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Description of a new species of *Ligia* Fabricius, 1798 (Crustacea: Isopoda: Ligiidae) from Samoa based on morphological and molecular data, with notes on *L. vitiensis* Dana, 1853

Valiallah **Khalaji-Pirbalouty**[1*], Carlos A. **Santamaria**[2**], Jayanthi D/O **Puniamoorthy**[3] & Jose Christopher E. **Mendoza**[3]

Abstract. *Ligia samoensis*, new species, is here described with specimens collected from Samoa, central Pacific, using morphological and molecular methods. This species can be distinguished from its closest congeners by the shape of the appendix masculina, which has a distinctive rectangular apical part with subtly rounded angles, and is equipped with long, narrow, pointed, and fully curved-down cuticular spines. Moreover, the inter-eye distance is ~0.6 of the eye length. DNA sequence analysis of the mitochondrial COI locus also supports the recognition of *L. samoensis*, new species, as it is highly divergent from other currently accepted *Ligia* species, including *L. vitiensis* Dana, 1853, a species thought to be widely distributed across coastal areas of the western, central, and southern Pacific as well as the Indian Ocean. The present COI analysis also shows some potential paraphyly within *L. vitiensis*, and the taxonomic ramifications of this are here discussed.

Key words. Peracarida, Oniscidea, *Ligia samoensis*, new species, *Ligia vitiensis*, CO1, SEM, Samoa, taxonomy

INTRODUCTION

The genus *Ligia* Fabricius, 1798 currently includes ~50 nominal species, most of which inhabit the supralittoral zone of rocky shores around the world (Ariyama & Hiki, 2024; Boyko et al., 2024). This, however, may be a severe underrepresentation of the species diversity in the genus as several new species of *Ligia* have been described in the past two decades (Taiti & Ferrara, 2004; Khalaji-Pirbalouty & Wägele, 2010; Santamaria, 2019; Ariyama & Hiki, 2024). Most of these newly described species are from remote oceanic islands, poorly studied regions, or previously unstudied populations. For instance, anatomical examinations of populations from the Persian Gulf and Yemen led to the description of two species in the region (Khalaji-Pirbalouty & Wägele, 2010). Meanwhile, the use of molecular taxonomic approaches led to the description of seven new species in the Hawaiian Archipelago (Santamaria, 2019). More recently, integrative approaches have led to the description of two novel species in Japan (Ariyama & Hiki, 2024). In addition to these recent descriptions, phylogeographic studies have uncovered highly divergent genetic lineages that appear to represent cryptic *Ligia* species in several other regions (Jung et al., 2008; Hurtado et al., 2010; Eberl et al., 2013; Santamaria et al., 2013, 2014, 2017; Raupach et al., 2014; Greenan et al., 2018; Hurtado et al., 2018). These findings, coupled with the poor dispersal capabilities of *Ligia* isopods (i.e., no planktonic larvae, poor desiccation resistance) and genetic isolation due to limited gene flow (Hurtado et al., 2010; Santamaria, 2019) suggest that poorly studied remote populations will harbour additional species in need of description.

One such region is the Samoan archipelago, which comprises nine oceanic islands of volcanic origin in the central Pacific Ocean that are thought to have formed during the Pliocene at the latest (reviewed by Keating, 1992). These islands are located ca. 1,000 km from Fiji, the type locality of *Ligia vitiensis*, a species described in 1853 by Dana from a mutilated specimen collected in the "Feejees" (i.e., Fiji) that has since been lost. The validity of this species has been questioned given its morphological similarity to the *L. exotica* and the *L. hawaiensis* cryptic species-complexes, with Jackson (1922) proposing *L. vitiensis* Dana, 1853 to be a junior synonym of *L. hawaiensis* Dana, 1853. Jackson later reinstated *L. vitiensis* as a valid species after examining specimens collected at the base of a waterfall in the Vaituha Valley in Eiao, an island in the Marquesas that is >4,500 km away from Fiji (Jackson, 1933). Taiti et al. (1992) also suggested that a unique *Ligia* species occurs within the reported range of *L. vitiensis* (viz. Sulawesi, Singapore,

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[1]Department of Biology, Faculty of Basic Science, Shahrekord University, Shahrekord, Iran; Email: vkhalaji@sci.sku.ac.ir, khalajiv@yahoo.com (*corresponding author)

[2]Department of Biology, College of Natural and Health Sciences, The University of Tampa, Tampa, Florida, United States of America; Email: csantamaria@ut.edu (**co-corresponding author)

[3]Lee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore, 2 Conservatory Drive, 117377, Singapore

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New Guinea, Melanesia, and Polynesia) after inspecting *Ligia* specimens from Indonesia, southern Melanesia, and southern Polynesia. They, however, deferred from describing any new species pending the resolution and stabilisation of the taxonomy of *L. vitiensis*.

Interestingly, *L. vitiensis* has not been reported from the Samoan Archipelago to date. Instead, the only two *Ligia* species previously reported from the region are *L. exotica* Roux, 1828, from Tutuila, and *L. perkinsi* (Dollfus, 1900) from Namua (Jackson, 1941; Schmalfus, 2003). The former is a widespread Asiatic species described by Roux (1828) from docks in Marseille (Mediterranean Sea) and that is known to have been introduced to artificial habitats around the world (Hurtado et al., 2018). The latter was described by Dollfus (1900) from specimens collected at elevation in the Hawaiian Archipelago and is currently thought to only inhabit mountainous habitats in the islands of Kaua‘i, O‘ahu, and Hawai‘i (Taiti & Ferrara, 1991; Taiti & Howarth, 1996; Taiti et al., 2003; Santamaria et al., 2013; Santamaria, 2019).

The complex taxonomic history of *L. vitiensis*, recent records of new *Ligia* species in poorly studied and insular habitats, and the distance between Fiji and Samoa suggest the possibility of a new species in the region. In this study, we use morphological and molecular approaches to characterise *Ligia* individuals from Samoa. We determine that these represent a novel species and herein describe *L. samoensis*, new species, from specimens collected in Lano beach, Savai‘i Island, Samoa.

MATERIAL AND METHODS

Morphological studies. Specimens for this study were collected primarily in Lano beach, Savai‘i Island, Samoa. Morphological studies were conducted using a Leica M205C stereomicroscope mounted with a Leica DFC450 camera and imaging system. Specimens were also prepared and studied with a JEOL scanning electron microscope (JSM-6700F) using previously described techniques (Khalaji-Pirbalouty & Wägele, 2010). Drawings of *L. samoensis* characters were made with a camera lucida on an Olympus BX51compound microscope and illustrations were electronically inked with Corel Draw vX6. Terminology follows Khalaji-Pirbalouty & Wägele (2010). Type material for *L. samoensis* is deposited in the Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum, National University of Singapore.

Molecular methodology. Genomic DNA was extracted from pereopods of four *L. samoensis* paratypes, five *L. vitiensis* topotypes from Fiji, and one putative *L. vitiensis* individual collected in Tonga. Extractions were carried out using the Qiagen DNeasy Blood and Tissue Kit following manufacturer’s instructions. The *L. vitiensis* topotypes are included as no current type exists for this species. As Dana’s (1853) description only provides “Feejees” as the locality, we included individuals from the island of Viti Levu, Fiji, near Komave. For all specimens, we PCR-amplified a 658-bp section of the mitochondrial Cytochrome c oxidase subunit I (COI) gene using the primer pair jgLCO1490 5′-TNTCNACNAAYCAYAARGAYATTGG-3′and jgHCO2198 5′-TANACYTCNGGRTGNCCRAA RAAYCA-3′. PCR reactions consisted of 12.5µl of Vazyme P222 Mastermix, 1µl of Bovine Serum Albumin (Promega) (1 mg/ml), 1µl of each primer (initial concentration of 10µM), 4.5µl of HyPure™ molecular biology grade water, and 5µl of template DNA for a total volume of 25µl and cycling conditions including an initial denaturation of 5 min at 95°C followed by 35 cycles of denaturation at 94°C (30 s), annealing at 45°C (1 min) and extension at 72°C (1 min), followed by a final extension of 5 min at 72°C. Positive amplicons were sequenced by Axil Scientific Pte Ltd. DNA extractions for *L. samoensis* paratypes have been deposited at the Lee Kong Chian Natural History Museum’s Cryo Collection.

Forward and reverse sequences produced for each specimen were assembled, checked for ambiguities and sequencing errors, and edited (i.e., had primer sequences removed) in Geneious Prime 2023. Sequences produced in this study were combined with COI sequences publicly available in GenBank for 112 *Ligia* individuals representing 28 currently valid species as well as possible undescribed ones (Table 1). Species represented in the dataset include all *Ligia* species currently known to occur in islands of the Pacific Ocean Islands except for *L. novizealandiae* (New Zealand) and *L. australiensis* (Australia) as preliminary analyses have shown them to be distantly related to *Ligia* from the Pacific Islands (Santamaria, unpub. data), and *L. rugosa* which is reported from French Polynesia (>2,000 km away from Samoa).

NGPhylogeny.fr (Lemoine et al., 2019) was used to align, curate, and reconstruct the phylogeny of the COI dataset. Our custom workflow consisted of an initial alignment of the COI dataset using MAFFT (Katoh & Standley, 2013) followed by the curation of the resulting alignment using trimAI (Capella-Gutiérrez et al., 2009). Both approaches were carried out using default settings. The resulting alignment was translated using the invertebrate mitochondrial translation table and inspected for evidence suggestive of pseudogenes or nmuts (e.g., early stop codons, indels). No evidence of nmuts was found in the alignment.

The curated alignment was then used to determine whether molecular data support the description of *L. samoensis* as a new species. To this end, we determined the placement of these specimens in a phylogenetic tree, estimated pairwise COI K2P distances between *L. samoensis* individuals and other species in the Pacific included in our dataset, and conducted distance-based and tree-based molecular species delimitation analyses (MSDAs). Phylogenetic reconstructions were conducted in NGPhylogeny.fr (Lemoine et al., 2019) as part of our custom workflow described above. Phylogenies were reconstructed in PhyML3 (Guindon et al., 2010) using standard settings, with bootstrap replicates enabled (200) and branch lengths estimated. The resulting tree was visualised and edited in iToL v6 (Letunic & Bork, 2024).

Table 1. GenBank accession numbers and locality information for taxa and COI sequences included in analyses. Entries in bold correspond to sequences produced in this study.

Species	GenBank Acc. No.	Locality
Ligia samoensis **(paratype)**	**PP766012**	**Lano beach, Savai‘i Island, Samoa**
Ligia samoensis **(paratype)**	**PP766013**	**Lano beach, Savai‘i Island, Samoa**
Ligia samoensis **(paratype)**	**PP766014**	**Lano beach, Savai‘i Island, Samoa**
Ligia vitiensis	**PQ040439**	**Navutoka, Tonga**
Ligia vitiensis **(topotype)**	**PQ040438**	**Komave, Viti Levu, Fiji**
Ligia vitiensis	KF546662	Dili, Timor-Leste
Ligia vitiensis	KF546663	Flores Island, Indonesia
Ligia vitiensis	MF805569	The Slipway, Dar-Es-Salaam, Tanzania
Ligia vitiensis	MF805570	Kilwa Masoko, Tanzania
Ligia vitiensis	MF805571	Basin Cabri, Aldabra Atoll, Seychelles
Ligia vitiensis	MF805572	Basin Cabri, Aldabra Atoll, Seychelles
Ligia vitiensis	MF805573	Silhouette Island, Seychelles
Ligia vitiensis	KF546665	Java, Indonesia
Ligia baudiniana	KF555843	Fort Sherman, Panama
Ligia baudiniana	KF555850	El Limon, Costa Rica
Ligia baudiniana	MF668214	End of Tiara Drive, Bradenton, FL, U.S.A.
Ligia dante	MH087709	Kealakukea Bay, Hawai‘i, U.S.A.
Ligia dante	MK034474	Kealakukea Bay, Hawai‘i, U.S.A.
Ligia dante	MK034475	Kealakukea Bay, Hawai‘i, U.S.A.
Ligia dante	MK034476	Kealakukea Bay, Hawai‘i, U.S.A.
Ligia dante	MK034477	Kealakukea Bay, Hawai‘i, U.S.A.
Ligia dante	MK034478	Miloli Beach Park, Hawai‘i, U.S.A.
Ligia dentipes	MF805566	Galle, Sri Lanka
Ligia dentipes	MF805576	L’Islette, W. Mahé, Seychelles
Ligia dentipes	MF805578	Cousine Island, Seychelles
Ligia dentipes	MF805585	Anse Parnel, S.E. Mahé, Seychelles
Ligia eleluensis	MK034483	Koki Beach Park, Maui, U.S.A.
Ligia eleluensis	MK034484	Koki Beach Park, Maui, U.S.A.
Ligia eleluensis	MK034485	Koki Beach Park, Maui, U.S.A.
Ligia eleluensis	MK034486	Koki Beach Park, Maui, U.S.A.
Ligia eleluensis	MK034487	Koki Beach Park, Maui, U.S.A.
Ligia exotica	KF546664	Veracruz Harbor, Veracruz, Mexico
Ligia exotica	KU906047	Indian Fields Creek, Virginia, U.S.A.
Ligia exotica	MH087511	VIMS Dock, Virginia, U.S.A.
Ligia exotica	MH087577	VIMS Dock, Virginia, U.S.A.
Ligia exotica	MN690248	Pulau Subar Laut, Singapore
Ligia hawaiensis	KF546598	Kalihiwai Beach, Kaua‘i, U.S.A.

Species	GenBank Acc. No.	Locality
Ligia hawaiensis	KF546601	Kalihiwai Beach, Kaua‘i, U.S.A.
Ligia hawaiensis	KF546603	Kalihiwai Beach, Kaua‘i, U.S.A.
Ligia hawaiensis	KF546604	Kalihiwai Beach, Kaua‘i, U.S.A.
Ligia hawaiensis	KF546605	Kalihiwai Beach, Kaua‘i, U.S.A.
Ligia hawaiensis	KF546606	Kalihiwai Beach, Kaua‘i, U.S.A.
Ligia honu	MK034513	Pu‘unalu Beach Park, Hawai‘i, U.S.A.
Ligia honu	MK034514	Pu‘unalu Beach Park, Hawai‘i, U.S.A.
Ligia italica	DQ182858	Patra, Peloponnisos, Greece
Ligia italica	DQ182859	Patra, Peloponnisos, Greece
Ligia italica	KF555842	Trieste, Italy
Ligia italica	MT521098	Giglio Porto, Italy
Ligia italica	MT521244	Giglio Porto, Italy
Ligia kamehameha	MK034515	South Point, Hawai‘i, U.S.A.
Ligia kamehameha	MK034516	South Point, Hawai‘i, U.S.A.
Ligia kamehameha	MK034517	South Point, Hawai‘i, U.S.A.
Ligia kamehameha	MK034518	South Point, Hawai‘i, U.S.A.
Ligia kamehameha	MK034519	South Point, Hawai‘i, U.S.A.
Ligia kamehameha	MK034520	Onekahakaha Beach Park, Hawai‘i, U.S.A.
Ligia mauinuiensis	MK034550	DT Fleming Beach Park, Maui, U.S.A.
Ligia mauinuiensis	MK034551	DT Fleming Beach Park, Maui, U.S.A.
Ligia mauinuiensis	MK034552	Hanakao‘o Park, Maui, U.S.A.
Ligia mauinuiensis	MK034553	Hanakao‘o Park, Maui, U.S.A.
Ligia mauinuiensis	MK034554	Hanakao‘o Park, Maui, U.S.A.
Ligia occidentalis	GU270916	Punta Sueño, Mexico
Ligia occidentalis	GU270917	San Lucas, Mexico
Ligia occidentalis	GU270918	Puerto Vallarta, Mexico
Ligia occidentalis	GU270919	El Requesón, Mexico
Ligia occidentalis	GU270920	Punta Chivato, Mexico
Ligia oceanica	KT208596	Wilhelmshaven, Nassauhafen, North Sea
Ligia oceanica	KT208931	Wilhelmshaven, Nassauhafen, North Sea
Ligia oceanica	KT209543	Wilhelmshaven, Nassauhafen, North Sea
Ligia oceanica	MT521177	Nassauhafen, Germany
Ligia oceanica	MT521189	Nassauhafen, Germany
Ligia pele	MK034562	Baby Beach, Maui, U.S.A.
Ligia pele	MK034563	Baby Beach, Maui, U.S.A.
Ligia pele	MK034564	Baby Beach, Maui, U.S.A.
Ligia pele	MK034565	Baby Beach, Maui, U.S.A.
Ligia pele	MK034566	Baby Beach, Maui, U.S.A.
Ligia perkinsi	KF546655	Haupu Range, Kaua‘i, U.S.A.

Species	**GenBank Acc. No.**	**Locality**
Ligia perkinsi	KF546659	Makaleha Mts, Kauaʻi, U.S.A.
Ligia perkinsi	KF546660	Mt. Kahili, Kauaʻi, U.S.A.
Ligia perkinsi	KF546661	Nuʻuanu Pali, Oʻahu, U.S.A.
Ligia rolliensis	MK034489	Kahaluu, Oʻahu, U.S.A.
Ligia rolliensis	MK034490	Kahaluu, Oʻahu, U.S.A.
Ligia rolliensis	MK034491	Kahaluu, Oʻahu, U.S.A.
Ligia rolliensis	MK034494	Kaena Point (South), Oʻahu, U.S.A.
Ligia rolliensis	MK034495	Kaena Point (South), Oʻahu, U.S.A.
Ligia rolliensis	MK034499	Kaena Point (North), Oʻahu, U.S.A.
Ligia rolliensis	MK034500	Kaena Point (North), Oʻahu, U.S.A.
Ligia sp. (Australia)	KR424601	Rapid Bay, Australia
Ligia sp. (Australia)	KR424602	Rapid Bay, Australia
Ligia sp. (Baja Pacific South)	HM569787	Bufadora Ensenada, Mexico
Ligia sp. (Baja Pacific South)	HM569788	Punta Baja, Mexico
Ligia sp. (Baja Pacific South)	HM569797	Bahía Asuncion, Mexico
Ligia sp. (Baja Pacific South)	HM569798	San Hipolito, Mexico
Ligia sp. (California)	HM569791	Corona Ensenada, Mexico
Ligia sp. (California)	HM569792	Ford Point, California, U.S.A.
Ligia sp. (California)	MK550637	White Point, California, U.S.A.
Ligia sp. (California)	MK550638	White Point, California, U.S.A.
Ligia sp. (California)	MK550639	White Point, California, U.S.A.
Ligia sp. (California)	MK550640	White Point, California, U.S.A.
Ligia sp. (California)	MK550641	White Point, California, U.S.A.
Ligia sp. (California)	MK550642	White Point, California, U.S.A.
Ligia sp. (California)	MK550643	White Point, California, U.S.A.
Ligia sp. (California)	MK550644	White Point, California, U.S.A.
Ligia sp. (California)	MK550652	White Point, California, U.S.A.
Ligia sp. (Careyes)	HM569882	Careyes, Mexico
Ligia sp. (Careyes)	HM569883	Careyes, Mexico
Ligia sp. (Central California)	HM569779	Coyote Point, California, U.S.A.
Ligia sp. (Central California)	HM569780	Harris Point, California, U.S.A.
Ligia sp. (Gulf of California North)	HM569861	La Cholla, Mexico
Ligia sp. (Gulf of California North)	HM569862	Puerto Penasco, Mexico
Ligia sp. (Gulf of California South)	HM569813	Mazatlan, Mexico
Ligia sp. (Gulf of California South)	HM569814	Mazatlan, Mexico
Ligia sp. (Southern California)	HM569806	Ithsmus Cove, California, U.S.A.
Ligia sp. (Southern California)	HM569807	Industrial Area, California, U.S.A.
Ligia sp. (Tanzania)	MF805568	Stone Town, Zanzibar, Tanzania
Ligia sp. (Thailand)	KF555841	Patong Beach, Phuket, Thailand

We estimated pairwise genetic distances between all sequences in the dataset using the Kimura-2-Parameter (K2P) correction (excluding ambiguous sites) in MEGA v11.0.13 (Tamura et al., 2021). MSDAs included both the tree-based Poisson Tree Processes model (Zhang et al., 2013) and distance-based ASAP describe. Tree-based analyses were conducted in the PTP server (http://species.h-its.org/) under both Maximum Likelihood and Bayesian Inferences. As this approach delineates putative species based on branching patterns in phylogenetic trees, we used the Maximum Likelihood phylogenetic tree we reconstructed from our COI dataset as input with other settings as follows: 500,000 MCMC iterations; a burn-in of 0.10; and a thinning value of 100. We also estimated the number of putative species in our dataset using ASAP (Puillandre et al., 2021) with analyses carried out in the ASAP Server (http://wwwabi.snv.jussieu.fr/public/abgd/abgdweb.html) under the Kimura 2-Parameter (K2P) nucleotide evolution model, a Pmin value of 0.01, Pmax of 0.20, and a relative width of 1. All other settings were as default.

RESULTS

TAXONOMY

Family Ligiidae Leach, 1814

Genus *Ligia* Fabricius, 1798

Diagnosis. The most recent diagnosis to the genus is that of Ariyama & Hiki (2024).

Remarks. Ariyama & Hiki (2024) provided an updated taxonomic diagnosis for this genus. The following statements are included here to augment their diagnosis. The character "Cephalon with large eyes, the distance between the eyes can be shorter, longer, or equal to the length of the eyes." can be useful in species identification. For example, in *Ligia hawaiensis* Dana, 1853, the distance between the eyes is less than their length, in *L. yemenica* it is equal, and in *L. pallasii* Brandt, 1833, this distance is greater than their length (Khalaji-Pirbalouty & Wägele, 2010).

According to Ariyama & Hiki (2024), the second [sic] article of antennula, has 3 or 4 short aesthetascs on mediodistal [sic] margin. This mistake likely stems from a visual error, with the authors mistakenly identifying the location of the aesthetascs as being on the mediodistal margin of the second article rather than the proximal part of the distal article. However, contrary to the text of the article, the figures by Ariyama & Hiki (2024: figs. 4A1, 9A1) show that these appendages are on the distal article. Contrary to Ariyama & Hiki (2024)'s assertion, these aesthetascs are located on the proximal part of the third article, a fact that has been correctly noted in prior research by Taiti & Ferrara (2004), and Khalaji-Pirbalouty & Wägele (2010). This observation is not limited to the genus in question but is consistent with other genera within the order Oniscidea, such as *Olibrinus* Budde-Lund, 1912, *Panchaia* Taiti & Ferrara, 2004, and *Tamarida* Taiti & Ferrara, 2004, where these aesthetascs are also found on the third article (Taiti & Ferrara, 2004). Finally, some characters that have not been mentioned in previous diagnoses, including the elongated antenna that is extending beyond pereon segments, the caudal surfaces of pereopods 6 and 7 with several rows of regular scales on ischium, merus, carpus and propodus (a path for water transport on these legs), and a tuft of very long thin setae on the tergal margin of dactylus, are included in this new species description.

Ligia samoensis, new species
(Figs. 1–6)

Material examined. Holotype. Male (14.2 mm without uropod) (ZRC 2023.0292), Lano Beach, Savai'i Island, Samoa, 13°36.499′S 172°12.082′W, coll. H. Wong & C.K. Chim, 6 August 2015. **Paratypes.** 2 males (13.0 mm, 14.0 mm) (ZRC 2023.0293), 3 males (12.5 mm, 13.8 mm, 14.2 mm) (ZRC 2023.0294), 1 male (14.6 mm) (ZRC 2023.0295), 1 female (12.1 mm) (ZRC 2023.0296), 1 female (10.0 mm) (ZRC 2023.0297), same data as holotype.

Diagnosis. Eyes relatively large, distance between eyes ca. 0.6 of the eye length; pleotelson length more than half of width; uropod peduncle more than twice length of pleotelson, about half length of rami, mesial margin with 6 robust setae; antennal flagellum extending to posterior margin of pleonite 3. Propodus of first pereopod without protruding triangular process on distal part; pereopods 6 and 7 dactyli with tuft of long, thin setae on tergal and subdistal margins. Appendix masculina apex tip not enlarged, apex blunt and slightly rounded, subapical margin equipped with several rows of slender and fully curved down cuticular spines.

Description of male. Body length 2.41 times greatest width (at pereonite 4) (Figs. 1A, 2A). Cephalon with large eyes, distance between eyes ~0.6 times as long as each eye length (Figs. 1B, C, 2A). Pereonite 7 posterolateral point extending to middle of pleonite 3. Pleonite 1 visible in dorsal view but largely concealed by pereonite 7; pleonites 3–5 with a subcrescentic epimera, pleonites 4 and 5 bearing a subcrescentic, thin dorsal depression. Pleotelson length ca. 0.7 times greatest width, bearing arcuate furrow dorsally, with pointed posteromedial margin; posterolateral corners acute but not reaching pleotelson apex; posterior margin with 5–7 submarginal foraminate tricorns on each side (Figs. 1D, 2F).

Antennula basal article with 2 simple setae on distoventral margin; article 2 covered with scaly setae, bearing 4 long setae on posterodistal angle; apical article with 4 aesthetascs (Fig. 2B).

Antenna peduncle article 3 longer than article 2, with simple seta on dorsodistal angle; article 5 about 1.6 times as long as article 4 (Figs. 1B, C, 2C); flagellum extending to posterior margin of pleonite 3, with 39 articles, last article (Fig. 2D) bearing a tuft of fine setae distally.

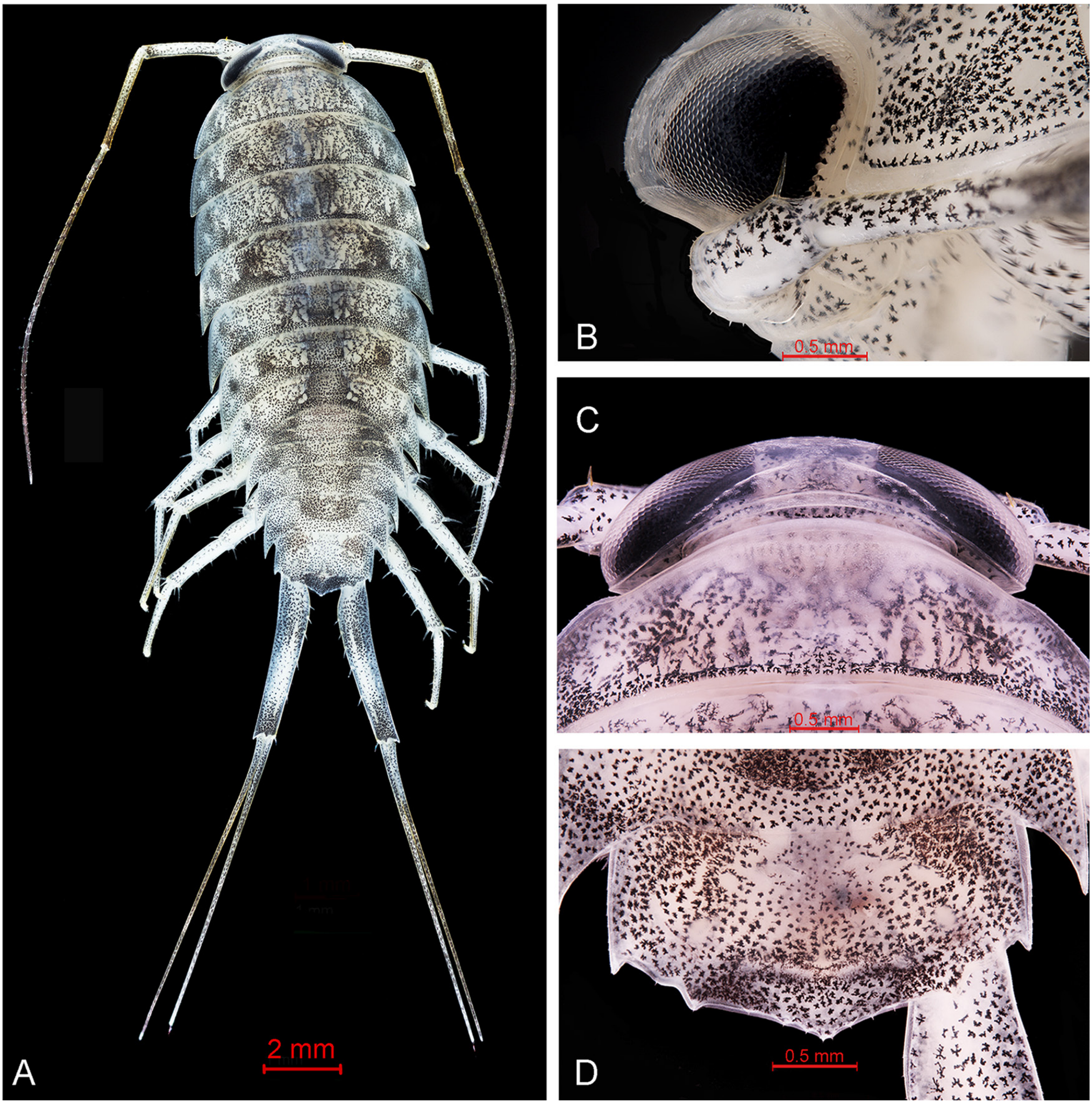

Fig. 1. *Ligia samoensis*, new species, male, holotype (ZRC 2023.0292). A, habitus, dorsal view; B, head, left lateral view; C, head, dorsal view; D, pleotelson, dorsal view.

Maxillula lateral endite apex with 5 robust spine-like teeth laterally, 5 robust serrate and 1 biserrate setae mesially, 2 robust simple setae medially; mesial endite with 3 stout, circumplumose setae (penicils), 1 submarginal stout simple seta, and fine setae on apical margin (Fig. 3A).

Maxilla lateral and mesial endite distally rounded, bearing fields with short, fine and dense setae as illustrated (Fig. 3B).

Maxilliped endite apex with 2 circumplumose setae (penicils), 6 robust marginal and 2 robust submarginal setae and scattered fine setae; palp with 5 separate articles, basal article with 1 medially and 1 apically bifid robust setae, article 2 with 2 medially and 4 apically bifid robust setae, articles 2–4 with transverse rows of slender setae on inner margins, article 3 with 3 distally bifid robust setae, article 4 with 4 distally and 1 laterally bifid robust setae, article 5 bearing about 20 simple apical setae, without marginal robust setae (Fig. 3C).

Mandible incisor and lacinia mobilis with three cusps; spine row of 11 serrate spines; molar process with many scattered fine setae (Fig. 3D).

Pereopod 1 basis ca. 2.2 times as long as greatest width, with some scale-like setae on inferior margin and some short setae on superior margin, superodistal corner with 1 robust seta; ischium and merus subequal in length, ischium

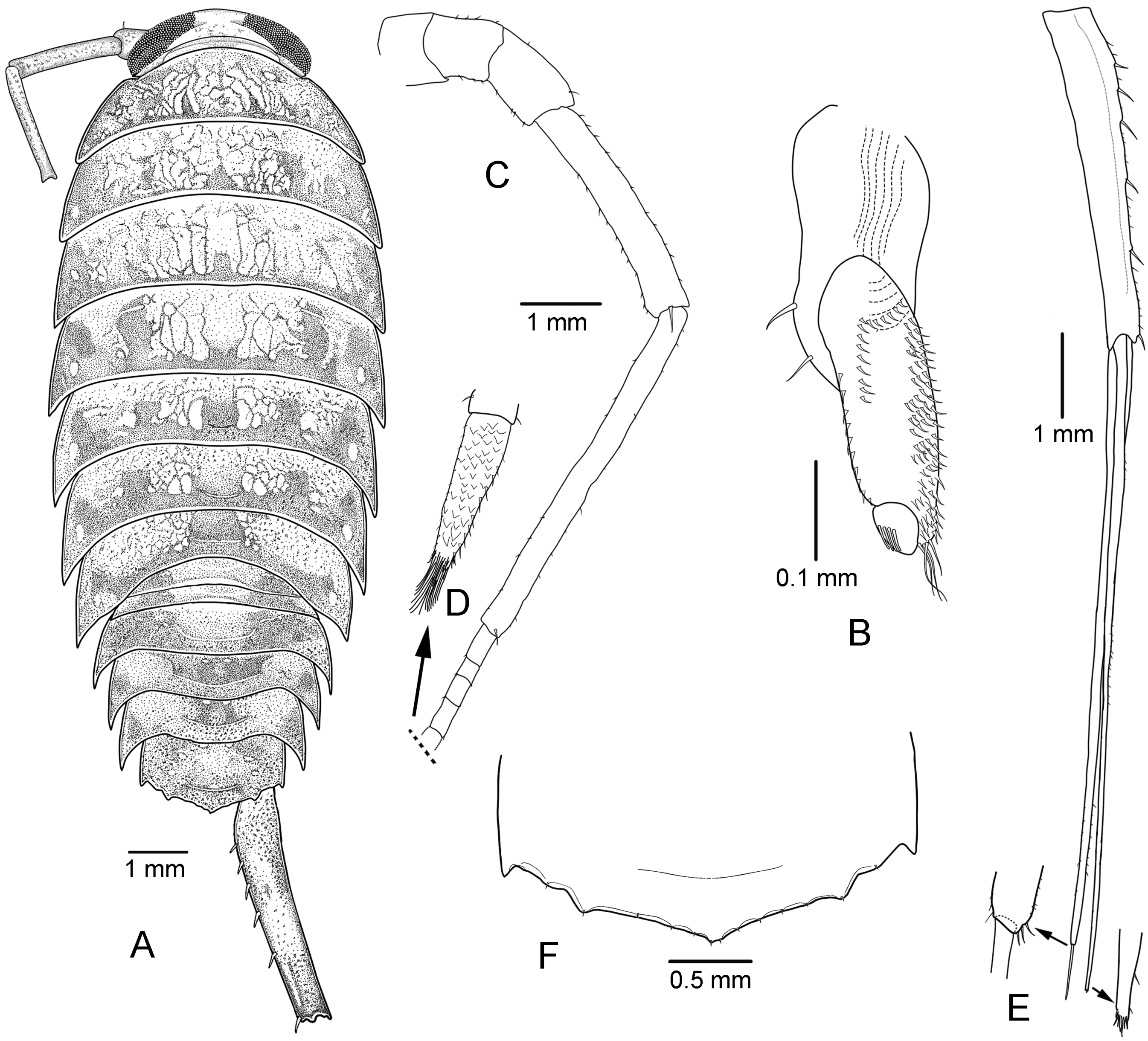

Fig. 2. *Ligia samoensis*, new species, male, holotype (ZRC 2023.0292). A, habitus, dorsal view; B, antennula; C, antenna; D, last (distalmost) article of antennal flagellum; E, uropod, dorsal view; F, pleotelson, dorsal view.

superior margin with 3 robust setae; merus and carpus with large papillar fields on inferior margins; carpus and propodus subequal in length; carpus length ca. 2.2 times greatest width; propodus curved, inferior margin with 5 marginal robust setae; dactylus with 6 short, scale-like setae on superior margin, distosuperior corner with 1 long club-tipped seta, secondary unguis small and shorter than main unguis (Fig. 4A).

Pereopod 3 basis length ca. 2.5 times greatest width; ischium longer than merus, with 3 robust setae on superior margin, dorsal surface with an oblique raw of 4 robust setae; merus with 6 robust and some short, simple setae on inferior margin; carpus longer than merus, inferior margin with 2 long robust setae and some short simple setae; propodus shorter than carpus, with some short, simple setae on inferior and superior margins; dactylus with 3 scale-like setae on superior margin, distosuperior corner with 1 long and distally noded seta (Fig. 4B).

Pereopod 5 basis about 2.2 times as long as wide, superior margin with 4 long setae, distal margin with 5 robust setae; ischium superodistal angle with 2 long robust setae; merus superodistal angle with 4 long robust setae, inferior margin with 5 long robust and some short setae; carpus longer than merus, carpus length ca. 2.2 times greatest width, distal and inferior margins with several robust setae; propodus elongated, ca. 1.23 times as long as carpus, with 6 robust setae on inferior margin; dactylus with 4 scale-like setae on superior margin, distosuperior angle with 1 long and distally noded seta (Fig. 4C).

Pereopod 7 with several fields of regular scales on basis, ischium and merus; basis length about 2 times as long as greatest width; ischium longer than merus, inferior margin with 6 short robust setae; with 1 long robust seta on superodistal corner, distal margin with 4 robust setae; merus superodistal corner with 3 long robust setae, inferior margin with 3 long and 7 short robust setae; carpus ca. 1.5 times as

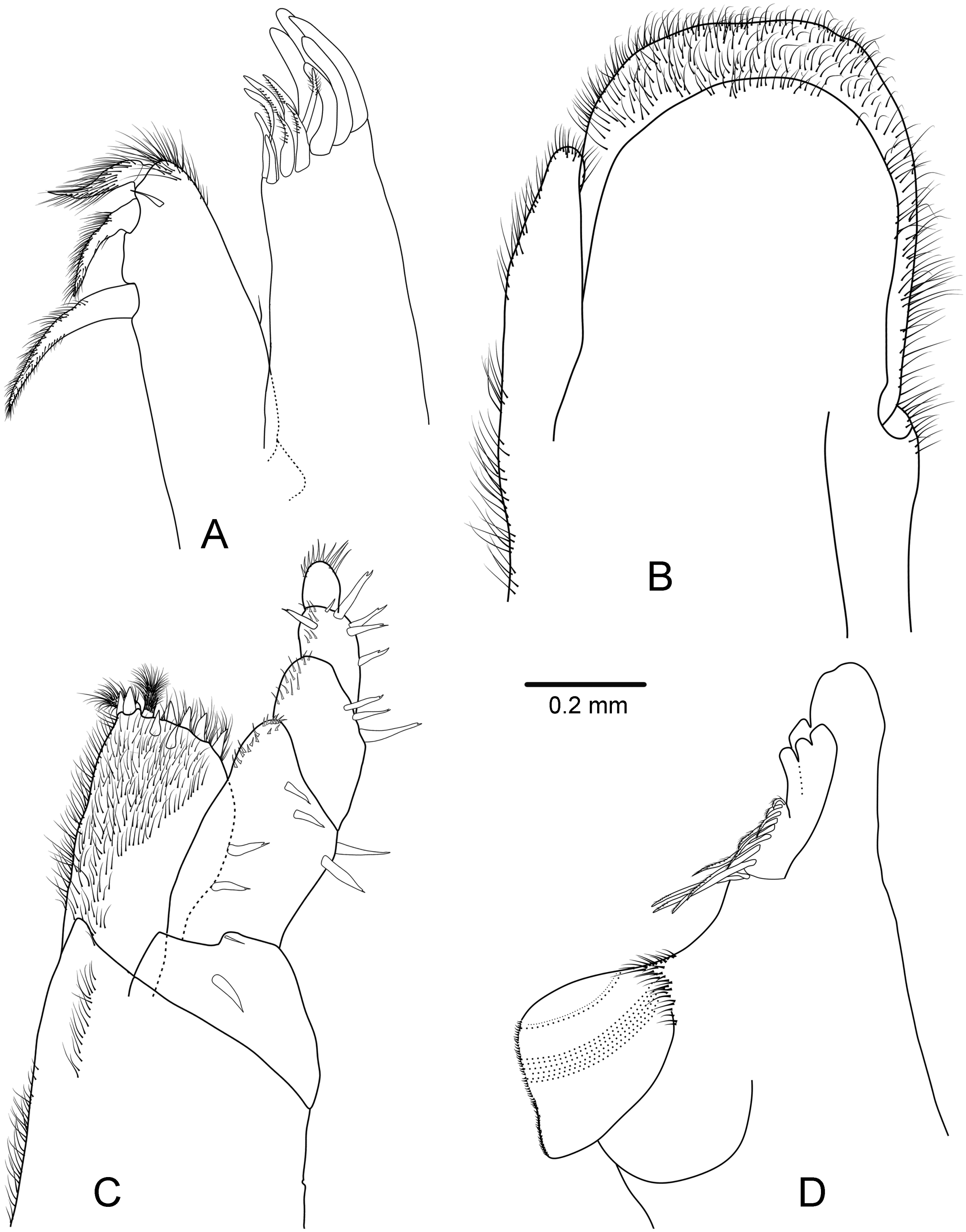

Fig. 3. *Ligia samoensis*, new species, male, holotype (ZRC 2023.0292). A, maxillula; B, maxilla; C, maxilliped; D, left mandible.

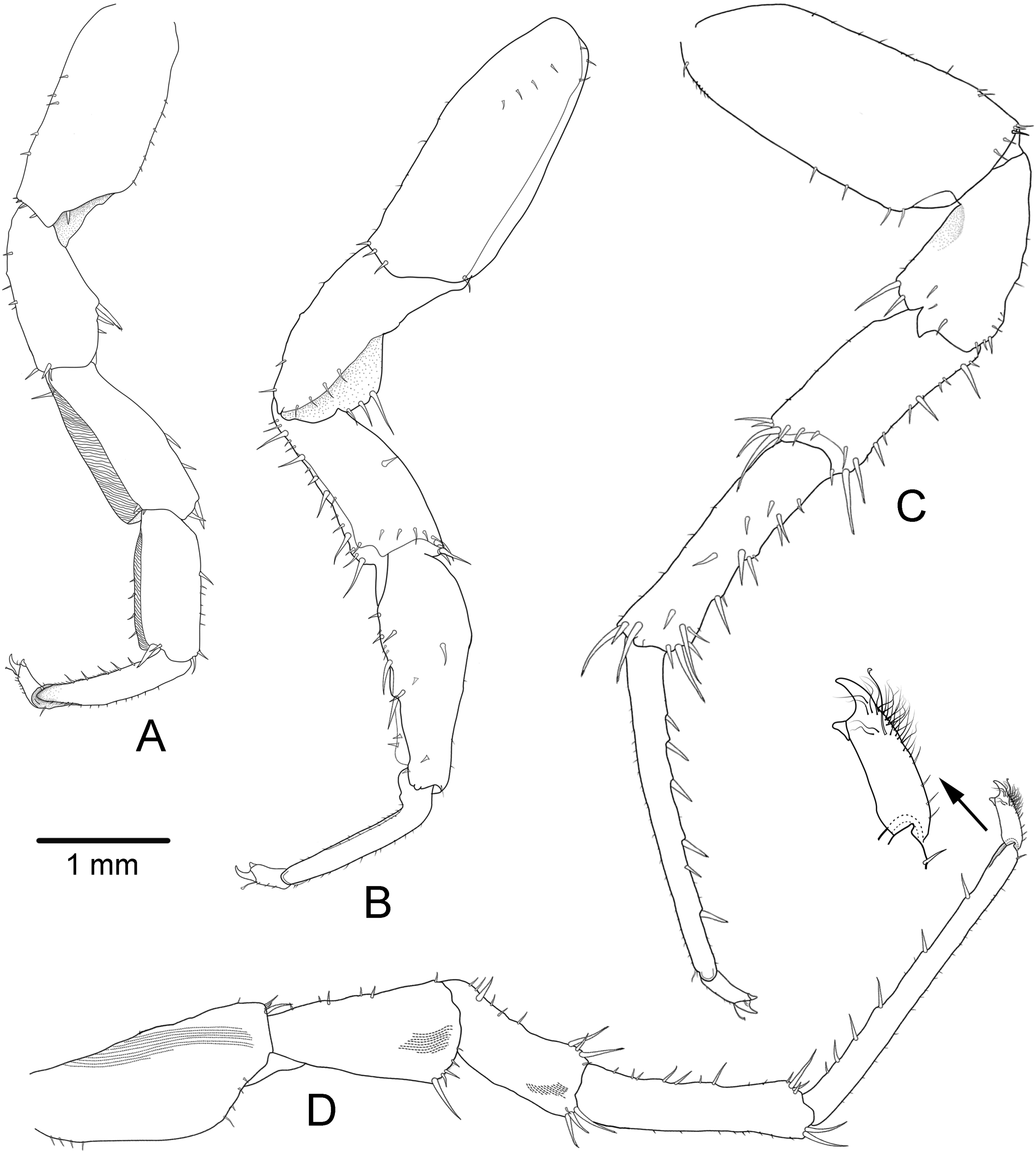

Fig. 4. *Ligia samoensis*, new species, male, holotype (ZRC 2023.0292). A, pereopod 1; B, pereopod 3; C, pereopod 5; D, pereopod 7.

long as merus, superodistal corner with 2 long robust setae; propodus elongated, ca. 1.4 times as long as carpus, with 6 robust setae on inferior margin; dactylus superior margin with a tuft of long and thin setae, distosuperior corner with 1 long and distally noded seta (Fig. 4D).

Pleopod 1 exopod bearing nearly rounded corners, with 23 plumose marginal setae (Fig. 5A).

Pleopod 2 exopod nearly oval, with row of 45 plumose marginal setae; appendix masculina (Figs. 5B, C, D, 6A, B) ca. 13.5 times as long as basal width, bearing tiny pectinate cuticular scales on proximal lateral margin (Fig. 6C, D); with blunt and slightly rounded apex, subapical medial margin not convex, equipped with several irregular and non-dense rows of narrow, acute, and fully curved-down cuticular spines.

Pleopod 3 similar to pleopod 4 as illustrated, exopod with 56 and 68 plumose marginal setae (Fig. 5E, F) respectively.

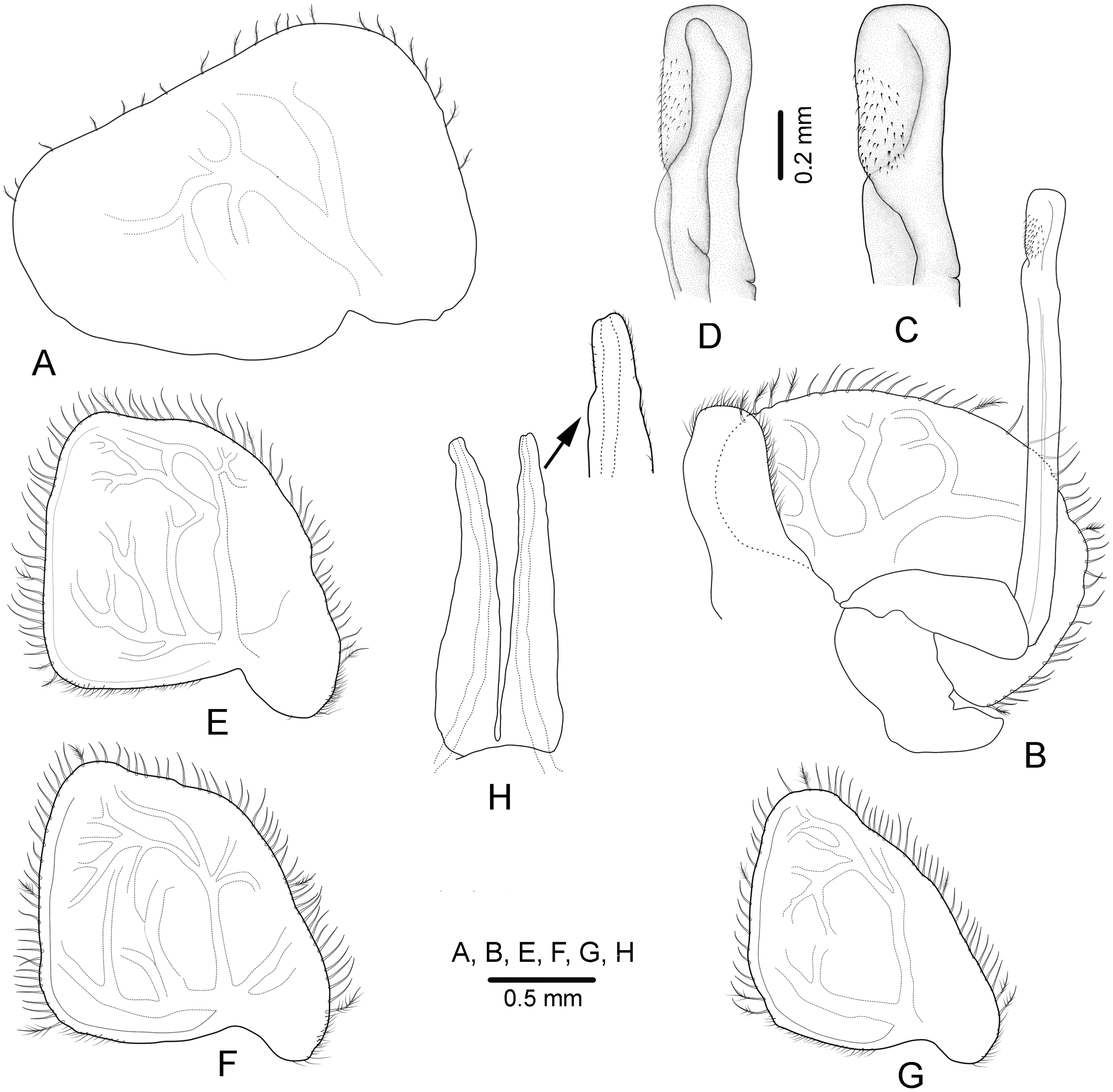

Fig. 5. *Ligia samoensis*, new species, male, holotype (ZRC 2023.0292). A, pleopod 1 exopod; B, pleopod 2; C, caudal surface of pleopod 2 endopod, distal part; D, rostral surface of pleopod 2 endopod, distal part; E–G, pleopod 3–5 exopod, respectively; H, penes.

Pleopod 5 exopod nearly triangular, with 51 plumose marginal setae (Fig. 5G).

Penes tapering evenly, apex with a small cleft, lateral margins bearing short, fine setae in distal part, about 5 times as long as basal width (Fig. 5H).

Uropod peduncle well extended beyond pleotelsonic apex, ca. 2.3 times as long as pleotelson; peduncle ca. 0.5 times as long as exopod, distolateral angle freely extending and acute, mesial margin with 6 robust and some short setae; exopod extending well beyond endopod main article, endopod with a tuft of small bristle distally (Figs. 1A, 2E).

Etymology. The specific epithet *samoensis* means "from Samoa" in Latin; used as an adjective.

Remarks. *Ligia samoensis*, new species, can be distinguished by the shape of the appendix masculina with its distinctive rectangular apex, characterised by subtly rounded angles. In addition, the subapical margin is not enlarged and is equipped with long, slender and fully curved-down cuticular spines. In other closely related and adjacently distributed species, the apical part of the appendix masculina is different: viz. enlarged with an obliquely truncate apex, with curved, short, but not dense cuticular spines in *L. hawaiensis* Dana, 1853 (type locality: Hawaiian Islands; see Taiti et al., 2003: fig. 6A); enlarged, truncate with short and somewhat dense cuticular spines in *L. vitiensis* Dana, 1853 (type locality:

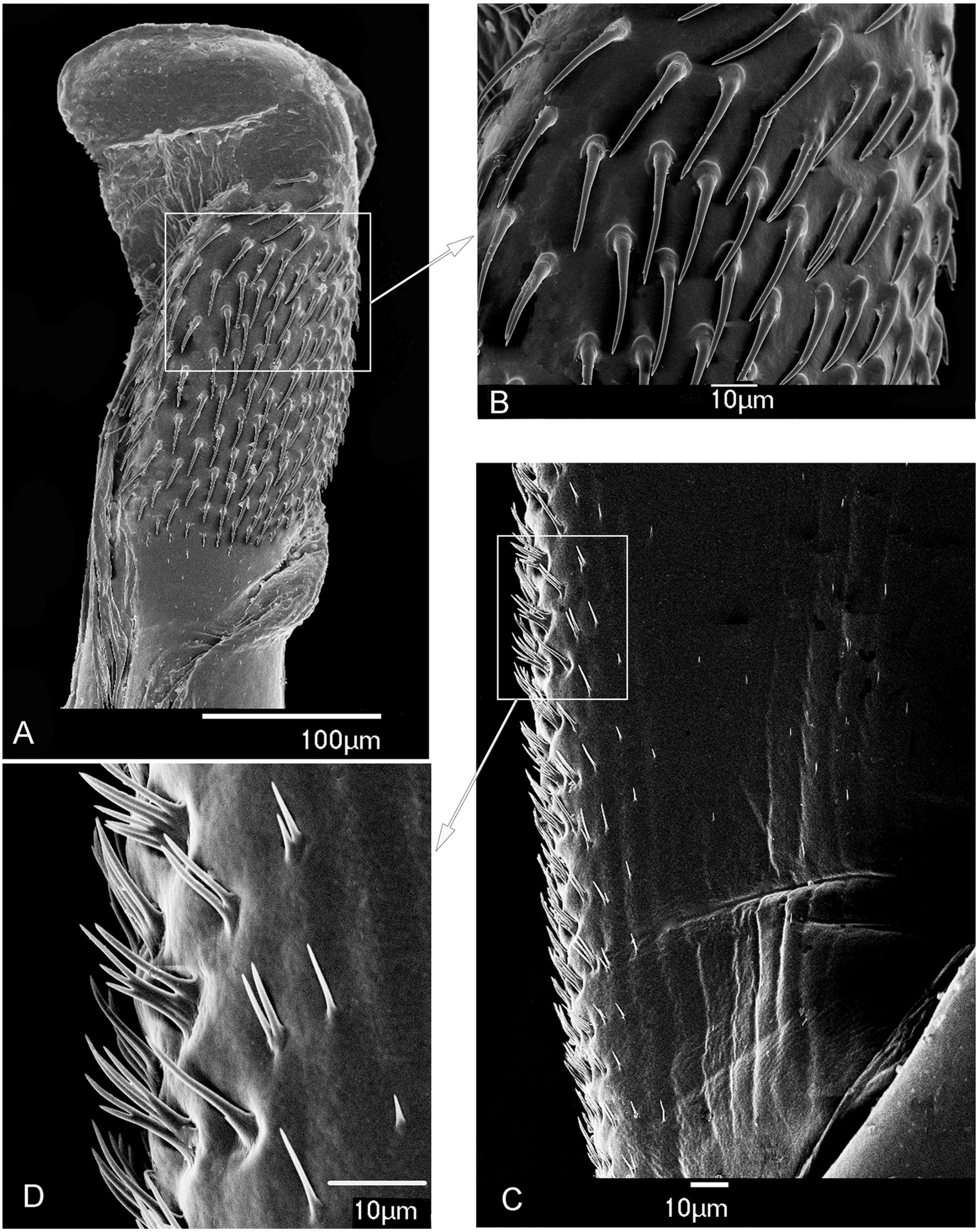

Fig. 6. *Ligia samoensis*, new species, male, holotype (ZRC 2023.0292), SEM. A, B, appendix masculina distal part with cuticular spines; C, D, appendix masculina proximal part with tiny pectinate cuticular setae.

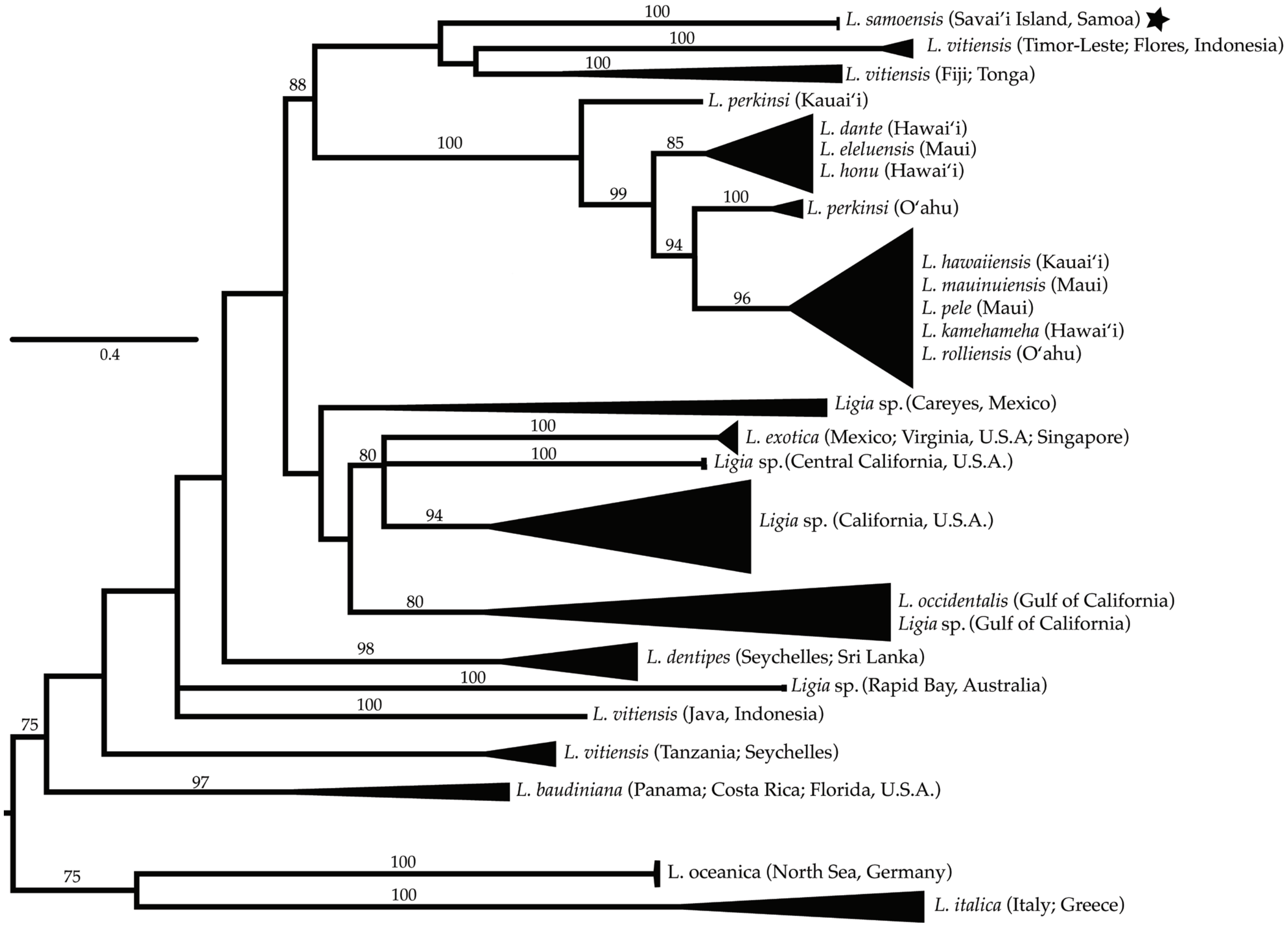

Fig. 7. Phylogeny of *Ligia* species included in this study inferred from COI sequences in PhyML. Tree presented corresponds to the most likely tree produced during analyses. Clades containing multiple closely related individuals or species are collapsed. Support values are provided for nodes supported by at least 75% of all bootstrap replicates. The star denotes *L. samoensis*, new species.

Fiji), as described and illustrated by Taiti et al. (1992) from a specimen from the Togian Islands in Sulawesi, Indonesia; and not enlarged, rounded, and slightly bilobed with short and dense cuticular spines in *L. perkinsi* Dollfus, 1900 (type locality: Hawaiian Islands; see Taiti et al., 2003: fig. 6B). Moreover, the new species possesses proportionally smaller inter-ocular distance than its relatives, with the distance between the eyes measuring ca. 0.6 times the length of the eye, compared to ca. 0.7 times in *L. hawaiensis* and ca. 1.0 times in *L. perkinsi*.

MOLECULAR RESULTS

The curated alignment produced in this study consisted of 592 base pairs (257 parsimony informative sites) and included 115 COI haplotypes from 29 species, including those recovered from *L. samoensis* paratypes (a single haplotype shared by all paratypes) and from *L. vitiensis* (one haplotype shared by all five Fiji topotypes and a separate one from Tonga). New COI haplotypes produced in this study have been deposited in GenBank under accession numbers PP766012–PP766014 and PQ040439–PQ040440 (Table 1).

Phylogenetic reconstructions recovered a well-supported clade consisting of all *L. samoensis* specimens (Bootstrap Support, BS = 100, dark blue in Fig. 7) but did not recover the monophyly of *L. vitiensis* (light blues in Fig. 7). We recovered three deeply divergent *L. vitiensis* lineages: (a) a well-supported clade consisting of individuals collected in Tanzania and the Seychelles (BS = 100), (b) a lineage reported from a single individual collected in Java; and (c) a poorly supported clade (BS < 75) composed of an Indonesian lineage consisting of individuals from Flores, Indonesia and Dili, Timor-Leste (BS = 100) and a Pacific lineage consisting of individuals from Fiji and Tonga (BS = 100). Phylogenetic reconstructions identified this latter *L. vitiensis* clade as the sister of the *L. samoensis*. However, the sister relationship between *L. samoensis*, a new species, and this *L. vitiensis* clade was not well supported (BS < 75).

The COI haplotype recovered from *L. samoensis* individuals was highly divergent from other *Ligia* species included in our dataset, with the average COI K2P distances between *L. samoensis* and other *Ligia* species ranging between 20.3 and 28.4% (Table 2). The COI K2P distance between the haplotype recovered from *L. samoensis* paratypes and those recovered from *L. vitiensis* individuals from nearby islands in the Pacific were: 20.0% for Fiji, 22.3% for Tonga, 22.8% for Flores, 22.3% for Timor-Leste, and 21.8% for Java.

Table 2. Average estimates of evolutionary divergence, as measured by Kimura 2-parameter distances, between Ligia species included in this study.

	L. samoensis	*L. vitiensis*	*L. dentipes*	*Ligia* sp. (Thailand)	*L. hawaiensis*	*L. kamehameha*	*L. rolliensis*	*L. pele*	*L. dante*	*L. honu*	*L. eleulensis*	*L. mauinuiensis*	*L. perkinsi*	*Ligia* sp. (Careyes, Mexico)	*Ligia* sp. (Gulf of California South)	*Ligia* sp. (Gulf of California North)	*L. occidentalis*	*Ligia* sp. (Baja Pacific North)	*Ligia* sp. (California)	*Ligia* sp. (Baja Pacific South)	*Ligia* sp. (Southern California)	*Ligia* sp. (Northern California)	*Ligia* sp. (California)	*L. exotica*	*L. baudiniana*	*Ligia* sp. (Tanzania)	*L. italica*	*Ligia* sp. (Australia)
L. vitiensis	23.1																											
L. dentipes	24.2	23.5																										
Ligia sp. (Thailand)	22.8	22.7	11.3																									
L. hawaiensis	24.6	23.3	22.1	24.5																								
L. kamehameha	25.4	22.1	22.6	18.9	13.0																							
L. rolliensis	25.1	21.9	24.1	20.3	13.8	5.0																						
L. pele	25.4	23.5	26.0	21.6	14.4	7.5	7.1																					
L. dante	23.0	23.9	21.1	21.6	14.9	15.3	15.3	16.1																				
L. honu	23.5	24.0	23.8	22.2	17.1	15.4	15.4	16.2	7.4																			
L. eleulensis	24.6	23.5	22.6	23.2	16.1	15.3	14.7	16.7	11.3	11.2																		
L. mauinuiensis	25.5	23.7	24.4	22.2	11.7	10.1	11.4	11.7	14.7	14.8	15.1																	
L. perkinsi	23.8	21.5	21.3	21.8	15.6	13.5	14.0	15.1	13.8	14.1	13.5	13.8																
Ligia sp. (Careyes, Mexico)	20.2	22.3	20.7	21.1	20.8	19.4	21.4	21.8	19.7	20.9	20.3	21.4	19.5															
Ligia sp. (Gulf of California South)	24.0	22.9	23.4	25.4	23.6	21.7	21.9	22.4	23.2	22.2	22.6	23.9	22.4	19.1														
Ligia sp. (Gulf of California North)	26.4	26.2	23.2	25.1	26.6	28.2	26.9	27.4	27.3	27.4	25.1	26.7	26.8	22.6	22.7													
L. occidentalis	23.2	24.4	22.5	21.1	22.6	23.8	24.5	25.3	23.6	24.9	24.2	24.7	23.9	21.7	18.0	23.5												
Ligia sp. (Baja Pacific North)	25.0	24.0	24.9	23.3	24.0	21.0	21.0	22.4	21.7	23.5	21.2	22.7	21.8	22.0	21.5	25.3	22.6											
Ligia sp. (California)	23.7	23.2	23.6	23.3	22.0	21.7	20.9	22.3	21.8	25.7	21.8	24.0	21.1	20.5	21.4	27.7	22.3	7.8										
Ligia sp. (Baja Pacific South)	24.1	22.8	23.0	22.4	21.3	22	22.6	22.6	22.0	23.2	18.8	22.6	21.0	19.1	20.9	23.3	21.0	13.7	13.9									
Ligia sp. (Southern California)	24.1	24.9	25.0	22.5	23.7	21.6	22.6	22.1	23.9	23.7	22.6	22.3	22.2	21.0	22.3	26.4	22.4	19.3	18.7	17.7								
Ligia sp. (Northern California)	23.6	23.4	25.4	22.9	24.2	23.2	23.9	24.9	25.3	25.9	25.4	24.4	22.3	20.8	21.2	24.7	21.7	21.3	21.8	22.4	20.8							
Ligia sp. (California)	24.7	25.2	24.0	23.9	22.4	21.6	21.7	21.8	22.9	23.5	22.5	22.3	22.4	21.3	22.0	27.8	23.3	18.3	18.5	17.4	7.7	23.2						
L. exotica	24.6	23.1	24.1	25.0	22.6	21.8	22.6	23.0	24.2	24.4	23.4	24.2	23.7	19.8	22.7	25.3	23.3	19.6	19.8	19.9	22.1	22.5	21.0					
L. baudiniana	27.0	25.2	24.6	26.2	25.6	26.3	26.3	26.5	24.3	25.2	23.6	26.3	22.5	24.0	24.8	27.9	29.0	25.1	25.2	23.9	25.8	25.5	25.7	27.1				
Ligia sp. (Tanzania)	25.1	24.8	24.3	25.6	23.2	23.5	23.1	24.4	22.9	25.1	24.5	23.8	23.9	23.3	24.9	27.1	23.5	22.6	23.4	22.6	27.4	24.4	24.6	22.6	24.5			
L. italica	25.9	25.8	26.2	25.7	24.6	24.1	24.1	23.5	23.9	25.1	25.4	24.4	23.5	25.4	25.6	28.0	24.0	25.0	23.9	25.9	26.0	25.6	26.2	30.1	26.2	26.7		
Ligia sp. (Australia)	28.3	25.1	22.9	23.7	26.4	24.5	24.0	25.0	25.0	25.4	23.5	23.5	22.9	23.2	23.2	26.1	26.9	25.8	24.5	24.2	27.5	26.3	27.0	24.6	26.5	25.9	24.9	
L. oceanica	27.2	26.8	27.4	26.6	24.9	24.5	23.8	25.2	24.7	25.8	24.8	26.7	24.7	23.4	27.4	27.5	28.9	25.3	24.7	24.4	25.6	26.5	26.6	26.6	26.7	27.0	26.7	29.5

All MSDAs consistently identified a putative species that consisted solely of *L. samoensis*, new species, and that excluded all other *Ligia* individuals in our dataset, including *L. vitiensis* topotypes. The Maximum Likelihood iteration of PTP identified 47 species while bPTP identified 58 species. In both PTP and bPTP analyses, *L. samoensis* was identified as a putative species separate from all other species in the dataset. In ASAP, the ten best partitions produced in our analyses recognised between 36–49 putative species in our dataset, with all partitions separating *L. samoensis* into a putative species that did not include any other *Ligia*.

The high level of differentiation between *L. samoensis* and other *Ligia* from the Pacific, the poor support for a monophyly of *L. vitiensis* and *L. samoensis* individuals, and the results of MSDAs all support the recognition of *L. samoensis*, new species, from Samoa.

DISCUSSION

Several new species of *Ligia* isopods have been described primarily from little-studied or remote coastal regions over the past two decades (Taiti & Ferrara, 2004; Khalaji-Pirbalouty & Wägele, 2010; Santamaria, 2019; Ariyama & Hiki, 2024). Additionally, phylogeographic studies have uncovered highly divergent lineages likely to represent cryptic species in need of description in isolated or insular populations (Jung et al., 2008; Hurtado et al., 2010; Eberl et al., 2013; Raupach et al., 2014; Santamaria et al., 2014; Santamaria et al., 2017; Greenan et al., 2018; Hurtado et al., 2018). By using an integrative taxonomic approach that includes morphological and molecular evaluations of *Ligia* specimens from Samoa, a highly remote archipelago in the Pacific, we have been able to uncover and describe *Ligia samoensis*, new species.

This species appears to be distinct when examining the morphological traits known to be diagnostic for *Ligia* species and/or species-complexes, such as the apex of the appendix masculina. The distinctive shape and ornamentation pattern of this structure provide a valuable tool to discern *Ligia* species that are otherwise difficult to tell apart based on appearance (Taiti et al., 2003; Khalaji-Pirbalouty & Wägele, 2010; Yin et al., 2013; Santamaria et al., 2014). The ornamentation pattern and shape of cuticular spines in *L. samoensis* shows a species-specific pattern that has not been documented in previously described *Ligia* species, including those reported for *L. vitiensis* from the Togian Islands, Indonesia (Taiti et al., 1992). The narrow, pointed, and fully curved-down cuticular spines that are distributed in an irregular and sparse arrangement in *L. samoensis* thus provide a diagnostic character for this novel species.

Molecular data also support the recognition of *L. samoensis* as a new species. While the phylogenetic tree (Fig. 7) producing the best likelihood score identified *L. samoensis* as the sister to a clade comprised of *L. vitiensis* lineages found in Fiji, Tonga, Timor-Leste, and Indonesia that may represent additional new species in need of description, this relationship was poorly supported (BS = 56). Pairwise comparisons of the COI haplotypes for *L. samoensis* and the aforementioned *L. vitiensis* individuals indicate that these two lineages are exceedingly divergent (COI K2P >20%). The COI K2P values observed in these pairwise comparisons are similar to those observed in comparisons between *L. samoensis* and other valid *Ligia* species (Table 2). Not surprisingly, both tree- and distance-based MSDAs consistently identified *L. samoensis*, new species, as a species separate from all others in our dataset. Interestingly, our analyses also identify multiple divergent lineages (pairwise COI K2P >20%) for *L. vitiensis* with phylogenetic reconstructions not supporting the monophyly of these lineages (also see Santamaria et al., 2017). These findings underscore the need for the proper redescription of *L. vitiensis* and suggest that previous reports of this species in the Indian Ocean (e.g., the Seychelles), and Southeast Asia (e.g., Java, Timor-Leste, the Togian Islands), may be misidentifications and refer to additional, potentially new species in need of description.

Admittedly, our molecular approaches only incorporated a single mitochondrial gene: COI. This gene, however, has been shown to closely correspond with other mitochondrial and nuclear markers in phylogeographic studies of *Ligia* (Santamaria et al., 2013; Santamaria et al., 2014; Santamaria et al., 2017; Greenan et al., 2018). Nonetheless, the use of additional markers and the incorporation of additional populations of *Ligia* from across the Pacific may allow for a better understanding of the phylogenetic relationship of *L. samoensis*, new species. Given the levels of divergence observed across *L. vitiensis* populations in the Pacific, such studies also may uncover other *Ligia* species in need of description in the islands of the Pacific Ocean, as *Ligia* are widely reported from the region (Jackson, 1933; Green et al., 1990; Taiti & Ferrara, 1991; Taiti et al., 1992; Schmalfuss, 2003). Such efforts, however, would be best served by the prior redescription of *L. vitiensis* and, as the original holotype is presumed lost, the designation of a neotype ideally from its type locality, Fiji, to stabilise the taxonomy of this species.

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