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Discovery of males of *Caligus grandiabdominalis* Yamaguti, 1954 (Copepoda: Caligidae) parasitic on redbelly yellowtail fusilier *Caesio cuning* (Bloch, 1791) from Sabah, Malaysia, with a redescription of the female of the species

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Abstract: *Caligus grandiabdominalis* was originally described from Indonesia based on adult females obtained from the redbelly yellowtail fusilier *Caesio cuning*, although it has not been subsequently reported. In this study, we describe the adult male of *C. grandiabdominalis* for the first time, along with a redescription of adult females, and present a molecular characterization based on materials collected from a fish market in Sabah, Malaysia, in 2022. *Caligus grandiabdominalis* is a member of the *Caligus bonito* group, with which it shares the following characteristics: (1) leg 4 three-segmented, (2) distal exopod segment of leg 4 with one outer and three terminal spines; (3) leg 1 with three well-developed setae along the inner margin of the distal exopod segment; and (4) a row of denticles present along the outer margin of the second endopod segment of leg 2. It can readily be distinguished from other species within the group by the absence of a sternal furca. The genital complex and abdomen of females were observed to differ in shape, which could be associated with the degree of maturation. In one of the females, the posterior corners of the genital complex were more conspicuously developed than in the original description. The genital complex and abdominal somites of the remaining three female specimens were not laterally expanded, consistent with the original description. COI sequence analysis revealed a perfect match for females, whereas the genetic distance between the sexes was 0.020. Consequently, molecular analysis revealed the examined individuals to be conspecific.

Key words: COI, ectoparasite, genital complex, marine fish, Siphonostomatoida

Introduction

The fish-parasitic siphonostomatoid copepod family Caligidae Burmeister, 1835, currently includes more than 500 species within 30 valid genera (see Walter & Boxshall 2024). Among these, the genus *Caligus* Müller, 1785 is the most specious, with 280 valid species recorded to date, followed by *Lepeophtheirus* von Nordmann, 1832, with 123 valid species (Walter & Boxshall 2024). A large major-

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ity of the *Caligus* species utilize fish as their hosts, with some species causing serious damage among aquaculture species (Costello 2009). Generally, the species of *Caligus* are comparatively well-studied and taxonomically well-defined, and there have also been a few attempts to study other aspects such as ecology, host–parasite interaction, and life cycles (Piasecki et al. 2023, Kondo et al. 2024). Among the species of *Caligus* known to be problematic in commercial aquaculture are *C. rogercresseyi* Boxshall & Bravo, 2000 and *C. elongatus* Nordmann, 1832, and accordingly, these have been well-studied (see González & Carvajal 2006, Arriagada et al. 2019, Abdel-Gaber et al. 2020, Hemmingsen et al. 2020). However, many species have not been recorded subsequent to their original descriptions, and most species descriptions are based on examinations of ovigerous females. Consequently, information on male morphology is lacking for many species, including the species that is the focus of this study: *Caligus grandiabdominalis* Yamaguti, 1954.

Caligus grandiabdominalis was described by Yamaguti (1954), based on an ovigerous female collected from the gills of the redbelly yellowtail fusilier *Caesio cuning* (Bloch, 1791) off Macassar, Sulawesi, Indonesia. However, the morphology of the males of this species has yet to be described. Following the original description, the species has not been reported, and hence a redescription based on fresh specimens is warranted. In this study, we describe both the female and male of *C. grandiabdominalis* based on material collected from the type host (*Cae. cuning*) at Sabah Fish Marketing Sdn Bhd, Sabah, Malaysia, in November 2022. We also provide cytochrome *c* oxidase I (COI) data for 3 individuals of this species.

Materials and Methods

Four redbelly yellowtail fusilier *Cae. cuning* (standard length: 25.4–27.2 cm) were purchased at a fish market (Sabah Fish Marketing Sdn Bhd) in Kota Kinabalu, Sabah, Malaysia on 10 and 11 November, 2022 (Fig. 1). The fish were identified following Nakabo (2013), then the body surfaces and gills were washed with fresh water, and four male and four female caligids were thereby obtained. The specimens were fixed in 99.5% ethanol, two females and two males were observed in lactophenol on Humes & Gooding (1964) slides, and illustrated using a drawing tube attached to a microscope (BX53, Olympus Corporation). Terminology follows Ho & Lin (2004). Two females and two males were used for molecular analysis. DNA extraction and preservation of the exoskeletons were performed using the method described by Nitta (2024). DNA extraction of one male was not successful. The exoskeletons of four preserved individuals were also used for morphological observation. All specimens are deposited in the Borneo Marine Research Institute's Repository & Museum, Universiti Malaysia Sabah, Kota Kinabalu (IPMB-Cr 01.00016 to IPMB-Cr 01.00023).

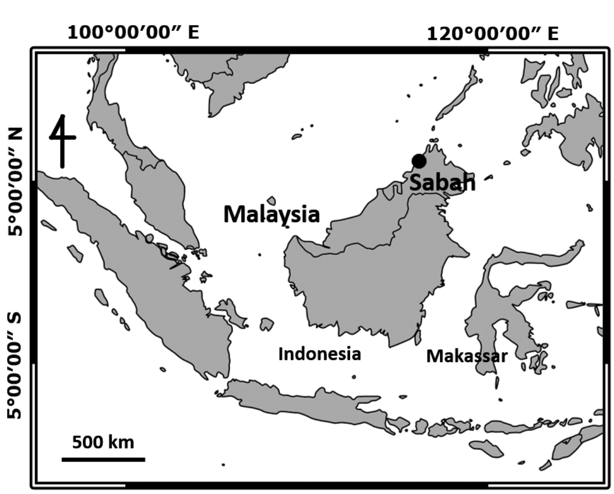

Fig. 1. Map of the sampling site.

The mtCOI region was PCR-amplified according to Øines & Heuch (2005), using primers LCO1490 (5′-GGTCAACAA ATCATAAAGATATTGG-3′) and HCO-2198 (5′-TAAACT TCAGGGTGACCAAAAAATCA-3′) (Folmer et al. 1994) for PCR-1, and WOBCOIF (5′-AGWGGRTTTTGATCHG-GNYT-3′) and WOBCOIR (5′-GGRTCAAAAAAYSTDG-TRTTTA-3′) for PCR-2 (Øines & Heuch 2005). The PCR reaction mixture totaled 25 μL in volume and consisted of 12.5 μL *Taq* PCR Master Mix (Qiagen Inc., Venlo, Nederland), 1.0 μL of each primer, 3.0 μL extracted DNA, and 7.5 μL distilled water. The PCR cycling conditions for PCR-1 were as follows: initial denaturing 95°C for 2 min, 37 cycles with denaturing at 95°C for 30 s, annealing temperature 46°C for 30 s and elongation at 72°C for 1 min. The final elongation step was 72°C for 2 min. The PCR cycling conditions for PCR-2 were as follows: initial denaturing 95°C for 2 min, 35 cycles with denaturing at 95°C for 30 s, annealing at 45°C for 30 s and elongation at 72°C for 1 min. The final elongation step was 72°C for 2 min (Øines & Heuch 2005). Amplification results were verified by 2% (w/v) agarose electrophoresis, PCR products obtained were purified using Exo-SAP-IT (USB Corporation, Cleveland, USA), and sequencing was performed commercially (Macrogen Japan Corp., Kyoto, Japan), with the sequences obtained being edited using MEGA 11 (Tamura et al. 2021). The sequences obtained were submitted to the DNA Data Bank of Japan (DDBJ). Sequence alignment was performed with CLUSTAL W (Thompson et al. 1994) in MEGA 11 (Tamura et al. 2021), using the sequence data for five other species within the *Caligus bonito* group obtained from International Nucleotide Sequence Database Collaboration (INSDC) (MN064566 for *Caligus bonito* Wilson C.B., 1905; OP425699 for *Caligus quadratus* Shiino, 1954; KF483690 for *Caligus mutabilis* Wilson C.B., 1905; and KR049058 for *Caligus hoplognathi* Yamaguti & Yamasu, 1959). The genetic distances (p-distances) of three selected specimens (one male and two females) were calculated based on the Kimura two-parameter model using MEGA 11 (Tamura et al. 2004, 2021).

Results

Description of the male of *Caligus grandiabdominalis* (Figs. 2, 3)

Body length 1.67–1.89 mm (1.75±0.10 mm, N=4) (Fig. 2A).

Habitus (Fig. 2A) in dorsal view, cephalothoracic shield subcircular, relatively narrow; fourth pediger fused to genital complex; genital complex barrel-shaped, ca. 1.1 times longer than wide, approximately 1/3 of maximum width of cephalothorax. Abdomen 2-segmented, first somite small, second (anal) somite ca. 2 times longer than first. Caudal ramus (Fig. 2B) short, armed with three short, subterminal setae and three long, terminal setae in addition to bearing row of fine sensillae along inner margin and one sensillate papilla.

Antennule (Fig. 2C) 2-segmented, proximal segment with 29 setae on anterodistal surface, distal segment shorter than proximal segment, with 1 subterminal seta on posterior margin and 11 naked setae plus 2 aesthetascs on distal margin. Antenna (Fig. 2D) 3-segmented: proximal segment elongate and unarmed; middle segment largest, armed with three corrugated adhesion pads; terminal segment smallest, with two medial setae in basal region and tooth-like projections. Postantennary process (Fig. 2E) large and sickle-shaped, with bisensillate and trisensillate papillae on basal part and trisensillate papilla on adjacent ventral cephalothoracic surface. Maxillule (Fig. 2G) dentiform, carrying subterminal seta, with 3 setae of unequal length on proximal papilla. Maxilla (Fig. 2H) 2-segmented; proximal segment (lacertus) unarmed; distal segment (brachium) slender, with flabellum located at approximately distal 1/3 of length, and calamus approximately 1.5 times as long as canna. Maxilliped (Fig. 2I) 3-segmented; first segment (corpus) long and unarmed; second (shaft) and third (claw) segments almost completely fused at mid-length with fusion line visible to comprise subchela with corpus; claw with barbel. Sternal furca absent.

Armature formula of legs as follows:

	Exopod	Endopod
Leg 1	1-0; III, 1, 3	(vestigial)
Leg 2	I-1; I-1; II, I, 5	0-1; 0-2; 6
Leg 3	I-0; I-1; III, 4	0-1; 6
Leg 4	I-0; I, III	(absent)

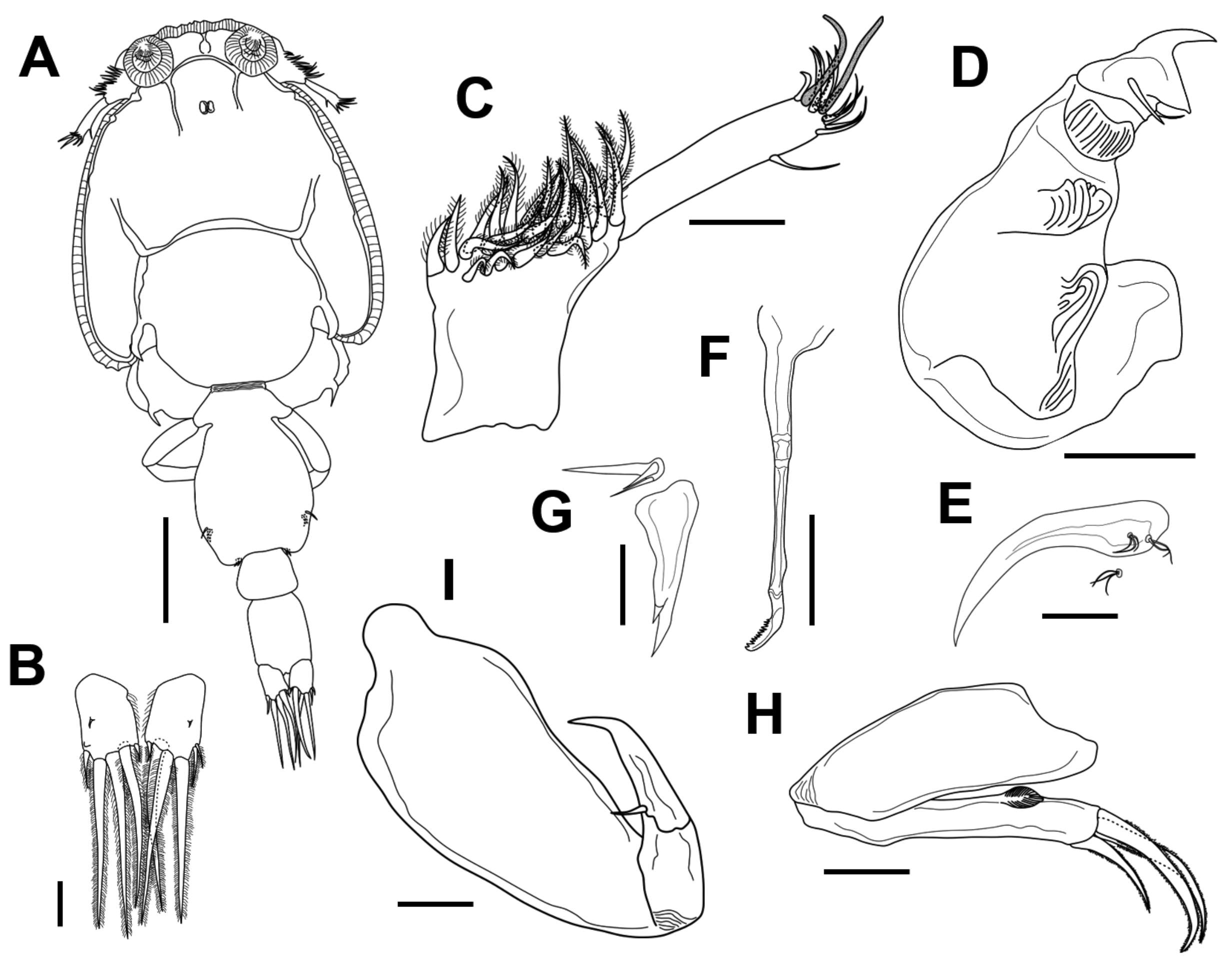

Fig. 2. *Caligus grandiabdominalis* Yamaguti, 1954, male. A. Habitus, dorsal view; B. Caudal ramus; C. Antennule; D. Antenna; E. Postantennal process; F. Mandible; G. Maxillule; H. Maxilla; I. Maxilliped. Scale bars: A=300 μm; B–I=50 μm.

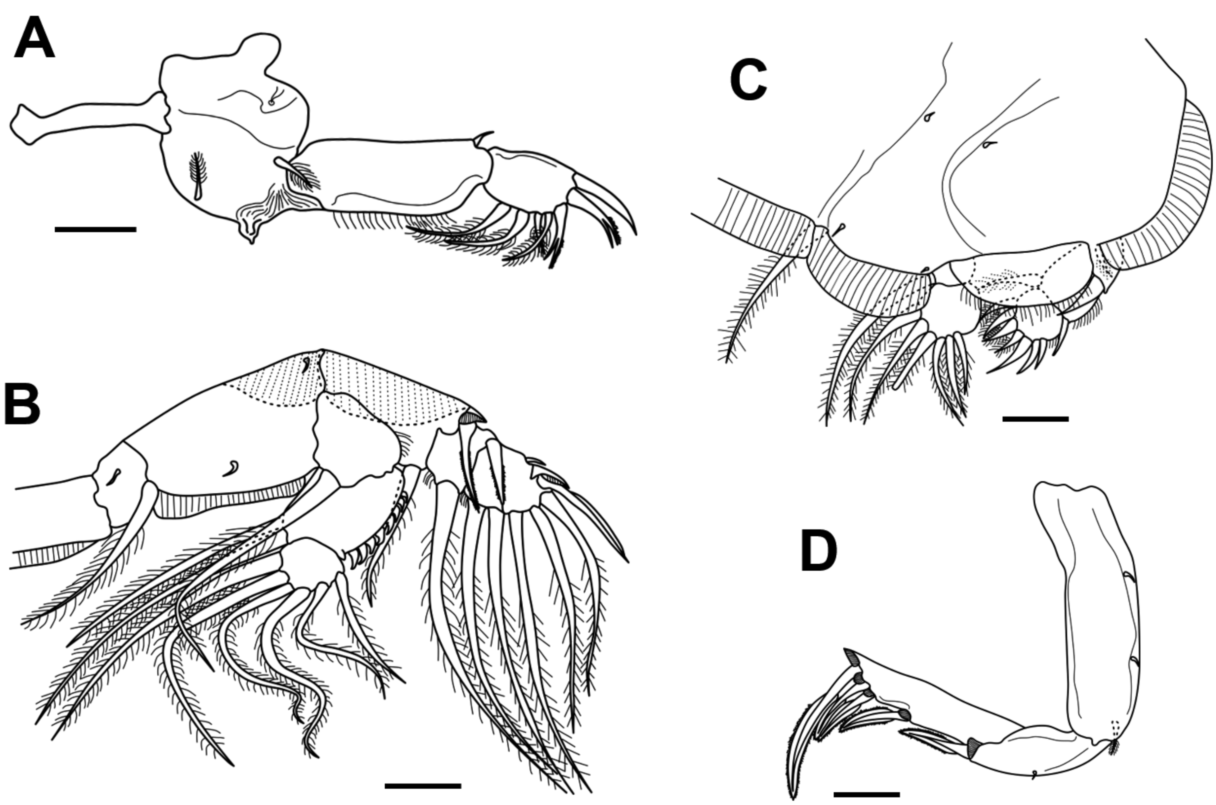

Fig. 3. *Caligus grandiabdominalis* Yamaguti, 1954, male. A. Leg 1; B. Leg 2; C. Leg 3; D. Leg 4. Scale bars: A–D=50 μm.

Leg 1 (Fig. 3A) with coxa and basis incompletely fused; intercoxal sclerite thin and long; coxa with branching outer sensilla subterminally; basis with plumose outer and inner setae; endopod vestigial, with minute vestigial element at tip; exopod 2-segmented, proximal segment long with row of fine sensillae along inner margin and short outer spine subterminally, distal segment with spines II and III, each having an accessory process.

Leg 2 (Fig. 3B) intercoxal sclerite rectangular, decorated with cuticular membrane along posterior margin; coxa small, having large inner plumose seta at distal corner and 1 surface sensilla; basis broad, with small, naked, outer seta at distal corner, medial sensilla on anterior surface, cuticular membrane along posterior margin and cuticular membrane reflexed over dorsal surface; exopod 3-segmented, first segment elongate, having outer spine obliquely crossing segment and large cuticular membrane along outer margin reflexed over dorsal surface, second segment with outer spine, third segment with 1 minute spine and pinnate spine on outer margin; endopod 3-segmented, outer margin of second segment decorated with row of denticles (Fig. 4).

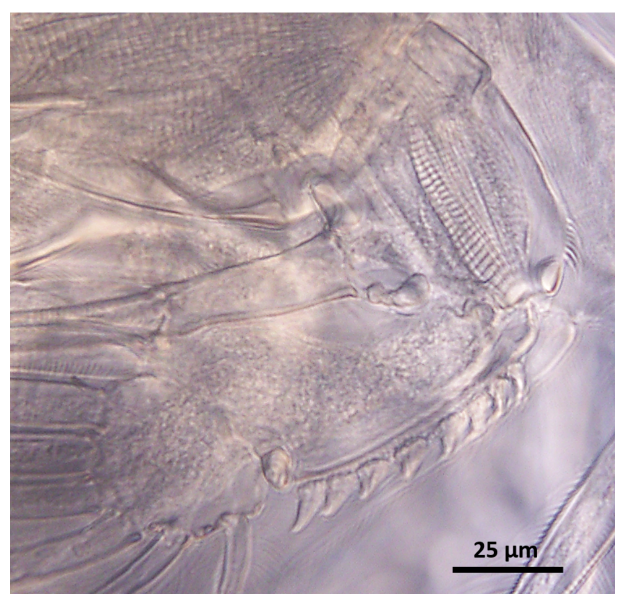

Fig. 4. Endopod of Leg 2 of *Caligus grandiabdominalis* Yamaguti, 1954, male.

Leg 3 (Fig. 3C) with protopod (apron) with large marginal membrane on outer and posterior margins, small plumose outer seta, large plumose inner seta, 2 sensilla along posterior margin and 2 sensillae on anterior surface; exopod 3-segmented, proximal segment with large outer spine, middle segment with 1 outer spine and 1 large inner plumose seta, distal segment with 3 spiniform elements and 4 plumose seta; endopod 2-segmented, proximal segment small, with large plumose inner seta, distal segment subcircular, having 6 plumose setae; velum well developed, furnished with fine sensillae along posterior margin.

Leg 4 (Fig. 3D): protopod with small plumose outer distal seta in addition to 2 discrete sensilla-bearing papillae along outer margin; exopod 2-segmented; proximal exopodal segment with large spine at outer distal corner; sensilla-bearing papilla on outer margin; pecten at base of each outer spine.

Leg 5 (Fig. 2A) represented by two papillae located on the posterolateral margin of genital complex, 1 tipped with a small seta and another with 2 similar setae.

Leg 6 (Fig. 2A) represented by 2 small setae located on margin of opercular plates closing off genital apertures on genital complex.

Redescription of the female of *Caligus grandiabdominalis* (Figs. 5–8)

Female. Body length 2.10–2.26 mm (2.17±0.08, N=3) (Fig. 5A).

Fully developed female. Body length 2.98 mm (N=1) (Fig. 5B).

Habitus (Figs. 5A, 6A) similar to male; fourth pediger fused to genital complex; genital complex with posterolateral corners produced posteriorly into lobe in pre-metamorphic females (Figs. 5A, 6A), and abdomen barrel-shaped without segmentation (Figs. 5A, 6A). In fully developed female, posterolateral corners more conspicuously produced backwards into triangular lobes (Figs. 5B, 6B). Abdomen unsegmented but clearly divided into 2 parts in fully developed female; anterior portion flattened peach-shaped, posterior portion semicircular (Figs. 5B, 6B).

Antennule (Fig. 7B) 2-segmented, proximal segment with 29 setae on anterodistal surface, distal segment shorter than proximal segment, with 1 subterminal seta on posterior margin and 11 naked setae plus 2 aesthetascs on distal margin. Antenna (Fig. 7C) 3-segmented, proxi-

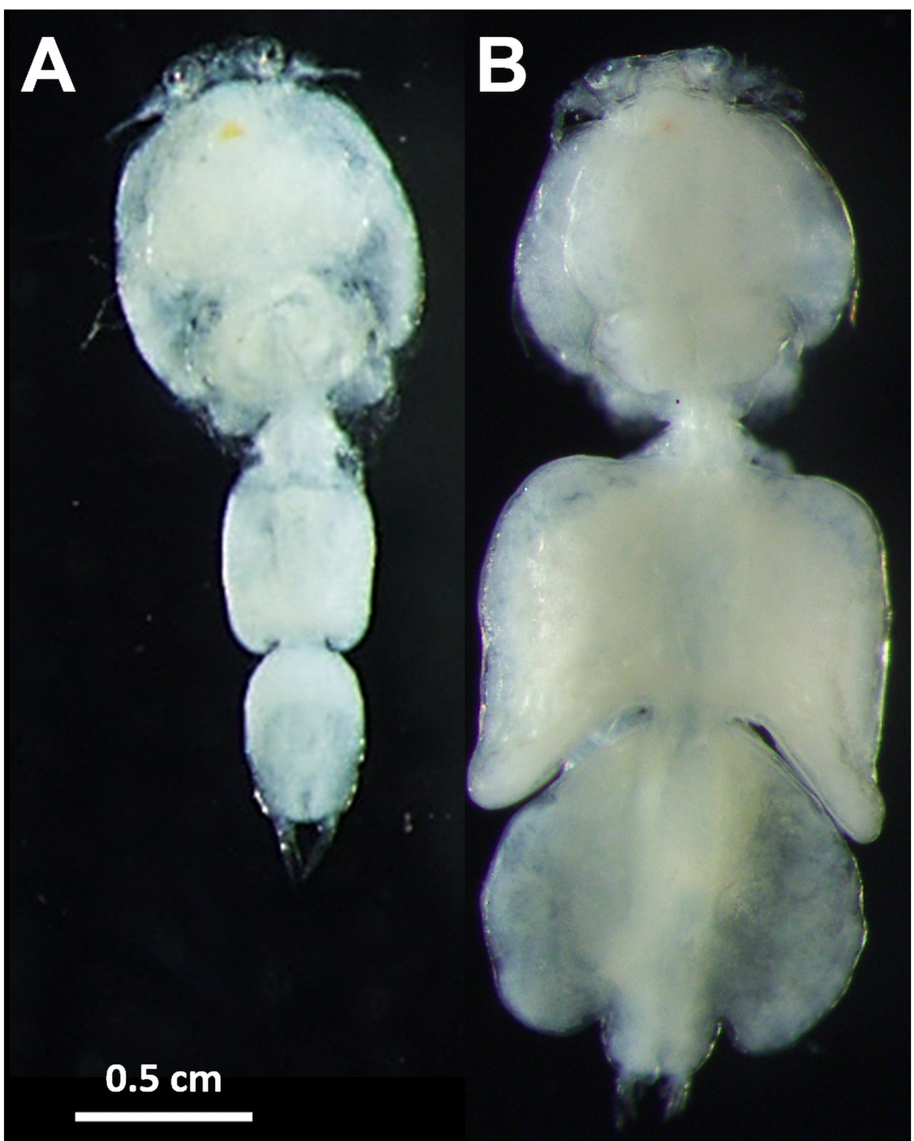

Fig. 5. *Caligus grandiabdominalis* Yamaguti, 1954. A. Female; B. Fully developed female.

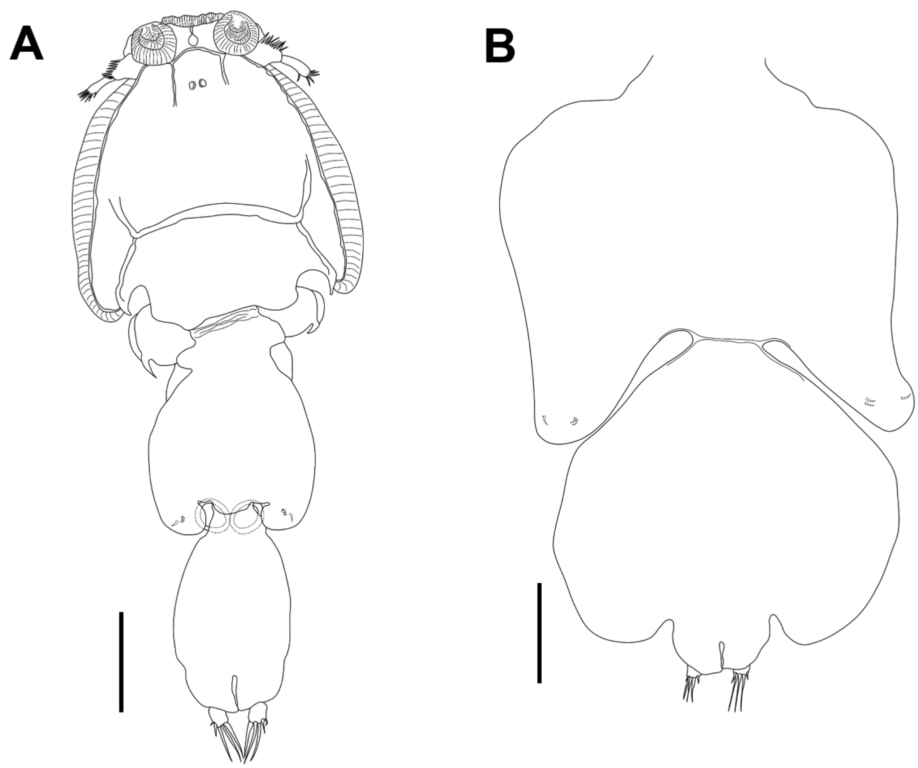

Fig. 6. *Caligus grandiabdominalis* Yamaguti, 1954, female. A. Habitus, dorsal view; B. Abdomen of a fully developed female. Scale bars: A, B=300 μm.

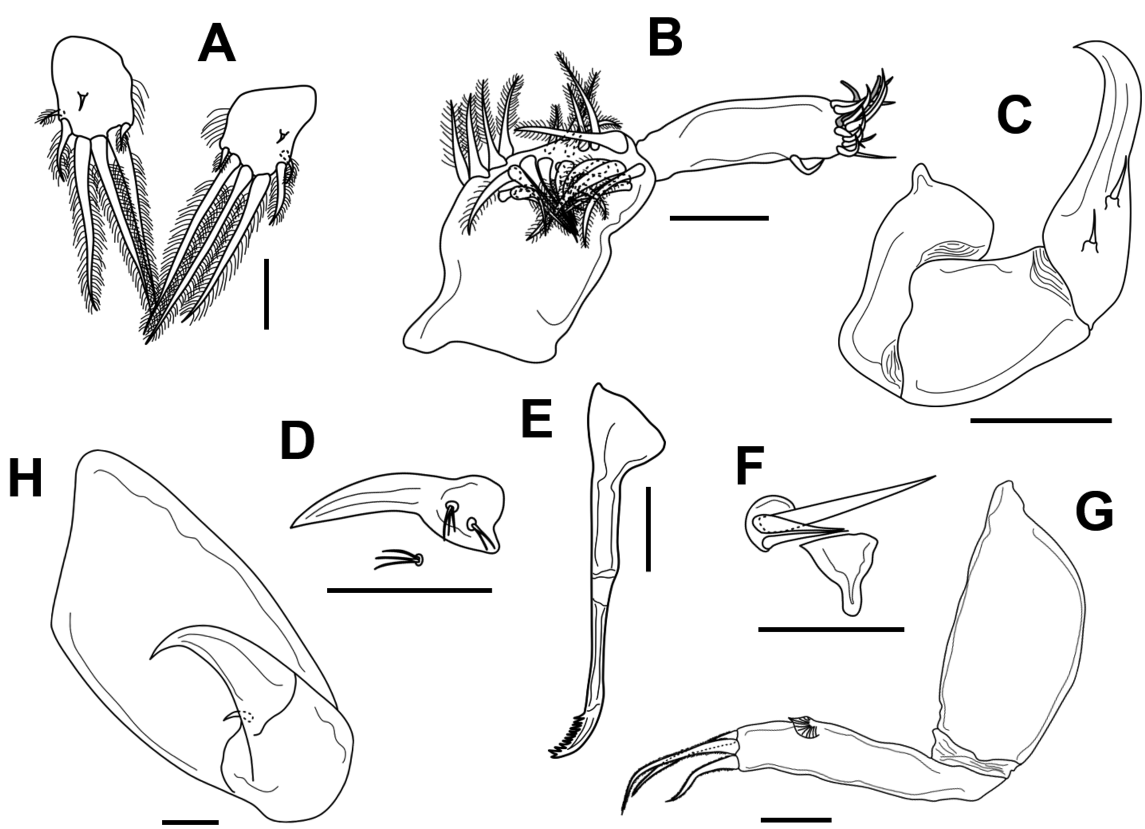

Fig. 7. *Caligus grandiabdominalis* Yamaguti, 1954, female. A. Caudal ramus; B. Antennule; C. Antenna; D. Postantennal process; E. Mandible; F. Maxillule; G. Maxilla; H. Maxilliped. Scale bars: A–H=50 μm.

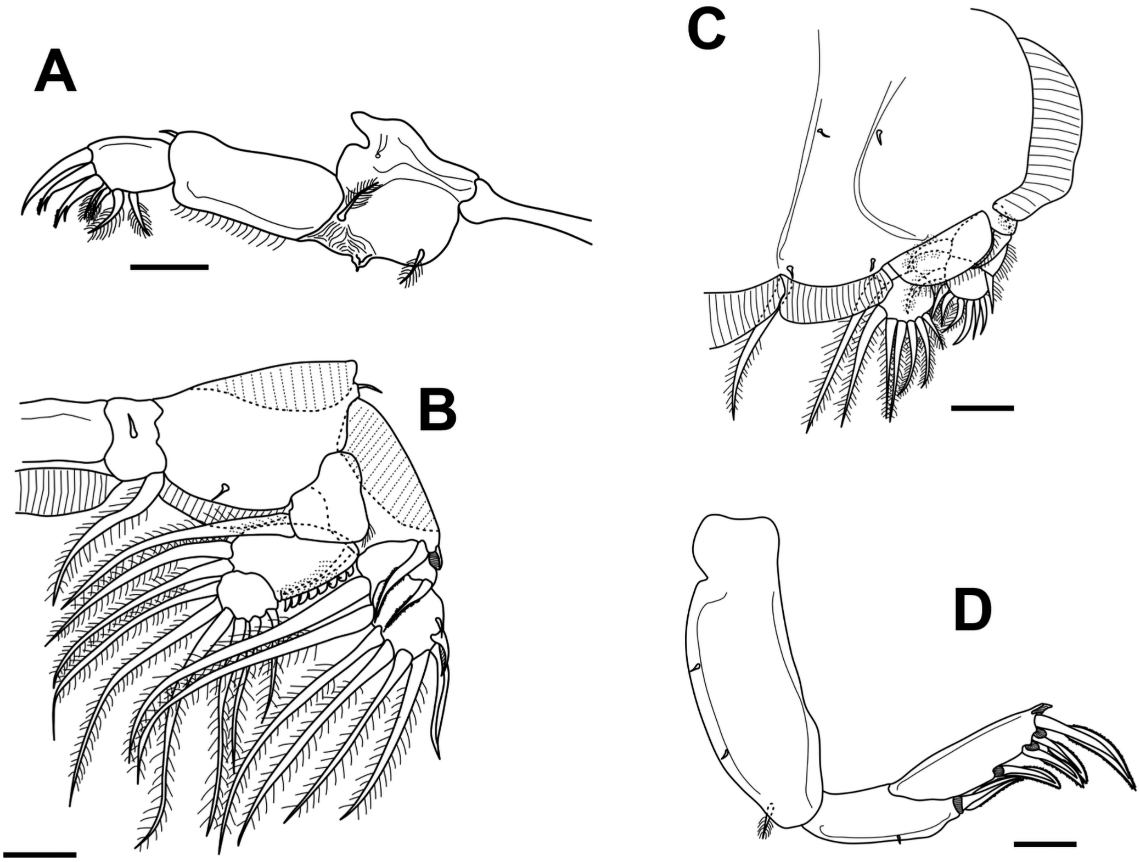

Fig. 8. *Caligus grandiabdominalis* Yamaguti, 1954, female. A. Leg 1; B. Leg 2; C. Leg 3; D. Leg 4. Scale bars: A–D=50 μm.

mal segment small; middle segment stout, unarmed; distal segment, curved claw bearing spiniform seta in basal and middle regions. Post-antennal process (Fig. 7D) weakly curved, with bisensillate and trisensillate papillae on basal part and trisensillate papilla on adjacent ventral cephalothoracic surface. Posterior process of maxillule (Fig. 7F) with more rounded tip than in male. Maxilliped (Fig. 7H) with corpus stouter than in males. Sternal furca absent. Leg 4 (Fig. 8D) generally as in male.

Molecular Analysis

We amplified 456-bp COI fragments from three specimens of *Caligus grandiabdominalis*. Genetic distances (*p*-distances) among the specimens were ≤0.020 (Table 1), with identical sequences from the two females showing a perfect match (*p*-distance=0) and 0.02 for the male. In contrast, there was a distance of more than 0.112 between *C. grandiabdominalis* and the other assessed species in the *Caligus bonito* group.

Discussion

To date, 15 species of *Caligus* have been reported in Malaysia (Ismail et al. 2024). To the best of our knowledge, this is the first record of *C. grandiabdominalis* in Malaysia. *Caligus grandiabdominalis* is a member of the *Caligus bonito* group, with which it has the following features in common: (1) leg 4 three-segmented, (2) distal exopod segment of leg 4 with one outer and three terminal spines; (3) leg 1 with three well-developed setae along the inner margin of the distal exopod segment; and (4) a row of denticles present along the outer margin of the second endopod segment of leg 2. The *Caligus bonito* group currently comprises the following 18 species: *C. asperimanus* Pearse, 1951; *C. asymmetricus* Kabata, 1965; *C. bonito*; *C. caudatus* (Gnanamuthu, 1950); *C. cossacki* Bassett-Smith, 1898; *C. dussumieri* Rangnekar, 1957; *C. formicoides* Redkar, Rangnekar & Murti, 1949; *C. grandiabdominalis*; *C. hoplognathi*; *C. malabaricus* Pillai N.K., 1961; *C. mutabilis*; *C. omissus* Cressey & Cressey, 1980; *C. pauliani* Nuñes-Ruivo & Fourmanoir, 1956; *C. phipsoni* Bassett-Smith, 1898; *C. quadratus*; *C. tenuifurcatus* Wilson C.B., 1937; *C. timorensis* (Izawa, 1995); and *C. triabdominalis* Byrnes T., 1987) (Boxshall 2018, Morales-Serna et al. 2014, Özak 2020, Boxshall & Barton 2023, Boxshall & Bernot 2023). *Caligus grandiabdominalis* can be readily distinguished from other species within this group based on the absence of a sternal furca. Although the following *Caligus* species similarly lack a sternal furca, each is a member of a different species group and also differ from *C. grandiabdominalis* in their morphological charac-

Table 1. Pairwise genetic distances (K2P) among selected species in the *Caligus bonito* group based on a comparison of a 456 bp fragment of the COI sequence.

No.	Speices name	Accession number	References	1	2	3	4	5	6	7
1	*Caligus grandiabdominalis* Fully developed female	LC860778	Present study							
2	*Caligus grandiabdominalis* Female	LC860779	Present study	0.000						
3	*Caligus grandiabdominalis* Male	LC860780	Present study	0.020	0.020					
4	*Caligus hoplognathi*	KF483707	Morales-Serna et al. (2014)	0.145	0.145	0.151				
5	*Caligus quadratus*	EF065619	Øines & Schram (2008)	0.125	0.125	0.137	0.090			
6	*Caligus bonito*	MN064566	Nikhila Reshmi et al. (2022)	0.140	0.140	0.146	0.090	0.080		
7	*Caligus mutabilis*	KF483690	Morales-Serna et al. (2014)	0.112	0.112	0.118	0.082	0.057	0.068	

teristics: *C. tenuis* (Beneden, 1852) (a member of the *Caligus diaphanus* group); *C. absens* Ho, Lin & Chen, 2000 (*Caligus macarovi* group); *C. enormis* Wilson C.B., 1913 (*Caligus productus* group); *C. cultellus* Özak, Kurt, Kamanli, Akbulut, Yanar & Boxshall, 2024, *C. rufus* Wilson C.B., 1908, *C. trichiuri* Krøyer, 1863, *C. unguidentatus* Rangnekar & Murti, 1950 (*Caligus trichiuri* group); and *C. yucatanensis* (Suárez-Morales, Kim & Escamilla, 2012) (*Caligus undulatus* group) (Boxshall 2018, Özak et al. 2024). In addition, *Caligus afurcatus* Wilson C.B., 1913, *C. carangis* Krøyer, 1863, *C. nibeae* Shen, 1957, *C. pharaonis* Nordmann, 1832, *C. reniformis* Prabha & Pillai, 1983, *C. stocki* (Cressey & Cressey, 1990), and *C. trachynoti* Heller, 1865, which are not members of any of the aforementioned groups, also lack a sternal furca (Krøyer 1863, Heller 1865, Wilson 1913, Shen 1957, Pillai 1985, Cressey & Cressey 1990, Dojiri & Ho 2013). However, they can be distinguished from *C. grandiabdominalis* by the following characteristics. *Caligus afurcatus*, *C. carangis*, *C. nibeae* and *C. trachynoti* differ from *C. grandiabdominalis* in the number of segments on the leg 4 (Krøyer 1863, Heller 1865, Wilson 1913, Shen 1957). *Caligus pharaonis* lacks external denticles on the second endopod segment of leg 2 (Pillai 1985). *Caligus reniformis* lacks a post-anntennal process (Dojiri & Ho 2013). *Caligus stocki* lacks 3 plumose setae on the distal segment of leg 1 (Cressey & Cressey 1990).

To date, males have been described for the following 10 *Caligus bonito* group species: *C. asperimanus*, *C. asymmetricus*, *C. bonito*, *C. formicoides*, *C. omissus*, *C. pauliani*, *C. phipsoni*, *C. quadratus*, *C. tenuifurcatus*, and *C. triabdominalis* (Byrnes 1987, Cressey & Cressey 1980, Cressey 1991, Lin & Ho 2001, Pillai 1985, Özak 2020, Shen 1957, Suárez-Morales et al. 2008). In each of these species, the males possess a sternal furca. The males of *C. grandiabdominalis* are similar to those of *C. omissus*, in that the inner margin of the corpus of the maxilliped is smooth in both species, although they differ with respect to the presence of the sternal furca in the latter. However, some protrusions are present on the myxal margin of the male maxilliped in the other species belonging to the *Caligus bonito* group. The males of *C. grandiabdominalis* and *C. omissus* also differ with respect to the number of setae on the proximal antennular segment, bearing 29 and 27 setae, respectively.

Our redescription of the female is fully consistent with the original description, with the exception of the number of setae on the antennule (Yamaguti 1954, present study). Although the females on which the original description was based had 11 terminal setae on the distal antennular segment, our recently collected specimens had 11 setae and two aesthetascs.

The genital complex and abdomen of the examined females differed in shape. The original description was based on two female specimens, the genital complex of which was described as rounded and quadrangular with the lateral margins rounded posteriorly into lobes (Yamaguti 1954). In addition, the abdomen was described as one-segmented although distinctly bifid, flat peach-shaped anteriorly, with rounded posterior corners, and quadrate posteriorly (Yamaguti 1954). In three of the four female specimens collected in the present study, the genital complex and abdominal somites were not laterally expanded, as indicated in the original description. However, these individuals carried paired spermatophores, indicating that they were adults and had mated. In the remaining fully developed female specimen examined in this study, the posterior corners of the genital complex were more notably developed than in the original description. In some *Caligus* species, the genital complex can be enlarged within the same species. For example, Shiino (1956) described two forms of *Caligus triangularis* Shiino, 1954, namely, a female with a large pentagonal genital complex, and a young female with a smaller quadrangular genital complex. In addition, based on their detailed observations of *C. dussumirei*, Boxshall & Barton (2023) proposed that expansion of the genital complex and abdomen is a late developmental phenomenon. We speculate that such changes in the morphology of the female genital complex could be associated with egg production. Consistent with this assumption, based on an examination of histological sections, Yanar et al. (2024) found that in *Caligus minimus* Otto, 1821, expansion of the genital complex occurred concomitantly with the development of eggs in the genital complex. However, given that in the present study, we obtained only a single fully developed female, it was not possible to prepare transparent specimens to examine the eggs in the genital complex. Nevertheless, taking into consideration previous findings, we suspect that the female genital complex is enlarged with increasing maturity in the following order: females with a small genital complex collected in this study, the original description by Yamaguti (1954), and the fully developed female with large genital complex collected in this study.

On the basis of genetic analysis, all the males, females, and fully developed female collected during this study were considered genetically conspecific. In this regard, Lefébure et al. (2006) have reported K2P values of between 0 and 0.094 within the same species in crustaceans, whereas in the present study, we obtained values of 0 between females and the fully developed female and 0.020 between males and females while other species in the *Caligus bonito* group were $>$0.112. Furthermore, morphologically, we observed no differences in the appendages of males and females. In contrast, we did detect sexual dimorphism with respect to the structures of the antenna, postantennal process, maxillule, and maxilliped, which is typical for *Caligus* species. We accordingly conclude that the specimens collected in this study were male and female *C. grandiabdominalis*.

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