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Revision of *Salmoneus cristatus* (Coutière, 1897) and Allied Forms (Decapoda: Caridea: Alpheidae)

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Salmoneus cristatus (Coutière, 1897) is one of the first described species in the alpheid genus *Jousseaumea* Coutière, 1897, a name later invalidated and replaced by *Salmoneus* Holthuis, 1955. The species was described based on material from Djibouti and was initially characterised by the presence of a pronounced, posteriorly extending carina on the mid-dorsal line of the carapace, a shoulder-like elevation of the orbital hoods, and a red-banded colour pattern. Relying mainly on morphological features, various authors reported *S. cristatus* from several localities in the Indo-West Pacific, from the Red Sea to southern China and Australia. However, recently collected material attributable to *S. cristatus* on morphological grounds allowed for the combination of morphological characters, molecular data and colour patterns, demonstrating the existence of at least four species under the name of *S. cristatus*, including three species that are morphologically similar to, but phylogenetically distant from *S. cristatus s. str*. Therefore, *S. cristatus* is redescribed herein based on recent material from Saudi Arabia and Iran, as well as older material from Israel and Madagascar, with designation of a neotype from the Red Sea coast of Saudi Arabia. Three new species, viz. *S. paracristatus* sp. nov., *S. franseni* sp. nov., and *S. alius* sp. nov., are described based on recent material from Papua New Guinea for the former two species, and New Caledonia, Papua New Guinea and the Solomon Islands for the latter species. However, at least two of these new species seem to have wider distributions in the Indo-West Pacific.

Key words: Marine biodiversity, Alpheid shrimps, *Salmoneus*, Phylogeny, Indo-West Pacific, New species

BACKGROUND

The caridean shrimp genus *Salmoneus* Holthuis, 1955 is presently the third largest genus in the family Alpheidae Rafinesque, 1815, with over 60 described species so far (Coutière 1897a b; De Grave and Fransen 2011; Anker 2022; Komai 2022). However, the actual species diversity of the genus appears to be far beyond what is currently known, considering the presence of numerous morphologically nearly identical species, the rapidly growing number of described species in the genus, and the fact that about two-thirds of all the species have been described in the past two decades (*e.g.*, Anker 2010; Komai and Anker 2012; Anker and Lazarus 2015; Anker 2019b; Anker and Ashrafi 2019; Anker et al. 2020; Marin 2021; Anker 2022; Komai 2022). The reason for this hidden diversity lies in these shrimps' small size and cryptic lifestyles, ranging from dwelling in small spaces under large boulders or in coral rubble crevices (Anker and Marin 2006; Anker 2011 2019a 2020; Ashrafi et al. 2020) to living in burrows of various fossorial animals (*e.g.*, De Grave 2004; Komai

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2009; Anker et al. 2014; Komai et al. 2021; d'Acoz et al. 2022), or in marine caves (Fransen 1991; Komai et al. 2015).

Salmoneus was subdivided into seven informal groups by Anker and Marin (2006), of which the *S. cristatus* (Coutière, 1897) group was defined by possession of a prominent mid-dorsal carina of variable posterior extension, and each of the major cheliped fingers being serrated, *i.e.*, armed with small, bluntly triangular teeth, on almost the entire cutting edge. The following species were originally assigned to the *S. cristatus* group, in addition to the group-nominal species: *S. auroculatus* Anker and Marin, 2006; *S. brevirostris* (Edmondson, 1930); and *S. tricristatus* Banner, 1959 (Anker and Marin 2006). Later, *S. chadwickae* Ďuriš and Horká 2016 was added to the *S. cristatus* group, thus resulting in five species presently assigned to this group (Ďuriš and Horká 2016). Within the *S. cristatus* group, *S. cristatus* is characterized by a striking, red-banded colour pattern, as described very briefly by Coutière (1987b 1899) and in more detail by L.B. Holthuis in Banner and Banner (1981), and by Banner and Banner (1983). The species is also morphologically rather distinctive, defined by the so called "shoulder" of the anterior region of the carapace, and somewhat elevating the orbital hoods (Coutière 1897b 1899; Banner and Banner 1981).

Salmoneus cristatus is one of the three species originally described by Coutière (1897a b) under the generic name *Jousseaumea* Coutière, 1897, the others being the type species *S. serratidigitus* (Coutière, 1897) and *S. latirostris* (Coutière, 1897). In the original description of *S. cristatus* from Djibouti, Coutière (1897b) did not provide any illustrations. However, some additional details and a few drawings were provided in a subsequent publication (Coutière 1899). Since the original account of the species, *S. cristatus* has been recorded from several localities throughout the Indo-West Pacific, including the Red Sea (Holthuis 1958; Banner and Banner 1981; Ďuriš and Horká 2016), East Africa (Bruce 1976; Banner and Banner 1983), Thailand (Banner and Banner 1966), Taiwan (Anker 2001, as *S.* cf. *cristatus*), eastern Australia (Anker 2003), Papua New Guinea (Ďuriš and Horká 2016, as *S.* aff. *cristatus*), and the South China Sea (Wang and Sha 2016; Sha et al. 2019). Importantly, Banner and Banner (1981) provided illustrations of the topotypic specimen of *S. cristatus* from Djibouti.

Ďuriš and Horká (2016) provided the first molecular phylogeny of the *S. cristatus* group, which included *S. chadwickae*, *S. auroculatus*, *S. tricristatus*, and two species tentatively identified as *S.* aff. *cristatus* and *S*. aff. *brevirostris*. However, the significance of this phylogeny is limited, as no specimens matching *S. cristatus sensu* Coutière (1897b 1899) from the western Indian Ocean were available at that time. Nevertheless, a comparative analysis of morphology and colour of *S. cristatus* and related forms in Ďuriš and Horká (2016) strongly indicated that *S. cristatus* may represent more than one species.

In the present study, morphological, ecological and molecular data are combined to perform a revision of *S. cristatus* and morphologically allied forms (see below). Firstly, the neotype of *S. cristatus* of Coutière (1897b) is designated, and the species is redescribed based on material from Iran and Saudi Arabia. The colour pattern of *S. cristatus* is illustrated for the first time. In addition, three new species are described based on material from Papua New Guinea (two species); and New Caledonia, Papua New Guinea, and the Solomon Islands (one species). Despite their morphological resemblance with *S. cristatus*, the herein described species markedly differ from *S. cristatus* by their live colours and are also phylogenetically distant from it.

MATERIALS AND METHODS

Material

The specimens of *Salmoneus* reported in the present study were collected during several expeditions organised by the Muséum National d'Histoire Naturelle, Paris, France (MNHN), and the Florida Museum of Natural History, University of Florida, Gainesville, USA (FLMNH UF). The MNHN expeditions include the Our Planet Reviewed Madang Expedition (Papua New Guinea) in 2012 [AA, ZĎ], the Our Planet Reviewed Kavieng Expedition (Papua New Guinea) in 2014 [ZĎ], Koumac Expedition (New Caledonia) in 2018 and 2019 [AA, ZĎ], and Madibenthos Expedition (Martinique) in 2016 [ZĎ]. The FLMNH expeditions include the survey of the Thuwal Reefs (Red Sea coast of Saudi Arabia) in 2013 [AA], Moorea Biocode Project (French Polynesia) in 2008 and 2009 [AA], and the Solomon Islands in 2016 [AA]. Additional material was collected in Iran (Abu-Musa Island) in 2019 [HA] and Saudi Arabia (Rabigh) in 2022 [AA]. Two older museum specimens, one of them deposited in the MNHN and the other in the Naturalis Biodiversity Center, Leiden, the Netherlands (RMNH), were also examined. Carapace length (cl, in mm) was measured along the mid-dorsal line from the tip of the rostrum to the posterior margin of the carapace.

DNA extraction, amplification, and sequencing

Tissues from the pleonal muscles and/or posterior

pleopods were used for total genomic DNA extraction using the DNeasy Blood and Tissue Isolation Kit (QIAGEN) following the manufacturer's instructions. The PCR was performed on partial segments of two genes, *i.e.*, the ribosomal 16S rRNA and mitochondrial CO1, using the pair primers Cari F/Cari R (Aznar-Cormano et al. 2015) and JgLCO1490/JgHCO2198 (Geller et al. 2013), respectively. A total volume of 20 µl including 4 µl 5× MyTaq™ Red Reaction buffer (including 15 mM $MgCl_2$ and 5 mM dNTPs), 1.2 µl DNA template, 13 µl ddH_2O, 0.8 µl of each primer, and 0.2 µl MyTaq™ Red DNA polymerase were used for the PCR. The thermocycler conditions for amplifying both 16S and CO1 genes followed the protocol described in Ashrafi et al. (2022). The PCR products were purified using the GenElute PCR Clean-up kit (Sigma-Aldrich). The final products were sent to Macrogen, Amsterdam, the Netherlands, for forward and in some cases reverse sequencing (by an ABI3730XL DNA Sequencer).

GenBank accession numbers for all newly created sequences (most of the material reported in this study) are provided in table 1. In addition to the specimens examined, subsampled and sequenced as part of this study, sequences of other species of the genus *Salmoneus* available on GenBank, including several members of the *S. cristatus* group, were included in the molecular analysis (Ďuriš and Horká 2016; Ashrafi et al. 2022; Komai 2022; see also Table 1).

Sequence alignment, pairwise distance analysis, and tree reconstruction

Obtained sequences were checked by eye using Chromas ver. 2.4.1 and then aligned by the software MUSCLE (Edgar 2004) implemented in MEGA-X (Kumar et al. 2018) with default parameters. For the non-protein coding gene, the partial fragment of 16S, the highly variable positions were eliminated from the alignments using Gblocks v0.91b (Castresana 2000) with default settings, except for allowing gap positions and less strict flanking positions. Pairwise distance analysis (*p*-distance) was conducted using the aligned CO1 gene dataset (~600 bp) in MEGA-X with default parameters. The best model of nucleotide substitution was selected based on BIC (Bayesian Information Criterion) using the software IQ-TREE ver. 2.0.5 (Kalyaanamoorthy et al. 2017). The maximum likelihood analysis was conducted with the software IQ-TREE ver. 2.0.5, whereas the Bayesian tree was constructed using MrBayes ver. 3.2.7 (Ronquist and Huelsenbeck 2003). The MCMC analysis was set for 18 $\times 10^6$ generations with four chains and two independent runs with a sampling frequency of 2500 for each run; at the end, the first 25% of trees were discarded as "burn-

Table 1. *Salmoneus* species used for sequencing and phylogenetic analysis. Collection information including country, collection numbers, GenBank accession numbers and references are provided

Species	Country	Collection number	GenBank Accession numbers 16S/CO1	References
S. aduncus Komai, 2022	Japan	CBM-ZC 17107	LC731708/-	Komai (2022)
S. alius sp. nov./HT	New Caledonia	MNHN-IU-2019-3495	OR438949/ OR438993	Present study
S. alius sp. nov./PT	PNG	MNHN-IU-2013-1471	OR485163/-	Present study
S. alius sp. nov./PT	Solomon Islands	FLMNH-UF-60000	OR485164/-	Present study
S. auroculatus Anker & Marin, 2006	PH/Panglao	OUMNH.ZC.2015-01-031	KR527200/ KT192564	Ďuriš and Horká (2016)
S. chadwickae Ďuriš & Horká, 2016/HT	RS/Jordan	OUMNH.ZC.2015-02-01	KP462861/ KT192561	Ďuriš and Horká (2016)
S. cristatus (Coutiere, 1897)	RS/Saudi Arabia	FLMNH-UF-68811	OR438956/ OR438996	Present study
S. cristatus (Coutiere, 1897)/NT	RS/Saudi Arabia	FLMNH-UF-36069	OR438955/-	Present study
S. cristatus (Coutiere, 1897)	PG/Iran	MNHN-IU-2019-3851	OR438948/ OR438991	Present study
S. franseni sp. nov./HT	PNG	MNHN-IU-2014-881	OR438950/ OR438994	Present study
S. franseni sp. nov.	PNG	MNHN-IU-2014-933	OR438952/ OR438998	Present study
S. paracristatus sp. nov./HT	PNG	MNHN-IU-2014-199	OR438951/ OR438995	Present study
S. paracristatus sp. nov./PT1	PNG	MNHN-IU-2014-205	KP462859/ OR438990	Ďuriš and Horká (2016), Present study
S. paracristatus sp. nov./PT2	PNG	MNHN-IU-2014-294	KP462858/-	Ďuriš and Horká (2016)
S. setosus Manning & Chace, 1990	FA/Martinique	MNHN-IU-2016-4648	OR438953/ OR438992	Present study
S. shojaei Ashrafi, Anker & Ďuriš, 2022	PG/Iran	MNHN-IU-2014-1257	ON128267/ ON128447	Ashrafi et al. (2022)
S. tricristatus A.H. Banner, 1959	FP/Moorea	FLMNH-UF-24069	OR438954/ OR438997	Present study

Abbreviations used: FA, French Antilles; FP, French Polynesia; PG, Persian Gulf; PH, Philippines; PNG, Papua New Guinea; RS, Red Sea; HT, holotype; NT, neotype; PT, paratype.

in". The online application ITOL (Letunic and Bork 2011) was used for displaying the final trees.

The phylogenetic tree was constructed for 15 specimens belonging to 10 species (Table 1), based on concatenation of two genes, 16S rRNA (488 bp) and mtCO1 (614 bp). It is important to note that this tree was built exclusively for taxonomic purposes, *i.e.*, to show genetic divergence between the specimens preliminarily identified as *S. cristatus*, and does not reflect the actual phylogenetic relationships between the 10 species included in the analysis. The voluntary omission of numerous distantly related taxa explains the low support for deeper branches of the tree. A more comprehensive phylogeny of *Salmoneus* and related genera will be provided elsewhere (Ashrafi et al. in preparation).

RESULTS

All specimens examined present a prominent mid-dorsal carina extending from the tip of the rostrum at least to the level of the eyes. However, in most cases, this carina extends beyond the middle of the carapace. All individuals are also characterised by the anterior region of the carapace having a distinct "shoulder", individualising the orbital hoods area from the rest of the carapace. However, some minor but seemingly consistent morphological differences between the western Indian Ocean (Saudi Arabia, Iran) and western Pacific (Papua New Guinea, New Caledonia, Solomon Islands) specimens, and also within the western Pacific material, were corroborated by our molecular results (see below). These differences affect, for instance, the posterior extension of the mid-dorsal carina, the configuration of the dentition of the major chela fingers, and the armature of the ischia of the third and fourth pereiopods (see below). In addition, only the western Indian Ocean specimens display bright red bands, as described for *S. cristatus* (Coutière 1899; Holthuis 1958), in contrast to the plain, creamy whitish or yellowish colour of the western Pacific individuals (see below).

The combined 16S + CO1 phylogenetic tree (Fig. 1) revealed the presence of four clades within the material initially identified as *S. cristatus* (or *S.* aff. *cristatus*). Each of these four clades clearly corresponds to a genetically distinctive lineage, with a minimal pairwise genetic distance of 9.1% for *COI* (Table 2). The three specimens from the western Indian Ocean clustered together as a sister clade of *S. tricristatus* Banner, 1959, whereas the specimens from the western

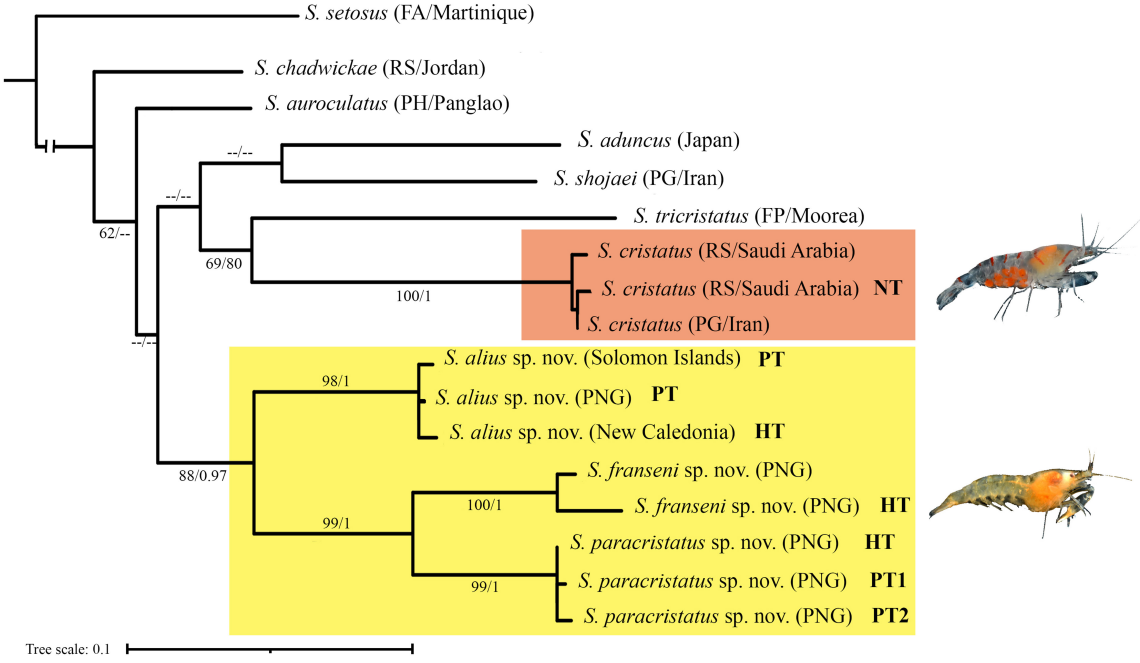

Fig. 1. Bayesian and Maximum Likelihood concatenated tree (based on 16S and *COI*) of selected species of *Salmoneus* with focus on the *S. cristatus* species group, showing two different clades morphologically allied to *S. cristatus*. Numbers above or under each branch are bootstrap supports and Bayesian posterior probabilities, respectively (supports and probabilities under 60/0.6 are not shown). Insert photographs show *S. franseni* sp. nov. (yellow clade) and *S. cristatus* (red clade). Abbreviations used: FA, French Antilles; FP, French Polynesia; PG, Persian Gulf; PH, Philippines; PNG, Papua New Guinea; RS, Red Sea; HT, holotype; NT, neotype; PT, paratype. Sequences for *S. aduncus*, *S. auroculatus*, *S. chadwickae*, and *S. shojaei* were obtained from GenBank (see Ďuriš and Horká 2016; Komai 2022; Ashrafi et al. 2022).

Pacific formed a clade containing three genetically well-differentiated lineages, though in a more distant position (Fig. 1). Therefore, the two most typical features of the carapace of *S. cristatus*, namely the strong, posteriorly extending mid-dorsal carina and the "shoulder" of the anterior region, seem to have evolved at least twice. These results, albeit preliminary, also indicate that the *S. cristatus* group as defined by Anker and Marin (2006) may not be monophyletic, as it includes *S. aduncus* from the *S. rostratus* group and *S. shojaei*, which was tentatively assigned to the *S. gracilipes* group (Komai 2022; Ashrafi et al. 2022).

Based on the morphological and molecular results, the specimens from the Red Sea (Saudi Arabia) and Persian Gulf (Iran) clearly represent *S. cristatus* sensu Coutière (1897b 1899), whereas the material from Papua New Guinea, New Caledonia, and the Solomon Islands is assigned to three new species, which are described below as *S. franseni* sp. nov., *S. paracristatus* sp. nov., and *S. alius* sp. nov. (Fig. 1). Within *S. cristatus*, the genetic distance of CO1 between the Red Sea and Persian Gulf specimens is minimal (1.0%, Table 2) and expected considering the geographic distance between these populations. On the other hand, the holotype of *S. franseni* sp. nov., was genetically more significantly different from the non-type specimen from the same locality (pairwise genetic distance of CO1 3.8%), which was tentatively attributed to the same species for it is missing its major cheliped.

RESULTS

TAXONOMY

Order Decapoda Latreille, 1802
Family Alpheidae Rafinesque, 1815

Genus *Salmoneus* Holthuis, 1955

Salmoneus cristatus (Coutière, 1897)
(Figs. 2–5)

Jousseaumea cristata Coutière 1897a: 234; Coutière 1899: 70, figs. 22, 23.

Salmoneus cristatus — Holthuis 1958: 18, fig. 7; (?) Bruce 1976: 44; Banner and Banner 1981: 54, fig. 6: Banner and Banner 1983: 88 (part.).

Not *Salmoneus cristatus* — Banner and Banner 1983: 88 [= *S. chadwickae* Ďuriš and Horká, 2016 or *S. auroculatus* Anker and Marin, 2006, see below].

Not *Salmoneus cristatus* — Anker 2003: 108, fig. 6 [possibly = *S. franseni* sp. nov., see below].

Not *Salmoneus cristatus* — Wang and Sha 2016: 1586, figs. 1–4 [= *S. paracristatus* sp. nov., see below]

Not *Salmoneus cristatus* — Sha, Wang, and Cui 2019: 206, figs 2.121–2.124 [= *S. paracristatus* sp. nov., see below]

Not *Salmoneus cristatus* — Banner and Banner 1966: 40, fig. 10 [possibly = *S. paracristatus* sp. nov., see below].

Material examined: Neotype: ovig. specimen (cl 2.5 mm), FLMNH UF 36069, Red Sea, Saudi Arabia, off Thuwal, Shib Nazar East, 22°19'19.94"N, 38°51'17.99"E, coral reef, depth 0−20 m, coll. A. Anker et al., 16.03.2016 (BDJRS-2832). Additional material: 1 non-ovig. specimen (cl 2.9 mm), FLMNH UF 68811, Red Sea, Saudi Arabia, north of Rabigh, 22°55'32.17"N, 38°51'21.45"E, back reef, shallow lagoon with sand and coral rubble, in coral rubble crevices, hand and hammer, depth 1 m, coll. A. Anker et al., 23.06.2022 (AA-22-140); 1 ovig. specimen (cl 3.5 mm), RMNH.CRUS. D.14354, Red Sea, Gulf of Aqaba, Israel, 03.12.1955, coll. H. Steinitz; 1 ovig. specimen (cl 3.3 mm), MNHN-IU-2019-3851, Persian Gulf, Iran, Abu-Musa Island, Qadir Park, sandy/rocky bottom with corals, shallow subtidal (depth less than 2 m), 17.07.2019, coll. H. Ashrafi; 1 ovig. specimen (cl 3.2 mm), MNHN-IU-2019-3852, same data as for previous specimen;

Table 2. Pairwise distance matrix of partial fragment of CO1 (bottom half) and 16S (top half) for *S. cristatus*, *S. paracristatus* sp. nov., *S. franseni* sp. nov., and *S. alius* sp. nov.

species	1	2	3	4	5	6	7	8	9	10
1) *S. alius* sp. nov (HT)		0.002	0.004	0.045	0.047	0.047	0.032	0.033	0.032	0.032
2) *S. alius* sp. nov (PNG)	-		0.002	0.043	0.044	0.045	0.030	0.031	0.030	0.030
3) *S. alius* sp. nov (SI)	-	-		0.045	0.047	0.047	0.032	0.033	0.032	0.032
4) *S. cristatus* (PG/Iran)	0.155	-	-		0.002	0.002	0.049	0.051	0.045	0.045
5) *S. cristatus* (RS/Saudi Arabia)	0.156	-	-	0.010		0.005	0.051	0.051	0.047	0.047
6) *S. cristatus* (NT)	-	-	-		-		0.051	0.053	0.047	0.047
7) *S. franseni* sp. nov.	0.137	-	-	0.150	0.152	-		0.007	0.026	0.026
8) *S. franseni* sp. nov. (HT)	0.153	-	-	0.168	0.166	-	0.038		0.027	0.027
9) *S. paracristatus* (HT)	0.135	-	-	0.182	0.181	-	0.095	0.107		0.000
10) *S. paracristatus* (PT)	0.140	-	-	0.184	0.182	-	0.091	0.107	0.005	

Abbreviations used: PG, Persian Gulf; RS, Red Sea; SI, Solomon Islands; HT, holotype; PT, paratype; NT, neotype.

1 ovig. specimen (cl 4.4 mm), MNHN-IU-2021-9769, Madagascar, Toliara (Tuléar), probably around 1977–1979, coll. M. Peyrot-Clausade.

Redescription: Small-sized alpheid shrimps (cl range 2.5–4.4 mm). Carapace (Fig. 3A–C) covered by short setae, with prominent mid-dorsal carina reaching to about distal fourth of carapace; frontal region entirely concealing eyes in dorsal view, distinctly elevated from anterolateral portion of carapace, shoulder-like; rostrum triangular in dorsal view, with subacute tip, reaching to about distal margin of second antennular article, approximately as long as broad; rostral carina prominent, continued by mid-dorsal carina on carapace; orbital teeth small, subacute, reaching to proximal third of first antennular article, distinctly longer than wide; anterolateral suture present, pterygostomial angle broadly rounded, cardiac notch deep.

Pleon (Fig. 3E) covered with short setae; pleura of first to forth pleonites rounded anteroventrally and posteroventrally; fifth pleuron subrounded posteroventrally; sixth pleuron with subtriangular projection flanking each side of telson, posteroventral suture incomplete.

Telson (Fig. 3D) subrectangular, tapering distally, about 4.5 times as long as distal width, covered by scattered short setae; dorsal surface with two pairs of spiniform setae located at about 0.5 and 0.8 telson length, respectively; posterior margin with broadly U-shaped, central notch furnished with 4 plumose setae, and two pairs of spiniform setae, mesial ones about 1.6 times as long as lateral ones and about 4 times as long as spiniform setae on dorsal surface.

Antennule (Fig. 3B, C) with peduncle relatively stout; first article approximately as long as broad; stylocerite robust, with blunt tip, reaching to or slightly overreaching second article; second article about 0.8 times as long as broad; third article about 1.2 times as long as second article; lateral antennular flagellum biramous, fused portion with two subdivisions, shorter ramus well developed, reaching to about sixth subdivision of longer ramus, with six or so groups of aesthetascs.

Antenna (Fig. 3B, C) with stout basicerite, its distoventral margin armed with subacute tooth and blunt subdistal projection, superior margin projecting as small subacute tooth; scaphocerite reaching to about middle of third article of antennular peduncle, lateral tooth slightly overreaching blade; carpocerite almost reaching distal margin of second article of antennular peduncle; flagellum not particularly stout, with second subdivision distinctly longer than others.

Third maxilliped (Fig. 5A, B) with coxa bearing strap-like epipod and broadly rounded lateral plate; antepenultimate article slender, about six times as long as broadest part; penultimate article relatively short, about 0.5 times as long as antepenultimate article; ultimate article about twice as long as penultimate article, distally armed with small, subapical, spiniform seta; exopod slender, reaching to about distal margin of antepenultimate article; arthrobranch normally developed.

First pereiopods (chelipeds) (Fig. 4) very different in size and shape. Major cheliped (Fig. 4A–D) robust, carried flexed under body when not in use; coxa with strap-like epipod and setobranch; ischium slender, four times as long as wide, unarmed ventrally; merus widening distally, about 2.3 times as long as ischium, with slightly concave ventral margin; carpus small, cup-shaped; chela enlarged, swollen, as long as combination of basis to carpus; palm robust, about twice as long as wide, subcylindrical, slightly flattened dorsally and with shallow depression mid-dorsally and deep complex groove proximally, about 1.4 times as long as fingers; fingers relatively slender, slightly twisted, with strongly crossing fingertips, not gaping when closed; pollex with cutting edge armed with about 15 teeth, proximal fourth of cutting edge concave and with eight small teeth, distal three-fourths of cutting edge straight and with seven teeth enlarging towards distal margin; dactylus with deep depression on proximal third part of mesial surface accommodating convex margin of opposed margin of pollex, with 11 teeth on cutting edge enlarging in size towards distal margin. Minor cheliped (Fig. 4E, F) significantly smaller and weaker than major cheliped; coxa with strap-like epipod and setobranch; ischium slender, about four times as long as broad, unarmed ventrally; merus slender, slightly longer than ischium; carpus slightly shorter than merus, widening distally; chela simple, with palm approximately as long as fingers; cutting edges of fingers unarmed.

Second pereiopod (Fig. 5C) moderately long, short, slender; coxa with strap-like epipod and setobranch; ischium about 6.5 times as long as wide, unarmed ventrally; merus slender, slightly longer than ischium; carpus 1.2 times as long as merus, with five subdivisions, proximal one as long as sum of others; chela about 0.3 times as long as carpus, palm and fingers subequal in length.

Third pereiopod (Fig. 5D) moderately slender; coxa with strap-like epipod and setobranch; ischium slightly widening distally, about 2.6 times as long as wide, with small spiniform seta on ventrolateral surface; merus slightly inflated, about 1.6 times as long as ischium; carpus slenderer and slightly shorter than merus, eight times as long as wide, with small spiniform seta on distoventral margin; propodus slightly shorter than carpus, ventral margin armed with two spiniform setae in addition to distal pair of spiniform setae

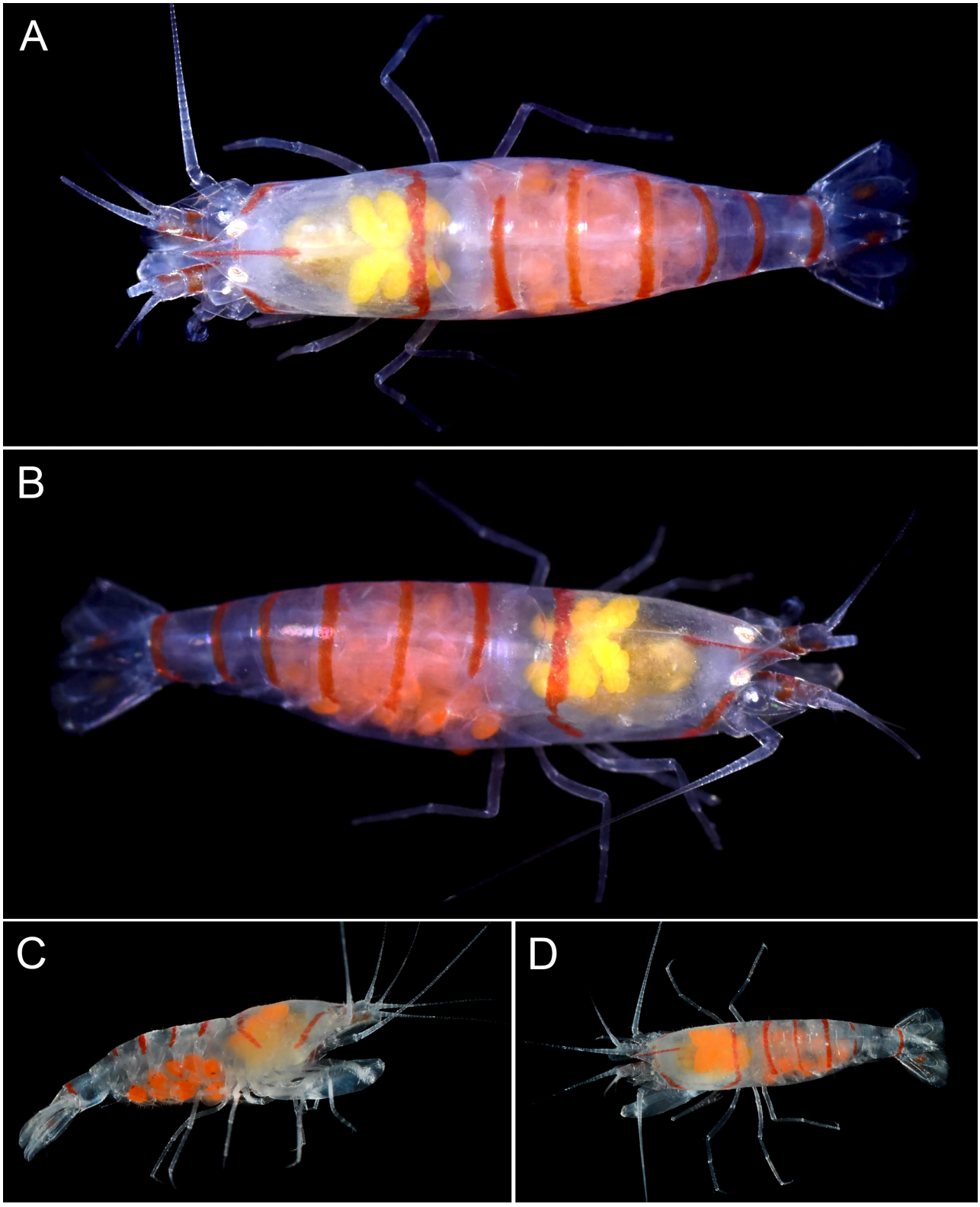

Fig. 2. *Salmoneus cristatus* (Coutière, 1897), shrimps in life; A, B, ovigerous specimen (cl 3.3 mm) from Abu-Musa Island, Iran (MNHN-IU-2019-3851), in dorsal (A) and dorsolateral (B) views [photographs courtesy of Rashed Abdollahi]; C, D, neotype, ovigerous specimen (cl 2.5 mm) from Shib Nazar East reef off Thuwal, Saudi Arabia (FLMNH UF 36069), in dorsal (A) and dorsolateral (B) views [photographs by AA].

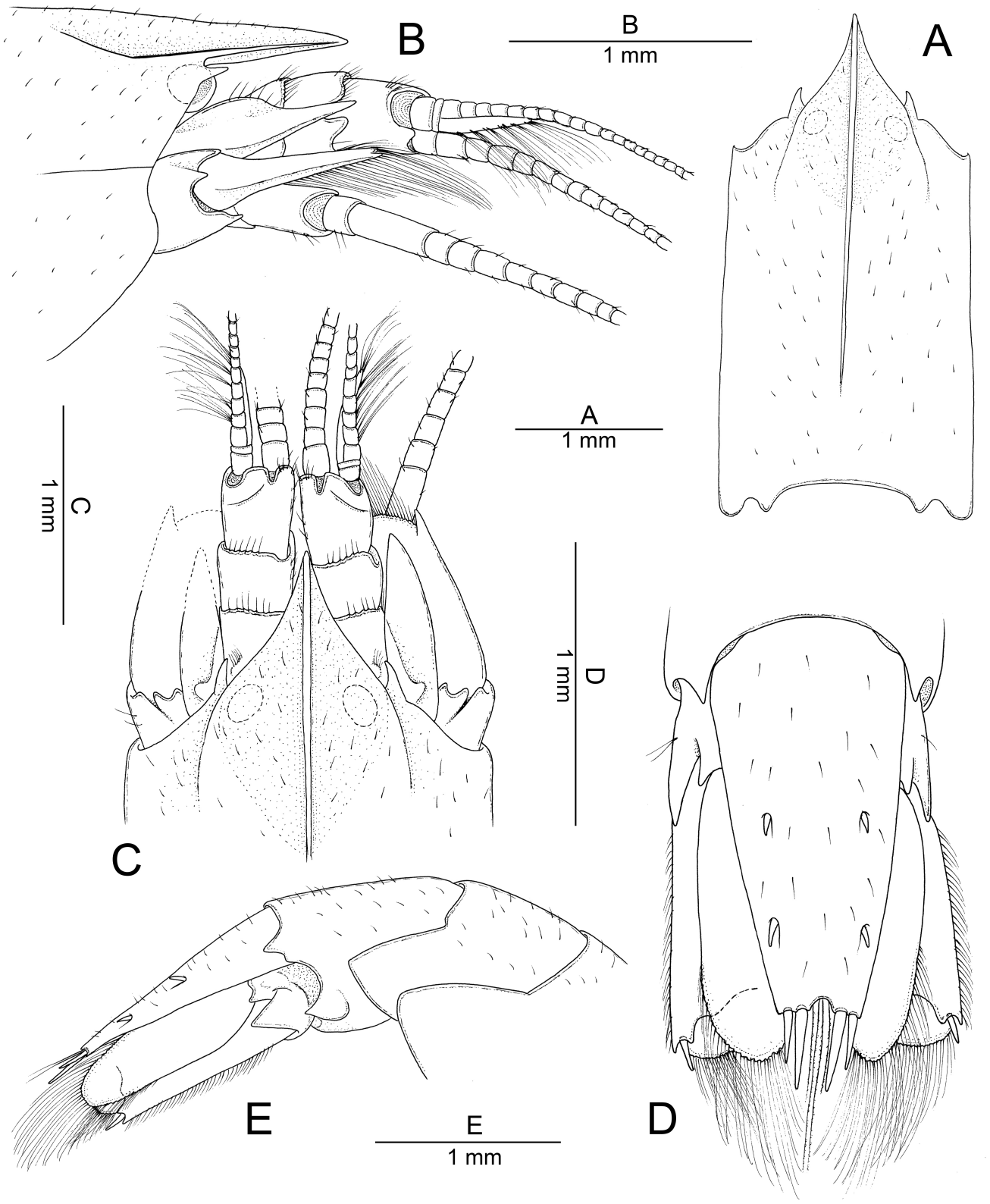

Fig. 3. *Salmoneus cristatus* Coutière, 1897, ovigerous specimen (cl 3.3 mm) from Abu-Musa Island, Iran (MNHN-IU-2019-3851): A, carapace, dorsal view; B, anterior region of carapace and frontal appendages, lateral view; C, same, dorsal view; D, telson and uropods, dorsal view; E, posterior pleonites, telson and right uropod, lateral view.

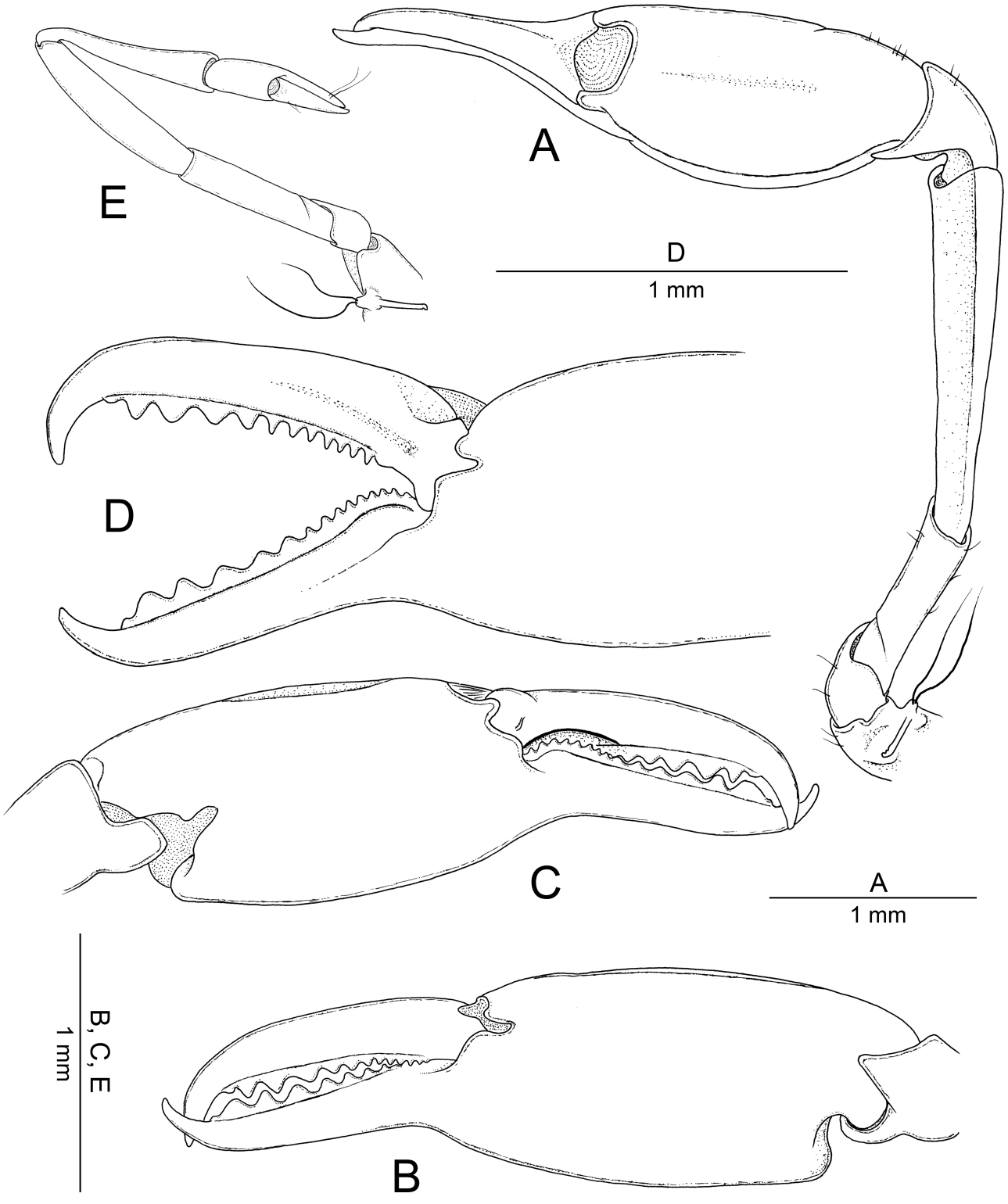

Fig. 4. *Salmoneus cristatus* Coutière, 1897, ovigerous specimen (cl 3.3 mm) from Abu-Musa Island, Iran (MNHN-IU-2019-3851): A, left (major) cheliped, lateral view; B, same, chela, lateral view; C, same, mesial view; D, same, distal half of palm and fingers open, lateral view; E, right (minor) cheliped, lateral view.

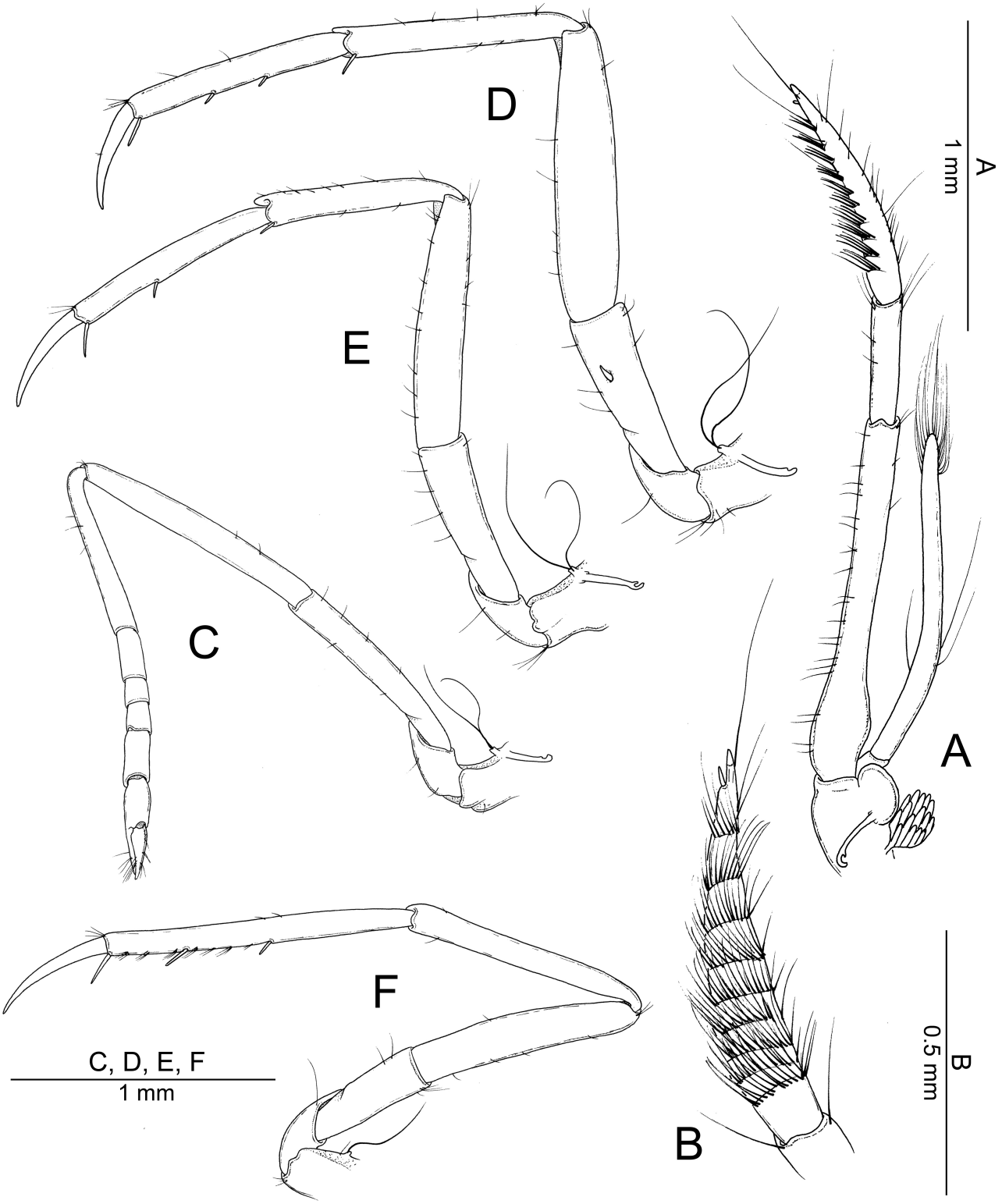

Fig. 5. *Salmoneus cristatus* Coutière, 1897, ovigerous specimen (cl 3.3 mm) from Abu-Musa Island, Iran (MNHN-IU-2019-3851): A, third maxilliped, lateral view; B, same, ultimate article, mesial view; C, second pereiopod, lateral view; D, third pereiopod, lateral view; E, fourth pereiopod, lateral view; F, fifth pereiopod, lateral view.

flanking dactylar base; dactylus simple, moderately slender, slightly curved, about half as long as propodus. Fourth pereiopod (Fig. 5E) generally similar to third one, somewhat more slender; ischium unarmed ventrally; propodus with one spiniform seta on ventral margin and one distal pair of spiniform setae adjacent to dactylus. Fifth pereiopod (Fig. 5F) similar to fourth pereiopod in length; coxa without strap-like epipod, with setobranch; carpus as long as merus, unarmed; propodus about 1.3 times as long as carpus, bearing seven rows of microserrulate setae on distoventral margin and two spiniform setae on ventral margin in addition to distal pair.

Uropods (Fig. 3D, E) with lateral lobe of protopod elongate, subacute distally; exopod ovate, distolateral margin with small triangular tooth adjacent to stout spiniform seta, diaeresis sinuous, with blunt lobe mesial to spiniform seta; endopod slightly longer than exopod, slender, ovoid, without specific features.

Colour in life: Background translucent whitish; carapace with several bright red bands disposed as following: one narrow, longitudinal band along anterior half of mid-dorsal carina; two narrow, oblique-transverse bands, one on each anterolateral surface, extending from just below each eye towards pterygostomial region; and moderately broad, transverse band across posterior one-fifth of carapace continued by narrower oblique band on each flank; pleon with six transverse, moderately broad, bright red bands, one per pleonite; antennular peduncles, telson and uropods with red markings; remaining appendages colourless; major cheliped hyaline white; fresh eggs bright yellow-orange; ovaries (visible by translucence) yellow (Fig. 2).

Variation: The present description is consistent for the neotype as well as Iranian material. However, one of the specimens from the Red Sea (FLMNH UF 68811) differs from the others in the armature of the ischium of the minor cheliped and that of the second pereiopod. In this specimen, each of these articles is armed with a small spiniform seta on the ventrolateral surface, contrasting to the unarmed ischia in the other specimens examined. Since the colour pattern of this specimen does not differ from that of the neotype or the Iranian specimen (Fig. 2) and since it is also genetically not different from the neotype (Fig. 1), there is no doubt that it represents *S. cristatus*.

Type locality: Djibouti (Coutière 1897).

Distribution: Red Sea (Coutière 1897 1899; locality not specified), including Gulf of Suez, Egypt (Banner and Banner 1981), Gulf of Aqaba, Israel (Holthuis 1958), and central coast of Saudi Arabia: Thuwal reefs and Rabigh (present study); Gulf of Aden: Djibouti (Coutière 1897a 1899; Banner and Banner 1981); Persian Gulf: Abu Musa Island, Iran (present study); Kenya: Malindi (Bruce 1976; Banner and Banner 1983); Madagascar: Toliara (Banner and Banner 1983); and Seychelles: Mahé (Banner and Banner 1983).

Remarks: The originally designated type specimen(s) of *S. cristatus* in Coutière (1897) could not be found in the MNHN collection neither by Banner and Banner (1981) nor by the present authors, and therefore, should be considered as non-extant. The topotypic specimen of *S. cristatus* collected by Ch. Gravier in Djibouti and illustrated by Banner and Banner (1981) (deposited under MNHN Na-2781) was also not located in the MNHN collection, despite several search attempts by the authors (HA, AA, pers. obs.). However, it must be noted that it is unlikely that this apparently lost specimen represented the original type (or one of the types) of *S. cristatus* in Coutière (1897). Since the herein reported material from the Red Sea fully aligns with Coutière's (1897 1899) descriptions and illustrations, as well as with the topotypic specimen examined by Banner and Banner (1981), one of the specimens from Saudi Arabia (FLMNH UF 36069) is designated as neotype for *S. cristatus*.

The ovigerous specimen from the Gulf of Aqaba reported by Holthuis (1958) (RMNH.CRUS.D.14354) is missing its major cheliped and therefore cannot be confirmed as *S. cristatus*, although nothing in its overall morphology (carapace, telson, third pereiopod, etc.) indicates the contrary. The original lot from Toliara (Tuléar), Madagascar, (MNHN-IU-2021-9769), which was reported by Banner and Banner (1983) under *S. cristatus*, contained three specimens. However, during our re-examination of this lot, only two specimens were found, and both lack all their pereiopods. One specimen appears to be *S. cristatus*, based on the general shape of the frontal region. However, the frontal region of the second specimen (separated under MNHN-IU-2021-9770 as *S.* cf. *chadwickae*) resembles more that of *S. chadwickae* or *S. auroculatus*.

***Salmoneus paracristatus* sp. nov.**

(Figs. 6–9)

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Salmoneus aff. *cristatus* — Ďuriš and Horká 2016: 783 (part.), fig. 11 a–c [not *S. cristatus* (Coutière, 1897)].

(?) *Salmoneus cristatus* — Anker 2003: 108, fig. 6 [not *S. cristatus* (Coutière, 1897)].

Material examined: Holotype: non-ovig. specimen (cl 2.9 mm), MNHN-IU-2014-199, Papua New Guinea, New Ireland, off Cape Nuan, Kavieng 2014 expedition, sta. KS13, 2°33'28.08"S, 150°47'25.98"E, sand with coral, depth 13 m, coll. MNHN team, 05.06.2014.

Paratypes: 1 non-ovig. specimen (cl 5.8 mm), MNHN-IU-2014-205, Papua New Guinea, New Ireland, E of North Cape, Kavieng 2014 expedition, sta. KB8, 2°33'10.02"S, 150°48'9"E, reef slope, brushing of dead corals, depth 13 m, coll. MNHN team, 05.06.2014 [infected with bopyrid isopod]; 1 non-ovig. specimen (cl 4.1 mm), MNHN-IU-2014-294, Papua New Guinea, New Ireland, between Big Nusa and Little Nusa Islands, Kavieng 2014 expedition, sta. KB16, 2°34'33.66"S, 150°46'20.88"E, oceanic front reef, brushing of dead corals, depth 13 m, coll. MNHN team, 07.06.2014.

Etymology: The new species' name integrates the Greek-derived prefix *para-* for beside, near, and the adjective *cristatus* for crested, referring to its morphological similarity with *S. cristatus*.

Description: small-sized alpheid shrimps (cl range of type material 2.9–5.8 mm). Carapace (Fig. 7A–C) sparsely setose, with prominent mid-dorsal carina reaching to about distal fourth of carapace; frontal region entirely concealing eyes in dorsal view, distinctly elevated from anterolateral portion of carapace, shoulder-like; rostrum triangular in dorsal view, with subacute tip, tapering distally, reaching to about distal margin of second antennular article, slightly longer than broad, rostral carina prominent, continued by mid-dorsal carina on carapace; orbital teeth small, subacute, approximately as long as broad; anterolateral suture present, pterygostomial angle broadly rounded, cardiac notch deep.

Pleon (Fig. 7D) sparsely covered by short setae; pleura of first to fourth pleonites rounded anteroventrally and posteroventrally; fifth pleuron subrounded posteroventrally; sixth pleuron with small triangular projection flanking each side of telson, posteroventral suture incomplete.

Telson (Fig. 7D, E) sub-rectangular, tapering distally, about 5.2 times as long as distal width, proximal margin about 2.4 times as broad as distal margin; dorsal surface with two pairs of spiniform setae located at about 0.5 and 0.8 telson length; posterior margin with broadly U-shaped, central notch furnished with 2 plumose setae, and two pairs of spiniform setae, mesial pair slightly shorter than plumose setae, about 1.8 times as long as lateral one and about five times as long as spiniform setae on dorsal surface.

Antennule (Fig. 7B, C) with peduncle relatively stout; first antennular article approximately as long as broad, stylocerite relatively robust, with blunt tip, reaching to distal margin of second article; second article about 1.3 times as broad as long; third antennular article about 1.7 times as long as second one, slightly longer than broad; lateral antennular flagellum biramous, fused portion with two subdivisions, shorter ramus well-developed, reaching to about seventh subdivision of longer ramus, with 9 or so groups of aesthetascs.

Antenna (Fig. 7B, C) with stout basicerite, its distoventral margin armed with subacute tooth and blunt subdistal projection, superior margin projecting as small subacute tooth; scaphocerite overreaching mid-length of third antennular article, blade slightly surpassing lateral tooth; carpocerite stout, slightly overreaching second antennular article, flagellum not particularly stout, second subdivision of flagellum remarkably longer than others.

Third maxilliped (Fig. 9A, B) with coxa bearing strap-like epipod and broadly rounded lateral plate; antepenultimate article slender, about 7.5 times as long as proximal width; penultimate article relatively short, about 0.3 times as long as antepenultimate article; ultimate article about 2.5 times as long as penultimate article, distally armed with small, subapical, spiniform seta; exopod slender, reaching to about distal margin of antepenultimate article; arthrobranch normally developed.

First pereiopods (Fig. 8) very different in size and shape. Major cheliped (Fig. 8A–C) robust, carried flexed under body when not in use; coxa with strap-like epipod and setobranch; ischium relatively slender, about four times as long as proximal width, unarmed ventrally; merus about 1.7 times as long as ischium, slightly widening distally; carpus vase-shaped, about 1.7 times as long as proximal width; chela enlarged, swollen, as long as sum of basis to carpus; palm robust, about 1.8 times as long as wide, subcylindrical, slightly flattened dorsally with shallow depression mid-dorsally and deep complex groove proximally, approximately as long as fingers; fingers with strongly crossing fingertips, not gapping when closed, pollex with cutting edge armed with about 11 evenly distributed teeth slightly enlarging toward distal margin, dactylus without depression on mesio-proximal side, armed with 10 evenly distributed teeth slightly enlarging towards distal margin. Minor cheliped (Fig. 8D, E) significantly smaller and weaker than major cheliped; coxa with strap-like epipod and setobranch; ischium slender, slightly widening distally, about four times as long as mid-width, unarmed ventrally; merus slightly swollen, slightly longer than ischium; carpus slightly longer than merus, widening distally; chela with palm approximately as long as fingers, cutting edge of fingers unarmed.

Second pereiopod (Fig. 9C) moderately long, slender; coxa with strap-like epipod and setobranch; ischium slender, about 8 times as long as wide, unarmed ventrally; merus slender, as long as ischium; carpus slender, 1.2 times as long as merus, with five subdivisions, proximal subdivision longest, slightly longer than sum of others, third and fourth subdivisions

subequal, second subdivision slightly longer than third one, last subdivision as long as second and third ones combined, chela about 0.3 times as long as carpus, palm and fingers subequal in length.

Third pereiopod (Fig. 9D) moderately slender; coxa with strap-like epipod and setobranch; ischium slightly widening distally, about four times as long as widest part, with small spiniform seta on ventrolateral surface; merus slightly inflated, about 1.5 times as long as ischium; carpus slenderer and slightly shorter than merus, 6.5 times as long as distal width, with small spiniform seta on distoventral margin; propodus slender, about 1.2 times as long as carpus, ventral margin with five spiniform setae in addition to distal pair of spiniform setae flanking dactylar base; dactylus simple, moderately slender, slightly curved, about 0.4 times as

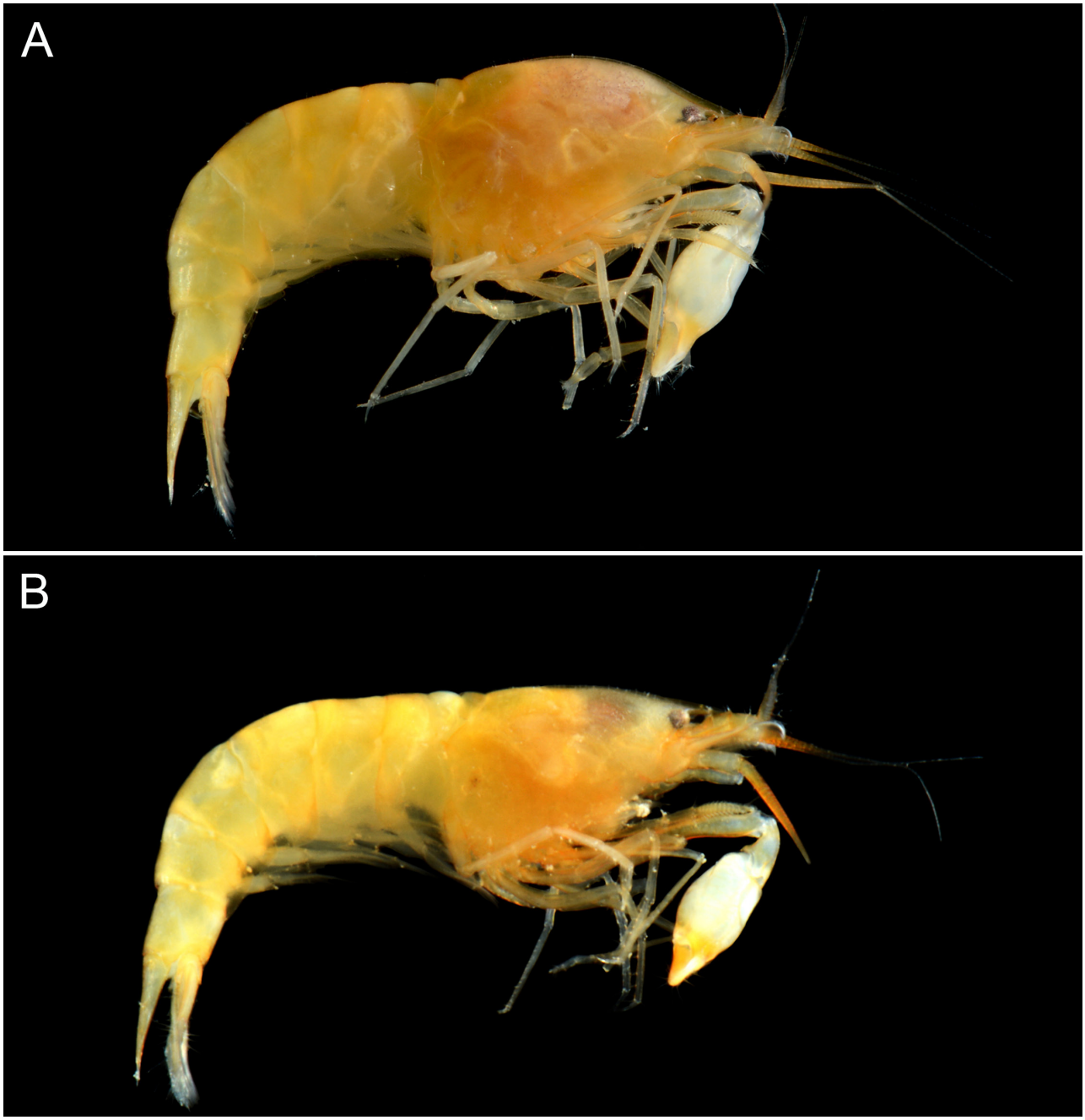

Fig. 6. *Salmoneus paracristatus* sp. nov., shrimps photographed *post-mortem*: A, paratype, non-ovigerous specimen (cl 5.8 mm) from New Ireland, Papua New Guinea (MNHN-IU-2014-205), in lateral view; B, paratype, non-ovigerous specimen (cl 4.1 mm) from New Ireland, Papua New Guinea (MNHN-IU-2014-294), in lateral view [photographs by ZĎ].

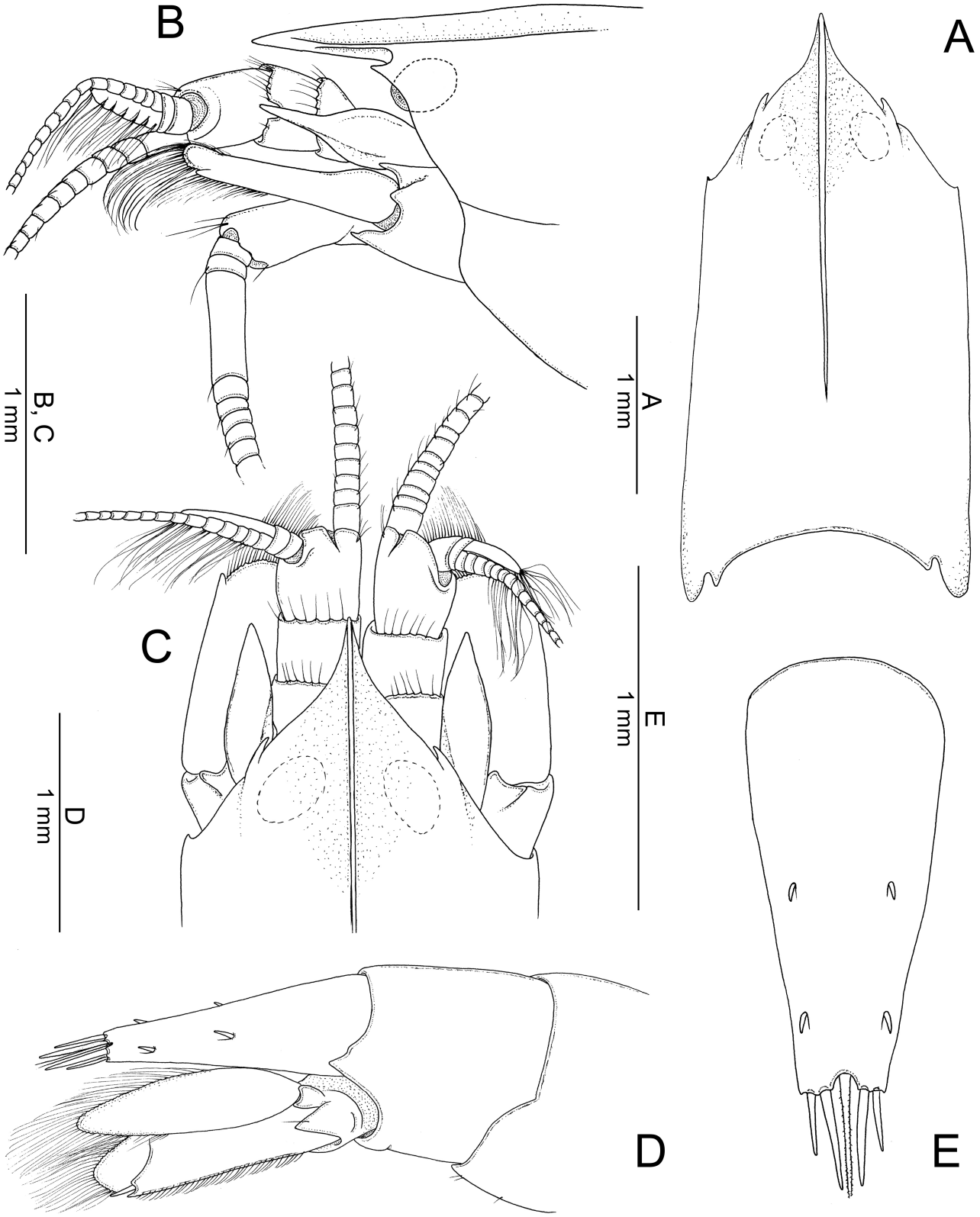

Fig. 7. *Salmoneus paracristatus* sp. nov., holotype, non-ovigerous specimen (cl 2.9 mm) from New Ireland, Papua New Guinea (MNHN-IU-2014-199): A, carapace, dorsal view; B, anterior region of carapace and frontal appendages, lateral view; C, same, dorsal view; D, posterior pleonites, telson and right uropod, lateral view; E, telson, dorsal view.

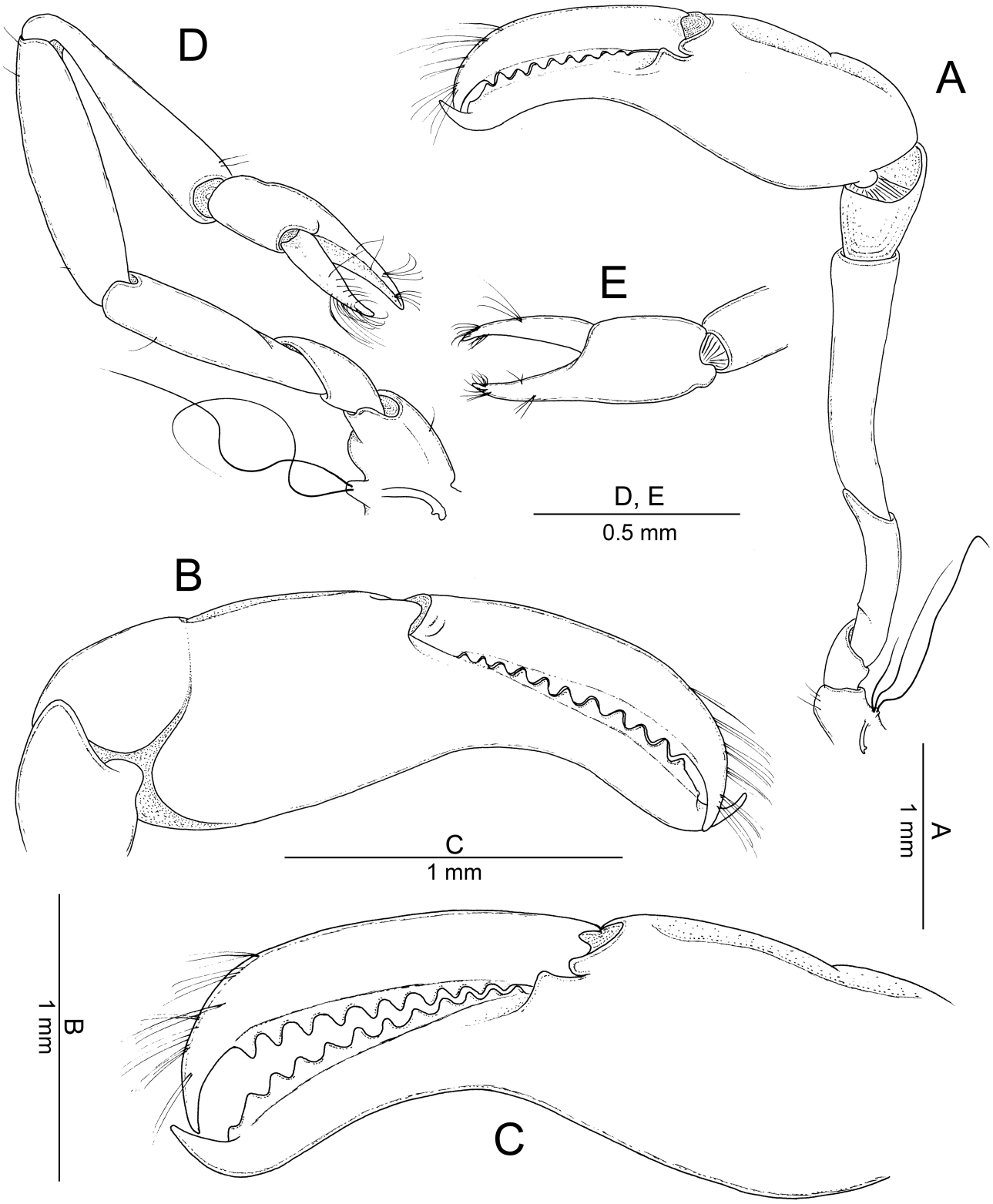

Fig. 8. *Salmoneus paracristatus* sp. nov., holotype, non-ovigerous specimen (cl 2.9 mm) from New Ireland, Papua New Guinea (MNHN-IU-2014-199): A, left (major) cheliped, lateral view; B, same, chela, mesial view; C, same, lateral view; D, right (minor) cheliped, lateral view; E, same, chela, mesial view.

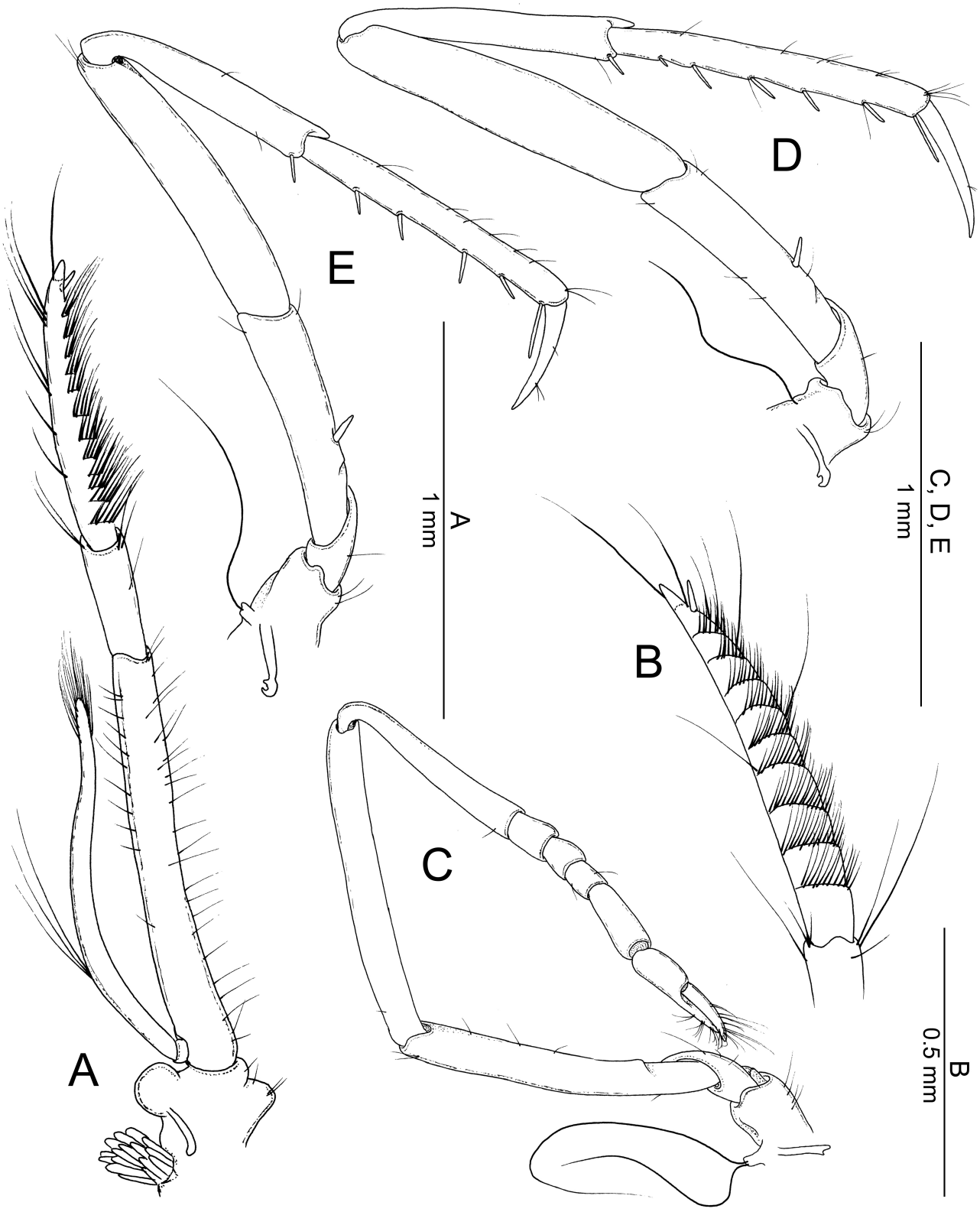

Fig. 9. *Salmoneus paracristatus* sp. nov., holotype, non-ovigerous specimen (cl 2.9 mm) from New Ireland, Papua New Guinea (MNHN-IU-2014-199): A, third maxilliped, lateral view; B, same, ultimate article, mesial view; C, second pereiopod, lateral view; D, third pereiopod, lateral view; E, fourth pereiopod, lateral view.

long as propodus. Fourth pereiopod (Fig. 9E) generally similar to third one but slightly slenderer; propodus armed with four spiniform setae on ventral margin in addition to distal pair. Fifth pereiopod missing.

Uropods (Fig. 7D) with lateral lobe of protopod broadly triangular; exopod ovate, anterolateral margin with small triangular tooth adjacent to relatively stout spiniform seta, diaeresis sinuous; endopod slightly longer than exopod, ovoid, without specific feature.

Colour in life: Body largely translucent with fawn-yellow tinge; pleon with faint, buff-yellow, transverse bands; antennular and antennal flagella pale orange; major cheliped hyaline white with orange-yellow tinge on fingers; remaining appendages colourless or with buff-yellow tinge (Fig. 6).

Type locality: Papua New Guinea (present study).

Distribution: Papua New Guinea: New Ireland (Ďuriš and Horká 2016, as *S.* aff. *cristatus*; present study); possibly Australia: Ashmore Reef off Queensland (Anker 2003, as *S. cristatus*).

Salmoneus franseni **sp. nov.**

(Figs. 10–13)

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Salmoneus aff. *cristatus* — Ďuriš and Horká 2016: 783 (part.) [not *S. cristatus* (Coutière, 1897)].

Salmoneus cristatus — Wang and Sha 2016: 1586, figs. 1–4 [not *S. cristatus* (Coutière, 1897)].

Salmoneus cristatus — Sha, Wang, and Cui 2019: 206, figs 2.121–2.124 [not *S. cristatus* (Coutière, 1897)].

(?) *Salmoneus cristatus* — Banner and Banner 1966: 40, fig. 10 [not *S. cristatus* (Coutière, 1897)].

Material examined: Holotype: non-ovig. specimen (cl 3.2 mm), MNHN-IU-2014-881, Papua New Guinea, Kavieng 2014 expedition, sta. KB60, 2°32'30"S, 150°35'18"E, sand and coarse rubble, brushing of dead corals, depth 20 m, coll. MNHN team, 23.06.2014. Additional material: 1 non-ovig. specimen (cl 2.7 mm), MNHN-IU-2014-933, same collection data as for holotype (see discussion below).

Etymology: The species is named after Dr. Charles H.J.M. Fransen (Naturalis Biodiversity Center, Leiden) for his major contribution to taxonomy of caridean shrimps, including description of a peculiar cave species of *Salmoneus* (Fransen 1991).

Description: Small-sized alpheid shrimps (cl 3.2 mm in holotype). Carapace (Fig. 11A–C) with prominent mid-dorsal carina reaching to about posterior fourth of carapace; frontal region fully concealing eyes in dorsal view, mid-dorsal carina prominent and reaching to about posterior fourth of carapace, distinctly elevated from anterolateral portion of carapace, shoulder-like; rostrum triangular in dorsal view, with subacute tip, reaching to about distal margin of second antennular article, as long as broad, rostral carina prominent, continued by mid-dorsal carina on carapace; orbital teeth small, subacute, as long as broad; anterolateral suture present, pterygostomial angle broadly rounded, cardiac notch deep.

Pleon (Fig. 11D) scarcely furnished with fine setae; pleura of first to third pleonites rounded anteroventrally and posteroventrally; fourth pleuron subrounded posteroventrally; fifth pleuron with small subacute projection posteroventrally; sixth pleuron with small subacute projection flanking each side of telson, posteroventral suture incomplete.

Telson (Fig. 11D, E) sub-rectangular, tapering distally, about 4.3 times as long as distal width, proximal margin about twice as broad as distal margin; dorsal surface with two pairs of spiniform setae located at about 0.5 and 0.8 telson length, respectively; posterior margin with broadly U-shaped, central notch furnished with two plumose setae, and two pairs of spiniform setae, mesial pair about 1.5 times as long as lateral one and about four times as long as spiniform setae on dorsal surface.

Antennule (Fig. 11B, C) with peduncle relatively stout; first antennular article approximately as long as broad, stylocerite relatively robust, with blunt tip, reaching to about distal margin of second article; second article about 1.6 times as broad as long; third article about 1.6 times as long as second article, slightly longer than wide; lateral antennular flagellum biramous, fused portion composed of one subdivision, shorter ramus well-developed, reaching to about ninth subdivision of longer ramus, with eight or so groups of aesthetascs.

Antenna (Fig. 11B, C) with stout basicerite, its distoventral margin armed with subacute tooth and blunt subdistal projection, superior margin projecting as small subacute tooth; scaphocerite reaching to about mid-length of third antennular article, blade slightly surpassing lateral tooth; carpocerite stout, slightly overreaching second antennular article.

Third maxilliped (Fig. 13A, B) with coxa bearing strap-like epipod and broadly rounded lateral plate; antepenultimate article slender, about nine times as long as proximal width; penultimate article relatively short, about 0.3 times as long as antepenultimate article; ultimate article about twice as long as penultimate article, distally armed with two subapical spiniform setae; exopod slender, reaching to about distal margin of antepenultimate segment; arthrobranch normally developed.

First pereiopods (Fig. 12) very different in size and shape. Major cheliped (Fig. 12A–D) robust, carried flexed under body when not in use; coxa with strap-like epipod and setobranch; ischium relatively slender,

about 4.3 times as long as proximal width, unarmed ventrally; merus slightly widening distally, about twice as long as ischium, ventral margin somehow flattened; carpus vase-shaped; chela enlarged, swollen, as long as combination of basis to carpus; palm robust, about 1.7 times as long as wide, subcylindrical, slightly flattened dorsally and with shallow depression mid-dorsally and deep complex groove proximally, approximately as long as fingers; fingers with strongly crossing fingertips, without gap when closed, with nine (dactylus) or 10 (pollex) evenly distributed teeth slightly enlarging towards distal margin; dactylus without concavity on proximal part of mesial surface. Minor cheliped (Fig. 12E, F) significantly smaller and weaker than major cheliped; coxa with strap-like epipod and setobranch; ischium slender, about 4.5 times as long as mid-width, unarmed ventrally; merus slightly swollen, slightly longer than ischium; carpus slightly longer than merus, widening distally; chela simple, with palm approximately as long as fingers, cutting edge of fingers unarmed.

Second pereiopod (Fig. 13C) slender; coxa with strap-like epipod and setobranch; ischium slender, about eight times as long as broad, unarmed ventrally; merus slender, as long as ischium; carpus slender, 1.5 times as long as merus, with five subdivisions, proximal

Fig. 10. *Salmoneus franseni* sp. nov., holotype, non-ovigerous specimen (cl 3.2 mm) from New Ireland, Papua New Guinea (MNHN-IU-2014-881), shrimp in life in dorsolateral (A) and lateral (B) views [photographs by ZĎ].

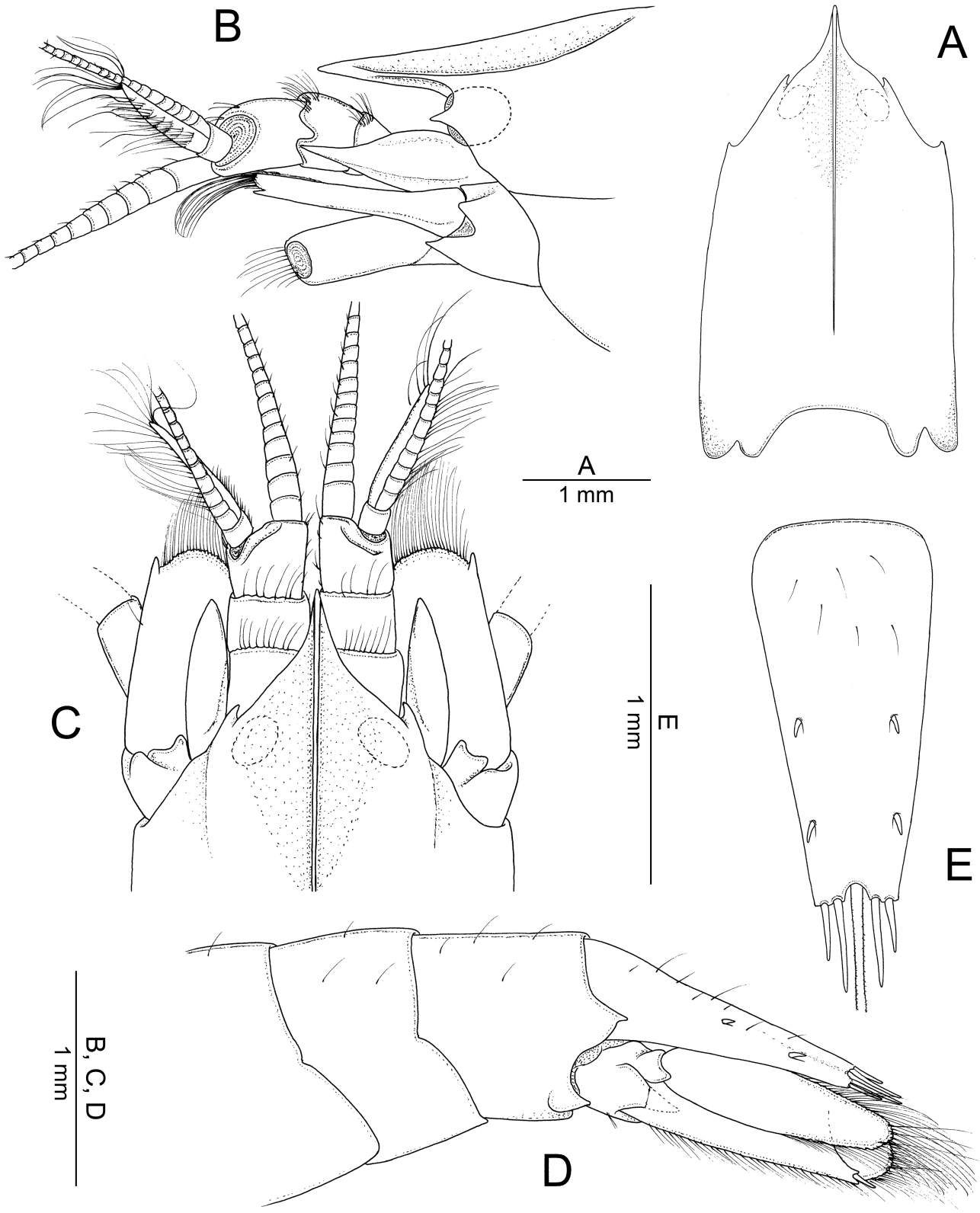

Fig. 11. *Salmoneus franseni* sp. nov., holotype, non-ovigerous specimen (cl 3.2 mm) from New Ireland, Papua New Guinea (MNHN-IU-2014-881): A, carapace, dorsal view; B, anterior region of carapace and frontal appendages, lateral view; C, same, dorsal view; D, posterior pleonites, telson and left uropod, lateral view; E, telson, dorsal view.

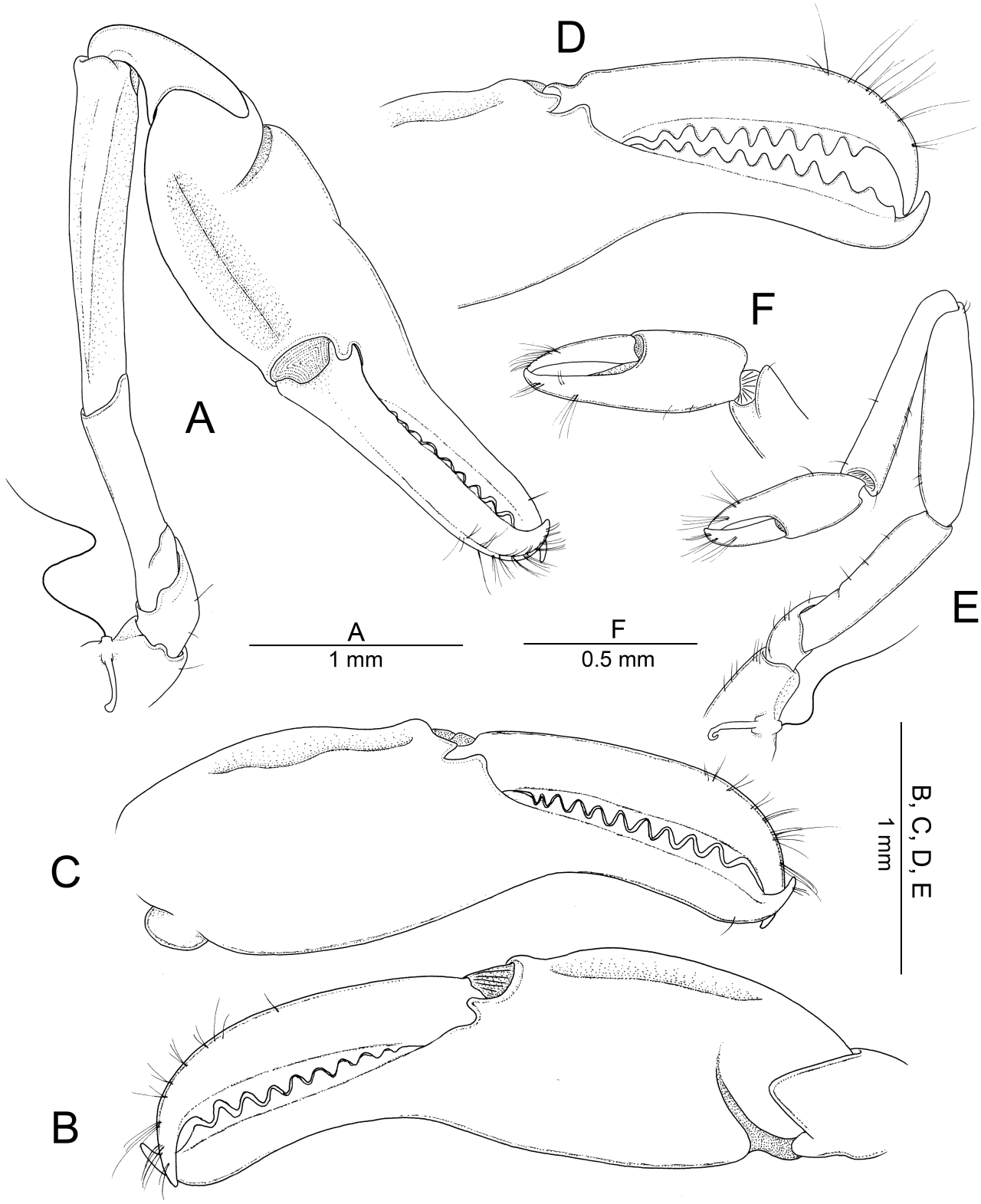

Fig. 12. *Salmoneus franseni* sp. nov., holotype, non-ovigerous specimen (cl 3.2 mm) from New Ireland, Papua New Guinea (MNHN-IU-2014-881): A, right (major) cheliped, lateral view; B, same, chela, mesial view; C, same, lateral view; D, same, distal portion of palm and fingers slightly open, lateral view; E, left (minor) cheliped, lateral view; F, same, chela, mesial view.

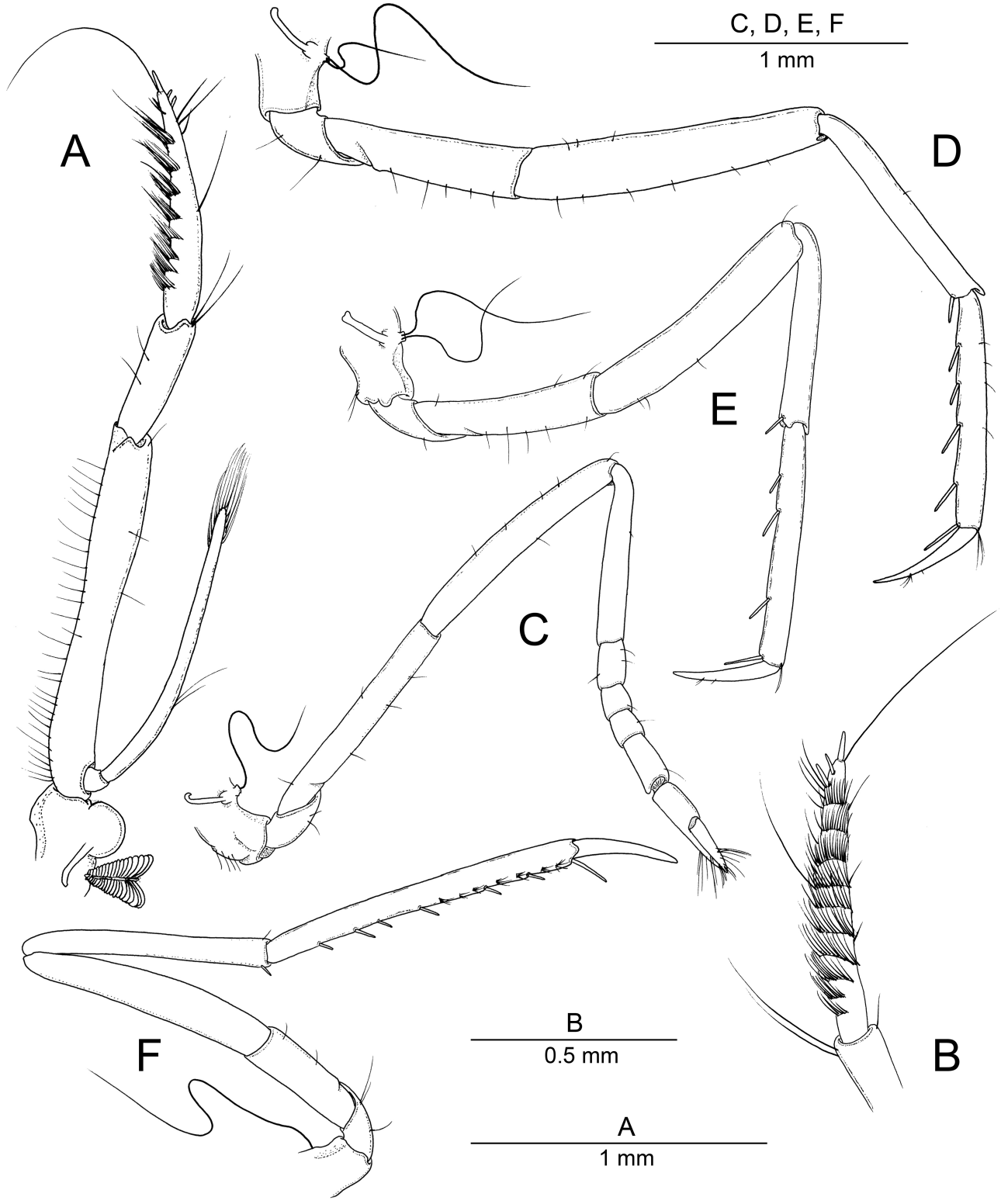

Fig. 13. *Salmoneus franseni* sp. nov., holotype, non-ovigerous specimen (cl 3.2 mm) from New Ireland, Papua New Guinea (MNHN-IU-2014-881): A, third maxilliped, lateral view; B, same, ultimate article, mesial view; C, second pereiopod, lateral view; D, third pereiopod, lateral view; E, fourth pereiopod, lateral view; F, fifth pereiopod, lateral view.

subdivision longest, slightly longer than sum of other subdivisions, third and fourth subdivisions subequal, second subdivision slightly longer than the third, last subdivision as long as second and third subdivisions combined; chela about 0.3 times as long as carpus, palm and fingers subequal in length.

Third pereiopod (Fig. 13D) moderately slender; coxa with strap-like epipod and setobranch; ischium slightly widening distally, about four times as long as distal margin, unarmed ventrally; merus slightly inflated, about 1.5 times as long as ischium; carpus more slender and slightly shorter than merus, 7.5 times as long as distal width, with spiniform seta on distoventral margin; propodus slender, approximately as long as carpus, ventral margin armed with four spiniform setae in addition to distal pair flanking dactylar base; dactylus simple, moderately slender, slightly curved, about 0.5 times as long as propodus. Fourth pereiopod (Fig. 13E) generally similar to third one but slightly more slender; propodus 1.2 times as long as carpus, ventrally armed with three spiniform setae and one distal pair. Fifth pereiopod (Fig. 13F) generally similar to fourth one; coxa without strap-like epipod; carpus slightly shorter than merus; propodus about 1.3 times as long as carpus, ventrally armed with six spiniform setae and one distal pair, bearing 7 rows of microserrulate setae on distoventral margin.

Uropod (Fig. 11D) with lateral lobe of protopod broadly triangular; exopod ovate, distolateral margin with small triangular tooth adjacent to spiniform seta, diaeresis sinuous; endopod slightly longer than exopod, ovoid, without specific features.

Colour in life: Body largely translucent with pale yellow or pale orange tinge; pleon with faint, buff-yellow, transverse bands; antennular and antennal flagella pale yellow; major cheliped whitish with orange-yellow tinge on fingers; remaining appendages colourless or with buff-yellow tinge (Fig. 10).

Type locality: Papua New Guinea (present study).

Distribution: Papua New Guinea: New Ireland (Ďuriš and Horká 2016; present study); southern China: Xisha Islands (Wang and Sha 2016; Sha et al. 2019 as *S. cristatus*); probably also in Thailand: Phuket (Banner and Banner 1966, as *S. cristatus*).

***Salmoneus alius* sp. nov.**

(Figs. 14–17)

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Material examined: Holotype: 1 non-ovig. specimen (cl 2.7 mm), MNHN-IU-2019-3495, New Caledonia, Koumac 2019 expedition, sta. HR2, Hienghène, 20°44'59.35"S, 165°16'34.86"E, reef slope, depth 10–34 m, coll. MNHN team, 09.11.2019. Paratypes: 1 ovig. specimen (cl 3.8 mm), FLMNH-UF-60000, Solomon Islands, New Georgia, Munda, Sosu Hite Island (informal name), shallow reef flat, less than 1.5 m, under corals and coral rubble, coll. A. Anker, 20.09.2016 (SOL-035); 1 specimen (cl not measured), MNHN-IU-2013-1471, Papua New Guinea, Madang 2012 expedition, sta. PR119, Madang lagoon, northern side of North Kranket Island, 5°11'20.04"S, 145°49'27.03"E, silty reef, depth 1–10 m, coll. A. Anker & Z. Ďuriš, 28.11.2012.

Etymology: The new species name is the Latin adjective *alius* for another or different, referring to yet another new species described in the genus *Salmoneus*, adding to over 40 species described over the last two decades.

Description: Small-sized alpheid shrimp (cl 2.7 mm). Carapace (Fig. 15A, B) with prominent mid-dorsal carina reaching to about posterior margin of eyes, frontal region entirely concealing eyes in dorsal view, distinctly elevated from anterolateral portion of carapace, shoulder-like; rostrum triangular in dorsal view, with subacute tip, reaching to about distal margin of second antennular article, slightly broader than long, rostral carina prominent, continued by mid-dorsal carina on carapace; orbital teeth small, subacute, as long as broad; anterolateral suture present, pterygostomial angle broadly rounded, cardiac notch deep.

Pleon (Fig. 15C) scarcely furnished with long fine setae; pleura of first to third pleonites rounded anteroventrally and posteroventrally; fourth and fifth pleura angular posteroventrally; sixth pleuron with subtriangular projection flanking each side of telson, posteroventral suture incomplete.

Telson (Fig. 15C, D) sub-rectangular, slightly tapering distally, about four times as long as distal width, proximal margin about 1.6 times as broad as distal margin; dorsal surface with two pairs of spiniform setae located on 0.6 and 0.8 telson length, respectively; posterior margin with broadly U-shaped, central notch furnished with two plumose setae, and two pairs of spiniform setae, mesial pair slightly shorter than plumose setae, much thicker than lateral pair, about 1.5 times as long as lateral one, about five times as long as spiniform setae on dorsal surface.

Antennule (Fig. 15A, B) with peduncle relatively stout; first article approximately as long as broad, stylocerite relatively robust, with blunt tip, slightly overreaching distal margin of second antennular article; second article about 1.5 times as broad as long; third article about 1.3 times as long as second article, as long as broad; lateral antennular flagellum biramous, fused portion with two subdivisions, shorter ramus well-developed, reaching to about seventh subdivision of

longer ramus, with seven or so groups of aesthetascs.

Antenna (Fig. 15A, B) with stout basicerite, distoventral margin with subacute tooth, superior margin projecting as small subacute tooth; scaphocerite slightly overreaching mid-length of third antennular article, blade slightly surpassing lateral tooth; carpocerite stout, slightly overreaching second antennular article, flagellum not particularly stout, with second subdivision distinctly longer than others.

Third maxilliped (Fig. 17A, B) with coxa bearing strap-like epipod and broadly rounded lateral plate; antepenultimate article slender, about 7.6 times as long as proximal width; penultimate article relatively short, about 0.2 times as long as antepenultimate article; ultimate article about 2.5 times as long as penultimate article, distally armed with two subapical spiniform setae; exopod slender, falling short of reaching distal margin of antepenultimate segment; arthrobranch normally developed.

First pereiopods (Fig. 16) very different in size and shape. Major cheliped (Fig. 16A−D) robust, carried flexed under body when not in use; coxa with strap-like epipod and setobranch; ischium relatively slender, about 3.3 times as long as proximal width, unarmed ventrally; merus about 1.9 times as long as ischium, slightly widening distally, ventral margin somehow flattened; carpus vase-shaped; chela enlarged, swollen, slightly shorter than combination of basis to carpus; palm robust, swollen, about 1.7 times as long as wide, subcylindrical, slightly flattened dorsally and with shallow depression mid-dorsally, with obsolete ridge on mid-lateral margin and small shallow depression on mid-ventral side of ridge, and with deep complex groove proximally, approximately as long as fingers; fingers with strongly crossing fingertips, no gapping when closed, with 10 (dactylus) or 12 (pollex) evenly distributed teeth slightly enlarging toward distal margin; dactylus without depression proximal part of mesial surface. Minor cheliped (Fig. 16E, F) significantly smaller and weaker than major cheliped; coxa with strap-like epipod and setobranch; ischium slender, about four times as long as mid-width, unarmed ventrally; merus slightly swollen, slightly longer than ischium; carpus slightly shorter than merus, widening distally; chela simple, with palm approximately as long as fingers; cutting edge of fingers unarmed.

Second pereiopod (Fig. 17C) moderately long, slender; coxa with strap-like epipod and setobranch; ischium slender, about 6.5 times as long as wide, unarmed ventrally; merus slender, slightly longer than ischium; carpus slender, 1.3 times as long as merus, with five subdivisions, proximal subdivision longest, slightly longer than sum of other subdivisions, third and fourth subdivisions subequal, second subdivision slightly longer than third one, distal subdivision as long as second and third subdivisions combined; chela about 0.4 times as long as carpus, palm and fingers subequal in length.

Third pereiopod (Fig. 17D) moderately slender, coxa with strap-like epipod and setobranch; ischium slightly widening distally, about three times as long as distal margin, with two strong spiniform setae on ventrolateral surface; merus slightly inflated, about 1.7 times as long as ischium; carpus slenderer and shorter than merus, 5.3 times as long as distal width, with spiniform seta on distoventral margin; propodus slender, approximately as long as carpus, with ventral margin armed with four spiniform setae in addition to distal pair of spiniform setae flanking dactylar base; dactylus simple, moderately slender, slightly curved, about 0.4 times as long as propodus. Fourth pereiopod (Fig. 17E) generally similar to the third, more slender somewhat; propodus 1.1 times as long as carpus, ventral margin armed with three spiniform setae and one pair distally. Fifth pereiopod (Fig. 17F) generally similar to fourth; coxa without strap-like epipod; ischium unarmed ventrally; carpus slightly longer than merus; propodus about 1.3 times as long as carpus, ventral margin armed with five spiniform setae and one pair distally, bearing seven rows of microserrulate setae on distoventral margin; dactylus conical, somewhat blunt distally (probably due to usage).

Uropod with lateral lobe of protopod broadly triangular; exopod ovate, distolateral margin with small triangular tooth adjacent to spiniform seta; diaeresis sinuous, with blunt lobe mesial to spiniform seta; endopod ovoid, without specific features.

Colour in life: Body largely translucent with yellow tinge; pleon with faint, yellow, transverse bands; antennular and antennal flagella pale yellow; major cheliped whitish with buff tinge on fingers; remaining appendages colourless; developing ovaries and eggs orange (Fig. 14).

Type locality: New Caledonia (holotype); additional type material from Papua New Guinea and Solomon Islands (present study).

Distribution: Presently known from the north-eastern coast of New Caledonia, Papua New Guinea (Kavieng), and the Solomon Islands (New Georgia).

DISCUSSION

Coutière (1897a) briefly described *Salmoneus cristatus* (as *Jousseaumea cristata*) based on an unspecified number of specimens collected in Djibouti, with some remarks on the species' colour pattern. Banner and Banner (1981: p. 51, table 2) stated

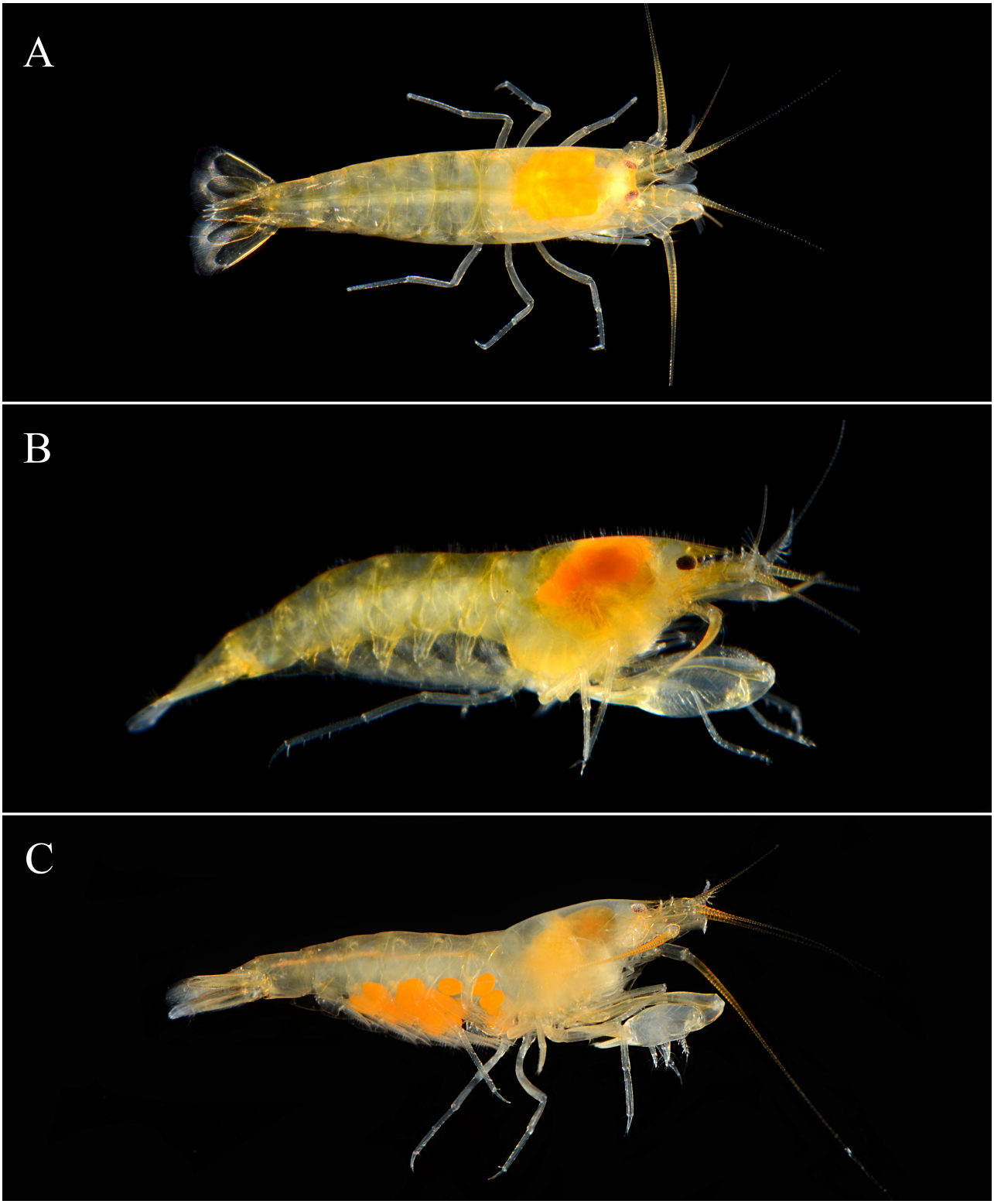

Fig. 14. *Salmoneus alius* sp. nov., holotype, non-ovigerous specimen (cl 2.7 mm) from New Caledonia (MNHN-IU-2019-3495), shrimp in life in dorsal view (A) lateral view (B); paratype, ovigerous specimen (cl 3.8 mm) from the Solomon Islands (FLMNH-UF-60000), shrimp in life in lateral view (C). [photographs A, B by ZĎ; and C by AA].

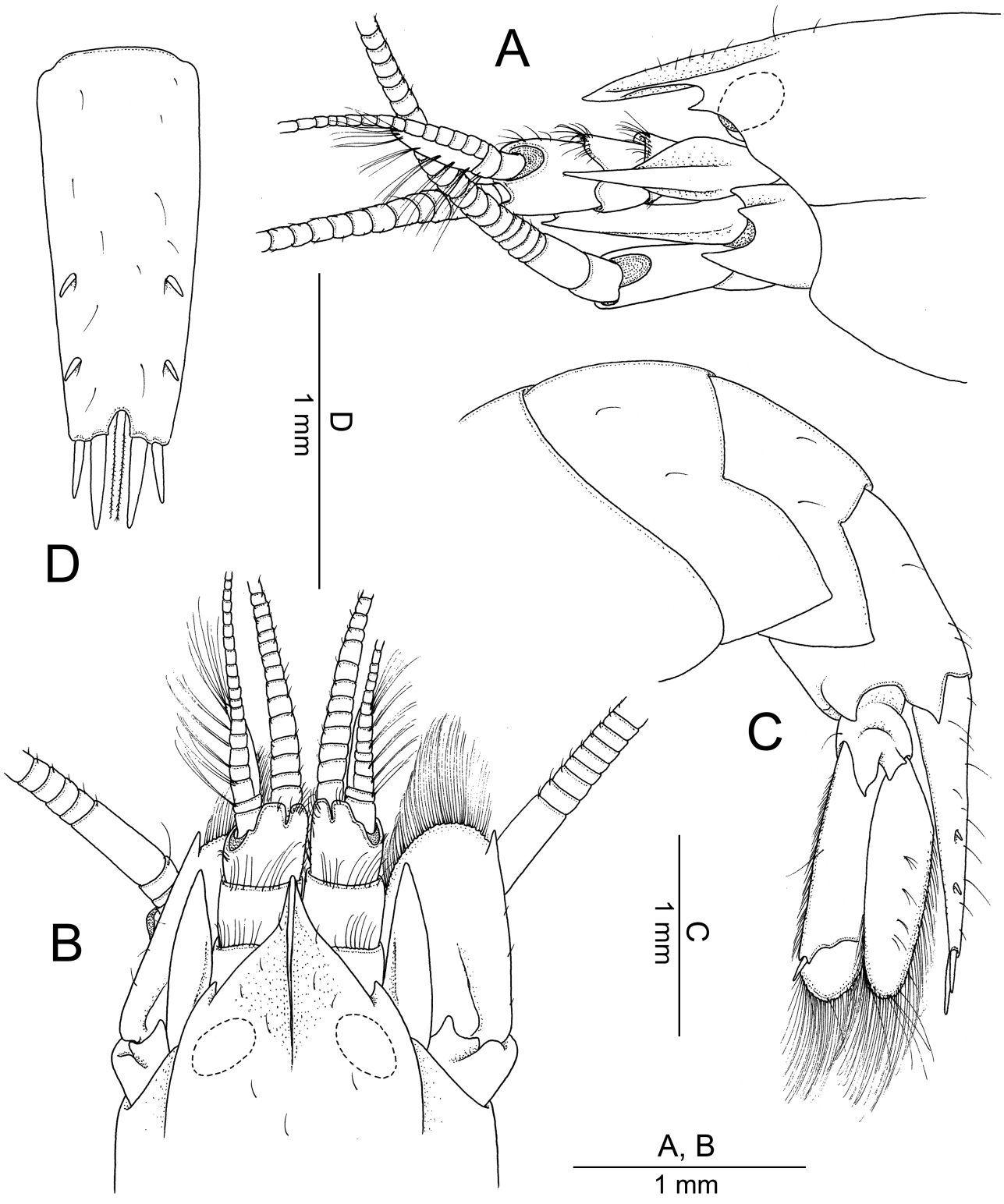

Fig. 15. *Salmoneus alius* sp. nov., holotype, non-ovigerous specimen (cl 2.7 mm) from New Caledonia (MNHN-IU-2019-3495): A, anterior region of carapace and frontal appendages, lateral view; B, same, dorsal view; C, posterior pleonites, telson and left uropod, lateral view; D, telson, dorsal view.

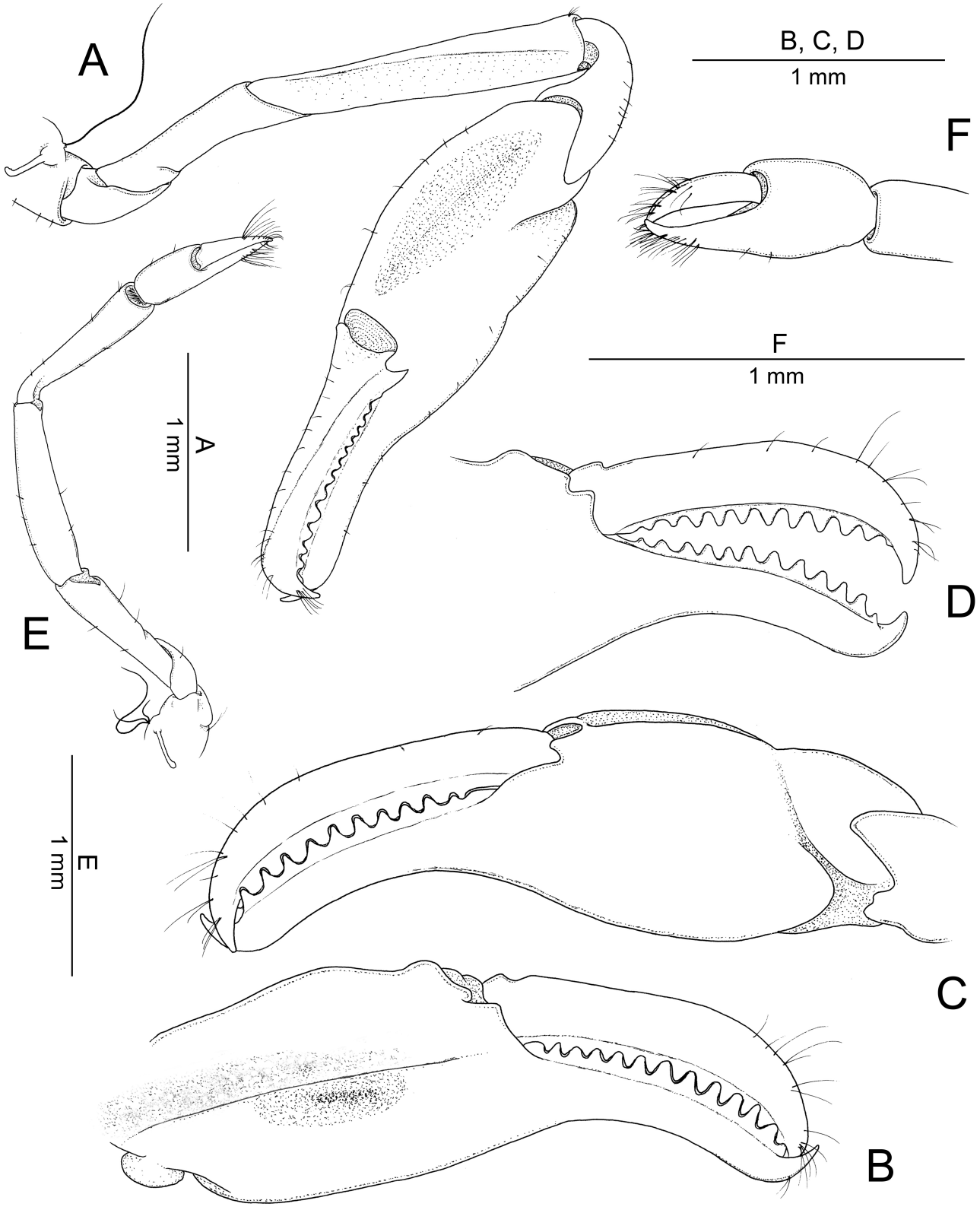

Fig. 16. *Salmoneus alius* sp. nov., holotype, non-ovigerous specimen (cl 2.7 mm) from New Caledonia (MNHN-IU-2019-3495): A, right (major) cheliped, lateral view; B, same, chela, lateral view; C, same, mesial view; D, same, distal portion of palm and fingers open, lateral view; E, left (minor) cheliped, lateral view; F, same, chela, mesial view.

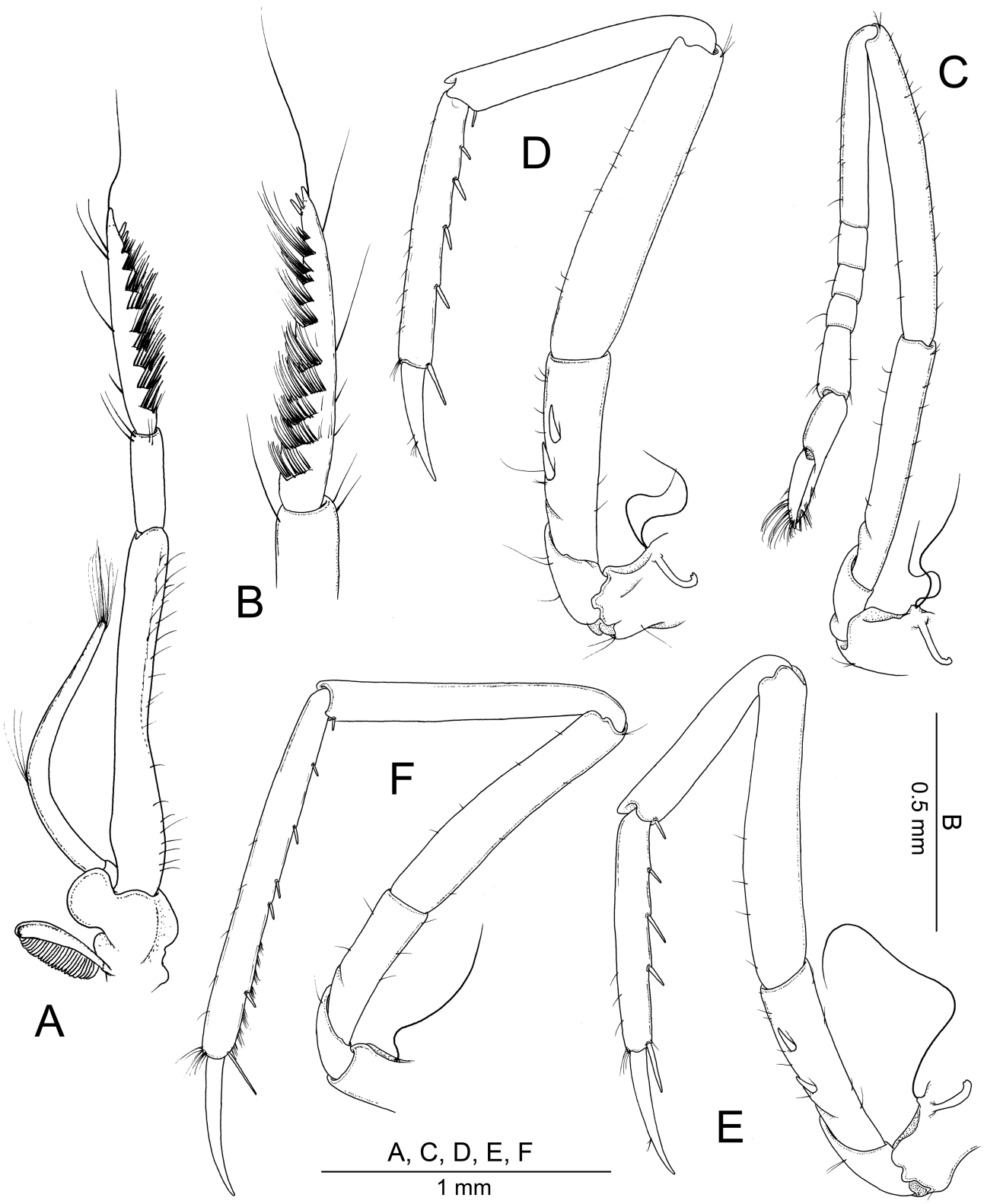

Fig. 17. *Salmoneus alius* sp. nov., holotype, non-ovigerous specimen (cl 2.7 mm) from New Caledonia (MNHN-IU-2019-3495): A, third maxilliped, lateral view; B, same, ultimate article, mesial view; C, second pereiopod, lateral view; D, third pereiopod, lateral view; E, fourth pereiopod, lateral view; F, fifth pereiopod, lateral view.

that Coutière (1897a) had only one type specimen of *S. cristatus*, although it remains unknown why this assumption was made. In his famous alpheid monograph, Coutière (1899) provided more details on the morphology of the species, including two superficial illustrations of the frontal region. The species has been reported or listed only a few times since its original description (Holthuis 1958; Banner and Banner 1966 1981; Bruce 1976; Anker 2003; Wang and Sha 2016; Sha et al. 2019). The two most diagnostic features of the species, viz. the strong mid-dorsal carina extending well beyond the middle of the carapace and the orbital hoods elevated from the rest of the carapace by two "shoulders" (term used by Banner and Banner 1981: 54), were used to morphologically distinguish *S. cristatus* from the other species of the genus. Based largely on morphological criteria (information on colour pattern was rarely available), *S. cristatus* has been recorded from several Indo-West Pacific localities ranging from the Red Sea and eastern Africa to Thailand, southern China, Papua New Guinea and eastern Australia (Holthuis 1958; Banner and Banner 1966 1981; Bruce 1976; Anker 2003; Ďuriš and Horká 2016, latter as *S.* aff. *cristatus*; Wang and Sha 2016).

The colour pattern of *S. cristatus*, as briefly described by Coutière (1897a 1899) and later in detail by L.B. Holthuis in Banner and Banner (1981), is highly diagnostic (Fig. 2). This colour pattern is also unique within the genus *Salmoneus* and the Alpheidae in general, enabling a quick identification of the species in the field. In addition to the description of the colour pattern of *S. cristatus* in Banner and Banner (1981) and herein reported material (Fig. 2), this colour pattern was recorded only for one of the specimens from the Seychelles (Banner and Banner 1983). Other species of *Salmoneus* with well-demarcated red bands, such as *S. latirostris* Coutière, 1897 and *S. venustus* Anker, 2009, have a different band arrangement and are morphologically very distinct from *S. cristatus* (Coutière 1899; Anker 2009b; AA, pers. obs.). Based on the present evidence, the geographical range of *S. cristatus* is restricted to the western Indian Ocean, from the Red Sea and the Persian Gulf to the Seychelles and Madagascar (see above). However, specimens identified as *S. cristatus* from Kenya (Bruce 1976) and the Gulf of Aqaba (Holthuis 1958) might yet belong to another species. Firstly, there is no information about the colour pattern in either record. Secondly, Bruce (1976) provided no information about the morphology of his specimens, while Holthuis provided only diagrammatic drawings of some morphological characters, mainly those of the major cheliped. The material reported by Holthuis, however, was examined in the present study, but the major cheliped is missing though it was drawn by Holthuis (1958: p. 19, fig 7d, e). Judging by the drawings of Holthuis, the material appears to be *S. cristatus* as the fingers of the major chela (see fig. 7e) somehow resemble those of *S. cristatus*.

The three herein described species, viz. *S. paracristatus* sp. nov., *S. franseni* sp. nov., and *S. alius* sp. nov., can be readily distinguished from *S. cristatus* by their creamy whitish or yellowish bodies, without bright red transverse bands (Figs. 6, 10, 14). They also differ from *S. cristatus* by the configuration of the dentation on the major chela fingers. In the three new species, the teeth of the major chela fingers are evenly distributed, with their size only slightly increasing towards the distal margin, and without a concavity on the proximo-mesial margin of the dactylus (Figs. 8A–C, 12A–D, 16A–D). In contrast, in *S. cristatus*, the proximal teeth are very small and located in a small convexity of the pollex, with the adjacent portion of the dactylus being deeply depressed to accommodate the proximal part of the pollex; the distal-most teeth are distinctly larger than the proximal ones (Fig. 4A–D).

Salmoneus paracristatus sp. nov. and *S. franseni* sp. nov. are very similar in most morphological features (Figs. 7–9, 11–13) and are also phylogenetically proximal to each other (Fig. 1). The only morphological difference that can be used to distinguish these two species is the armature of the ischium of the third and fourth pereiopods. Both ischia are each armed with a spiniform seta in all specimens of *S. paracristatus* sp. nov. (Fig. 9D, E), being unarmed in the two specimens of *S. franseni* sp. nov. (Fig. 13D, E). The posterior extension of the mid-dorsal carina of *S. paracristatus* sp. nov. and *S. franseni* sp. nov. is similar to that of *S. cristatus* (Figs. 3A, 7A, 11A). In contrast, in *S. alius* sp. nov., the mid-dorsal carina of the carapace is markedly shorter than in *S. paracristatus* sp. nov., *S. franseni* sp. nov. and *S. cristatus*, reaching only to the posterior margin of the eyes (Fig. 15B) *vs.* extending well beyond the carapace middle in the other three species. In addition, the shoulder of the frontal region in *S. alius* sp. nov. appears to be weaker compared to that of the other three species. In *S. alius* sp. nov., the ischia of the third and fourth pereiopods are each armed with two strong spiniform setae (Fig. 17D, E), contrasting with each ischium armed with only one spiniform seta in *S. paracristatus* sp. nov. (Fig. 9D, E) and the completely unarmed ischia in *S. franseni* sp. nov. (Fig. 13D, E). In *S. cristatus*, only the ischium of the third pereiopod is armed with one (Fig. 5D) or two (Banner and Banner 1981: fig. 6h) spiniform setae; the ischium of the fourth pereiopod is unarmed.

The three new species are presently known with certainty only from their type localities, although some previous records of *S. cristatus* suggest that some of

them may be more widespread in the western Pacific and perhaps also in the eastern Indian Ocean. For instance, *S. franseni* sp. nov. seems to have a wider distribution ranging from Papua New Guinea (Ďuriš and Horká 2016, as *S.* aff. *cristatus*; present study) to the Sourth China Sea (Wang and Sha 2016) and possibly to the Indian Ocean coast of Thailand (Banner and Banner 1966). The material of *S. cristatus* from Phuket, western Thailand, reported by Banner and Banner (1966) is morphologically closest to *S. franseni* sp. nov., with the only notable difference in the length of the mid-dorsal carina of the carapace, which in the Phuket specimen extends only to the mid-length of the carapace, rather than to the posterior fourth of the carapace, as in the type specimens of *S. franseni* sp. nov. from Papua New Guinea. Similarly, the record of *S. cristatus* from Queensland, eastern Australia in Anker (2003) most likely represents *S. paracristatus* sp. nov. Anker's (2003) specimen was missing the major cheliped and its colour pattern has not been recorded. Although *S. cristatus* and *S. paracristatus* sp. nov. are impossible to separate morphologically without observation of the major chela dentition and without colour pattern, based on geographical criteria, the Australian specimen is tentatively assigned to *S. paracristatus* sp. nov. The identity of the Taiwanese material tentatively reported as *S.* cf. *cristatus* by Anker (2001) remains unknown as only the major cheliped was illustrated, which is, however, different from that of *S. cristatus*. Finally, the third and morphologically most distinctive of the four species treated herein, *S. alius* sp. nov., extends further south, ranging from Papua New Guinea and the Solomon Islands to New Caledonia.

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Authors' contributions: HA performed the molecular analysis, prepared all line drawings and the first draft of the manuscript. AA reviewed and substantially edited the original draft, and also prepared one of the colour plates. ZĎ reviewed and checked the final draft, including all the illustrations and species descriptions. All the authors read and approved the final version of the manuscript.

Competing interests: The authors declare that they have no competing interests.

Availability of data and materials: All sequences generated for this study are available on GenBank,

with corresponding accession numbers provided in table 1. The material used in the study is deposited in the collections of MNHN, FLMNH and RMNH (see above).

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

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