

**A new infaunal species of the alpheid shrimp genus *Salmoneus*
Holthuis, 1955 (Crustacea: Decapoda: Alpheidae)
and a new crustacean association from anoxic mangrove habitats
in southern Vietnam**

**Новый инфаунный вид креветок-альфеид рода *Salmoneus*
Holthuis, 1955 (Crustacea: Decapoda: Alpheidae) и новая
ассоциация ракообразных из бескислородных мангровых
местообитаний на юге Вьетнама**

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KEY WORDS: biodiversity, Crustacea, mangrove, communities, burrowing fauna, association, Vietnam, Indo-West Pacific.

КЛЮЧЕВЫЕ СЛОВА: биоразнообразие, Crustacea, мангры, сообщества, роющая фауна, ассоциации, Вьетнам, Индо-Вест Пацифика.

ABSTRACT. A new infaunal shrimp of the genus *Salmoneus* Holthuis, 1955 (Crustacea: Decapoda: Alpheidae) is described from the burrows of the mangrove-dwelling alpheid shrimps *Alpheus* cf. *euphrosyne* de Man, 1897, *Alpheus* aff. *lobidens* De Haan, 1849 and upogebiid mud shrimp *Wolffogebia phuketensis* (Sakai, 1982) in a deep mangrove swamps of the Can Gio Mangrove Biosphere Reserve, South Vietnam. *Salmoneus spiridonovi* sp.n. appears morphologically close to the eastern Atlantic *S. erasimorum* Dworschak, Anker et Abed-Navandi, 2000, *S. caboverdensis* Dworschak, Anker et Abed-Navandi, 2000, the western Atlantic *S. degravei* Anker, 2010, and the Indo-West Pacific *S. seticheles* Anker, 2003, *S. brucei* Komai, 2009, *S. yoyo* Anker, Firdaus et Pratama, 2014 and *S. durisi* Anker, 2019, which are characterized by both pereiopods I (chelipeds) being enlarged, subequal in size, but asymmetrical in the shape, clearly separating them from other species in the genus. Moreover, the new species is the first representative of the genus *Salmoneus* recorded as an infaunal associate of upogebiid burrows.

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РЕЗЮМЕ. Новый вид инфаунных креветок рода *Salmoneus* Holthuis, 1955 (Crustacea: Decapoda: Alpheidae) описан из нор альфеидных креветок *Alpheus* cf. *euphrosyne* de Man, 1897, *Alpheus* aff. *lobidens* De Haan, 1849 и уропегебидов *Wolffogebia phuketensis* (Sakai, 1982), обитающих в глубоких мангровых болотах мангрового биосферного заповедника Канзе (Can Gio), Южный Вьетнам. *Salmoneus spiridonovi* sp.n. морфологически близок к восточно-атлантическому *S. erasimorum* Dworschak, Anker et Abed-Navandi, 2000, *S. caboverdensis* Dworschak, Anker et Abed-Navandi, 2000, западно-атлантическому *S. degravei* Anker, 2010 и индо-пацифических *S. seticheles* Anker, 2003, *S. brucei* Komai, 2009, *S. yoyo* Anker, Firdaus et Pratama, 2014 и *S. durisi* Anker, 2019, которые характеризуются увеличенными и субэквивалентными по размеру, но асимметричными хелипепдами (переоподами I), что четко отделяет их от других видов рода. Более того, новый вид является первым представителем рода *Salmoneus*, зарегистрированным в качестве инфаунного партнера (симбионта) нор креветок-уропегебидов.

Introduction

The Can Gio Mangrove Biosphere Reserve (10°22'–10°40'N, 106°46'–107°00'E), mainly forested by about 20-year-old monocultural forests of *Rhizophora apicu-*

lata Bl. (Rosaceae: Rhizophoraceae), was declared a UNESCO Biosphere Reserve in 2000, although a significant part of the territory of this area is still used as agricultural land, in particular for shrimp farming. After the establishment of the national park, an active study on the biological diversity and structure of mangrove communities was started there [Van Xuân, 1992, 2001; Diele *et al.*, 2013; Kuenzer, Vo, 2013; Costa-Böddeker *et al.*, 2016; Pham, 2017; Ashelby *et al.*, 2018; David *et al.*, 2018, 2019; Shih *et al.*, 2019; Vinh *et al.*, 2020; Marin, 2021]. Continued research on mangroves is critical, as they play a predominant role in tropical coastal areas around the world, providing a wide range of biological diversity, environmental and social services, such as protection from storms and coastal erosion [Moberg, Rönnbäck, 2003; Walters *et al.*, 2008]. In addition, especially in Southeast Asia, mangroves are seriously threatened: about 20% of the total mangrove area has been lost since 1980 [FAO, 1993, 2007], while at least 35% of this area was lost between 1980 and 2000 worldwide [Valiela *et al.*, 2001].

As in many other mangrove ecosystems of the Indo-West Pacific, deep areas of mangrove forests provide a source of accumulation of alluvial sediment, and are formed by dark gray or black marsh mangrove soils, which are characterized by low level of oxygen and the presence of hydrogen sulfide, mostly because of the activity of anaerobic sulfur-reducing bacteria (e.g., *Desulfobacter* sp.) [Ng, Sivasothi, 2002; Hossain, Nuruddin, 2016]. Such conditions are very difficult for various burrowing species to live in, so most of the species that inhabit mangrove swamps are habitat-specific, in contrast to the outer areas of mangrove forests, where bioturbation effect is sufficient.

A detailed study on the crustacean biodiversity in the central parts of the Can Gio Mangrove Biosphere Reserve in April 2020 revealed several specific infaunal species associated with larger burrowing animals. In the presented contribution, a new species of the genus *Salmoneus* Holthuis, 1955 (Crustacea: Decapoda: Alpheidae) from burrows of large burrowing crustaceans, which are also specific to anoxic mangrove swamps, is described as new to science.

Material and methods

Sampling was carried out within the scientific program of the Joint Russian-Vietnamese Tropical Research and Technological Center (Tropical Center) in the upper channel zone of the deep mangrove forests in the Can Gio Mangrove Biosphere Reserve near the Vietnam-Russian Climatic Research Station (CRS “Can Gio”) ($10^{\circ}27'19.1''N$ $106^{\circ}53'32.9''E$) (Fig. 1) in March–April (dry season) 2020. The animals were collected from different burrows on the muddy substrate using a bait suction pump (yabby-pump). Some burrows of large burrowing and infaunal animals located above the water level and the adjacent areas were carefully excavated with a shovel, and then manually with hands. All collected animals were photographed alive using a Canon G16 digital camera and then fixed with 90% ethanol solu-

tion. The drawings were made using lucida camera attached to Olympus SZX10 stereo microscope.

Carapace length (cl., in mm), measured from the tip of the rostrum to the midpoint of the posterodorsal margin of the carapace, and total body length (tbl., in mm), represented by the dorsal length from the tip of rostrum to the posterior margin of telson, are used as standard measurements. Although it is quite difficult to determine the sex of representatives of the genus *Salmoneus* as both sexes have appendix masculina on pereopods II, it is still possible to clearly habitually distinguish two groups in the collected individuals (see Fig. 2) — conditionally related to females (\varnothing), individuals with eggs/developed pleurae and relatively less developed pereopods I (chelipeds), and conditionally related to males (σ), individuals always without eggs, less developed pleurae and relatively more developed pereopods I (chelipeds). Further, they will be mentioned in this way as \varnothing (female) or σ (male), respectively, but it is worth mentioning that the real gender may be erroneous.

Barcode segment of the cytochrome c oxidase subunit I (COI) mtDNA, used as one of the most informative gene markers for genetic studies at population and species level [Avise, 1993], was amplified with the help of the universal primers COIF (5'-CCAGCTGGAGGAGGAYCC-3') and H7188 (5'-CATTCTAGGCCTAAGAAGTGTG-3') [Kessing *et al.*, 1989; Knowlton *et al.*, 1993]. PCR products were performed on amplifier T100 (Bio-Rad, USA) under the following standard recommended conditions. The volume of 10 μ L of reaction mixture contained 1 μ L of total DNA, 2 μ L of 5xPCR mix (Dialat, Russia) and 1 μ L of each primer. The amplification products were separated by using gel electrophoresis of nucleic acids on a 1.5% agarose gel in 1xTBE, and then stained and visualized with 0.003% EtBr using imaging UV software. DNA nucleotide sequences were determined using Genetic Analyzer ABI 3500 (Applied Biosystems, USA) and BigDye 3.1 (Applied Biosystems, USA) with direct and reverse primers. Aligned sequences of COI mtDNA gene marker, 658 base pairs in length, are deposited in GenBank (NCBI). No further phylogenetic analysis was performed, as only two sequences of the genus *Salmoneus* are currently present in genetic databases.

The type material is deposited in the collection of the Zoological Museum of Moscow State University, Moscow, Russia (ZMMU) and the Laboratory of Ecology and Evolution of Marine Invertebrates of A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences, Moscow, Russia (LEMMI).

Taxonomy

Order Decapoda Latreille, 1802

Family Alpheidae Rafinesque, 1815

Genus *Salmoneus* Holthuis, 1955

Salmoneus spiridonovi sp.n.

Figs 2–8.

HOLOTYPE σ (non-ovigerous specimen), cl. 5.0 mm, tl. 15.3 mm, ZMMU Ma-6186 — VIETNAM, Ho Chi Minh District, Can Gio Mangrove Biosphere Reserve, $10^{\circ}27'30.7''N$ $106^{\circ}53'35.7''E$, inside burrows of *Alpheus* cf. *euphrosyne* along the banks of canals deep in mangroves, yabby-pump sampling, coll. I. Marin & S. Sinelnikov, 25.04.2020.

PARATYPES, 1 σ (non-ovigerous specimen), cl. 4.7 mm, tl. 15.0 mm, ZMMU Ma-6186 (dissected); 1 ovigerous \varnothing , cl. 5.3 mm, tl. 16.5 mm, ZMMU Ma-6187 — same locality as for holotype, inside burrows of *Alpheus* cf. *euphrosyne* and *Alpheus* aff. *lo-*

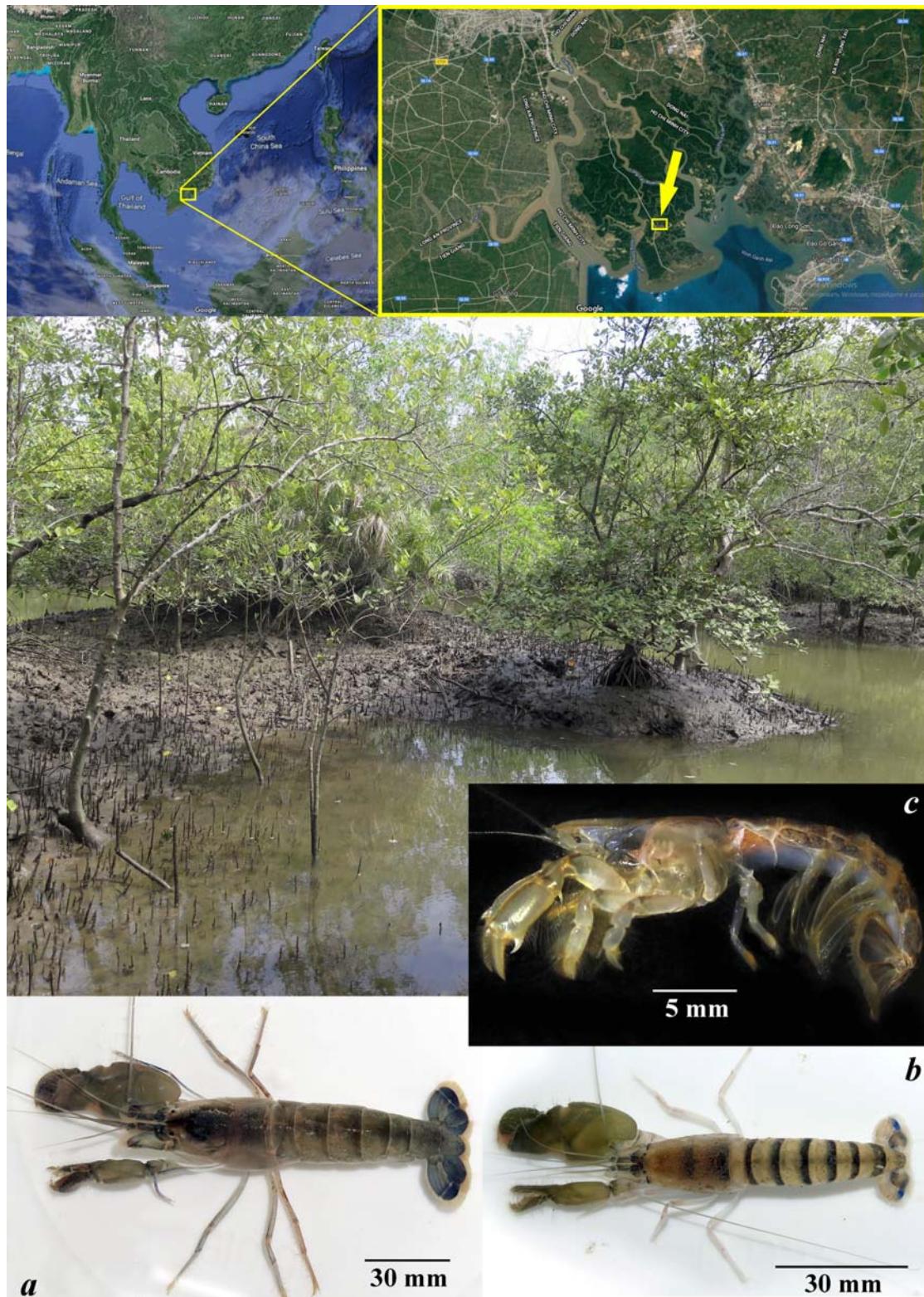


Fig. 1. The location of the Can Gio Mangrove Biosphere Reserve in South Vietnam (upper map) and typical biotopes in the locality, where *Salmoneus spiridonovi* sp.n. was collected (lower) with the other burrowing crustaceans (*Alpheus* cf. *euphrosyne* de Man, 1897 (a), *Alpheus* sp. aff. *lobidens* De Haan, 1849 (Alpheidae) (b) and mudshrimp *Wolffogebia phuketensis* K. Sakai, 1982 (Upogebiidae) (c)).

Рис. 1. Расположение мангрового биосферного заповедника Канзэ в Южном Вьетнаме (верхняя карта) и типичные биотопы в местности, где был собран *Salmoneus spiridonovi* sp.n. (нижнее фото) совместно с другими роющими ракообразными (*Alpheus* cf. *euphrosyne* de Man, 1897 (a), *Alpheus* sp. aff. *lobidens* De Haan, 1849 (Alpheidae) (b) и креветками *Wolffogebia phuketensis* K. Sakai, 1982 (Upogebiidae) (c)).

bidens, 17.04–2.05.2020; 1 ovigerous ♀, cl 5.2 mm, tl 16.0 mm (LEMMI), ZMMU Ma-6188 — same locality as for holotype, inside manually excavated burrow of *Wolffogebia* cf. *phuketensis*, coll. I. Marin & S. Sinelnikov, 25.04.2020.

ADDITIONAL MATERIAL, 2 ovigerous ♀♀; 2 non-ovigerous ♀♀; 6 non-ovigerous ♂♂ (LEMMI) — same locality as for holotype, inside burrows of *Alpheus* cf. *euphrosyne* and *Alpheus* aff. *lobidens*, 17.04–2.05.2020.

DESCRIPTION. Small-sized (maximum cl. 5.3 mm, tl. 16.3 mm) alpheid shrimp with subcylindrical body form (Figs 2, 8). Carapace covered with fine, erect setae dorsally (Figs 2, 3b, d). Rostrum well developed, flattened dorsoventrally, triangular in dorsal view, broad at base, reaching mid-length of second article of antennular peduncle, directed forward, nearly straight; tip acute, dorsal surface non-carinate; ventral margin with distinct subapical tooth; lateral margins sharply edged (Fig. 3a, b, d); carapace anterior margin with well-developed, acute orbital teeth, directed somewhat mesially in dorsal view, anteriorly in lateral view (Fig. 3a, b, d); pterygostomial region broadly rounded; anterolateral suture present (Fig. 3b, d); cardiac notch deep (Fig. 2). Epistomial sclerite with low protuberance. Upper lip with crested median lobe.

Eyestalks (Fig. 3a, b, d, e) visible dorsally and exposed laterally, concealed by anterior part of carapace for about 1/3, with dorsomesial distal tubercle; cornea (Fig. 3e) located at anterolateral part of eyestalk, darkly pigmented, somewhat reduced:

Pleon with pleurae I–IV broadly rounded to slightly angular, pleura V with posteroventral margin forming subacute angle (Fig. 2); pleura VI without articulated flap, posterior margin blunt, not acutely produced (Fig. 7g); pre-anal plate rounded and medially depressed.

Telson (Fig. 7h) moderately slender, subtrapezoidal, tapering distally, about 2.5 times as long as proximal width; dorsal surface with two pairs of short stout spines at about 0.5 and 0.8 of telson length; posterior margin with deep U-shaped notch filled with 7–9 long plumose setae, and flanked by 3 pairs of long spines.

Antennular peduncle moderately stout (Fig. 3f, g); stylocerite (Fig. 3f) moderately slender, falling slightly short of distal margin of antennular article 2; ventromesial carina with small, anteriorly directed tooth (Fig. 3h); antennular article 2 about as long as wide, shorter than basal antennular article; outer flagellum subdivided almost at base, with 6–7 fused articles, and secondary ramus with 6–7 groups of aesthetascs.

Antenna (Fig. 3i) moderately robust; basicerite bearing sharp, triangular distoventral tooth; scaphocerite broad and ovoid in shape, about 1.5–1.7 times as long as wide, just reaching distal end of antennular peduncle, with straight lateral margin and broadly convex blade, distolateral tooth sharp, slightly overreaching distal margin of blade; carpocerite short, cylindrical, slightly overreaching mid-length of scaphocerite.

Mouthparts typical for genus. Mandible (Fig. 4a) incisor process armed with 5 or 6 teeth; molar process well developed; palp 2-articulated. Maxilla I (Fig. 4b) with distal endite broad, bearing spinules on distomesial margin; endopod bilobed, subterminal lobe bearing long spine, terminal lobe unarmed. Maxilla II (Fig. 4c) with distal endite broad, bilobed, edged with fine simple setae; proximal endite well developed, bilobed, edged with fine simple setae; scaphognathite well developed. Maxilliped I (Fig. 4d) with endite bilobed, distally with row of short fine setae; exopod well developed, with broad caridean lobe; endopod slender, un-

segmented, with 2 long setae subdistally and several plumose setae along mesial margin; episod broad. Maxilliped II (Fig. 4e) with well-developed exopod and ear-shaped episod. Maxilliped III (Fig. 4f) slender, pediform; coxa (Fig. 4g) with rounded lateral plate, and strap-like episod with terminal hook; antepenultimate article slightly flattened ventrolaterally; penultimate article less than 7 times as long as wide; ultimate article tapering distally, with numerous rows of short serrulate setae and long simple setae, tip (Fig. 4h) with sharp corneous point and 2 long spiniform setae subdistally; arthrobranch well-developed, multi-lamellate (Fig. 4g).

Pereiopods I (chelipeds) usually subequal in length, asymmetrical in shape, carried flexed (Fig. 8); coxae each with strap-like episod and setobranch consisting of 2 moderately long setae; bases as long as wide, unarmed. Major cheliped almost similar between males (Fig. 5a–c) and females (Fig. 6a, b); coxa as long as wide; ischium slightly flattened ventrolaterally, 3–3.5 times as long as wide, with small movable spine proximoventrally; merus about 6 times as long as maximal width, somewhat wider near mid-length, smooth, unarmed, ventrolateral surface distinctly depressed to accommodate flexed carpus and chela; carpus constricted proximally, cup-shaped, with three lobes distally; chela (Figs 5b, 6b) subcylindrical, rounded in cross-section; palm subequal to fingers in length, smooth, flexor margin with a dense row of fine setae extending inward onto pollex, extensor margin with some long fine setae subdistally; fingers (Figs 5c, 6b) not gaping when closed, subequal in length, crossing distally, with evenly serrated cutting edges; cutting edges of both dactylus and pollex with 13–15 subtriangular teeth; dactylus with a dense row of long fine setae extending inward along its dorsal margin. Minor cheliped similar in proportion to major cheliped with slightly stouter chela, near similar between males (Fig. 5d–f) and females (Fig. 6c–e); ischium slightly flattened ventrolaterally, about 4 times as long as wide, with small movable spine proximoventrally; merus 6–6.5 times as long as maximal width, somewhat wider near mid-length, smooth, ventrolateral surface depressed; carpus somewhat bent, cup-shaped, with three lobes distally; chela (Figs 5e, 6d) slightly compressed, oval in cross-section; palm about 1.5 times as long as dactylus, smooth, flexor margin with a dense row of long fine setae extending onto inward pollex, extensor margin also with row of long fine setae distodorsally; fingers (Figs 5f, 6e) somewhat gaping when closed, crossing distally; dactylus longer than pollex, slightly twisted, strongly curved distally, its cutting edge armed with one proximal low tooth-like process and two distinct teeth, distal portion unarmed, hiatus-like, dorsal margin with a dense row of long fine setae directed inward along its dorsal margin; pollex less strongly curved compared to dactylus, its cutting edge armed with two large teeth intercalating with dactylar teeth, distal part significantly sloped, with 2 or 3 triangular teeth in males (Fig. 5g) and less stronger teeth in females (Fig. 6f).

Pereiopod II (Fig. 7a) slender. Coxa as long as wide, with strap-like episod and setobranch consisting of 2 setae. Basis as long as wide, unarmed. Ischium unarmed, about 7 times as long as wide. Merus equal in length to ischium, unarmed. Carpus with 5 subarticular with ratio 4.5/1/1/1.5. Chela longer than distal-most carpal subarticle.

Pereiopod III (Fig. 7b) moderately slender. Coxa about 1.4 times as long as wide, with strap-like episod and setobranch consisting of 2 setae. Basis as long as wide, unarmed. Ischium about 4 times as long as wide, with 2 mov-

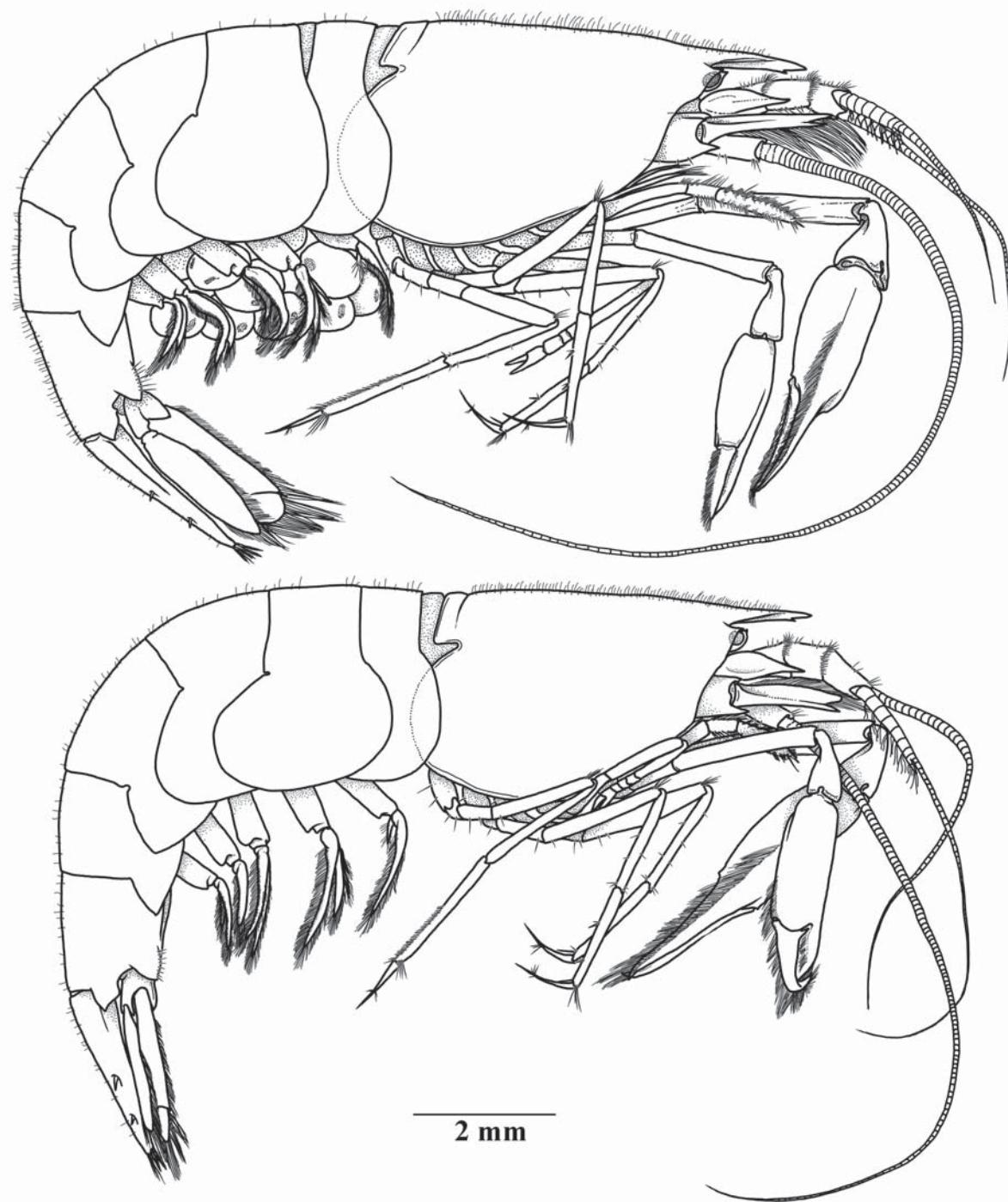


Fig. 2. *Salmoneus spiridonovi* sp.n., habitus in lateral view. Upper, paratype, ZMMU Ma-6187, conditionally ovigerous female, ♀; lower, holotype, ZMMU Ma-6185, conditionally male, ♂ (non-ovigerous specimen).

Рис. 2. *Salmoneus spiridonovi* sp.n., общий вид, вид сбоку. Верхний, параптип, ZMMU Ma-6187, условно половозрелая самка с яйцами, ♀; нижний, голотип, ZMMU Ma-6185, условно самец, ♂ (не-яйценосная особь).

able spines on ventrolateral surface. Merus 7–7.5 times as long as wide, unarmed. Carpus almost subequal in length to merus, noticeably slender, about 10–11 times as long as wide, with small spiniform setae distoventrally. Propodus subequal in length to carpus, about 10 times as long as wide, with 2 widely spaced spiniform setae on flexor margin, in

addition to long spiniform setae at flexor distal margin, which is about 1/3 of the length of dactylus; dactylus (Fig. 7c) about half-length of propodus, slender, gently curving distally, terminating in sharp tip.

Pereiopod IV (Fig. 7d) almost similar but slightly robust than pereiopod III; coxa about 1.5 times as long as wide,

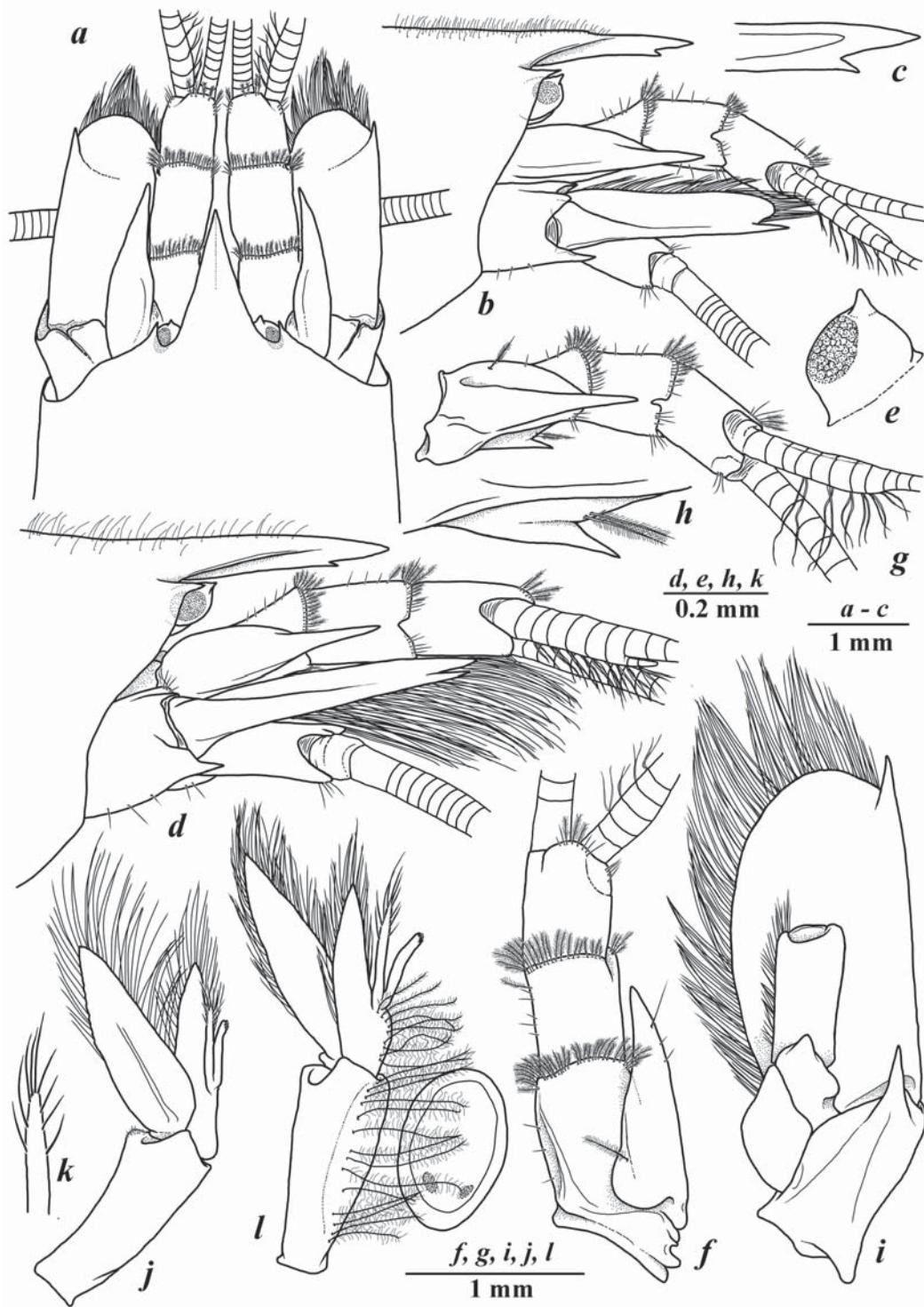


Fig. 3. *Salmoneus spiridonovi* sp.n., holotype, ♂ (non-ovigerous specimen) (ZMMU Ma-6186) (a–c), paratype ♂ (non-ovigerous specimen) (LEMMI) (e–k), paratype, ovigerous ♀ (LEMMI) (d, l): a — rostrum, anterior part of carapace and cephalic appendages, dorsal view; b, d — rostrum and anterior part of carapace, lateral view; c — tip of rostrum, lateral view; e — eye, dorsal view; f, g — right antennule, flagella partially omitted; h — ventromesial tooth of basal article of right antennular peduncle; i — left antenna, ventral view; j, l — left pleopod II, dorsal view; k — tip of appendix masculina, dorsal view.

Рис. 3. *Salmoneus spiridonovi* sp.n., голотип, ♂ (не-яйценосная особь) (ZMMU Ma-6186) (a–c), паратип, ♂ (LEMMI) (e–k), паратип, ♀ с яйцами (LEMMI) (d, l): a — рострум, передняя часть карапакса и головные придатки, вид сверху; b, d — рострум и передняя часть карапакса, вид сбоку; c — кончик рострума, вид сбоку; e — глаз, вид сверху; f, g — правая антenna, жгутики частично обрезаны; h — вентромезиальный зубец базального членика правого antennalного стебелька; i — левая антenna, вид снизу; j, l — левый плеопод II, вид сверху; k — кончик appendix masculina, вид сверху.

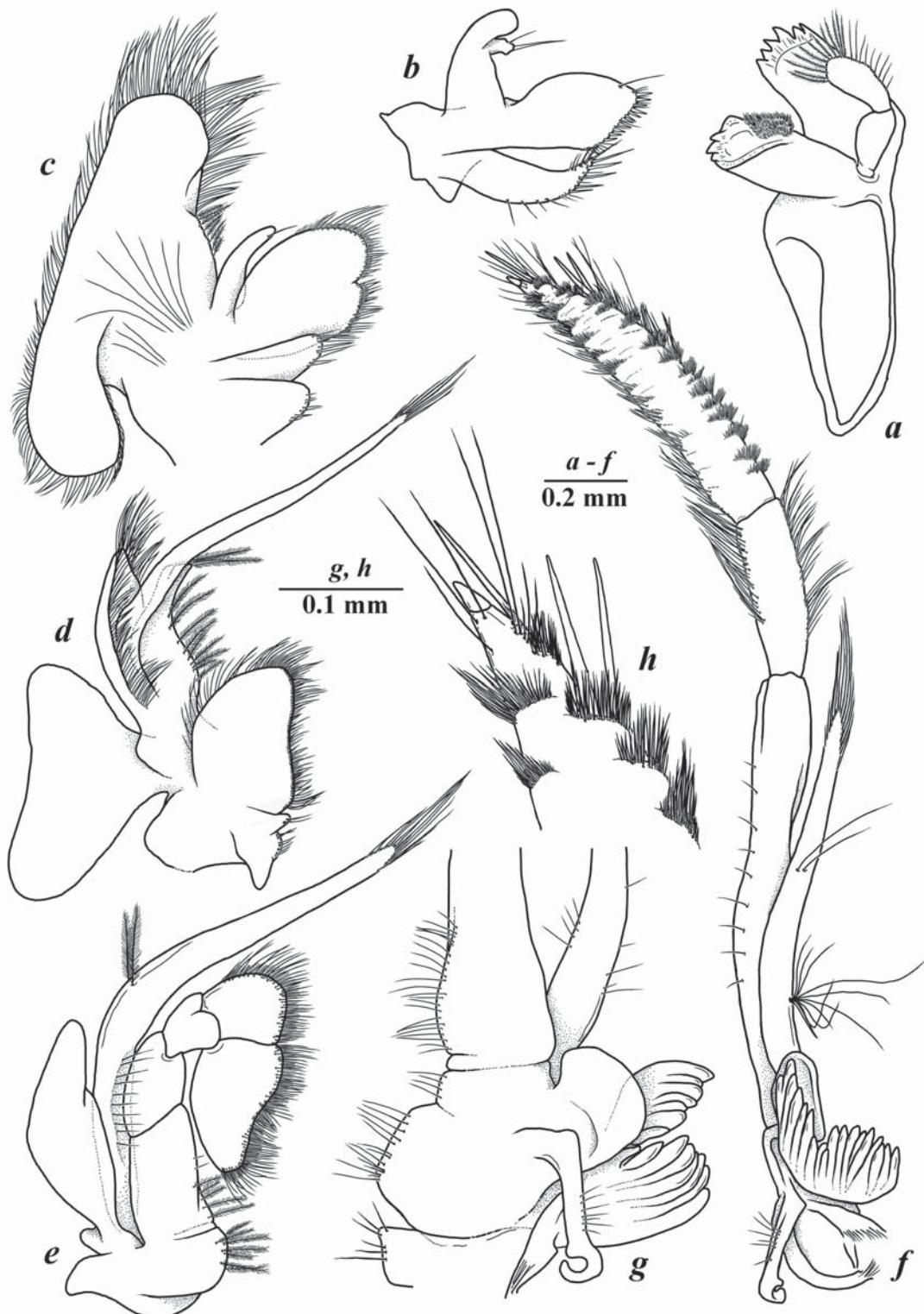


Fig. 4. *Salmoneus spiridonovi* sp.n., paratype, ♂ (non-ovigerous specimen) (ZMMU Ma-6186): *a* — right mandible, internal view; *b* — left maxillula, outer view; *c* — left maxilla, outer view; *d* — left maxilliped I, outer view; *e* — left maxilliped II, outer view; *f* — left maxilliped III, lateral view; *g* — coxa and basal part of antepenultimate article of left maxilliped III, ventral view; *h* — tip of ultimate article of maxilliped III, lateral view.

Рис. 4. *Salmoneus spiridonovi* sp.n., параптип, ♂ (не-яйценосная особь) (ZMMU Ma-6186): *a* — правая мандибула, вид изнутри; *b* — левая максиллула, вид снаружи; *c* — левая максилла, вид снаружи; *d* — левая максиллипеда I, вид снаружи; *e* — левая максиллипеда II, вид снаружи; *f* — левая максиллипеда III, вид сбоку; *g* — кокса и базальная часть предпоследнего членика левой максиллипеды III, вентральный вид; *h* — кончик дистального членика максиллипеды III, вид сбоку.

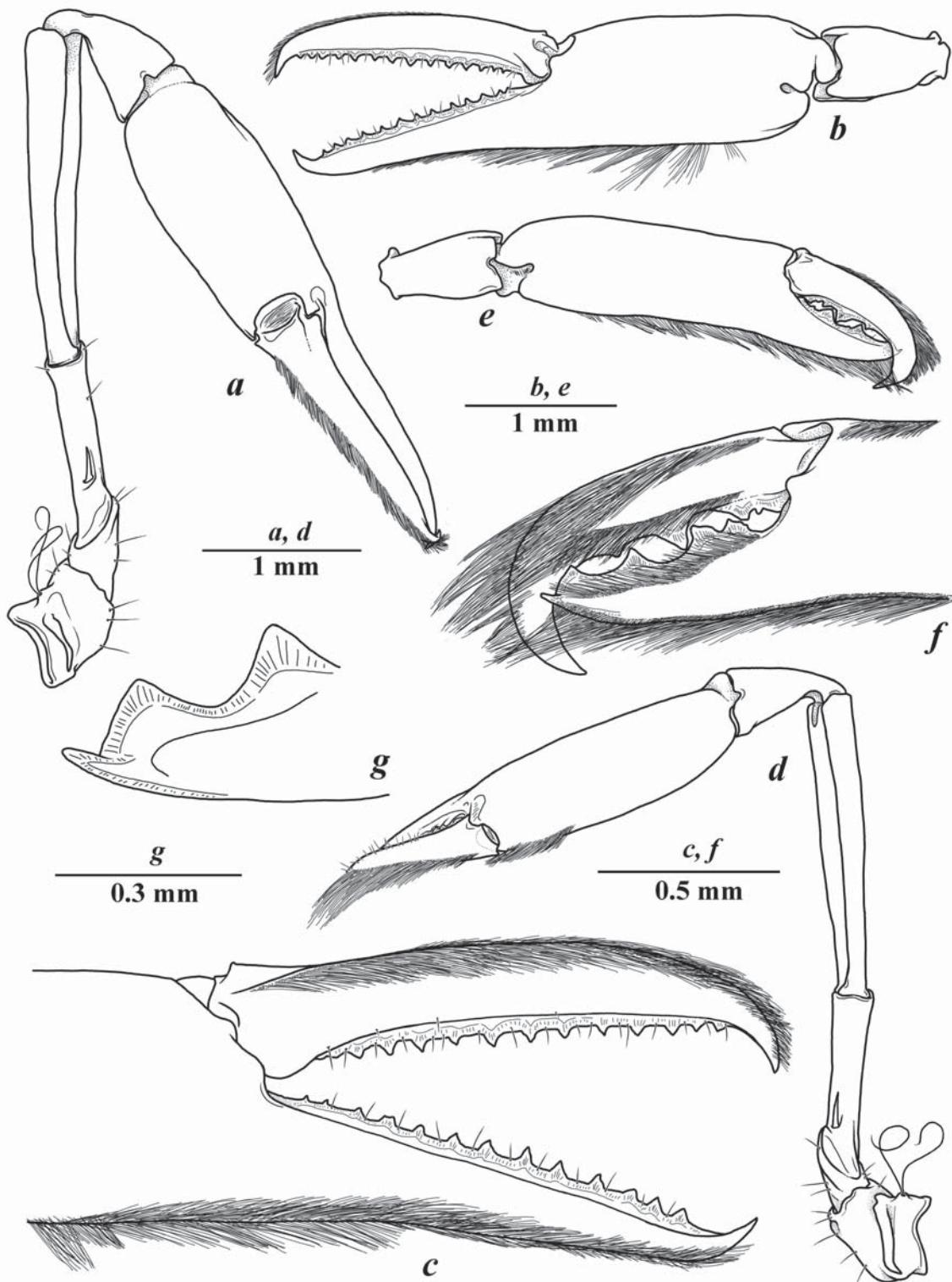


Fig. 5. *Salmoneus spiridonovi* sp.n., paratype, ♂ (non-ovigerous specimen) (ZMMU Ma-6186): *a* — major (right) pereiopod I (cheliped), lateral view; *b* — same, carpus and chela, extensor view; *c* — fingers of major pereiopod I, internal view; *d* — minor (left) pereiopod I (cheliped), lateral view; *e* — same, carpus and chela, extensor view; *f* — fingers of minor pereiopod I, flexor view; *g* — distal part of polex (fixed finger) of minor pereiopod I, flexor view.

Рис. 5. *Salmoneus spiridonovi* sp.n., параптип, ♂ (не-яйценосная особь) (ZMMU Ma-6186): *a* — большая (правая) переопода I (хелипеда), вид сбоку; *b* — тот же, карпус и клемшия, вид изнутри; *c* — пальцы большой переоподы I, вид изнутри; *d* — малая (левая) переопода I (хелипеда), вид сбоку; *e* — тот же, карпус и клемшия, вид изнутри; *f* — пальцы малой переоподы I, вид изнутри; *g* — дистальная часть полекса (неподвижного пальца) малой переоподы I, вид изнутри.

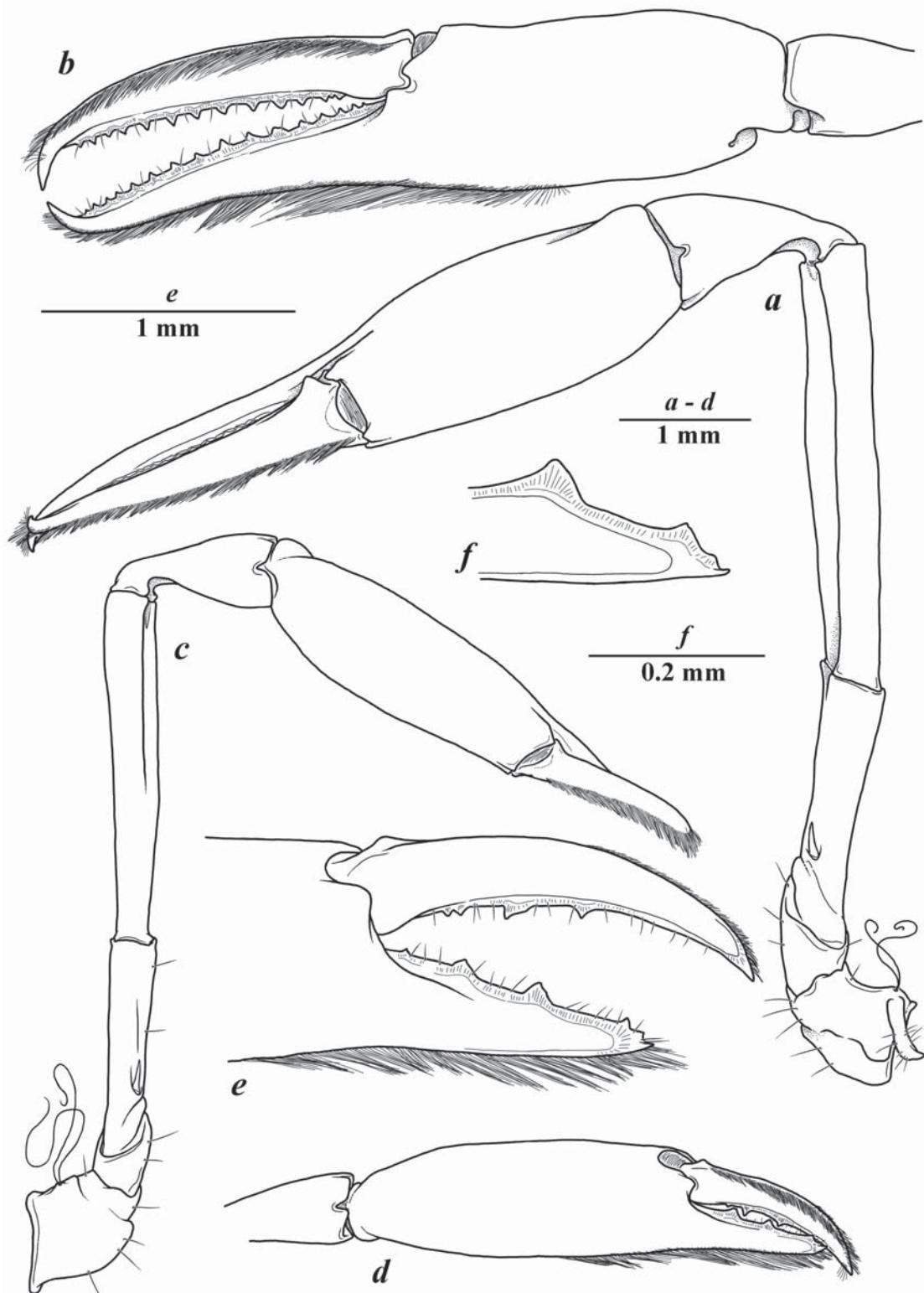


Fig. 6. *Salmoneus spiridonovi* sp.n., paratype, ovigerous ♀ (LEMMI): *a* — major (left) pereiopod I (cheliped), lateral view; *b* — same, carpus and chela, internal view; *c* — minor (right) pereiopod I (cheliped), lateral view; *d* — same, carpus and chela, internal view; *e* — fingers of major pereiopod I, internal view; *f* — distal margin of polex (fixed finger) of minor pereiopod I, internal view.

Rис. 6. *Salmoneus spiridonovi* sp.n., параптип, яйценосная ♀ (LEMMI): *а* — большая (левая) переопода I (хелипеда), вид сбоку; *б* — то же, карпус и клемша, вид сбоку; *в* — малая (правая) переоподия I (хелипеда), вид сбоку; *г* — то же, карпус и клемша, вид изнутри; *д* — пальцы большой переоподы I, вид изнутри; *е* — дистальный край полекса (неподвижного пальца) малой переоподы I, вид изнутри.

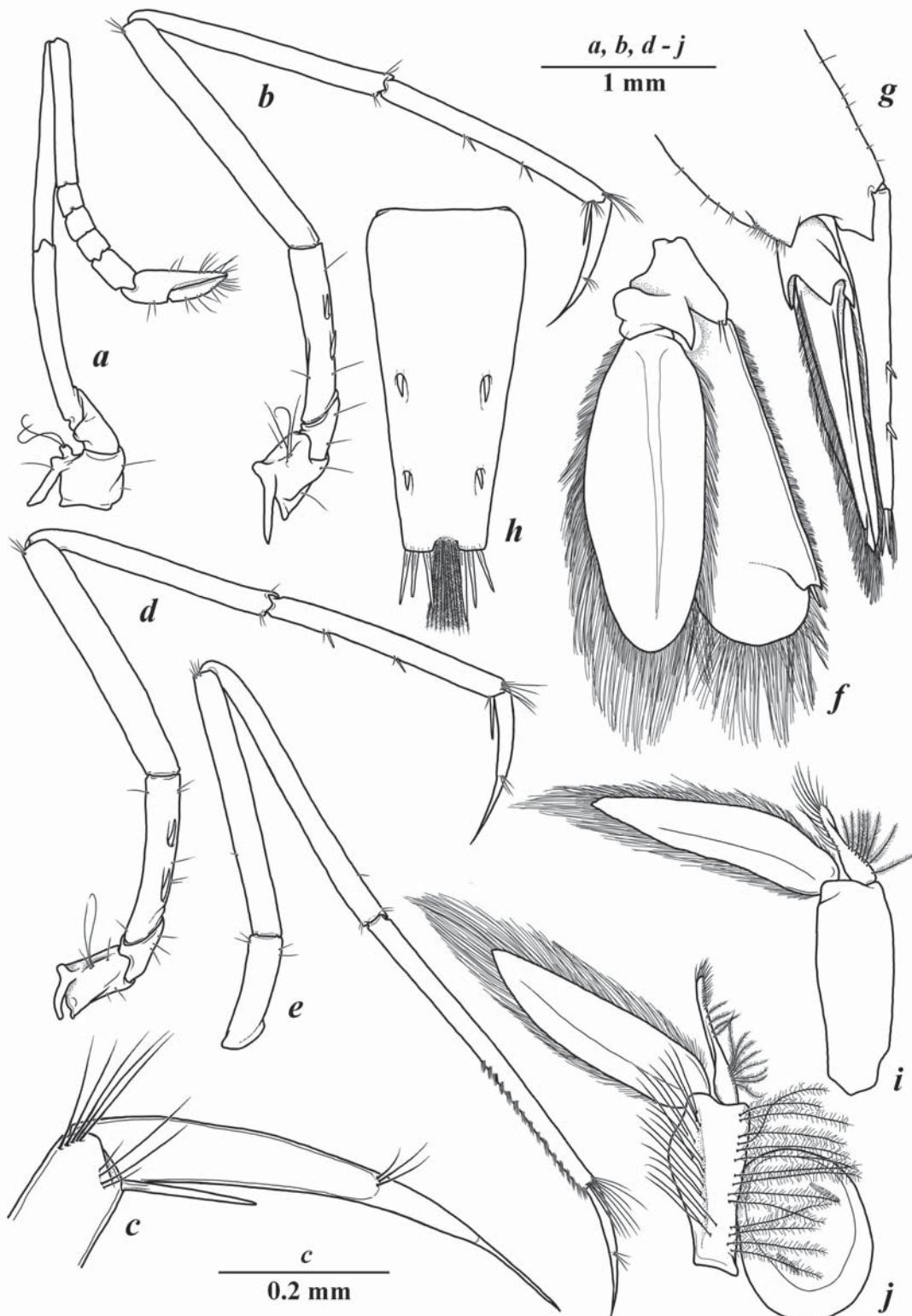


Fig. 7. *Salmoneus spiridonovi* sp.n., paratype, ♂ (non-ovigerous specimen) (ZMMU Ma-6186) (a–i) and paratype ♀ (LEMMI) (j): a — pereiopod II, outer view; b — pereiopod III, lateral view; c — dactylus of pereiopod III, lateral view; d — pereiopod IV, lateral view; e — pereiopod V, lateral view; f — uropods, internal view; g — telson and uropods, lateral view; h — telson, dorsal view; i, j — left pleopod I, dorsal view.

Рис. 7. *Salmoneus spiridonovi* sp.n., параптип, ♂ (не-яйценосная особь) (ZMMU Ma-6186) (a–i) и параптип ♀ (ZMMU Ma-6186) (j): а — переопод II, вид снаружи; б — переопод III, вид сбоку; в — дактилус переопод III, вид сбоку; г — переопод IV, вид сбоку; д — переопод V, вид сбоку; е — уроподы, вид изнутри; ж — тельсон и уроподы, вид сбоку; з — тельсон, вид сверху; и, ж — левый плеопод I, вид сверху.

with strap-like epipod and 2 setobranchs; basis as long as wide, unarmed; ischium about 4 times as long as wide, with 2 movable spines proximoventrally; merus about 6–7 times as long as wide, unarmed; carpus almost subequal to merus, noticeably slender, about 9–10 times as long as wide, with small spiniform setae distoventrally; propodus noticeably subequal to carpus, about 9 times as long as wide, with 2 widely spaced spiniform setae on ventral margin, in addition to long spiniform setae near dactylar base, which is about 1/3 of the length of dactylus; dactylus about half-length of propodus, moderately slender, simple, smoothly curving distally, with sharp tip.

Pereiopod V (Fig. 7e) more slender than pereiopods III–IV; coxa 1.5 times as long as wide, unarmed; basis as long as wide, unarmed; ischium about 2.5 times as long as wide, unarmed; merus about 7 times as long as wide, unarmed; carpus noticeably more slender and slightly longer than merus, about 10 times as long as wide, shorter than propodus, unarmed; propodus long, slender, about 13–14 times as long as wide, with two dozens of serrulate setae forming moderate cleaning brush on distal ventrolateral surface, without spiniform setae; dactylus about 0.3 times length of propodus, distally curved, otherwise similar to dactyli of pereiopods III–IV.

Pleopods similar in males and females. Pleopod I (Fig. 7i, j) with appendix interna, furnished with simple setae distally and subdistally, and plumose setae along the mesial margin. Pleopod II (Fig. 3j, l) with appendix masculina slightly shorter than appendix interna, appendix masculina furnished with 7–8 stiff setae on apex and subapical area (Fig. 3k).

Uropod (Fig. 7f, g) with protopod ending in sharp curved posterolateral tooth and median spine on posterodorsal margin just lateral to the base of the endopod. Exopod broadly ovoid, with small distolateral tooth and well-developed distolateral spine; diaeresis sinuous. Endopod as long as exopod, ovoid, unarmed.

Gill-exopod formula typical for genus, consisting of 1 arthrobranch above base of maxilliped III, 1 pleurobranch on each thoracomeses IV–VIII, corresponding to pereiopods I–V, epipods on maxillipeds I–III and pereiopods I–IV, exopods on maxillipeds I–III and setobranch on pereopods I–V, corresponding to epipod on maxilliped III and pereiopods I–IV.

COLOURATION IN LIFE. Body and appendages semi-translucent-whitish, dorsal surface of basal segments of antennules and antennae, carapace, pleon and telson densely covered with small red chromatophores; chelipeds, ambulatory pereiopod and uropods semitranslucent-whitish; eyes cornea red; eggs yellow (Fig. 8).

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ETYMOLOGY. The new species is named in honour of the Russian carcinologist Dr. Vassily Albertovich Spiridonov (7.04.1957–17.12.2020), who, amongst other lines of study, worked on mangrove crustaceans in the Can Gio Mangrove Biosphere Reserve of South Vietnam [Chertoprud *et al.*, 2012].

TAXONOMIC REMARKS. *Salmoneus spiridonovi* sp.n. morphologically similar to the eastern Atlantic *S. erasimorum* Dworschak, Anker et Abed-Navandi, 2000, *S. caboverdensis* Dworschak, Anker et Abed-Navandi, 2000, the western Atlantic *S. degravei* Anker, 2010, and the Indo-West Pacific *S. seticheles* Anker, 2003, *S. brucei* Komai, 2009, *S. yoyo* Anker, Firdaus et Pratama, 2014 and *S. durisi* Anker,

2019 [Dworschak *et al.*, 2000; Anker, 2003, 2010, 2019; Komai, 2009; Anker *et al.*, 2014]. All of these species are characterized by both pereiopods I (chelipeds) being enlarged, subequal in size, but asymmetrical in the shape, clearly separating them from other species in the genus (except some species from the “*Salmoneus jarli*” species group (see below)). However, the monophyly of this group is not phylogenetically tested and proven [Anker, 2019]. The monotypic genus *Deioneus* Dworschak, Anker et Abed-Navandi, 2000 is morphologically close to those species of *Salmoneus* [Dworschak *et al.*, 2000].

In most of diagnostic features, the new species is similar to the Indo-Pacific *Salmoneus seticheles* and *S. durisi* in the presence of a distoventral tooth on the rostrum, the general shape of the pereiopods I and the presence of rows of long fine setae on the flexor and extensor margins of the chelae of both pereiopods I.

From *Salmoneus seticheles* (see Anker [2003]), morphologically the most closely related species, the new species can be separated by 1) rostrum triangular in dorsal view, with well-developed lateral carina, reaching the mid-length of antennular article 2, with more developed distoventral tooth on rostrum; 2) ischium of both pereiopods I (chelipeds) armed with well-marked strong tooth; 3) the presence of dense row of long fine setae directed inward along dorsal margin of dactylus and ventral margin of polex and palm in both major and minor pereiopods I (vs. just row of long simple setae in *S. seticheles* [Anker, 2003: Figs 3B, 4]); 4) significantly sloped distal part of polex both in males and females (vs. “normal” sharp distal margin of polex in *S. seticheles* [Anker, 2003: Fig. 4B]); and 5) shorter distoventral spines on propodus of ambulatory pereiopods, especially pereiopod III, which are about 1/3 of the length of dactylus (vs. about 1/5 of the length of dactylus in *S. seticheles* [Anker, 2003: Fig. 3E]). Moreover, the holotype of *S. seticheles* [Anker, 2003] and the specimen from Singapore [Anker, De Grave, 2016] possess very asymmetrical and different in size pereiopods I, while all collected specimens of the new species, both non-ovigerous and ovigerous, have subequal pereiopods I.

From *Salmoneus durisi*, the new species can be separated by 1) relatively longer rostrum with well-developed distoventral tooth (vs. relatively shorter, without distoventral tooth in *S. durisi* [Anker, 2019: Fig. 1a, b, j]; 2) relatively slender telson, about 2.5 times as long as proximal width, in *S. spiridonovi* sp.n. (vs. about 2 times in *S. durisi*) [Anker, 2019: Fig. 1d]; 3) ischium of both pereiopods I (chelipeds) armed with well-marked movable spine; 4) the presence of dense and wide row of long fine setae along distoventral margin of palm, dorsal margin of dactylus and distal margin of polex in both major and minor pereiopods I in *S. spiridonovi* sp.n. (Figs 5, 6) (vs. one row of sparse long simple setae in *S. durisi* [Anker, 2019: Fig. 3]); 4) oblique distal part of polex both in males and females (see Figs 5g, 6f) (vs. “normal”, pointed and elongated, distal part of polex in *S. durisi* [Anker, 2019: Fig. 3g]); and 5) different living coloration: carapace and pleon with deep red chromatophores in *S. spiridonovi* sp.n. (Fig. 8) (vs. entirely translucent whitish body in *S. durisi* [Anker, 2019: Fig. 4]).

The reduced cornea of the eyes easily separates the new species from *Salmoneus yoyo* and *S. brucei*. Moreover, these species can be further separated from the new species by the absence of a distoventral tooth on the rostrum and the morphology of chelipeds: *S. yoyo* has a number of blunt tubercles on the ventromesial margin of the merus and the propo-

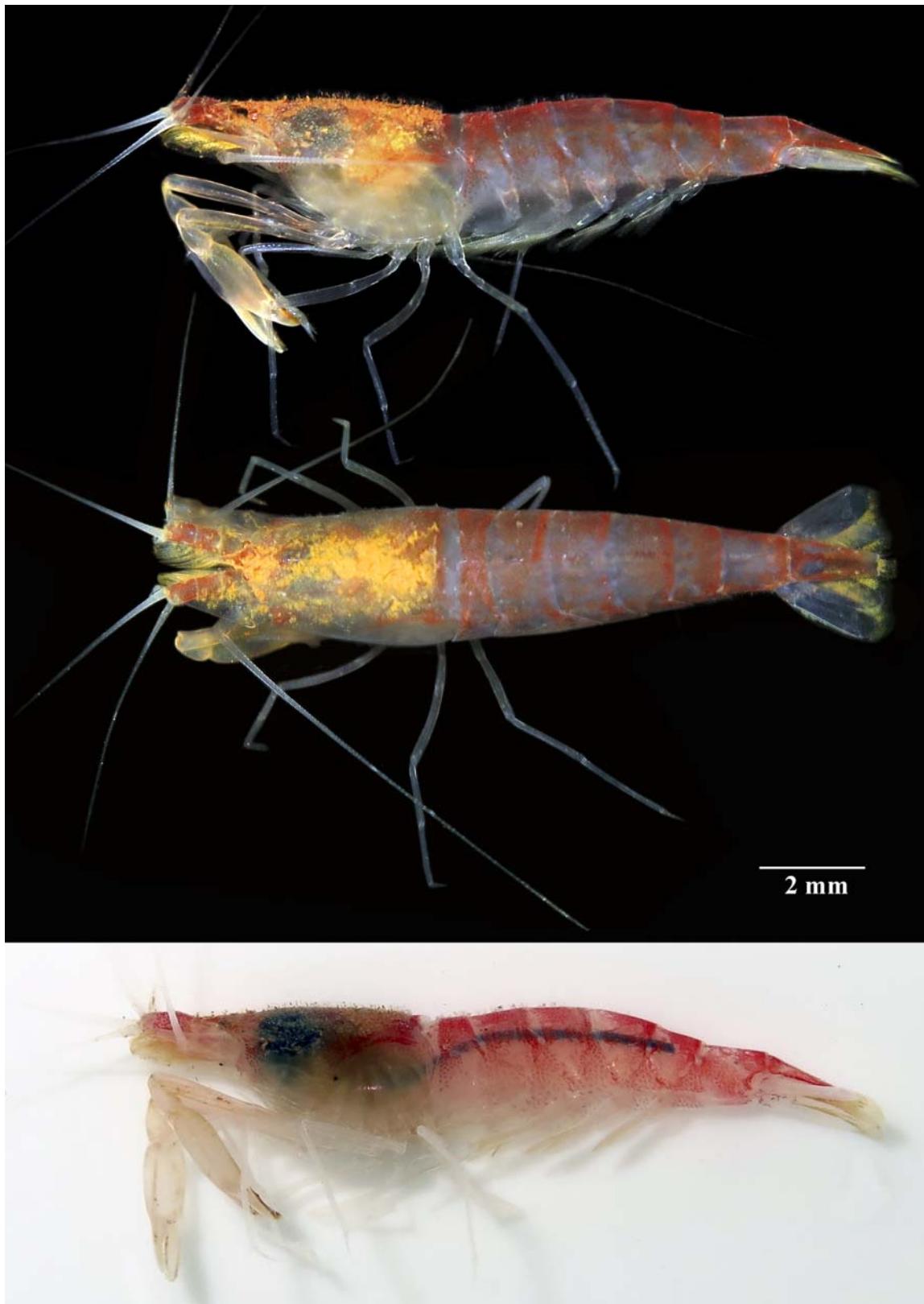


Fig. 8. *Salmoneus spiridonovi* sp.n., habitus of ♂ (non-ovigerous specimen), showing living coloration. The yellow color on the carapace and antennae is due to particles derived from mangrove mud.

Рис. 8. *Salmoneus spiridonovi* sp.n., общий вид ♂ (не-яйценосной особи), прижизненная окраска. Желтые частицы на карапаке и антеннах представляют собой частицы мангровой грязи.

dus of the pereiopod I (chelipeds), and lacks a row of fine setae along margins of the palm and dactylus [Anker *et al.*, 2014: Fig. 2]; the beveled shape of the distal margin of psolex in *S. yoyo* [Anker *et al.*, 2014: Fig. 2F, G, H] is very similar to the new species. At the same time, *S. brucei* is rather distinctive in lacking supraorbital spines on the carapace and more robust pereiopods I (chelipeds), in particular, the meri, compared with the new species [Komai, 2009: Fig. 4; Anker, 2019: Fig. 5].

The eastern Atlantic *S. erasimorum*, *S. caboverdensis*, and the western Atlantic *S. degravei* Anker, 2010, which also have subequal pereiopods I (chelipeds), are easily distinguished from the new species by the unarmed ischia of both pereiopods I and the shape of their fingers, with very slender pincer-like fingers of the major cheliped and the stouter, subequal fingers of the minor chelipeds [Anker, 2010; Dworschak *et al.*, 2000].

Three more species from the tropical western Pacific, namely *Salmoneus komaii* Anker, 2011, *S. paulayi* Anker, 2011 and *S. poupinii*, presently referred to the “*S. jarli*” species group [Anker, 2011], also have more or less similar pereiopods I, but differ from the new species in numerous features, including absence of the rostral teeth, better developed cornea of the eye, a different shape of fingers of the pereiopods I, the presence of 2 spines on the ischium of the pereiopod II and of 3 spines on the ischium of the pereiopod III and a translucent whitish body coloration [Anker, 2011].

HABITAT AND ECOLOGY. Sampling using a yabby-pump allowed to obtain adult individuals of *Salmoneus spiridonovi* sp.n. from the burrows of two species of the alpheid shrimp genus *Alpheus*, the only species of the genus inhabiting mangrove swamps of the Can Gio mangrove forests — *Alpheus cf. euphrosyne* de Man, 1897 and *Alpheus aff. lobidens* De Haan, 1849 (Fig. 1) (both are from species complexes [e.g., Cunha *et al.*, 2020]) One adult ovigerous specimen (♀) of the new species was collected from a vertical burrow (with a total length of up to 10–15 cm) of the upogebiid mud shrimp *Wolffogebia cf. phuketensis* Sakai, 1982 (Fig. 1c) during a manual burrow excavation together with the host. All individuals of *Salmoneus spiridonovi* sp.n. were collected individually per the host’s burrow, sometimes with a single unidentified goby fish. Other burrowing and burrow-associated animals found in the same area during yabby-pump sampling were the mangrove stomatopod *Clorida rotundicauda* (Miers, 1880) (Stomatopoda: Squillidae), numerous burrowing sesarmid crabs (Decapoda: Sesarmidae), *Metaplas* spp. (Decapoda: Varunidae) and *Uca* spp. (Decapoda: Ocypodidae), *Wolffogebia* spp. (Decapoda: Upogebiidae), mud amphipods of the genus *Victoriopispa* Karaman et Barnard, 1979 (Amphipoda: Eriopisidae), different gobies, and the recently described alpheid shrimps *Potamalpheops kisi* Marin, 2021 (Decapoda: Alpheidae) [Marin, 2021]. All of them are specific to this biotope, representing a stable community characteristic of deep mangrove swamps, wetland pools and tidal creeks in the C?n Gi? Mangrove Biosphere Reserve, and have not been found on intertidal mudflats or the mangrove estuary.

DISTRIBUTION. Presently known only from the Can Gio Mangrove Biosphere Reserve, South Vietnam.

Discussion

The genus *Salmoneus* Holthuis, 1955 currently contains 50 species worldwide [De Grave, Fransen, 2011;

Anker *et al.*, 2020; De Grave *et al.*, 2020; Komai *et al.*, 2021]. Most of the known species of the genus are free-living, inhabiting crevices among coral rubbles, under rocks and boulders in tropical to temperate regions of all oceans [Anker, Marin, 2006; Anker, 2011; Komai, Anker, 2012; Anker, Lazarus, 2015; Komai *et al.*, 2015; Īuriš, Horká, 2016; Anker *et al.*, 2015, 2020]. Some species are, however, known as infaunal symbionts of various burrowing marine invertebrates, such as echiuran worms [Anker *et al.*, 2020; De Grave *et al.*, 2020], larger burrowing alpheid shrimps of the genus *Alpheus* (Decapoda: Caridea: Alpheidae), as well as axiidean ghost shrimps of the family Callianassidae and Callichiridae (Decapoda: Axiidea) [Dworschak *et al.*, 2000; De Grave, 2004; Anker, Marin, 2006; Komai, 2009; Anker, 2010] (Table 1). Several more described species also appear to be infaunal, but their hosts remain unknown [Felder, Manning, 1986; Anker *et al.*, 2014; Komai *et al.*, 2021].

The habitat conditions of burrowing animals at the collection site in the Can Gio Mangrove Biosphere Reserve (see Fig. 1) are very difficult due to the anoxic fetid deep mud of alluvial origin with a high content of hydrogen sulfide beneath the surface (see above). The burrowing fauna here should be tolerant to low level of oxygen (hypoxia). It is very specific, and very likely endemic, and is represented here by the most prominent mudskippers and amphibious crabs, as well as a very limited number of other large burrowing crustaceans (see above). Amphibious caridean shrimps, such as *Merguia* spp. (Merguiidae) and *Potamalpheops* spp. (Alpheidae) are also characteristic for such deep mangrove swamp conditions [Gillikin *et al.*, 2001; Marin, 2021]. The new species was mostly obtained from the burrows of large alpheid shrimps of the genus *Alpheus*, while the ovigerous female collected from the burrow of *W. cf. phuketensis* could be an accidental association. Actually, mud shrimps of the genus *Wolffogebia* are one of the few numerous burrowing crustaceans in the area, whereas *W. phuketensis* is known as a specialized deep mangrove swamp dwelling species, digging tunnels/burrows in or near mounds excavated by mud lobsters of *Thalassina* spp. (Decapoda: Gebiidae: Thalassinidae) in the upper littoral zone of such mangrove swamps [Ng, Kang, 1988]. The reduced cornea of the eyes of the *Salmoneus* appears to be linked to permanent cryptogenic habitats inside deep burrows of larger burrowing host as well as cloudy waters of mangrove communities.

Among the species of the genus *Salmoneus*, only *Salmoneus carvachoi* Anker, 2007 is known as infaunal associate of the western Atlantic gebiid ghost shrimps *Axianassa australis* Rodrigues et Shimizu, 1992 (Decapoda: Gebiidae: Axianassidae) [Anker, 2007; Oliveira *et al.*, 2015] (Table 1). Thus, the present new species is the first representative of the genus *Salmoneus* known as infaunal associate of *Wolffogebia* and mud shrimps of the family Upogebiidae (Decapoda: Gebiidae), while *Salmoneus* became the sixth genus

Table 1. Known infaunal crustacean associations of the genera *Salmoneus* and *Deioneus*.
 Таблица 1. Известные ассоциации инфаунных креветок родов *Salmoneus* и *Deioneus*.

| Associated species | Host | Reference |
|--|---|---|
| <i>Alpheus</i> spp. (Caridea: Alpheidae) | | |
| <i>Salmoneus alpheophilus</i> Anker et Marin, 2006 | in burrow of large goby-associated <i>Alpheus</i> sp. | Anker, Marin, 2006 |
| <i>Salmoneus carvachoi</i> Anker, 2007 | in burrow of <i>Alpheus estuariensis</i> Christoffersen, 1984, <i>Alpheus chacei</i> Carvacho, 1979 | Anker, 2007; Oliveira et al., 2015 |
| <i>Salmoneus colinorum</i> De Grave, 2004 | larger snapping shrimps of <i>Alpheus malabaricus</i> (Fabricius, 1775) species complex | De Grave, 2004; Anker et al., 2015; Anker, 2019 |
| <i>Salmoneus rostratus</i> Barnard, 1962 | in burrow of large goby-associated <i>Alpheus</i> sp. | Anker, 2003; Anker, Marin, 2006; De Grave, Wilkins, 1997. |
| Ghost shrimps of the family Callianassidae (Axiidea) | | |
| <i>Salmoneus brucei</i> Komai, 2009 | callianassid ghost shrimps <i>Lepidophthalmus tridentatus</i> (von Martens, 1868) and <i>L. cf. rosae</i> (Nobili, 1904) | Komai, 2009; Anker, 2019 |
| <i>Salmoneus erasimorum</i> Dworschak, Anker et Abed-Navandi, 2000 | <i>Gilvoissius tyrrhena</i> (Petagna, 1792) | Dworschak et al., 2000 |
| Ghost shrimps of the family Callichiridae (Axiidea) | | |
| <i>Salmoneus caboverdensis</i> Dworschak, Anker e Abed-Navandi, 2000 | <i>Neocallichirus pachydactylus</i> (A. Milne-Edwards, 1870) | Dworschak et al., 2000 |
| <i>Salmoneus degravei</i> Anker, 2010 | <i>Neocallichirus grandimana</i> (Gibbes, 1850) | Anker, 2010 |
| <i>Salmoneus durisi</i> Anker et Ashrafi, 2019 | <i>Neocallichirus calmani</i> (Nobili, 1904) | Anker, Ashrafi, 2019 |
| <i>Salmoneus ikaros</i> Anker, Al-Kandari et De Grave, 2020 | <i>Balsscallichirus masoomi</i> (Tirmizi, 1970) | Anker et al., 2020 |
| <i>Deioneus sandizelli</i> Dworschak, Anker et Abed-Navandi, 2000 | <i>Corallianassa intesi</i> (de Saint Laurent & Le Loeuff, 1979) and <i>Neocallichirus pachydactylus</i> (A. Milne-Edwards, 1870) | Dworschak et al., 2000 |
| Host unknown | | |
| <i>Salmoneus pouponi</i> Anker, 2011 | possibly, associated with a burrow of <i>Glypturus</i> sp. (Callianassidae) | Anker, 2011 |
| <i>Salmoneus singaporensis</i> Anker, 2003 | possibly, associated with burrows of <i>Alpheus rapacida</i> De Man, 1908 (Alpheidae) | Johnson, 1962; Anker, 2003; Anker, De Grave, 2016 |
| <i>Salmoneus tricristatus</i> Banner, 1959 | possibly, burrows of large <i>Alpheus</i> sp. | Anker et al., 2015 |
| <i>Salmoneus venustus</i> Anker, 2019 | possibly, associated with a burrow of <i>Glypturus</i> sp. (Callianassidae) | Anker, 2019 |

among Alpheidae known in association with upogebiid mudshrimps. Representatives of *Athanas* Leach, 1814, *Betaeus* Dana, 1852, *Leptalpheus* Williams, 1965, *Lep-tathanas* De Grave et Anker, 2008 and *Stenalpheops* Miya, 1997 are also known in associations with the upogebiid mudshrimps, mostly from the genus *Upoge-bia* Leach, 1814 (Table 2).

With the new species, the diversity of the genus *Salmoneus* in coastal waters of Vietnam now consists of 8 species. All other species, namely *S. rostratus*

Barnard, 1962, *S. nhatrangensis* Anker et Marin, 2006, *S. auroculatus* Anker et Marin, 2006, *S. falcidactylus* Anker et Marin, 2006, *S. pusillus* Anker et Marin, 2006, *S. alpheophilus* Anker et Marin, 2006 and *S. venustus* Anker, 2019 were recorded and described from Nha Trang Bay, central Vietnam [Anker, Marin, 2006; Anker, 2019]. This is, of course, potentially very far from the true diversity, and research will be continued, and there are more unknown species awaiting discovery.

Table 2. Infaunal alpheid shrimps (Alpheidae) known from burrows of mudshrimps of the genus *Upogebia* Leach, 1814 (Gebiidea: Upogebiidae).
 Таблица 2. Инфаунные креветки-альфеиды (Alpheidae), известные из нор роющих креветок рода *Upogebia* Leach, 1814 (Gebiidea: Upogebiidae).

| Associated species | Host | Reference |
|--|--|---|
| <i>Athanas dentirostris</i> Anker, Jeng et Chan, 2001 | <i>Upogebia</i> aff. <i>takaoensis</i> Sakai and Türkay, 1995 | Anker <i>et al.</i> , 2001 |
| <i>Betaeus levifrons</i> Vinogradov, 1950 | <i>Upogebia major</i> (De Haan, 1841) | Marin, 2010; Marin, Antokhina, 2020 |
| <i>Betaeus longidactylus</i> Lockington, 1877 | <i>Upogebia pugettensis</i> (Dana, 1852) | Hart, 1964; Campos <i>et al.</i> , 2009 |
| <i>Betaeus ensenadensis</i> Glassell, 1938 | <i>Upogebia pugettensis</i> (Dana, 1852) and <i>U. macginitaeorum</i> (Williams, 1986) | Campos <i>et al.</i> , 2009 |
| <i>Betaeus harrimani</i> Rathbun, 1904 | <i>Upogebia pugettensis</i> (Dana, 1852) | Hart, 1964; Campos <i>et al.</i> , 2009 |
| <i>Leptalpheus felderii</i> Anker, Vera Caripe et Lira, 2006 | <i>Upogebia omissa</i> Gomes Corrêa, 1968 | Anker <i>et al.</i> , 2006 |
| <i>Leptalpheus forceps</i> Williams, 1965 | <i>Upogebia affinis</i> (Say, 1818) | Williams, 1965; Saloman, 1971 |
| <i>Leptalpheus mexicanus</i> Ríos et Carvacho, 1983 | <i>Upogebia dawsoni</i> Williams, 1986 | Ríos, Carvacho, 1983; Ríos, 1992; Campos <i>et al.</i> , 1995 |
| <i>Leptathanas powelli</i> De Grave et Anker, 2008 | <i>Upogebia furcata</i> (Aurivillius, 1898) | De Grave, Anker, 2008 |
| <i>Stenalpheops anacanthus</i> Miya, 1997 | <i>Upogebia major</i> De Haan | Miya, 1997 |
| <i>Stenalpheops koreanus</i> Kim, 1998 | <i>Upogebia edulis</i> Ngoc-Ho et Chan, 1992 and <i>U. major</i> De Haan | Miya, 1997; Hayashi 1998; Kim, 1998; Anker <i>et al.</i> , 2001 |

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