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ORIGINAL PAPER

Description of a new endoparasitic copepod genus and species (Lamippidae) that induces gall formation in leaves of the sea pen *Ptilosarcus gurneyi* (Octocorallia) from British Columbia

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Abstract A new genus and species of gall-forming endoparasitic copepod of the family Lamippidae is described from the orange sea pen *Ptilosarcus gurneyi* (Gray, 1860) collected in British Columbia, Canada. Lamippid copepods (over 50 species) are obligate endoparasites, some of which form galls in a variety of soft corals (Alcyonacea and Pennatulacea). *Ptilosarcoma athyrmata* n. gen., n. sp. is the first lamippid formally described from any species of *Ptilosarcus* Verrill, 1865. In total, 143 galls from six sea pens were dissected and found to typically contain one female and male copepod pair. Infested leaves of *P. gurneyi* had 1.4 ± 0.6 (n = 143) galls per leaf. Using light and scanning electron microscopy, the copepods were examined and found to most closely resemble those belonging to the genus *Isidicola* Gravier, 1914, based on the presence of maxillipeds and lack of acicules on the caudal rami; however, they are distinct from the sole species of *Isidicola* based on aspects of antennal morphology. We conclude that *Lamippina laubieri* Bouligand, 1960 is a synonym of *L. aciculifera* (Zulueta, 1908), thus the family presently contains 52 species and one subspecies. A key to lamippid genera and a table of all lamippid genera and species with all known hosts and locality records are provided.

Keywords Cnidaria · Copepod · Lamippid · Northeast Pacific · Parasite

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Introduction

Octocorals are known as hosts for a range of symbionts, including endoparasitic copepods (Watling et al. 2011; Baillon et al. 2014; De Clippele et al. 2015; Rogers et al. 2016). Copepods of the family Lamippidae are obligate endoparasites of soft corals (Alcyonacea and Pennatulacea) where they live embedded within polyps and other regions of hosts (Bouligand 1960; Boxshall and Halsey 2004); species belonging to three lamippid genera induce prominent galls visible on the surfaces of the hosts. Currently, there are ten lamippid genera containing 51 species and one subspecies: *Enalcyonium* Olsson, 1869 (31 species), *Gorgonophilus* Buhl-Mortensen and Mortensen 2004 (one species), *Isidicola* Gravier, 1914 (one species), *Lamippella* Bouligand and Delamare-Deboutteville, 1959 (three species), *Lamippe* Bruzelius, 1858 (four species and one subspecies), *Lamippina* Bouligand, 1960 (two species, not including *Lamippina laubieri* Bouligand, 1960), *Lamippula* Bouligand, 1966 (four species), *Linaresia* Zulueta, 1908 (three species), *Magnippe* Stock, 1978 (one species), and *Sphaerippe* Grygier, 1983 (one species) (Boxshall 2015; see Table 1). Lamippidae are further separated into two subfamilies: Linaresiinae and Lamippinae (Stock 1988). Linaresiinae includes *Linaresia* and *Magnippe*, all species of which have females with stelliform bodies and a simple, reduced mouth for both sexes (Stock 1988). Females of species in Lamippinae have fusiform bodies and both sexes have a prominent buccal cone (Stock 1988).

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Table 1 List of Lamippidae species with host, geographic distribution, and depth data; * = type species. Classification of host taxa follows van Ofwegen (2016). Blanks in the Depth column indicate that depths were not provided in the original description

Copepod	Host(s)	Host family	Host suborder	Host order	Locality/Localities	Depth (m)
Lamippinae Joliet, 1882						
Enalcyonium Olsson, 1869						
Enalcyonium affinis Zulueta, 1908	*Eunicella verrucosa* (Pallas, 1766)	Gorgoniidae	Holaxonia	Alcyonacea	France (Mediterranean)	
Enalcyonium albidum Zulueta, 1908	*Pteroeides griseum* (Linnaeus, 1767)	Pennatulidae	Subsessiliflorae	Pennatulacea	France (Mediterranean)	
Enalcyonium alcyonii Joliet, 1882	*Paralcyonium spinulosum* Delle Chiaje, 1822	Paralcyoniidae	Alcyoniina	Alcyonacea	Coast of Africa (Mediterranean)	
Enalcyonium auriculatum Kim, 2004	*Lobophytum schoedei* Moser, 1919	Alcyoniidae	Alcyoniina	Alcyonacea	New Caledonia	1
Enalcyonium bullatum Kim, 2004	*Siphonogorgia variabilis* (Hickson, 1903)	Nidaliidae	Alcyoniina	Alcyonacea	New Caledonia	30
Enalcyonium caledonensis Kim, 2004	*Lobophytum schoedei* Moser, 1919	Alcyoniidae	Alcyoniina	Alcyonacea	New Caledonia	1
Enalcyonium capillatum Kim, 2004	*Rumphella antipathes* (Linnaeus, 1758)	Gorgoniidae	Holaxonia	Alcyonacea	New Caledonia	1
Enalcyonium carrikeri Dudley, 1973	*Gersemia rubiformis* (Ehrenberg, 1834)	Nephtheidae	Alcyoniina	Alcyonacea	Maine; Massachusetts; Block Island, USA (40°39.5′N, 69°47.8′W)	25–35
Enalcyonium ceramensis Kim, 2007	*Rumphella aggregata* (Nutting, 1909)	Gorgoniidae	Holaxonia	Alcyonacea	Moluccas (03°17′00″S, 130°44′48″E)	10
Enalcyonium ciliatum Stock, 1972	*Dendronephthya hemprichi* Klunzinger, 1877	Nephtheidae	Alcyoniina	Alcyonacea	Israel (Red Sea); Ethiopia	3
Enalcyonium circulatum Kim, 2007	*Muricella* sp.	Acanthogorgiidae	Holaxonia	Alcyonacea	Moluccas (03°17′00″S, 130°44′48″E)	2
Enalcyonium concinnum Humes, 1957	*Virgularia schultzei* Kükenthal, 1910	Virgulariidae	Subsessiliflorae	Pennatulacea	Sierra Leone	<5
Enalcyonium confusum Stock, 1988	*Alcyonium palmatum* Pallas, 1766	Alcyoniidae	Alcyoniina	Alcyonacea	France (Mediterranean)	60–80
	Alcyonium acaule Marion, 1878	Alcyoniidae	Alcyoniina	Alcyonacea	France (Mediterranean)	10
Enalcyonium digitigerum Ho, 1984	*Bellonella rigida* Putter, 1900	Alcyoniidae	Alcyoniina	Alcyonacea	Sado Island, Japan	
Enalcyonium euniceae Stock, 1973	*Eunicea mammosa* Lamouroux, 1816	Plexauridae	Holaxonia	Alcyonacea	Puerto Rico	3
Enalcyonium forbesi Scott, 1901	*Alcyonium digitatum* Linnaeus, 1758	Alcyoniidae	Alcyoniina	Alcyonacea	United Kingdom; France (Atlantic)	20–22
Enalcyonium grandisetigerum Kim, 2009	*Dendronephthya cirsium* Kükenthal, 1905	Nephtheidae	Alcyoniina	Alcyonacea	Madagascar (13°15′50″S, 48°08′35″E)	
Enalcyonium heegaardi Bouligand, 1960	*Gersemia rubiformis* (Ehrenberg, 1834)	Nephtheidae	Alcyoniina	Alcyonacea	Davis Strait, NW Atlantic (63°06′N, 56°00′W)	2258
Enalcyonium humesi Kim, 2004	*Lobophytum schoedei* Moser, 1919	Alcyoniidae	Alcyoniina	Alcyonacea	New Caledonia	1
Enalcyonium kohsiangi Uyeno, 2015	*Pteroeides* sp.	Pennatulidae	Subsessiliflorae	Pennatulacea	Johor Strait, Indonesia	
Enalcyonium lobophyti Kim, 2004	*Lobophytum schoedei* Moser, 1919	Alcyoniidae	Alcyoniina	Alcyonacea	New Caledonia	1
Enalcyonium nudum Stock, 1973	*Plexaura homomalla* (Esper, 1792)	Plexauridae	Holaxonia	Alcyonacea	Puerto Rico	3
Enalcyonium olssoni Zulueta, 1908	*Alcyonium digitatum* Linnaeus, 1758	Alcyoniidae	Alcyoniina	Alcyonacea	Sweden	
Enalcyonium pusillum Zulueta, 1908	*Leptogorgia sarmentosa* (Esper, 1789)	Gorgoniidae	Holaxonia	Alcyonacea	France (Mediterranean)	
Enalcyonium ramosum Stock, 1973	*Plexaura homomalla* (Esper, 1792)	Plexauridae	Holaxonia	Alcyonacea	Puerto Rico	3
Enalcyonium robustum Kim, 2009	*Dendronephthya regia* Verseveldt, 1966	Nephtheidae	Alcyoniina	Alcyonacea	Madagascar (13°15′50″S, 48°08′35″E)	
Enalcyonium rubicundum Olsson, 1869*	*Alcyonium digitatum* Linnaeus, 1758	Alcyoniidae	Alcyoniina	Alcyonacea	Sweden; United Kingdom	22
Enalcyonium scorpio Stock, 1973	*Leptogorgia virgulata* (Lamarck, 1815)	Gorgoniidae	Holaxonia	Alcyonacea	North Carolina, USA	5
Enalcyonium setigerum Zulueta, 1908	*Paramuricea chamaeleon* (Koch, 1887)	Plexauridae	Holaxonia	Alcyonacea	Not Stated	
	Alcyonium coralloides (Pallas, 1766)	Alcyoniidae	Alcyoniina	Alcyonacea	France (Mediterranean)	
Enalcyonium sympodii Zulueta, 1910	*Leptogorgia sarmentosa* (Esper, 1789)	Gorgoniidae	Holaxonia	Alcyonacea	France (Mediterranean)	
Enalcyonium variicauda Stock, 1973	*Briareum asbestinum* (Pallas, 1766)	Briareidae	Scleraxonia	Alcyonacea	Puerto Rico	1–8
Gorgonophilus Buhl-Mortensen and Mortensenm 2004						
Gorgonophilus canadensis Buhl-Mortensen and Mortensen, 2004*	*Paragorgia arborea* (Linnaeus, 1758)	Paragorgiidae	Scleraxonia	Alcyonacea	Davis Strait, W of Greenland (41°60′N, 65°39′W)	445–560

Table 1 (continued)

Copepod	Host(s)	Host family	Host suborder	Host order	Locality/Localities	Depth (m)
Isidicola Gravier, 1914						
Isidicola antarctica Gravier, 1914*	*Primnoisis gracilis* (Gravier, 1914)	Isididae	Calcaxonia	Alcyonacea	Antarctica (due S tip of South America, 67°45′S, 68°33′W)	254
	Primnoisis formosa Gravier, 1914	Isididae	Calcaxonia	Alcyonacea	Antarctica (due S tip of South America, 67°45′S, 68°33′W)	254
Lamippe Bruzelius, 1858						
Lamippe anthoptili Jungersen, 1904 (*nomen nudum*; = *L. bouligandi*)	*Anthoptilum grandiflorum* (Verrill, 1865)	Anthiloptiidae	Subsessiliflorae	Pennatulacea	Not Stated	
Lamippe bouligandi Laubier, 1972	*Anthoptilum grandiflorum* (Verrill, 1865)	Anthiloptiidae	Subsessiliflorae	Pennatulacea	Labrador Sea (63°10′N, 53°40′W)	1210
Lamippe proteus Claparéde, 1867	*Alcyonium digitatum* Linnaeus, 1758	Alcyoniidae	Alcyoniina	Alcyonacea	Italy	
Lamippe pteroidis Zulueta, 1910	*Pteroeides griseum* (Linnaeus, 1767)	Pennatulidae	Subsessiliflorae	Pennatulacea	France (Mediterranean)	
Lamippe rubra Bruzelius, 1858*	*Pennatula phosphorea* Linnaeus, 1758	Pennatulidae	Subsessiliflorae	Pennatulacea	Norway; France (Mediterranean)	
Lamippe rubra decolor Zulueta, 1908	*Pennatula phosphorea* Linnaeus, 1758	Pennatulidae	Subsessiliflorae	Pennatulacea	France (Mediterranean)	
Lamippella Bouligand and Delamare-Deboutteville, 1959						
Lamippella acanellae Grygier, 1983	*Acanella arbuscula* (Johnson, 1862)	Isididae	Calcaxonia	Alcyonacea	NE Atlantic (off France) (47°44.3′N, 08°51′W)	1010
Lamippella delamarei Bouligand, 1965	*Kophobelemnon stelliferum* (Müller, 1776)	Kophobelemnidae	Sessiliflorae	Pennatulacea	France (Mediterranean)	
Lamippella faurei Bouligand and Delamare-Deboutteville, 1959*	*Alcyonium palmatum* Pallas, 1766	Alcyoniidae	Alcyoniina	Alcyonacea	France (Mediterranean)	
	Alcyonium acaule Marion, 1878	Alcyoniidae	Alcyoniina	Alcyonacea	France (Mediterranean)	
	Eunicella verrucosa (Pallas, 1766)	Gorgoniidae	Holaxonia	Alcyonacea	France (Mediterranean)	
	Alcyonium coralloides (Pallas, 1766)	Alcyoniidae	Alcyoniina	Alcyonacea	France (Mediterranean)	
	Rolandia coralloides de Lacaze Duthiers, 1900	Clavulariidae	Stolonifera	Alcyonacea	France (Mediterranean)	
Lamippina Bouligand, 1961						
Lamippina aciculifera Zulueta, 1908*	*Alcyonium palmatum* Pallas, 1766	Alcyoniidae	Alcyoniina	Alcyonacea	France (Mediterranean)	
	Alcyonium acaule Marion, 1878	Alcyoniidae	Alcyoniina	Alcyonacea	France (Mediterranean)	
Lamippina aequalis Stock, 1973	*Antillogorgia acerosa* (Pallas, 1766)	Gorgoniidae	Holaxonia	Alcyonacea	Curaçao	3–4
	"Pseudopterogorgia sp." (probably *Antillogorgia* sp.)	Gorgoniidae	Holaxonia	Alcyonacea	Curaçao	3
Lamippina laubieri Bouligand, 1960 (= *L. aciculifera*; new synonomy, see text)	*Leptogorgia sarmentosa* (Esper, 1789)	Gorgoniidae	Holaxonia	Alcyonacea	Not Stated (but probably Mediterranean coast of France)	
Lamippula Bouligand, 1966						
Lamippula chattoni Zulueta, 1908*	*Pennatula phosphorea* Linnaeus, 1758	Pennatulidae	Subsessiliflorae	Pennatulacea	France (Mediterranean)	
Lamippula duthiersi Joliet, 1882	*Paralcyonium spinulosum* Delle Chiaje, 1822	Paralcyoniidae	Alcyoniina	Alcyonacea	France (Mediterranean)	
Lamippula pallida Zulueta, 1908	*Veretillum cynomorium* (Pallas, 1766)	Veretiliidae	Sessiliflorae	Pennatulacea	France (Mediterranean)	
Lamippula parva Zulueta, 1908	*Paramuricea chamaeleon* (Koch, 1887)	Plexauridae	Holaxonia	Alcyonacea	France (Mediterranean)	
Ptilosarcoma, new genus Williams, Anchaluisa, Boyko and McDaniel						
Ptilosarcoma athyrmata, new species Williams, Anchaluisa, Boyko and McDaniel*	*Ptilosarcus gurneyi* (Gray, 1860)	Pennatulidae	Subsessiliflorae	Pennatulacea	Strait of Georgia, BC, Canada and Puget Sound, WA, USA	5–10
Sphaerippe Grygier, 1980						
Sphaerippe caligicola Grygier, 1980*	*Callogorgia* sp.	Primnoidae	Calcaxonia	Alcyonacea	Bahamas (26°31′N, 98°51′W)	366
Linaresiinae Stock 1988						

Table 1 (continued)

Copepod	Host(s)	Host family	Host suborder	Host order	Locality/Localities	Depth (m)
Linaresia Zulueta, 1908						
Linaresia bouligandi Stock, 1979	*Placogorgia* sp.	Plexauridae	Holaxonia	Alcyonacea	Gulf of Mexico (27°37'N, 84°13'W)	73
Linaresia magna Grygier, 1980	*Placogorgia* sp.	Plexauridae	Holaxonia	Alcyonacea	Oahu, Hawaii (21°19'N, 157°34'W)	366
Linaresia mammillifera Zulueta, 1908*	*Paramuricea clavata* (Risso, 1826)	Plexauridae	Holaxonia	Alcyonacea	France (Mediterranean)	
Magnippe Stock, 1978						
Magnippe caputmedusae Stock, 1978*	*Thesea citrina* Diechmann, 1936	Plexauridae	Holaxonia	Alcyonacea	Gulf of Mexico (27°37'N, 83°58'W)	54.9
	Thesea parviflora Diechmann, 1936	Plexauridae	Holaxonia	Alcyonacea	Gulf of Mexico (26°24'N, 83°43'W)	73.2
	Thesea rugosa Diechmann, 1936	Plexauridae	Holaxonia	Alcyonacea	Gulf of Mexico (27°37'N, 83°58'W)	54.9

Unlike many other sedentary organisms that require solid surfaces for settlement and attachment, sea pens thrive in benthic marine habitats comprising sand, mud, and rubble from intertidal to deep-sea regions (Williams 2011). One of the unique characteristics of pennatulaceans is the presence of an initial or primary polyp that allows for anchorage in the sediment by a muscular peduncle. Sea pens can exhibit high densities of individuals, forming "forests" on the sea floor and providing refuge for a range of species (Williams 2011). The orange sea pen *Ptilosarcus gurneyi* (Gray, 1860) is a large (up to ca. 50 cm tall) conspicuous species found in coastal waters in depths up to 135 m along the west coast of North America from Alaska to southern California (Batie 1972). *Ptilosarcus gurneyi* is restricted to sand and silt substrates in which it anchors by means of peristaltic movements of the expansible, bulbous peduncle. Population densities as high as 129 individuals/m^2 have been reported from Puget Sound on sandy bottoms swept by tidal currents (Birkeland 1969).

Ptilosarcus gurneyi[1] exhibits a colour range from pale to vivid orange, although specimens from deep water in southern California are reportedly more variable, with yellow, violet, and orange-red specimens (Nutting 1909; Batie 1972). The species is feather-shaped, with a thick rachis bearing polyps and a cylindrical, extensible peduncle without polyps. Internally, a flexible calcareous rod supports the rachis. The rachis bears a series of paired, kidney-shaped leaves on either side that support two rows of polyps used to capture plankton (Best 1988). A second type of polyp, which lacks tentacles, is found on the rachis. These siphonozooids form two bands down the dorsal tract of the rachis and function in the movement of water internally for the expansion/contraction of the colony. The sea pen expels water and retracts into the sediment in response to abiotic factors (e.g., light, water velocity, and turbidity) and to escape from predators (e.g., sea stars or nudibranchs) (Birkeland 1974; Dickinson 1978; Weightman and Arsenault 2002).

An unidentified gall-inducing parasitic copepod was recently found in numerous specimens of *P. gurneyi* by one of us (N. McDaniel) from several locations in the Strait of Georgia, British Columbia. Previous studies had documented purported undescribed species of endoparasitic copepods, identified as belonging to *Lamippe*, associated with this host (Johnstone 1969; Batie 1971). Johnstone (1969) and Batie (1971) found the copepod to be highly prevalent in *P. gurneyi* collected from Puget Sound, WA, USA. The purpose of the present study was to describe the newly discovered copepods from the British Columbia *P. gurneyi* specimens based on scanning electron microscopy (SEM). A key to the lamippid genera is provided along with a table of all genera and species with host and locality data.

[1] Batie 1972 considered *Ptilosarcus quadrangularis* Moroff 1902 to be a synonym of *Ptilosarcus gurneyi*; see also Williams 1995.

Materials and methods

Specimens of *Ptilosarcus gurneyi* were collected on 14 January 2014 and 28 August 2014 from localities in the Strait of Georgia, British Columbia, Canada, at 5–10 m using scuba (collectors D. Swanston and N. McDaniel). The leaves of *P. gurneyi* were cut off after collection and fixed in 95 % ethanol. Before dissection of galls, length and width measurements were recorded. Incisions around the outer perimeter of the galls were made and then opened and examined for copepods with a dissecting microscope.

For scanning electron microscopy (SEM), the extracted copepods were dehydrated in three exchanges of 100 % ethanol and placed in a critical point drier (SAMDRI-795). After drying, the specimens were attached with double-sided sticky tape to aluminum stubs and coated with gold in an EMS-550 sputter coater. Images were taken using a FEI Quanta 250 SEM. Specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM) and the Zoological Reference Collection, Lee Kong Chian Natural History Museum (formerly The Raffles Museum) (ZRC). References for all lamippid taxa included in Table 1 are provided in the literature cited. While dates of description are given for host taxa, we included these as references only when the hosts are mentioned in the body of the paper, but not when they are solely listed in Table 1. Although for free-living copepods it is typical for descriptions of new species to be accompanied by line drawings, this is not always the case with parasitic species. Because of their highly derived morphology and loss of features, these species sometimes have their morphology documented primarily with SEM (e.g., Salmen et al. 2008; Schwabe and Maiorova 2015). We have likewise relied on SEM herein, supplemented by light microscopy observations.

Results

Systematic description

Class Crustacea Pennant, 1777
Subclass Copepoda Milne Edwards, 1840
Order Poecilostomatoida Thorell, 1859
Family Lamippidae Joliet, 1882
Subfamily Lamippinae Stock, 1988
Genus *Ptilosarcoma*, new genus

Diagnosis Maxillipeds present, unsegmented antennule shorter than antenna, antenna segmented with terminal hook, legs without endopods, and caudal rami without acicules present. Induces galls in host (Fig. 1), typically occupied by one female and male copepod pair.

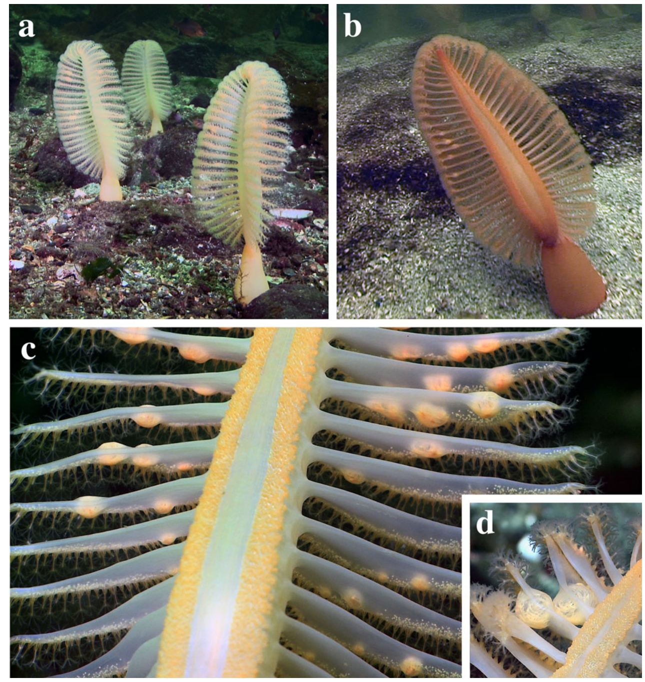

Fig. 1 In situ photographs of the orange sea pen *Ptilosarcus gurneyi* (Gray, 1860). **a**, three *Ptilosarcus gurneyi* parasitized by *Ptilosarcoma athyrmata* n. gen., n. sp., photographed on 9 Jan 2013 at Sakinaw Rock, Sechelt Inlet, British Columbia; **b**, individual *Ptilosarcus gurneyi* parasitized by *Ptilosarcoma athyrmata* n. gen., n. sp., photographed on April 2006 at Maltby Islets, Clayoquot Sound, British Columbia; **c**, close-up view of one individual shown in A, 1–3 galls are present on nearly all leaves of the sea pen; **d**, close-up of two galls induced by *Ptilosarcoma athyrmata* n. gen., n. sp

Etymology The generic name is a combination of the host genus (*Ptilosarcus)* and *sarcoma* (derived from the Greek σάρξ, meaning flesh; contemporarily referring to a tumor of the connective tissues). This combination refers to the galls or "tumors" that the copepods induce in their host sea pens.

Remarks *Ptilosarcoma* is similar to *Isidicola* in the following characters: presence of maxillipeds, unsegmented antennule, and caudal rami without acicules. However, *Ptilosarcoma* differs from *Isidicola* in antennal morphology (*Isidicola* with antennule longer than antenna, antenna unsegmented with terminal hook vs. *Ptilosarcoma* with antennule shorter than antenna, antenna segmented with terminal hook). *Ptilosarcoma* is also morphologically close to *Gorgonophilus*, based on the form of the antennae and legs, but is differentiated by the lack of a well-formed maxilliped in *Gorgonophilus* (present in *Ptilosarcoma*) and well-defined endopods on the legs (lacking in *Ptilosarcoma*). This degree of differentiation between these genera is comparable to that found between other lamippid genera (see Key to Genera), which are distinguished by differentiation of endopods and other similar characters. Molecular studies should be undertaken to independently confirm the distinctiveness of these genera.

Ptilosarcoma athyrmata, new genus, new species
Figs. 1, 2, 3, and 4

Synonomy "First *Lamippe* species" Johnstone 1969: 17–41, figs. 9–21. (not "Second *Lamippe* species" Johnstone 1969: 42–50, figs. 22–25).

Lamippe sp. Batie 1971: 31, 32, 39.

"parasitic isopod" Shimek 2005; Carefoot, n.d.

Material examined Holotype: mature female (2.1 mm), from *Ptilosarcus gurneyi*, 7–10 m depth, Roberts Bank, Strait of Georgia, British Columbia, Canada (49°0′55.17″N, 123°10′48.2″W), coll. D. Swanston, 28 August 2014 (USNM 1421905); allotype: mature male (1.4 mm), from same gall as holotype (USNM 1421906).

Paratypes: 112 females and 52 males from six *Ptilosarcus gurneyi*, same collection data as holotype (100 females and 40 males in USNM 1421907 – 1421979; 12 females and 12 males in ZRC 2016.0490; all in 95 % EtOH); seven females and eight males from *Ptilosarcus gurneyi*, 5–10 m depth, off Tsawwassen Jetty, Strait of Georgia, British Columbia, Canada (49°0′33.66″N, 123°7′7.38″W), coll. N. McDaniel, 14 January 2014 (USNM 1421980 – 1421987; 2 females and 3 males on SEM stubs, rest of specimens in 95 % EtOH).

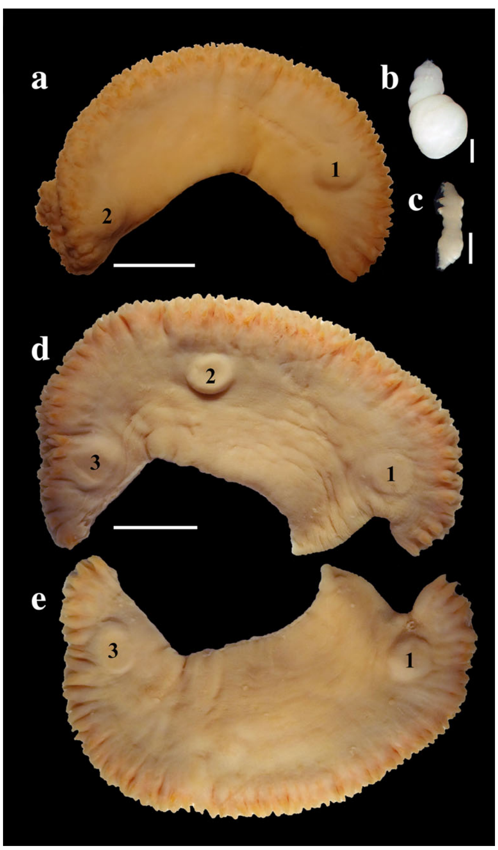

Fig. 2 Preserved leaves of the orange sea pen *Ptilosarcus gurneyi* (Gray, 1860) with galls induced by *Ptilosarcoma athyrmata* n. gen., n. sp. **a**, leaf with two galls (gall 1 contained the holotype and allotype pair); **b**, holotype (USNM 1421905) of *Ptilosarcoma athyrmata* n. gen., n. sp., ventral view; **c**, allotype (USNM 1421906) of *Ptilosarcoma athyrmata* n. gen., n. sp., lateral view; **d**, leaf showing 3 galls observed on one side; **e**, opposite side of same leaf shown in d, note that gall 2 is not observable in this view. *Scale bars* = 5 mm (**a**, **d**, **e**), 500 μm (**b**, **c**)

Diagnosis See generic diagnosis.

Description

Female Body bulbous, maximal width at approximately 2/3 of body length, tapering gradually anteriorly, rounded posteriorly (Figs. 2b and 3a); body white after preservation. Hototype 2.1 mm long, 1.0 mm maximal width. Body composed of cephalosome, two pedigerous somites, fused middle somites, and trunk with caudal rami; cephalosome often retracted partially into body and deflexed downward; segmentation indistinct between pedigerous somites. Paired depressions on body surface (possible remnants of legs).

Two pairs of antennae present; antennules lacking clear segmentation, nub-like, with approximately ten stout terminal setae (Fig. 3b and d); antennae approximately 4–5 times as long as antennules, with five segments, terminal segment produced into curved, claw shape with single seta at base (Fig. 3b, b inset, d), additional single seta on side of fourth segment. Labrum triangular, concave on posterior margin, with lobes extending posteriolaterally; lobes overlying sharply pointed maxillipeds projecting into buccal cavity; knob-shaped post oral plate between bases of maxillipeds, single seta at base of each maxilliped (Fig. 3c and d).

Leg 1 (Fig. 3d and e) immediately posterior to oral region, uniramous, with unsegmented exopod extending and oriented medially and four or five stout spines, small depression in cuticle at posteriolateral base of leg 1. Leg 2 (Fig. 3d and f) similar in morphology to leg 1, with unsegmented exopod extending to medially oriented curved point and with three or four stout spines.

Genital area a large medial depression, composed of one anal somite and pair of caudal rami, gonopores not observed. Caudal rami (Fig. 3a and g) semi-circular with 4–6 small nub-like extensions (Fig. 3g inset) in a patch oriented toward ventral side.

Male Body cylindrical anteriorly, maximal width at large, bulbous fifth somite, cephalosome smaller in diameter than rest of body (Fig. 4a); body white after preservation. Allotype 1.4 mm long, 0.4 mm maximal width. Body composed of cephalosome, two pedigerous somites, three limbless somites, genito-abdomen region and caudal rami.

Two pairs of antennae present; antennules lacking clear segmentation, but ring around middle suggestive of two fused segments, extending distally to terminal point, with approximately 10 setae along antennule (Fig. 4b–d); antennae approximately twice as long as antennules, with four segments, terminal segment produced into curved, claw shape with single

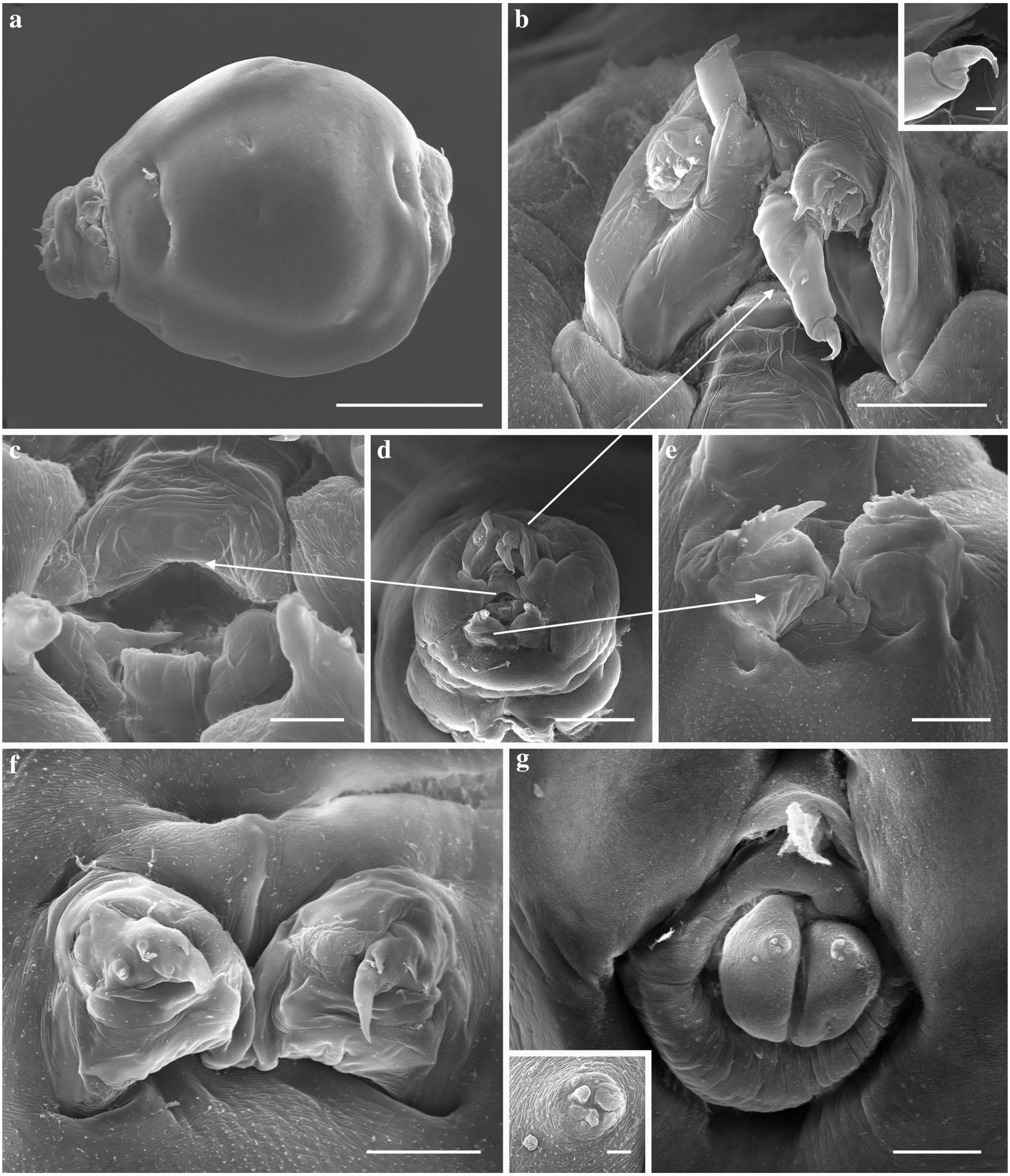

Fig. 3 Female of *Ptilosarcoma athyrmata* n. gen., n. sp. (A-G, USNM 1421980). **a**, whole specimen, ventral view; **b**, antennules and antennae, inset shows close-up of terminal hook on left antenna; **c**, buccal cone with maxilliped; **d**, overview of anterior end with antennae, buccal cone and first thoracopods indicated with arrows; **e**, first pair of thoracopods; **f**, second pair of thoracopods; **g**, posterior end, inset shows close-up of extensions on caudal rami. *Scale bars* = 500 μm (**a**), 50 μm (**b**, **e**, **f**), 5 μm (b inset), 20 μm (**c**), 150 μm (**d**), 100 μm (**g**), 10 μm (g inset)

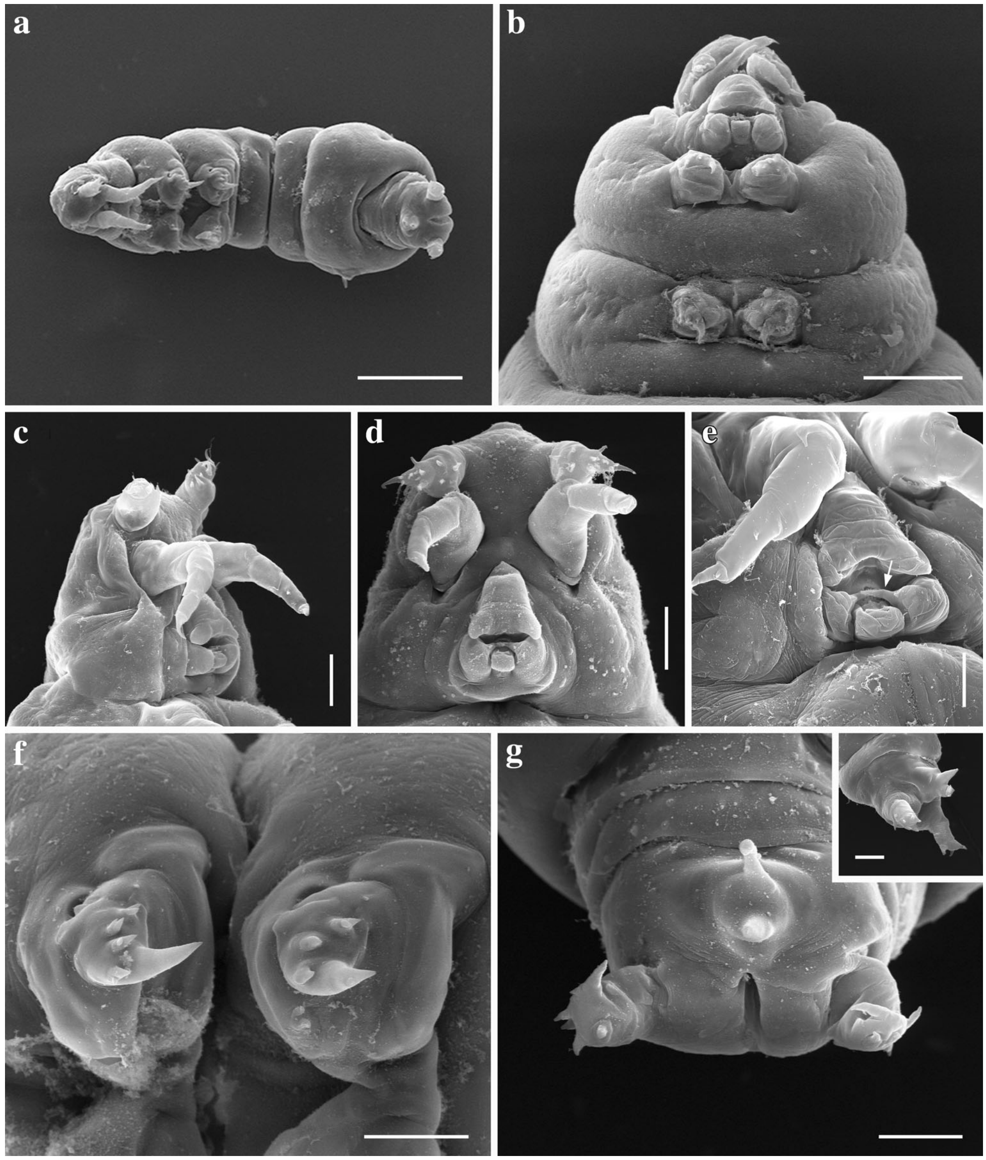

Fig. 4 Male of *Ptilosarcoma athyrmata* n. gen., n. sp. (A-G, USNM 1421980). **a**, whole specimen, ventral view; **b**, overview of anterior end with antennae, buccal cone and thoracopods; **c**, lateral view of anterior end with antennae and buccal cone; **d**, ventral view of anterior end with antennae and buccal cone; **e**, buccal cone with maxilliped indicated by arrow; **f**, first and second pair of thoracopods; **g**, genito-abdomen region, inset shows close-up in lateral view. *Scale bars* = 250 μm (**a**), 150 μm (**b**), 50 μm (**c**, **d**, **f**, **g**), 25 μm (**e**), 10 μm (g inset)

seta at base (Fig. 4c–d), additional single seta on side of first and third segments. Oral region as in female; labrum triangular, concave on posterior margin, with lobes extending posteriolaterally; lobes overlying sharply pointed maxillipeds that project into buccal cavity; knob-shaped post oral plate between base of maxillipeds, single seta at base of maxillipeds (Fig. 4c–e).

Leg 1 (Fig. 4b and f) uniramous, with unsegmented exopod extending to large, curved point oriented medially and with four stout bifurcated spines. Leg 2 (Fig. 4b and f) similar in morphology to leg 1, with unsegmented exopod extending to large, curved point oriented medially and with three stout spines; spines simple or bifurcated.

Genito-abdomen region of two slender, cylindrical somites (presumably comprising the genital and abdominal somites) anterior to caudal rami. Caudal rami (Fig. 4a and g, g inset) digitiform, semi-circular with 5–7 spines; prominent mid-ventral process anteromedial to caudal rami, mid-ventral process bifurcated, extending to one larger anterior point and one smaller posterior point (Fig. 4g, g inset); slit-like anal opening between caudal rami.

Ecology The copepods induce the formation of galls in their hosts that appear as pale orange spherical enlargements in the leaves of the sea pens (Figs. 1 and 2). The galls vary in size and shape, with smaller female copepods inducing less pronounced galls, to larger swellings where connective tissue of the host can easily be observed in living sea pens (Figs. 1c and d and 2a, d, and e). In some cases the copepods induce galls that can be observed as spherical swellings on both sides of the sea pen leaves, in other cases they are only observable from one side (Fig. 2d and e).

In total, 143 leaves from six *P. gurneyi* were dissected; the maximal number of galls per leaf was three and the average was 1.4 ± 0.6 (n = 143). Most galls had either a single female copepod (61 galls) or female and male pair (51 galls); four galls had ≥2 females, 11 galls had only a male copepod, and 16 galls had no copepods present. Those cases where copepods were not present may have been swellings from host reproductive tissue or instances where the copepods had died; most female copepods are large and conspicuous, so it is unlikely they were overlooked. Females were 1.9 ± 0.2 mm (n = 30) in length, males were 1.3 ± 0.2 mm (n = 22) in length. Developing eggs of the copepods were loose in the galls and measured 137.7 ± 11.4 μm (n = 33) in diameter; nauplius larvae were also occasionally found in the galls and measured 183.5 ± 5.0 μm (n = 7) in length.

Johnstone (1969) reported two morphologically distinct species of "*Lamippe*" from *P. gurneyi*: one found only in the leaves and one found in the peduncle and water vascular canals. Batie (1971) reported only on the species found in the leaves. As all our specimens were recovered from leaf galls, it seems likely that the copepods reported from that habitat by Johnstone (1969) and Batie (1971) and examined in the present study represent the same taxon. Johnstone (1969) indicated that *P. gurneyi* from Puget Sound (Des Moines, Pierce County and Gordon Point, King County, WA, USA) were "nearly always infested" with this copepod, while Batie (1971) reported the copepod in 73.5 % of *P. gurneyi* from Dash Point, Puget Sound, WA, USA in June. Johnstone (1969) suggested that the copepods reach their peak intensities by May (~1 copepod gall per leaf; 81 galls on a sea pen with 82 leaves) versus only 16 galls present on a single sea pen in February. Johnstone (1969) completed studies on living copepods, including providing details on the life cycle of the parasites. These studies represent some of the very few observations on the reproduction and development of lamippid copepods, as well as description of males depositing spermatophores on females. Unfortunately, the specimens of Johnstone (1969) are not known to exist at the University of Puget Sound (Peter Wimberger, pers. comm.) and attempts to locate the specimens of Batie (1971) were unsuccessful.

Distribution and Hosts Known from Strait of Georgia, British Columbia, Canada and Puget Sound, WA, USA in *Ptilosarcus gurneyi*. Galls observed widely along the south coast of British Columbia (McDaniel, pers. obs.) and *Ptilosarcoma athyrmata*, n. gen., n. sp. should be looked for wherever *P. gurneyi* occurs in order to determine the extent of host/parasite range overlap. To our knowledge, galls have not been noted in the literature from *P. gurneyi* in its southern range (e.g., Nutting 1909).

Etymology The specific name is derived from the ancient Greek noun ἄθυρμα, meaning, in the plural, beautiful objects or adornments, as the galls induced by the copepods are reminiscent of ornaments on a Christmas tree. The adornments, being harmful to the sea pens, are only beautiful to the eye of the beholder. The name is used as a noun in apposition.

Remarks and discussion

There are now 11 genera in Lamippidae (see Key) and with the description of the new species, currently there are 52 species and one subspecies of lamippid copepods found in 17 families of octocorals belonging to Alcyonacea and Pennatulacea (Table 1). At present, species of Helioporacea belong to the only octocoral order not known to be parasitized by lamippids. However, new species descriptions (Uyeno 2015) and records of potentially undescribed species (Baillon et al. 2014; De Clippele et al. 2015) indicate that the family is more diverse than currently recognized. Overlooked species are probably more common in the non-gall forming genera than those that induce galls in hosts (e.g., *Gorgonophilus, Isidicola*, *Ptilosarcoma* n. gen., and *Sphaerippe*), where hosts are more easily recognized as being parasitized.

Females of the new genus and species are similar to those of *Gorgonophilus canadensis* Buhl-Mortensen and Mortensen, 2004 and *Sphaerippe caligicola* Grygier, 1980 in general morphology and in that they induce the formation of galls in their hosts [*Paragorgia* sp. and *Callogorgia* sp., respectively]. However, individuals of *G. canadensis* and *S. caligicola* have well-defined endopods and males of both species lack mid-ventral processes. Also, in contrast to the galls made by *Ptilosarcoma athyrmata*, n. gen., n. sp. that typically have only one female or one female and one male per gall, *G. canadensis* was reported to regularly contain two females and one male per gall (Buhl-Mortensen and Mortensen 2004) as well as seven or eight egg sacs. Egg sacs were never encountered in the galls examined in this study, only loose eggs. The galls produced by *G. canadensis* extend into chimney-like structures not found in sea pens parasitized by *Ptilosarcoma athyrmata*, n. gen., n. sp. The prominent mid-ventral process on males of *Ptilosarcoma athyrmata*, n. gen., n. sp. is similar to those observed by Stock (1973) on males of *Enalcyonium scorpio* Stock, 1973 and he noted that this structure was found in species belonging to other lamippid genera. The function of the structure remains unknown. The new species shares some characters with *Isidicola antarctica* Gravier, 1914 but this Antarctic species that parasitizes *Primnoisis* spp. is poorly known and in need of redescription.

Note that two websites (Shimek 2005; Carefoot, n.d.) contain images of infested *P. gurneyi* but erroneously identified the galls as being produced by parasitic isopods. There are no isopods known to parasitize any cnidarians.

Key to genera of Lamippidae

1. Female body stelliform, with large lateral processes . . 2
Female body fusiform or swollen, without long processes 3
2. Female with 6 pairs of tapering body processes . . . . *Magnippe*
Female with 9 pairs of body processes, 5 with bifid tips . . . . *Linaresia*
3. Maxillipeds present or vestigial 4
Maxillipeds absent 7
4. Antennule segmented, caudal rami with acicules 5
Antennule unsegmented, caudal rami without acicules . . 6
5. Legs 1 and 2 with well-developed endopods bearing digitate processes . . . . *Lamippina**
Legs 1 and 2 without well-developed endopods . . . . *Lamippe*
6. Antennule longer than antenna;
antenna unsegmented with terminal hook. . . . . . *Isidicola*
Antennule shorter than antenna;
antenna segmented with terminal hook. . . . *Ptilosarcoma*, new genus
7. Caudal rami without acicules 8
Caudal rami with acicules . . . . *Lamippula*
8. Antennule clearly segmented 9
Antennule unsegmented or weakly segmented 10
9. Body with minute papillae . . . . *Enalcyonium*
Body without minute papillae . . . . *Sphaerippe*
10. Legs 1 and 2 with well developed endopods;
female with lateral lobes on the cephalosome. . . . . *Gorgonophilus*
Legs 1 and 2 with reduced, unarmed endopods; body fusiform . . . . *Lamippella*

*A note on *Lamippina laubieri* Bouligand, 1960. This species name was introduced in a table and was very poorly described in that there was no descriptive text, and the species was not indicated as being a new species. It was stated by Bouligand (1960) to be very close to *L. aciculifera* (Zulueta, 1908). However, only a year later, the same author (Bouligand 1961) did not mention the species in another paper dealing with, in part, *Lamippina*. The "description" of *L. laubieri* is technically valid and the name is available in that characters, however minor, were provided in the table of Bouligand (1960) to distinguish it from *L. aciculifera*. However, even Bouligand did not recognize *L. laubieri* as a distinct species in any of his subsequent papers (e.g., Bouligand 1961, 1965, 1966). The host of *L. laubieri*, *Leptogorgia sarmentosa*, is also from the same region (eastern Atlantic) as *L. aciculifera*. Finally, although *L. aciculifera* was described from the host *Alcyonium palmatum*, Bouligand (1966: 299) indicated that juvenile *L. aciculifera* were found in *Leptogorgia sarmentosa*. We therefore consider *L. laubieri* to apply to juveniles of *L. aciculifera* and the two names are synonymous.

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