THE RAFFLES BULLETIN OF ZOOLOGY 2007 Supplement No. **16**: 21–27
Date of Publication: 31 Dec.2007

PSEUDOPAGURODES MCLAUGHLIN, 1997 (CRUSTACEA: ANOMURA: PAGUROIDEA: PAGURIDAE) REVISITED

Patsy A. McLaughlin
Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Road, Anacortes, WA 98221-9081B (USA)
Email: hermit@fidalgo.net

Dwi Listyo Rahayu
Research Center for Oceanography, Indonesian Institute of Sciences (LIPI), Jl. Pasir Putih 1, Ancol Timur, Jakarta 14430 (Indonesia)
E-mail: dwilistyo@yahoo.com

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 *Pseudopagurodes* 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 *Pseudopagurodes*, 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.

TAXONOMY

PAGURIDAE Latreille, 1802

Pseudopagurodes McLaughlin, 1997 emended

Pagurodes Henderson, 1888: 94 (in part); Alcock, 1901: 224 (in part); Alcock, 1905: 106 (in part); Gordan, 1956: 314 (in part); de Saint Laurent, 1969: 740 (in part).
Pseudopagurodes McLaughlin, 1997: 487; McLaughlin, 2003: 126.
Nematopaguroides – Wang & McLaughlin, 2000: 957 (in part, not *Nematopaguroides* Forest & de Saint Laurent, 1968; see remarks).

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 corneous spinules or spines on ventral margins. Fourth pereopods semichelate; propodal rasp 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; unpaired left pleopods on pleomeres 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 unequally biramous left pleopods on pleomeres 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 *Nematopaguroides* Forest & de Saint Laurent, 1968. The genus, known previously only from the western Atlantic off Brazil, had been distinguished by its authors from *Nematopagurus* 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 *Nematopaguroides* 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, 14º00.8'N 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 120º17.8'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.

PANGLAO 2004: 1 female (3.6 mm) (MNHN Pg 7714), stn T3, Panglao Island, Bolod, 9°31.5'N 123°46.8'E, 150 m, 31 May 2004; 1 male (3.5mm), 1 ovig. female (3.3mm) (NMP), stn T17, Bohol Island, Cortes, 9°41.8'N 123°49.1'E, 132–137 m, 19 Jun.2004; 1 female (2.6 mm) (MNHN Pg 7715), stn T25, Bohol Island, Cortes, 9°41.1'N 123°49.3'E, 160–210 m, 24 Jun.2004.
PANGLAO 2005: 7 males (2.6–3.8 mm), 8 females (2.7–4.0 mm), 1 ovig. female (3.2 mm) (ZRC, NMP), stn CP 2348, 09º29.6'N 123º52.5'E, 164–196 m, 24 May 2005.

Redescription. **–** Shield (Figs. 1A, 3) slightly longer than broad to somewhat broader than long, with tufts of sparse setae outlining gastric region. Rostrum broadly rounded, not reaching to slightly over-reaching level of triangular lateral projections, unarmed but often with few short setae. Lateral projections each with small marginal or submarginal spine. Posterior median plate moderately broad, membranous or very weakly calcified anteriorly.

Ocular peduncles 0.6–0.8 shield length; corneas noticeably dilated, 0.4–0.8 peduncular length; ocular acicles narrowly triangular, each with prominent submarginal spine; separated by slightly less to slightly more than basal width of one acicle.

Antennular peduncles overreaching distal margins of corneas by 0.7–0.8 lengths of ultimate segments; dorsal surface of ultimate segment with short, slightly oblique row of moderately long setae distally; penultimate segment with few scattered short setae; basal segment with small spine on distolateral margin of statocyst lobe.

Antennal peduncles overreaching distal margins of corneas by at least 0.5 lengths of ultimate segments; fifth and fourth segments each with few sparse setae; third segment with small spine at ventrodistal angle; second segment with dorsolateral distal angle prominently produced, terminating in small spine, dorsomesial distal angle with small to moderately large spine; first segment with lateral surface unarmed, ventrodistal angle with small spine. Antennal acicle reaching to proximal half of ultimate peduncular segment, not overreaching distal margin of cornea. Antennal flagellum usually reaching to tip

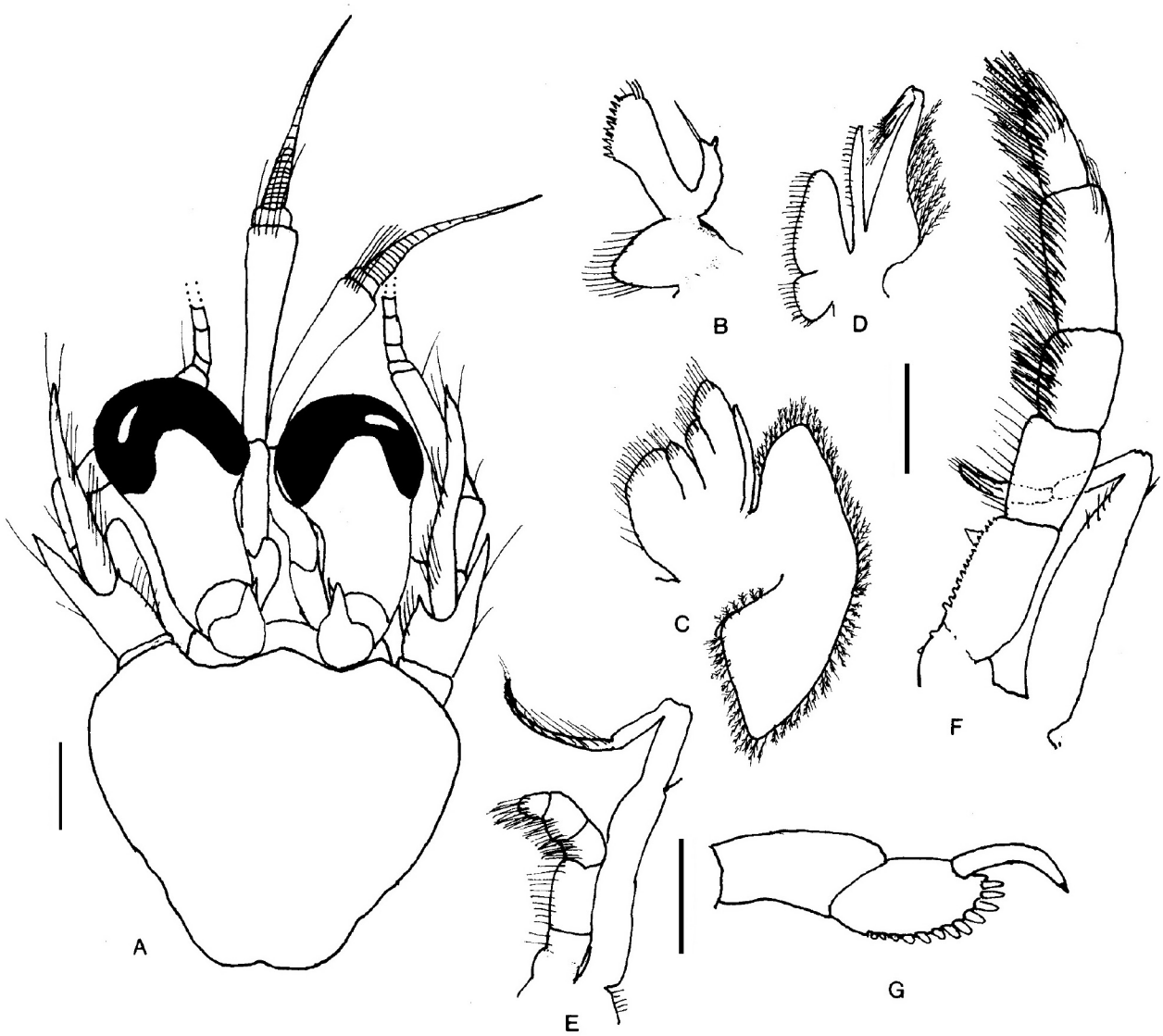

Fig. 1. *Pseudopagurodes piliferus* (Henderson, 1888). Male from MUSORSTOM 3, stn CP 145 (3.6 mm, MNHN Pg 7713). A, shield and cephalic appendages (aesthetascs omitted); B–F, mouthparts left, internal view); B, maxillule; C, maxilla; D, first maxilliped; E, second maxilliped; F, third maxilliped; G, carpus, propodus and dactyl of right fourth pereopod (lateral view). Scales = 1 mm.

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, dorsal surface with covering of moderately short stiff setae; mesial and ventral surfaces unarmed but with scattered tufts of sparse 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 on dorsal surface, lateral and mesial faces with similar rows of setae at least dorsally; ventromesial margin with one spine distally, partially concealed by transverse ridges of long, sometimes capsulate setae extending onto ventral surface

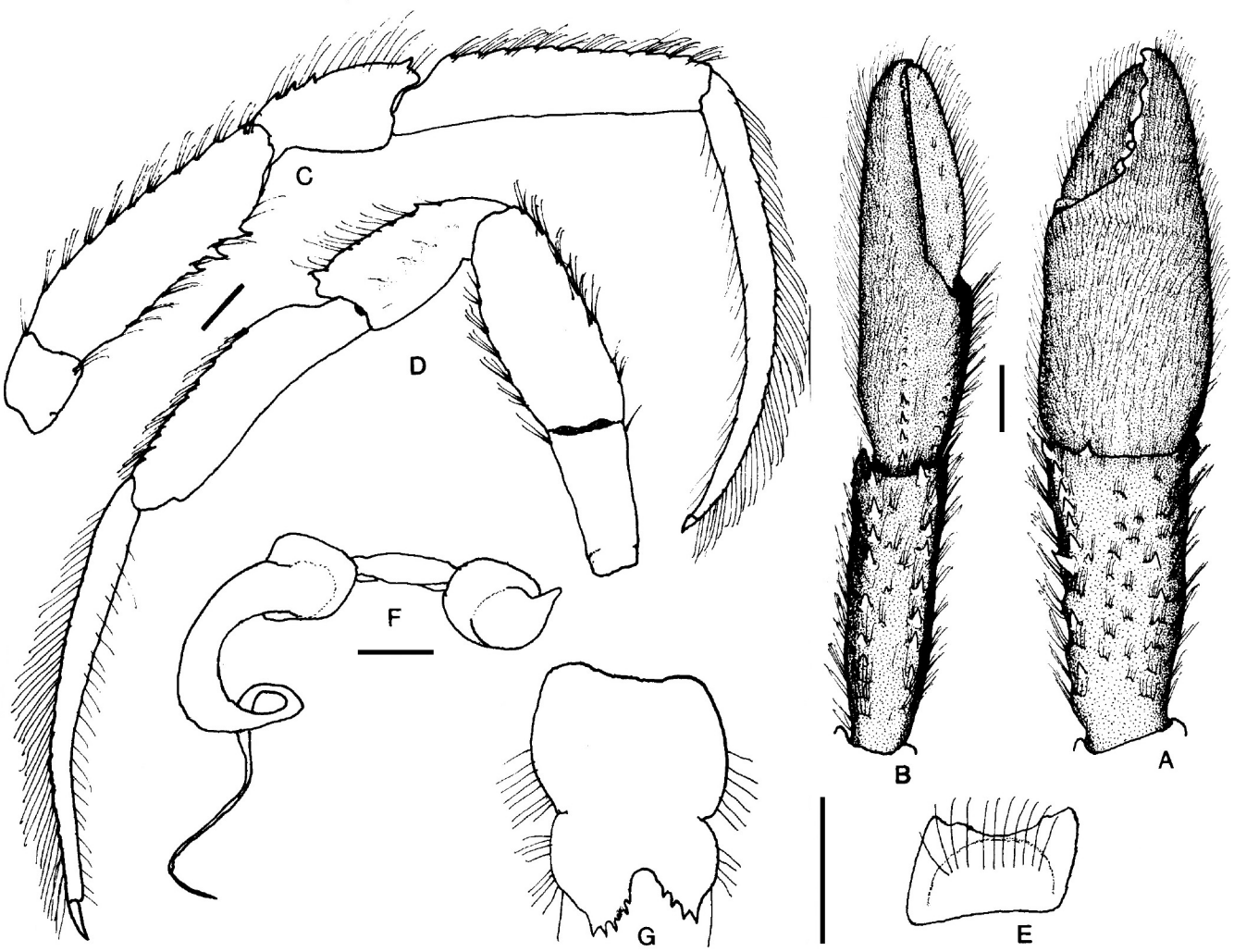

Fig. 2. *Pseudopagurodes piliferus* (Henderson, 1888). Male from MUSORSTOM 3, stn CP 145 (3.6 mm, MNHN Pg 7713). A, carpus and chela of right cheliped; B, carpus and chela of left cheliped; C, right second pereopod (lateral view); D. left third pereopod (lateral view); E, anterior portion of sternite of third pereopods; F, coxae and sternite of fifth pereopods; G, telson. Scales = 1 mm.

mesially, ventrolateral margin with two widely-spaced spines distally, also partially concealed by transverse ridges of long, often capsulate setae extending onto ventral surface laterally. Ischium with two or three low protuberances and few setae on ventrolateral margin.

Left cheliped (Figs. 2B, 3) slender, slightly shorter to slightly longer than right; dactyl and fixed finger slightly arched ventrally; dactyl 1.2–1.3 length of palm; dorsomesial margin delimited by row of long setae; dorsal and ventral surfaces each with row of moderately widely-spaced tufts of sparse setae in midline; mesial face unarmed. Palm approximately 0.5 length of carpus, elevated in midline; dorsomesial margin with row of long setae and row of small spines or spinules in larger individuals, dorsal midline with two or three spines proximally in small individuals, short to moderately long row of small spines in larger specimens, not extending onto fixed finger, dorsolateral margin with row of long setae, frequently concealing row of small spines or spinules. Carpus approximately equal to length of merus; dorsomesial and dorsolateral margins each with row of spines, dorsal surface with scattered low protuberances and long setae, often forming transverse rows of long setae in large individuals; lateral and mesial faces each with transverse rows of long, sometimes capsulate, setae, at least dorsally; ventral surface also with few transverse rows of long setae. Merus with transverse rows of setae on dorsal surface and mesial and lateral faces dorsally, ventromesial and ventrolateral faces and margins cut to form prominent ridges, each with row of long, sometimes capsulate (at least in large individuals) setae, distal-most ridge with distinct marginal spine. Ischium with two or three low protuberances and sparse tufts of setae on ventrolateral margin.

Ambulatory legs (Figs. 2C, D) generally similar; dactyls 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. Dactyls 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 capsulate setae definitely appeared to be a function of animal size, as no capsulate setae were observed in small individuals. However, when capsulate 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.

Fig. 3. *Pseudopagurodes piliferus* (Henderson, 1888). Ovigerous female from stn T3, Panglao Island (3.6 mm, MNHN Pg 7714).

***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 weakly 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 dorsodistal margin of the merus of the third maxilliped is unarmed 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 Lemaitre & 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 spinules 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 Lemaitre (2004). Such variability is interpreted in those genera, as well as in *Pseudopagurodes*, as reflection of intrageneric evolutionary transition.

ACKNOWLEDGEMENTS

The authors are indebted to Drs. Alain Crosnier, USM Taxonomie-Collections, Départment Systématique et Évolution, Muséum national d'Histoire naturelle, Paris; and Peter K.L. Ng, Department of Biological Sciences, National Univeristy of Singapore, for making the material available for study. This is, in part, a scientific contribution from the Shannon Point Marine Center, Western Washington University.

LITERATURE CITED

Alcock, A., 1901. *A descriptive catalogue of the Indian deep-sea Crustacea Decapoda Macrura and Anomala, in the Indian Museum. Being a revised account of the deep-sea species collected by the royal Indian marine survey ship Investigator. Part II Anomala or Anomura*. Indian Museum, Calcutta, 286 pp.

Alcock, A., 1905. Anomura. Fasc. I. Pagurides. *Catalogue of the Indian decapod Crustacea in the collections of the Indian Museum*, 2: i–xi, 1–197. Indian Museum, Calcutta.

Asakura, A., 2000. A review of Japanese species of *Pylopaguropsis* Alcock, 1905 (Decapoda: Anomura: Paguridae). *Crustacean Research*, **29**: 70–108.

Forest, J., 1989. Compte rendu de la Campagne MUSORSTOM 3 aux Philippines (32 mai–7 juin 1985). In: Forest, J. (ed.), Résultats des Campagnes MUSORSTOM, volume 2. *Mémoires du Muséum national d'Histoire naturelle*, (A), **143**: 9–23.

Forest, J. and M. de Saint Laurent, 1968. Résultats scientifiques des campagnes de la "Calypso", Part VII. Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961–1962). 6. Crustacés Décapodes: Pagurides. *Annales de l'Institut Océanographique de Monaco*, n.s. **45**(2): 45–172.

Gordan, J., 1956. A bibliography of pagurid crabs, exclusive of Alcock, 1905. *Bulletin of the American Museum of Natural History*, **108**: 253–352.

Henderson, J.R., 1888. Report on the Anomura collected by H.M.S. *Challenger* during the years 1873-76. *Scientific Results of the Exploratory Voyage of HMS Challenger, (Zoology)* **27**: i–xi, 1–221. Her Majesty's Stationary Office, Edinburgh etc.

Lemaitre, R., 2004. Crustacea Decapoda: A worldwide review of the hermit crab species of the genus *Sympagurus* Smith, 1883. In: Marshall, B. & B. Richer de Forges (eds.), Tropical Deep-Sea Benthos, volume 23. *Mémoires du Muséum national d'Histoire naturelle*, **191**: 85–149.

Lemaitre, R. & P.A. McLaughlin, 2003. New species of *Goreopagurus* (Decapoda: Anomura: Paguridae) from Tasmania and reevaluation of sexual tubes in hermit crab systematics. *Memoirs of Museum Victoria*, **60**(2): 221–227.

McLaughlin, P.A., 1997. Crustacea Decapoda: Hermit crabs of the family Paguridae from the KARUBAR cruise in Indonesia. In: Crosnier, A. & P. Bouchet (eds), Résultats des Campagnes MUSORSTOM, volume 16. *Mémoires du Muséum national d'Histoire naturelle*, **172**: 433–572.

McLaughlin, P.A., 2003. Illustrated keys to the families and genera of the superfamily Paguroidea (Crustacea: Decapoda; Anomura), with supplemental diagnoses of the genera of the Paguridae. *Memoirs of the Museum Victoria*, **60**(1): 111–144.

McLaughlin, P.A., 2004. A review of the hermit crab genus *Nematopagurus* A. Milne-Edwards & Bouvier, 1892 and the descriptions of five new species. In: Marshall, B. & B. Richer de Forges (eds.), Tropical Deep-Sea Benthos, volume 23. *Mémoires du Muséum national d'Histoire naturelle*, **191**: 151–229.

McLaughlin, P.A. and A. Asakura, 2004. Reevaluation of the hermit crab genus *Parapagurodes* McLaughlin & Haig (Decapoda: Anomura: Paguridae) and a new genus for *Parapagurodes doederleini* (Doflein). *Proceedings of the Biological Society of Washington*, 117(1): 42–56.

McLaughlin, P.A. & J. Haig, 1989. On the status of *Pylopaguropsis zebra* Henderson, *P. magnimanus* (Henderson), and *Galapagurus teevanus* Boone, with descriptions of seven new species of *Pylopaguropsis* (Crustacea: Anomura: Paguridae). *Micronesica*, **22**: 123–171.

McLaughlin, P.A., R. Lemaitre & U. Sorhannus, 2007. Hermit crab phylogeny: A reappraisal and its "fall-out". *Journal of Crustacean Biology*, **27**(1): 97–115.

Miers, E.J., 1884. Crustacea. In: *Report on the zoological collections made in the Indo-Pacific Ocean during the voyage of H.M.S. "Alert" 1881–2*. British Museum, London, Pp. 178–322, 513–575.

Milne-Edwards, A. and E.-L. Bouvier, 1892. Observations préliminaires sur les paguriens recueillis par les expéditions du *Travailleur* et du *Talisman*. *Annales des Sciences Naturelles, Zoologie et Paléontologie*, (7)**13**: 185–226.

Saint Laurent, M. de, 1969. Révision des genres *Catapaguroides* et *Cestopagurus* et description de quatre genres nouveaux. III. *Acanthopagurus* de Saint Laurent (Crustacés Décapodes Paguridae). *Bulletin du Muséum national d'Histoire naturelle*, (2) **41**(3): 731–741.

Schram, F.R. & S. Koenemann, 2004. Developmental genetics and arthropod evolution: on body regions of Crustacea. In: Scholtz, G. (ed.), Evolutionary Developmental Biology of Crustacea. *Crustacean Issues*, **15**: 75–92. A.A. Balkema Publishers, Lisse, etc.

Smith, S.I., 1883. Preliminary report on the Brachyura and Anomura dredged in deep water off the south coast of New England by the United States Fish Commission in 1880, 1881, and 1882. *Proceedings of the United States National Museum*, **6**(1): 21–57.

Wang, Y.-L. & P. A. McLaughlin, 2000. First report of *Nematopaguroides* (Crustacea: Decapoda: Paguridae) in the Indo-Pacific, and the description of a new species. *Proceedings of the Biological Society of Washington*, **113**(4): 956–963.