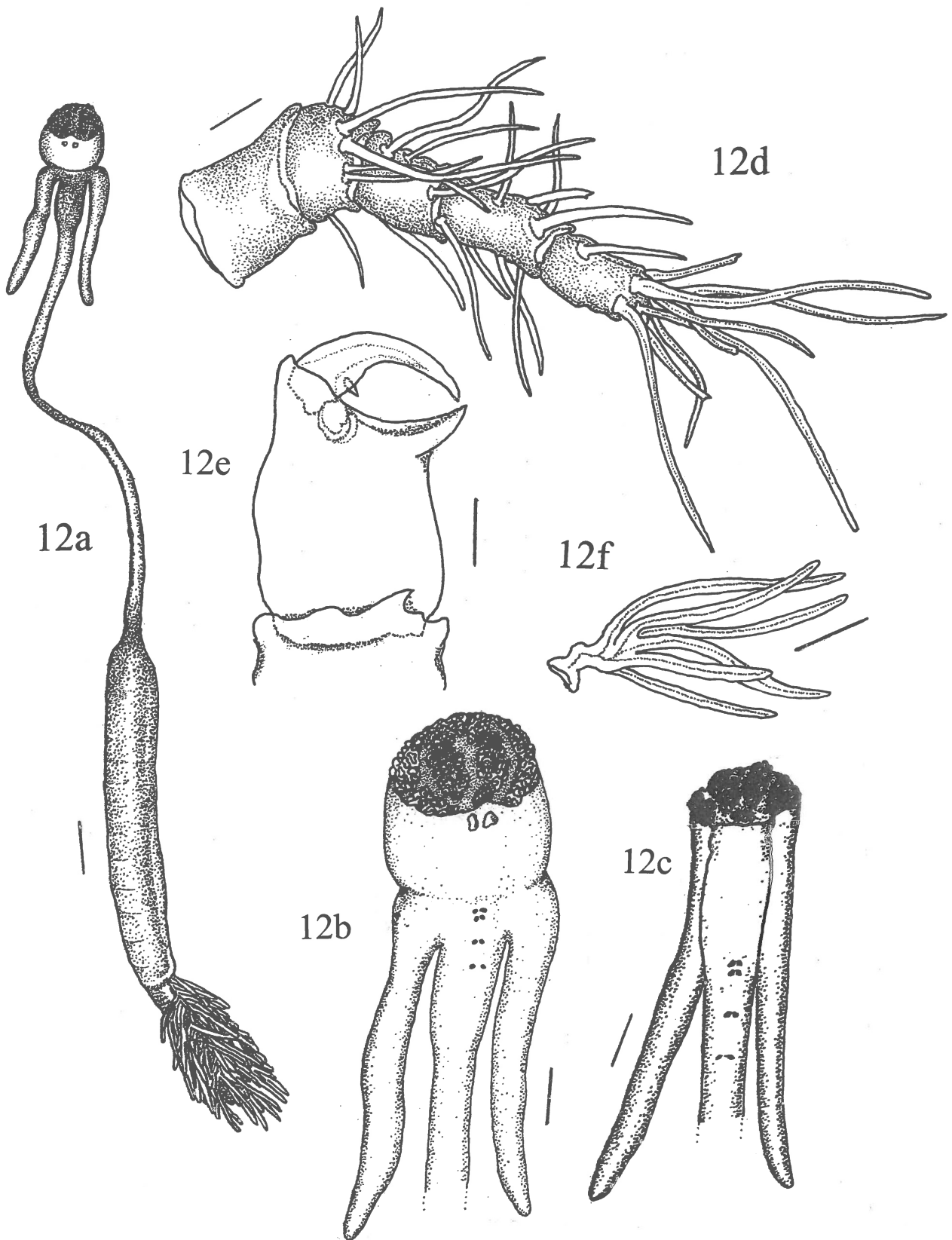


FIGURE 12. *Pennella instructa*, a. habitus, ventral; b. cephalothorax, ventral; c. cephalothorax (different specimen), ventral; d. first antenna, dorsal; e. terminal segment, second antenna, dorsal; f. abdominal plumes (b, c from Hogans 1986). Scale bars: a = 5.0 mm; b, c = 3.0 mm; d, e = 0.02 mm; f = 2.0 mm.

three), always directed posteriorly, and a cephalothoracic papillae field which is configured in distinct bands (on *P. filosa* the papillae are random, not organized in groups or bands). *Pennella instructa* has a two-segmented first antenna; *P. filosa* exhibits 3 segments on this appendage. *Pennella instructa* exhibits a somewhat variable second antenna, the structure of the terminal segment is not consistent between specimens; whether this is due to age, atrophy or site of infestation is not known. Unlike *P. filosa* which generally infests only muscle tissue, *P. instructa* is often found with the cephalothorax embedded in the tissues of an individual organ (ex: ovaries) or inserted into the dorsal aorta of the heart of the host (Wilson 1932; Hogans *et al.* 1985; Merella *et al.* 2003).

***Pennella intricata* (Costa, 1847)**

Not valid. Reported, but not described or figured. *Nomen nudum* (Walter & Boxshall 2015).

***Pennella liouvillei* Quidor, 1912**

Not valid. From flyingfish *Exocoetus* sp., South Pacific. Incompletely described and validity based on torsion of the neck/cephalothorax, proven unreliable character: Wilson (1917). A variable form and synonym of *P. exocoeti* (Wilson 1917; Hogans 1988a). Accepted as *P. exocoeti* (Walter & Boxshall 2015).

***Pennella longicauda* Gnanamuthu, 1957**

(Fig. 13)

Synonyms. *Pennella oxyporhamphi* Sebastian, 1966

Type host and locality. *Cypselurus bahiensis*, Madras, Indian Ocean..

Morphology. Size: 35 mm. Papillae: partial coverage, clavate and tubiform, not spherical, unorganized arrangement. Holdfasts: two only, short. First antenna with five segments, second with three segments. Plumes: simple, single or double,

Remarks. *Species inquirendae*. Described from the flyingfish, *species inquirendae* according to Hogans (1988a), based on missing type material. A brief account of a new species, figures in the original description show that the single specimen documented is sufficiently different from other *Pennella* to warrant consideration as a distinct species. *Pennella longicauda* is another small *Pennella* and exhibits unique cephalothoracic papillae (elongate, tubiform, not spherical- Fig. 13b); the specimen described by Gnanamuthu (1957) was a gravid female with eggs strings. It has not been reported since the original record.

***Pennella makaira* Hogans, 1988**

(Fig. 14)

Synonyms. None

Type host and locality. *Makaira nigricans*, Caribbean Sea.

Morphology. Size: 27–29 mm. Papillae: full coverage, spherical, clavate and tubiform, simple branching; unorganized arrangement. Holdfasts: two only, short. First antenna with three segments, second with two segments. Plumes: simple, single or double.

Remarks. A valid species. Found so far only on blue marlin (*M. nigricans*) in the south Atlantic (Hogans 1988c; Williams & Bunkley-Williams 1996). A small species with a unique overall shape and uniform papillae structure between specimens. The only small (<50 mm) *Pennella* known to infest large scombriform fishes.

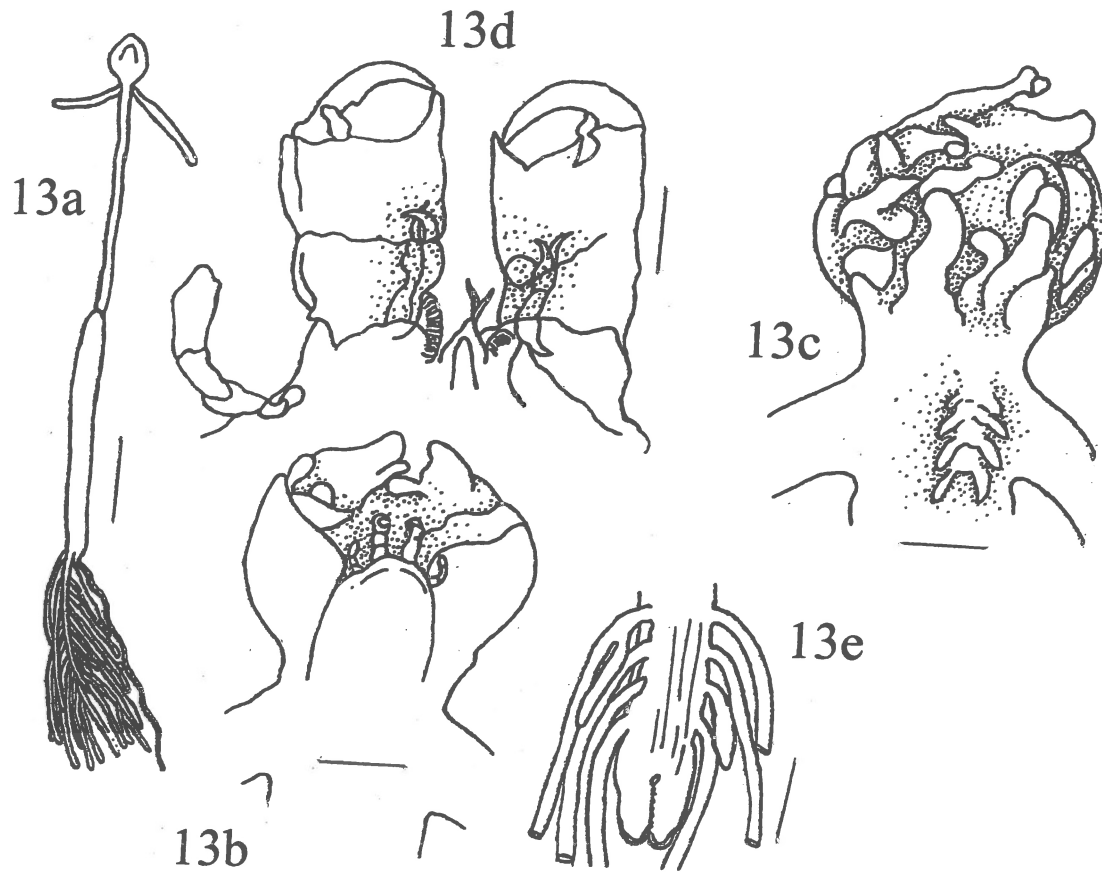


FIGURE 13. *Pennella longicauda*, a. entire parasite; b. cephalothorax, dorsal; c. cephalothorax, ventral. d. detail of appendage area, dorsal; e. abdomen and plumes (from Gnanamuthu, 1957). Scale bars: a = 5.0 mm; b, c = 1.0 mm; d = 0.02 mm.

***Pennella orthogorisci* Wright, 1870**

Not valid. A large *Pennella* species described from ocean sunfish (*Mola mola*) in the eastern Atlantic (Ireland). Wilson (1917) redescribed *P. orthogorisci* collected from ocean sunfish caught off Massachusetts. There is nothing within these two accounts which would indicate that this species differs in any way from *P. filosa* which was first documented from, and has repeatedly been found on the same host (Benz & Hogans 1993 and references therein). Wilson (1917) in redescribing *P. orthogorisci*, differentiated his specimens from *P. instructa*, but failed to explain how they were different from *P. filosa*. The morphological variability of specimens of *P. filosa* from ocean sunfish (Hogans 1988a) easily encompasses any features of *P. orthogorisci*. Synonym of *P. filosa* (Kabata 1979; Hogans 1988a). accepted as *P. filosa* (Walter & Boxshall 2015).

***Pennella oxyporhamphi* Sebastian, 1966**

Not valid. Found on the halfbeak, *Oxyporhamphus* sp. (now placed in the flyingfish family Exocoetidae; Dasilao *et al.* 1997), Indian Ocean. The original description is from one apparent adult, and 2 immature parasites. It is brief and the figures are not detailed enough to warrant separation of this species from another small species apparently found on flyingfish in the Indian Ocean, *P. longicauda*. Sebastian (1966) stated that *P. oxyporhamphi* closely resembled *P. longicauda*, but considered it a separate species based on its only slightly different overall structure. *Pennella oxyporhamphi* has not been reported since the original record. Probable synonym of *P. longicauda*.

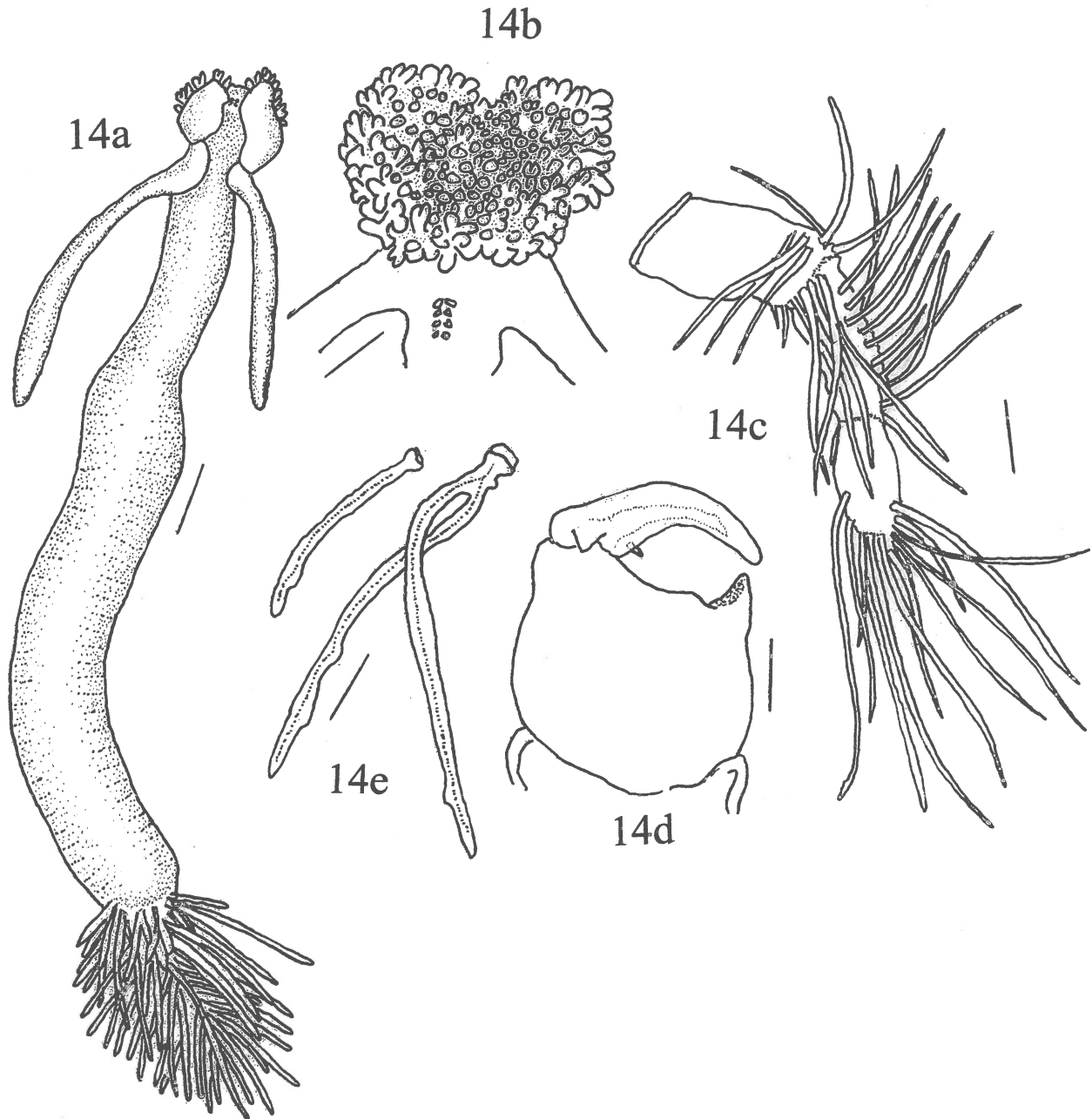


FIGURE 14. *Pennella makaira*, a. habitus, lateral; b. cephalothorax, ventral; c. first antenna, dorsal; d. terminal segment, second antenna, dorsal; e. abdominal plumules (redrawn from Hogans 1988c). Scale bars: a = 3.0 mm; b = 1.0 mm; c, d = 0.02 mm; e = 0.5 mm.

***Pennella platycephalus* Gnanamuthu, 1957**

(Fig. 15)

Synonyms. None.

Type host and locality. *Cypselurus* sp., Indian Ocean.

Morphology. Size: 37 mm. Papillae: partial coverage, a few spherical only, configured in a single small group. Holdfasts: two only, short. First and second antenna (not described or figured- no information). Plumules: simple, all but one single or double; one set shown with four plumules (original figures).

Remarks. *Species inquirendae*. Original description from a single specimen found on a flyingfish

(*Cypselurus*). *Species inquirendae* according to Hogans (1988a), based on missing type material and brief description/ figures. *Pennella platycephalus* is one of several new species of small *Pennella* described from flyingfish in the Indian Ocean by Gnanamuthu (1957) in a single paper. *Pennella platycephalus* exhibits a cephalothorax shape (Figure 15b) unique amongst *Pennella* species; the cephalothoracic papillae are few in number and spherical, a feature not found in any other species parasitizing flyingfish. The original specimen was described from a gravid female with eggs strings. There have been no reports of this species since the initial record.

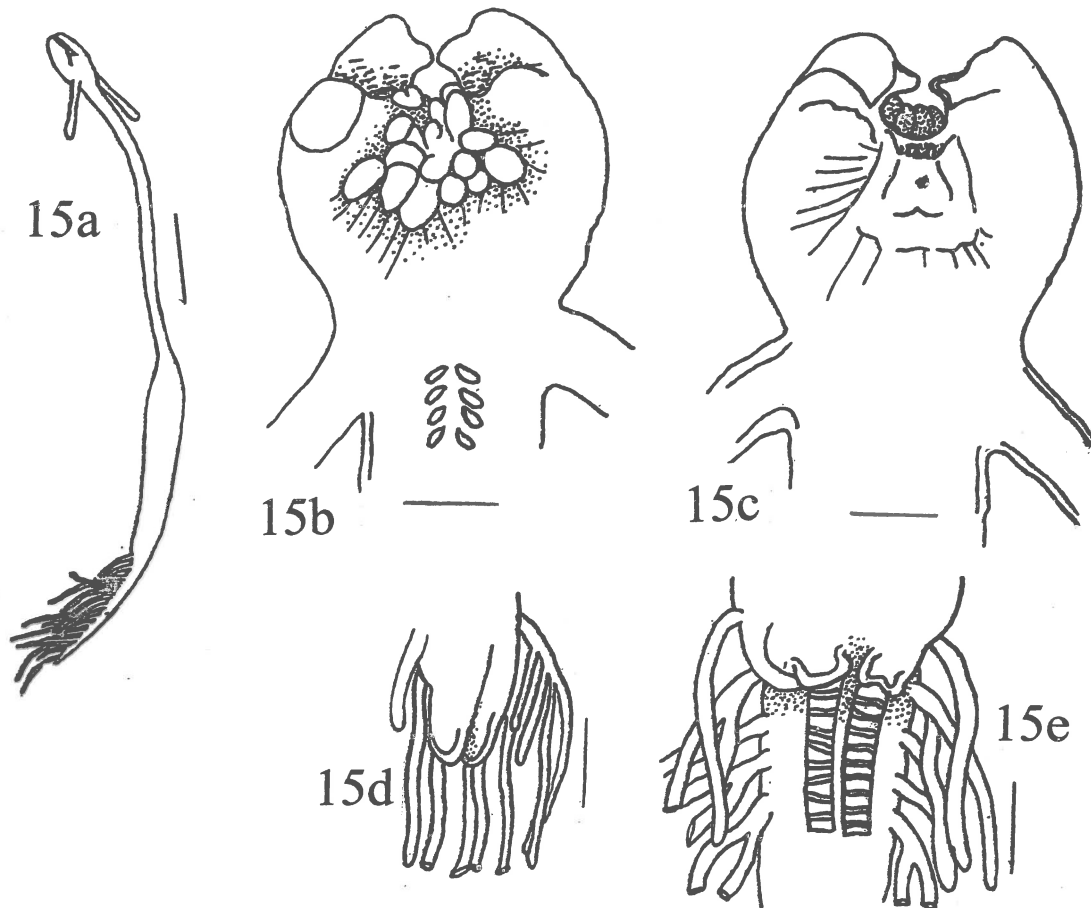


FIGURE 15. *Pennella platycephalus*, a. entire parasite; b. cephalothorax, ventral; c. cephalothorax, dorsal; d. posterior end of abdomen with plumes; e. abdomen, ventral (from Gnanamuthu, 1957). Scale bars = a = 5.0 mm; b-d = 1.0 mm; e = 0.5 mm.

***Pennella plumosa* (Dekay, 1844)**

Not valid. Described from a damaged specimen from *Diodon pilosus* (= *D. holocanthus*) (Dekay 1844). Wilson (1917) considered *P. plumosa* to be a synonym of *P. sagitta*, but this species does not parasitize *Diodon*. The brief description of the incomplete parasite indicates that the specimen is likely *P. diodontis*. Considered herein a synonym of *P. diodontis*.

***Pennella pustulosa* Baird, 1850**

Not valid. Described from a specimen collected from *Corpyphaena* sp., Australia (Baird, 1850). The single specimen was without a cephalothorax or holdfasts (i.e. only the external portion of the parasite was documented). Inadequate description and insufficient information; synonym of *P. filosa* (Leigh-Sharpe 1928); accepted as *P. filosa* (Walter & Boxshall 2015).

***Pennella remorae* Murray, 1856**

(Fig. 16)

Synonyms. None

Type host and locality. *Echeneis remora*, Atlantic Ocean.

Morphology. Size: 99 mm. Papillae: partial coverage, generally spherical, variable in size and shape, found in distinct, organized groups. Holdfasts: three, two laterals short; dorsal horn shorter. First antenna with five segments, second with two segments. Plumes: dendritic, complex branching.

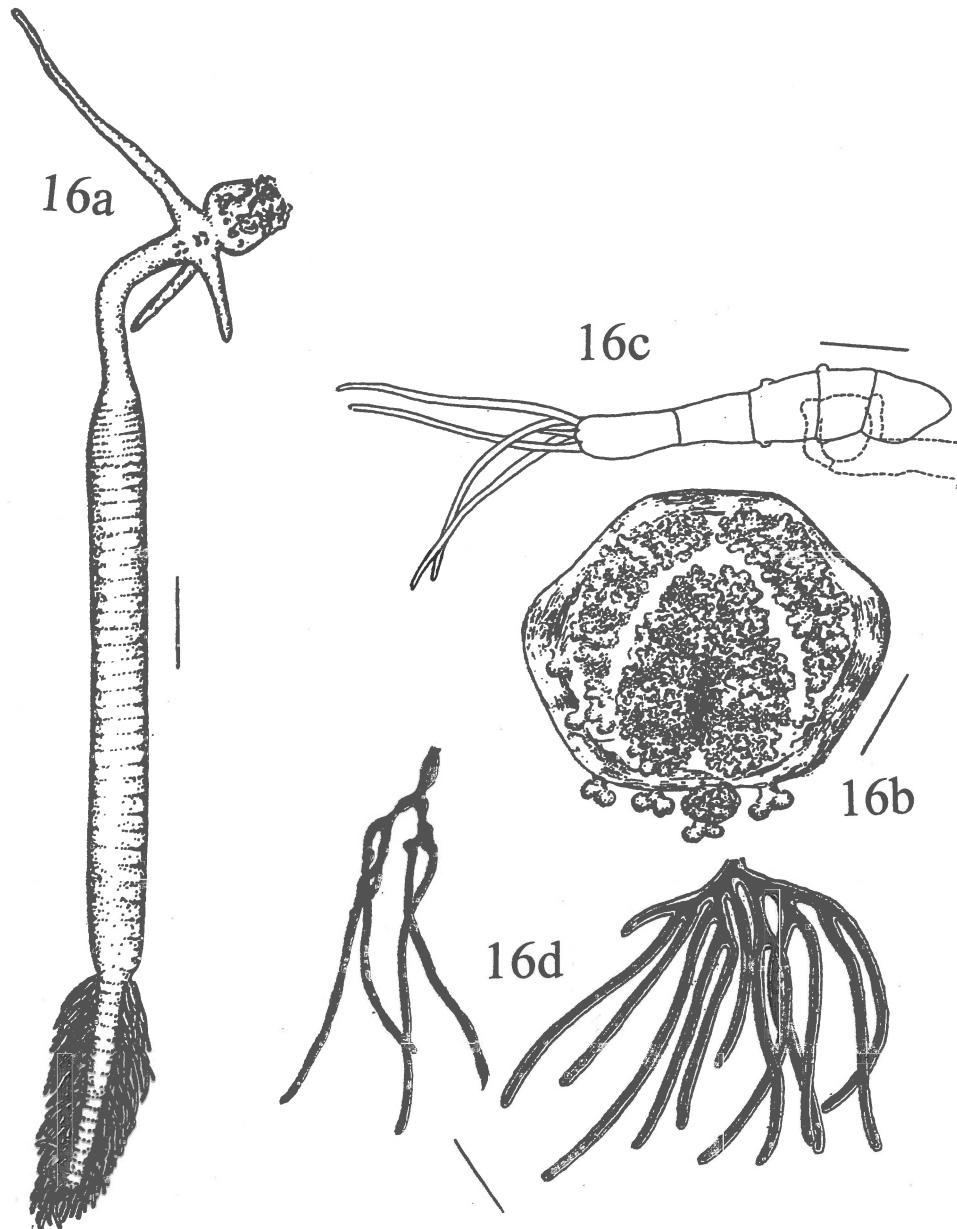


FIGURE 16. *Pennella remorae*, a. habitus, dorsal; b. apical end of cephalothorax; c. first antenna, dorsal; d. abdominal plumes (from Delamare Deboutteville and Nunes-Ruivo 1951). Scale bars: a = 5.0 mm; b = 0.5 mm; c = 0.02 mm; d = 2.0 mm.

Remarks. *Species inquirendae.* Delamare Deboutteville and Nunes-Ruivo (1951) redescribed *P. remorae* from a single whole specimen collected from *Echeneis remora* (= *E. naucrates*). Original description (Murray, 1856) from a specimen (without anterior embedded portion of the parasite) collected from the same host species, also in the Atlantic Ocean. Hogans (1988a) incorrectly considered *P. remorae* to be a synonym of *P. filosa*. Although Delamare Deboutteville & Nunes-Ruivo had only a single specimen, both the description and figures are well-

executed and show that *P. remorae* has several features which may distinguish it from other valid species. These include the unique host species (a remora), overall length (90mm- which places it in the intermediate size group of *Pennella* species), cephalothoracic papillae configured in distinct groups or bands, and a five-segmented first antenna (as far as can be determined, the only other species of *Pennella* with a five-segmented first antenna are *P. longicauda*, a much smaller species from flyingfish and *P. instructa*, a larger species from billfish).

***Pennella robusta* Gnanamuthu, 1957**

(Fig. 17)

Synonyms. None.

Type host and locality. *Paraexocoetus brachypteris*; Indian Ocean.

Morphology. Size: 55 mm. Papillae: partial coverage, spherical, clavate and branching tubiform, random arrangement. Holdfasts: two only, short. First antenna with three segments, second with three segments. Plumes: simple, single or double.

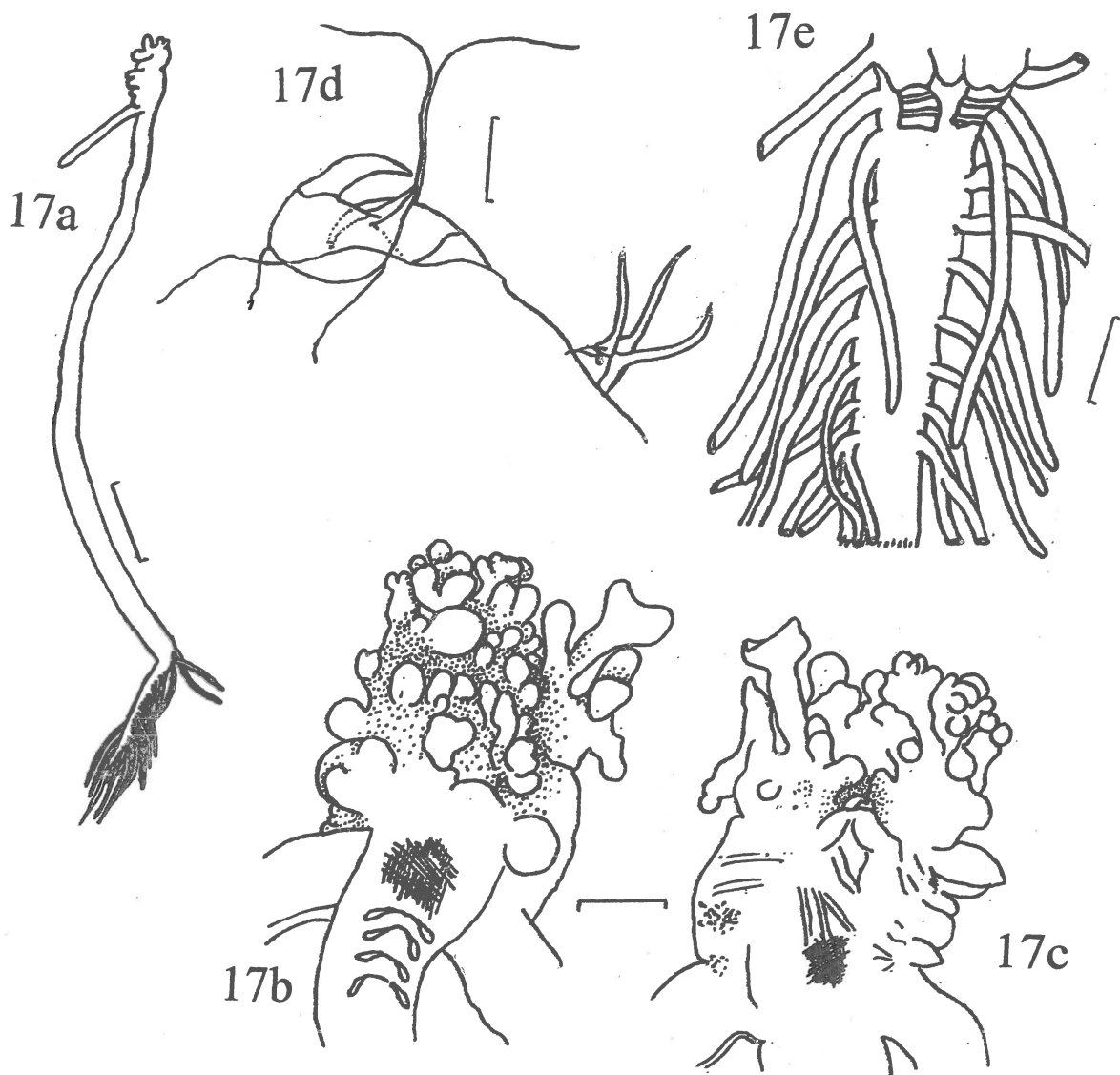


FIGURE 17. *Pennella robusta*, a. entire parasite; b. cephalothorax, ventral; c. cephalothorax, dorsal; d. appendage area with partial figure of second antenna and first maxilla, dorsal; e. abdomen and plumes, ventral (from Gnanamuthu 1957). Scale bars : a = 5.0 mm; b, c = 1.0 mm; d = 0.02 mm; e = 1.0 mm.

Remarks. *Species inquirendae*. An intermediate sized species of *Pennella* described from a flyingfish, based on a single specimen. Hogans (1988a) considered *P. robusta* as *species inquirendae* based on a lack of type material, although the original description and figures do portray the species. The cephalothoracic papillae (tubiform and spherical and configured in an elongate field- Figure 17b), of *P. robusta* are different than those found in any other species of *Pennella* and much different from other species also found on flyingfish. Egg strings were present on the specimen originally described. Not reported since the original record.

***Pennella rubra* Brian, 1906**

Not valid. Described from a single specimen (without anterior embedded end) from the ocean sunfish in the Mediterranean. Brian (1912) re-evaluated the original designation and considered his *P. rubra* a synonym of *P. filosa* (Wilson 1917). Accepted as *P. filosa* (Walter & Boxshall 2015).

***Pennella sagitta* (Linnaeus, 1758)**

(Fig. 18)

Synonyms. *Pennella bocconii* Lamartinier, 1798, *P. branchiata* (Blainville, 1822)

Type host and locality. *Antennarius* sp (?), Atlantic Ocean.

Morphology. Size: 20–25 mm. Papillae: full coverage, clavate and tubiform, simple branching. Holdfasts: two only, short. First antenna with three segments, second with two segments. Plumes: simple, single or double.

Remarks: A valid species. Found so far only on sargassum fish of the family Antennariidae. Redescribed from *Histrio histrio*, Atlantic Ocean (Hogans 1988a). Possibly found on another frogfish, *Antennarius* sp. (Mediterranean) (Brian 1908), but this record is not based on adequate descriptions or figures. Previously confused with *P. diodontis*, but *P. sagitta* is the smallest *Pennella* and is a separate, distinct species (Hogans 1988a). *Pennella sagitta* has been repeatedly shown by many authors to be a soft, delicate parasite with uniform external morphology among specimens (Hogans 1988a and references therein).

***Pennella selaris* Kirtisinghe, 1964**

(Fig. 19)

Synonyms. None.

Type host and locality. *Selar malam*, Indian Ocean.

Morphology. Size: 26 and 29 mm. Papillae: full coverage, few, tubiform, branching. Holdfasts: two. First and second antenna (not described or figured- no information). Abdominal plumes; simple, single.

Remarks: *Species inquirendae*. Original description from the blackfin trevally (*S. malam* = *Alepes melanoptera*); type material not available. The two specimens were described based on one immature and one apparent adult (which did not have egg strings). Kirtisinghe (1964) provided undetailed figures and used the rationale of Leigh-Sharpe (1928: species distinctness based on neck length to trunk length ratio) to differentiate *P. selaris* from other *Pennella* species. Neck and trunk length change significantly through metamorphosis and are poor characters for defining species. *Pennella selaris* is apparently a small species which exhibits an unusual, unique arrangement and structure of the cephalothoracic papillae. No other *Pennella* has been found on *A. melanoptera*, although *P. filosa* (a much larger parasite) has been found on the closely-related amberjack, *Seriola dumerilini* (Tuncer *et al.* 2010). Based on its size, unusual host and papillae structure, *P. selaris* could be considered as a distinct member of *Pennella*; additional specimens are required to confirm its status. Not reported since the original record.

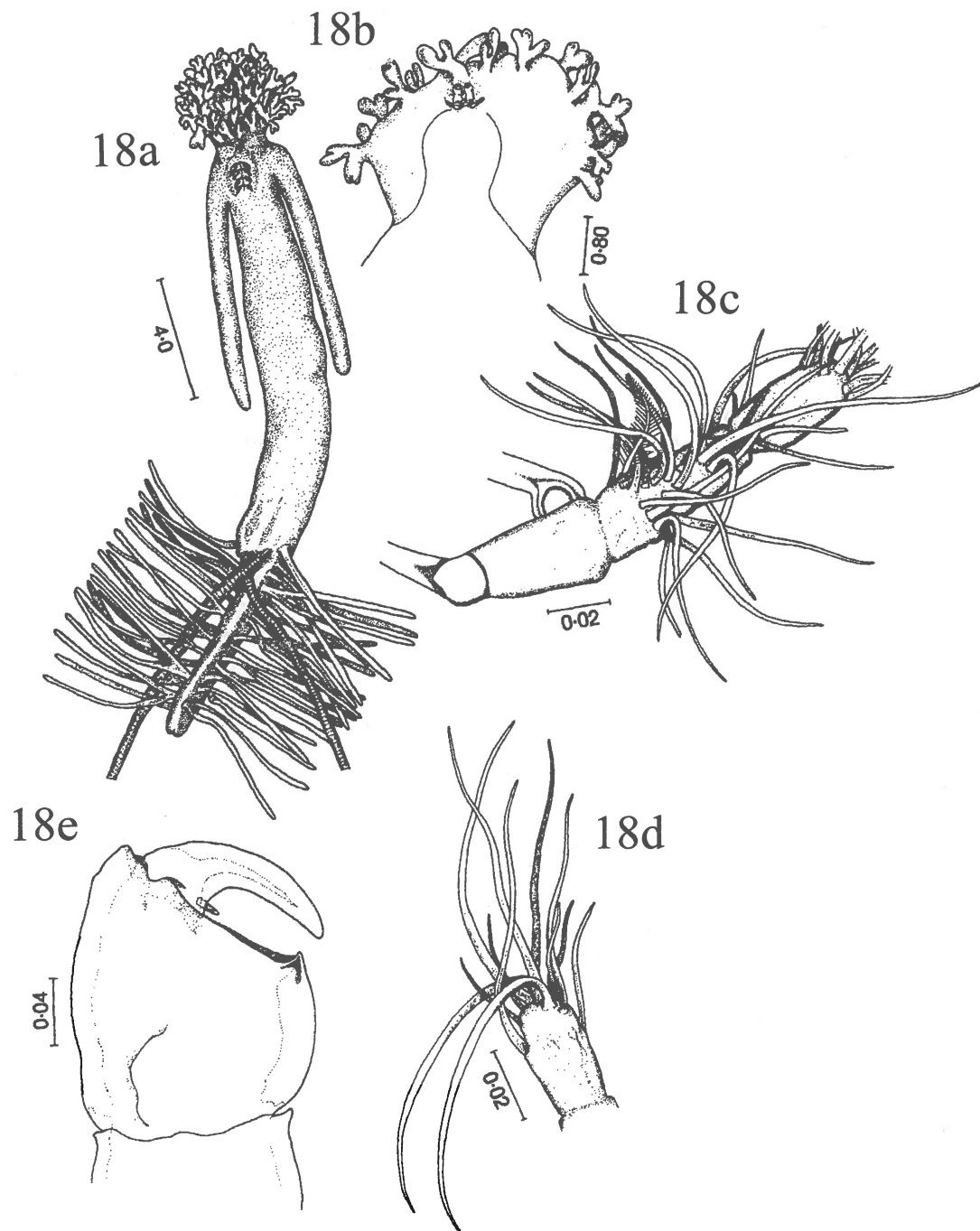


FIGURE 18. *Pennella sagitta* a. habitus, ventral; b. cephalothorax, dorsal; c. first antenna, dorsal; d. apical armature of first antenna, dorsal; e. terminal segment, second antenna, dorsal (from Hogans 1988a).

***Pennella sultana* Nordmann, 1864**

Poor original description (Nordmann 1864). Not a *Pennella*, but a species of the genus *Lernaeolophus* (Pennellidae). Accepted as *Lernaeolophus sultanus* (Walter & Boxshall 2015).

***Pennella tridentata* Listowsky, 1893**

Not valid. The original description was from a specimen recovered from swordfish (*Xiphias*) in the Mediterranean

Sea. *Pennella tridentata* is identical with many specimens of *P. filosa* (also found on swordfish) in size and external morphology. Listowsky's specimen exhibited three holdfast horns (two lateral, one dorsal) a condition often found in *P. filosa*. There is nothing in the original account which serves to differentiate *P. tridentata* from a variable form of *P. filosa*. Synonym of *P. filosa*.

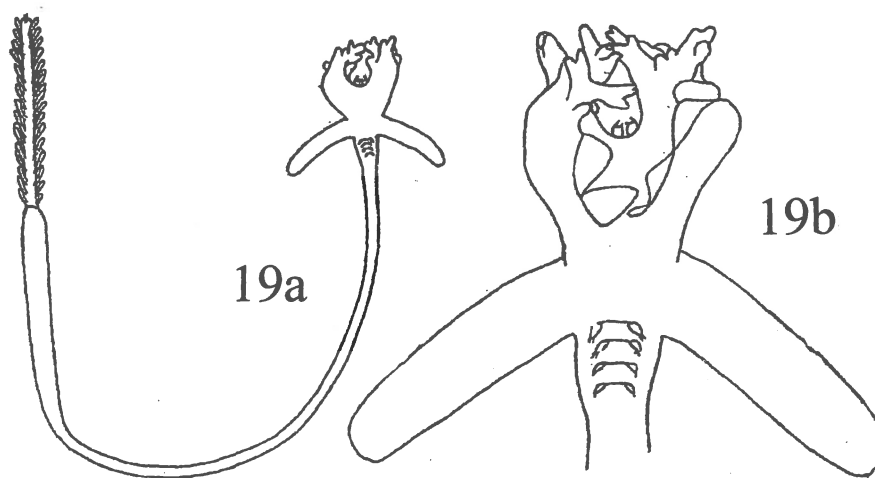


FIGURE 19. *Pennella selaris*, a. entire parasite, young specimen, ventral; b. cephalothorax, oldest specimen, ventral (from Kirtisinghe 1964). No scale bars on original figures.

***Pennella varians* Steenstrup & Lutken, 1861**

Not valid. Described from both the copepodid stage recovered from the intermediate host (squid) and the adult female collected from dolphinfish, *Coryphaena* sp. in the Atlantic Ocean. There is nothing in the original report which positively proves that the larval form on squid is the same species as the adults found on *Coryphaena*. Adult specimens of *P. varians* from *Coryphaena* exhibited short holdfast horns (Steenstrup & Lutken 1861). Steenstrup & Lutken (1861) found specimens of *P. varians* in various stages of metamorphosis on the dolphinfish and competently described and figured each. However, they also found adults of *P. filosa* on the same host species. *Pennella varians* from the original description was likely a younger female of *P. filosa* in the midst of development. In all other structural aspects they strongly resemble *P. filosa* (also frequently found on this host; Wilson 1917; Garcia *et al.* 2010) in overall size, cephalothoracic papillae, holdfast horn configuration and trunk/ abdomen structure. The adult form of *P. varians* has not been reported since the original record. As the adult parasite on the definitive host, a phenotype and synonym of *P. filosa*.

***Pennella zeylanica* Kirtisinghe, 1933**

Not valid. Reported from Pacific sailfish, *Istiophorous gladius* (= *I. platypterus*), Ceylon. The original description and figures clearly indicate that *P. zeylanica* is identical with *P. instructa* of Wilson (1917) (cephalothoracic papillae and holdfast horn configuration is the same between the two species) which is also found on sailfish (Hogans 1986 and references therein). Synonym of *P. instructa* (Hogans 1986); accepted as *P. instructa* (Walter & Boxshall 2015).

Undetermined *Pennella* sp.

A *Pennella* which is likely a distinct species, but has not previously been assigned to any known member of the genus has been documented. Nagasawa *et al.* (1984) identified a *Pennella* sp. from the saury (*Cololabris saira*) in the north Pacific. The parasite is clearly different from any of its congeners based on photographs of recovered

specimens (Nagasawa *et al.* 1984). The cephalothoracic papillae are dendritic and form a large mass covering the entire apical end of the parasite, a feature not yet reported from any other species of *Pennella*. Nagasawa *et al.* (1984, 1988) reported on the population dynamics and geographical distribution of the parasite; the authors were reluctant to classify the specimens further than the generic diagnosis based on the poor taxonomic condition of the genus.

Discussion

This review of *Pennella* suggests that 15 of 44 reported species exhibit unique and distinct characteristics and are substantiated, or are potentially valid members of the genus. Six species (*P. elegans*, *P. longicauda*, *P. platycephalus*, *P. robusta*) described from single specimens on flyingfish (Gnanamuthu 1957), *P. selaris* from trevally (Kirtisinghe 1964) described from two specimens (one immature and one apparent adult) and *P. remorae* (also described from a single specimen), are now included in this group although no type material, or any other specimens exist. We have only the original descriptions and figures, which indicate that the mature parasites exhibited unique characters, to consider the species as valid. Additional specimens of these six species are required to discover the true nature of each.

One objective of this present review has been to define a set of characters which can be effectively used to differentiate species of *Pennella*. Wilson (1917) had previously indicated in his discussion on the taxonomy of *Pennella*: “scarcely any two authors have described their species similarly”. If species of previously documented *Pennella* had been treated in a similar manner, with descriptions based on a consistent set of differentiating characters, the confusion in the taxonomy of the genus would be much reduced. It would be useful to incorporate those characters which are now suggested for distinguishing species into any future descriptions of new *Pennella*. The salient morphological features useful for differentiating species are the parasite size, cephalothoracic papillae shape and configuration, segmentation of the first and second antenna, holdfast horn number and arrangement, and abdominal plume structure. The non-morphological character based on host type is also useful. For *Pennella*, the key to confident assessment of any species is the application of defined character states to multiple specimens.

In the present review, the alignment of species groups by size is amended from previous assessments, there are four large species (>100 mm): *P. balaenoptera*, *P. benzi* **sp. nov.**, *P. filosa* and *P. instructa*; 3 species are intermediate in size (50–100 mm): *P. hawaiiensis*, *P. remorae* and *P. robusta* and eight are small species (<50mm): *P. diodontis*, *P. elegans*, *P. exocoeti*, *P. longicauda*, *P. makaira*, *P. platycephalus*, *P. sagitta*, and *P. selaris*.

Species grouping and diversity based on the host type is evident: *P. balaenoptera* is parasitic on marine mammals, *P. filosa* is a parasite of large pelagic fish (billfish, tunas, ocean sunfish, amberjack, and dolphinfish), *P. benzi* **sp. nov.** occurs on escolars, *P. hawaiiensis* occurs on boarfish, *P. instructa* is found on swordfish and sailfish, *P. remorae* parasitizes remoras, *P. exocoeti*, *P. elegans*, *P. longicauda*, *P. elegans* and *P. platycephalus* are parasites of several species of flyingfish, *Pennella makaira* is found on blue marlin, *P. diodontis* is found on porcupine fish, *P. selaris* parasitizes the blackfin trevally and *P. sagitta* infests frogfish. Species richness and diversity of the genus is re-affirmed; based on this current review using external morphology and phenotypic characters to define species, it is suggested that there are a variety of *Pennella* species which exhibit a wide range of shapes and sizes, and type of hosts infested.

If *Pennella* was subjected to molecular phylogenetic analysis some confusion as to what defines a legitimate species could be eliminated. Castro-Romero *et al.* (2016) documented morphological variability in cephalothorax and holdfast structures between specimens of single species of three pennellid genera (*Peniculus* Nordmann, 1832, *Metapeniculus* Castro-Romero & Baeza-Kuroki, 1985, and *Trifur* Wilson, 1917) based on DNA barcoding; this method when applied to *Pennella* may show similar results. It would be very useful to determine the polyphyletic distribution within *Pennella* based on host designation as this could indicate if there are fewer valid species within the genus, individuals of which exhibit wide structural variability depending on the type of host parasitized.

Summary of the proposed taxonomic status of 44 species of *Pennella*

Valid (substantiated) species (9): *P. balaenoptera*, *P. benzi* **sp. nov.**, *P. diodontis*, *P. exocoeti*, *P. filosa*, *P. hawaiiensis*, *P. instructa*, *P. makaira*, *P. sagitta*

Species inquirendae (6): *P. elegans*, *P. longicauda*, *P. platycephalus*, *P. remorae*, *P. robusta*, *P. selaris*

Invalid (unsubstantiated) species (29): *P. antarctica*, *P. anthonyi*, *P. biloba*, *P. blainvillii*, *P. bocconii*, *P. brachiata*, *P. cervicornis*, *P. cetti*, *P. charcoti*, *P. costai*, *P. crassicornis*, *P. cylindrica*, *P. elongata*, *P. germonia*, *P. germonia fagei*, *P. gracilis*, *P. histiophori*, *P. holteni*, *P. incerta*, *P. intricata*, *P. liouvillei*, *P. orthagoriscola*, *P. oxyporhamphi*, *P. plumosa*, *P. rubra*, *P. sultana*, *P. tridentata*, *P. varians*, *P. zeylanica*

Hosts reported for *Pennella* spp. listed as valid or species inquirendae

***P. balaenoptera*:** *Balaenoptera acutorostrata*, *Balaenoptera physalus*, *Balaenoptera borealis*, *Grampus griseus*, *Phocaena phocaena*, *Mirounga angustirostris*, *Stenella coeruleoalba*, *Turisops truncatus*

***P. benzi* sp. nov.:** *Lepidocybium flavobrunneum*

***P. diodontis*:** *Diodon holacanthus*, *Zanclus cornuta* (?)

***P. elegans*:** *Cypselurus* sp.

***P. exocoeti*:** *Exocoetus* sp., *Cheilopogon melanurus*

***P. filosa*:** *Coryphaena hippurus*, *Istiophorus platypterus*, *Makaira nigricans*, *Mola mola*, *Seriola dumerilini*, *Tetrapterus audax*, *Thunnus thunnus*, *Thunnus alalunga*, *Xiphias gladius*

***P. hawaiiensis*:** *Pentoceros richardsoni*

***P. instructa*:** *Istiophorus platypterus*, *Xiphias gladius*

***P. longicauda*:** *Cypselurus bahiensis*

***P. makaira*:** *Makaira nigricans*

***P. platycephalus*:** *Cypselurus* sp.

***P. remorae*:** *Echeneis naucrates*

***P. robusta*:** *Paraexocoetus brachypterus*

***P. sagitta*:** *Histrio histrio*, *Antennarius* sp. (?)

***P. selaris*:** *Alepes melanoptera*

Key to species of *Pennella* listed as valid or species inquirendae

Parasites of marine mammals	<i>P. balaenoptera</i>
Parasites of marine teleost fish	2
2. Total length of <50mm	3
2. Total length 50-100mm	4
2. Total length of >100mm	5
3. Parasitic on flyingfish genus <i>Cypselurus</i>	3a
3. Parasitic on other fish genera	3b
3a1. Size 35mm, cephalic papillae short, clavate and spherical	<i>P. elegans</i>
3a2. Size 35mm, cephalic papillae elongate, clavate, tubiform	<i>P. longicauda</i>
3a3. Size 37mm, cephalic papillae spherical only, in single small group	<i>P. platycephalus</i>
3b1. Size 25mm, cephalic papillae clavate only; on <i>Diodon</i>	<i>P. diodontis</i>
3b2. Size 40mm, cephalic papillae tubiform, branched; on <i>Exocoetus</i>	<i>P. exocoeti</i>
3b3. Size 28mm, cephalic papillae tubiform, branched, on <i>Makaira</i>	<i>P. makaira</i>
3b4. Size 23mm, cephalic papillae tubiform, branched; on <i>Histrio</i>	<i>P. sagitta</i>
3b5. Size 28mm, cephalic papillae few, large, tubiform; on <i>Selar</i>	<i>P. selaris</i>
4a. Size 85mm, cephalic papillae not organized, on <i>Pentoceros</i>	<i>P. hawaiiensis</i>
4b. Size 90mm, cephalic papillae in distinct groups, on <i>Echeneis</i>	<i>P. remorae</i>
4c. Size 55mm, cephalic papillae clavate, branched, on <i>Paraexocoetus</i>	<i>P. robusta</i>
5a. Without dorsal horn; cephalic papillae in distinct groups	6
5b. With dorsal horn; cephalic papillae not in distinct groups	7
6. Two holdfast horns only, cephalic papillae in distinct groups	<i>P. instructa</i>
7. Three holdfast horns, dorsal horn bifurcate; on <i>Lepidocybium</i>	<i>P. benzi</i> sp. nov.
7. Three holdfast horns, dorsal horn not bifurcate; on other fish	<i>P. filosa</i>

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