

Kallograea kulolasi n. gen., n. sp. and *K. jolliveti* (Guinot & Segonzac, 2018) from the hydrothermal Kulo Lasi Volcano Caldera, West Pacific; and a reappraisal of *Austinograea* Hessler & Martin, 1989 and *Gandalfus* McLay, 2007 (Decapoda, Brachyura, Bythograeoidea)

Danièle GUINOT & Peter K. L. NG

DIRECTEUR DE LA PUBLICATION / *PUBLICATION DIRECTOR*: Gilles Bloch
Président du Muséum national d'Histoire naturelle

RÉDACTRICE EN CHEF / *EDITOR-IN-CHIEF*: Laure Desutter-Grandcolas

ASSISTANTE DE RÉDACTION / *ASSISTANT EDITOR*: Anne Mabilille (zoosyst@mnhn.fr)

MISE EN PAGE / *PAGE LAYOUT*: Anne Mabilille

COMITÉ SCIENTIFIQUE / *SCIENTIFIC BOARD*:

Nesrine Akkari (Naturhistorisches Museum, Vienne, Autriche)
Maria Marta Cigliano (Museo de La Plata, La Plata, Argentine)
Serge Gofas (Universidad de Málaga, Málaga, Espagne)
Sylvain Hugel (CNRS, Université de Strasbourg, France)
Marco Isaia (Università degli Studi di Torino, Turin, Italie)
Rafael Marquez (CSIC, Madrid, Espagne)
Jose Christopher E. Mendoza (Lee Kong Chian Natural History Museum, Singapour)
Annemarie Ohler (MNHN, Paris, France)
Jean-Yves Rasplus (INRA, Montferrier-sur-Lez, France)
Wanda M. Weiner (Polish Academy of Sciences, Cracovie, Pologne)

COUVERTURE / *COVER*:

Kallograea kulolasi n. gen., n. sp. *in situ*, Kulo Lasi Caldera, video, PL729, 1472 m, associated with Siboglinidae and easily recognisable by its long chelipeds with elongated and slender merus.

Zoosystema est indexé dans / *Zoosystema is indexed in*:

- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Agriculture, Biology, and Environmental Sciences®
- Scopus®

Zoosystema est distribué en version électronique par / *Zoosystema is distributed electronically by*:

- BioOne® (<http://www.bioone.org>)

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Zoosystema* sont référencés par /
Articles and nomenclatural novelties published in Zoosystema are referenced by:

- ZooBank® (<http://zoobank.org>)

Zoosystema est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris / *Zoosystema is a fast track journal published by the Museum Science Press, Paris*

Les Publications scientifiques du Muséum publient aussi / *The Museum Science Press also publish*:

Adansonia, *Geodiversitas*, *Anthropozoologica*, *European Journal of Taxonomy*, *Naturae*, *Cryptogamie* sous-sections *Algologie*, *Bryologie*, *Mycologie*, *Comptes Rendus Palevol*.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2025
ISSN (imprimé / *print*): 1280-9551/ ISSN (électronique / *electronic*): 1638-9387

***Kallograea kulolasi* n. gen., n. sp. and *K. jolliveti* (Guinot & Segonzac, 2018) from the hydrothermal Kulo Lasi Volcano Caldera, West Pacific; and a reappraisal of *Austinograea* Hessler & Martin, 1989 and *Gandalfus* McLay, 2007 (Decapoda, Brachyura, Bythograeoidea)**

Danièle GUINOT

Institut de Systématique, Évolution, Biodiversité (ISYEB)
Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE,
Université des Antilles, case postale 53,
57 rue Cuvier, F-75231 Paris cedex 05 (France)
daniele.guinot@mnhn.fr

Peter K. L. NG

Lee Kong Chian Natural History Museum, Conservatory Drive,
National University of Singapore, Singapore 117377 (Republic of Singapore)
peterng@nus.edu.sg

Submitted on 5 March 2025 | Accepted on 3 June 2025 | Published on 18 December 2025

[urn:lsid:zoobank.org:pub:C235ADA7-C6F4-491F-B5F8-D990E772801E](https://zoobank.org/pub:C235ADA7-C6F4-491F-B5F8-D990E772801E)

Guinot D. & Ng P. K. L. 2025. — *Kallograea kulolasi* n. gen., n. sp. and *K. jolliveti* (Guinot & Segonzac, 2018) from the hydrothermal Kulo Lasi Volcano Caldera, West Pacific; and a reappraisal of *Austinograea* Hessler & Martin, 1989 and *Gandalfus* McLay, 2007 (Decapoda, Brachyura, Bythograeoidea). *Zoosystema* 47 (33): 773–797. <https://doi.org/10.5252/zoosystema2025v47a33>. <http://zoosystema.com/47/33>

ABSTRACT

The French multidisciplinary CHUBACARC 2019 cruise in the western Pacific sampled hydrothermal fauna at 18 different vent fields from five vent zones spanning 5000 km and explored the Kulo Lasi Volcano, an area with intense hydrothermal activity. At the periphery of the Kulo Lasi Caldera, a new species belonging to a new genus of bythograeoid crab was collected, here named *Kallograea kulolasi* n. gen., n. sp. *Kallograea kulolasi* n. gen., n. sp. is a small species, being already mature at a carapace width of 12 mm, and having well-differentiated gonopods and vulvae. It possesses several distinctive characters: carapace transversally elliptical and flat; chelipeds elongate, especially the very long and slender merus; major chela with blunt fingers; and a white setal patch on the cheliped propodus, resembling a downy pubescence that covers the superior margin of the cheliped palm and that extends over its inner and outer surfaces. Another species, *Austinograea jolliveti* Guinot & Segonzac, 2018, is provisionally assigned to the same genus. *Kallograea jolliveti* (Guinot & Segonzac, 2018) n. comb. differs by several characters: the second gonopod is relatively much shorter, the epistome is differently structured, the chela has a setal patch that is only present on the inner side of the palm, and there is a distinct coloured spot at the base of the fixed finger. The two congeneric species share the following characters: long chelipeds with elongated and slender meri; major cheliped (crusher) with thick blunt-tipped fingers; male sternopleonal cavity gently concave, relatively wide distally, and without any obvious depression for the tips of G1; G1 almost straight, obliquely directed, not crossing each other along distal parts; and G2 with a flagellum only slightly longer or shorter than the basal part. The vulvae are also rather large in the two species, occupying most of the surface of thoracic sternite 6. Comparison of *Kallograea* n. gen. with other bythograeoids of the western Pacific provided the opportunity to define and illustrate in greater detail the type species of *Austinograea* Hessler & Martin, 1989, *A. williamsi* Hessler & Martin, 1989, endemic to the North Western Pacific, as well as the two known species of *Gandalfus* McLay, 2007. The characters used to separate *Austinograea* and *Gandalfus*, and the taxonomy of the two genera are discussed.

KEY WORDS

Hydrothermal vent crabs,
CHUBACARC 2019,
FUTUNA 1 and 3,
Futuna volcanic Arc,
Austinograea williamsi,
Gandalfus puia,
G. yunohana,
new genus,
new species.

RÉSUMÉ

Kallograea kulolasi n. gen., n. sp., de la caldera du volcan hydrothermal Kulo Lasi, Pacifique Ouest, and *K. jolliveti* (Guinot & Segonzac, 2018); et réévaluation d'*Austinograea* Hessler & Martin, 1989 et de *Gandalfus* McLay, 2007 (Crustacea, Decapoda, Brachyura, Bythograeidea).

La campagne multidisciplinaire française CHUBACARC 2019 dans le Pacifique Ouest a échantillonné la faune hydrothermale de 18 sites hydrothermaux différents dans cinq zones s'étendant sur 5000 km et a exploré le volcan Kulo Lasi, à l'intense activité hydrothermale. À la périphérie de la caldera du volcan Kulo Lasi une nouvelle espèce appartenant à un nouveau genre de Bythograeidae a été récoltée, ici nommée *Kallograea kulolasi* n. gen., n. sp. *Kallograea kulolasi* n. gen., n. sp. est une petite espèce déjà mature avec une largeur de carapace de 12 mm, et avec des gonopodes et des vulves déjà différenciés. Elle possède plusieurs caractères distinctifs : carapace transversalement elliptique, plate; chélipèdes allongés, notamment avec un mérus très long et étroit; grand chélipède, avec des doigts à extrémité émoussée; et une touffe de soies sur le propode du chélipède sous forme d'une pubescence blanche couvrant le bord supérieur de la main et s'étendant de part et d'autre des faces externe et interne. Une autre espèce, *Austinograea jolliveti* Guinot & Segonzac, 2018 est provisoirement attribuée au même genre. *Kallograea jolliveti* (Guinot & Segonzac, 2018) n. comb. se distingue par plusieurs caractères : le second gonopode est relativement plus court, l'épistome est différemment structuré, la pince a une touffe de soies qui est seulement présente à la face interne de la main, et il y a une tache distinctement pigmentée à la base du doigt fixe. Les deux espèces cogénériques partagent les caractères suivants : longs chélipèdes, avec un mérus très allongé et étroit; grand chélipède (broyeur) avec des doigts épais et à bout émoussé; cavité sternopléonale mâle légèrement concave, relativement large distalement, sans dépression marquée pour l'extrémité des G1; G1 presque droit, obliquement dirigé, avec les parties distales de l'un et l'autre ne s'entrecroisant pas; G2 avec un flagelle seulement légèrement plus long ou plus court que la partie basale. Les vulves sont aussi d'assez grande taille chez les deux espèces, occupant la plus grande partie de la surface du sternite 6. La comparaison de *Kallograea* n. gen. avec les autres bythograeoides du Pacifique Ouest nous donne l'opportunité de mieux définir et d'illustrer largement l'espèce type d'*Austinograea* Hessler & Martin, 1989, *A. williamsi* Hessler & Martin, 1989, endémique du Pacifique Nord-Ouest, ainsi que les deux espèces connues de *Gandalfus* McLay, 2007. Les caractères utilisés pour séparer *Austinograea* et *Gandalfus* et la taxonomie des deux genres sont discutés.

MOTS CLÉS

Crabes hydrothermaux,
CHUBACARC 2019,
FUTUNA 1 et 3,
arc volcanique Futuna,
Austinograea williamsi,
Gandalfus puia,
G. yunohana,
nouveau genre,
nouvelle espèce.

INTRODUCTION

Of the 304 active confirmed vent sites/fields listed in the InterRidge Vents Database 3.4 (Beaulieu & Szafranski 2020), 44% are in the western Pacific Ocean, a region of complex tectonic plate interactions where nearly all hydrothermalism occurs on back-arc spreading ridges and volcanic arcs (Ruellan & Lagabrielle 2005; fig. 1; Tunnicliffe *et al.* 2024; fig. 1). Over 90% of all explorations of volcanic arcs over the last decades have shown that intense hydrothermal activity occurs along these back-arc ridges, with a high proportion of submarine volcanoes of island arcs (Fig. 1). In the southwest Pacific, at the southeast of Futuna Island and at the transition between the northern end of the Tonga Trench and the North Fiji fracture zone, tectonic movements are reputed to be the fastest in the world, at 18–24 cm per year. Within a region characterised by a change in the tectonic fabric between a NE-SW oriented volcanic graben and the N-S oriented Alofi ridge (Fig. 2), a broad zone of volcanism takes place.

The French multidisciplinary cruise in the western Pacific, CHUBACARC 2019, endeavoured to sample the fauna at 18 different vent fields from five hydrothermal zones spanning 5000 km (Fig. 1). One of these sites is the Kulo Lasi

Volcano, notably the Kulo Lasi Caldera, which has long-extinct sulphide deposits without high temperature emissions (Hourdez & Jollivet 2023: 6, 41, 56, fig. 53, tables 1, 15, 19, 20). Only one dive with a remotely operated vehicle (ROV), PL729 (Fig. 3) was at the periphery of the Kulo Lasi Caldera, found sporadic faunal patches and collected a few mussels, *Arcovestia* tubeworms, *Ifremeria* snails, and small bythograeoid crabs consisting of five males and one female. These crabs are here recognised as a new genus and new species, *Kallograea kulolasi* n. gen., n. sp.

In fact, it is during regional mapping by the FUTUNA 1 cruise in 2010, with the R/V *Atalante* and the manned submersible *Nautille* (<https://doi.org/10.17600/10010110>) or the autonomous underwater vehicle (AUV) *Idef-X*, to explore the French Exclusive Economic Zone (EEZ) (Fouquet *et al.* 2015), that a volcano with an intense hydrothermal activity was discovered in the centre of this vast volcanic zone. The major target of FUTUNA 1, as well that of the FUTUNA 3 cruise in 2012 (Fig. 3), was the investigation of the Kulo Lasi Volcano and its caldera (Fouquet *et al.* 2015, 2018; Konn *et al.* 2016: figs 1, 6; Szitkar *et al.* 2020: figs 1, 2, 6A). In the southwestern sector of the caldera, the biota was particularly dense and varied, with various sessile and motile organisms, including large clusters of siboglinid

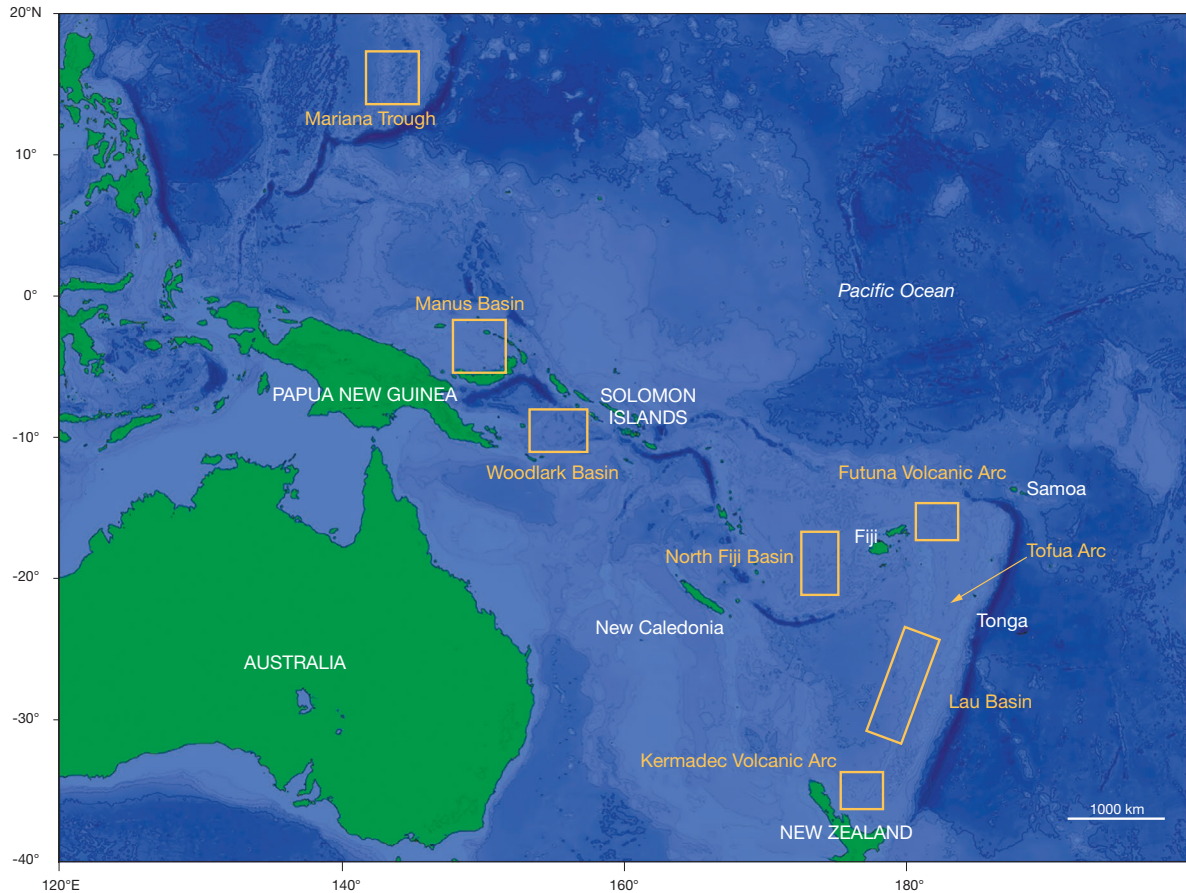


FIG. 1. — Map of the five hydrothermal areas of the Western Pacific explored by the Chubacarc 2019 Cruise, with sampling locations (yellow rectangles): Lau Basin, North Fiji Basin, Futuna Volcanic Arc (see Pelletier *et al.* 2017), Woodlark Basin, and Manus Basin. The Mariana Trough (see Hessler & Lonsdale 1991) and Kermadec Volcanic Arc have been added. Courtesy Stéphane Hourdez.

worms, shrimps, and galatheids. Brachyuran crabs were found associated with tubeworms in an area of diffuse venting in the southwestern sector of the caldera wall (Fouquet *et al.* 2018: 322, fig. 10D).

The FUTUNA 1 2010 cruise had collected two small brachyuran specimens at the periphery of the Kulo Lasi Caldera, a young male (MNHN-IU-2009-4046) and a small female (MNHN-IU-2018-5226), first identified as *Austinograea* sp. by M. Segonzac and deposited in the MNHN: they remain unidentifiable. Another specimen (MNHN-IU-2009-4045) collected by the FUTUNA 1 cruise by the same dive and exactly in the same place of the Kulo Lasi Caldera, but not examined by the first author at the time of the study of Guinot & Segonzac (2018), belongs to *Austinograea jolliveti* Guinot & Segonzac, 2018, which is known from the North Fiji Basin and Lau Back-Arc Basins (Guinot & Segonzac 2018: 89, figs 9A-H, 10A-E, 11A-E). Three other specimens collected by the FUTUNA 3 cruise, from station PL06 in the Kulo Lasi Caldera (MNHN-IU-2024-6075), previously preserved at the IFREMER and not previously examined by the present authors, were recently sent to the MNHN where they are now deposited (MNHN-IU-2024-6075).

They belong to the same species, *A. jolliveti*. Comparisons with *Kallograea kulolasi* n. gen., n. sp. revealed that they are two distinct species but should both be referred, although with some reservation, to the same new genus *Kallograea* n. gen., distinct from *Austinograea* Hessler & Martin, 1989. *Kallograea jolliveti* (Guinot & Segonzac 2018) n. comb. is therefore also present in the volcanic arc of Futuna, Kulo Lasi, like *K. kulolasi* n. gen., n. sp.

The CHUBACARC 2019 campaign did not find *Kallograea jolliveti* n. comb. in the Kulo Lasi volcanic area, but collected it further away, in the Manus Basin, northern New Britain, Papua New Guinea (Fig. 1), which occupies a back-arc position relative to the New Britain arc-trench system and contains an active plate boundary (Ross *et al.* 1986). Therefore, in addition to its original collection location, *K. jolliveti* n. comb. appears to be present in two relatively distant regions: the Kulo Lasi Volcano and the Manus Basin (MNHN-IU-2024-6026 and MNHN-IU-2024-6551). The Pac Manus Vent Field extends over a large area and consists of sites with different levels of activity (Hourdez & Jollivet 2023: 63, 160, with a figure showing crabs).

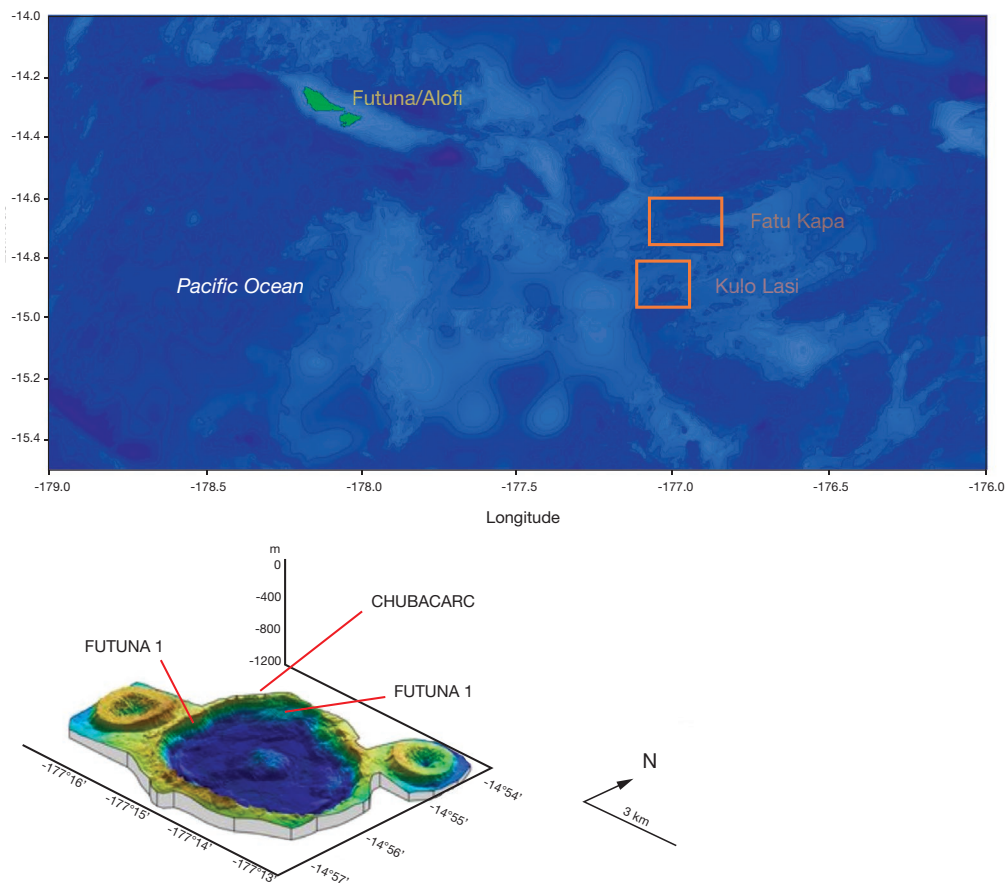


FIG. 2. — Location of the Alofi Ridge in the Futuna area, the Fatu Kapa hydrothermal field (explored by the CHUBACARC 2019 cruise) and the Kulo Lasi Volcano (indicated by **red rectangles**), showing depths of the various locations. Composite figure including the high-resolution bathymetry modified after Konn *et al.* (2016). Courtesy Stéphane Hourdez.

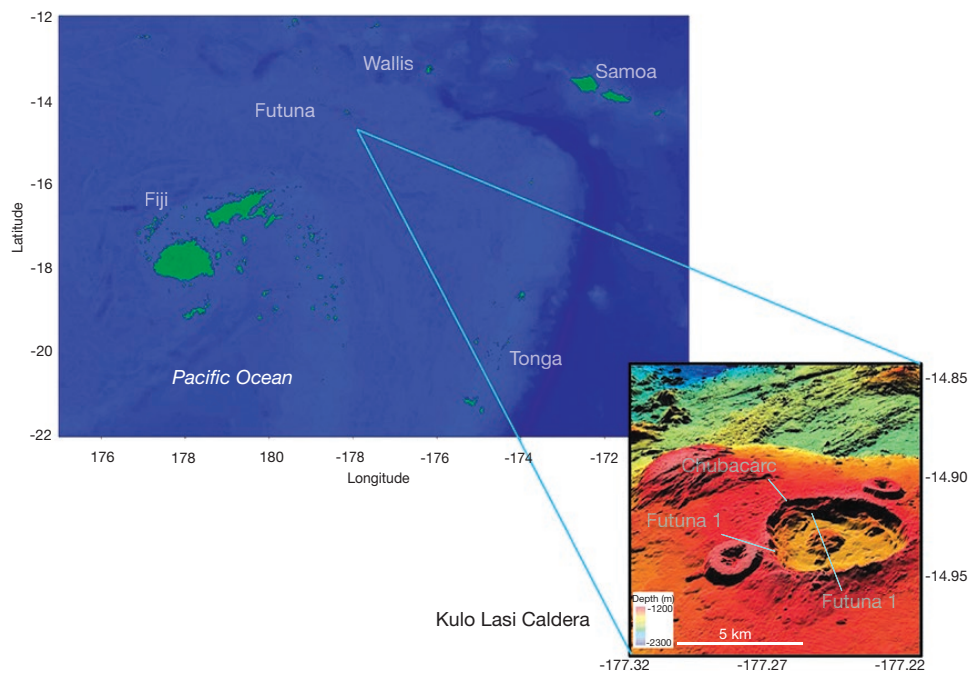


FIG. 3. — Visualisation of the Wallis and Futuna volcanic areas, especially the Kulo Lasi volcanic area and its caldera, with the sampling locations of the FUTUNA 1 (two sites) and CHUBACARC 2019 cruises. Composite figure including the high-resolution bathymetry modified after Sztikar *et al.* (2020). Depths coloured as: **red**, 1200-1500 m; **green**, 1500-1800 m; **blue**, 1800-2300 m. Courtesy Stéphane Hourdez.

THE GEOGRAPHY OF THE LOCATIONS OF THE MATERIAL STUDIED

Located around 100 km southeast of Futuna Island and at a water depth of 1500 m, Kulo Lasi is a shield volcano 20 km diameter with numerous active and inactive hydrothermal fields on the floor and walls of the caldera. It represents the most recent volcanic episode in the Futuna area. The roughly circular caldera, 5 km in diameter, which exhibits a flat bottom, with the top located at a depth of 1200 m and the base only 400 m deeper (c. 1600 m below sea level), is covered by recent lava flows and a central mound composed of older tectonic lava flows (Konn *et al.* 2016: figs 1, 6; Sztikar *et al.* 2020: figs 1, 2, 6A). The south-western sector of the caldera (Fouquet 2018: 321, figs 9, 10D, 13), with a depth of 1418 m and a temperature less than 6°C, was characterised by a dense and varied biota. In the north-western and eastern sectors of the caldera, with active black smoker chimneys located on the floor and in areas of diffuse venting, marine organisms were also abundant, i.e., only motile animals such as fish, shrimps, galatheids, and brachyurans crabs. During this first cruise and during the FUTUNA 3 cruise in 2012, diving operations with the manned submersible *Nautille* revealed the presence of organisms inside the caldera.

The CHUBACARC 2019 cruise in the western Pacific, on board of the R/V *Atalante* and the remotely operated vehicle (ROV) *Victor 6000*, sampled the fauna in five hydrothermal zones: Lau Basin, Futuna volcanic Arc, North Fiji Basin, Woodlark Basin, and Manus Basin (Boulart *et al.* 2022; Hourdez & Jollivet 2023) (Fig. 1). The aim was to understand the biodiversity in each zone so as to ascertain the degree of connectivity of species within and between the basins. One of the studied sites was the periphery of the Kulo Lasi Caldera, a long-extinct formation with sulphide deposits and without high temperature emissions (Hourdez & Jollivet 2023: 6, 41, 56, fig. 53, tables 1, 15, 19, 20). The Lau and North Fiji Basins had in fact been explored earlier by the French-Japanese STARMER 2 cruise in 1989 (chief scientist: Daniel Desbruyères, R/V *Nadir*, manned submersible *Nautille* <https://doi.org/10.17600/89003312>) while the American expedition MGLN07MV in 2006 (chief scientist: C. R. Fisher, R/V *Melville*, manned submersible *Jason II*) explored the Lau Back-Arc Basin (see Guinot & Segonzac 2018: tables 1, 2).

MATERIAL AND METHODS

ABBREVIATIONS

Institutions

IFREMER	Institut français de recherche pour l'exploitation de la mer, Plouzané;
JAMSTEC	Japan Marine Science Technology Center, Yokohama;
MNHN	Muséum national d'Histoire naturelle, Paris;
NIWA	National Institute of Water and Atmospheric Research, Auckland;
ZRC	Zoological Reference Collection, Lee Kong Chian Natural History Museum, National University of Singapore.

Morphology

G1	male first pleopod;
G2	male second pleopod;
Mxp3	external or third maxilliped;
P2–P5	pereopods 2–5 (first to fourth ambulatory legs, respectively).

Equipment

ASPI	undersea suction collector;
AUV	autonomous underwater vehicle;
DSS	deep-sea manned submersible;
GBT	large collection box ('grande boîte de collecte');
PI	diving operations;
ROV	remotely operated vehicle;
R/V	research vessel;
Stn	station.

Genetics

CHU	research code for DNA sequencing.
-----	-----------------------------------

For the list of stations of the CHUBACARC 2019 cruise, see Hourdez & Jollivet (2019) <https://doi.org/10.17600/18001111>

COMPARATIVE MATERIAL

Austinograea williamsi Hessler & Martin, 1989: **Paratypes. Western North Pacific** • 1 ♂ (21.6 × 34.2 mm), 1 ♀ (22.5 × 35.3 mm), 1 small ♂ (15.2 × 23.8 mm); dive 1845; Alice Springs vent field; 3640 m; 6.V.1987; 18°12.599'N, 144°42.431'E; MNHN-IU-2008-11121 (= MNHN-B20910).

Austinograea hourdezi Guinot & Segonzac, 2018: **Paratypes. Western Pacific** • 1 ♂ (21.4 × 34.3 mm); dive 232, Tu'i Malila site; Lau Back-Arc Basin; 1891 m; 11.IX.2006; 21°59.34'S, 176°34.09'W; MNHN-IU-2016-10740 • 1 ♀; dive 427, ABE site, Lau Back-Arc Basin; 2130 m; 7.IX.2009; 20°45.65'S, 176°11.45'W; MNHN-IU-2016-10744.

Austinograea alayseae Guinot, 1990: **Western Pacific** • 1 ♂, 1 ♀; western Pacific: TUIM06MV cruise; dive PL142, slurp 1, Lau Basin, Cam Tow; 2719 m; 19.V.2005; 20°19'S, 176°08'W; ZRC 2024.0727, ex MNHN-IU-2022-4049.

Gandalfus puia McLay, 2007: **Western Pacific** • holotype ♂ (15.5 × 24.3 mm); stn TAN0107/128; Rumble III; 35°44.22–44.04'S, 178°29.72–29.63'E; 270–239 m; 21.V.2001; NIWA 27855 • 1 paratype ♂ (21.3 × 33.5 mm); Macauley Caldera, Kermadec Islands; 337 m; 12.IV.2005; 30°12.78'S, 181°33.04'E; NIWA 18017 • 1 paratype ♂ (22.9 × 36.4 mm); Brothers Seamount, dive KOK0506/32; 1647 m; 2.V.2005; 34°51.70'S, 179°3.58'E; NIWA 18019 • 1 ♂ (22.6 × 36.7 mm) [coated with a brown ferric deposits, slightly damaged], 1 ♂ (11.6 × 18 mm); Kermadec Islands, Macauley Caldera, stn KOK0506/22; 337 m; 12.IV.2005; 30°12.78'S, 181°33.04'E; NIWA 18018 • 1 ♂ (entirely white) (18.8 × 29.0 mm); stn TAN1213/59; 405.0–408 m; 26.X.2012; NIWA 86453 • 1 ♂, 6 ♀ [1 ♀ 10.4 × 14.3 mm, ZRC 2024.0726]; Haungaroa Caldera; HYDROTHERMADEC cruise; dive 413; stn 026; 707 m; 31.XII.2016; 32°37.04'S, 179°37.51'E; MNHN-IU-2024-6553 (ex SH162-065).

Gandalfus yunohana Takeda, Hashimoto & Ohta, 2000: **Western Pacific** • 1 ♀ (28.2 × 42.2 mm); off central Japan, Philippine Sea Plate, Kaikata Seamount, *Shinkai 2000*, dive #1014; 26°42.35'N, 141°04.67'E; 448 m deep; 18.V.1998; MNHN-IU-2024-6053 (= MNHN-B28759) (ex JAMSTEC) • 1 ♀ (43.4 × 28.4 mm); same data; MNHN-IU-2024-6054 (= MNHN-B28759) (ex JAMSTEC) • 1 ♂ (20.5 × 29.9 mm); same data; MNHN-IU-2024-6055 (= MNHN-B28759) (ex JAMSTEC) • paratype ♂ (20.5 × 29.9 mm); off central Japan, Philippine Sea Plate, Myojin Knoll, *Shinkai 2000*, dive # 1007, 32°06.19'N, 139°52.04'E, 1263 m deep, 5.V.1998; MNHN-IU-2008-11865 (= MNHN-B28419).

SYSTEMATICS

Section EUBRACHYURA Saint Laurent, 1980
 Subsection HETEROTREMATA Guinot, 1977
 Superfamily BYTHOGRAEOIDEA Williams, 1980 *sensu lato*
 Family BYTHOGRAEIDAE Williams, 1980 *sensu lato*

Kallograea n. gen.

[urn:lsid:zoobank.org:act:4AA24DD0-6035-4ED5-8075-54ECFABE95E6](https://doi.org/10.21203/rs.3.rs-3111111/v1)

TYPE SPECIES. — *Kallograea kulolasi* n. sp., by present designation.

OTHER INCLUDED SPECIES. — *Austinograea jolliveti* Guinot & Segezac, 2018 (see below).

ETYMOLOGY. — The name is derived from the Greek “*kallo*” for “beautiful”, and the name for marine crabs “*graea*” (cf. Liddell & Scott 1940); alluding to the slender and delicate chelipeds of the two constituent species. The gender is feminine.

DIAGNOSIS. — Carapace transversely elliptical. Dorsal surface of carapace almost flat; regions indistinct. Eyestalk absent, podophthalmite fused to floor of orbital region; cornea absent, no visible pigment. Antennules, antennae recessed under front. Mxp3 ischium distinctly elongate; merus subtriangular, distally produced. Adult male chelipeds prominently elongate; merus long, slender; palm elongated (especially in *K. kulolasi* n. sp.), with setal patch either exclusively on inner surface and between fingers of both chelipeds (*K. jolliveti* n. comb.) or on either side of superior margin (including the superior margin itself), thus on both sides of palm and extending between fingers (*K. kulolasi* n. sp.); crusher with thick blunt-tipped fingers. No spot on anterior portion of palm near base of dactylus, but coloured spot at base of fixed finger (*K. jolliveti* n. comb.). Adult male ambulatory legs slender, elongate, especially merus, propodus. Thoracic sternum short, wide. Male sternopleonal cavity gently concave, relatively wide distally, but without obvious depression for G1 tips. Longitudinal median line along entire male and female thoracic sternite 8, deep. G1 almost straight, obliquely directed, not crossing each other along distal parts. G2 either rather long, with the flagellum slightly longer than basal part, or shorter and with a small flagellum. Vulvae relatively large, occupying most of surface of thoracic sternite 6.

REMARK

The genera closest to *Kallograea* n. gen. are *Austinograea* Hessler & Martin, 1989 and *Gandalfus* McLay, 2007, for which we deem necessary to give detailed illustrations of the species for comparisons of these two genera with the new genus established here; see below.

Kallograea kulolasi n. sp. (Figs 4–7)

[urn:lsid:zoobank.org:act:8E69D842-1647-45A5-8EB9-AC968353F769](https://doi.org/10.21203/rs.3.rs-3111111/v1)

TYPE MATERIAL. — **Holotype.** Western Pacific • ♂ (right-handed) 7.3 × 12.7 mm; CHUBACARC 2019 cruise, Leg 1; Futuna Volcanic Arc, Kulo Lasi Caldera; 15°10.0692'S, 14°42.9563', 177°28.4632', 177°00.5768'W (latitude minimum/maximum and longitude minimum/maximum, respectively); PL729 - GBT1; 1472 m; MNHN-IU-2024-6067.

Paratypes. Western Pacific • 1 ♂ (right-handed) 7.5 × 12.0 mm; same data as holotype; MNHN-IU-2024-6084 • 1 ♂ 9.7 × 15.4 mm (without chelipeds); MNHN-IU-2024-6035 [CHU 036] • 1 ♀ 8.1 × 12.6 mm (with detached chelipeds in tube); MNHN-IU-2024-6033 • 1 ♂ 9.6 × 16.4 mm; MNHN-IU-2024-6552 [CHU 035] • 1 ♂ (left-handed) 8.8 × 14.1 mm; ZRC 2024.0724 (ex MNHN-IU-2024-6085).

TYPE LOCALITY. — Kulo Lasi Caldera, on periphery.

ETYMOLOGY. — Named after the Kulo Lasi Volcano where the species was discovered. Kulo lasi is a common name meaning ‘big cauldron’ in Futunian. Used as a noun in apposition.

DESCRIPTION

Carapace

Small size (carapace width 12.0–16.4 mm). Carapace elliptical, very short, very elongated transversely, width-to-length ratio 1.59–1.74, flat; regions indistinct (Figs 4A, C; 5A; 6A). Dorsal surface entirely smooth, glabrous (Figs 4A, C; 5A; 6A). Anterolateral margin regularly rounded, with minute, barely discernible granules; supra-orbital margin with more obvious granules (Figs 4A, C, E; 5A, C; 6A, E). Posterolateral margins convergent posteriad; posterior margin slightly concave (Figs 4A, C; 5A; 6A). Subhepatic regions entirely glabrous (Figs 4E; 5B, C; 6E). Front broad, not protruded, practically straight, not emarginate medially, barely pointed medially, with two indistinct lobes; margin without discernible granules (Figs 4A, C, E; 5A; 6A, E). Infra-orbital region with scattered small granules (Figs 4E; 6E). Eyes, antennules, antennae recessed below front (Figs 4E; 6E). Orbit not delimited; orbital region extending as groove, lateral to area with vestigial eyestalks and antennae (Figs 4E; 5A, C; 6E). Eyestalk absent; podophthalmite barely visible, as small fixed piece fused to floor of orbital region; cornea absent but a tiny dark pigment barely visible (Figs 4E; 5A, C; 6E). Antennules folded horizontally (Figs 4E; 5C; 6E). Antenna very small; urinary article fixed, recessed; basal article (2 + 3) cylindrical, moveable; article 4 slightly elongated, inclined; flagellum not long. Proepistome very thin (Figs 4E; 5C, E; 6E). Posterior margin of epistome wide, with lateral margins distinctly concave, median projection obtusely triangular (Figs 4E; 6E). Pterygostomial lobe with small granules; pterygostomial region smooth (except minute granules along lateral line), glabrous, except along lateral line (Figs 4E; 5B, C; 6E).

Mxp3

Mxp3 completely closing buccal cavity, on all parts, especially between antero-external margin of merus and pterygostomial lobe. Ischium long, external margin oblique; longitudinal internal groove weak. Merus: external margin proximally straight, then obliquely directed; distal and external margins almost touching pterygostomial lobe; merus distal part markedly narrow, produced; internal margin bluntly angled medially. Carpus inserted on distal part of antero-internal margin of merus; propodus thick, short; dactylus long, reaching about three-quarters length of ischium; inner margins of propodus and dactylus with brush-like setae. Mxp3 coxa with only proximal portion visible, lateral projection hidden by junction

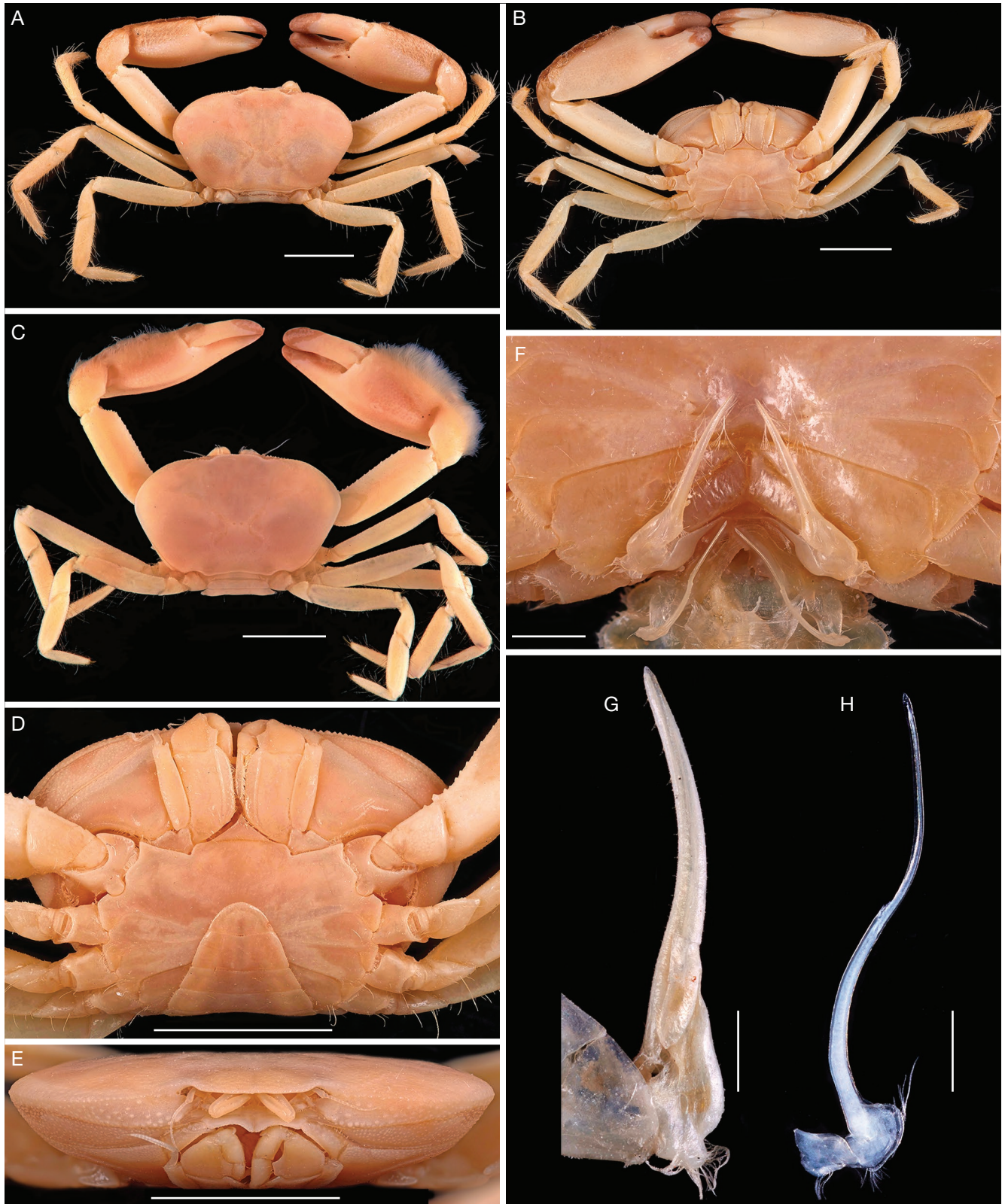


FIG. 4. — *Kallograea kulolasi* n. gen., n. sp. **A, B, D-H**, holotype, ♂ 7.3 × 12.7 mm, Futuna Volcanic Arc, Kulo Lasi Caldera (MNHN-IU-2024-6067); **C**, paratype, ♂ 7.5 × 12.0 mm, Futuna Volcanic Arc, Kulo Lasi Caldera (MNHN-IU-2024-6084): **A, C**, dorsal habitus (**C**, see prominent down-like pubescence on chelae); **B**, ventral habitus; **D**, buccal cavity, thoracic sternum and pleon, ventral view; **E**, frontal view of cephalothorax; **F**, sternopleonal cavity showing gonopods, ventral view; **G**, right G1, dorsal view; **H**, right G2. Scale bars: A-E, 5 mm; F, 1 mm; G, H, 0.5 mm. Credits: MNHN-Soubzmaigne.

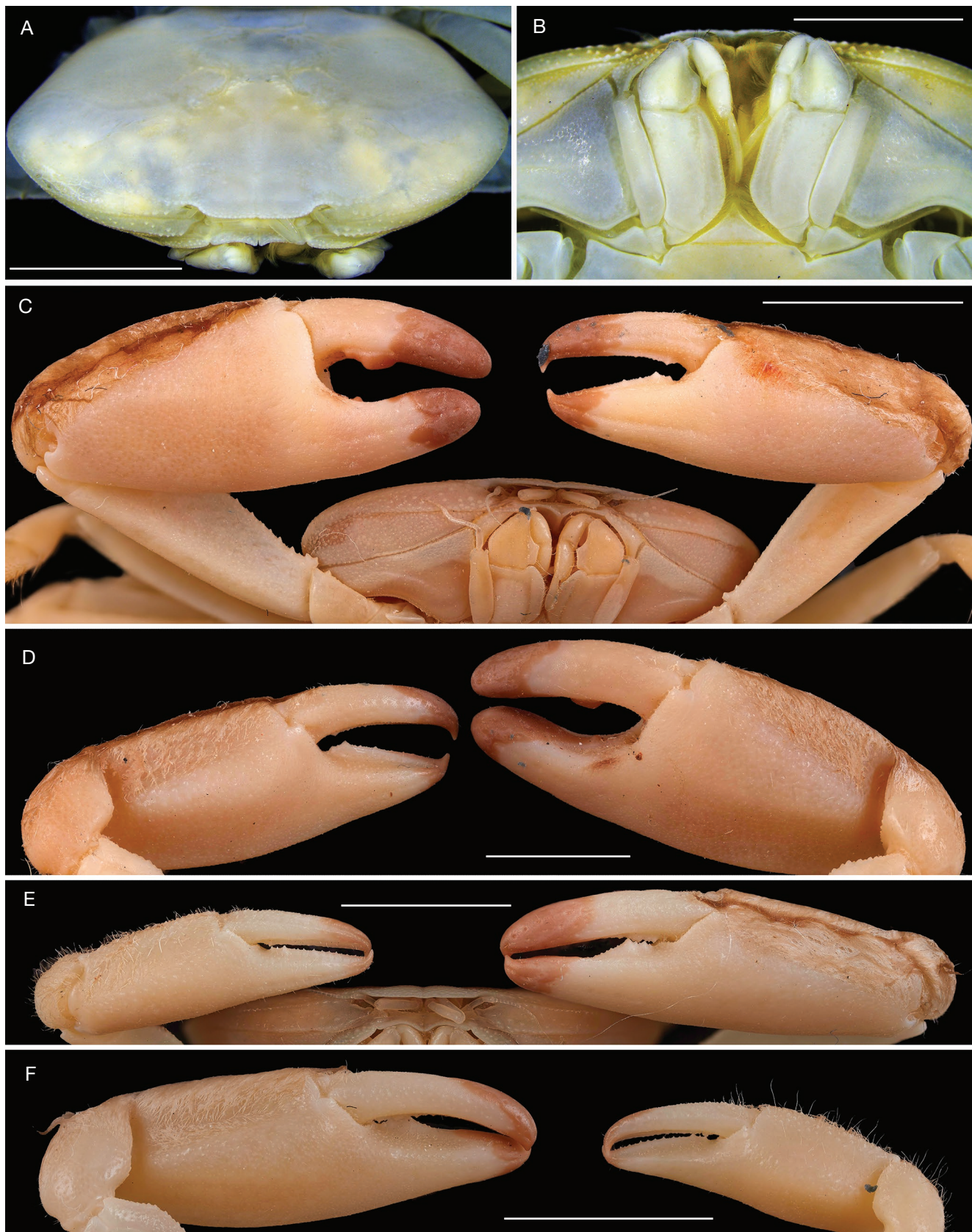


FIG. 5. — *Kallograea kulolasi* n. gen., n. sp. **A, B, E, F**, paratype, ♂ 8.8 × 14.1 mm, Futuna Volcanic Arc, Kulo Lasi Caldera (ZRC 2024.0724, ex [MNHN-IU-2024-6085](#)); **C, D**, [MNHN-IU-2024-6067](#), holotype, ♂ 7.3 × 12.7 mm, Futuna Volcanic Arc, Kulo Lasi: **A**, anterodorsal view of carapace; **B**, buccal cavity and mxp3, ventral view; **C, E**, outer view of chelae; **D, F**, inner view of chelae. Scale bars: 5 mm. Credits: C-F, MNHN-Soubzmaigne.

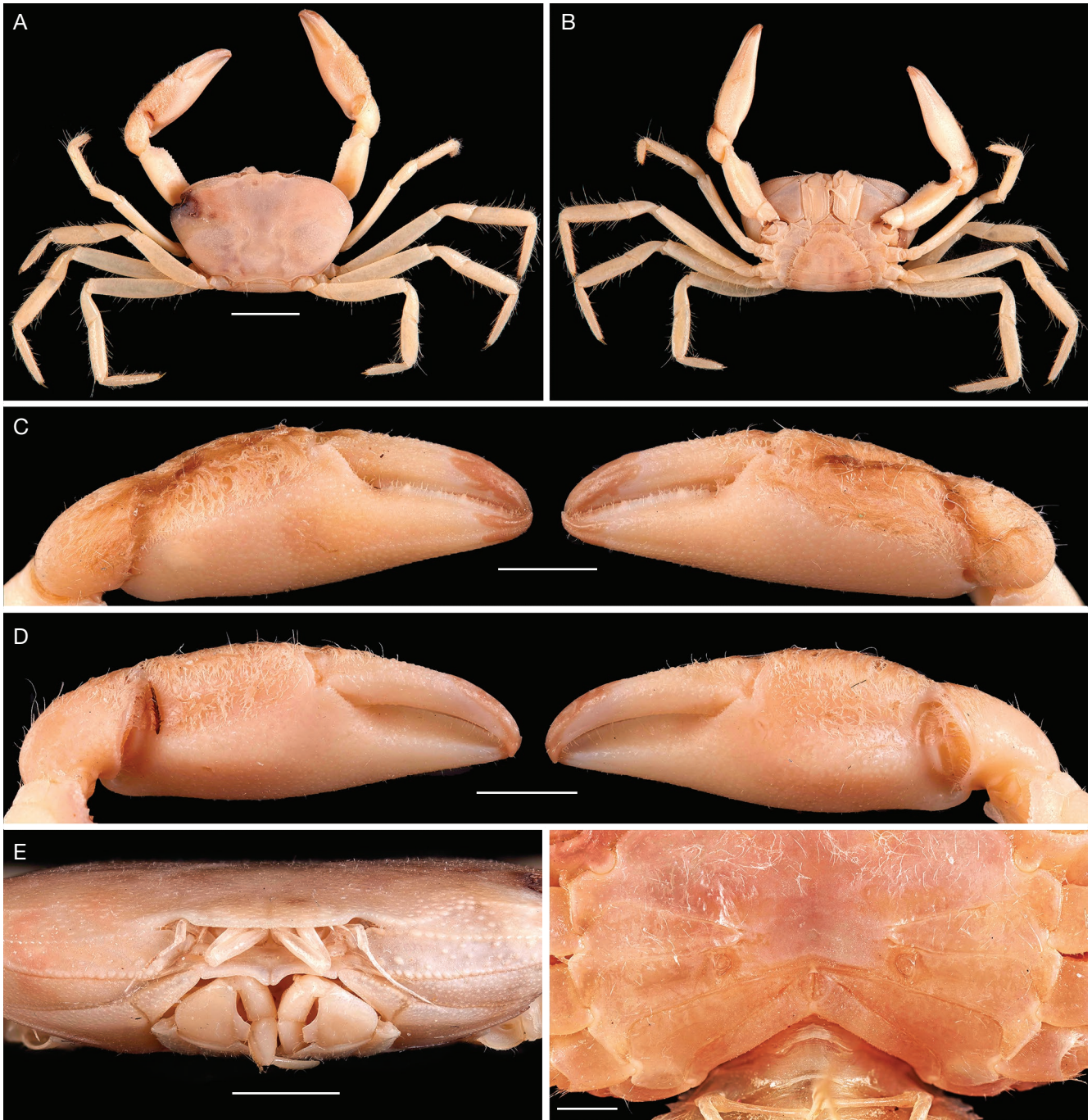


FIG. 6. — *Kallograea kulolasi* n. gen., n. sp., paratype, ♀ 8.1 × 12.6 mm, Futuna Volcanic Arc, Kulo Lasi Caldera (MNHN-IU-2024-6033): **A**, dorsal habitus; **B**, ventral habitus; **C**, outer view of chelae; **D**, inner view of chelae; **E**, frontal view of cephalothorax; **F**, sternopleonal cavity showing vulvae, ventral view. Scale bars: A, B, 5 mm; C-E, 2 mm; F, 1 mm. Credits: MNHN-Soubzmaigne.

of thoracic sternum (sternite 4) with pterygostome. Exopod thick, longer than endopod ischium (Figs 4D, E; 5B; 6E).

Male chelipeds

Male chelipeds elongate, not clearly heteromorphic (weak heterochely in females, see below) (Figs 4A-C; 5C-F). Merus very long, slender, extending far beyond margin of carapace, subcylindrical, triangular in cross section, anterior border straight (without expansion), with regularly spaced small

granules. Carpus covered with thick patches of thin soft setae on whole external surface; propodus of both chelipeds very long, with superior margin covered by thick patches of thin soft setae, appearing as a white down-like pubescence (Fig. 4C) (more developed on major chela), partially extending on both outer and inner parts of palm (more on inner part) and extending partially to basal part of dactylus. Fingers distinctly shorter than palm, with dark colour extending along distal third- or quarter-length; no setae along occluding margins.

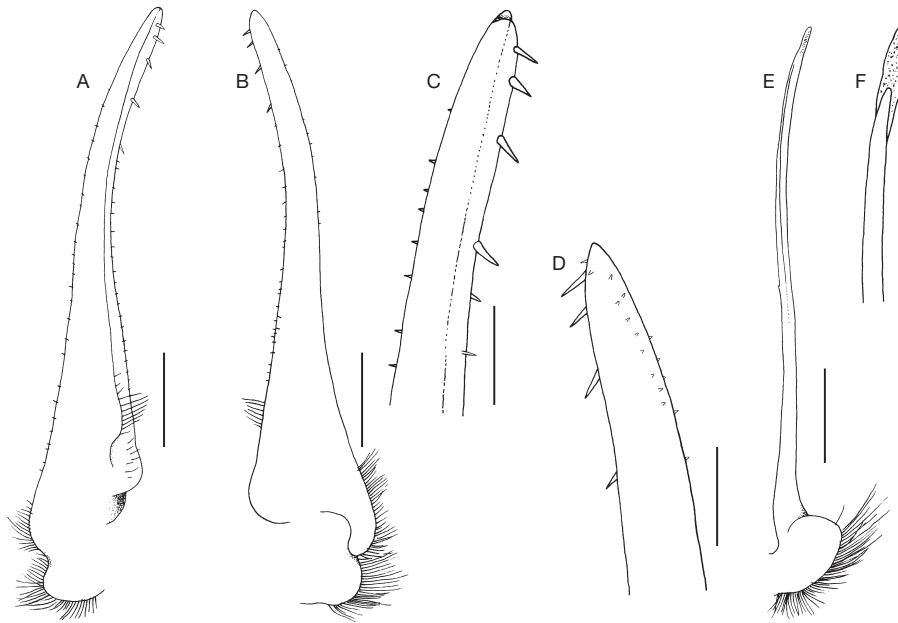


FIG. 7. — *Kallograea kulolasi* n. gen., n. sp., paratype, ♂ 8.8 × 14.1 mm, Futuna Volcanic Arc, Kulo Lasi Caldera (ZRC 2024.0724, ex MNHN-IU-2024-6085). Gonopods: **A**, right G1 (ventral view); **B**, right G1 (dorsal view); **C**, distal part of right G1 (ventral view); **D**, distal part of right G1 (dorsal view); **E**, right G2; **F**, distal part of right G2. Scale bars: A, B, E, 0.5 mm; C, D, F, 0.2 mm.

No obvious spot at base of propodus. Dark pigmentation on fingers not extending to palm, confined to tips in males (as in females) (Fig. 5C-E).

In right-handed males (like holotype), major cheliped (crusher) stouter, slightly shorter than minor chela (cutter); both fingers very thick, distinctly blunt-tipped, weakly gaping; dactylus with small tooth, then molariform tooth on occluding margin; fixed finger thick, with some small denticles on occluding margin; dark colour extending dorsally on only distal part of fingers. Minor cheliped (cutter) with finger tips pointed. Merus as in major chela; palm rather long, outer surface slightly convex, smooth; both fingers not gaping at occluding margin, both tips curved, crossed; dactylus elongate, with occluding margin lined with some minute proximal teeth; fixed finger very thick, with thin extension bearing nearly straight occluding margin, with some small proximal teeth (Figs 4A, B; 5C, D).

In left-handed male (e.g., ZRC 2024.0724, ex MNHN-IU-2024-6085), chelae less developed; fingers of major chela much stouter than pointed fingers of minor chela; both fingers relatively thinner, only very weakly gaping, less blunt-tipped, slightly curved at tip; minor chela elongated, with less dense patch of thin soft setae on superior margin; fixed finger regularly toothed (medially granular in left-handed males) (Fig. 5E, F).

Female chelipeds

Female chelipeds (♀ 8.1 × 12.6 mm mm, MNHN-IU-2024-6033) not as developed as those of males, with merus distinctly shorter and narrower than in males (Fig. 6A, B). Chelae slightly heteromorphic, not blunt-tipped, with both

fingers not gaping, crossing at tips; major chela only a little stouter as minor chela. As in males, patches of thin soft setae, appearing as down-like pubescence, on superior margin of carpus, propodus, extending on both outer and inner part of palm. Dark pigmentation of fingers in most part confined to tips (as in males) (Fig. 6C, D).

Ambulatory legs

P2-P5, in particular meri, distinctly long, slender. P2 much shorter than chelipeds; P3, P4 longest. Merus of P2-P4 smooth, without patches of setae, only with a few sparse setae; carpus, propodus and dactylus of P2-P5 with sparse setae on ventral margins (Figs 4A-C; 6A, B).

Thoracic sternum

Thoracic sternum very wide, short, extending laterally, elliptical; suture 2/3 complete; sutures 4/5-7/8 incomplete; sutures 6/7 and 7/8 medially less calcified (Fig. 4D, F). Junction of sternite 4 with pterygostome represented by only short juxtaposition, without patch of setae. Median line at level of sternite 8 in both sexes, reaching to junction with sternite 7 (Fig. 4F). In males, press-button of locking mechanism acute, on sternite 5 abutting against suture 5/6 (Fig. 4F). Entirely smooth, glabrous in both sexes (Figs 4D, F; 6B, F).

Pleon

Both sexes with six free somites and telson. Male pleon rather wide, regularly triangular; pleonal somite 3 widest; pleonal somite 6 longest; telson very short, bluntly semicircular (Fig. 4B, D). Press-button on narrow portion of sternite 5, absent in females (Fig. 4F).

Female pleon almost round, covering most of thoracic sternites; telson semicircular (Fig. 6B).

Gonopods

G1 almost straight, directed obliquely into sternopleonal cavity, never contiguous, and even distant throughout their entire length, including their tips which are apart, not recessed in medial depression at end of sternopleonal cavity. Only some setae along mid distal part (Figs 4G; 7A-D). G2 relatively long, flagellum slightly longer than basal part, curved, blade-like, distal part slightly dilated (Figs 4H; 7E, F).

Vulvae

Vulvae distant from each other, subhemispherical; close to but separate from thoracic sternal suture 5/6, occupying 2/3 of surface of sternite 6 (Fig. 6F).

REMARKS

Five males and one female of *Kallograea kulolasi* n. gen., n. sp., all small specimens, have been collected by the French CHUBACARC 2019 cruise on the periphery of the caldera of Kulo Lasi Volcano, through a unique dive in the north sector (Figs 2; 3). Immediately suspected of being new by Stéphane Hourdez (pers. comm.), they are here confirmed to represent an undescribed species.

Kallograea kulolasi n. gen., n. sp. is a small-sized species, however, with well-developed gonopods and vulvae. It is also the smallest bythograeid known in the world. The smallest bythograeid previously was *Bythograea microps* Saint Laurent, 1984 (Saint Laurent 1984: 356) from the East Pacific Rise (between 21°N and 9°50'N), which is indicated as having a maximum carapace width 40 mm according to Guinot & Segonzac (2006b: 468), but it seems that this size may be overestimated: the male collected during the Hot 96 mission measuring 13 × 24 mm likely represents the largest *B. microps* known to date (Guinot & Segonzac 1997: 139; Guinot & Hurtado 2003: 437). *Kallograea kulolasi* n. gen., n. sp. is distinctly smaller, with specimens measuring 12 mm in carapace width already mature (e.g., MNHN-IU-2024-6084).

Kallograea kulolasi n. gen., n. sp. is characterised by a flat carapace, the males possessing distinctly elongate chelipeds, with especially blunt fingers on the major chela, and a prominent setal patch on the propodus that appears as a white down-like pubescence on the superior margin of the cheliped palm and extending on the inner and outer surfaces. This pubescence is best observed in water or ethanol, as the setae collapse and clump together when the specimen is studied dried (compare Fig. 4C with Fig. 5E, F). Since in most *Austinograea* species the setal patch is exclusively located on the inside of the palm, its presence on either side of the upper palm margin is a unique feature of *K. kulolasi* n. gen., n. sp. A setal patch is also present over the entire external surface of the carpus, which is not found in other bythograeids, which have a glabrous carpus instead. The markedly thick and blunt-tipped fingers of the crusher cheliped is also a remarkable character of *K. kulolasi* n. gen., n. sp. The condition of these finger tips is unusual and perhaps functions similarly to the spoon-tipped fingers

of other crabs. As indicated by Davie *et al.* (2015), not much is known about the precise function of spoon-tipped fingers, but they seem to be generally used for feeding on detritus, scooping up mucus from corals or picking up other soft foods, scraping off encrusting algae, effective gripping of filamentous algae, or scraping epilithic algae off coral rock. The rounded finger tips of the major chelae of *K. kulolasi* n. gen., n. sp. may be adapted for harvesting the filamentous bacterial matter in its habitat.

The palm and fingers of male adult chelipeds appear very heavy relative to the long and slender merus, in which the apodemes and attached muscles have little room, and together with the flat carapace, gives the crab a very distinctive appearance. Male *Kallograea kulolasi* n. gen., n. sp. clearly prioritises investing in strong chelipeds but in females, the chelipeds are proportionately shorter and the chelae are less strongly developed. This marked sexual dimorphism suggests the male chelipeds may have a role in reproductive selection.

DISTRIBUTION

Known only from the Futuna volcanic Arc, on the periphery of the Kulo Lasi Caldera.

Kallograea jolliveti (Guinot & Segonzac, 2018) n. comb.
(Figs 8; 9)

Austinograea jolliveti Guinot & Segonzac, 2018: 89, figs 9A-H, 10A-E, 11A-E.

MATERIAL EXAMINED. — **Holotype.** Western Pacific • ♂ 12.8 × 20.0 mm (right-handed); North Fiji Basin; STARMER II cruise, dive 18 (PL 18); Mussel Valley site; 18°50'S, 173°29'E; 2750 m; 3.VII.1989; MNHN-IU-2016-10769.

Paratypes. Western Pacific • 1 ♂ (slightly right-handed) 14.7 × 25.4 mm, 1 ♀ 12.4 × 21.6 mm; same data as for holotype; MNHN-IU-2016-10770.

OTHER MATERIAL. — **Western Pacific** • 1 ♀ 13.6 × 22.0 mm (left-handed); Lau Back-Arc Basin; MGLN07MV cruise, dive 237; ABE site; 20°45.65'S, 176°11.45'E; 2130 m; 25.IX.2006; MNHN-IU-2016-10751.

NEW MATERIAL. — **Western Pacific** • 1 ♂ 14.3 × 22.7 mm (slightly left-handed), Futuna 1 cruise, Kulo Lasi, PL1776-4 – aspi 4; 14°56.35'S, 177°15.57'W; 1406 m; 12.IX.2010; L. Menot coll.; R/V *Atalante*; ROV *Nautil*; M. Segonzac 06.2011 det. *Austinograea* sp.; ZRC 2024.0725 (MNHN-IU-2009-4045) • 2 ♂ 8.0 × 13.4 mm, 9.0 × 12.4 mm, 1 ♀ 8.4 × 13.8 mm (most of legs and chelipeds detached), Futuna 3 cruise, PL06 – aspi 04; MNHN-IU-2024-6075 • 1 ♀ 13.5 × 20.0 mm, CHUBACARC cruise, PL734 - GBT2, Manus Basin, Pac Manus, Roman's Ruins; 03°43'649, 151°40'861; 1725 m; MNHN-IU-2024-6026 [CHU 511] • 1 ♂ 12.2 × 16.8 mm (right-handed); CHUBACARC cruise, PL733 - GBT5; Manus Basin, Pac Manus, Fenway; MNHN-IU-2024-6551.

REMARKS

See description by Guinot & Segonzac (2018: 89, figs 9A-H; 10A-E; 11A-E) and remarks on *K. kulolasi* n. gen., n. sp.

In *Kallograea jolliveti* n. comb., the pigmented spot near the base of the fixed finger and more or less in continuity with the dark colour of the fixed finger, and present on both chelae in

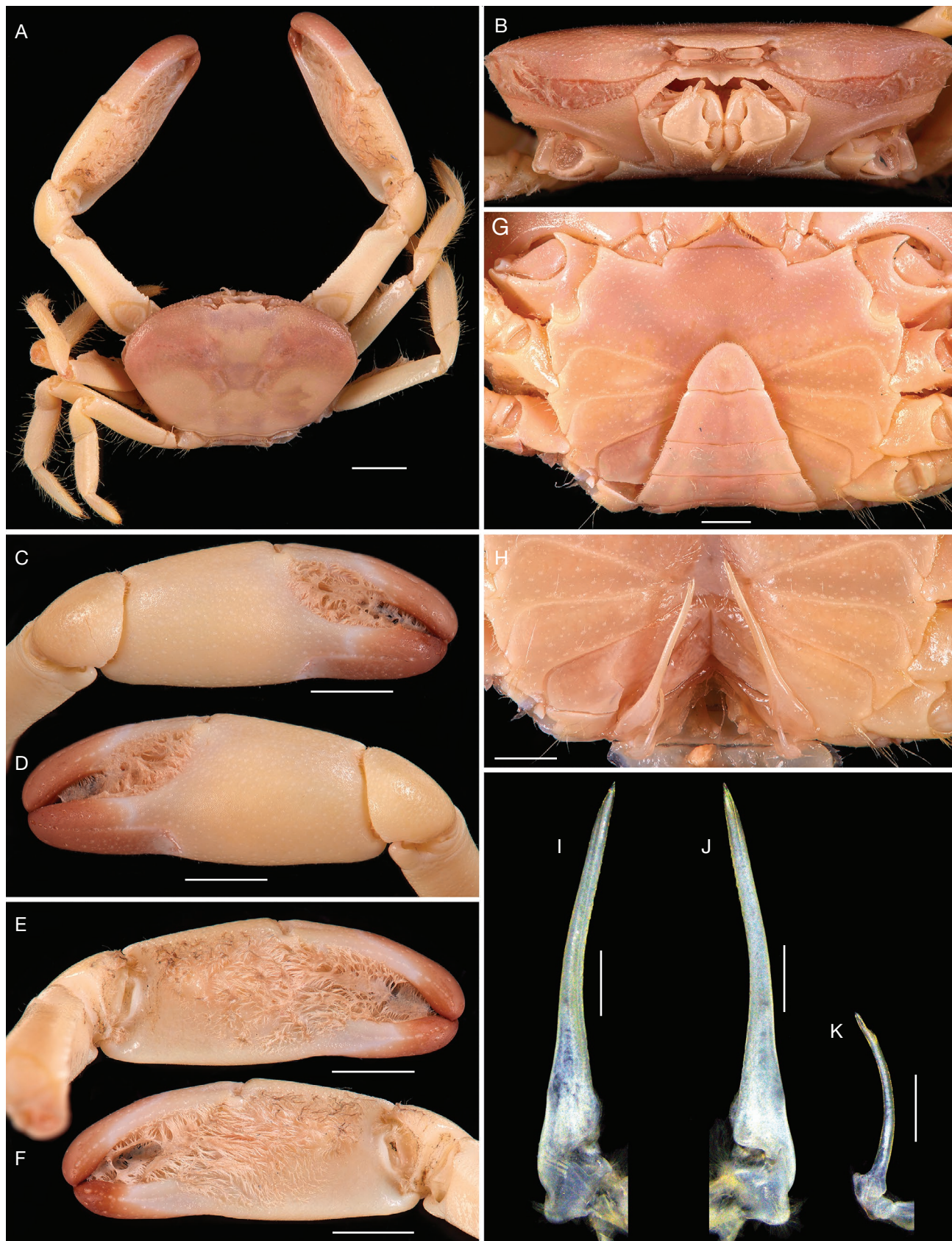


FIG. 8. — *Kallograea jolliveti* (Guinot & Segonzac, 2018) n. comb., ♂ 14.3 × 22.7 mm, Futuna Volcanic Arc, Kulo Lasi Caldera (ZRC 2024.0725, ex [MNHN-IU-2009-4045](#)): **A**, dorsal habitus; **B**, frontal view of cephalothorax; **C**, **D**, outer view of chelae; **E**, **F**, inner view of chelae; **G**, thoracic sternum and pleon, ventral view; **H**, sternopleonal cavity showing locking structures and gonopods, ventral view; **I**, right G1, ventral view; **J**, right G1, dorsal view; **K**, right G2. Scale bars: A-F, 5 mm; G, H, 2 mm; I-K, 1 mm. Credits: MNHN-Soubzmaigne.

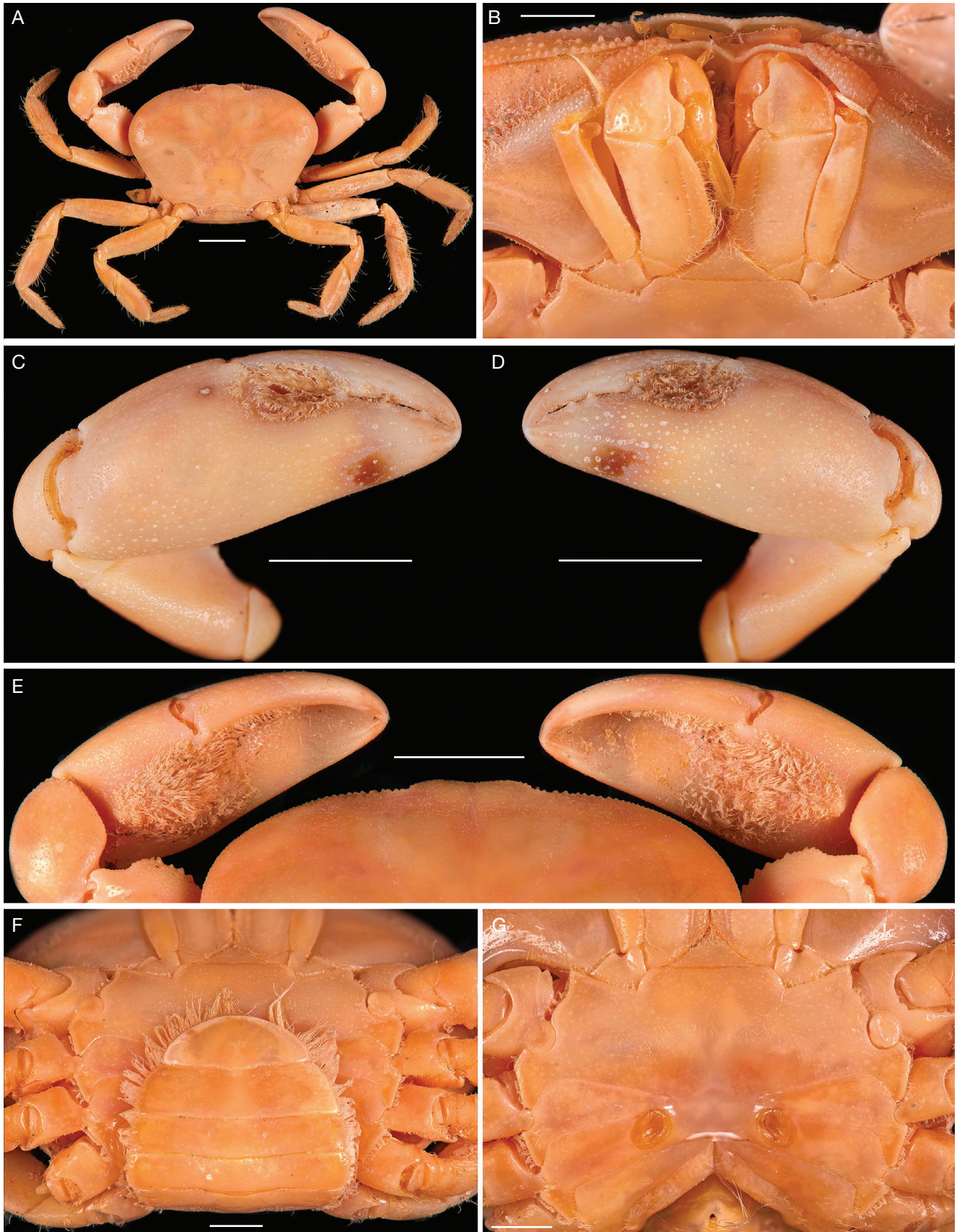


FIG. 9. — *Kallograea jolliveti* (Guinot & Segonzac, 2018) n. comb., MNHN-IU-2024-6026, ♀ 13.5 × 20.0 mm, Manus Basin, Roman's Ruins: **A**, dorsal habitus; **B**, buccal cavity and mxp3, ventral view; **C**, **D**, outer view of chelae showing pigmented spot at base of fixed finger; **E**, inner view of chelae; **F**, thoracic sternum and pleon, ventral view; **G**, sternopleonal cavity showing vulvae, ventral view. Scale bars: A, C-E, 5 mm, B, F, G, 2 mm. Credits: MNHN-Soubzmaigne.

both sexes (Figs 8C; 9C, D), recalls the distinctly coloured, more or less purplish, oval spot of *Bythograea microps* Saint Laurent, 1984, located practically in the same place and also present in both sexes (Saint Laurent 1984: pl. 1F; Guinot & Segonzac 2006b: fig. 5). In addition to the similarly coloured spot on the cheliped palm, these two species are both relatively small; but, whereas *B. microps* shows only a drastic reduction of the eyestalks (Saint Laurent 1984: 386; 1988; Guinot & Segonzac 2006b: fig. 2), *K. jolliveti* n. comb. is entirely blind: the eyestalks are absent, the podophthalmite is fused to the floor of the orbital region, and the cornea is absent, without any visible pigment (Fig. 8B).

DISTRIBUTION

Kallograea jolliveti n. comb. has a wide distribution in the western Pacific: initially, North Fiji and Lau Basins, now Kulo Lasi Volcano and Manus Basin.

COMPARISON BETWEEN *KALLOGRAEA KULOLASI* N. GEN., N. SP. (Figs 4–7) AND *K. JOLLIVETI* N. COMB. (Figs 8, 9)

Kallograea kulolasi n. gen., n. sp. can easily be distinguished from *K. jolliveti* n. comb. by the suborbital region being glabrous or almost so (Figs 4E; 5A; 6E) (vs densely setose in *K. jolliveti* n. comb.; Fig. 8B); median lobe of the posterior epistomial margin being obtusely triangular, with the lateral margins concave (Figs 4E; 5C; 6E) (vs median lobe more acutely triangular with lateral margins gently sinuous to almost straight in *K. jolliveti* n. comb.; Fig. 8B); the mxp3 completely closes the buccal cavity across the anterior part, with the distal and external margins of the merus almost touching the pterygostomial lobe (Figs 4E; 5C; 6E) (vs distinct gap between the distal and external margins of the merus and the pterygostomial lobe in *K. jolliveti* n. comb.; Fig. 8B); the P2–P5, in particular the meri, are distinctly longer and more slender (Figs 4A–C; 6A, B) (vs shorter and stouter in *K. jolliveti* n. comb.; Figs 8A; 9A); the ventral margins of P2–P4 have only scattered setae (vs with dense tomentum in *K. jolliveti* n. comb.); in both sexes, the dorsal margin of palm as well as the upper third or half of the outer surface (including the superior margin) and the upper third of the inner surface of adult male palm are densely setose but the rest of the inner surface is glabrous (Figs 4A–C; 5C–F; 6A–D) (vs dorsal and outer surfaces glabrous although the inner surface is densely setose in *K. jolliveti* n. comb.; Figs 8A, C–F; 9A, C–E); there is no spot at the base of the male pollex (Figs 5C, E; 6C) (vs with a visible pale-coloured spot in *K. jolliveti* n. comb.; Figs 8C, D; 9, D); the fingers of the male chela are relatively shorter than the palm, with the pigmentation extending along the distal third or quarter (Figs 5C–F; 6C, D) (vs the fingers of the male chela are as long as the palm, with the pigmentation extending along the distal half in *K. jolliveti* n. comb.; Figs 8A, C–F; 9A, C–E); the male thoracic sternum is proportionately wider, in relation with the short body of the species (Fig. 4B, D, F) (vs thoracic sternum less wide in *K. jolliveti* n. comb.; Figs 8G; 9G); the longitudinal median line on sternite 8 is relatively deeper (Figs 4F; 6F) (vs median line less deep in *K. jolliveti* n. comb.; Figs 8H; 9G); the male

pleon is distinctly wider, with the telson semicircular in form (Fig. 4B, D) (vs pleon less wide with the telson more triangular in *K. jolliveti* n. comb.; Fig. 8G); the G1 is more strongly curved outwards (Figs 4G; 7A, B) (vs distinctly straighter in *K. jolliveti* n. comb.; Fig. 8I, J); the G2 is proportionately much longer in *K. kulolasi* n. gen., n. sp., with the flagellum slightly longer than basal part (Figs 4H; 7E) (vs G2 relatively shorter, with a small flagellum in *K. jolliveti*; Fig. 8K); and the medially positioned subhemispherical vulva occupying slightly more than half the space of sternite 6 (Fig. 6F) (vs relatively larger, ovate and occupying most of the space of sternite 6, with the anterior edge touching sternal suture 5/6 in *K. jolliveti* n. comb.; Fig. 11G).

The differences in the structure of the posterior epistomial margin (i.e., whether the mxp3 completely closes the anterior part of the buccal cavity), shape of the male telson, the very different proportions of the flagellum and basal part of the G2, and the structures of the vulvae, however, are significant, and may suggest *K. jolliveti* n. comb. is not a member of *Kallograea* n. gen. That being said, the flat carapace, wide male anterior thoracic sternum, wide male pleon, and elongate male chelipeds with the rounded finger tips are important shared characters with *K. kulolasi* n. gen., n. sp., and indicate that placing *Austinograea jolliveti* in *Kallograea* n. gen. is the best decision for the time being.

It is interesting to find two distinct species in a narrow perimeter on the periphery of the circular caldera of the Kulo Lasi Volcano, an area with a diameter of only 5 km. The biota in this area, however, is known to be very dense and varied. *Kallograea kulolasi* n. gen., n. sp. seems confined to the Kulo Lasi Volcano, whereas the geographic range of *K. jolliveti* now extends from west to east, up to the Manus Basin (Figs 1–3).

COMPARISON BETWEEN *KALLOGRAEA* N. GEN. (Figs 4–9) AND *AUSTINOGRAEA* HESSLER & MARTIN, 1989 (Figs 10; 11)

The genus *Austinograea* is known from four species from the western Pacific: the type species *A. williamsi* Hessler & Martin, 1989, *A. alayseae* Guinot, 1990 (note that genetic differences have been found between individuals of *A. alayseae* from the Tofua Arc and the Manus Basin, see Kim *et al.* 2014), *A. bourdezi* Guinot & Segonzac, 2018, and *A. chubacarc* Guinot, 2025. A fifth species, *A. rodriguezensis* Tsuchida & Hashimoto, 2002, occurs in the western Indian Ocean.

Austinograea williamsi (see Hessler & Martin 1989: figs 1, 2, 4, 5a, 6a, 7a, 8b, 9–11, 13a, 14a–d; Tsuchida & Fujikura 2000: figs 3, 5, 6, 8; Segonzac 2006: figs 1–4; see also Desbruyères *et al.* 2006; Kojima & Watanabe 2015: figs 25.1, 25.2), found in abundance in beds of the snail *Alviniconcha hessleri* Okutani & Ohta, 1988 that is common at the vent openings, is endemic to the Mariana Trough in the north-western Pacific, in the Mariana Back-Arc Basin, just west of the Mariana Island Arc. It should be noted that the ocular region of adult *A. alayseae* is not significantly different from that of adult *A. williamsi* (Hessler & Martin 1989: fig. 4): the orbital region is only more recessed in *A. williamsi*, but, likewise, the eye is vestigial, fused to the orbital floor, and replaced by a small oval region in the posterior orbital wall

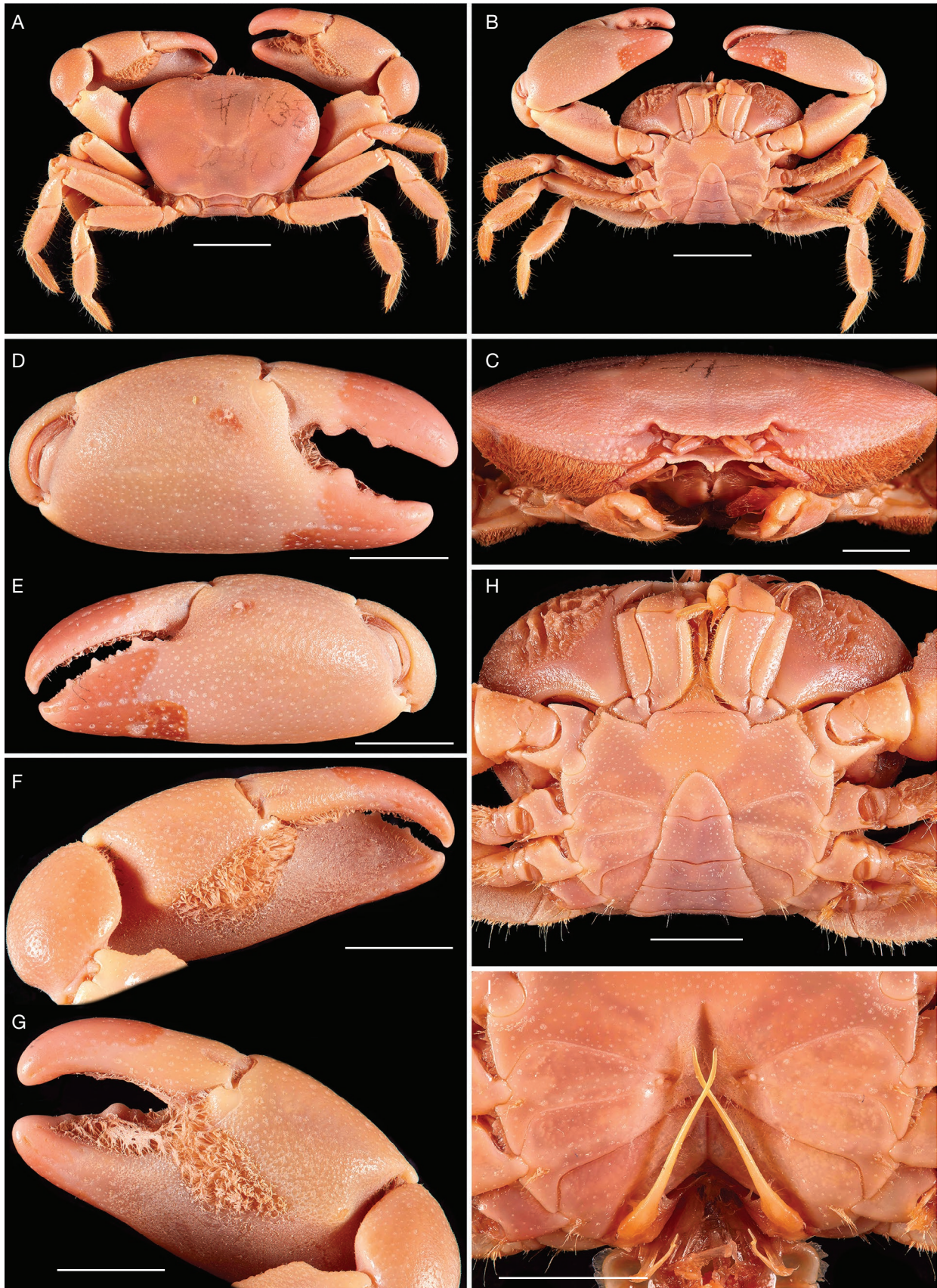


FIG. 10. — *Austino-graea williamsi* Hessler & Martin, 1989, paratype, ♂ 21.6 × 34.2 mm, Mariana Back-Arc Basin, Alice Springs ([MNHN-IU-2008-11121](#) = MNHN-B20910): **A**, dorsal habitus; **B**, ventral habitus; **C**, frontal view of cephalothorax; **D**, **E**, outer view of chelae; **F**, **G**, inner view of chelae; **H**, buccal cavity, thoracic sternum and pleon, ventral view; **I**, sternopleonal cavity showing locking structures and gonopods, ventral view. Scale bars: A, B, 10 mm, C-I, 5 mm. Credits: MNHN-Soubzmaigne.



FIG. 11. — *Austinograea williamsi* Hessler & Martin, 1989, paratype, ♀ 22.5 × 35.3 mm, Mariana Back-Arc Basin, Alice Springs (MNHN-IU-2008-11121 = MNHN-B20910). **A**, dorsal habitus; **B**, sternopleonal cavity showing vulvae, ventral view; **C**, **D**, outer view of chelae; **E**, inner view of chelae. Scale bars: A, 10 mm; B, 2 mm; C-E, 5 mm. Credits: MNHN-Soubzmaigne.

lateral to the antenna, and with a trace of cornea that is more or less discernible and virtually unpigmented (sometimes a small spot) (cf. Hessler & Martin 1989: figs 4, 5a for *A. williamsi*; Guinot 1990: fig. 1A, B for *A. alysaeae*). A key to the species of *Austinograea* was provided by Guinot & Segonzac (2018: 96). One species described from the western Pacific, *Austinograea yunohana* Takeda, Hashimoto & Ohta, 2000, was subsequently transferred by McLay (2007) to his new genus *Gandalfus* (see below).

Kallograea n. gen. is markedly different from *Austinograea* in that the dorsal surface of the carapace is almost flat (Figs 4A, C, E; 5A; 6A, E) (vs surface gently but distinctly convex in frontal view in *Austinograea*; Figs 10A, C; 11A); the posterior margin of the epistome is relatively wider (Figs 4E; 6E) (vs transversely narrower in *Austinograea*; Fig. 10C); the ischium

of the mxp3 is distinctly elongate (Fig. 5B) (vs shorter in *Austinograea*, except in *A. williamsi*; Fig. 10H); the merus of the mxp3 is subtriangular in shape, with the anterior part much produced (Figs 4E; 5B; 6E) (vs subquadrate in *Austinograea*, except in *A. williamsi*; Fig. 10H); the male anterior thoracic sternum is short and very wide (Fig. 4B, D, F) (vs transversely narrower in *Austinograea*; Fig. 10B, H, I); the adult male chelipeds are distinctly more elongate and slender, especially the merus that is longer, distinctly extending well beyond the carapace margin, and slender, narrow on its whole length, and regularly toothed on the dorsal margin (Figs 4A-C; 5C, D) (vs distinctly shorter and stouter, of moderate length and width in *Austinograea* [the chelipeds are relatively longer in *A. williamsi* but still distinctly shorter than in *Kallograea* n. gen.]; Fig. 10A, B); the adult male ambulatory legs are proportionately

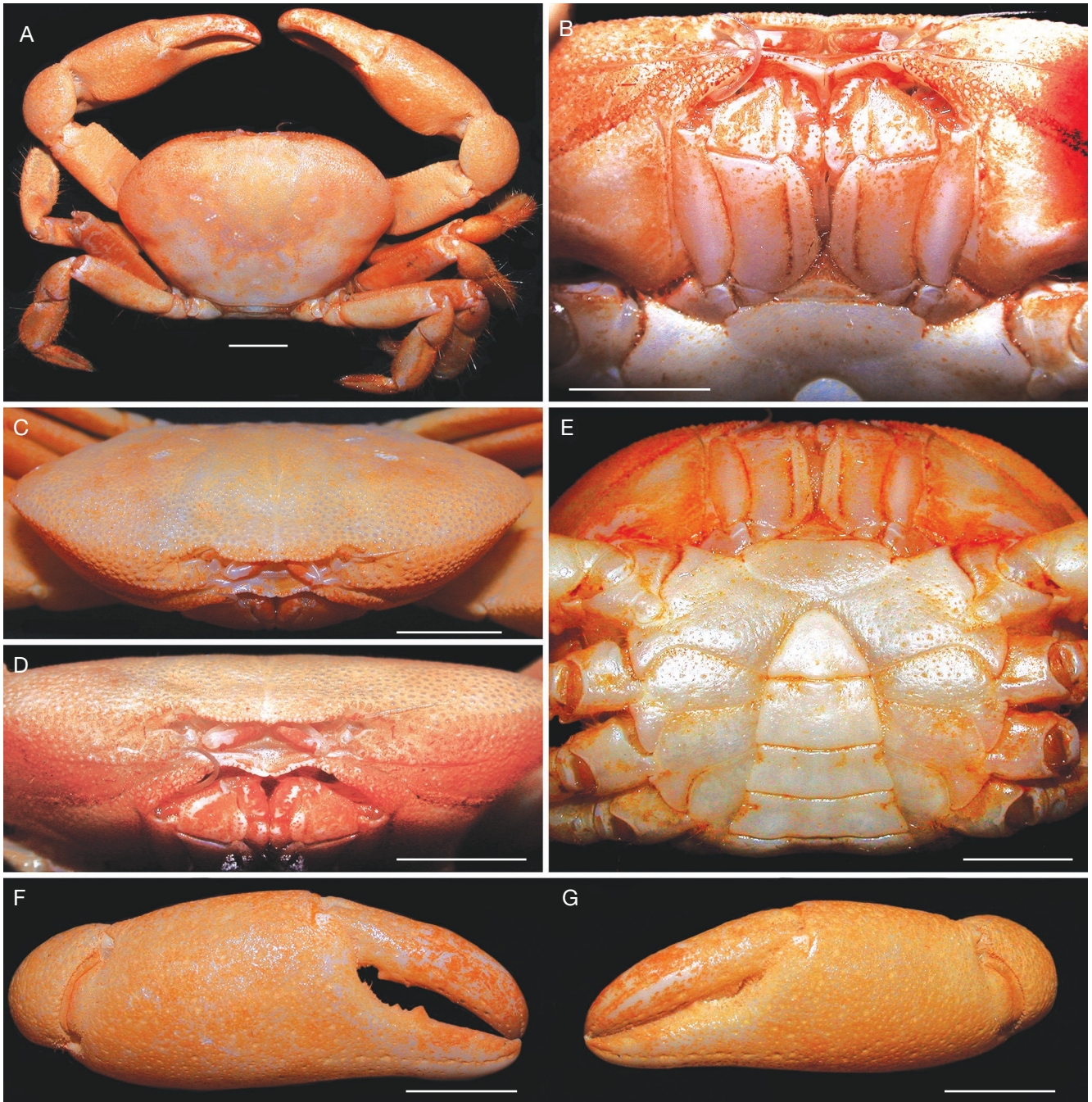


FIG. 12. — *Gandalfus puia* McLay, 2007, holotype, ♂ 15.5 × 24.3 mm, Rumble III, Kermadec Islands (NIWA 27855). **A**, dorsal habitus; **B**, buccal cavity and mxp3, ventral view; **C**, anterodorsal view of carapace; **D**, frontal view of cephalothorax; **E**, buccal cavity, thoracic sternum and pleon, ventral view; **F**, **G**, outer view of chelae. Scale bars: 5 mm.

more slender and elongate, especially the merus and propodus (Fig. 4A-C) (vs relatively shorter and stouter in *Austinograea*; Fig. 10A, B); the male sternopleonal cavity is gently concave, relatively wide distally and without a concavity for the G1 tip (Fig. 4F) (vs cavity relatively deeper, relatively narrowing distally Fig. 10I, sometimes with a distinct depression for the G1 tips, in *Austinograea*); and the almost straight G1 is positioned more or less longitudinally with the distal parts of each not overlapping (Figs 4F, G; 7A-D) (vs distinctly sinu-

ous or straight with the distal parts of each overlapping to some degree in *Austinograea* (Fig. 10I) [condition not clear for *A. rodriguezensis*, cf. Tsuchida & Fujikura 2000: fig. 8].

The form of the median lobe on the posterior epistomial margin of *K. kulolasi* n. gen., n. sp., being obtusely triangular (Figs 4E; 6E), is different from that of *Austinograea* species (acutely triangular in form; Fig. 10C); and is more similar in condition to that in *Gandalfus* (Figs 12B-D; 14B, C; 15B; 16B), although the overall margin of *K. kulolasi*

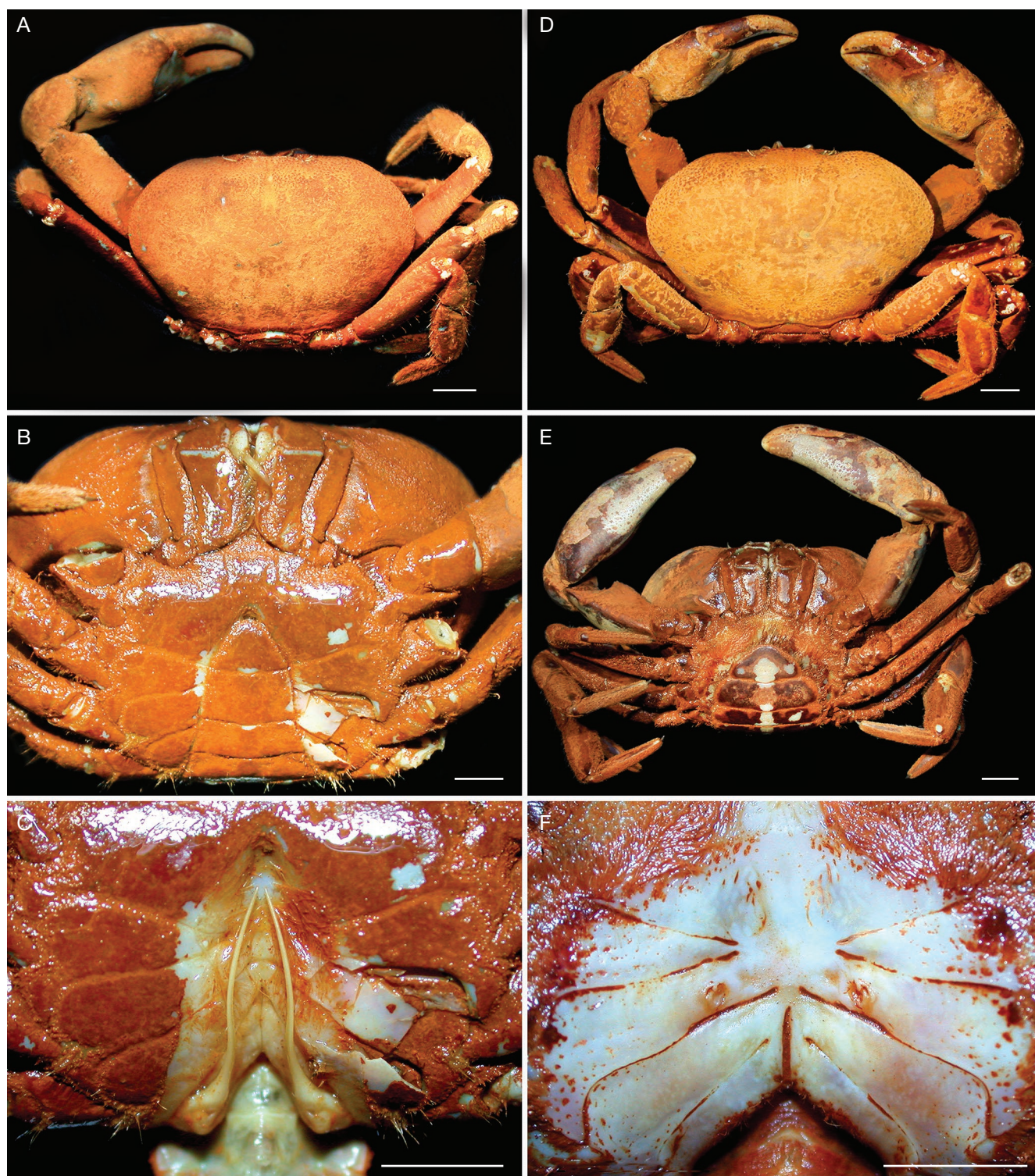


FIG. 13. — *Gandalfus puia* McLay, 2007: **A-C**, paratype, ♂ 21.3 × 33.5 mm, Macauley Caldera, Kermadec Islands (NIWA 18017); **D-F**, paratype, ♀ 22.9 × 36.4 mm, Brothers Seamount, Kermadec Islands (NIWA 18019): **A, D**, dorsal habitus; **B**, buccal cavity, thoracic sternum and pleon, ventral view; **C**, thoracic sternum and sternopleonal cavity showing gonopods, ventral view; **E**, ventral habitus; **F**, sternopleonal cavity showing vulvae, ventral view. Scale bars: 5 mm.

n. gen., n. sp. is distinctly wider. On the other hand, the median lobe of the margin in *K. jolliveti* n. comb., being acutely triangular (Figs 8B; 9B), is more similar in form to that of *Austinograea* species, although the overall margin is still wider in *K. jolliveti* n. comb.

In *Austinograea alayseae* Guinot, 1990, the extremities of the G1 join at the tips at the end of the sternopleonal cavity in situ and are positioned in a small deep depression (cf. Guinot 1990: 884, 891, fig. 2C; Guinot & Segonzac 2006a: fig. 5). In *A. hourdezi* Guinot & Segonzac, 2018 (Guinot

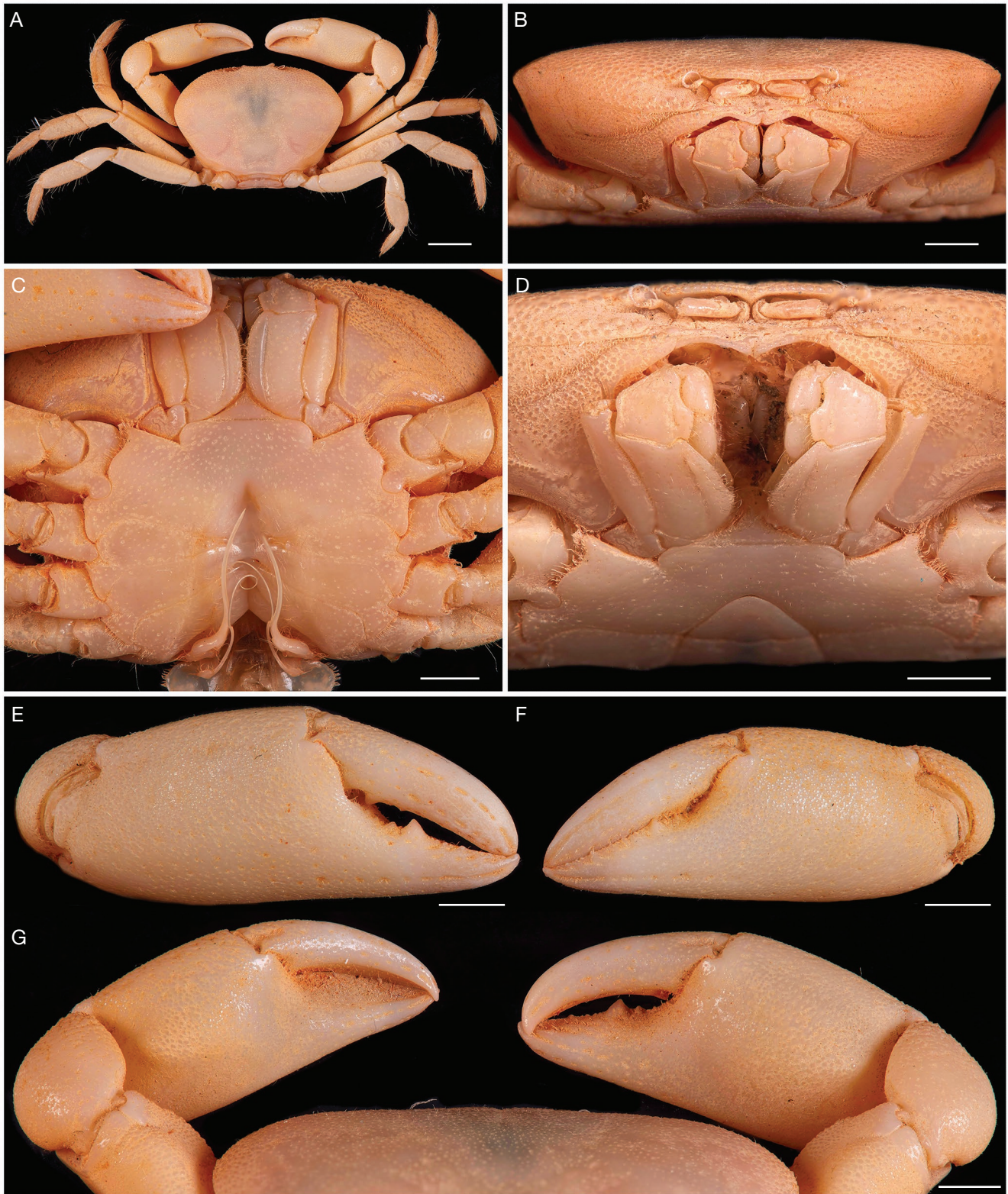


FIG. 14. — *Gandalfus puia* McLay, 2007, ♂ 11.6 × 18.0 mm, Macauley Caldera, Kermadec Islands (NIWA 18018): **A**, dorsal habitus; **B**, frontal view of cephalothorax; **C**, thoracic sternum and sternopleonal cavity showing gonopods 1 and 2, ventral view; **D**, buccal cavity and mxp3, anteroventral view; **E**, **F**, outer view of chelae; **G**, inner view of chelae. Scale bars: A, 5 mm; B-G, 2 mm. Credits: MNHN-Soubzmaigne.

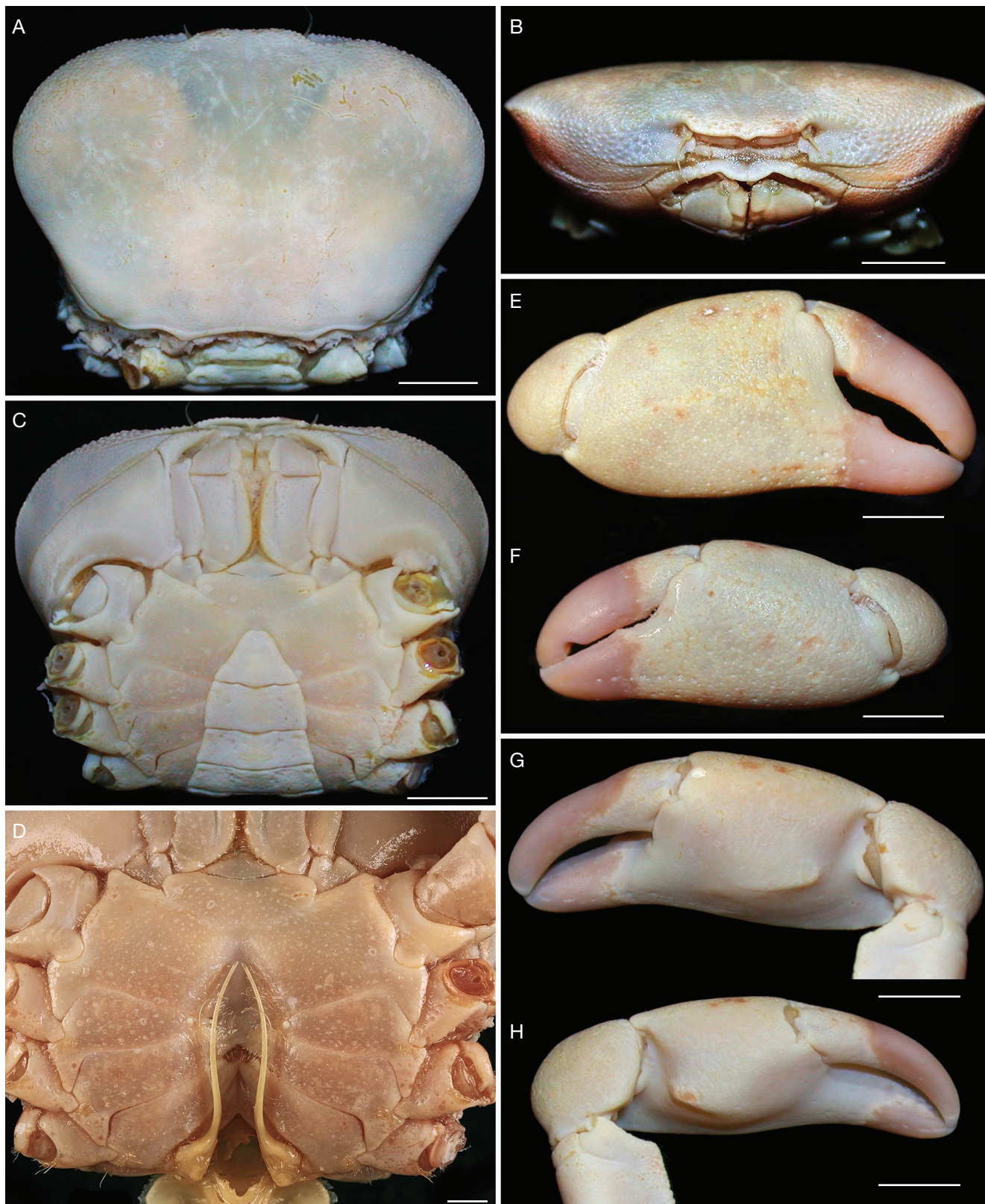


FIG. 15. — *Gandalfus yunohana* (Takeda, Hashimoto & Ohta, 2000), ♂ 20.5 × 29.9 mm, Kaikata Seamount (MNHN-IU-2024-6055): **A**, carapace, dorsal view; **B**, frontal view of cephalothorax; **C**, buccal cavity, thoracic sternum and pleon, ventral view; **D**, sternopleonal cavity showing locking structures and gonopods, ventral view; **E**, **F**, outer view of chelae; **G**, **H**, inner view of chelae. Scale bars: A-C, E-H, 5 mm; D, 2 mm. Credits: MNHN-Soubzmaigne.



FIG. 16. — *Gandalfus yunohana* (Takeda, Hashimoto & Ohta, 2000), ♀ 28.2 × 42.2 mm, Kaikata Seamount (MNHN-IU-2024-6053). A, dorsal habitus; B, frontal view of fronto-orbital and buccal region; C, buccal cavity and mxp3, ventral view; D, E, outer view of chelae; F, buccal cavity, thoracic sternum and pleon, ventral view; G, sternopleonal cavity showing vulvae, ventral view. Scale bars: 5 mm. Credits: MNHN-Soubzmaigne.

1990: figs 4C, 6C) and *A. williamsi* (Fig. 10I), the G1 tips also cross distally and are positioned in a narrow channel at the anterior part of the sternopleonal cavity. In contrast, in *Kallograea* n. gen., the obliquely directed G1 have the tips well separated and the anterior part of the sternopleonal cavity is proportionally wider, flatter and without a special distal depression to receive the G1 tips (Figs 4F; 8H).

Another significant distinction between *Austinograea* and *Kallograea kulolasi* n. gen., n. sp. is observed in the length of the flagellum of G2. It is much shorter than the basal article in *Austinograea* species (Fig. 10I) and is as long as the basis in *Kallograea kulolasi* n. gen., n. sp. (Figs 4H; 7E). In *K. jolliveti* n. comb., the G2 is proportionally shorter and the flagellum much shorter than that



FIG. 17. — **A, B**, *Kallograea kulolasi* n. gen., n. sp. in situ. CHUBACARC 2019 cruise, Futuna Volcanic Arc, Kulo Lasi Caldera, PL729, 1472 m, with probably the holotype, ♂ 7.3 × 12.7 mm (MNHN-IU-2024-6067), associated with Siboglinidae *Arcovestia ivanovi* Southward & Galkin, 1997. The species is easily recognisable by its small, flat carapace, long chelipeds, notably with elongated and slender merus, the setal patch on the superior border of the palm, and the shape of propodus; **C, D**, unidentified *Gandalfus* sp. from Kulo Lasi Caldera.

in *K. kulolasi* n. gen., n. sp. (Fig. 8K); Guinot & Segonzac 2018: figs 9D, 11C-E).

No other *Austinograea* species, except *A. williamsi*, in which the male crusher has rounded finger tips (Fig. 10B, D, G), has finger tips as blunt as those on the crusher of *Kallograea* n. gen. Their overall cheliped structures, however, differ significantly, with that of *Kallograea* n. gen. being elongate and slender (Figs 4A-C; 5C-F; 8A, C-F) and that of *Austinograea*, short and stout (Fig. 8A, B, D, G).

The above-discussed differences justify the transfer of *Austinograea jolliveti* into *Kallograea* n. gen., albeit with some reservations (see previously: Comparison between *Kallograea kulolasi* n. gen., n. sp. and *K. jolliveti* n. comb.).

COMPARISON BETWEEN *KALLOGRAEA* N. GEN. (Figs 4-9) AND *GANDALFUS* MCLAY, 2007 (Figs 12-16)

The type species, *Gandalfus puia*, has been collected from hydrothermal sites of the Kermadec Arc in the south-west Pacific Ocean, the longest underwater volcanic ridge on the planet, particularly in three active volcanoes between 30°12'S-35°44'S

and 181°33'E-178°29'E (at 270-239 m, at 1604-1647 m, and at 337 m). The ridge, which forms the base of the Kermadec Islands, is linear for about 1000 km and is a prolongation of the Tonga ridge. The Tonga-Kermadec Ridge is underlying the Tonga-Kermadec island arc and, on its western side, it is flanked by the back-arc-basin, the Lau Basin, which is at the boundary of the Australian and Pacific Plates (De Ronde *et al.* 2001; Wright 2001; Wright *et al.* 2002; Hauff *et al.* 2021).

The carapace of adult *Gandalfus* species is distinctly higher, with the dorsal surface more convex (Figs 12A, C, D; 13A, D; 14A, B; 15A; 16A) compared to those of *Kallograea* spp. which are lower and flatter (Figs 4A, C, E; 5A; 6A, E; 8A, B; 9A). The chelipeds of *G. puia* and *G. yunohana* are relatively short, have a short merus that is irregularly serrated and triangular in cross section, and a granulous and glabrous palm ending in relatively acute fingers that are armed with several proximal teeth of variable size, including one larger tooth at midlength of fixed finger (Figs 12A, F, G; 13A; 14A, E-G; 15E-H; 16A, D, E) (vs adult male chelipeds distinctly more elongate, with the merus distinctly longer, slender along its

entire length, with the dorsal margin dentate, and extending well beyond carapace margin; the stout palm possessing setal patches and ending in thick and blunt fingers, and on the major chela, there is only a molariform tooth on the fixed finger in *Kallograea* n. gen.; Figs 4A-C; 5C-F; 8A, C-F). While adult *Gandalfus* spp. are generally larger (carapace width: 36.7 mm in *G. puia*; 42.2 mm in *G. yunohana*), we have subadult specimens of *G. puia* (e.g., female 10.4 × 14.3 mm, ZRC 2024.0726, ex [MNHN-IU-2024-6553](#)) which are comparable in size to the two *Kallograea* species, but these differences remain valid.

McLay (2007: fig. 2D-F, table 2) recognised a new genus for his new species, *Gandalfus puia*, arguing that its G2 was quite different from those of *Austinograea* s. str. In *G. puia*, the G2 is approximately as long as the G1, with the flagellum as long as or longer than the basal article. Because of this character, McLay (2007) transferred *Austinograea yunohana* Takeda, Hashimoto & Ohta, 2000 to *Gandalfus* (see Takeda *et al.* 2000: 164, 168, figs 4I, 6c, e) and, in doing so, he restricted *Austinograea* for species in which the G2 is clearly shorter than the G1, and has a shorter flagellum as well. The G2 is distinctly less than half the length of the G1 in *A. williamsi* (Fig. 10I; Hessler & Martin 1989: fig. 14a; Tsuchida & Fujikura 2000: fig. 6; Guinot & Segonzac 2006c: fig. 4) and *A. rodriguezensis* (cf. Tsuchida & Hashimoto 2002: fig. 8; Tsuchida 2006: fig. 3); about half the length of the G1 in *A. hourdezi* Guinot & Segonzac, 2018 (cf. Guinot & Segonzac 2018: fig. 6D, E); and more than half the length of the G1 (which is curved and armed with spiniform setae along its whole length) in *A. alayseae* Guinot, 1990 (cf. Guinot 1990: fig. 3A-C; Guinot & Segonzac 2006a: fig. 6).

The discovery of the relative lengths of G2/G1 in *Kallograea kulolasi* n. gen., n. sp. and *K. jolliveti* n. comb. reinforces the value of this character as a key taxonomic index. In both species of *Kallograea* n. gen., the G2 is curved, and is as long as or shorter than the G1 (Figs 4H; 7E; 8K); with the flagellum slightly longer than the basal part. This is also one of the main characters that distinguishes *Gandalfus* from *Austinograea*.

Another distinctive character of *Gandalfus* documented by McLay (2007), the slightly sinuous posterior epistomial margin (vs the strongly sinuous margin in *Austinograea*; see Tsuchida & Hashimoto 2002: fig. 3), was difficult to appreciate because, unfortunately, the shape of the epistome of *G. puia* was not clearly illustrated in McLay's paper. Our examination of the two genera shows that the median lobe of the margin is obtusely triangular in *Gandalfus* (Figs 12B-D; 14B, D; 15B; 16B, C) but more distinctly acutely triangular in *Austinograea* (Fig. 8C; Tsuchida & Hashimoto 2002: fig. 3). The posterior epistomial margin in both *Kallograea* species is distinctly wider than those of *Gandalfus* or *Austinograea*. As discussed earlier under *Austinograea*, the median lobe of this margin is obtusely triangular in *K. kulolasi* n. gen., n. sp. (Figs 4E; 5C; 6E).

McLay (2007: 7) described the vulva in a female of *Gandalfus puia* (carapace width 36.5 mm) as "slit-like", oriented along anterior posterior body axis, not operculate, but he did not give an illustration. *Gandalfus puia* has a rounded vulva, with

a distinct pointed tubercle at the anterior edge, which may be interpreted as a narrow sternal cover (Fig. 13F), as that of *G. yunohana* illustrated by Takeda *et al.* (2000: 166, fig. 4 E, as *Austinograea yunohana*; Fig. 16G). The vulva of *K. kulolasi* n. gen., n. sp. (Fig. 6F) and *K. jolliveti* n. comb. (Fig. 9G; Guinot & Segonzac 2018: fig. 10E, as *Austinograea jolliveti*) is large, occupying most of the surface of sternite 6, and rounded, without any trace of an anterior tubercle. The vulva of *Austinograea* species is rounded, closed by soft membrane: in *A. williamsi* (Fig. 9B) and *A. hourdezi* (Guinot & Segonzac 2018: fig. 10E), without any trace of an anterior tubercle.

The larvae of *Gandalfus yunohana* were reported on by Nakajima *et al.* (2010) and Hamasaki *et al.* (2010). The complete mitogenome of *G. yunohana*, from the Nikko Seamount on the Izu-Ogasawara Ridge, was reported by Yang *et al.* (2010: fig. 3) who showed that it had highly conserved characteristics and appeared to be related to brachyurans such as *Pseudocarcinus gigas* (Lamarck, 1818). *Pseudocarcinus gigas* is at present in its own family (see Ng & Davie 2020), and this supposed relationship needs to be revisited. The complete mitochondrial genome of *G. puia*, from the Tonga Arc, was obtained by Kim *et al.* (2015: fig. 1), showing that the genetic data of this taxon is distinct from that of *Austinograea* s. str. The phylogenetic tree of Wang *et al.* (2019: fig. 1) includes *Gandalfus puia*, *G. yunohana*, *Austinograea alayseae*, *A. rodriguezensis* and *Segonzacia mesatlantica* (Williams, 1988), and they show the same separation, indicating *Gandalfus* and *Austinograea* are separate genera (see also the Bayesian inference tree in Ma *et al.* 2024). Barcoding sequences of the mitochondrial COI gene of *G. yunohana*, from four vent fields (including two on the Izu Arc, one on the northern Mariana Arc and one in the Okinawa Trough), have shown a similar genetic diversity of populations on the Izu and northern Mariana Arcs and a sharing of the dominant haplotypes, without genetic subdivision regardless of the habitat depth, the whole suggesting a high dispersal capability for *G. yunohana* (cf. Watanabe *et al.* 2020).

Unidentifiable species

REMARK

As discussed earlier, a number of small or damaged specimens examined cannot be conclusively identified with known taxa. These are listed below.

MATERIAL EXAMINED. — 1 ♀ 9.0 × 12.0 mm (left-handed, very damaged, in two pieces and many detached legs and with only left cheliped (cutter), covered with dark substance; FUTUNA 3; Kulo Lasi Volcano; Fu-3-PL04 - Aspi 4-001 (PL-04-1825); 1825 m; n°sample 001 [there is no patch of setae on the upper margin of the damaged palm; the only chela is covered with granules on the carpus and propodus, and has no spot; the fingers cross at the tips and their black colour is very reduced; the mxp3 are completely closing the buccal cavity]; 14°54.96'S, 177°14.60'W; [MNHN-IU-2024-6074](#) • 1 young ♂ 8.2 × 13.2 mm (with detached chelipeds, left-handed); FUTUNA 1; Kulo Lasi; PL1778-06 - aspi 4; 14°54.96'S, 177°14.60'W; 1477 m; 15.IX.2010; R/V *Atalante*, ROV *Nautille*, M. Segonzac 2011 det. *Austinograea* sp.; [MNHN-IU-2009-4046](#) • 1 ♀; same data as for preceding; [MNHN-IU-2018-5226](#).

Acknowledgements

We would like to express our cordial thanks to the captain and crew of the R/V *Atalante* as well as to the operation teams of the ROV *Victor*, and in particular to the chief scientists of the CHUBACARC 2019 cruise, Stéphane Hourdez and Didier Jollivet (<https://doi.org/10.17600/18001111>). We are grateful to Stéphane Hourdez, who provided the specimens studied here, allowed all the material collected by several campaigns to be entrusted to us, and made useful corrections and suggestions on a preliminary draft. We also thank Lenaick Menot, who sent us the brachyuran material collected by the FUTUNA 3 cruise (2012), initially preserved at the Centre IFREMER. From the MNHN, we would like to warmly acknowledge the unfailing help of Sébastien Soubzmaigne for the photographs, the valuable and constant assistance of Paula Martin-Lefèvre (MNHN, Direction des Collections) and the support of Laure Corbari (Curator of the Crustacean collection). Jean-François Bernardet helped us with the first sorting of the material and the measurement of specimens. Analia Martin-Lefèvre helped us in the very first phase of the preparation of the iconography. We would like to extend our warmest thanks to Kareen Schnabel and Saddle Mills (NIWA) for their kind and professional help in loaning the types and other material of *Gandalfus puia* in their collection. Thanks are addressed to the editorial staff of *Zoosystema*, Laure Desutter-Grandcolas, editor in chief, and especially to Anne Mabilie for her highly professional and friendly support. The paper has benefited greatly from many useful corrections, suggestions and comments from J. C. Mendoza and an anonymous reviewer.

REFERENCES

- BEAULIEU S. E. & SZAFRAŃSKI K. M. 2020. — InterRidge global database of active submarine hydrothermal vent fields version 3.4 [dataset]. *PANGAEA*. <https://doi.org/10.1594/PANGAEA.917894>
- BOULART C., ROUXEL O., SCALABRIN C., LE MEUR P., PELLETER E., POITRIMOL C., THIÉBAUT E., MATABOS M., CASTEL J., TRAN LU Y. A., MICHEL L., CATHALOT C., CHÉRON S., BOISSIER A., GERMAIN Y., GUYADER V., ARNAUD-HAOND S., BONHOMME F., BROQUET T., CUEFF-GAUCHARD V., LE LAYEC V., L'HARIDON S., MARY J., LE PORT A.-S., TASIEMSKI A., KUAMA D., HOURDEZ S. & JOLLIVET D. 2022. — Active hydrothermal vents in the Woodlark Basin may act as dispersing centres for hydrothermal fauna. *Communications Earth & Environment* 3 (1): 64 (16 p.). <https://doi.org/10.1038/s43247-022-00387-9>
- DAVIE P. J. F., GUINOT D. & NG P. K. L. 2015. — Anatomy and functional morphology of Brachyura (Chapter 71-2), in CASTRO P., DAVIE P. J. F., GUINOT D., SCHRAM F. R. & VON VAUPEL KLEIN J. C. (eds), *Decapoda: Brachyura, Treatise on Zoology – Anatomy, Taxonomy, Biology*. Vol. 9C-1, Crustacea. Brill, Leiden and Boston: 11-163. https://doi.org/10.1163/9789004190832_004
- DESBRUYÈRES D., HASHIMOTO J. & FABRI M. 2006. — Composition and biogeography of hydrothermal vent communities in Western Pacific Back-Arc Basins, in CHRISTIE D. M., FISHER C. R., LEE S.-M. & GIVENS S. (eds), *Back-Arc Spreading Systems: Geological, Biological, Chemical, and Physical Interactions. Geophysical Monographs* 166: 215-234.
- DE RONDE C. E. J., BAKER E. T., MASSOTH G. J., LUPTON J. E., WRIGHT I. C., FEELEY R. A. & GREENE R. R. 2001. — Intra-oceanic subduction-related hydrothermal venting, Kermadec volcanic arc, New Zealand. *Earth & Planetary Science Letters* 193: 359-369.
- FOUQUET Y., ALIX A. S., BIROT D., CHÉRON S., CHARLOU J. L., DONVAL J. P., ÉTOUBLEAU J., GERMAIN Y., GUILLOU M., GUÉRIN C., GUYADER V., KONN C., LABANIEH S., PELLETER E., PIERRE D., DUPRÉ S., SCALABRIN C., CAMBON M. A., MENOT L., PRADILLON F., CHAZOT G., DYMENT J., SZITKAR F. & GOUIN J. 2015. — Discovery of Extensive Hydrothermal Fields in the Wallis and Futuna Back-Arc Environment (SW Pacific), in ANDRÉ-MAYER A. S., CATHELINÉAU M., MUCHEZ P., PIRARD E. & SINDERN S. (eds), *Mineral Resources in a Sustainable World*, 1-5: 1223-1226.
- FOUQUET Y., PELLETER E., KONN C., CHAZOT G., DUPRÉ S., ALIX A. S., CHÉRON S., DONVAL J. P., GUYADER V., ÉTOUBLEAU J., CHARLOU J. L., S. LABANIEH SCALABRIN C. 2018. — Volcanic and hydrothermal processes in submarine calderas: the Kulo Lasi example (SW Pacific). *Ore Geology Reviews* 99: 314-343
- GUINOT D. 1990. — *Austinograea alayseae* sp. nov., crabe hydrothermal découvert dans le bassin de Lau, Pacifique sud-occidental (Crustacea Decapoda Brachyura). *Bulletin du Muséum national d'Histoire naturelle 4^e sér.*, 11, section A (4): 879-903.
- GUINOT D. 2025. — *Austinograea chubacarc* n. sp. from the Manus and Woodlark Basins (western Pacific), and new records of *A. alayseae* Guinot, 1990 and *A. hourdezi* Guinot & Segonzac, 2018 (Crustacea, Decapoda, Brachyura, Bythograeidae). *Zoosystema* 47 (12): 167-184. <https://doi.org/10.5252/zoosystema2025v47a12>. <http://zoosystema.com/47/12>
- GUINOT D. & HURTADO L. A. 2003. — Two new species of hydrothermal vent crabs of the genus *Bythograea* from the southern East Pacific Rise and from the Galapagos Rift (Crustacea Decapoda Brachyura Bythograeidae). *Compte Rendus Biologies* 326: 423-439. [https://doi.org/10.1016/S1631-0691\(03\)00126-4](https://doi.org/10.1016/S1631-0691(03)00126-4)
- GUINOT D. & SEGONZAC M. 1997. — Description d'un crabe hydrothermal nouveau du genre *Bythograea* (Crustacea Decapoda Brachyura) et remarques sur les Bythograeidae de la dorsale du Pacifique oriental. *Zoosystema* 19 (1): 121-149.
- GUINOT D. & SEGONZAC M. 2006a. — *Austinograea alayseae* Guinot, 1990, in DESBRUYÈRES D., SEGONZAC M. & BRIGHT M. (eds), *Handbook of Deep-Sea Hydrothermal Vent Fauna*. Second completely revised edition. *Denisia* 18: 460-461.
- GUINOT D. & SEGONZAC M. 2006b. — *Bythograea microps* de Saint Laurent, 1984, in DESBRUYÈRES D., SEGONZAC M. & BRIGHT M. (eds), *Handbook of Deep-Sea Hydrothermal Vent Fauna*. Second completely revised edition. *Denisia* 18: 468.
- GUINOT D. & SEGONZAC M. 2006c. — *Austinograea williamsi* Hessler & Martin, 1989, in DESBRUYÈRES D., SEGONZAC M. & BRIGHT M. (eds), *Handbook of Deep-Sea Hydrothermal Vent Fauna*. Second completely revised edition. *Denisia* 18: 468.
- GUINOT D. & SEGONZAC M. 2018. — A review of the brachyuran deep-sea vent community of the western Pacific, with two new species of *Austinograea* Hessler & Martin, 1989 (Crustacea, Decapoda, Brachyura, Bythograeidae) from the Lau and North Fiji Back-Arc Basins. *Zoosystema* 40 (1): 75-107. <https://doi.org/10.5252/zoosystema2018v40a5>. <http://zoosystema.com/40/5>
- HAMASAKI K., NAKAJIMA K., TSUCHIDA S., KADO R. & KITADA S. 2010. — Number and duration of zoeal stages of the hydrothermal vent crab *Gandalfus yunohana* from laboratory reared specimens. *Journal of Crustacean Biology* 30 (2): 236-240. <https://doi.org/10.1651/09-3199.1>
- HAUFF F., HOERNLE K., GILL J., WERNER R., TIMM C., GARBE-SCHÖNBERG D., GUTJAHN M. & JUNG S. 2021. — R/V SONNE Cruise SO255 «VITIAZ»: an integrated major element, trace element and Sr-Nd-Pb-Hf isotope data set of volcanic rocks from the Colville and Kermadec Ridges, the Quaternary Kermadec volcanic front and the Havre Trough backarc basin, Version 1.0. Interdisciplinary Earth Data Alliance (IEDA). <https://doi.org/10.26022/IEDA/111723>
- HESSLER R. R. & LONSDALE P. 1991. — Biogeography of Mariana Trough hydrothermal vent communities. *Deep-Sea Research*

- Part a-Oceanographic Research Papers 38: 185-199. [https://doi.org/10.1016/0198-0149\(91\)90079-U](https://doi.org/10.1016/0198-0149(91)90079-U)
- HESSLER R. R. & MARTIN J. W. 1989. — *Austinograea williamsi*, new genus, new species, a hydrothermal vent crab (Decapoda: Bythograeidae) from the Mariana Back-Arc Basin, western Pacific. *Journal of Crustacean Biology* 9 (4): 645-661. <https://doi.org/10.2307/1548594>
- HOUREZ S. & JOLLIVET D. 2019. — CHUBACARC cruise, RV L'Atalante. IFREMER. <https://doi.org/10.17600/18001111>
- HOUREZ S. & JOLLIVET D. 2023. — CHUBACARC Cruise Report. CNRS; Sorbonne University; Ifremer. Hal-04100305.
- KIM S.-J., KIM H. S. & JU S. J. 2014. — Mitochondrial genome of the hydrothermal vent crab *Austinograea alayseae* (Crustacea: Bythograeidae): genetic differences between individuals from Tofua Arc and Manus Basin. *Mitochondrial DNA* 25: 251-252.
- KIM S.-J., MOON J.-W. & JU S.-J. 2015. — Complete mitochondrial genome of the blind vent crab *Gandalfus puia* (Crustacea: Bythograeidae) from the Tonga Arc. *Mitochondrial DNA* 27 (4): 1-2.
- KOJIMA S. & WATANABE H. 2015. — Vent Fauna in the Mariana Trough, in ISHIBASHI J.-I., KYOKO O. & MICHINARI S. (eds), *Subseafloor Biosphere Linked to Hydrothermal Systems*. TAIGA Concept. Chapter 25. Springer, Tokyo Heidelberg New York Dordrecht London: 313-324.
- KONN C., FOURRÉ E., JEAN-BAPTISTE P., DONVAL J. P., GUYADER V., BIROT D., ALIX A. S., GAILLOT A., PEREZ F., DAPOIGNY A., PELLETIER E., RESING J. A., CHARLOU J. L. & FOUQUET Y., PARTIES A S 2016. — Extensive hydrothermal activity revealed by multi-tracer survey in the Wallis and Futuna region (SW Pacific). *Deep-Sea Research Part I*, 116: 127-144.
- LIDDELL H. G. & SCOTT R. 1940. — *A Greek-English lexicon, a new (ninth) edition*. Oxford University Press, London. xlviii + 2111 p.
- MA S., CHEN Z., SUN Y., QU M., WANG X., JIANG W., QIN G. & LIN Q. 2024. — Morphological convergence from independent crab lineages contributes to the flourishing symbiotic diversity between crabs and branching corals. *Coral Reefs* 43: 1013-1022. <https://doi.org/10.1007/s00338-024-02517-5>
- MCLAY C. L. 2007. — New crabs from hydrothermal vents of the Kermadec Ridge submarine volcanoes, New Zealand: *Gandalfus* gen. nov. (Bythograeidae) and *Xenograpsus* (Varunidae) (Decapoda: Brachyura). *Zootaxa* 1524: 1-22. <https://doi.org/10.5281/zenodo.177502>
- NAKAJIMA K., HAMASAKI K., TSUCHIDA S., KADO R. & KITADA S. 2010. — First zoal stage of the hydrothermal vent crab, *Gandalfus yunohana* (Decapoda, Brachyura, Bythograeidae). *Crustaceana* 83 (5): 525-537. <https://doi.org/10.1163/001121610X491022>
- NG P. K. L. & DAVIE P. J. F. 2020. — A new family and superfamily for the Southern Giant Crab of Australia, *Pseudocarcinus gigas* (Lamarck, 1818) (Decapoda: Brachyura). *Journal of Crustacean Biology* 40 (5): 607-626. <https://doi.org/10.1093/jcbiol/ruaa058>
- ROSS B., CROOK K., TAYLOR B., BROGAN S., CHAPPELL B., FRANKEL E., LIU L., SINTON J. & TIFFIN D. 1986. — Hydrothermal chimneys and associated fauna in the Manus Back-Arc Basin, Papua New Guinea. *Eos* 67 (21): 489, 490.
- RUELLAN E. & LAGABRIELLE Y. 2005. — Subductions et ouvertures océaniques dans le Sud-Ouest Pacifique. Oceanic subductions and active spreading in the Southwest Pacific. *Géomorphologie: relief, processus, environnement* 11 (2): 121-142. 2. <https://doi.org/10.4000/geomorphologie.307>
- SAINT LAURENT M. DE 1984. — *Crustacés Décapodes d'un site hydrothermal actif de la dorsale du Pacifique oriental (13° Nord), en provenance de la campagne française Biocyatherm*. *Comptes Rendus de l'Académie des Sciences* 299: 355-360.
- SAINT LAURENT M. DE 1988. — Biologie et écologie des sources hydrothermales. *Oceanologica Acta*, special vol. 8, 1987 (1988): 99-107.
- SEGOZAC M. 2006. — *Austinograea williamsi* Hessler & Martin, 1989, in DESBRUYÈRES D., SEGOZAC M. & BRIGHT M. (eds), *Handbook of Deep-Sea Hydrothermal Vent Fauna*. Second completely revised edition. *Denisia* 18: 463.
- SZITKAR F., DYMENT J. & FOUQUET Y. 2020. — Widespread volcanism Southeast of Futuna Island (SW Pacific Ocean): near-seafloor magnetic dating and regional consequences. *Journal of Volcanology and Geothermal Research* 431: 107646 (1-9).
- TAKEDA M., HASHIMOTO J. & OHTA S. 2000. — A new species of the family Bythograeidae (Crustacea, Decapoda, Brachyura) from the hydrothermal vents along volcanic front of the Philippine Sea Plate. *Bulletin of the National Science Museum Series A*, 26: 159-172.
- TSUCHIDA S. 2006. — *Austinograea rodriguezensis* Tsuchida & Hashimoto, 2002 in DESBRUYÈRES D., SEGOZAC M. & BRIGHT M. (eds), *Handbook of Deep-Sea Hydrothermal Vent Fauna*. Second completely revised edition. *Denisia* 18: 462.
- TSUCHIDA S. & FUJIKURA K. 2000. — Heterochely, relative growth, and gonopod morphology in the bythograeid crab, *Austinograea williamsi* (Decapoda, Brachyura). *Journal of Crustacean Biology* 20: 407-414.
- TSUCHIDA S. & HASHIMOTO J. 2002. — A new species of bythograeid crab, *Austinograea rodriguezensis* (Decapoda, Brachyura), associated with active hydrothermal vents from the Indian Ocean. *Journal of Crustacean Biology* 22 (3): 642-650. <https://www.jstor.org/stable/1549747>
- TUNNICLIFFE V., CHEN C., GIGUÈRE T., ROWDEN A. A., WATANABE H. K. & BRUNNER O. 2024. — Hydrothermal vent fauna of the western Pacific Ocean: distribution patterns and biogeographic networks. *Diversity and Distributions* 30: e13794. 1- 16 p. <https://doi.org/10.1111/ddi.13794>
- WANG Z., TANG D., SHI X., GUO H., CHEN X., ZHANG D. & TANG B. 2019. — Genetic basis of hydrothermal vent adaptation in Bythograeidae crabs: insights from adaptive evolution of mitochondrial protein coding genes. *Pakistan Journal of Zoology* 51 (5): 1721-1731. <https://doi.org/10.17582/journal.pjz/2019.51.5.1721.1731>
- WATANABE H. K., CHEN C., KOJIMA S., KATO S. & YAMAMOTO H. 2020. — Population connectivity of the crab *Gandalfus yunohana* (Takeda, Hashimoto & Ohta, 2000) (Decapoda: Brachyura: Bythograeidae) from deep-sea hydrothermal vents in the north-western Pacific. *Journal of Crustacean Biology* 40 (5): 556-562. <https://doi.org/10.1093/jcbiol/ruaa045>
- WRIGHT I. C. 2001. — In situ modification of modern submarine hyaloclastic/pyroclastic deposits by oceanic currents: an example from the southern Kermadec arc (SW Pacific). *Marine Geology* 172: 287-307.
- WRIGHT I. C., STOFFERS P., HANNINGTON M., DE RONDE C. E. J., HERZIG P., SMITH I. E. M. & BROWNE P. R. L. 2002. — Towed-camera investigations of shallow-intermediate water-depth submarine stratovolcanoes of the southern Kermadecarc. *Marine Geology* 185: 207-218. [https://doi.org/10.1016/S0025-3227\(01\)00285-7](https://doi.org/10.1016/S0025-3227(01)00285-7)
- YANG J.-S., NAGASAWA H., FUJIWARA Y., TSUCHIDA S. & YANG W.-J. 2010. — The complete mitogenome of the hydrothermal vent crab *Gandalfus yunohana* (Crustacea: Decapoda: Brachyura): a link between the Bythograeidea and Xanthoidea. *Zoologica Scripta* 39 (6): 621-630. <https://doi.org/10.1111/j.1463-6409.2010.00442.x>

Submitted on 5 March 2025;
accepted on 3 June 2025;
published on 18 December 2025.