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Partial revision of the Indo-West Pacific alcyonarian-associated shrimp genus *Propontonia* Bruce, 1969 (Decapoda: Palaemonidae) with the description of a new species from the Line Islands

Частичная ревизия рода *Propontonia* Bruce, 1969 (Decapoda: Palaemonidae), ассоциированного с кораллами-альционариями, с описанием нового вида с островов Лайн

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KEY WORDS: Symbiosis; phylogeny; corals; Octocorallia; Alcyonaria; diversity; community; tropical; Indo-West Pacific.

КЛЮЧЕВЫЕ СЛОВА: Симбиоз; филогения; кораллы; октокораллы; альционарии; разнообразие; сообщество; тропики; Индо-Западная часть Тихого океана.

ABSTRACT. The Indo-West Pacific palaemonid shrimp genus *Propontonia* Bruce, 1969 (Decapoda: Palaemonidae), associated with the alcyonarian soft corals (Anthozoa: Octocorallia), is partially revised. *Periclimenes kempi* Bruce, 1969 is transferred to the genus, as well as a new species is described from the Line Islands. The diagnosis of the genus is modified and clarified, while the absence/presence of a well-developed exopodal flagellum of maxilliped III is considered only as a species-level morphological feature. The identification key to all known species of the genus *Propontonia* is presented.

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РЕЗЮМЕ. Частично ревизирован индо-западнотихоокеанский род креветок-палаемонид *Propontonia* Bruce, 1969 (Decapoda: Palaemonidae), ассоциированный с мягкими кораллами-альционариями (Anthozoa: Octocorallia). *Periclimenes kempi* Bruce, 1969 перенесен в этот род, а также описан новый вид с островов Лайн (Центральные Полинезийские Спорады). Диагноз рода модифицирован и уточнен, в то время как отсутствие/наличие хорошо развитого жгутика экзопода максиллипед III рассматривается только как морфологический признак видового уровня. В статье представлен определительный ключ ко всем известным видам рода *Propontonia*.

Introduction

Representatives of the family Palaemonoidea Rafinesque, 1815 (Decapoda: Caridea), or palaemonid shrimps, are among the most diverse and specialized marine caridean shrimps, whose huge biological diversity is due to symbiosis with various marine invertebrates. Corals, both soft and scleractinian, occupy an important place among the hosts of these shrimps, with which a number of strictly specialized relationships (associations) are known [Bruce, 1977; Horká *et al.*, 2016a; Chow *et al.*, 2021]. The diversity of coral reefs is also determined by palaemonid shrimps, participating in symbiotic relationships with almost all invertebrates, along with representatives of other caridean shrimp families, Alpheidae and Hippolytidae [Horká *et al.*, 2016a; Bruce, 1976a]. Association of palaemonid shrimps with soft corals could be classified as protective epibiosis [Horká *et al.*, 2016a; Morton, 1988].

Symbiotic associations are considered as one of the main driving forces of speciation and evolution [Moran, 2006, 2007; Joy, 2013]. Association with a large host living on its surface or inside the body often leads to significant changes in the ancestral (usually free-living) set of morphological features of smaller symbiotic species demonstrating such high ecological plasticity that allows them to adapt to different hosts, as is observed in palaemonid shrimps. Among such available adaptations, reduction of various protruding parts of the body, such as rostrum, spines and others, is more common. Currently, an active molecular genetic study of palaemonid shrimp (family Palaemonidae) [Kou *et* *al.*, 2013; Gan *et al.*, 2015; Horká *et al.*, 2016a; Chow *et al.*, 2021] has made it possible to clarify their phylogenetic relationships and revealed previously unknown interspecific (generic) relationships, regrouping known genera previously established only on the basis of morphology. In addition, these studies have made it possible to identify/determine different levels of phylogenetic significance of certain morphological features.

The Indo-West Pacific palaemonid shrimp genus *Propontonia* Bruce, 1969 was designated for *Propontonia pellucida* Bruce, 1969, described as associated with soft coral *Sarcophyton crassicaule* Moser, 1919 (Anthozoa: Octocorallia: Sarcophytidae) [Bruce, 1969a]. Based on several morphological features, especially the completely reduced exopodal flagellum on maxilliped III, Bruce [Bruce, 1969a] pointed out that *Propontonia* is most closely related to the Indo-West Pacific genus *Hamodactylus* Holthuis, 1952, which is also associated with corals, mainly alcyonarians, and the Eastern Pacific genus *Waldola* Holthuis, 1951. The most distinctive morphological feature of the genus *Propontonia*, in addition to the absence of an exopodal flagellum of maxilliped III, is the specific flattened and curved shape of the dactylus of the minor pereiopod (cheliped) II, which probably corresponds to the nutritional preferences of these shrimps in collecting surface coral mucus. Such form of dactyli of chelipeds is also characteristic for other coral-associated palaemonid shrimps, for example, *Periclimenes diversipes* Kemp, 1922, *P. watamuae* Bruce, 1976, *P. mahei* Bruce, 1969 and some others.

During the study of the collection of palaemonid shrimps deposited at the University of Florida, Gainesville, FL, USA (UF), a small collection from the Line Islands was studied. As a result, a single ovigerous female of an interesting palaemonid shrimp species, very similar to *P. pellucida* and also associated with soft corals, was found. However, the specimen under study has a well-developed exopodal flagellum on maxilliped III, while it is completely reduced in *P. pellucida*, which just led to the separation of the latter species into a separate genus [Bruce, 1969a]. Phylogenetic analysis based on 16S rRNA gene marker (see Suppl. Fig. 1), which was used to clarify the phylogenetic relationships of *P. pellucida*, confirmed its close phylogenetic relationships with *Periclimenes kempi* Bruce, 1969, which is also associated with alcyonarians, but has a well-developed exopodal flagellum on maxilliped III [Bruce, 1969b, 1981]. Thus, the conducted phylogenetic analysis indicates that the presence/absence of the flagellum of exopod on maxilliped III is just a species-level morphological feature for these palaemonid shrimps, but not the generic one. As the result, the diagnosis of the genus *Propontonia* is clarified and changed, while *Periclimenes kempi* is transferred to *Propontonia*, as well as a new species of the genus is described, increasing the known diversity of the genus up to three species, all of which are associated with alcyonarian soft corals in tropical shallow waters of the Indo-West Pacific.

Materials and Methods

The type material is deposited in the University of Florida, Gainesville, FL, USA (UF), the other studied material is deposited in the authors' personal collection at A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences, Moscow, Russia (LEMMI). Postorbital carapace length (pcl., in mm) is used as a standard measurement of the size. Only primary synonyms are given.

Dataset of aligned sequences of 16S mitochondrial rRNA gene marker, about 415 base pairs in length used for the phylogenetic study was taken from GenBank (NCBI) database (see Supplement). The alignment of all sequences was obtained with MEGA 7.0 [Kumar *et al.*, 2016]. The best evolutionary substitution model was determined using MEGA 7.0 and jModeltest2.1.141 (Diego Darriba, Universidade da Coruña as part of the Computer Architecture Group (GAC), Coruña, Spain). A phylogenetic analysis was conducted using PhyML 3.0 [Guidon *et al.*, 2010] with several models based on BIC (Bayesian Information Criterion) and AIC (Akaike Information Criterion). The trees based on Maximum Likehood (ML) and Neighbor Joining (NJ) algorithms with the higher bootstrap probability were used for graphic display of the phylogenetic relationships within the family Palaemonidae. Bootstrap support is presented. The final visualization is presented in the Supplement only, since phylogenetic analysis is not the purpose of this study.

Pairwise genetic divergences (*p*-distances) was calculated based on available sequences using MEGA 7.0 with the Kimura 2-Parameter (K2P) model of evolution [Kimura, 1980].

Results

Phylogenetic analysis

The data of the obtained phylogenetic analysis based on 16S rRNA gene marker (see Supplement) confirm the close genus-specific relationships between *Propontonia pellucida* and *Perilclimenes kempi* in all accomplished scenarios. At the same time, the taxonomic position of this clade (*P. pellucida* + *P. kempi*) varies in various phylogenetic constructions, being closely related to *Coralliocaris*+*Jocaste*+*Harpiliopsis* clade (MS analysis, see Suppl. Fig. 1), *Manipontonia* spp. and *Hamopontonia* spp. (NJ analysis, see Suppl. Fig. 1), while multi-locus analysis mostly shows its close relationships with the actinian-associated *Actinimenes* spp. [Gan *et al.*, 2015; Horká *et al.*, 2016a; Chow *et al.*, 2021]. In this regard, at the moment it is quite difficult to determine the phylogenetic position and related taxa for this clade, while any relationships with *Hamodactylus*, suggested by Bruce [1969a], were not proved.

The intraspecific pairwise distances (*p*-distances) between *P. pellucida* and *P. kempi* is about 8% that correspond to other genetic distances characteristic for congeneric species within the family Palaemonidae [Murphy, Austin, 2003; Kou *et al.*, 2013].

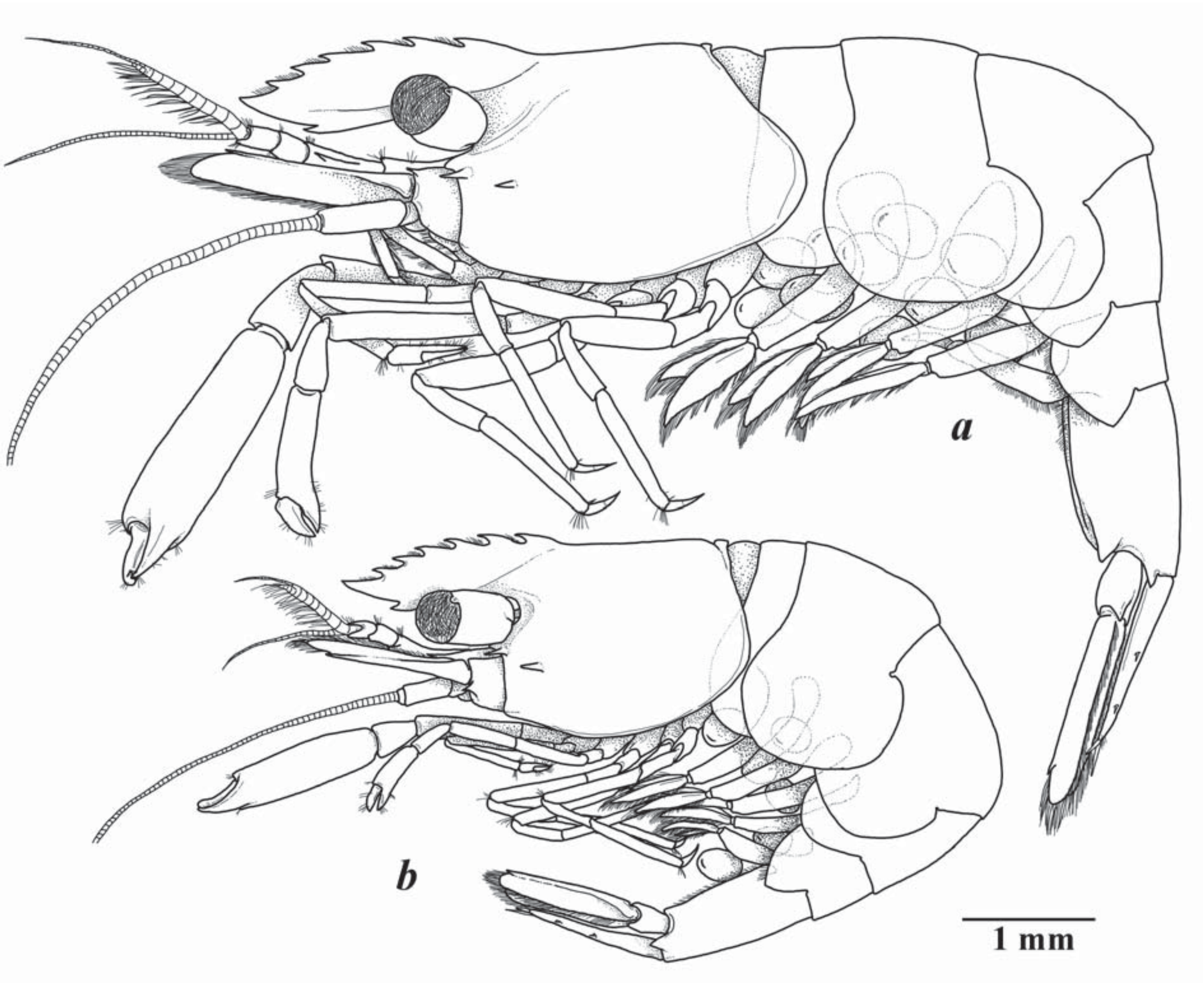

Fig. 1. *Propontonia alexanderbrucei* sp.n., holotype ♀, pcl. 1.8 mm (UF 11677, KINB3) (a) and *Propontonia pellucida* Bruce, 1969, ovigerous ♀, pcl. 1.4 mm (LEMMI) (b), general mesial view.

Рис. 1. *Propontonia alexanderbrucei* sp.n., голотип ♀, pcl. 1,8 мм (UF 11677, KINB3) (а) и *Propontonia pellucida* Bruce, 1969, яйценосная ♀, pcl. 1,4 мм (LEMMI) (б), общий мезиальный вид.

Taxonomic part

Order Decapoda Latreille, 1802
Family Palaemonidae Rafinesque, 1815
Genus *Propontonia* Bruce, 1969

SPECIES INCLUDED. *Propontonia pellucida* Bruce, 1969, *P. kempi* (Bruce, 1969) comb.n. and *P. alexanderbrucei* sp.n. (see below).

DIAGNOSIS (modified after Bruce [1969a]). Small commensal palaemonid shrimps associated with alcyonarian corals (Alcyonacea). Carapace smooth with well-marked antennal and hepatic spines; rostrum well-developed, deep and compressed, dorsally and ventrally dentate. Abdominal segments smooth, with first 5 pleura rounded. Telson elongate, with two pairs of dorsal spines and three pairs of terminal spines. Eyes well developed with globular cornea, without any outgrowths. Antennule with broad basal segment, with well-developed stylocerite and acute distolateral tooth; intermediate and distal peduncular segments short; upper and lower flagella well-developed, upper flagellum biramous with rami fused proximally. Scaphocerite broad with strong distolateral tooth exceeded by lamella; antennal flagellum long and slender. Mandible without palp; molar and incisor processes fine, normally developed. Maxillula with simple palp. Maxilla with well-developed palp and bilobed endite; scaphognathite broad. Maxilliped I with small palp, well-developed exopod with large caridean lobe, and bilobed epipod. Maxilliped II with well-developed exopod and simple epipod. Maxilliped III slender with large epipod and rudimentary arthrobranch; exopod completely reduced or present and well-developed. Pereiopods I slender; chela with subspatulate fingers, with entire or serrated cutting margins. Pereiopods II relatively large, unequal in size, dissimilar, with subspatulate fingers. Ambulatory pereiopods III–V slender, with simple dactyli. Fourth thoracic sternite unarmed. Pleopods normal, endopod of male pleopod I with distomedial process. Uropods normal, with large mobile distolateral spinule.

Propontonia pellucida Bruce, 1969
Figs 1b, 2.

Propontonia pellucida Bruce, 1969a: 141–151, figs 1–5 [type locality — Seychelles].

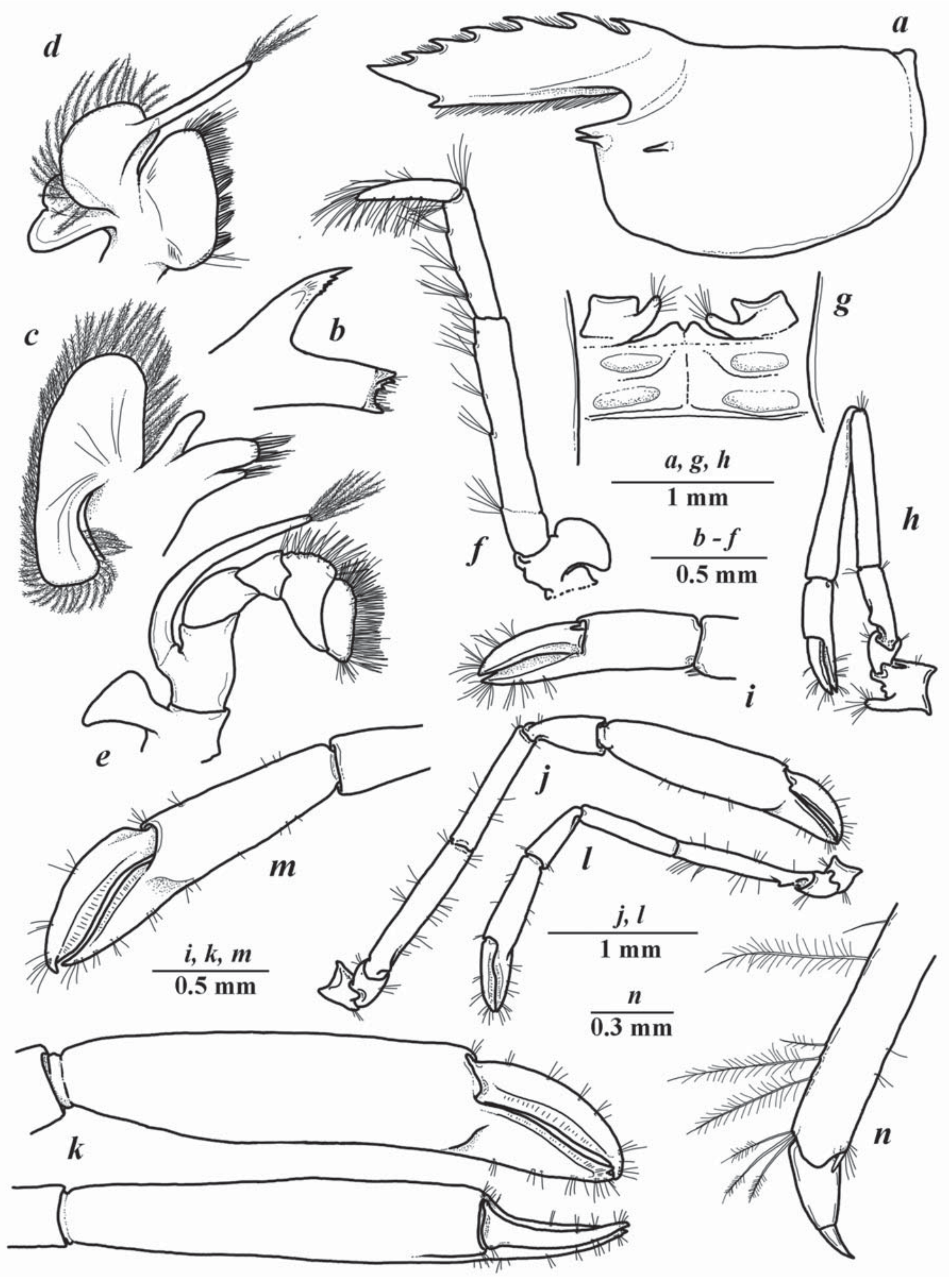

Fig. 2. *Propontonia pellucida* Bruce, 1969, ovigerous ♀ (LEMMI): a — carapace, lateral view; b — mandible; c — maxilla II; d — maxilliped I; e — maxilliped II; f — maxilliped III; g — 4th thoracic sternite; h — pereiopod I; i — chela of pereiopod I; j — major pereiopod II; k — chela of major pereiopod II; l — minor pereiopod II; m — chela of minor pereiopod II; n — dactylus and distal propodus of pereiopod III.

Рис. 2. *Propontonia pellucida* Bruce, 1969, яйценосная ♀ (LEMMI): a — карапакс, вид сбоку; b — мандибула; c — максилла II; D — максиллипед I; E — максиллипед II; F — максиллипед III; G — 4-й грудной сегмент; h — переопода I; i — клешня переоподы I; J — большая переопода II; k — клешня большой переоподы II; L — малая переопода II; m — клешня малой переоподы II; N — дактилус и дистальная часть проподуса переоподы III.

MATERIAL EXAMINED. 1 ovigerous ♀ (pcl 1.7 mm), 1 ♂ (pcl 1.4 mm), LEMMI – Vietnam, Nhatrang Bay, Mun Island, depth 10 m, on alcyonarian *Sarcophyton* sp., SCUBA, coll. O. Savinkin, T. Dautova, 17.04.2006; 2 ovigerous ♀♀ (pcl 2.0 and 1.5 mm), UF 572, UGML-0510 – Mariana Islands, Guam, N of Haputo, fore reef, depth 15 m, coll. G. Paulay, 09.07.2000 (GP-830: 31-32, 36).

SHORT DESCRIPTION. Small-sized palaemonid shrimp with cylindrical slightly depressed body. Carapace swollen in central part, smooth, with large antennal and hepatic teeth, without supraorbital teeth; rostrum deep, compressed, turned forward, pointing distally, reaching to distal margin of antennular peduncle; rostral formula 0+6/1 (Fig. 2*a*); orbit well developed, deep, unarmed; inferior orbital angle bluntly produced distally. Maxilliped III (Fig. 2*f*) of normal form, with slender unarmed segments; flagellum of exopod completely reduced, with large rounded epipod and rudimentary arthrobranch. Pereiopod I (Fig. 2*h*) with carpus about 3 times as long as wide, equal to merus and about 2 times longer than propodus; propodus about 2 times longer than wide, subcylindrical, twice shorter than carpus; fingers subspatulate, with entire cutting margins. Pereiopods II (Fig. 2*j, i*) dissimilar in shape and unequal in size; with robust and smooth segments; major pereiopod II with palm (Fig. 2*k*) cylindrical, smooth, about 4 times as long as wide, with almost straight margins; fingers about 2.5 times shorter than palm, about 2.5 times longer than wide, subspatulated; minor pereiopod II with palm (Fig. 2*m*) cylindrical, smooth, about 2.5 times as long as wide, with almost straight margins; fingers subspatulated, about 3.5 times longer than wide, subspatulated. Pereiopod III with relatively stout dactylus (Fig. 2*n*), with basal part about 1.5 times as long as wide, with simple slender and curved unguis.

REMARKS. The studied specimens well correspond to the original description of the species [Bruce, 1969]. Maxilliped III with completely reduced flagellum of exopod (see Fig. 2*f*) clearly separating the species from the congeners.

ECOLOGY. In Nhatrang Bay, the species was found in association with alcyonarian *Sarcophyton* sp. (Anthozoa: Octocorallia: Sarcophytidae). Known as a symbiont of soft corals *Sarcophyton* spp. and *Lobophytum* spp. (Anthozoa: Octocorallia: Sarcophytidae) [Bruce, 1969a; Fransen, 1994; Okuno, 2002].

DISTRIBUTION. The species is known from the western Indian Ocean, Seychelles, Vietnam, Japan and Marianna Islands [Bruce, 1969a, 1978; Fransen, 1994; Okuno, 2002; Marin, Savinkin, 2007; present study].

Propontonia kempi (Bruce, 1969) **comb.n.**

Periclimenes (*Ancylocaris*) *diversipes* Kemp, 1922: 179–184, figs 36–39 (partim).

Periclimenes kempi Bruce, 1969b: 260–262 [type locality, Hurghada, Egypt]. — Bruce, 1981: 80.

REMARKS. The species is clearly separated from *P. pellucida* by well-developed exopodal flagellum of maxilliped III, showing that this feature is a species-specific within the genus. For the differences from the new species (see below).

HOSTS. The species was found in association with alcyonarian *Rumphella aggregata* (Nutting, 1910) (Anthozoa: Octocorallia: Isididae) and *Sinularia* sp. (Anthozoa: Octocorallia: Sinulariidae) [Bruce, 1981; De Grave, 2000].

DISTRIBUTION. Type locality, Hurghada, Egypt, Red Sea [Bruce, 1969]. Also known from Zanzibar, Kenya, Andaman Islands, Singapore, Fiji and the Great Barrier Reef [Bruce, 1981; De Grave, 2000].

Propontonia alexanderbrucei **sp.n.**

Figs 1a, 3, 4.

MATERIAL EXAMINED. Holotype, ovigerous ♀, pcl. 1.8 mm (UF 11677, KINB3), Line Islands, Kingman Reef, NE/E of atoll, outer reef slope, on soft coral, 0–13.3 m, coll. M. Malay, 26.08.2005 (photo).

ETYMOLOGY. The species is named in a memory of Dr. Alexander James (“Sandy”) Bruce (25 February 1929 – 27 July 2022), the famous carcinologist, who made a significant contribution to the study of palaemonid shrimps, as well as greatly contributed to the interest of the author of this article to these shrimps.

DESCRIPTION. Small-sized palaemonid shrimp with cylindrical slightly depressed body. Carapace swollen in central part, smooth, with large antennal and hepatic teeth, without supraorbital teeth (Fig. 3*a*). Rostrum deep, compressed, turned forward, pointing distally, reaching to distal margin of antennular peduncle; rostral formula 0+6/1 (Fig. 3*a*); dorsal rostral carina well developed reaching to distal third of carapace length, with small dorsal teeth; ventral rostral carina less developed, but well-marked; proximal lateral rostral lamina non-developed. Orbit well developed, deep, unarmed; inferior orbital angle bluntly produced distally. Pterygostomial angle produced, bluntly rounded distally.

Abdominal somites smooth; pleura of abdominal somites I–V rounded (Fig. 1*a*).

Telson (Fig. 3*c*) relatively slender, about 3.5 times as long as proximal width, narrow medially and distally, with 2 pairs of medium submarginal dorsal spines at 0.45 and 0.7 of telson length; distal margin of telson armed with 3 pairs of distal spines.

Eyes well developed, large; eyestalk smooth, cylindrical, about 1.5 times as long as wide; cornea well developed, medium, subovate (Fig. 3*e*).

Antennula (Fig. 3*f*) well-developed; basal segment stout, about 2 times longer than wide, with well-developed slender acute stylocerite, distolateral angle with large acute triangular tooth and small rounded lobe medially; ventromedial tooth well-marked; intermediate segment stout, about as long as wide, with well-developed lateral lobe; distal segment stout, as long as wide, slightly smaller than to previous segment; proximal part of upper antennular flagellum with 8–9 segments, shorter ramus with more than 25 segments; about 7 or 8 groups of aesthetascs present.

Antenna (Fig. 3*g*) well-developed, basicerite about 1.5 times longer than wide, smooth, without distoventral tooth; scaphocerite wide, about twice longer than maximal width, overreaching distal margin of antennular peduncle, distolateral tooth well developed, acute, small, not reaching to distal margin of blade.

Mouthparts. Mandible (Fig. 3*h*) without palp, molar process stout, subcylindrical, expanding distally, incisor process well developed, distally oblique. Maxillula (Fig. 3*i*) with bilobed palp, lower lobe with small ventral tubercle bearing short simple seta, upper lacinia broader proximally, tapering distally to transverse distal margin, with numerous short simple setae; lower lacinia elongate, with short slender spines and simple setae. Maxilla (Fig. 3*g*) with slender palp, about 3 times longer than basal width, tapering slightly distally, basal endite deeply bilobed, upper and lower lobes simple, armed with small setae distally, scaphognathite normal, about 3 times longer than central width, anterior lobe about 1.5 times longer than basal width. Maxilliped I (Fig. 3*k*) with slender tapering palp, basal endite well-developed, broad, distally rounded, medial margin straight, armed with

Fig. 3. *Propontonia alexanderbrucei* sp.n., holotype ♀ (UF 11677, KINB3): a — carapace, lateral view; b — 4th thoracic sternite; c — telson and uropods; d — distolateral margin of exopod of uropod; e — eyes; f — antennula; g — antenna; h — mandible; i — maxilla I; g — maxilla II; k — maxilliped I; l — maxilliped II; m — maxilliped III.

Рис. 3. *Propontonia alexanderbrucei* sp.n., голотип ♀ (UF 11677, KINB3): a — карапакс, вид сбоку; b — 4-й грудной стернит; c — тельсон и уроподы; d — дистолатеральный край экзопода уроподы; e — глаз; f — антеннула; g — антенна; h — мандибуда; i — максилла I; g — максиллипеда II; k — максиллипеда I; l — максиллипеда II; m — максиллипеда III.

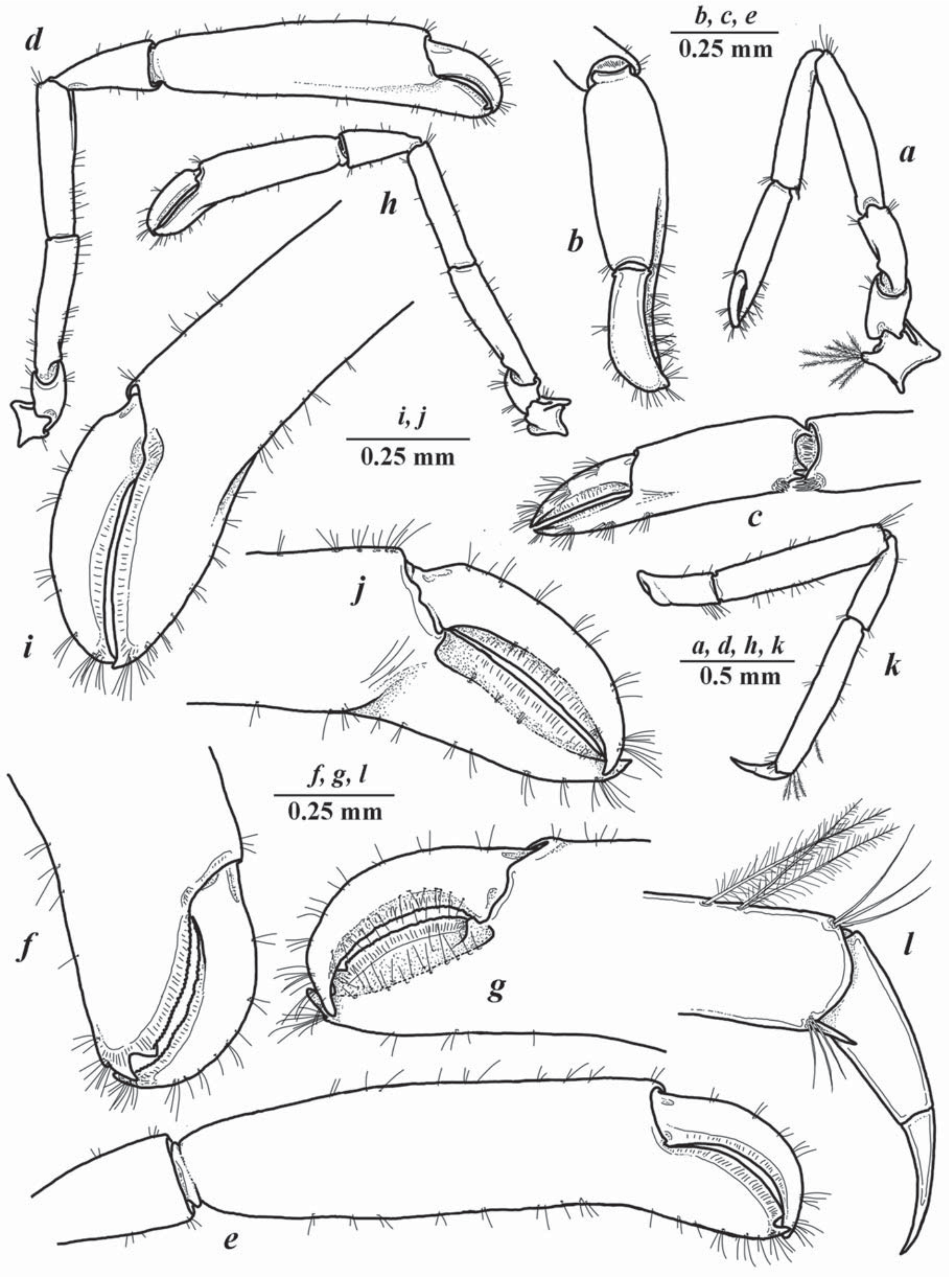

Fig. 4. *Propontonia alexanderbrucei* sp.n., holotype ♀ (UF 11677, KINB3): a — pereiopod I; b, c — chela of pereiopod I, different views; d — major pereiopod II; e — chela of major pereiopod II; f, g — fingers of major pereiopod I; h — minor pereiopod II; i — distal chela of minor pereiopod II; j — fingers of major pereiopod II; k — pereiopod III; l — dactylus and dis-tal propodus of pereiopod III.

Рис. 4. *Propontonia alexanderbrucei* sp.n., голотип ♀ (UF 11677, KINB3): a — переопода I; b, c — клешня переоподы I, разные виды; D — большая переопода II; e — клешня большой переоподы II; f, g — пальцы большой переоподы I; H — малая переопода II; I — дистальная часть клешни малой переоподы II; j — пальцы большой клешни переоподы II; k — переопода III; l — дактилус и дистальная часть проподуса переоподы III.

numerous simple marginal and submarginal setae, coxal endite non separated from basal, medial margin convex with sparser similar setae; exopod with well-developed flagellum, caridean lobe large, with numerous plumose marginal setae; epipod rounded, bilobed. Maxilliped II (Fig. 3*l*) of normal form, endopod with dactylar segment broad, armed with numerous stout serrulate spines medially, propodal segment with distal margin broadly rounded with numerous spiniform marginal setae, carpus, merus and ischiomerus without special features; exopod with well-developed flagellum; coxa with medial margin slightly produced, with subquadrate epipod, without podobranch. Maxilliped III (Fig. 3*m*) of normal form, with slender unarmed segments; ischiomeral segment about 4 times longer than wide; antepenultimate segment about 4.5 times longer than wide; penultimate segment tapering distally, about 4.5 times longer than wide., with well-developed flagellum of exopod, reaching to the distal margin of ischiomeral segment, with large rounded epipod and rudimentary arthrobranch.

Pereiopod I (Fig. 4*a*) with relatively slender segments; coxal segment as long as wide, with distoventral lobe; basis as long as wide; ischium about 2 times longer than wide; merus slender, about 5 times as long as wide; carpus about 4 times as long as wide, shorter than merus; propodus (Fig. 4*b*, *c*) about 4 times longer than wide, subcylindrical, equal to carpus; fingers subspatulate, about 4 times as long as wide, about 1.5 times shorter than propodus, with straight and serrated cutting margins.

Pereiopods II (Fig. 4*d*, *h*) dissimilar in shape and unequal in size; with robust and smooth segments; Major pereiopod II (Fig. 4*d*) with coxal segment as long as wide, with small distoventral lobe; basis as long as wide; ischium about 4.5 times longer than wide; merus robust, about 5 times longer than wide, with straight lateral margins, equal to ischium; carpus triangular, stout, flaring distally, with smooth distal margin; palm (Fig. 4*e*) cylindrical, smooth, about 4 times as long as wide, with almost straight margins; fingers (Fig. 4*f*, *g*) stout, subspatulated, about 3.5 times shorter than palm; fixed finger (pollex) stout, compressed, about 1.5 times longer than wide, with two distal triangular teeth and serrated cutting margin; movable finger (dactylus) slender, compressed, with simple curved tip and serrated cutting margin. Minor pereiopod II (Fig. 4*h*) about 1.5 times smaller than major one, with coxal segment as long as wide, with small distoventral lobe; basis as long as wide; ischium about 4.5 times longer than wide; merus slender, about 4.5 times longer than wide, with straight lateral margins, equal to ischium; carpus triangular, stout, flaring distally, with smooth distal margin; palm (Fig. 4*e*) cylindrical, smooth, about 3.5 times as long as wide, with almost straight margins; fingers (Fig. 4*i*, *j*) stout, subspatulated, about 2 times shorter than palm; fixed finger (pollex) stout, compressed, about 2 times longer than wide, with simple tip and serrated cutting margin; movable finger (dactylus) slender, compressed, with simple curved tip and serrated cutting margin.

Pereiopod III (Fig. 4*k*) with smooth slender unarmed segments; coxal segment as long as wide, unarmed; basis as long as wide; ischium robust, about twice longer than wide; merus slender, about 4.5 times as long as wide; carpus about 3 times as long than wide, about half of propodus and merus; propodus relatively stout, about 5.5 times as long as proximal its width, with smooth unarmed margins, without ventral or distoventral teeth; dactylus (Fig. 4*l*) simple, with basal part about 2 times as long as wide, with simple slender and curved unguis. Pereiopods III–V similar.

Pleopods normal, without specific features. Uropods (Fig. 3*c*) slender, slightly exceeding telson; distolateral margin of uropodal exopod rectangular with small fixed tooth and large movable distolateral spine (Fig. 3*d*).

COLOURATION. Unknown.

DIFFERENTIAL DIAGNOSIS. The species clearly differs from its congeners in a relatively short carpus of pereiopod I, which is equal in size to propodus (Fig. 4*a*).

From *P. pellucida*, the species could be also easily separated by well-developed flagellum of exopod on maxilliped III (Fig. 3*m*).

HOST. The holotype specimen of the new species was collected from unidentified soft coral.

DISTRIBUTION. The species is presently known only from the type locality, Line Islands.

Discussion

The relationship between the known species of the genus *Propontonia* is confirmed both morphologically and genetically, while such a previously considered important feature as the reduction of the exopodal flagellum of maxilliped III is seems to be an interspecific, but not a generic-level in this group (genus) of palaemonid shrimps. Similar reduction of the exopodal flagellum of maxillipeds II–III, is characteristic of a number of other soft corals associated palaemonid shrimp genera , for example, the Indo-West Pacific genera *Hamodactylus* [Fransen, 2013; Fransen, Rauch, 2013; Horká *et al.*, 2016b], *Hamodactyloides* Fujino, 1973 [Holthuis, 1958; Fujino, 1973], *Ctenopontonia* Bruce, 1979 [Fujino, 1973], *Fennera* Holthuis, 1951 [Holthuis, 1951; Bruce, 1979], *Mesopontonia* Bruce, 1967 [Holthuis, 1951] and *Pontonides* Borradaile, 1917 [Marin, 2007], the Eastern Pacific *Veleronia* Holthuis, 1951, *Pseudoveleronia* Marin, 2008 [De Ridder, Holthuis, 1979; Marin, 2008] and *Waldola* Holthuis, 1951 [Holthuis, 1951; Bruce, 1969a]. Additionally, Exopodal flagellum of maxilliped III is partially reduced in coral-associated *Anapontonia denticauda* Bruce, 1966, *Ischnopontonia lophos* (Barnard, 1962) and *Metapontonia fungiacola* Bruce, 1967 [Bruce, 1966, 1967; Marin, 2008, 2011]. Analysis of the literature data indicates that the reduction of the flagellum of maxillipeds, especially maxilliped III, is very common in palaemonid shrimp species associated with corals, whereas in the species, associated with other invertebrates, such reduction is not observed and flagellum is well developed, even in related switching lineages. It is very likely that different involvement in symbiotic relationships, both in time and in interaction, leads to the reduction of this organ. At the same time, exopodal flagellum of maxilliped III is well developed and significantly reduced in related coral-associated palaemonid genera *Pliopontonia furtiva* Bruce, 1973 and *M. fungicola*, respectively [Bruce, 1967, 1973].

Unfortunately, it is currently difficult to accurately determine the phylogenetic position of the genus *Propontonia* within the family Palaemonidae, since different construction algorithms lead to different positions, but in the future it is molecular genetic methods that will allow it to be evaluated, since the morphology of the palaemonid shrimps has too many convergent cases of similarity when living on the same taxon or group of related host [Kou *et al*., 2013; Gan *et al*., 2015; Horká *et al*., 2016a; Chow *et al*., 2021]. However, conducted molecular genetic analysis allowed to refute the previously put forward hypothesis about the relationship of *P. pellucida* and *P. diversipes* [Bruce, 1969a, b]. Scleractinian coral-associated *Periclimenes diversipes*, *P. watamuae*, *P. gonioporae* Bruce, 1989, *P. mahei* are most likely not related to *Propontonia*, despite having very similar fingers of both pereiopods (chelipeds) I and II. Similar subspatulate form of dactyli of pereiopod (chelipeds) II, especially minor one, probably showing a convergent adaptation in several coral-associated palaemonid lineages, could be associate with the probable feeding of these shrimp on coral mucus, and such specific form allows raking and accumulating mucus, using fingers of chelipeds like a shovel.

It is currently believed that symbiotic interaction usually begins with a simple topical association (commensalism) of smaller symbiont with different larger hosts just for protection, and then gradually moves to more dependent and specialized relationships, leading to a gradual morphological specialization of the symbiont [Chow *et al.*, 2021; Van As, Van As, 2019]. Modified morphological forms are often common to species with different host affiliations, potentially representing convergence in dietary character or apomorphic traits restricted to a small group of closely related species. For example, the reduction of the incisor process on mandible is characteristic for sponge-associated species, which probably correlated with their diet preferences [Ïuriš *et al*., 2011; Chow *et al*., 2021]. The similar examples are presented in modified dactyli of ambulatory pereiopods III–V [Bruce, 1976b; De Grave, 1999], uropods [Bruce, 1966, 1967] and telson [Bruce, 1085; Marin, 2012, 2014]. For most of the morphological features and adaptations there is no direct connection with the associated host, and it seems that the evolution of the morphology of the symbiont is mainly based on its phylogenetic relationships [Chow *et al*., 2021]. At the same time, a number of new phylogenetic data [Horká *et al.*, 2016a; Chow *et al*., 2021] indicate that the entire phylogeny of Palaemonidae is characterized by a constant dynamic spectrum of host change (switching), which potentially disrupts and redirects the ongoing adaptive evolutionary process and causes intermittent distribution of the species with similar morphology, but different host association. This situation indicates that it is problematic to use any morphological features or the spectrum of associated hosts to construct any phylogenetic conclusions, which is also additional evidence against orthogenetic evolution in the family Palaemonidae [Chow *et al*., 2021].

The identification key for the known species of the genus *Propontonia* Bruce, 1969

1. Flagellum of exopod of maxilliped III greatly reduced ... . *Propontonia pellucida* Bruce, 1969
– Flagellum of exopod of maxilliped III greatly well-developed 2
2. Carpus of pereiopod I equal to chela (propodus + fingers) .... *Propontonia kempi* (Bruce, 1969) comb.n.
– Carpus of pereiopod I significantly longer than chela (propodus + fingers) ..... *Propontonia alexanderbrucei* sp.n.

Supplementary data. The following Supplementary Figure is available online.

Supplementary Figure 1. Different reconstruction (tree) (ML — Maximum Likehood and NJ — Neighbor Joining algorithms) of molecular phylogenies (16S mitochondrial rRNA gene marker) for the family Palaemonidae with the higher bootstrap probability based on the sequences from the GenBank (NCBI) database. The support of nodes is marked. The arrows indicate the position of *Propontonia pellucida* and *Periclimenes kempi.*

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