ABSTRACT. – Pseudopagurodes piliferus (Henderson, 1888), heretofore known only from its female holotype, is redescribed and illustrated based on recent collections, and an error in the stated type locality is corrected. Additionally, a superficially very similar species, previously assigned to the genus Nematopaguroides, N. reconditus Wang & McLaughlin, 2000, is transferred to Pseudopagurodes. The rationale for the transfer and the similarities between the two species are discussed.

KEY WORDS. – Crustacea, Decapoda, Anomura, Paguridae, Pseudopagurodes piliferus redescription, Pseudopagurodes reconditus new combination, Philippine Islands.

INTRODUCTION

De Saint Laurent (1969) speculated that the three species assigned to Pagurodes Henderson, 1888 by that author actually represented three distinct genera. She designated Pagurodes inarmatus Henderson, 1888 as the type species, and indicated that new genera would be proposed for Pagurodes limatulus Henderson, 1888 and Pagurodes piliferus Henderson, 1888 in a subsequent publication. Both species were, at that time, based on single specimens, although a second specimen had been doubtfully included in Pagurodes piliferus by Henderson (1888). De Saint Laurent’s subsequent publication was never completed. After finding several specimens among the collections of the 1991 French-Indonesian expedition to the Kai and Tanimbar Islands of Indonesia that appeared to agree with Henderson’s (1888) original description of P. limatulus and Alcock’s (1905) supplemental diagnosis, McLaughlin (1997) examined the type specimens of all three taxa.

For P. limatulus, McLaughlin proposed the genus Michelopagurus McLaughlin, 1997, and provided a detailed redescription based on the holotype and Indonesian specimens. At the same time, she also proposed the genus Pseudopagurobes McLaughlin, 1997 for Pagurodes piliferus, and determined that the doubtfully assigned specimen actually represented Pagurus compressipes (Miers, 1884). Although McLaughlin (1997, Figs. 13 e, f; 37a, b) illustrated the female holotype of P. piliferus, because it was not part of the Indonesian fauna, she did not redescribe the species. Despite McLaughlin’s (2003) subsequent report of sexual tube development in the male of Pseudopagurobes, detailed information on P. piliferus was still woefully inadequate. In recent examinations of paguroid material from the MUSORSTOM Philippine expeditions (1976, 1985), the PANGLAO 2004 and the PANGLAO 2005 expeditions, the authors independently first assigned several of their specimens to Nematopaguroides reconditus Wang & McLaughlin, 2000. However, when it was recognized that McLaughlin (2003) had described identical male sexual tube development for Pseudopaguristes piliferus, the status of both species was re-evaluated. The Philippine material available proved to represent P. piliferus. We now present a complete redescription of Henderson’s (1888) taxon and compare and contrast it with the very superficially similar N. reconditus.

MATERIALS AND METHODS

The specimens described herein have come from the collections of the Muséum national d’Histoire naturelle, Paris, France (MNHN, with the suffix Pg), the Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore, Republic of Singapore (ZRC), and the National Museum of the Philippines (NMP), Manila, the Philippines; all have been deposited in or returned
to these institutions. Terminology for the descriptions generally follows that of McLaughlin (2004), with the exception of the substitution of pleon for abdomen as recommended by Schram & Koenemann (2004). The abbreviations NHM, HMS, DW, CP, stn, and ovig. refer to the Natural History Museum, London, His Majesty’s Ship, Warén dredge, beam trawl, station, and ovigerous, respectively. MUSORSTOM is the acronym for the joint expeditions of the MNHN and the Office de la Recherche scientifique et technique d’Outre-Mer (ORSTOM), now Institute de Recherche pour le Développement (IRD). Panglao is the name of the Philippine island around which the expeditions surveyed. One measurement, shield length, measured from the midpoint of the rostral lobe to the midpoint off the posterior margin of the shield provides an indication of animal size and is given in parentheses following the specimen’s sex. Ocular peduncle length was measured on the lateral surface of the left peduncle from the distal margin of the cornea to the proximal margin of the ultimate peduncular segment; corneal diameter represented the maximum diameter of the cornea measured across the dorsal surface. Data for MUSORSTOM 3 stations were provided by Forest (1989). Data for the Panglao expedition were obtained in the field by the second author, a participant in the expeditions. Latitudes and longitudes are given only for the beginning of each trawl.

**TAXONY**

**PAGURIDAE** Latreille, 1802

**Pseudopagurodes** McLaughlin, 1997 emended


**Type species.** – By original designation, *Pagurodes piliferus* Henderson, 1888; gender masculine.

**Diagnosis.** – Eleven pairs of biserial or distally quadriserial phyllobranchiate gills. Rostrum reduced and rounded. Ocular acicles slender, well separated. Maxillule with external lobe of endopod obsolete or well developed, not recurved. Third maxilliped with well developed crista dentata and one accessory tooth; merus with or without prominent dorsodistal spine. Sternite of third maxillipeds (thoracic sternite IX) unarmed, with or without median indentation. Chelipeds subequal. Dactyls of ambulatory legs without conoecous spinules or spinies on ventral margins. Fourth pereopods semiciliate; propodal rarl with single row of scales; with or without preungual process at base of dactylar claw.

Males with stout sexual tube developed from coxa of right fifth pereopod, directed posteriorly or toward exterior and drawn out into long filament; coxa of left usually with papilla or short tube; unequal left pleopods on pleomerers three to five with external rami long, slender, internal rami reduced, vestigial or absent. Females with paired gonopores, no paired and modified first pleopods, three unequivally biramous left pleopods on pleomerers two to four, pleopod five as in males. Uropods asymmetrical. Telson with transverse indentations, posterior lobes symmetrical or only weakly asymmetrical, separated by median cleft; oblique terminal margins with each few spines or spinules.

**Remarks.** – During a study of paguroids in the collections of the Institute of Oceanology of the Chinese Academy of Sciences at Qingdao, People’s Republic of China, Wang & McLaughlin (2000) described a species that they assigned to *Nematopagurides* Forest & de Saint Laurent, 1968. The genus, known previously only from the western Atlantic off Brazil, had been distinguished by its authors from *Nematopagus* A. Milne-Edwards & Bouvier, 1892 by having the right male sexual tube directed toward the exterior rather than passing ventrally across the body from right to left, and by the absence, in females, of paired and modified first pleopods. Having no knowledge of males of *Pseudopagurodes* at that time, Wang & McLaughlin compared and contrasted *N. reconditus* Wang & McLaughlin, 2000 only with the species of *Nematopagurus* occurring regionally. However, when specimens seemingly identifiable with both *P. piliferus* and *N. reconditus* were found in the in the Philippines, we felt it imperative to make a critical re-examination of Henderson’s (1888) species. We found the two taxa so similar morphologically that assignment to two different genera could not be justified. Our rationale for transferring *N. reconditus* to *Pseudopagurodes* rather than placing that genus in synonymy with *Nematopaguridae* is given in the discussion that follows the taxonomic account.

**Pseudopagurodes piliferus** (Henderson, 1888)

(Figs. 1–3)

*Pagurodes piliferus* Henderson, 1888: 96 (in part), Pl. 9 Fig. 5; *Pseudopagurodes piliferus*: McLaughlin, 1997, Figs. 35 e, f; 37a, b.

**Material examined.** – Holotype, ovig. female (4.5 mm), HMS CHALLENGER, stn 204a or b, the Philippines, 12º43’N 122º09’E, 189 or 210 m, 2 Nov.1874 (NHM 88.33) (see Remarks).

**Other material.** – MUSORSTOM 1: 1 male (4.8 mm) (MNHN Pg 7705), stn 12, 14º00.8N 120º20.5’E, 210–187 m, 20 Mar.1976; 1 male (2.9 mm) (MNHN Pg 7706), stn 26, 14º00.9’N 120º16.8’E, 186 m, 22 Mar.1976; 1 male (2.1 mm) (MNHN Pg 7707), stn 30, 14º01.3’N 120º18.7’E, 186–177 m, 22 Mar.1976. MUSORSTOM 3: 2 males (3.2, 3.7 mm) (MNHN Pg 7708), stn CP 86, 14º00.4’N 120º17.5’E, 187–192 m, 31 May 1985; 2 males (3.0, 3.0 mm), 1 female (2.4 mm), 1 ovig. female (3.8 mm) (MNHN Pg 7709), stn CP 87, 14º00.6’N 120º19.6’E, 197–191 m, 31 May 1985; 1 male (3.3 mm) (MNHN Pg 7710), stn CP 92, 14º03.0’N 120º11.5’E, 224 m, 31 May 1985; 4 males (1.8–4.7 mm), 1 female (3.0 mm) (MNHN Pg 7711), stn CP 100, 14º00.15’N 120º17.6’E, 189–199 m, 1 Jun.1985; 4 males (2.6–3.3 mm) (MNHN Pg 7712), stn CP 101, 14º00.15’N 120º19.5’E, 196–194 m, 1 Jun.1985; 2 males (2.6, 3.6 mm) (MNHN Pg 7713), CP 145, 11º01.6’N 124º04.2’E, 214–246 m, 7 Jun.1985.
Fig. 1. *Pseudopagurodes piliferus* (Henderson, 1888). Male from MUSORSTOM 3, stn CP 145 (3.6 mm, MNHN Pg 7713). A, shield and cephalic appendages (aesthetascs omitted); B–F, mouthparts left, internal view); B, maxillule; C, maxilla; D, first maxilliped; E, second maxilliped; F, third maxilliped; G, carpus, propodus and dactyl of right fourth pereopod (lateral view). Scales = 1 mm.
McLaughlin & Rahayu: *Pseudopagurodes* vs *Nematopaguroides*

of right cheliped or slightly beyond; one or two moderate to long setae every four to six articles.

Maxillule (Fig. 1B) with external lobe of endopod moderately well developed, not recurved. Maxilla (Fig. 1C) with proximal lobe of scaphognathite very broad. First maxilliped (Fig. 1D) with slender exopod. Second maxilliped (Fig. 1E) with exopod only approximately 1.3 longer than endopod. Third maxilliped (Fig. 1F) with unarmed merus and carpus. Sternite of third maxillipeds with small median indentation.

Right cheliped (Figs. 2A, 3) moderately slender, stouter, but not necessarily longer than left; dactyl 0.7–0.8 length of palm, dorsomesial margin usually delimited by row of closely-spaced, moderate to long setae; cutting edge with two broad calcareous teeth in proximal 0.7, row of corneous teeth distally, terminating in small corneous claw, slightly overlapped by fixed finger. Palm 0.8–0.9 length of carpus; dorsomesial margin delimited by row of tiny to small spines and adjacent row of moderately long to long setae, convex dorsal surface with abundance of moderately long, quasi stiff setae rather closely-spaced but not obscuring integument, often with two to four small spines in dorsal midline proximally, dorsolateral margin with row of long setae extending full length of fixed finger, occasionally few small tubercles or spinules proximally; mesial, lateral and ventral surfaces unarmed but with tufts of long setae. Carpus slightly longer than merus; dorsodistal margin usually with small spine mesially, dorsomesial margin with row of small to prominent spines not concealed by row of long setae, dorsolateral margin with row of spines accompanied by transverse rows of stiff setae, dorsal surface with scattered spinulose tubercles or protuberances, each accompanied by few stiff setae; mesial, lateral and ventral surfaces all with scattered tufts of setae, longest and most numerous ventrally. Merus with short transverse rows of moderately short setae; small spine distally, partially concealed by transverse ridges of long, sometimes capsulate setae extending onto ventral surface.
prominently curved dactyl. Fourth pereopods (Fig. 1G) each with long, subsemicircular anterior lobe (Fig. 2E), with row of setae. Ischia unarmed, but each with few setae. Sternite sparse setae on second pereopods, third unarmed but with each with one to few spines or spinulose protuberances and each with row of low transverse ridges and setae on dorsal pereopods; lateral surfaces each with row of sparse setae. Meri occasionally irregular row of small spines on second transverse, slightly spinulose ridges and long setae, or each with one to three smaller spines in proximal half and Carpi each with dorsodistal spine, dorsal surfaces unarmed and each with one to three smaller spines in proximal half and transverse, slightly spinulose ridges and long setae, occasionally irregular row of small spines on second pereopods; lateral surfaces each with row of sparse setae. Meri each with row of low transverse ridges and setae on dorsal margin; mesial and lateral faces glabrous; ventral surfaces each with one to few spines or spinulose protuberances and sparse setae on second pereopods, third unarmed but with sparse setae. Ischia unarmed, but each with few setae. Sternite of third pereopods with roundly subrectangular or subsemicircular anterior lobe (Fig. 2E), with row of setae subdistally. Fourth pereopods (Fig. 1G) each with long, prominently curved dactyl.

Ambulatory legs (Figs. 2C, D) generally similar; dactyl long, 1.3–1.9 length of propodi, slender, in dorsal view straight, in lateral view, curved ventrally; dorsal margins each with row of long stiff bristles and often additional ventral row of rather widely-spaced long setae, mesial faces each with weak longitudinal sulcus, sometimes also with median row of tufts of sparse setae, row of long setae ventrally accompanied by few widely-spaced tiny corneous spinules proximally. Propodi each with row of transverse low ridges and long setae dorsally; lateral faces each with row of sparse setae; ventrodistal margins each with one small corneous spine. Carpi each with dorsodistal spine, dorsal surfaces unarmed or each with one to three smaller spines in proximal half and transverse, slightly spinulose ridges and long setae, occasionally irregular row of small spines on second pereopods; lateral surfaces each with row of sparse setae. Meri each with row of low transverse ridges and setae on dorsal margin; mesial and lateral faces glabrous; ventral surfaces each with one to few spines or spinulose protuberances and sparse setae on second pereopods, third unarmed but with sparse setae. Ischia unarmed, but each with few setae. Sternite of third pereopods with roundly subrectangular or subsemicircular anterior lobe (Fig. 2E), with row of setae subdistally. Fourth pereopods (Fig. 1G) each with long, prominently curved dactyl.

Males with elongate right sexual tube (Fig. 2F) and very short to short left. Coxae of fifth pereopods in females each with tuft of long setae, much denser on left.

Telson (Fig. 2G) with slightly asymmetrical posterior lobes separated by broad median cleft; terminal margins slightly to distinctly oblique, with three to five spines often increasing in size toward outer angles.

**Colouration.** – Colour generally red-orange (Fig. 3). Shield red-orange; ocular peduncles transparent with yellow area proximal to each black cornea; antennal and antennular peduncles transparent or pale orange. Dactyls and propodi of both chelipeds white with faint speckles of pale orange; carpi red-orange; meri red-orange with small white area on each mesial face. Dactyly of ambulatory legs white, each with orange patch distally and proximally; propodi and meri white, each with orange patch ventrally and proximally; meri mottled red-orange and white. Pleon mottled red-orange and white.

**Distribution.** – The Philippines; 154–246 m.

**Variation.** – Seemingly characteristic of *P. piliferus* is the abundance of stiff setae on the dorsal surfaces of the chelae and the delimiting marginal rows of longer simple setae; however, the three males from the first MUSORSTOM expedition had sparser and longer setae on the dorsal surfaces of the chelae and lacked the distinctive marginal setation. The development of capsule setae definitely appeared to be a function of animal size, as no capsule setae were observed in small individuals. However, when capsule setae were present, they were primarily restricted in their distribution to the carpi and meri of the chelipeds, exclusive of the dorsal surfaces of these segments.

As indicated in the redescription, another variable is seen in the ratio of corneal diameter to peduncular length, which, on the basis of limited sample size, does not appear to be a function of sex or animal size. In contrast, the development of the sexual tubes does seem to be size related, with shorter right and small left tubes characteristic of smaller males.
Remarks. – The type locality, HMS CHALLENGER station 204 (a or b) was cited in the species description by Henderson (1888) as off Tablas Island, but in the station data list, off Panay Island is given as the locality for station 204. In his text, Henderson gave the depth for *P. piliferus* as 100 or 115 fms (189 or 210 m), which is the depth listed in the station data for Panay Island. The station data depth for the station of Tablas Island (stn 207) is 700 fms (1,280 m). It seems safe to assume that the report of off Tablas Island as the type locality for this species is in error and that the correct type locality is off Panay Island.

**Pseudopagurodes reconditus** (Wang & McLaughlin, 2000) new combination

*Nematopaguroides* reconditus Wang & McLaughlin, 2000: 957, Figs. 1, 2.

**Remarks.** – Not only in the development of male sexual tubes and absence of female paired and modified first pleopods are *P. reconditus* and *P. piliferus* extremely similar, but in virtually all of their readily apparent attributes. They share a short, moderately broad shield, rounded rostral lobe, short, stout ocular peduncles with dilated corneas and slender ocular acicles, long antennular and antennal peduncles, subequal and weekly armed chelipeds, elongate and slender ambulatory legs, and similarly shaped telson. That they can justifiably be considered distinct species is based on four characters in particular: 1) The gills of *P. piliferus* are distally quadriserial, while those of *P. reconditus* are biserial; 2) The external lobe of the maxillulary endopod is well developed in *P. piliferus*, obsolete in *P. reconditus*; 3) The dorso-distal margin of the merus of the third maxillipeds is not armed in *P. piliferus*, but provided with a prominent spine in *P. reconditus*; 4) When viewed dorsally, the dactyls of the ambulatory legs are straight in *P. piliferus*, whereas they are distinctly twisted in *P. reconditus*. Additionally, but potentially subject to more variation is the absence of a preungual process at the base of the claw of the fourth pereopod of *P. piliferus* and the more uniform covering of setae on the dorsal surfaces of the chelae with accompanying longer setae on dorsomesial and dorsolateral margins. A well developed preungual process is usually present on the fourth pereopod in *P. reconditus* and the setation of the chelipeds is sparser and the marginal setae usually not forming uniform rows.

**DISCUSSION**

As previously indicated, *Nematopaguroides* was proposed for two western Atlantic species, *N. fagei* Forest & de Saint Laurent, 1968 and *N. pusillus* Forest & de Saint Laurent, 1968. However, the assignment of the latter species was considered questionable by the authors because their single male had not only an elongate, filiform right sexual tube but a similar but slightly shorter left tube. Of the genera possessing sexual tubes known at the time, Forest & de Saint Laurent pointed out that when two tubes were present, one was always less developed, often rudimentary, thus the practically equal development of the tubes in *N. pusillus* was exceptional among pagurids. Nonetheless, they were reluctant to establish a second new genus for a single specimen based on that character alone. Because their South China Sea species exhibited development of a short left sexual tube, Wang & McLaughlin (2000) considered the species intermediate between the two western Atlantic species and confirmation of the accurate assignment of *N. pusillus* to the genus. We now consider that interpretation incorrect. Wang & McLaughlin’s species is more appropriately assigned to *Pseudopagurodes*.

The number of genera now known to have male sexual tube development has increased considerably in the last three decades, and both intrageneric and intraspecific variation in development of one or both tubes is recognized as much commoner. It would appear that *Nematopaguroides* and *Pseudopagurodes* share apparently identical development of the right male sexual tube, with variability in development of the left seen in *P. piliferus* and *P. reconditus* and unknown in *N. fagei* and *N. pusillus*. Although sexual tube development is acknowledged as a significant character in defining genera, that character alone can not be considered to the exclusion of others, as pointed out by McLaughlin & Asakura (2004), and may not always be indicative of phylogenetic relationships as demonstrated by Lemaire & McLaughlin (2003). Another character shared by the first three species is the lack of female paired first pleopods; females are unknown in *N. pusillus*. However, the loss of female paired and modified first pleopods is an evolutionary advance shared by a large number of paguroid genera (McLaughlin et al., 2007), thus not indicative of any phylogenetic relationship between these two genera.

If secondary sexual characters are excluded, what other evidence is available to substantiate the assignment of Wang & McLaughlin’s (2000) taxon to *Pseudopagurodes* rather than simply considering *Nematopaguroides* the senior synonym? Significant morphological attributes shared by *P. piliferus* and *P. reconditus* that are not similarly shared with *N. fagei* and *N. pusillus* include the narrow ocular acicles, subequal chelipeds, shape and length of the left chelae, and most importantly, the lack of corneous spines on the ventral margins of the dactyls of the ambulatory legs. The unarmed sternite of the third maxillipeds is not mutually exclusive to *P. piliferus* and *P. reconditus*, but is not a common pagurid character state. However, it, like characters of the mouthparts, is not known for *Nematopaguroides* species. Nonetheless, we believe that the aforementioned attributes are sufficiently diagnostic to justify the recognition of both genera.

Although the differences in maxillulary endopodal development and gill structure might have been reasons not to consider the two species congeneric at one time, variability in maxillulary endopodal structures has been demonstrated for species in the pagurid genus *Pylopaguropsis* Alcock, 1905 by McLaughlin & Haig (1989) and Asakura (2000) and in gill structure in the parapagurid genus *Sympagurus* Smith, 1883 by Lemaire (2004). Such variability is interpreted in those genera, as well as in *Pseudopagurodes*, as reflection of intrageneric evolutionary transition.
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LITERATURE CITED


