

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)

Danièle GUINOT

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 Mabilie (zoosyst@mnhn.fr)

MISE EN PAGE / *PAGE LAYOUT*: Anne Mabilie

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*:

Still frame from video (190527174907236_15_1080) of the vent site La Scala in Woodlark Basin: see numerous *Austinograea chubacarc* n. sp. among gastropods *Alviniconcha* Okutani & Ohta, 1988. In the middle of the still, see two crabs copulating: the small male, below, holds the much larger female with its two chelae.

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

***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)**

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

Submitted on 16 July 2024 | Accepted on 25 September 2024 | Published on 15 April 2025

urn:lsid:zoobank.org:pub:FF6E38D0-DBEF-41B9-B200-6D9A61E5C77B

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>

ABSTRACT

Collected in the Woodlark Basin and Manus Basin during the French CHUBACARC 2019 cruise, a species of the genus *Austinograea* Hessler & Martin, 1989 (Bythograeidae Williams, 1980) was found to be distinct from its four congeners from the western Pacific: *A. williamsi* Hessler & Martin, 1989, *A. alayseae* Guinot, 1990, *A. hourdezi* Guinot & Segonzac, 2018, and *A. jolliveti* Guinot & Segonzac, 2018. Established here as *A. chubacarc* n. sp., it displays an original and unique character, which is regarded as having specific importance, namely in the male a narrow depression on the upper margin of the dactylus of the major chela (but not in the female). The presence of *A. chubacarc* n. sp. at a depth of around 1750 m in the Manus Basin and at a much greater depth, around 3388 m, in the Woodlark Basin reinforces the view that the brachyuran community of Woodlark, although very deep, can be connected to much shallower populations in the Manus Basin, as has already been demonstrated by the barcoding studies of vent gastropod species. New records of *A. alayseae* and of *A. hourdezi* are also reported.

RÉSUMÉ

Austinograea chubacarc n. sp. des bassins de Manus et Woodlark (Pacifique occidental), et nouveaux signalements d'*A. alayseae* Guinot, 1990 et *A. hourdezi* Guinot & Segonzac, 2018 (Crustacea, Decapoda, Brachyura, Bythograeidae).

Une nouvelle espèce du genre *Austinograea* Hessler & Martin, 1989 (Bythograeidae Williams, 1980), récoltée dans le bassin de Woodlark et le bassin de Manus lors de la campagne française CHUBACARC 2019, s'est révélée distincte de ses quatre congénères du Pacifique occidental : *A. williamsi* Hessler & Martin, 1989, *A. alayseae* Guinot, 1990, *A. hourdezi* Guinot & Segonzac, 2018 et *A. jolliveti* Guinot & Segonzac, 2018. Établie ici sous le nom d'*A. chubacarc* n. sp., elle présente un caractère original et unique, considéré comme revêtant une importance spécifique, à savoir, chez le mâle, une étroite dépression sur le bord supérieur du dactyle de la grande pince (et non chez la femelle). La présence d'*A. chubacarc* n. sp. à une profondeur de 1750 m environ dans le bassin de Manus et à une profondeur beaucoup plus élevée, 3388 m environ, dans le bassin de Woodlark renforce l'idée que la communauté brachyourienne de Woodlark, bien que très profonde, peut être reliée à des populations beaucoup moins profondes dans le bassin de Manus, comme l'ont déjà démontré les études de barcoding d'espèces hydrothermales de gastéropodes. De nouveaux signalements d'*A. alayseae* et d'*A. hourdezi* sont également rapportés.

KEY WORDS
CHUBACARC 2019
cruise,
hydrothermal site,
western Pacific,
Lau Basin,
genus *Austinograea*,
new records,
new species.

MOTS CLÉS
Campagne
CHUBACARC 2019,
site hydrothermal,
Pacifique occidental,
bassin de Lau,
genre *Austinograea*,
signalements nouveaux,
espèce nouvelle.

INTRODUCTION

The French multidisciplinary CHUBACARC 2019 cruise in the western Pacific Ocean on board of the R/V *L'Atalante* aimed to sample the hydrothermal fauna at 18 different vent fields from five hydrothermal zones spanning 5000 km: Lau Basin, Futuna Volcanic Arc, North Fiji Basin, Woodlark Basin, and Manus Basin (Fig. 1) (Hourdez & Jollivet 2023). The possible connectivity of deep vent populations within and between the back-arc basins of the western Pacific, which altogether represents a discontinuous ridge system, needed to be studied. The inventory of the biodiversity of each area of the basins investigated has so far focused mainly on certain invertebrates so that many organisms belonging to numerous hydrothermal-associated groups have already been studied, combining morphological descriptions and genetic sequence datasets (e.g. Chabert 2021; Poitrimol 2022; Boulart *et al.* 2022; Poitrimol *et al.* 2022; Castel *et al.* 2022).

Our current project is to devote two taxonomic papers to the brachyuran crabs collected during the CHUBACARC 2019 cruise, of which the material was not sent to us in its entirety (S. Hourdez, pers. comm. June 3, 2024). The purpose of this first article is the description of a new bythograeid species, established here as *Austinograea chubacarc* n. sp., which has been found in two basins: in the Woodlark Basin on La Scala vent Field at a great depth, c. 3388 m, and in the Manus Basin only at c. 1750 (Fig. 2). This new species of *Austinograea* Hessler & Martin, 1989 (Bythograeidae Williams, 1980) proved to be distinct from its four western Pacific congeners: *A. williamsi* Hessler & Martin, 1989, *A. alayseae* Guinot, 1990, *A. hourdezi* Guinot & Segonzac, 2018, and *A. jolliveti* Guinot & Segonzac, 2018. A second article will consist mainly of the revision of *A. jolliveti* and the description of a new species collected on the Futuna Volcanic Arc (exclusively on the Kulo Lasi Volcano), a species close to, although different from, *A. jolliveti*: this study, with P. K. L. Ng, is ongoing.

REMARKS

Previous papers by various geneticists, such as Mateos *et al.* (2012: 9, 10, figs 2, 3) have shown that the Bythograeidae (and *Bythograeoidea* Williams, 1980) include two distinct clades: one comprising members of the genus *Bythograea* Williams, 1980, and the other containing the remaining genera. The phylogenetic analysis by Lee *et al.* (2019b: 9) found two main clades of bythograeid crabs: “a Bythograea clade” and “a clade composed of *Austinograea*, *Gandalfus* [McLay, 2007], *Allograea* [Guinot, Hurtado & Vrijenhoek, 2002], *Cyanograea* [Saint Laurent, 1984] and *Segonzacia* [Guinot, 1989]” (see also Leignel *et al.* 2017). However, recent genetic studies by the author and colleagues have found strong support for two groups that are not sister groups, but are unrelated lineages. Ongoing unpublished morphological and genetic studies by the author with her colleagues show the same pattern.

The origin of the bythograeids *sensu lato*, which represent a ubiquitous and abundant group of macroinvertebrates that colonised deep-sea hydrothermal vents, is not yet resolved (see Yang *et al.* 2013).

Several genetic analyses have been conducted on bythograeids: on *Austinograea williamsi* Hessler & Martin, 1989, the type species of the genus; on *A. alayseae* Guinot, 1990; and on other species of the western Pacific. The monophyly of the group *Austinograea-Gandalfus*, supported by the molecular analysis of Mateos *et al.* (2012: 11), is confirmed by morphology. Mateos *et al.* (2012: 10, fig. 2) found that nucleotide divergence for the mitochondrial 16S rDNA gene between *Austinograea* aff. *williamsi* [i.e., *A. hourdezi*] and *A. williamsi* was 5.5%; between *A. aff. williamsi* [i.e., *A. hourdezi*] and *A. alayseae* was 7%, whereas between *A. williamsi* and *A. alayseae* it was 5.9%. Wang *et al.* (2024: fig. 3) recognised a family Bythograeidae, with three assemblages: *A. alayseae* + *A. rodriguezensis* Tsuchida & Hashimoto, 2002; *Gandalfus puia* McLay, 2007 + *G. yunohana* (Takeda, Hashimoto & Ohta, 2000); and *Segonzacia mesatlantica* Williams, 1988. Similarly, Tan *et al.* (2018: fig. 1) recovered two groups; one with *Austinograea alayseae* and *A. rodriguezensis*; and another one with *Gandalfus puia* and *G. yunohana*. The complete mitogenome of *Gandalfus yunohana* was determined by Yang *et al.* (2010); that of an *Austinograea* sp. collected from the Carlsberg Ridge, the mid-ocean ridge in the northwestern Indian Ocean, which is probably *A. rodriguezensis*, by Xu *et al.* (2020).

Environmental DNA metabarcoding (eDNA) was made by Komai *et al.* (2019: table 1) for ‘*Austinograea alayseae* Guinot, 1990’ and ‘*A. alayseae*’. Genomic DNA extraction, sequencing and gene annotation of *A. alayseae* were performed by Kim *et al.* (2013). Kim *et al.* (2014: table 1) found slight genetic differences (82.29% nucleotide similarity) between individuals (assumed to be *A. alayseae*) from the Manus Basin and the Tofua Volcanic Arc, 24°6'S, 176°9'W, east of the Lau Basin, located about 3000 km apart in the southwestern Pacific. Based on *Austinograea alayseae* (collected from the South China Sea, 3°42'47.259"S, 151°52'50.084"E, at a depth of 1995 m and a temperature of 1.01°C), a species with vestigial eyes and in which chemical communication should be the predominant mode of behaviour, such as predation and mating, transcriptome analysis by Hui *et al.* (2017) revealed a comprehensive set of genes expressed in four different tissues, resulting in 725 461 unigenes and 134 489 annotated genes. Genes related to sensory, circadian rhythm, hormone, hypoxia stress, metal detoxification were identified, and, in particular, ten olfactory receptor and three gustatory receptor genes in the degraded eyestalk; most of which were involved in immune responses, indicating their important roles in crab adaptation to a harsh environment.

In a genetic study of *Austinograea alayseae* from three adjacent vent systems (Manus Basin, North Fiji Basin, and Tonga Arc), using the sequences of two mitochondrial genes (COI and 16S rDNA) and one nuclear gene (28S rDNA), Lee *et al.* (2019b: 6, 8, figs 2, 3, tables 4, 5) found identical 28S rDNA sequences for three *A. alayseae* populations: Manus population with 10 individuals, North Fiji population with 11 individuals and Tonga population with 17 individuals, with the Manus population differ-

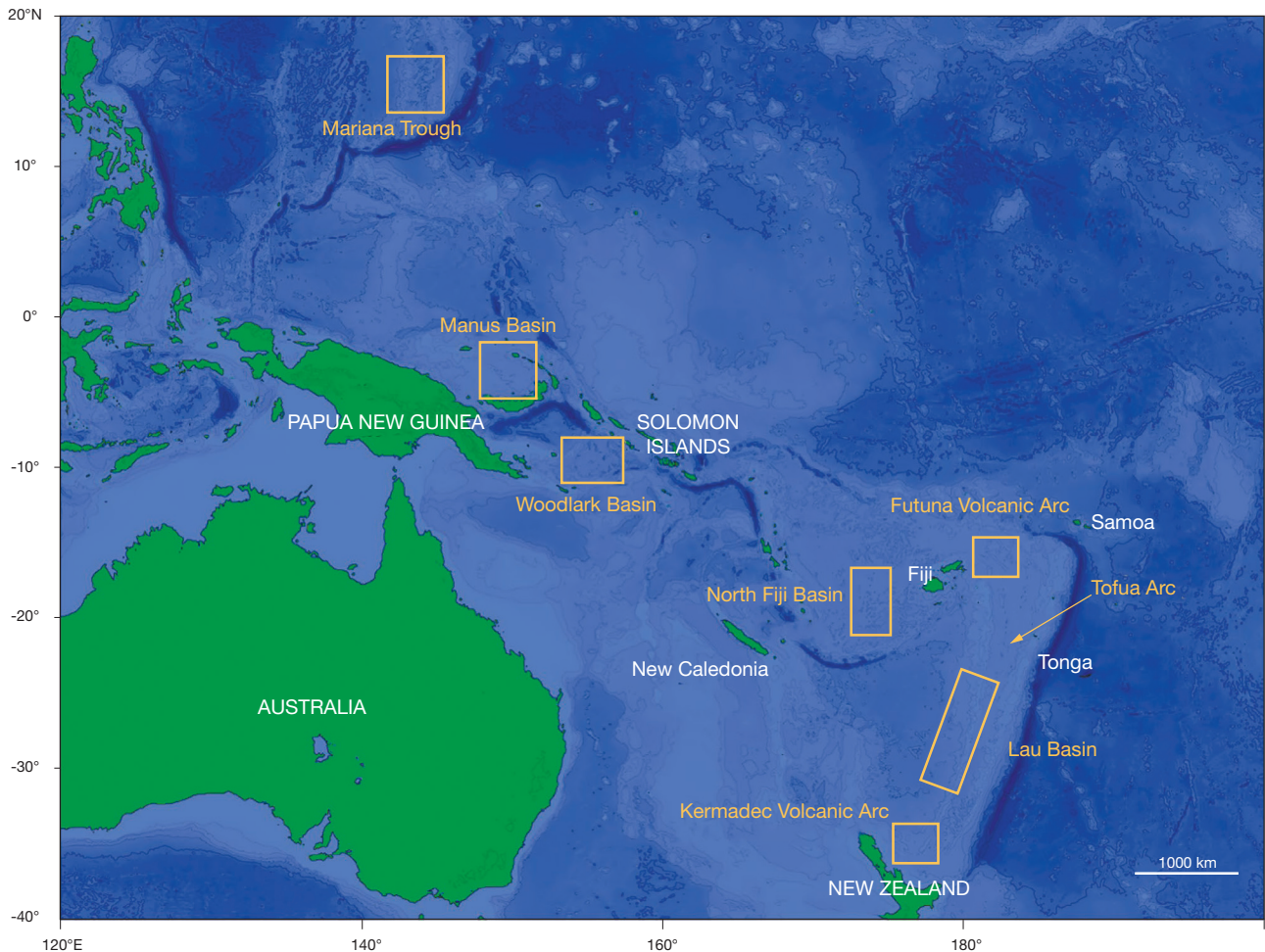


FIG. 1. — Map of the five hydrothermal areas of the western Pacific explored by the CHUBACARC 2019 cruise and sampling locations: Lau Basin, North Fiji Basin, Futuna Volcanic Arc, Woodlark Basin, and Manus Basin. The Mariana Through and Kermadec Volcanic Arc have been added. Courtesy Stéphane Hourdez.

ing significantly from the North Fiji and Tonga populations, and without any difference between the North Fiji and Tonga populations. They recognised two segregated populations formed in the Manus and North Fiji-Tonga regions, corresponding to two clades: a Manus clade and a North Fiji-Tonga clade, despite the current absence of morphological traits enabling them to be distinguished. How can we interpret these results and identify these different populations? At this phase of the research, it is not possible for us to exploit or use the results of all these genetic analyses, namely to relate the species thus investigated to those we have described previously (Guinot 1990; Guinot & Segonzac 2018).

MATERIAL AND METHODS

Measurements provided (in mm) are for the carapace length followed by the maximum carapace width. The material examined is deposited in the Muséum national d'Histoire naturelle (MNHN), Paris.

PROVENANCE OF OF THE MATERIAL STUDIED

The Woodlark Basin (Figs 1; 2), located in the Solomon Sea, is one of the few places on Earth where active seafloor spreading into continental crust can be studied (Laurila *et al.* 2012). Composition analysis has highlighted a split between the western basins (i.e., Manus and Woodlark) and the eastern basins (North Fiji and Lau Basins) and also the Futuna Volcanic Arc (Poitrimol 2022: 32, 150, table 3.4.B). Incipient speciation may be underway in the Manus Basin for a crab population, whereas no exchange is detected with the Lau or North Fiji Basins (Lee *et al.* 2019b). The discovery and sampling of hydrothermal biological communities in the Woodlark Ridge may help to establish an intermediate milestone between the Lau Basin in the east and the Manus Basin in the west. Some hydrothermal species are clearly endemic to the Woodlark Ridge, with specific attributes due to the greater depth (3388 m b.s.l.) at which the vent sources are located, compared to the shallower vent sites in the Manus Basin. Other species may use the Woodlark Ridge as a stepping stone during the colonisation of the present day back-arc basins of the Western Pacific. Preliminary barcod-

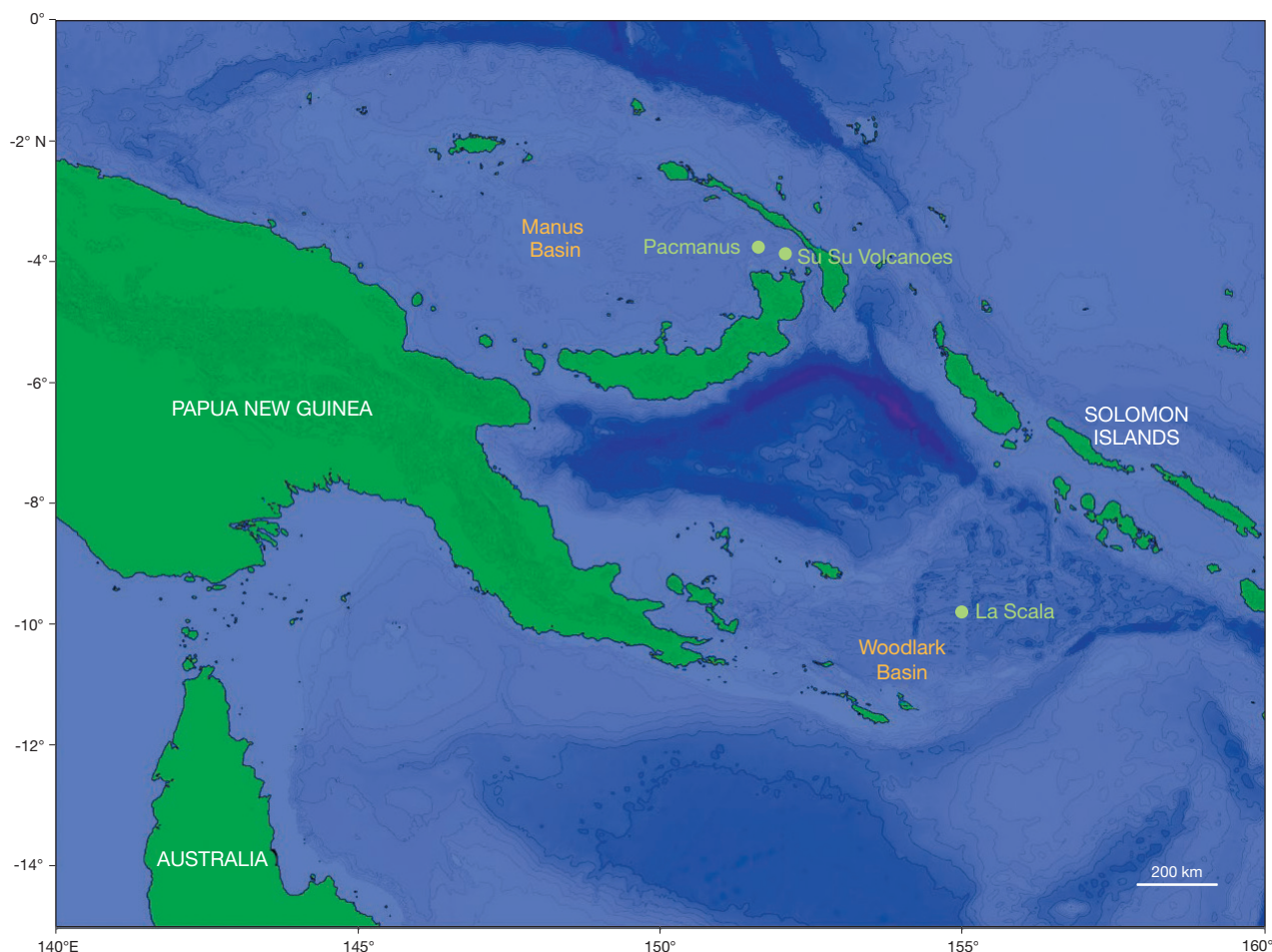


FIG. 2. — Map showing the Woodlark Basin (with the La Scala vent Field) and Manus Basins (with the Pacmanus vent Field). Courtesy Stéphane Hourdez.

ing analyses of key species suggest that the Woodlark Basin may act as a biodiversity dispersal centre for hydrothermal vent fauna and as a crossroad between the east/west basins in this region of the Pacific (Boulart *et al.* 2022). Studying the crabs found in the Woodlark Basin, well sampled by the CHUBACARC 2019 cruise (Hourdez & Jollivet 2023: 74, table 11), will allow us to test these hypotheses.

We have identified as a new species several samples of *Austinograea* collected at the La Scala Vent Field, discovered in segment 3B of the Woodlark Ridge of the CHUBACARC 2019 cruise (see Material examined), the only vent site in the Woodlark Basin (Fig. 2) at about 3388 m b.s.l. and with high-temperature hydrothermal activity. It extends over the slopes of a submarine relief of the Woodlark ridge over nearly 70 m depth and comprises two main very active areas (black smoker chimneys) and several inactive zones dominated by variably altered basaltic rocks, indicating that an active and stable hydrothermal circulation has been maintained over a long period (Boulart *et al.* 2022: 1). The La Scala vent Field is characterised by very large beds of gooseneck barnacles colonising diffusion areas that are poorly active on old chimneys. At the top of the site and on its periphery, black smokers are

very active (Hourdez & Jollivet 2023: 74, figs 5, 6, 11, 71, tables 2, 10, 11).

In the Woodlark Basin, Boulart *et al.* (2022: 8, 10, 14) reported that copepods, the shrimp *Rimicaris variabilis* (Komaï & Tsuchida, 2015) and polychaetes were the dominant taxa in patches of species of the snail *Alviniconcha* Okutani & Ohta, 1988, as well as bythograeoid crabs found on black smokers. An *Austinograea* sp., depicted in their figure 5c, e, was 'likely to represent a new species'. It is possible indeed that the putative new species of these authors and the crabs depicted in their figure represent the new species described here, *A. chubacarc* n. sp.

The Manus Basin (Figs 1; 2), north of New Britain, Papua New Guinea, occupies a back-arc position relative to the New Britain arc-trench system and contains an active plate boundary (Ross *et al.* 1986). The Pacmanus vent Field extends over a large area and consists of sites with different levels of activity (Hourdez & Jollivet 2023: 63, fig. 1, and p.160, figs showing crabs). In this area, the vent site Solwara 8, located at the base of the ridge, is densely populated with animals living on chimneys, including *A. chubacarc* n. sp., represented by three specimens, and *Austinograea alayseae*.

For the list of stations of the CHUBACARC 2019 cruise, see Hourdez & Jollivet 2019 and <https://campagnes.flotte-oceanographique.fr/campagnes/18001111>

For the videos of the Chubacarc Expedition: <https://video.ifremer.fr/index> of the La Scala vent Field, PL738 (Fig. 8A), <https://video.ifremer.fr/index>

ABBREVIATIONS

Institutions

MNHN Muséum national d'Histoire naturelle, Paris;
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 maxillipeds;
P2–P5 pereopods 2–5 (first to fourth ambulatory legs, respectively);
coll. collected by;
det. identified by;
leg. donated by;
m b.s.l. metres below sea level;
♀ female;
♂ male.

Equipment (see Hourdez & Jollivet 2023)

ASPI Suction sampler;
GBT Large collection box ('Grande boîte de collecte');
Panier Basket
PBT Small collection box ('Petite boîte de collecte');
PL# Dive number #;
ROV Remotely Operated Vehicle;
R/V Research/Survey Vessel.

Genetics

CHU Code for DNA study, Stéphane Hourdez, Observatoire océanologique de Banyuls-sur-mer.

SYSTEMATICS

Section EUBRACHYURA Saint Laurent, 1980
Subsection HETEROTREMATA Guinot, 1977
Family BYTHOGRAEIDAE Williams, 1980

Genus *Austinograea* Hessler & Martin, 1989

TYPE SPECIES. — *Austinograea williamsi* Hessler & Martin, 1989, by original designation and monotypy.

REMARKS

The genus *Austinograea* currently consists of four species in the western Pacific: 1) *A. williamsi* Hessler & Martin, 1989, which seems to be confined to the northwestern Pacific, in the Mariana Back-Arc Basin (just west of the Mariana Island Arc) and found in abundance in snail beds filling the vent openings of the Mariana Trough; 2) *A. alayseae*, originally collected from the Lau Back-Arc Basin, subsequently found distributed across hydrothermal vent areas in the Southwest

Pacific Ocean, e.g. along the Eastern Lau Spreading Center and also reported from the North Fiji Basin, Tonga Arc and Manus Basin (see below); 3) *A. hourdezi*, a widespread species encountered in the southwestern Pacific from numerous vent fields of the Lau and North Fiji Back-Arc Basins, now identified in the Woodlark Basin (see still from the video 190527174907236_15_1080 of La Scala vent Site) (Fig. 8A) and which cohabits with *A. alayseae* at a number of sites (see below); and 4) and the rare and enigmatic *A. jolliveti* from the southwestern Pacific, collected so far only from one site in the Lau Basin (ABE Site) and one site in the North Fiji Basin (Mussel Valley Site). Another species, *A. rodriguezensis* Tsuchida & Hashimoto, 2002, is located well apart, in the western Indian Ocean. The new *Austinograea* found in the Woodlark and Manus Basins described here would be the sixth species of the genus.

Austinograea chubacarc n. sp. (Figs 3–7; 8A, B)

urn:lsid:zoobank.org:act:4946C58F-0337-4C49-8898-CF60271B3265

Austinograea sp. – Boulart *et al.* 2022: 7, 8, ?fig. 5c, e.

Crabs – Hourdez & Jollivet 2023: 74, tables 10, 11.

TYPE LOCALITY. — Woodlark Basin, La Scala vent Field.

TYPE MATERIAL. — **Holotype.** SW Pacific • ♂ 22.8 × 35.7 mm, right-handed; Woodlark, La Scala vent Field; PL738 - ASPI2; 9°47.943'S, 155°3.160'E; 3388 m; 27.V.2019; CHUBACARC 2019 cruise; Hourdez det. *Austinograea*; Chu-025 written on carapace; MNHN-IU-2024-6548.

Paratypes. SW Pacific • 1 ♂ 6.3 × 8.1 mm, right-handed, 1 juvenile ♂ 9.8 × 14.6 mm, 1 ♀ 8.5 × 12.4 mm; Woodlark, La Scala vent Field; PL738 - ASPI3; 9°47.943'S, 155°3.160'E; 3374 m; 27.V.2019; CHUBACARC 2019 cruise; Hourdez det. *Austinograea hourdezi*; MNHN-IU-2024-6549 • 1 ♀ 13.5 × 19, 3 mm; same data as for preceding; Chu-026 written on carapace; MNHN-IU-2024-6550 • 1 ♀ 24.7 × 39.2 mm, with two chelae gaping; Woodlark, La Scala, PL738 - GBT10; 9°47.943'S, 155°3.164'E; 3388 m; 27.V.2019; CHUBACARC 2019 cruise CHU-027; MNHN-IU-2024-6092 • 1 ♀ 28.6 × 45.7 mm, right-handed, but cutter bigger than crusher; same data as for preceding; CHU-028; MNHN-IU-2018-5228 • 1 ♀ 18.2 × 28.3 mm, slightly right-handed; same data as for preceding; CHU-029; MNHN-IU-2024-6090 • 1 ♀ 17.7 × 28.3 mm, with two cutters; same data as for preceding; CHU-030; MNHN-IU-2024-6089 • 1 ♂ 15.6 × 25.0 mm, right-handed; same data as for preceding; det. *Austinograea* sp., CHU-031; MNHN-IU-2024-6036 • 5 ♀, 1 ♀ 14.6 × 22.2 mm; with two cutters; same data as for preceding; CHU-032; MNHN-IU-2024-6091 • 1 ♂ 14.0 × 22.4 mm, right-handed; same data as for preceding; Hourdez det. *Austinograea*; CHU-033; MNHN-IU-2024-6032 • 1 ♂ (right-handed) 14.3 × 22.4 mm; same data as for preceding; det. *Austinograea*; CHU-034 written on carapace; MNHN-IU-2024-6022 • 1 juvenile ♂ 11.8 × 18.3 mm, right-handed; same data as for preceding; Hourdez det. *Austinograea* sp.; MNHN-IU-2024-6034 • 1 ♂ 10.0 × 15.3 mm (without chelipeds); same data as for preceding; MNHN-IU-2018-5227.

OTHER MATERIAL. — SW Pacific • 1 ♂ 14 × 21.6 mm, left-handed (gonopods detached); Manus Basin, Pacmanus, Solwara 8, PL733 - ASPI7; 3°43.819'S, 151°40.454'E; c. 1750 m; 18.V.2019;

CHUBACARC 2019 cruise; MNHN-IU-2024-6086 • 1 ♂ 10.3 × 15.9 mm, right-handed; MNHN-IU-2024-6088 • 1 ♀ 22.5 × 34.6 mm; slightly right-handed, unreadable numbers written on carapace; MNHN-IU-2024-6087.

ETYMOLOGY. — The expedition name CHUBACARC 2019 cruise rhymes with one *Star Wars* character; and the specific name *chubacarc* is an oblique reference to *Chewbacca*, the furry hero of the popular American *Star Wars* saga by George Lucas (Lucas film), alluding to the dense setae on the internal surface of the cheliped palm of the species. The name is used as a noun in apposition.

DESCRIPTION

Carapace

Carapace transversely elliptical, flat. Dorsal surface with regions indistinct, smooth, except for a few granules on frontal and suborbital regions; may have very sparse, extremely short setae, only discernible at high magnification. Front not protruding, straight or slightly convex, bluntly pointed medially (see Variations), with tiny granules. Anterolateral margin marked by rounded edge, slightly granular proximally. Posterolateral margins convergent. Posterior margin slightly concave. Proepistome sunken, very thin. Margin of epistome formed of two minutely granular, moderately concave lobes, with a median projection. Pterygostomial lobe tuberculous; pterygostomial region smooth. Subhepatic regions covered by patches of setae (see Variations).

Cephalic structures

Eyes, antennules and antennae retracted. Suborbital plate absent. Orbit not delimited, only an orbital area that extends as groove lateral to region containing vestigial eyestalks and antennae; outer side of orbital area tuberculated. Eyestalk not moveable, showing as fixed piece fused to floor of orbital region; no cornea, no pigment. Antennules folded horizontally. Antenna inserted in wide supraorbital notch; urinary article fixed, broad, retracted; basal article (2 + 3) cylindrical, moveable, retracted; article 4 slightly elongated, inclined; flagellum short, curved.

Third maxillipeds

Third maxillipeds closing buccal cavity, except anteriorly where there is a gap between them and pterygostomial lobe. Ischium long, with marked longitudinal internal groove. Merus short; external margin entirely and regularly curved, oblique, without marked angle; distal part distinctly narrower and produced; internal margin with proximal half produced as squarish lobe. Carpus inserted in notch of antero-internal margin of merus; propodus thick, developed; dactylus thick and moderately extending beyond articulation of ischium/merus; inner margins of propodus and dactylus with some brush-like setae. Mxp3 coxa with only proximal portion visible, its lateral projection hidden by junction of thoracic sternum (sternite 4) with pterygostome. Exopod with relatively long flagellum.

Chelipeds

Chelipeds heteromorphic: distinctive heterochely (also in females, see below) and marked heterodonty, with two types of chelae. Major chela (crusher, see below) stout and short,

with blunt tips, gaping in large males; minor chela (cutter, see below) narrower, with elongate, more pointed fingers. Ischio-basis glabrous or with potentially very small setal patch. Merus relatively short, triangular in cross section; anterior border sinuous, with strong teeth; merus glabrous in males; in contrast, in females usually each with patch of setae (see Variations). Carpus glabrous on outer part, with patch of setae only along margin articulating on propodus or more developed; surface pitted. Propodus of both chelae having outer surface of palm near base of dactylus either with two coalescing spots of variable dark colour or with a single elongated spot (actually composed of two more or less coalescing spots) and another one rounded forming a depression (see holotype Fig. 3E, G), these spots more or less distinct, tending to fade, then disappearing (see Variations, below). Spots absent in females (see below). Inner surface of both chelae and fixed finger with a depressed surface on half posterior part; on internal median part of palm, thick, well-circumscribed patch of dense light brown setae, extending thinly along occluding margins.

Crusher. Palm convex, inflated, smooth, pitted, with one or two more or less distinct spots, with depressed posterior portion on inner posterior surface. Fingers thick, not gaping at occluding margins, with blunt tips; two main, proximal and median, teeth on occluding margin of dactylus, becoming blunt in large males as holotype; a marked subproximal tooth and two smaller ones on occluding margin of fixed finger, becoming blunt, and only one remaining in large males as holotype. Median surface of thick dactylus of major male chela hollowed out by deep depression extending distally into fissure, becoming thinner and up to subdistal portion of dactylus (see Variations), this character constituting the most distinctive trait of the species. In females, such a depression absent, but more or less replaced along most part of dactylus by thin, interrupted line. In males, dark colour extending over approximately two-thirds of dactylus and most part of fixed finger.

Cutter. Palm elongate, with subparallel borders; surface smooth, except for two spots of different size and shape (one as a depression, like in holotype) near base of dactylus, more or less similar to those of crusher. Both fingers not gaping at occluding margins; dactylus elongate, hollowed, with occluding margin smooth; fixed finger very thick, depressed on inner surface; occluding margin nearly straight, with two or three small teeth, decreasing in size gradually forward, becoming blunt in large individuals. In males, dark colour extending over approximately most part of both dactylus and fixed finger, but sometimes fading.

In females, both chelae either similar and showing as two elongate and thin cutters or slightly heteromorphic and showing as a crusher and a cutter but without significant differences between them. Palm and fixed finger with posterior half part markedly depressed. Fingers very long, narrow, without depression on superior margin of dactylus, sometimes being replaced by thin interrupted line along most of dactylus of crusher; this line sometimes indistinct, for example in female



FIG. 3. — *Austinograea chubacarc* n. sp., holotype, ♂ 23.8 × 35.7 mm, right-handed, Woodlark, La Scala, PL738 - Aspi2 (MNHN-IU-2024-6548). **A**, dorsal view; **B**, ventral view; **C**, ventral surface of cheliped with large setal patches inside chela and fingers, and smaller on ischio-basis and carpus; **D**, ventral surface of pleon and telson showing deep socket on somite 6; **E-H**, right and left chelae, inner surface with setal patch and outer surface with two spots (**E**, **F**, crusher; see the depression on the dactylus; **G**, **H**, cutter); **I**, thoracic sternum and gonopods *in situ*; **J**, G1 crossing distally and with tips but not lodging in special distal depression of sterno-pleonal cavity, and G2. Scale bars: A, B, C, I, 10 mm; E, F, G, H, 5 mm; D, J, 2 mm (credits: MNHN-Soubzmaigne).



FIG. 4. — *Austinograea chubacarc* n. sp., paratype, ♂ 14.3 × 22.4 mm, right-handed, Woodlark, La Scala (MNHN-IU-2024-6022). **A**, dorsal view; **B**, frontal view; **C**, ventral view; **D**, thoracic sternum, with pleon; **E**, **F**, two frontal views and chelipeds (see the deep depression on dactylus of major chela). Scale bars: A, C, E, F, 5 mm; B, D, 1 mm (credits: MNHN-Soubzmaigne).



FIG. 5. — *Austinograea chubacarc* n. sp., paratype, ♂ 14.3 × 22.4 mm, right-handed, Woodlark, same data as for fig. 4 (MNHN-IU-2024-6022): **A**, ventral anterior view: mpx3, thoracic sternum; **B**, thoracic sternum and gonopods *in situ* crossing at tips but not lodging in distal depression; **C**, **E**, right and left chelae, outer surface of palm and fingers: crusher (**C**) with blunt tips; no coloured spot visible at outer surface of palm near base of dactylus; see deep depression on dactylus; cutter (**E**); **D**, **F**, right and left chelae, inner surface: palm and proximal portion of fingers with setal patches on mid part and with depressed half posterior part: crusher (**D**), cutter (**F**). Scale bars: A, C, D, E, F, 5 mm; B, 1 mm (credits: MNHN-Soubzmaigne).

22.5 × 34.6 mm, MNHN-IU-2024-6087 (Fig. 7C, D), with dark (reddish) colour very marked, located only in subdistal tips of both dactylus and fixed finger. Inner surface of palm with well circumscribed thick patch of dense light brown setae, weakly extending along occluding margins; patches of setae also present on ischio-basis and proximal part of carpus and merus.

Ambulatory legs

P2-P5 shorter than chelipeds; P3 and P4 longest. Ischio-basis, merus and propodus with thick patches of dense setae on ventral margins (thicker on P2 and P3, weak on P5), mixed with sparse longer setae; superior border of carpus and propodus fringed with setae. Dactyli relatively stout, also with patches of short setae.

Thoracic sternum

Thoracic sternum with incomplete sutures 4/5-7/8, separated by short gap; suture 2/3 complete. Median line only along sternite 8. Junction of sternite 4 with pterygostome only represented by short juxtaposition. At level of antero-external portion of sternite 4 and of episternites 5, 6, 7, some setal patches in males, denser in young adult females, and, in larger females, becoming well circumscribed patches with decreasing size from front to back. Press-button of locking mechanism very acute, close to suture 5/6.

Pleon

Male pleon of six free somites and telson, regularly triangular; pleonal somites 1, 2 dorsally exposed; pleonal somite 3 widest; pleonal somite 6 longest; telson triangular, slightly rounded distally. On posterior angles of somite 6, a deep socket delineated by raised, thick margin.

Penis and gonopods

Penis emerging from anterior margin of coxo-sternal P5 condyle. Both G1 crossing subdistally, joining at tips, the latter not lodged in special depression but normally ending in relatively wide extremity of sterno-pleonal cavity at this level. G1: slender, faintly curved, with only short, small spiniform setae arranged in two rows along mid-part only. G2: short, a little less half length of G1, bent to slightly less three-quarters of length at level of small setiferous area; flagellum curved, flattened, bladelike.

Vulvae

Vulvae big, rounded, occupying most of sternite 5, with thick curved membrane on inner side; large median opening.

VARIATIONS

In males, the depression on the superior margin of the major cheliped dactylus is relatively long and deep, both in the right-handed male holotype 22.8×35.7 mm (MNHN-IU-2024-6548) (Figs 3E; 8) and in the right-handed paratype male 14.3×22.4 mm (MNHN-IU-2024-6022) (Figs 4E, F; 5C) from the Woodlark Basin. Only in a small right-handed paratype male 15.6×25.0 mm (MNHN-IU-2024-6036), the depression is shallow and short, as if atrophied (Fig. 6D), whereas in the right-handed juvenile paratype male 11.8×18.3 mm (MNHN-IU-2024-6034) the depression of the dactylus is already present and as developed as in the holotype. Such a depression is absent in female chelae (Fig. 7A, C).

The frontal margin is straight or slightly bluntly pointed medially (Figs 3A; 4A, B, E, F; 5A).

The degree of setation varies: it is more developed in females, particularly on the subhepatic area and in the latero-anterior angles of sternite 4; there are usually patches of setae on the ischio-basis and carpus of the chelipeds of females and, at less extent, in large males such as the holotype (Fig. 3C); but the merus is glabrous in males (Figs 3C, I; 4C). The setal patch on the suborbital margin is regularly dense (such as in the holotype, Fig. 3B) or denser medially than externally.

The spots on the outer surface of the male palm are variable but usually present in *Austinogreaa chubacarc* n. sp. from the Woodlark Basin, whereas spots are absent on the chelae of females (Fig. 7C, E). In the right-handed holotype ♂ 22.8×35.7 mm (MNHN-IU-2024-6548) (Fig. 3E), the palm of the major chela bears two dark spots, an elongated one with a depression near the base of the dactylus and a rounded one in a depression at its upper middle, whereas the minor chela has two coalescent spots, the upper one with depression (Fig. 3G). Only a trace, difficult to perceive (and not really visible in the photograph), can be guessed on the minor chelae of the right-handed male 14.3×22.4 mm (MNHN-IU-2024-6022) (Fig. 4C, E, F). In the right-handed male paratype 14.3×22.4 mm (MNHN-IU-2024-6036) (with an atrophied depression), two spots are visible on the palm of the minor chela, whereas only one is clearly visible and a second one barely discernible on the palm of the major chela (Fig. 6D). In *A. chubacarc* n. sp. from the Manus Basin, only one spot is clearly visible on each chela of the left-handed male 14×21.6 mm (MNHN-IU-2024-6086) and in the right-handed ♂ 10.3×15.9 mm (MNHN-IU-2024-6087).

REMARKS

Austinogreaa chubacarc n. sp. differs from all known species of *Austinogreaa* in that the movable finger – the dactylus – of the male major chela has a long, deep depression (it can also be defined as a ‘wide groove’) on its outer superior border (Figs 3E; 4E, F); this depression is absent in females. Such a deeply grooved dactylus is an unusual, unique feature that we have never observed in other brachyuran crabs, and its function remains unclear. It is a singular species character admittedly but it is probably not that weird. Many crabs do have the outer surface of the dactylus lined with narrow grooves and, in some cases, there is a dorsal crest that highlights the longitudinal groove. Are these structures homologous?

Interestingly, the depression on the dactylus of *A. chubacarc* n. sp. can be discerned on the major palm of certain crabs seen *in situ* from video images (Fig. 8B, close-up).

The overall shapes and occlusal geometries of the cheliped dactylus (which probably correspond strongly with diet) and its micro- and ultrastructure have been described in detail, with each cheliped having a range of mechanical advantages at its disposal and a diversity in occlusive design (e.g. Brown *et al.* 1979: 157; Masunari *et al.* 2015, 2020). Agnew (2008), who investigated the evolutionary patterns of the dactylus in decapod crustaceans, including the fossils (where the mobile finger is often the only represented remnant in fossil assemblages), and Fujiwara & Kawai (2016), for whom the decapod chela is a suitable structure to analyse the evolutionary process of functional diversifications, do not mention the existence of such a curious feature (namely the wide groove on the dactylus) that cannot alter in any way – apparently – the crushing, chipping, gripping and pinching abilities of the dactylus.

Austinogreaa chubacarc n. sp. has fairly strong chelae in both males (Figs 3A-C, E-H; 4A, C E, F; 5C-F; 6D) and females (Fig. 7A-F), admittedly, without any teeth and complex armouring; however, it seems clear that chelae are used for

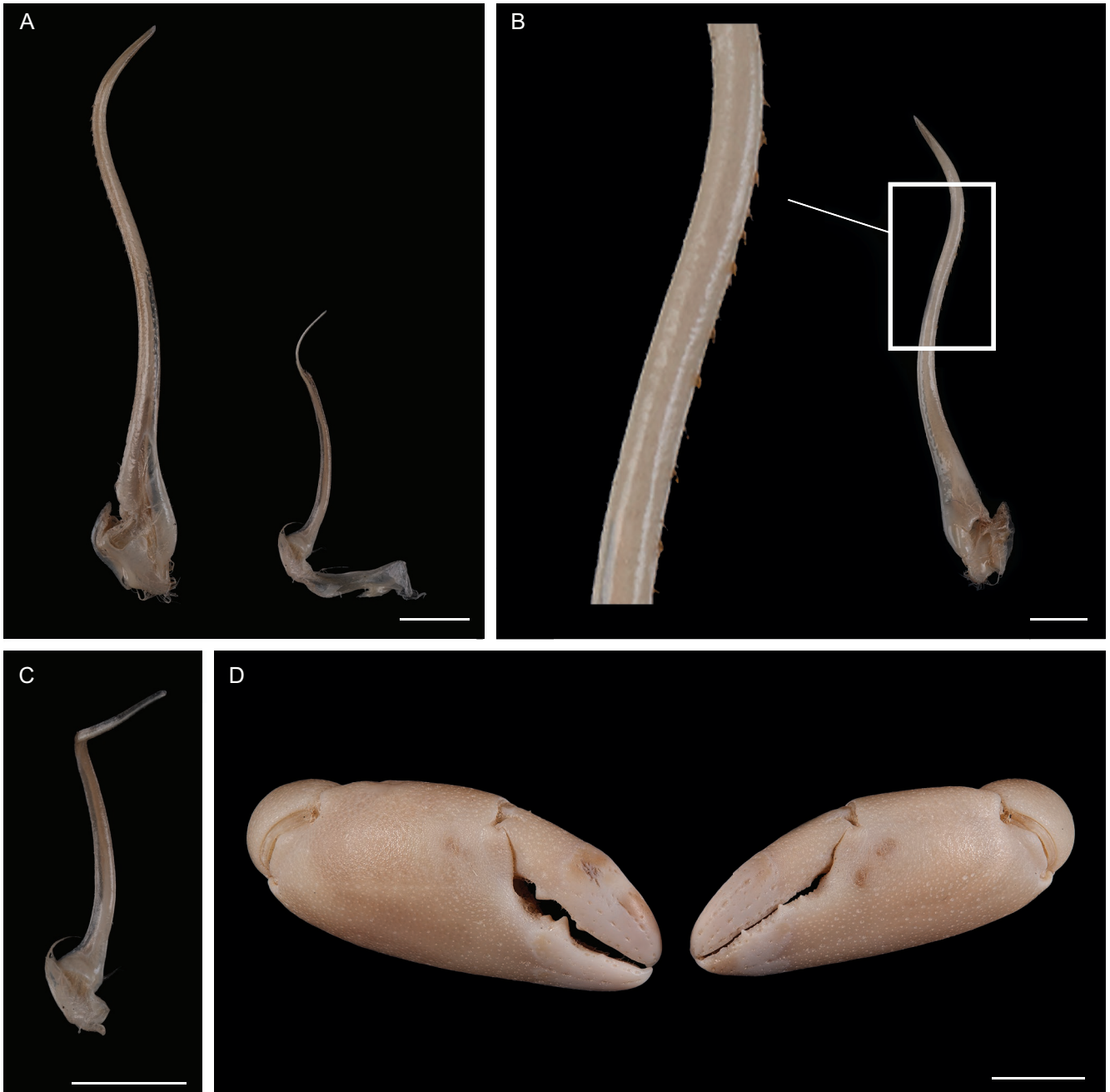


FIG. 6. — *Austinograea chubacarc* n. sp.: **A–C**, ♂ 14 × 21.6 mm, left-handed, Manus Basin, Pacmanus (MNHN-IU-2024-6086): **A**, G1 and G2 at same scale; **B**, G1 and close up to show setae; **C**, G2. **D**, paratype, ♂ 15.6 × 25.0 mm, right-handed, Woodlark, La Scala (MNHN-IU-2024-6036): dactylus with atrophied depression; outer surface of palm with one weak spot on crusher and two spots on cutter. Scale bars: A, B, C, 1 mm; D, 5 mm (credits: MNHN-Soubzmaigne).

competition and for foraging. Chelipeds, sexually dimorphic, also play a role in reproduction: although they are much less robust in males than in females, they hold the female firmly during mating (see below, Fig. 8C).

In *Austinograea chubacarc* n. sp., the outer surface of the palm may bear, near the base of the dactylus of the major and minor chelae, more-or-less coloured spots: either very dark and partly in the form of depressions, as in the male right-handed holotype 22.8 × 35.7 mm (Fig. 3E, G) and paratype 15.6 × 25.0 mm (Fig. 6D); or superficial and tending to fade or even disappear, as for example in the right-handed paratype

male 14.3 × 22.4 mm (Fig. 4E, F and see Variations). There are also two characteristic depressions on the propodus of male chelae, crusher and cutter, of *A. hourdezi* (Guinot & Segonzac 2018: figs 3A; 4A, B; 5E, G), similarly located in all the individuals examined, variously delineated by a raised margin and appearing fairly deep or shallower, and almost always coloured, appearing as dark spots. As in *A. chubacarc* n. sp., the spots are absent in the females of *A. hourdezi* (Guinot & Segonzac 2018: fig. 7E, G).

Austinograea chubacarc n. sp. shares with *A. hourdezi* the following characters: setal patches on the inner surface of

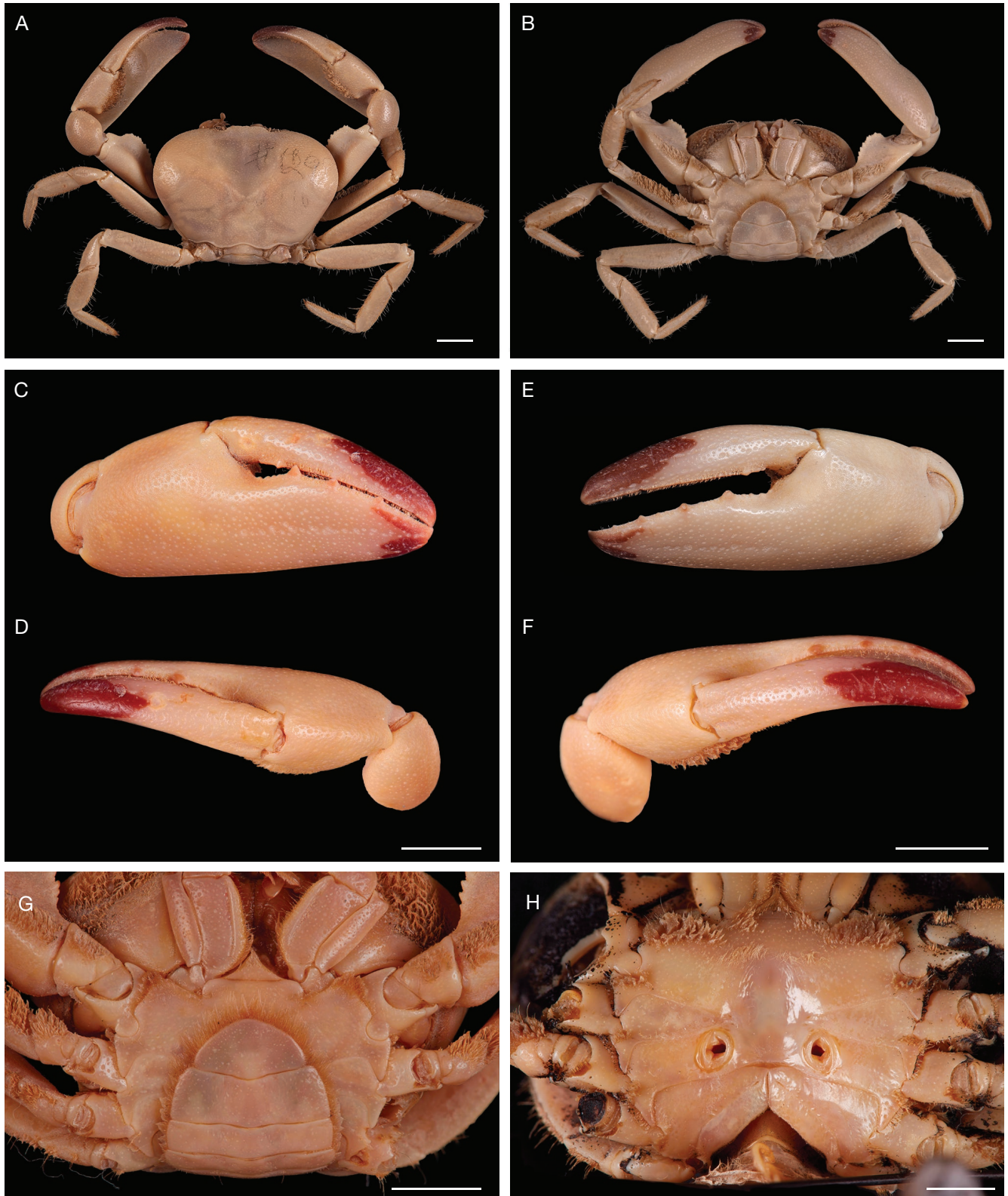


FIG. 7. — *Austinograea chubacarc* n. sp.: **A-G**, ♀ 22.5 × 34.6 mm, slightly right-handed, Manus Basin, Pacmanus (MNHN-IU-2024-6087), **A**, dorsal view; **B**, ventral view; **C-F**, right and left chelae, palm and fingers with red pigmentation: **C**, **E**, outer surface; **D**, **F**, other view: crusher (**C**, **D**); cutter (**E**, **F**); **G**, thoracic sternum and pleon; **H**, paratype, ♀ 24.7 × 39.2 mm, right-handed, Woodlark Basin, La Scala (MNHN-IU-2024-6092): thoracic sternum and vulvae; see setal patches in lateral parts of sternite 4 and at level of episternites 4-6. Scale bars: A-H, 5 mm (credits: MNHN-Soubzmaigne).

the palm of the major and minor chelae in both sexes, on the subhepatic region and on the inner surface of the legs; triangular male pleon. *Austinograea chubacarc* n. sp. and *A. hourdezi* differ in the following characters: G1 slightly curved in *A. chubacarc* n. sp., straighter in *A. hourdezi*; flagellum of G2 proportionally shorter in *A. chubacarc* n. sp. (see Fig. 6A–C); merus of mxp3 shorter in *A. chubacarc* n. sp. (Figs 4B, F; 5A, C); merus of the chelipeds cylindrical and weakly toothed in *A. hourdezi* (Guinot & Segonzac 2018: fig. 5A), instead of being shorter and with marked teeth in *A. chubacarc* n. sp. (Fig. 3A, B); thoracic sternum completely glabrous in male *A. hourdezi* (Guinot & Segonzac 2018: fig. 5C, D), whereas it has tufts of setae on the antero-external portion of sternite 4 and at level of episternites 5, 6, 7 in male *A. chubacarc* n. sp. (Figs 3I; 4D); ischio-basis and carpus of chelipeds may bear small setal patches in males and females of *A. chubacarc* n. sp. (Figs 3C; 7G, respectively), but not in *A. hourdezi*.

In *Austinograea chubacarc* n. sp. the tips of the G1s, crossing subdistally, normally end in the relatively wide extremity of the sterno-pleonal cavity at this level, instead to end in the extremity of the sterno-pleonal cavity that is narrower at this level in *A. hourdezi* (Guinot & Segonzac 2018: figs 4C, 6C). These two dispositions differ significantly from that of *A. alayseae*, in which Guinot (1990: 884, 891, fig. 2C) described the extremities of the G1 as joining in a small deep, well-delineated depression (d) at the narrow end of the sterno-pleonal cavity. In *A. jolliveti*, the morphology is quite different: the G1s are directed obliquely, separated even at their tips, and the sterno-pleonal cavity is not excavated distally, without a small special distal depression to receive the distant G1 tips (see Guinot & Segonzac 2018: figs 9B–D; 11C–E). *Austinograea chubacarc* n. sp. can be distinguished from *A. williamsi* by the G1 (Fig. 6A, B) that is more curved than that, straighter, of *A. williamsi* (see Hessler & Martin 1989: fig. 14a, c, d; Tsuchida & Fujikura 2000: figs 6; 7A; Tsuchida & Hashimoto 2002: fig. 8). In *A. rodriguezensis* Tsuchida & Hashimoto, 2000, the G1s are nearly straight (Tsuchida & Hashimoto 2002: fig. 8), but it is not known whether or not they meet at their tips: we can predict that they are distant. Note that in *Gandalfus puia* and *G. yunohana* the tips of the G1s reach the extremity of the sterno-abdominal cavity that is relatively wide at this level.

The G2 of *A. chubacarc* n. sp. (Fig. 6B, C) is short, a little less half the length of G1, bent at a slightly less three-quarters of the length.

The most diagnostic feature of *A. chubacarc* n. sp. remains the depression on the cheliped dactylus of males (Figs 3E; 4E, F).

The larval morphology may in the future confirm the distinction of *Austinograea chubacarc* n. sp. It was carried out in certain vent species from the Indian Ocean and the western Pacific: megalopa of *Austinograea rodriguezensis* from the Indian Ocean (Demidow *et al.* 2021); 16 pre-zoeal stages and first zoeal stage of *A. rodriguezensis* from Kairei Hydrothermal Vent field (Kihara *et al.* 2024), with a well-developed spinature on carapace and plenoal somites, not only attributed to defence from predators but considered an

effective adaptation that helps in the dispersal of the zoeal stages to maintain the resident population; first zoeal stage of *Gandalfus yunohana* (Nakajima *et al.* 2010); and three zoeal stages and megalopa of the same species (Hamasaki *et al.* 2010), with larval data supporting the recognition of *Austinograea* and *Gandalfus* as two distinct clades comprising *A. rodriguezensis* and *G. yunohana*, respectively (Kihara *et al.* 2024).

A phylogenetic analysis based on the CHUBACARC material was published by Chabert (2021: 26, 27, 32, table 2) for her master thesis. We support the Chabert's result (Chabert 2021: 11, 26, 32, table 2) that the specimens from the Woodlark Basin identified as 'Gen. sp. B' would be a new species: they could well belong to *A. chubacarc* n. sp.

Austinograea hourdezi
Guinot & Segonzac, 2018

Austinograea hourdezi Guinot & Segonzac, 2018: 880, figs 3A; 4A–E; 5A–H; 6A–E; 7A–H. — Lee *et al.* 2019a: fig. 1B, D. — Chabert 2021: table 2.

MATERIAL EXAMINED. — 3 ♀ 28.0 × 44.1 mm, 28.6 × 44.6 mm, 25.0 × 38.6 mm; Lau Basin, Tow Cam; PL730 – Panier; 20°19.080'S, 176°8.264'W; 2710 m; 26.IV.2019; CHUBACARC 2019 cruise; Hourdez det. *Austinograea*; MNHN-IU-2024-6023.

REMARKS

The Tow Cam Site in the Lau Basin is the type locality of *Austinograea hourdezi*, a widespread species in the southwestern Pacific, found in numerous vent fields of the Lau and North Fiji Back-Arc Basins (Guinot & Segonzac 2018: 80).

In a still from the video 190527174907236_15_1080 <https://video.ifremer.fr/index> of the La Scala vent Field, PL738 (Fig. 8A), *A. hourdezi* is easily recognised by the thick patch of setae on the inner surface of the chelipedal palm: its presence is confirmed in the Woodlark Basin at the La Scala vent Field, where it coexists with *A. chubacarc* n. sp.

Chabert (2021: table 2), using a barcode approach with the cytochrome c oxidase subunit I (COI) gene, identified *Austinograea* aff. *hourdezi* in the Woodlark Basin, and *A. hourdezi* in the North Fiji. In addition, she identified *A. aff. williamsi* in the Manus and Lau Basins, but we cannot determine which species they correspond to. S. Hourdez plans to carry out the correspondence between these genetic results and the different bythograeid species, after the publication of this paper (pers. comm.).

We did not identify *A. williamsi* among the bythograeids collected during the CHUBACARC 2019 cruise, and so far the species appears to be endemic to the Mariana Trough, a back-arc basin in the northwest Pacific (Fig. 1) (Kojima & Watanabe 2015).

Lee *et al.* (2019a), who determined the COI sequence of *Austinograea hourdezi* from three hydrothermal vent regions in the North Fiji Basin, found that all were identical. Lee *et al.* (2019b: 10, tables 3, 4, S1 table) obtained sequences of two mitochondrial genes (COI and 16S rDNA) of the species.

Austinograea alayseae Guinot, 1990

Austinograea alayseae Guinot, 1990: 880, 898, figs 1-3, pl. 1 figs A-F. — Guinot & Segonzac 2018: 75, 79, 76, 78, 96 (key), 99, 100, 101. — Tsuchida & Fujikura 2000: 407, 413. — Tsuchida & Hashimoto 2002: 643, 646, 647, 649 (key), figs 5, 6, 8. — Kim *et al.* 2013: 1, 2, 5-9, fig. 2, tables 1-3. — Lee *et al.* 2019b: 2, 3, 6-11, figs 1-3, tables 2, 3-5, S1.

MATERIAL EXAMINED. — **SW Pacific** • 1 young ♀, without chelae; Manus Basin, PL733 - PBT7; SnowCap/Big papi; 3°43.263'S, 151°40.485'E; 1669 m; 19.V.2019; CHU-512; MNHN-IU-2024-6027 • 1 very small ♀ with one chelae; Manus Basin, Pacmanus; PL734 - ASPI3; 3°43.040'S, 151°40.375'E; 1769 m; 19.V.2019; MNHN-IU-2024-6081 • 1 ♀ 16.3 × 24.6 mm, native right-handed; Manus Basin; PL736 - Aspi7, North Su/Solwara 1; 3°47.957'S, 152°6.090'E; 1195 m; 23.V.2019; CHU-510; Hourdez det. *Austinograea*; MNHN-IU-2024-6024 • 4 ♀: 1 ♀ 33.9 × 53.2 mm, left-handed, CHU-660; 1 ♀ 30.6 × 48.3 mm, with two cutters, the left being bigger, CHU-661, 1 ♀ 28.5 × 35 mm, with two cutters, the left being bigger, 1 ♀ 28.8 × 45.4 mm, native right-handed; PL736 - GBT3, North Su/Solwara 1, PL736 - GBT3; 3°47.942'S, 152°6.060'E; 1210 m; 22.V.2019; Hourdez det. *Austinograea* sp., CHU-662; MNHN-IU-2024-6028 • 1 ♀ 35.5 × 57.7 mm, left-handed; Manus Basin; PL736 - GBT4, North Su/Solwara 1; 3°47.957'S, 152°6.090'E; 1195 m; 23.V.2019, Hourdez det. *Austinograea*; CHU-509; MNHN-IU-2024-6030 • 1 ♂ 9.7 × 14.2 mm, right-handed; Manus Basin; PL734 - GBT4; 3°43.649'S, 151°40.866'E; 1725 m; 19.V.2019; Roman's Ruins/Solwara 6, 7 and 8; Hourdez det. *Austinograea*; CHU-513; MNHN-IU-2024-6025 • 1 ♀ 12.0 × 18.0 mm, native right-handed; same data as for preceding; Hourdez det. *Austinograea*, CHU-514 MNHN-IU-2024-6029 • 1 ♀ 26.2 × 41.2 mm, native right-handed; Manus Basin; PL737 - Panier, South Su, Pacmanus area; 3°48.565'S, 152°6.314'E; 1330 m; 24.V.2019; Hourdez det. *Austinograea* sp.; MNHN-IU-2024-6031.

OTHER MATERIAL. — We add one specimen collected in high temperature vent site by the BAMBUS cruise in 2011 (see participants in Bach *et al.* 2011), and sent to the MNHN in 2011 (see Bach *et al.* 2011).

SW Pacific • 1 ♂ 12.9 × 20.5 mm, left-handed; Manus Basin, site Pacmanus, R/V *Sonne*; ROV QUEST; BAMBUS cruise; éch. 49 ROV 5, site Solwara 8/Fenway; 03°43.72'S, 151°40.33'E; 1716 m; 9.VII.2011; W. Bach coll., ex-Bremen University collection, M. Segonzac det. ?*A. alayseae*, XII.2011 (but not studied further MNHN-IU-2024-6068).

REMARKS

Austinograea alayseae, originally collected in the Lau Back-Arc Basin, west of the Tonga Islands, along the Valu Fa Ridge, at around 176°38'W and between 22°34'S and 22°10'S, at 1750 m depth (Guinot 1990) and already found in the Eastern Lau Spreading Center (Corbera & Segonzac 2010; Podowski *et al.* 2010; Sen *et al.* 2013, 2014, 2016) (Fig. 1), is distributed over a wide geographical range. It has been reported from the North Fiji Basin (Jollivet *et al.* 1989, as bythograeid sp.; Guinot 1997 in Desbruyères & Segonzac 1997; Galkin 1997; Hashimoto *et al.* 1999, as bythograeid sp.; Guinot & Segonzac 2006a; Desbruyères *et al.* 2006; Shields & Segonzac 2007), and from the Tonga Arc and Manus Basin (Lee *et al.* 2019b). It has been reported from both active and inactive sites (Kowalczyk and Binns sites, respectively) (Erickson *et al.* 2009).

All the *Austinograea alayseae* material from the CHUBAC-ARC 2019 cruise studied here was collected in abundance in the Manus Basin, and more precisely in the Pacmanus

area. Scavenger and carnivore, abundant at vent openings, crawling actively on snail thickets, this species dominates the Manus Basin fauna (Galkin 1992, 1997: fig. 1; Tsuchida & Hashimoto 2002; López-González *et al.* 2005; Guinot & Segonzac 2006; Lee *et al.* 2019b: table 2). Females of *A. alayseae* are much more numerous and reach a much larger size than males: the maximum size of males in the material from the CHUBACARC 2019 cruise is 14.2 mm carapace wide, that of females is 57.7 mm wide. In the material from the Vai Lili Site of Lau Basin studied by Guinot (1990: 899), the largest male measured 51.3 mm carapace wide, and the largest female 63 mm.

According to Chabert (2021: 11, 26, 32, table 2), phylogenetic analysis, which allowed her to define the delimitation of nine bythograeid species in the Woodlark Basin, has demonstrated the presence within the morpho-species *Austinograea alayseae* of at least three cryptic species, each with different distributions. Her study recognised in the Woodlark Basin: two specimens of '*A. alayseae* A' (also present in the North Fiji and Lau Basins, and the Futuna Volcanic Arc), five specimens of 'Gen. sp. B' (apparently endemic to the La Scala vent Field), one specimen of the 'Gen. sp. C', and one specimen of '*A. aff. hourdezi*'. Unfortunately, from the material analysed by Chabert (2021: table 2, p. 15), we received only the one that identified as '*A. alayseae* A'. As, we did not obtain the material identified as '*A. alayseae* B, C and D', in this article we will leave aside the interpretation of these results.

In the Manus Basin, Chabert (2021: 27, 32, table 2) did not report a 'Gen. sp. B' but recognised seven '*Austinograea alayseae* B' there, which were not located in any other basin, and one specimen of *A. aff. williamsi*, which she also found, with two specimens, in the Lau Basin. The material in our hands, however, does not allow us to relate these various *Austinograea* to any known species.

DISCUSSION

Austinograea chubacarc n. sp. is distributed in the Woodlark and Manus Basins. In the Woodlark Basin, the dive PL738 at the La Scala vent Field was at around 3888 m (Hourdez & Jollivet 2023: table 2). It is likely that the five specimens from the Woodlark Basin identified as "Gen. sp. B" by the phylogenetic analysis of Chabert (2021: 11, 26, 32, table 2) and considered endemic to the La Scala vent Field belong to *A. chubacarc* n. sp. Similarly, it is more than probable that the crabs found on the black smokers of the Woodlark Basin "likely to represent a new species" and shown on videos within an aggregation of *Alviniconcha kojimai* vent snails, polynoid polychaete worms, and alvinocarid shrimps (Boulart *et al.* 2022: 8, 14, fig. 5c, e) are in fact *A. chubacarc* n. sp., even though the dactylus of the major chela is too small to detect a depression on the upper margin, the key distinguishing feature of *A. chubacarc* n. sp. The same depression is present in the *A. chubacarc* n. sp. from the Manus Basin, that lives at a much shallower depth, 1750 m, which suggests that this species has developed adaptive mechanisms to acquire



FIG. 8. — **A**, still frame from video (190527174907236_15_1080) of the vent site La Scala in Woodlark Basin: see numerous *Austinograea chubacarc* n. sp. among gastropods *Alviniconcha* Okutani & Ohta, 1988; **B**, close-up of the video 8A showing a small male specimen (located at the bottom and left of the video still) of *Austinograea chubacarc* n. sp., with the dactylus of the major chela grooved by the characteristic depression of the species visible *in situ*; **C**, close-up of the video 8A showing two crabs (located up and to the left of the video still) copulating face to face: the small male, below, holds the much larger female with its two chelae. Top, middle and far right, several individuals of *A. hourdezi* Guinot & Segonzac, 2018 recognisable by setal patch inside chelae.

an enhanced physiological tolerance, including a depth and temperature lability, and also ability to disperse (see Wang *et al.* 2019).

A still from video (190527174907236_15_1080) taken by ROV onboard camera from the La Scala vent Field (Fig. 8A) depicts several crabs, including one in the lower left where the depression on the dactylus of the major chela is visible in situ (see close-up Fig. 8B), and which are therefore unambiguously *A. chubacarc* n. sp. On the same video, two crabs can be seen copulating face to face: the small male holds the much larger female above it with its two chelae (Fig. 8C). It is difficult to detect with certainty a depression on the dactylus of the small right male chela, but we can guess it.

The dive PL738 at the La Scala vent Field, at around 3388 m, brought back numerous specimens of *Austinograea chubacarc* n. sp., while, from the five dives in the Manus Basin, only the dive PL733 at c. 1750 m provided three specimens (Hourdez & Jollivet 2023: tables 1, 2). It is therefore certain that *A. chubacarc* n. sp. is not endemic to the Woodlark Basin and also occurs in the Manus Basin. We have identified as *A. hourdezi* four specimens that were collected in the Woodlark Basin during the same dive 738 at La Scala vent Field (see above under *A. hourdezi*), and this species, easily recognised in the field by the patch of dense setae on the inner surface of the chelae and a dark spot on the outer surface, is clearly visible on the still from the video 190527174907236_15_1080 from the La Scala Vent (Fig. 8A). A third species, *A. alayseae*, is abundant in the Manus Basin and, although it has not been collected from the Woodlark Basin, it is likely to be present there, as its distribution is very wide (see above under *A. alayseae*).

Chabert (2021: 27, 32, table 2) did not report her “Gen. sp. B” (here considered to correspond to *Austinograea chubacarc* n. sp.) from the Manus Basin, around 1752 m. It is indeed surprising to find the same species at this shallow depth and at a much greater depth, around 3388 m, in the Woodlark Basin. According to Boulart *et al.* (2022: 215), despite faunistic similarities with other western Pacific communities, the Woodlark Basin communities may have specific attributes due to the greater depth (3330 m) at which the vent sources are located compared to the shallower vent sites found elsewhere in the western Pacific. *Austinograea chubacarc* n. sp., coming into contact from these two basins, highlights the stepping-stone role of the Woodlark Basin in the dispersal of the Southwest Pacific vent fauna between the Manus and Woodlark Basins.

In this context, it is interesting to compare the carcinological vent fauna with that of the vent gastropods *Alviniconcha*, even if the latter is represented by a much higher number of species. And this is all the more true given that bythograeoid crabs, and in particular *Austinograea chubacarc* n. sp., are, among other organisms, part of the dominant taxa found in *Alviniconcha* spp. patches (Fig. 8A) (Boulart *et al.* 2022: 8, fig. 5c, e). Combining morphological description and DNA sequence datasets of three species of vent snails across five basins, Castel *et al.* (2022) confirmed that some species, easily distinguished on the basis of their external morphology, while partially overlapping over their range, display high levels of divergence. Using a DNA barcoding approach, analyses of

the genetic divergence of six genera of vent gastropods across South West Pacific back-arc basins and the La Scala site on the Woodlark Ridge showed contrasting phylogeographic patterns among species, even between closely related species: some species were widely distributed across basins, without evidence of strong barriers to gene flow, and other species were restricted to one basin only; whereas individuals from the Woodlark Basin were either endemic to this area or, coming into contact from these basins, exhibited intermediate patterns of isolation (Poitrimol *et al.* 2022).

Acknowledgements

We would like to express our cordial thanks to the captain and crew of the R/V *L'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 also thank Lenaïck Menot (Ifremer, Centre de Bretagne), who sent us the brachyuran material collected by the Futuna 3 cruise (2012, <https://doi.org/10.17600/12010040>), initially preserved at the Centre Ifremer of Plouzané (Finistère), and which will be studied later. We gratefully acknowledge the help of Sébastien Soubzmaigne (MNHN) for the photographs and the valuable assistance of Paula Martin-Lefèvre (MNHN, Direction des Collections) for identifying the dives, her exceptional curatorial support and reading the manuscript. Jean-François Bernardet (Volunteer) helped us with the first sorting of the material and the measurement of specimens. Analia Martin-Lefèvre put all her young talent and kindness into the preparation of the iconography. We are very grateful to Stéphane Hourdez (Observatoire océanologique de Banyuls-sur-mer), who provided the specimens studied here and the videotapes of the dives where they were sampled, prepared the maps featured in this article, patiently answered our many questions, and made some corrections and suggestions on a preliminary draft. We would also like to thank Laure Corbari (Curator of the Crustacean collection, MNHN) for access to the collections. We gratefully acknowledge the involvement of Peter K. L. Ng and an anonymous referee who greatly contributed to improving the manuscript with constructive comments.

REFERENCES

- AGNEW J. G. 2008. — *Dactyls reveal evolutionary patterns in decapod crustaceans*. Doctoral Dissertations. 9 LSU (Louisiana State University) 4: i-iv, 1-193. https://repository.lsu.edu/gradschool_dissertations/94
- BACH W. AND CRUISE PARTICIPANTS 2011. — Report and preliminary results of RV SONNE Cruise SO 216, Townsville (Australia) - Makassar (Indonesia), June 14 - July 23, 2011. BAMBUS, Back-Arc Manus Basin Underwater Solfataras. *Berichte aus dem Fachbereich Geowissenschaften der Universität Bremen* 280: 1-87.
- 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>
- BROWN S. C., CASSUTO S. R. & LOOS R. W. 1979. — Biomechanics of chelipeds in some decapod crustaceans. *Journal of Zoology* (London) 188: 143-159. <https://doi.org/10.1111/j.1469-7998.1979.tb03397.x>
- CASTEL J., HOURDEZ S., PRADILLON F., DAGUIN-THIÉBAUT C., BALENGHIEN M., RUAAULT S., CORRE E., TRAN LU Y. A., MARY J., GAGNAIRE P.-A. ET AL. 2022. — Inter-specific genetic exchange despite strong divergence in deep-sea hydrothermal vent gastropods of the genus *Alviniconcha*. *Genes* 13: 985. <https://doi.org/10.3390/genes13060985>
- CHABERT A. 2021. — *Diversity of western pacific (sic) Back-arc Basins invertebrates reevaluated through a barcode approach – Results on decapods and polychaetes*. Master thesis. Dissertations, Thèses and Masters Projects. International Master of Science in Marine Biological Resources (IMBRSea): 1-43.
- CORBERA J. & SEGONZAC M. 2010. — A new *Styloptocuma* species (Crustacea, Cumacea) from hydrothermal vent fields of the Lau and North Fiji basins (West Pacific). *Zoosystema* 32 (3): 439-447. <https://doi.org/10.5252/z2010n3a5>
- DEMIDOW O., KIHARA T. C., MARTÍNEZ ARBIZU P. & CLARK P. F. 2021. — The megalopal stage of the hydrothermal vent crab *Austinograea rodriguezensis* Tsuchida & Hashimoto, 2002 (Decapoda: Bythograeidae): a morphological description based on CLSM images. *Zootaxa* 5040 (3): 365-387. <https://doi.org/10.11646/zootaxa.5040.3.3>
- DESBRUYÈRES D. & SEGONZAC M. (EDS) 1997. — *Handbook of deep-sea hydrothermal vent fauna*. Éditions IFREMER, Brest.
- DESBRUYÈRES D., SEGONZAC M. & BRIGHT M. (EDS) 2006. — *Handbook of deep-sea hydrothermal vent fauna*. Second completely revised edition. *Denisia* 18: 1-455.
- ERICKSON K. L., MACKO S. A. & VAN DOVER C. L. 2009. — Evidence for a chemoautotrophically based food web at inactive hydrothermal vents (Manus Basin). *Deep-Sea Research II* (56): 1577-1588. <https://doi.org/10.1016/j.dsr2.2009.05.002>
- FUJIWARA S.-I. & KAWAI H. 2016. — Crabs grab strongly depending on mechanical advantages of pinching and disarticulation of chela. *Journal of Morphology* 277 (10): 1259-1272. <https://doi.org/10.1002/jmor.20573>
- GALKIN S. V. 1992. — Bottom fauna of the hydrothermal vents in the Manus Basin. *Okeanologiya* 32 (6): 1102-1110. [in Russian; English translation in *Oceanology* 32 (6): 768-774]
- GALKIN S. V. 1997. — Megafauna associated with hydrothermal vents in the Manus Back-Arc Basin (Bismarck Sea). *Marine Geology* 142 (1): 197-206. [https://doi.org/10.1016/S0025-3227\(97\)00051](https://doi.org/10.1016/S0025-3227(97)00051)
- 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. & SEGONZAC M. 2006. — *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. 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 (5): 75-107. <https://doi.org/10.5252/zoosystema2018v40a5>
- 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.
- HASHIMOTO J., OHTA S., FIALA-MÉDIONI A., AUZENDE J.-M., KOJIMA S., SEGONZAC M., FUJIWARA Y., HUNT J. C., GENA K., MIURA T., KIKUCHI T., YAMAGUCHI T., TODA T., CHIBA H., TSUCHIDA S., ISHIBASHI J., HENRY K., ZBINDEN M., PRUSKI A., INOUE A., KOBAYASHI H., BIRRIEN J.-L., NAKA J., YAMANAKA T., LAPORTE C., NISHIMURA K., YEATS C., MALAGUN S., KIA P., OYAZU M. & KATAYAMA T. 1999. — Hydrothermal vent communities in the Manus Basin, Papua New Guinea - Results of the BIOACCESS cruise '96 and '98. *InterRidge News* 8: 12-18.
- 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.
- HOURDEZ S. & JOLLIVET D. 2019. — CHUBACARC cruise, RV L'Atalante. IFREMER <https://doi.org/10.17600/18001111>
- HOURDEZ S. & JOLLIVET D. 2023. — CHUBACARC Cruise Report. CNRS; Sorbonne University; Ifremer. Hal-04100305.
- HUI M., SONG C., LIU Y., LI C. & CUI Z. 2017. — Exploring the molecular basis of adaptive evolution in hydrothermal vent crab *Austinograea alayseae* by transcriptome analysis. *PLoS ONE* 12 (5): e0178417. <https://doi.org/10.1371/journal.pone.0178417>
- JOLLIVET D., HASHIMOTO J., AUZENDE J. M., HONZA E., RUELLE E., DUTT S., IWABUCHI Y., JARVIS P., JOSHIMA M., KAWAI T., KAWAMOTO T., KISIMOTO K., LAFOY Y., MATSUMOTO T., MITSUZAWA K., NAGANUMA T., NAKA J., OTSUKA K., OTSUKI A., BHASKARRAO Y. J., TANAHASHI M., TANAKA T., TEMAKON J. S., URABE T., VEIVAU T. & YOKOKURA T. 1989. — First observations of faunal assemblages associated with hydrothermalism in the North-Fiji back-arc basin. *Comptes rendus de l'Académie des Sciences sér. III Sciences de la Vie A* 309 (8): 301-308.
- KIHARA T. C., CLARK P. F. & MEYN K. H. 2024. — First zoeal stage of the Indian Ocean hydrothermal vent crab, *Austinograea rodriguezensis* Tsuchida & Hashimoto, 2002 (Decapoda: Brachyura: Bythograeidae). *Zootaxa* 5476 (1): 192-206. <https://doi.org/10.11646/zootaxa.5476.1.18>
- KIM S. J., LEE K. Y. & JU S.-J. 2013. — Nuclear mitochondrial pseudogenes in *Austinograea alayseae* hydrothermal vent crabs (Crustacea: Bythograeidae): effects on DNA barcoding. *Molecular Ecology Resources* 13 (5): 781-787. <https://doi.org/10.1111/1755-0998.12119>
- 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 (4): 251-252. <https://doi.org/10.3109/19401736.2013.800489>
- KOJIMA S. & WATANABE H. 2015. — Vent Fauna in the Mariana Trough, in ISHIBASHI J.-I. et al. (eds), *Subseafloor Biosphere Linked to Hydrothermal Systems: TAIGA Concept*. https://doi.org/10.1007/978-4-431-54865-2_25
- KOMAI T., GOTOH R. O., SADO T. & MIYA M. 2019. — Development of a new set of PCR primers for eDNA metabarcoding decapod crustaceans. *Metabarcoding and Metagenomics* 3: 1-19. <https://doi.org/10.3897/mbmg.3.33835>
- LAURILA T. E., PETERSEN S., DEVEY C. W., BAKER E. T., AUGUSTIN N. & HANNINGTON M. D. 2012. — Tectonic and magmatic controls on hydrothermal activity in the Woodlark Basin: hydrothermalism in the Woodlark Basin. *Geochemistry, Geophysics, Geosystems* 13 (9): 1-13. <https://doi.org/10.1029/2012GC004247>
- LEE W.-K., JU S.-J., HOU B. K. & KIM S.-J. 2019a. — DNA Barcoding for the hydrothermal vent crab *Austinograea* species (Crustacea: Bythograeidae) from the North Fiji Basin, Southwestern Pacific Ocean. *Animal Systematics, Evolution and Diversity* 35 (1): 30-32. <https://doi.org/10.5635/ASED.2019.35.1.004>
- LEE W. K., KIM S. J., HOU B. K., VAN DOVER C. L. & JU S. J. 2019b. — Population genetic differentiation of the hydrothermal vent crab *Austinograea alayseae* (Crustacea: Bythograeidae) in the southwest Pacific Ocean. *PLoS ONE* 14 (4): 1-15. <https://doi.org/10.1371/journal.pone.0215829>

- LEIGNEL V., HURTADO L. A. & SEGONZAC M. 2017. — Ecology, adaptation and acclimatisation mechanisms of Bythograeidae Williams, 1980, a unique endemic hydrothermal vent crabs family: current state of knowledge. *Marine and Freshwater Research* 69 (1). <https://doi.org/10.1071/MF17007>
- LÓPEZ-GONZÁLEZ P. J., RODRÍGUEZ E. & SEGONZAC M. 2005. — A new species of sea anemone (Cnidaria: Anthozoa: Actiniaria) from Manus Basin hydrothermal vents, South-western Pacific. *Marine Biology Research* 1 (5): 326-337.
- MASUNARI N., HIRO-OKU M., DAN S., NANRI T., KONDO M., GOTO M., TAKADA Y. & SAIGUSA M. 2015. — Chela asymmetry in a durophagous crab: predominance of right-handedness and handedness reversal is linked to chela size and closing force. *Journal of Experimental Biology* 218: 3658-3670. <https://doi.org/10.1242/jeb.120196>
- MASUNARI N., SEKINE K., KANG B. J., TAKADA Y., HATAKEYAMA M. & SAIGUSA M. 2020. — Ontogeny of cheliped laterality and mechanisms of reversal of handedness in the durophagous Gazami Crab, *Portunus trituberculatus*. *Biological Bulletin* 238 (1): 25-40. <https://doi.org/10.1086/707648>
- MATEOS M., HURTADO L. A., SANTAMARIA C. A., LEIGNEL V. & GUINOT D. 2012. — Molecular systematics of the deep-sea hydrothermal vent endemic brachyuran family Bythograeidae Williams, 1980: a comparison of three Bayesian species-tree methods. *PLoS ONE* 7 (3): e32066 (14 p.). <https://doi.org/10.1371/journal.pone.0032066>
- 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 zoeal stage of the hydrothermal vent crab, *Gandalfus yunohana* (Decapoda, Brachyura, Bythograeidae). *Crustaceana* 83 (5): 525-537. <https://www.jstor.org/stable/27822635>
- PODOWSKI E. L., MA S., LUTHER III G. W., WARDROP D., FISHER C. R. 2010. — Biotic and abiotic factors affecting distributions of megafauna in diffuse flow on andesite and basalt along the Eastern Lau Spreading Center, Tonga. *Marine Ecology Progress Series* 418: 25-45. <https://doi.org/10.3354/meps08797>
- POITRIMOL C. 2022. — *Distribution et partitionnement de la biodiversité hydrothermale dans un système discontinu de dorsales : le cas des bassins arrière-arc de l'ouest Pacifique. Biodiversité*. Sorbonne Université. <https://theses.hal.science/tel-03900421>
- POITRIMOL C., THIÉBAUT É., DAGUIN-THIÉBAUT C., LE PORT A.-S., BALLENGHIEN M., TRAN LU Y. A. ET AL. 2022. — Contrasted phylogeographic patterns of hydrothermal vent gastropods along South West Pacific: Woodlark Basin, a possible contact zone and/or stepping-stone. *PLoS ONE* 17 (10): e0275638. <https://doi.org/10.1371/journal.pone.0275638>
- 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, Transactions of the American Geophysical Union* 67 (21): 489-490. <https://doi.org/10.1029/EO067i021p00489>
- SEN A., BECKER E. L., PODOWSKI E. L., WICKES L. N., MA S., MULLAUGH K. M., HOURDEZ S., LUTHER G. W. III & FISHER C. R. 2013. — Distribution of mega fauna on sulfide edifices on the Eastern Lau Spreading Center and Valu Fa Ridge. *Deep-Sea Research Part I: Oceanographic Research Papers* 72: 48-60. <https://doi.org/10.1016/j.dsr.2012.11.003>
- SEN A., PODOWSKI E. L., BECKER E. L., SHEARER E. A., GARTMAN A., YÜCEL M., HOURDEZ S., LUTHER G. W. III & FISHER C. R. 2014. — Community succession in hydrothermal vent habitats of the Eastern Lau Spreading Center and Valu Fa Ridge, Tonga. *Limnology and Oceanography* 59: 1510-1528. <https://doi.org/10.4319/lo.2014.59.5.1510>
- SEN A., KIM S., MILLER A. J., HOVEY K. J., HOURDEZ S., LUTHER III G. W. & FISHER C. R. 2016. — Peripheral communities of the Eastern Lau Spreading Center and Valu Fa Ridge: community composition, temporal change and comparison to near-vent communities. *Marine Ecology* 37: 599-617. <https://doi.org/10.1111/maec.12313>
- SHIELDS J. D. & SEGONZAC M. 2007. — New nemertean worms (Carcinonemertidae) on bythograeid crabs (Decapoda: Brachyura) from Pacific hydrothermal vent sites. *Journal of Crustacean Biology* 27 (4): 681-692. <https://doi.org/10.1651/S-2794.1>
- TAN M. H., GAN H. M., LEE Y. P., LINTON S., GRANDJEAN F., BARTHOLOMEI-SANTOS M. L., MILLER A. D. & AUSTIN C. M. 2018. — ORDER within the chaos: insights into phylogenetic relationships within the Anomura (Crustacea: Decapoda) from mitochondrial sequences and gene order rearrangements. *Molecular Phylogenetics and Evolution* 127: 320-331. <https://doi.org/10.1016/j.ympev.2018.05.015>
- TSUCHIDA S. & FUJIKURA K. 2000. — Heterochely, relative growth, and gonopod morphology in the bythograeid crab, *Austinoergaea williamsi* (Decapoda, Brachyura). *Journal of Crustacean Biology* 20: 407-414. <https://doi.org/10.1163/20021975-99990052>
- TSUCHIDA S. & HASHIMOTO J. 2002. — A new species of bythograeid crab, *Austinoergaea 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>
- 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>
- WANG Z., XU X., ZHENG Y., XU Z., LI Y. & CHEN H. 2024. — Analysis of the overlength Main noncoding region in *Metacarcinus magister* (Decapoda: Brachyura) and a phylogenetic study of the Cancroidea species. *Genes* 15: 437 (16 p.). <https://doi.org/10.3390/genes15040437>
- XU P., ZHOU Y. & WANG C. 2020. — Complete mitochondrial genome sequence of the genus *Austinoergaea* (Malacostraca: Brachyura: Bythograeidae) and its phylogenetic analysis. *Mitochondrial DNA part B* 5 (3): 3487-3488. <https://doi.org/10.1080/23802359.2020.1821823>
- 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 Bythograeoidea and Xanthoidea. *Zoologica Scripta* 39 (6): 621-630. <https://doi.org/10.1111/j.1463-6409.2010.00442.x>
- YANG J. S., LU B., CHEN D. F., YU Y. Q., YANG F., NAGASAWA H. & YANG W. J. 2013. — When did decapods invade hydrothermal vents? Clues from the Western Pacific and Indian Oceans. *Molecular Biology and Evolution* 30: 305-309. <https://doi.org/10.1093/molbev/mss224>

Submitted on 16 July 2024;
accepted on 25 September 2024;
published on 15 April 2025.