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

Danièle GUINOT
Michel SEGONZAC
Institut de Systématique, Évolution, Biodiversité (ISYEB),
Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, EPHE,
case postale 53, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
guinot@mnhn.fr (corresponding author)
segonzac@mnhn.fr

ABSTRACT

Two new species of the genus *Austinograea* Hessler & Martin, 1989 (Bythograeidae Williams, 1980), distinct from *A. williamsi* Hessler & Martin, 1989 and *A. alayseae* Guinot, 1990, are here reported from hydrothermal vent fields of the southwestern Pacific: *A. hourdezi* n. sp. and *A. jolliveti* n. sp., both in the Lau and North Fiji Back-Arc Basins. *Austinograea hourdezi* n. sp. is characterised by two depressions appearing as dark spots on the palm of both chelipeds in males and differs from the more northern *A. williamsi* and the Indian *A. rodriguezensis* Tsuchida & Hashimoto, 2002, which show only one spot on the male chelae, near the base of the dactylus. Some individuals exhibiting all morphological characters of *A. hourdezi* n. sp. bear only one spot on the chelae, near the base of dactylus; the fact that most are left-handed corresponds to the presence of a regenerated cheliped, with handedness reversal after the accidental loss of the major cheliped: these atypical individuals are here treated as *A. hourdezi* n. sp. The single spot that characterises each chela of *A. jolliveti* n. sp. is located at the base of the fixed finger in both sexes and shows as a differently pigmented, violaceous "pustule", being similar to that of *Bythograea microps* Saint Laurent, 1984 from the East Pacific Rise. Moreover, *A. jolliveti* n. sp. can be distinguished by the shortest G2 found in *Austinograea*, especially by its reduced flagellum. *A. hourdezi* n. sp., represented by numerous specimens, was found to co-occur with *A. alayseae* in several vent sites of the Lau and North Fiji Back-Arc Basins, and both are probably distributed across a wide geographical range, whereas *A. jolliveti* n. sp., represented by only a few specimens, was collected from only two vent sites (ABE and Mussel Valley). In the northwestern Pacific, *A. williamsi* is apparently restricted to the Mariana Trough, where it is the only one member of the family Bythograeidae. The Manus Basin perhaps hosts an additional *Austinograea* species. In the western Pacific, vent fields are the only hydrothermal systems, except the East Pacific Ridge, that are not linearly distributed; different basins may host different species within the same brachyuran genus (five congeneric species of *Austinograea*, including *A. rodriguezensis* from the western Indian Ocean). The morphological distinction between the *Austinograea* species is supported by molecular analyses, for *A. williamsi*, *A. alayseae*, and *A. hourdezi* n. sp. A key to the five species of *Austinograea* is provided, in order to be able to potentially identify the crabs photographed *in situ* in their natural environment.

KEY WORDS
Gandalfus,
hydrothermal site,
western Pacific,
Lau Back-Arc Basin,
North Fiji Back-Arc Basin,
Manus Basin, Mariana Trough,
deep-sea fauna,
new species.

RÉSUMÉ

*Révision de la communauté hydrothermale brachyourienne du Pacifique occidental, avec deux espèces nouvelles d'*Austinograea *Hessler & Martin, 1989 (Crustacea, Decapoda, Brachyura, Bythograeidae) des bassins arrière-arc de Lau et Nord-Fidjien.*

Deux nouvelles espèces du genre *Austinograea* Hessler & Martin, 1989 (Bythograeidae Williams, 1980), distinctes d'*A. williamsi* Hessler & Martin, 1989 et d'*A. alayseae* Guinot, 1990, sont décrites des sources hydrothermales du Pacifique Sud-Ouest: *A. hourdezi* n. sp. et *A. jolliveti* n. sp., toutes deux récoltées dans les bassins arrière-arc de Lau et Nord-Fidjien. *Austinograea hourdezi* n. sp. est caractérisée par deux dépressions apparaissant comme des taches sombres sur la main des deux chélipèdes chez le mâle; elle diffère d'*A. williamsi*, plus septentrional, et d'*A. rodriguezensis* Tsuchida & Hashimoto, 2002, de l'océan Indien, qui, toutes deux, montrent une seule tache sur la main des pinces des mâles, près de la base du dactyle. Certains individus, qui présentent tous les caractères morphologiques d'*A. hourdezi* n. sp., ne portent qu'une seule tache sur les pinces, à la base du dactyle; ils sont pour la plupart gauchers, ce qui correspond à la présence d'un chélipède régénéré avec réversion de la dextralité, après la perte accidentelle du grand chélipède: ces individus atypiques sont traités ici comme *A. hourdezi* n. sp. L'unique tache qui caractérise chaque pince d'*A. jolliveti* n. sp. est située à la base du doigt fixe dans les deux sexes et se présente comme une sorte de pustule différemment pigmentée, violacée, ressemblant à celle de *Bythograea microps* Saint Laurent, 1984, de la dorsale du Pacifique oriental. De plus, *A. jolliveti* n. sp. se distingue par le plus court G2 connu chez *Austinograea*, surtout par son flagellum très réduit. *Austinograea hourdezi* n. sp., représentée par de nombreux spécimens, cohabite avec *A. alayseae* sur de nombreux sites des bassins arrière-arc de Lau et Nord-Fidjien, et ces deux espèces ont probablement une large répartition géographique; à l'inverse, *A. jolliveti* n. sp., représentée seulement par quelques spécimens, n'a été trouvée que sur deux sites (ABE et Mussel Valley). Dans le Pacifique Nord-Ouest, *A. williamsi* est apparemment distribuée dans la seule zone d'accrétion des Mariannes, où elle est le seul représentant de la famille des Bythograeidae. Il est possible que le bassin de Manus abrite une espèce encore différente d'*Austinograea*. Dans le Pacifique occidental, les champs de cheminées sont les seuls sites hydrothermaux, excepté sur la dorsale du Pacifique oriental, qui ne sont pas répartis de manière linéaire; des bassins différents peuvent abriter différentes espèces appartenant au même genre de Brachyoures (cinq espèces congénériques d'*Austinograea*, y compris *A. rodriguezensis* de l'océan Indien occidental). La distinction morphologique des espèces d'*Austinograea* est confirmée par les analyses moléculaires, pour *A. williamsi*, *A. alayseae* et *A. hourdezi* n. sp. Une clé d'identification des cinq espèces d'*Austinograea* est proposée, dans le but de permettre l'identification des crabes photographiés *in situ* dans leur environnement naturel.

INTRODUCTION

Two brachyuran genera, *Austinograea* Hessler & Martin, 1989 and *Gandalfus* McLay, 2007, both characterised by the most highly reduced, degenerate eyes of the family Bythograeidae Williams, 1980, are known from the northwestern and southwestern Pacific Back-Arc Basins (Fig. 1). To date, *Austinograea*, one of the most widespread of the known bythograeid genera, is represented by two species in the western Pacific:

1) *Austinograea williamsi* Hessler & Martin, 1989 (type species by original designation) from vent west of the Mariana Islands (southernmost region of the Mariana Trough, Mariana Back-Arc Basin). *Austinograea williamsi* was originally collected in abundance on three active vent fields along the crest of the spreading center, at about latitude 18°N and longitude 144°E, 3600 m depth; later found on vent sites of the Mariana Trough at 13°23.7'N, 143°55.2'E, about 1450 m depth, and at 18°12.9'N, 144°42.5'E, about 3600 m depth (Hessler *et al.* 1988; Hessler & Martin 1989; Guinot 1990; Hessler & Lonsdale 1991; Tsuchida & Fujikura 2000; Tsuchida & Hashimoto 2002; Martin & Haney 2005; Segonzac 2006; McLay 2007; Ng *et al.* 2008; Zelnio & Hourdez 2009; Hamasaki *et al.* 2010: fig. 1; Podowski *et al.* 2010; Sen *et al.* 2013, 2014,

2016; Kojima & Watanabe 2015). Records of *A. williamsi* from the Lau and North Fiji Back-Arc Basins appear to be quite doubtful and at the very least need to be checked.

And 2) *Austinograea alayseae* Guinot, 1990, originally collected from the Lau Back-Arc Basin, west the Tonga Islands (behind the Tonga subduction zone), along the Valu Fa Ridge, at about 176°38'W and between 22°34'S and 22°10'S, from 3595 to 3660 m depth; subsequently found distributed over a wide geographical range along the Eastern Lau Spreading Center (Fig. 2), and also reported from the North Fiji Basin (Jollivet *et al.* 1989, as bythograeid sp.; Hashimoto *et al.* 1989, as bythograeid sp.; Guinot 1990, 1997 *in* Desbruyères & Segonzac 1997; Galkin 1997; Tsuchida & Hashimoto 2002; Komai & Segonzac 2004; Martin & Haney 2005; López-González *et al.* 2005; Segonzac 2006; Guinot & Segonzac 2006a, b; Desbruyères *et al.* 2006b; McLay 2007; Shields & Segonzac 2007; Ng *et al.* 2008; Erickson *et al.* 2009; Corbera & Segonzac 2010; Podowski *et al.* 2010; Mateos *et al.* 2012; Kim *et al.* 2013, 2014; Sen *et al.* 2013, 2014, 2016; Yang *et al.* 2013; Hui *et al.* 2017). Some of these records, however, deserve to be checked.

Another *Austinograea* species, *A. rodriguezensis* Tsuchida & Hashimoto, 2002, was found in the western Indian Ocean, from four vent sites on the Central Indian Ridge, 22 km N
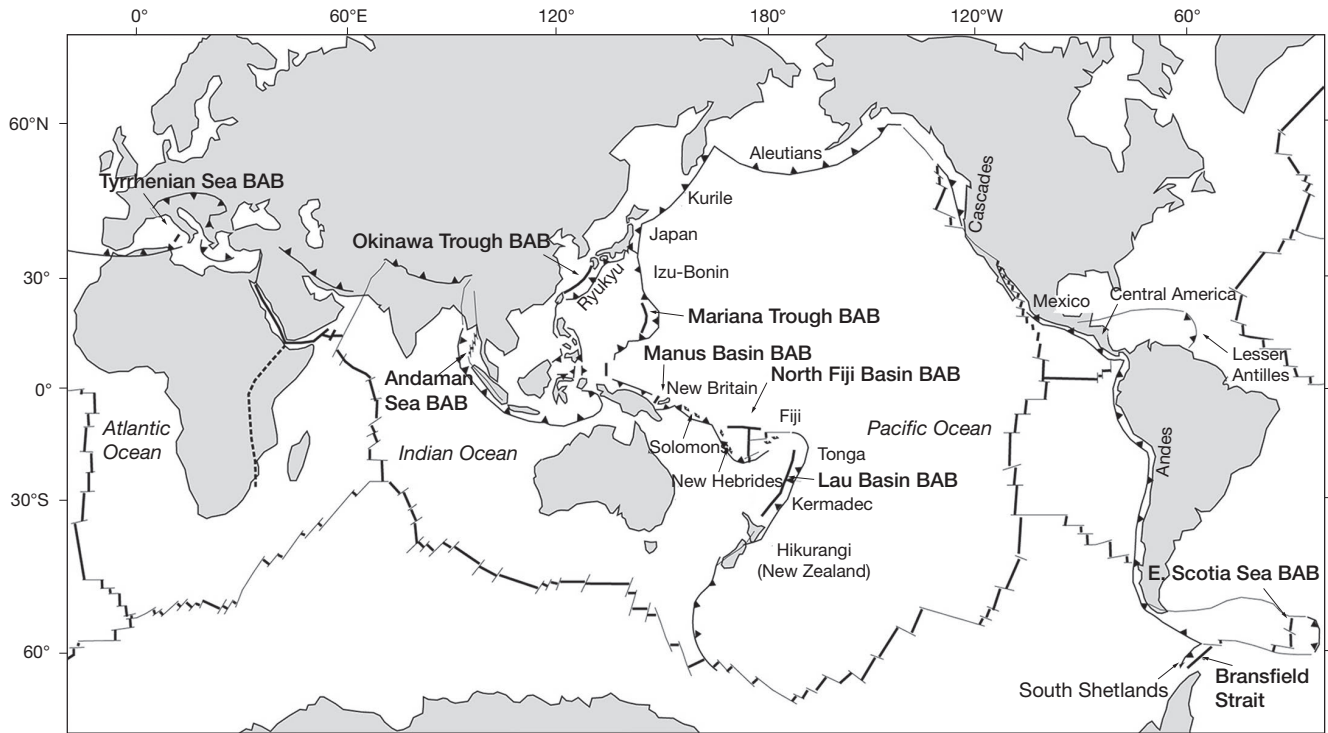
Fig. 1. — Map of active Back-Arc Basins of the world.

of the Rodriguez Triple Junction (Van Dover *et al.* 2001: fig. 2D, as "*Austinograea* n. sp."; Van Dover 2002: 761, tables 1-4, as "*Austinograea* n. sp."; Tsuchida & Hashimoto 2002; Tsuchida 2006; Ng *et al.* 2008; Haimin *et al.* 2010; Kojima & Watanabe 2015). It is distributed over a relatively wide area of brownish stained lava around the vent fields, being most abundant adjacent to the black smoker chimneys (Nakamura *et al.* 2012: figs 2A, 4A, B, E, F, table 1), without genetic differences between local populations (Van Dover *et al.* 2001; Beedessee *et al.* 2013: figs 4, 5, tables 2, 3; Watanabe & Beedessee 2015: table 16.1). Its main characteristics are: chelae not markedly dimorphic; sexual dimorphism weak; external surface of male chela with one spot on propodus, described as "small blackened mark located near base of dactylus" (Tsuchida & Hashimoto 2002: fig. 6); inner surface of chela propodus glabrous, and dense patch of setae only near occluding margins; on cutter, occluding margins straight, with teeth of similar size; G1 only with four small stout spines arranged along dorsal surface.

The genus *Gandalfus*, sister genus of *Austinograea*, is mainly distinguished from *Austinograea* by the epistomial margin being gently sinuous (versus strongly sinuous in *Austinograea*) and G2 approximately as long as G1 (versus distinctly shorter than G1 in *Austinograea*) (McLay 2007: 15). *Gandalfus* contains two species:

– *G. puia* McLay, 2007 (type species by original designation), from vent fields in the Tonga-Kermadec Arc between 30°12'S-35°44'S and 181°33'E-178°29'E, at depths varing from 270-239 m to 1647 m (McLay 2007; de Ronde & Stucker 2015: fig. 47.1);

– *G. yunohana* (Takeda, Hashimoto & Ohta, 2000), distributed at eastern edge of Philippine Sea Plate, 32°06.19'N, 139°52.04'E, 1263 m, and from vents on the Suiyo, Kaikata and Nikko Seamounts, all off central Japan, occurring in great abundance at some sites (Hashimoto *et al.* 1995, as bythograeid sp.; Tsuchida *et al.* 1998; Takeda *et al.* 2000; Kojima 2002; Martin & Haney 2005; Hashimoto 2006; McLay 2007; Miyake *et al.* 2007; Ng *et al.* 2008; Hamasaki *et al.* 2010; Nakajima *et al.* 2010; Yang *et al.* 2010; Ma 2011; Mateos *et al.* 2012; Yorisue *et al.* 2012; de Ronde & Stucker 2015: fig. 47.1; see also Kabasawa 1992). On the Izu-Ogasawara Ridge *G. yunohana* has been found at the massive Nikko Seamount, 472 m (Yang *et al.* 2010) that is only located 5 km from the Northeast Nikko Seamounts, an area without any hydrothermalism (except weak shimmering near the top of the seamount) where three brachyuran species collected at depths of 520-680 m do not belong to Bythograeidae (Komai & Tsuchida 2014).

Most vent crabs in the family Bythograeidae are typically found at great depths. In contrast, the two species of *Gandalfus* are by far the shallowest bythograeids, from 270-239 m to 1647 m (see Tarasov *et al.* 2005), whereas *Austinograea williamsi* shows the deepest records, 3600 m depth, in the western Pacific.

When describing *Austinograea alayseae* collected by the French BIOLAU 1989 cruise, Guinot (1990: 900) suspected the presence of a second species, probably a new *Austinograea* in two explored sites of the Lau Back-Arc Basin (Vai Lili and Hine Hina sites, see Fig. 2) and suggested that it should be distinguished as *Austinograea* sp. aff. *williamsi*. Since then, a large number of specimens of this unnamed species have been
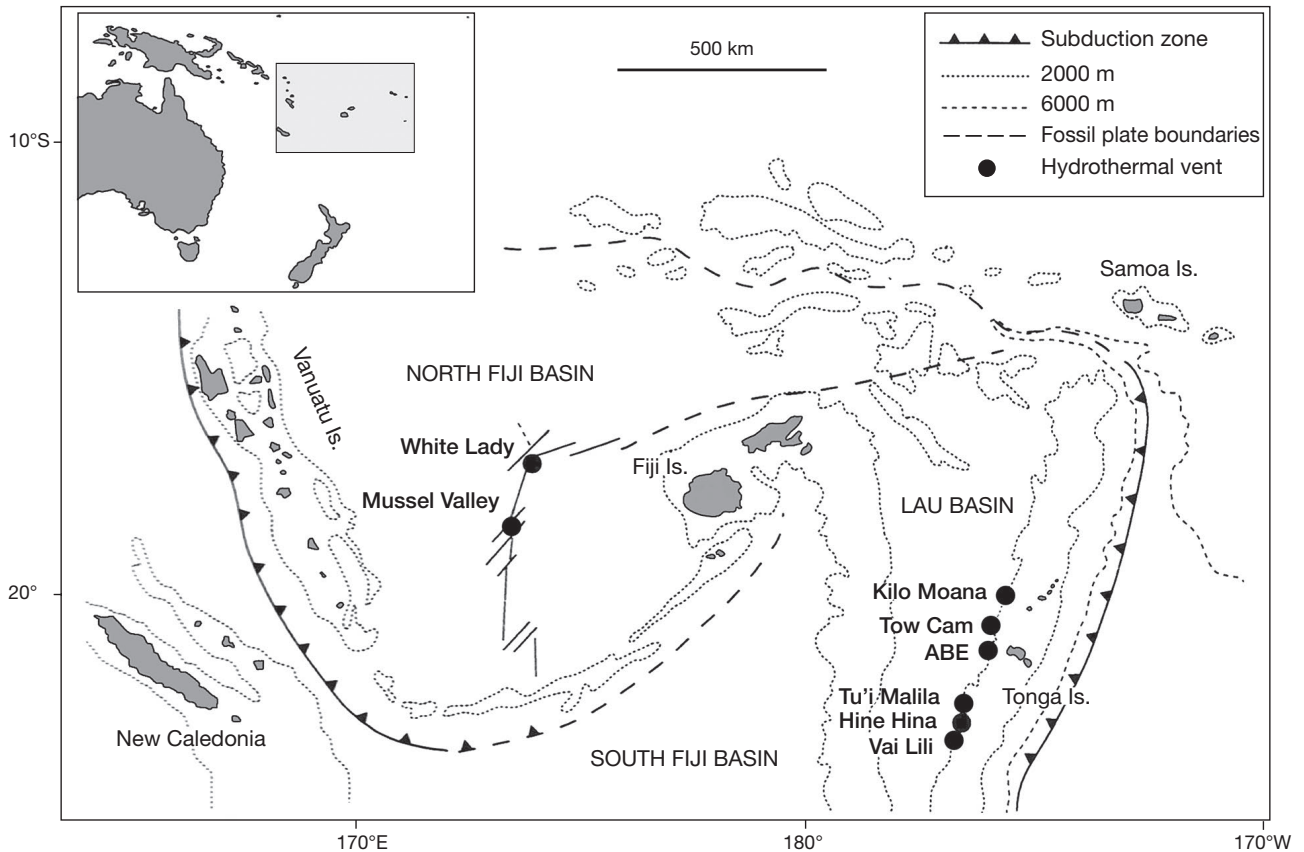
Fɪɢ. 2. — Map of the Lau and North Fiji Back-Arc Basins showing the vent field location along the Eastern Lau Spreading Center and Valu Fa Ridge. After Corbera & Segonzac (2010).

found in the material collected by several cruises in the Lau and North Fiji Basins, notably French-Japanese STARMER II; American cruises (TUIM06MV, TUIM07MV, MGLN07MV, Lau Basin 2009) (Tables 1, 2). This allows us now to describe with confidence this unnamed crab as *Austinograea hourdezi* n. sp. The presence of a species distinct from *A. alayseae* and *A. hourdezi* n. sp. was supported by molecular sequence data (Mateos *et al.* 2012). Unfortunately, the existence of this separate, new species *Austinograea* sp. aff. *williamsi* close to *A. williamsi* and *A. alayseae* has been largely overlooked, although clearly mentioned in the *Handbook of Deep-Sea Hydrothermal Vent Fauna* of Desbruyères *et al.* (2006b) by Guinot & Segonzac (2006a, b: 460) and included in a molecular phylogenetic analysis by Mateos *et al.* (2012: 1, 3, 6, 10, fig. 2, table 1).

The need to bring this issue to a conclusion and give a name to this species is pressing. In fact, various papers on the faunal communities of the western Pacific recently reported either only *A. alayseae* or two bythograeid species, one as *A. alayseae* and a second one, often named *A. williamsi*. We have re-examined the morphological characters of all the individuals sampled from across numerous sites in the southwestern Pacific. We will show that the investigated hydrothermal fields of the Lau and North Fiji Basins host not only two but three *Austinograea* species. The re-identification of all *A. alayseae* housed in various institutions is required in the event of confusion with the widespread *A. alayseae* and *A. hourdezi* n. sp.

In this study, which examines a representative sample of the hydrothermal brachyuran fauna from the deep-sea vent communities of the western Pacific, some males and females could not be first readily identified as *A. hourdezi* n. sp. Most of these individuals, atypical with regards to the pattern of spot(s) on the chelae but, however, without other equivocal morphological evidence, proved to be left-handed, with a small regenerated cheliped (see below, *Individuals with regenerated chelae*).

The perplexing results on the genome of southwestern Pacific bythograeids published in several recent papers suggested the presence of at least two species, formally designated as *A. alayseae* and *A. williamsi* (a species that was previously found confined to the northwestern Pacific), and even more, as *Austinograea* spp. These published accounts deserve to be inspected. One reason for such shortcomings is that obtained data may have been biased by possible incorrect identifications of specimens used for molecular sequences. Such an assumption means that, in these genetic studies, the assignment to *A. williamsi* of the crabs inhabiting the Lau and North Fiji vent fields was probably erroneous, being likely *A. hourdezi* n. sp. that seems rather common.

Another new species has been found in the Lau Back-Arc Basin (ABE site, MGLN07MV cruise) and North Fiji Back-Arc Basin (Mussel Valley site, STARMER II cruise, see Table 1) and, although represented by only a few specimens, it is established here as *Austinograea jolliveti* n. sp.

TABLE 1. — Cruises to the southwestern and northwestern Pacific Ocean where the *Austinograea* crabs here studied were collected. Abbreviations: **LB**, Lau Back-Arc Basin; **NFB**, North Fiji Back-Arc Basin; **MA**, Mariana Back-Arc Basin; **SM**, manned submersible.

Cruise	Location	Dates	Vessel	SM	Chief Scientist	Organism
American cruise DWC	MA	04.V.1987	*Atlantis II*	*Alvin*	P. Lonsdale	Scripps Institution of Oceanography, USA
BIOLAU	LB	12-27.V.1989	*Nadir*	*Nautile*	A.-M. Alayse	Ifremer, France
STARMER II	LB & NFB	30.VI-19.VII.1989	*Atalante*	*Nautile*	D. Desbruyères & S. Ohta	Ifremer, France & JAMSTEC, Japan
BIOACCESS 98	MB	13-25.XI.1998	*Natsuchima*	*Shinkai 2000*	Jun Hashimoto	JAMSTEC, Japan
TUIM06MV	LB & NFB	15-03.V.2005	*Melville*	*Jason II*	R. C. Vrijenhoek	Mbari, USA
TUIM07MV	LB	08-30.V.2005	*Melville*	*Jason II*	C. R. Fisher	Penn State University, USA
MGLN07MV	LB	05.IX-20.X.2006	*Melville*	*Jason II*	C. R. Fisher	Penn State University, USA
Lau Basin 2009	LB	16.V-08.VI.2009	*Thomas Thompson*	*Jason II*	C. R. Fisher	Penn State University, USA

TABLE 2. — List and location of the vent sites from where the material here studied was collected.

Cruises, dive	Basin	Vent site	Coordinates	Depth (m)	Date
American cruise DWC, dive 1845	Mariana Basin	Alice Springs	18°12.60'N, 144°42.42'E	3640	06.V.1987
BIOLAU, BL 03	Lau Basin	Hine Hina	22°32'S, 176°43'W	1900	15.V.1989
BIOLAU, BL 12	Lau Basin	Vai Lili	23°13'S, 176°38'W	1750	24.V.1989
TUIM06MV, dive 140	Lau Basin	Kilo Moana	20°03.23'S, 176°08.01'W	2623	17.V.2005
MGLN07MV, dive 230					07.IX.2006
Lau Basin 2009, dive 424					07.IX.2009
TUIM06MV, dive 142	Lau Basin	Tow Cam	20°19.07'S, 176°08.24'W	2719	19.V.2005
MGLN07MV, dives 231, 237	Lau Basin	ABE	20°45.65'S, 176°11.45'W	2130	09.IX.2006, 01.X.2006
Lau Basin 2009, dive 425					25.V.2009
Lau Basin 2009, dive 427					28.V.2009
TUIM06MV, dive 143	Lau Basin	Tu'i Malila	21°59.34'S, 176°34.09'W	1891	20.V.2005
MGLN07MV, dive 232					11.IX.2006
Lau Basin 2009, dive 428					30.V.2009
STARMER II, PL 11, PL 16, PL 20	North Fiji Basin	White Lady	16°59.50'S, 173°55.47'E	2000	06.VII.1989, 11.VII.1989
TUIM06MV, dives 151 & 152					15.VII.1989
					30.V.2005, 31.V.2005
STARMER II, PL 18	North Fiji Basin	Mussel Valley	18°50'S, 173°29'E	2750	13.VII.1989

MATERIAL AND METHODS

Specimens studied here were collected during several deep-sea surveys at the hydrothermal vents of the Lau and North Fiji Basins, southwestern Pacific, by a long series of cruises, operating manned submersibles *Alvin*, *Nautile*, *Shinkai 2000* and the ROV *Jason II*, deployed on board of RV *Atlantis II*, *Nadir*, *Atalante*, *Natsuchima*, *Melville*, and *Thomas Thompson* (Table 1). Individuals were caught with a suction sampler or by baited traps. A list, with the location of the vent sites from where the material was collected is provided Table 2.

To provide a report as comprehensive as possible, in addition to the material separated by Guinot (1990) as *Austinograea* sp. aff. *williamsi* we have included all the specimens of the genus deposited in the MNHN, either preliminarily identified or unsorted. In total, the material from eight cruises (Table 1) has been examined and has allowed discovery of two new species, and a new appreciation of the abundance of specimens of *A. alayseae*.

Measurements provided (in mm) are for the carapace length (cl) followed by the maximum carapace width (cw). The abbreviations P1, P2, P3, P4, P5 are used for the first to fifth pairs of pereopods, respectively, P1 being the chelipeds; G1, G2 for the male first and second pleopods or gonopods, respectively; mxp3 for external maxillipeds; PL, dive; ROV, remotely operated vehicle; RV, research vessel; SM, submersible.

The material examined is deposited in the Muséum national d'Histoire naturelle (MNHN), Paris. Specimens sent in loan from Pennsylvania State University are housed in USA (Collection C. R. Fisher). Paratypes of *A. hourdezi* n. sp. will be sent to some institutions.

COMPARATIVE MATERIAL OF *AUSTINOGRAEA ALAYSEAE* (SEE GUINOT 1990)
Lau Basin, BIOLAU 2009 cruise, Valu Fa Ridge, Vai Lili site, 22°13'S, 176°38'W, 1900 m: dive BL09, 21.V.1989: ♂ 16 × 24 mm, holotype, MNHN-IU-2008-11305 (= MNHN-B24021), 1 ♀ 21 × 32 mm, allotype, 1 ♂ 18.0 × 27.5 mm, 1 ♀ 24.0 × 37.0 mm, paratypes, MNHN-IU-2008-11306 (= MNHN-B24022); dive BL04, 16.V.1989: 3 ♂, 2 ♀, paratypes, MNHN-IU-2008-11305 (= MNHN-B24056); dive BL06, 18.V.1989: 11 ♂, 19 ♀, paratypes, MNHN-IU-2016-10767 (= MNHN-B24057); dive BL10, 22.V.1989: 35 ♂, 52 ♀, paratypes, MNHN-IU-2008-11309 (= MNHN-B24055); dive BL11, 23.V.1989: 2 ♀ 17.0 × 27.0 mm, 24.0 × 38.0 mm, MNHN-IU2016-10768 (= MNHN-B24058).

COMPARATIVE MATERIAL OF *AUSTINOGRAEA WILLIAMSI*
Mariana Back-Arc Basin, dive 1845, Alice Springs site, 18°12.805'N, 144°42.425'E, 3640 m, 06.V.1987: 2 ♂, 2 ♀, all paratypes, MNHN-IU-2008-11121 (= MNHN-B20910).

COMPARATIVE MATERIAL OF *GANDALFUS YUNOHANA*
Izu-Ogasawara Arc, *Shinkai 2000*, dive #1007, Myojin Knoll site, 32°06.19'N, 139°52.04'E, 1263 m, 05.V.1998: ♂ 24.9 × 38.0 mm, paratype, MNHN-IU-2008-11865.

SYSTEMATICS

Family BYTHOGRAEIDAE Williams, 1980
Genus *Austinograea* Hessler & Martin, 1989

TYPE SPECIES. — *Austinograea williamsi* Hessler & Martin, 1989.

Austinograea hourdezi n. sp.
(Figs 3A; 4A-E; 5A-H; 6A-E; 7A-H)

Austinograea sp. aff. *williamsi* Guinot, 1990: 898 (Addenda), 900, 901. — Guinot & Segonzac 2006b: 460, fig. 1. — Mateos *et al.* 2012: 1, 5, 6, 10, figs 1, 2, table 1.

TYPE MATERIAL. — **Holotype**. MNHN-IU-2016-10737, ♂ 25.7 × 40.2 mm, southwestern Pacific, Lau Back-Arc Basin, TUIM06MV cruise, dive 142, Tow Cam site, 20°19.07'S, 176°08.24'W, 2719 m, 19.V.2005: right-handed individual, with left cheliped and all P2-P5 detached (Figs 4A-C; 6A-E).
Paratypes. MNHN-IU-2016-10738, same data, 1 ♂ 29.8 × 48.1 mm (left-handed, two spots on both chelae, with weak heterochely and heterodonty) (Fig. 5A-H), 1 ♂ 24.7 × 36.0 mm (left-handed, with small regenerated right chela, bearing only one spot).
MNHN-IU-2016-10745 (= MNHN-B24060), 3 ♂ 21.0 × 32.8 mm, 18.7 × 28.0 mm, 18.3 × 29.2 mm, 5 ♀ 25.0 × 40.0 mm (two P1 lacking), 19.1 × 32.2 mm, 18.3 × 28.2 mm, 18.3 × 28.4 mm (Fig. 7A-H), cl 19.1 mm (bad condition), Lau Back-Arc Basin, BIOLAU cruise, BL 12, Vai Lili site, 23°13'S, 176°38'W, 1750 m, 24.V.1989.
MNHN-IU-2016-10747 (= MNHN-B24059), 2 ♂ 18.0 × 31.0 mm, 17.0 × 28.0 mm, 1 ♀ 16.4 × 26.8 mm, Lau Back-Arc Basin, BIOLAU cruise, dive BL 03, Hine Hina site, 22°32'S, 176°43'W, 1853 m, 15.V.1989.
MNHN-IU-2016-10739, 1 ♀ (with two cutters) 28.4 × 46.8 mm, Lau Back-Arc Basin, Lau Basin 2009 cruise, dive 424, Kilo Moana site, 20°03.23'S, 176°08.01'W, 2623 m, 07.IX.2009.
MNHN-IU-2016-10741, 1 ♀ 25.3 × 40.0 mm, Lau Back-Arc Basin, TUIM06MV cruise, dive 140, Kilo Moana site, 20°03.23'S, 176°08.01'W, 2623 m, 17.V.2005.
MNHN-IU-2016-10740, 1 ♂ 21.4 × 34.3 mm, Lau Back-Arc Basin, MGLN07MV cruise, dive 232, Tu'i Malila site, 21°59.34'S, 176°34.09'W, 1891 m, 11.IX.2006 (preserved in ethanol 85%).
MNHN-IU-2016-10743, 1 big damaged ♂ (with detached legs), Lau Back-Arc Basin, MGLN07MV cruise, dive 231, ABE site, 20°45.65'S, 176°11.45'W, 2130 m, 09.IX.2006 (preserved in formalin 10% then transferred to ethanol 70%).
MNHN-IU-2016-10746 (= MNHN-B27831), 1 ♀ cl 28.2 mm (left part broken), North Fiji Basin, STARMER II cruise, dive PL 16, White Lady site, 16°59.50'S, 173°55.47'E, 2000 m, 11.VII.1989.
MNHN-IU-2016-10742, 4 ♀ 19.4 × 39.3 mm, 20.5 × 33.2 mm, 19.0 × 30.0 mm, 25.0 × 40.0 mm, TUIM06MV cruise, dive 151, box 2, North Fiji Basin, White Lady site, 16°59.50'S, 173°55.47'E, 2000 m, 30.V.2005.

TYPE LOCALITY. — Southwestern Pacific, Lau Back-Arc Basin, Tow Cam site, 20°19.07'S, 176°08.24'W, 2719 m.

OTHER MATERIAL EXAMINED. — MNHN-IU-2016-10748 (= MNHN-B27827), 1 ♀ cl 29.2 (damaged, left P1 lacking), North Fiji Basin, STARMER II cruise, dive PL 20, White Lady site, 16°59.50'S, 173°55.47'E, 2000 m.

MNHN-IU-2016-10744, 2 ♀ 26.0 × 42.0 mm, 26.0 × 40.0 mm, Lau Back-Arc Basin, Lau Basin 2009 cruise, dive 427, ABE site, 20°45.65'S, 176°11.45'W, 2130 m, 28.V.2009 (preserved in ethanol 85%). This sample with two typical females devoid of spots on chelae palm also contains a female 27.1 × 44.6 mm with a spot (a unique spot) on each chela (see *Individuals with regenerated chelae*).
MNHN-IU-2016-10752, 1 ♀ 30.0 × 48.5 mm, Lau Back-Arc Basin, MGLN07MV cruise, dive 230, Kilo Moana site, 20°03.23'S, 176°08.01'W, 2623 m, 07.IV.2006 (preserved in formalin 10% and then transferred into ethanol 70%). This large right-handed female, with heterochely and heterodonty (Fig. 4D, E), is atypical due to the presence two spots on the chelae (on the crusher, one marked dark spot plus a faint another one, only discernible as yellow trace; on the cutter, two indistinct spots, only as yellow traces), conversely to typical females that are devoid of any spot.
MNHN-IU-2016-10768 (= MNHN-B27834), 1 ♀ 22.7 × 36.5 mm, North Fiji Basin, STARMER II cruise, dive PL 18, Mussel Valley, 18°50'S, 173°29'E, 2750 m, 13.VII.1989. This atypical female bears a spot on each chela.
MNHN-IU-2016-10765, only one big crusher chela (with two spots) and several pereopods, Lau Back-Arc Basin, no other data.
Collection C. R. Fisher. 2 ♀, southwestern Pacific, Lau Back-Arc Basin, MGLN07MV, dive J2-232, Tu'i Malila site, 21°59.34'S, 176°34.09'W, 1891 m, 11.IX.2006 (preserved in formalin 10% and then transferred into ethanol 70%); 2 ♀, Lau Back-Arc Basin, MGLN07MV, dive 231, ABE site, 20°45.65'S, 176°11.45'W, 09.IX.2006 (preserved in formalin 10% and then transferred into ethanol 70%); 2 ♀, Lau Back-Arc Basin, Lau Basin 2009 cruise, dive 425, ABE site, 20°45.65'S, 176°11.45'W, 2130 m, 25.V.2009 (preserved in ethanol 85%).

ETYMOLOGY. — Dedicated to Stéphane Hourdez (CNRS, Station biologique de Roscoff, France) in recognition of his valuable contribution to the knowledge of hydrothermal fauna sites (taxonomy, ecology, physiology, adaptation, phylogeny). He actively participated in the taxonomic sampling during the C. R. Fisher's cruises in the Lau Basin, suspecting the presence of new *Austinograea*.

DISTRIBUTION. — *Austinograea hourdezi* n. sp. is a widespread species encountered in the southwestern Pacific from numerous vent fields of the Lau and North Fiji Back-Arc Basins. It cohabits with *A. alayseae* at a number of sites, and the two species seem to share a similar distribution.
As *A. alayseae*, *A. hourdezi* n. sp. has not been found in the northwestern Pacific, at least after the revision of the MNHN collection and without, however, the examination of an extensive material from the Mariana Trough. For its part, *A. williamsi* seems to be confined to the northwestern Pacific, in the Mariana Back-Arc Basin, and vent sites of the Mariana Trough.

DESCRIPTION (MALE)
Carapace
Carapace transversely elliptical, flat; regions indistinct. Dorsal surface nearly smooth, except for rare small granules on frontal region and small tubercles on orbital region; numerous small pits. Anterolateral margin marked by rounded edge, slightly granulous. Posterolateral margins convergent; posterior margin slightly concave. Subhepatic regions entirely covered by patches of dense setae. Front broad, not protruded, bluntly pointed medially and with two slightly concave lobes. Eyes, antennules and antennae recessed under front. Suborbital plate absent. Orbit not delimited, only an orbital region that extends as groove lateral to region containing vestigial eyestalks and antennae. Outer side of orbital region tuberculated.
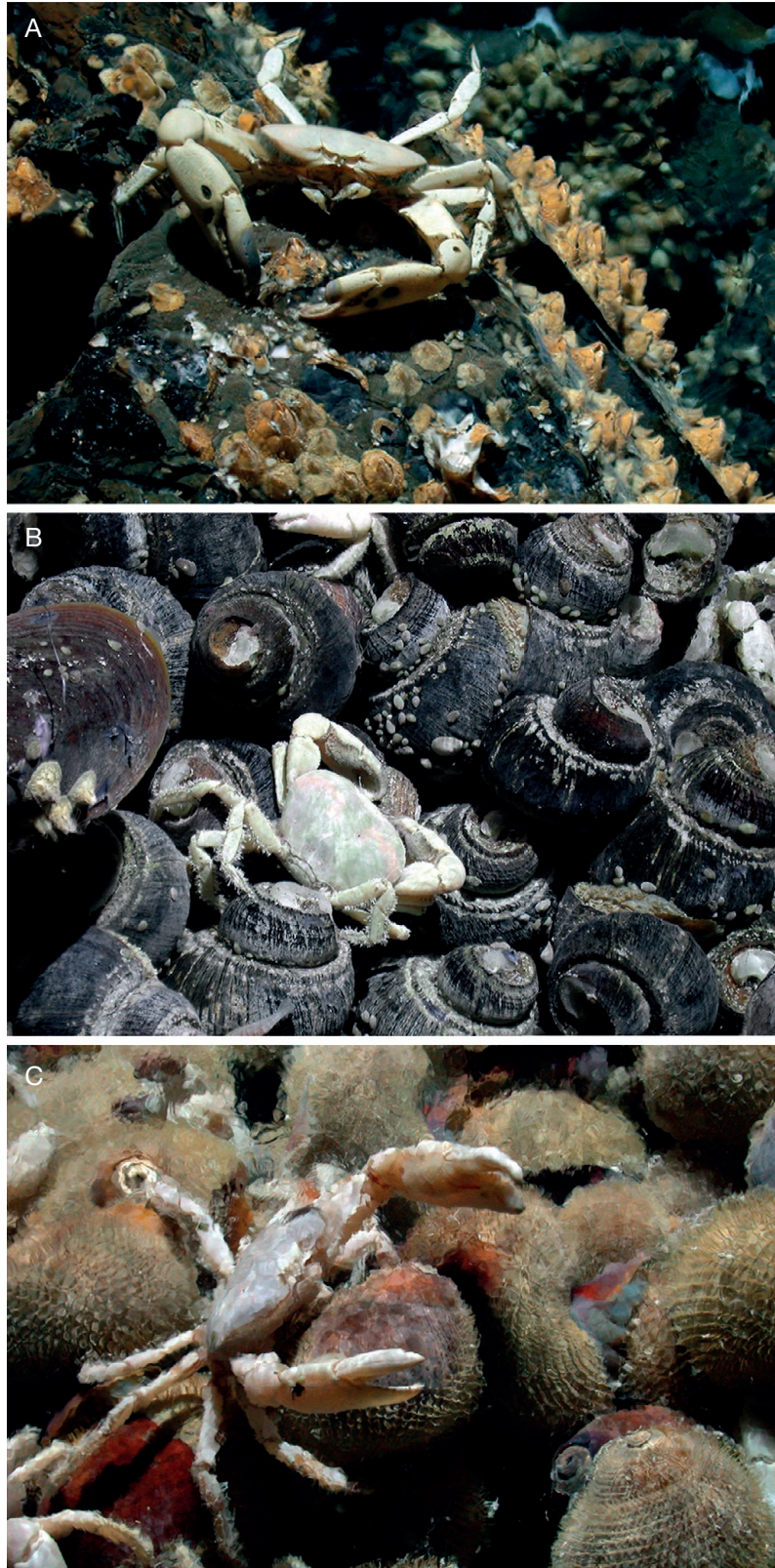
FIG. 3. — *Austinograea hourdezi* n. sp. photographed *in situ*: **A**, Lau Basin, Lau Basin 2009 cruise, dive 432, Tow Cam site, 20°18.98'S, 176°08.19'W, 2723 m, 05.VI.2009 (type locality), among sessiles barnacles *Eochionelasmus ohtai ohtai* Yamaguchi, 1990. The two dark spots on outer surface of palm of both chelae indicate a male; see patches of dense setae on inner surface of both chelae, and the darkly coloured two-thirds of dactylus of right cheliped; **B**, **C**, *Austinograea hourdezi* n. sp., due to the patch of dense setae on inner surface of both chelae: **B**, Lau Basin, TUIM07MV cruise, dive 163, ABE site, 20°45.65'S, 176°11.45'W, 2130 m, 23.VI.2005; on a bed of gastropod *Ifremeria nautilei* Bouchet & Warén, 1991; **C**, Lau Basin, Lau Basin 2009 cruise, dive 431, ABE site, 20°45.65'S, 176°11.45'W, 2130 m, 03.VI.2009. The crab and the gastropods *Alviniconcha hessleri sensu lato* are blurry, the photography *in situ* having been taken in hydrothermal diffuse area with the emanating fluid visible as shimmering water. Photographies courtesy of C. R. Fisher (Penn State University, USA).
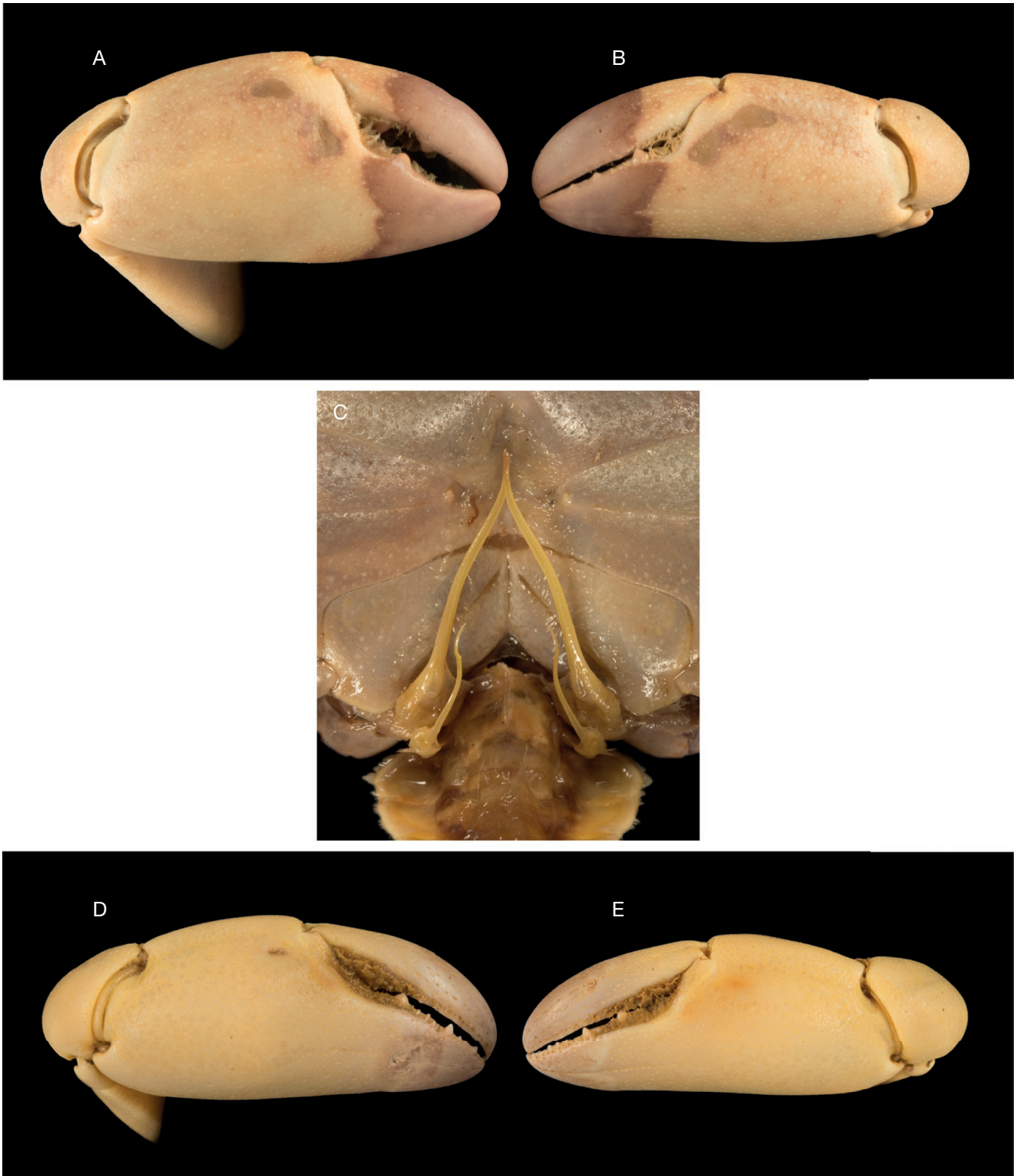
FIG. 4. — **A-C**, *Austinograea hourdezi* n. sp., holotype, ♂ 25.7 × 40.2 mm (right-handed), Lau Back-Arc Basin, TUIM06MV cruise, dive 142, Tow Cam site, 20°19.07'S, 176°08.24'W, 2719 m, MNHN-IU-2016-10737: **A, B**, chelae with two coloured spots on outer surface of palm of right crusher (**A**) and left cutter (**B**); **C**, G1 and G2 photographed *in situ*; **D, E**, *Austinograea hourdezi* n. sp., atypical ♀ 30.0 × 48.5 mm (right-handed), Lau Back-Arc Basin, MGLN07MV cruise, dive 230, Kilo Moana site, 20°03.23'S, 176°08.01'W, 2623 m, MNHN-IU-2016-10752: **D**, crusher with one marked dark spot and the other one, only discernible by a yellow trace (wound at base of fixed finger is not a spot comparable to that of *A. jolliveti* n. sp.); **E**, cutter with two indistinct spots, only as yellow traces.

FIG. 5. — *Austinograea hourdezi* n. sp., paratype, ♂ 29.8 × 48.1 mm (left-handed, with weak heterochely and heterodonty), Lau Back-Arc Basin, TUIM06MV cruise, dive 142, Tow Cam site, MNHN-IU-2016-10738: **A**, dorsal view; **B**, frontal view; **C**, mxp3; **D**, ventral view; **E**, **G**, both chelae with two typical spots on outer surface; **F**, **H**, both chelae with patches of setae on inner surface: **E**, **F**, cutter situated at right; **G**, **H**, crusher situated at left.

Eyestalk not moveable, showing as fixed piece fused to floor of orbital region; no cornea. Antennules folded horizontally. Antenna inserted in wide supraorbital notch; urinary article fixed, broad, recessed; basal article (2 + 3) cylindrical, moveable; article 4 slightly elongated, inclined; flagellum of about 10 articles. Proepistome incomplete. Margin of epistome with moderate median projection and formed of two moderately concave lobes, marked by row of low granules. Pterygostomial lobe tuberculous; pterygostomial region smooth, except for small curved ridge.

Thoracopods

Third maxillipeds completely closing buccal cavity. Ischium long, with marked longitudinal internal groove. Merus: external margin regularly curved, oblique, without marked angle, with distal part markedly narrow and produced; internal margin with prominent lobe in half proximal portion. Carpus inserted in notch of antero-internal margin of merus; propodus thick; dactylus about as long as merus; inner margins of propodus and dactylus with brush-like setae. Exopod longer than endopod ischium. Mxp3 coxa with only proximal portion visible, its lateral projection hidden by junction of thoracic sternum (sternite 4) with pterygostome. Chelipeds heteromorphic, marked heterochely (also in females, see below), with two types of chelae: major cheliped blunt-tip (crusher), stouter and shorter than pointed-tip minor chela (cutter). Carpus with setae on superior margin and inner surface; merus long, triangular in cross section, anterior border straight, with blunt teeth, smaller distally. Propodus of both chelae with two conspicuous, deep depressions at outer surface of palm near base of dactylus (absent in females), both as two dark spots, even well visible in specimens photographed *in situ*. Inner surface of both chelae dished on half posterior part; thick patches of dense setae largely extending on half anterior part of propodus and partially extending along occluding margins. Dark colour extending on about three-quarters of fixed finger and practically on whole part of dactylus of both crusher and cutter. Crusher: palm convex, inflated, smooth, except for two depressions located near base of dactylus: one horizontally directed and the largest; the other obliquely directed, smaller. Fingers thick, slightly gaping at occluding margins; two weak, blunt teeth, proximal and median, on occluding margin of dactylus; a blunt but marked subproximal tooth and smaller ones on occluding margin of fixed finger. Cutter: palm elongate, with subparallel borders, smooth, except for two depressions near base of dactylus, similar to those of the crusher; both fingers not gaping at the occluding margins; dactylus elongate, hollowed, with occluding margin smooth; fixed finger very thick, dished on inner surface; occluding margin nearly straight, with 2-3 small teeth, size progressively diminishing forwards. P2-P5 shorter than chelipeds; P3 and P4 longest; meri with patch of dense setae on ventral margins, carpi, propodi fringed on dorsal and ventral margins with felt of short, stiff setae, mixed with sparse longer setae, the patch being dense, thicker on inferior margin. Dactyli rather stout, with patches of short setae.

Thoracic sternum

Thoracic sternum with sutures 4/5-7/8 incomplete but separared by short gap; suture 2/3 complete. Median line only along sternite 8, hardly continuying along sternite 7. Junction of sternite 4 with pterygostome represented by only short juxtaposition, without patch of setae. Press-button of locking mechanism acute, very close to suture 5/6.

Pleon

Pleon of six free segments and telson regularly triangular; pleonal somite 3 widest; pleonal somite 6 longest, anterointernally delineated by raised, thick margin; telson triangular, rounded distally. Both G1 joining at tips. G1: slender, faintly curved, with only short, spiniform setae arranged in two rows along mid-part only. G2: about half the length of G1, with bend about two-thirds length at level of small setiferous area; flagellum rather long, curved, flattened, bladelike.

DESCRIPTION (FEMALE)

Chelipeds weakly dimorphic (versus dimorphic in males), having almost cutters on both sides. On both chelipeds: inner surface markedly dished on half posterior part of propodus and on fixed finger; thick patches of dense setae extending on half or anterior two-thirds part of propodus and along occluding margins of dactyli. Dark colour extending on about three-quarters of fixed finger and on two-thirds of dactylus of both crusher and cutter. Weak heterochely and heterodonty; cutter however smaller than crusher. Crusher: palm hardly inflated, elongated, smooth, without depressions; fingers thick, not or only slightly gaping at the occluding margins; two tiny blunt teeth on occluding margin of dactylus; two tooth and a few smaller ones on occluding margin of fixed finger. Cutter: palm similar to crusher but fingers more elongated, not gaping at occluding margins; palm smooth, without depressions; both fingers; dactylus elongate, hollowed, with occluding margin practically smooth; fixed finger very thick, with occluding margin nearly straight, bearing small teeth, two being more marked. P2-P5 with felt of short, stiff setae, mixed with numerous longer setae. Median line along sternite 8, hardly continuying along sternite 7. Dense patches of setae on thoracic sternum near junction of sternite 4 with pterygostome. No pleonal locking mechanism in mature females. Margins of pleon densely fringed with setae. Vulvae large, rounded, with thick membranous area all around median opening.

REMARKS AND COMPARATIVE DIAGNOSIS

The two characteristic depressions on the propodus of both male chelae, crusher and cutter, of *Austinograea hourdezi* n. sp. (Figs 3A; 4A, B; 5E, G), typically absent in females (Fig. 7E, G), are similarly located in all the individuals examined, but they are variously delineated by a raised margin and thus may appear quite deep or shallower but practically always coloured as dark or coloured spots, always with a different texture and colour but commonly referred to as "dark spots". The function of the pigmented pits or spots present on the palm of chelipeds (also on the subocular regions in others species) of certain bythograeids is supposed to be sensory.
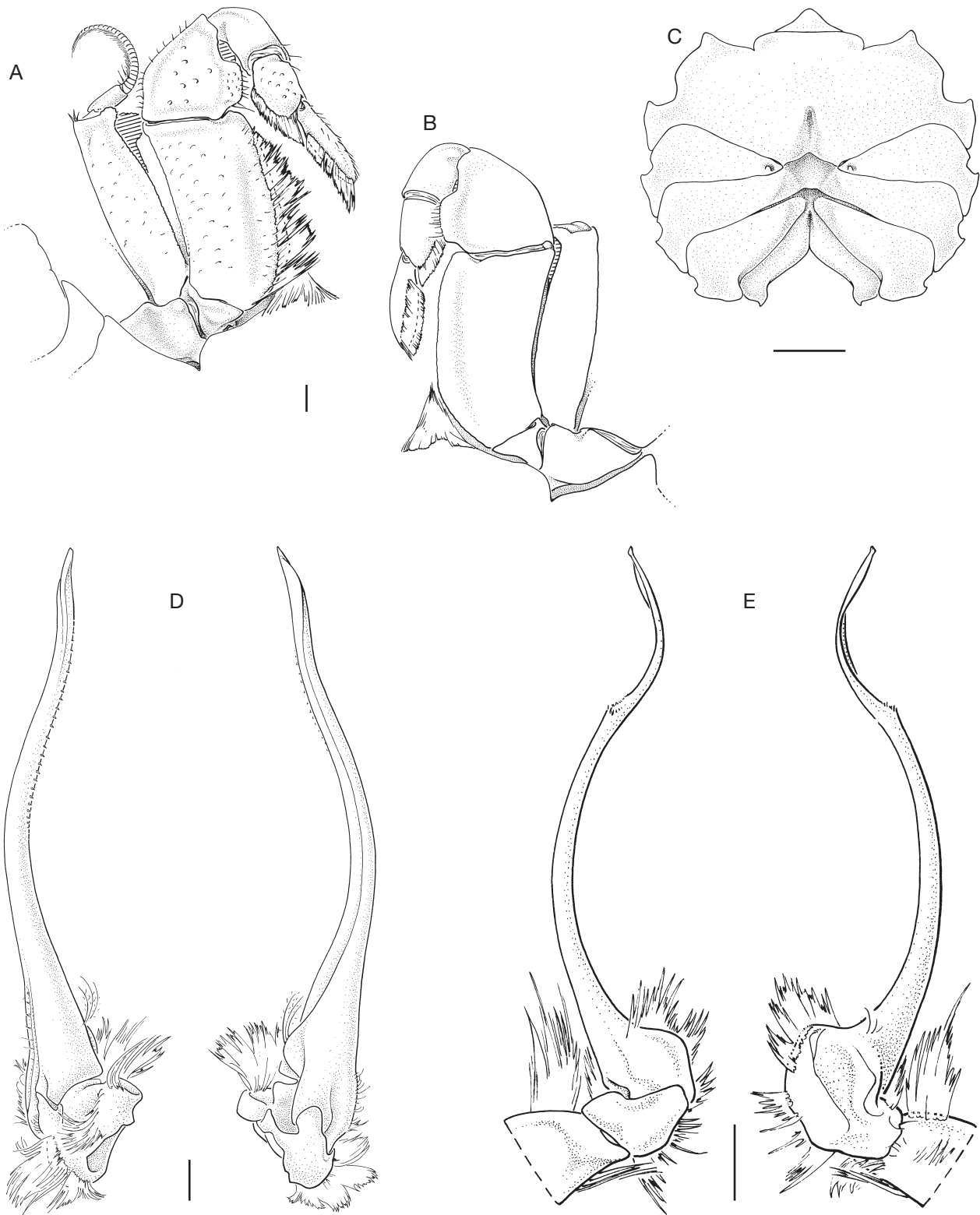
FIG. 6. — *Austinograea hourdezi* n. sp.: **A-C**, holotype, ♂ 25.7 × 40.2 mm (right-handed), Lau Back-Arc Basin, TUIM06MV cruise, dive 142, Tow Cam site, 20°19.07'S, 176°08.24'W, 2719 m, MNHN-IU-2016-10737: **A**, **B**, right and left mxp3, with and without ornamentation; **C**, thoracic sternum. **D**, **E**, paratype, ♂ 29.8 × 48.1 mm (left-handed), Lau Back-Arc Basin, TUIM06MV cruise, dive 142, Tow Cam site, MNHN-IU-2016-10738: **D**, G1, two views; **E**, G2, two views. Scale bars: A, B, D, E, 1 mm; C, 5 mm. Note the scale bars of the two gonopods, the G2 being about half-length of G1.

For atypical specimens of *A. hourdezi* n. sp., see below *Individuals with regenerated chelae*.

Austinograea hourdezi n. sp. may be easily distinguished from *A. alayseae* (Fig. 8A, B), with which it cohabits in several sites, by:

1) subhepatic region covered by patch of dense setae in both sexes (no setae in *A. alayseae*); 2) mxp3: external border oblique, distal end strongly produced (in *A. alayseae* forming a marked angle: proximal portion vertically oriented, with slightly concave border, half distal portion abruptly tilted; distal end weakly produced); inner margin produced in marked lobe (without lobe in *A. alayseae*); 3) both male chelae with two deep, dark depressions, marked as spots (without any spot in *A. alayseae*); 4) in both sexes patches of dense setae on inner surface of palm and along fingers (without setae in *A. alayseae*); 5) marked heterochely: male crusher with short, stout propodus, and short, thick fingers; 6) fixed finger coloured; dactylus coloured on two thirds (in *A. alayseae* pronounced heterochely but propodus of male crusher more elongated; fingers more elongated, narrower); 7) male cutter with occluding margin of dactylus smooth; 8) fixed finger very thick, almost entirely coloured, occluding margin with three small teeth, size progressively diminishing forwards (in *A. alayseae* fingers elongated, armed on both occluding margins with several small teeth interspersed with smaller ones; dactylus coloured at distal end in males and only at tip in females); 9) thoracic sternum with median line at level of sternite 8 and practically not continuying along sternite 7 in both sexes (extending on most part of sternite 7 in both sexes of *A. alayseae*, see Guinot 1990: fig. 2C); 10) male pleon with triangular telson (rounded in *A. alayseae*); and 11) G1 rather straigt, with only minute setae along subdistal half (more curved, with several rows of rather long, acute setae along most of length in *A. alayseae*).

The most distinctive character between *Austinograea hourdezi* n. sp. and *A. williamsi* is in the presence of a two spots in male chelae of *A. hourdezi* n. sp. (Figs 3A; 4A, B; 5E, G) ([versus one spot on the palm of crusher and cutter male chelipeds of *A. williamsi*, described by Hessler & Martin (1989: 651, figs 1b, 9a-c) as "small, often brown-stained, pitted area just proximal to, and in line with, ventral border of dactylus" in "larger males" and absent in females (see also Tsuchida & Fujikura 2000: fig. 2]). Heterochely and heterodonty are pronounced in males of *A. hourdezi* n. sp. and *A. williamsi*. The male cutter chela of *A. hourdezi* n. sp. has a thick, broad fixed finger, and an occluding margin armed with a few teeth. In *A. williamsi* the cutter chela is more elongate; the fixed finger is more inflated and broader, with a deeply dished inner surface, and a markedly convex, much toothed occluding margin that fits flush against dactylus. In *A. hourdezi* n. sp. the chelae show a sexual dimorphism that is distinctive from that of *A. williamsi* (see Hessler & Martin 1989: figs 9, 10), in which females have cutters for both chelipeds with a markedly concave propodal inner margin and a well dished fixed finger at occluding margin that bears numerous, sharper, delicate teeth. The mxp3 merus of *A. hourdezi* n. sp. is very similar to that of *A. williamsi*, both having an oblique external border,

a produced ending and a pronounced inner lobe. Another marked difference is the subhepatic region: covered by dense setae in *A. hourdezi* n. sp., whereas the patch of setae is much more larger in *A. williamsi*, in which it considerably extends below the lateral line.

For the distinction between *A. alayseae* and *A. williamsi*, see the comparative illustrations in Tsuchida & Hashimoto (2002). The inner surface of palm and most inner surface of the dactylus of the two chelae bear patches of setae in both sexes of *A. hourdezi* n. sp. (Figs 3A-C; 5A, F, H; 7A, B, F, H), as in *A. williamsi*, whereas in both sexes of *A. alayseae* the chelae of both sides are glabrous on palm and dactylus. The G1 and G2 of *A. hourdezi* n. sp. and *A. williamsi* (in which the G2 is about less than half the G1's length) are similar, whereas in *A. alayseae* the G1 bears numerous long setae scattered over its entire length.

DISTINCTION OF FEMALES

As the spots on the cheliped propodus are typically absent in female *A. hourdezi* n. sp. and in both sexes of *A. alayseae*, the more useful significant character to differentiate the females of the two species is the patch of setae at the inner surface of the palm of females of *A. hourdezi* n. sp. (Fig. 7A, B, F, H), as in the males (Figs 3A; 5A, F, H). In contrast, in *A. alayseae* (Fig. 8A, B) the chelae are devoid of setae, in females as in males. The same character allows identification of females of *A. williamsi*, with setose patch at the inner chela surface (Hessler & Martin 1989: fig. 10), from females of *A. alayseae*, which have glabrous chelae. See the comparative illustration of female *Austinograea* chelae by Tsuchida & Hashimoto (2002: fig. 6), which does not show any spot in *A. williamsi* and *A. alayseae*, in contrast with *A. rodriguezensis*, which is shown bearing a spot, as in the males. In *A. alayseae* a thick posterior membrane may cover most of the vulva, leaving a variously developed opening, sometimes only a lateral slit, whereas in *A. hourdezi* n. sp. the medial opening is entirely surrounded by thick membrane (Fig. 7D).

INDIVIDUALS WITH REGENERATED CHELAE

A few male specimens that display most characters of *A. hourdezi* n. sp. (including mxp3 shape and patches of setae on inner surface of chelae) exhibit a single spot on the outer surface chelae palm, instead of two. The holotype (MNHN-IU-2016-10737), from the Lau Basin, Tow Cam site, a large right-handed male 25.7 × 40.2 mm, typically bears the two characteristic spots on each chela (Fig. 4A, B), such as most of other males that we have examined. Although left-handed and with weak heterochely and heterodonty, a larger male from the same site 29.8 × 48.1 mm, paratype, MNHN-IU-2016-10738, also shows the two typical spots on chelae, even on regenerated cheliped (Fig. 5E, G). But a smaller left-handed male 24.7 × 36.0 mm, from the same sample, has an obviously regenerated minor chela that bears only one spot; its left chela, having become the major chela, shows the two typical spots.

Two samples of female *A. hourdezi* n. sp., instead of being devoid of any spot on the chela, bear a spot on both chelae:
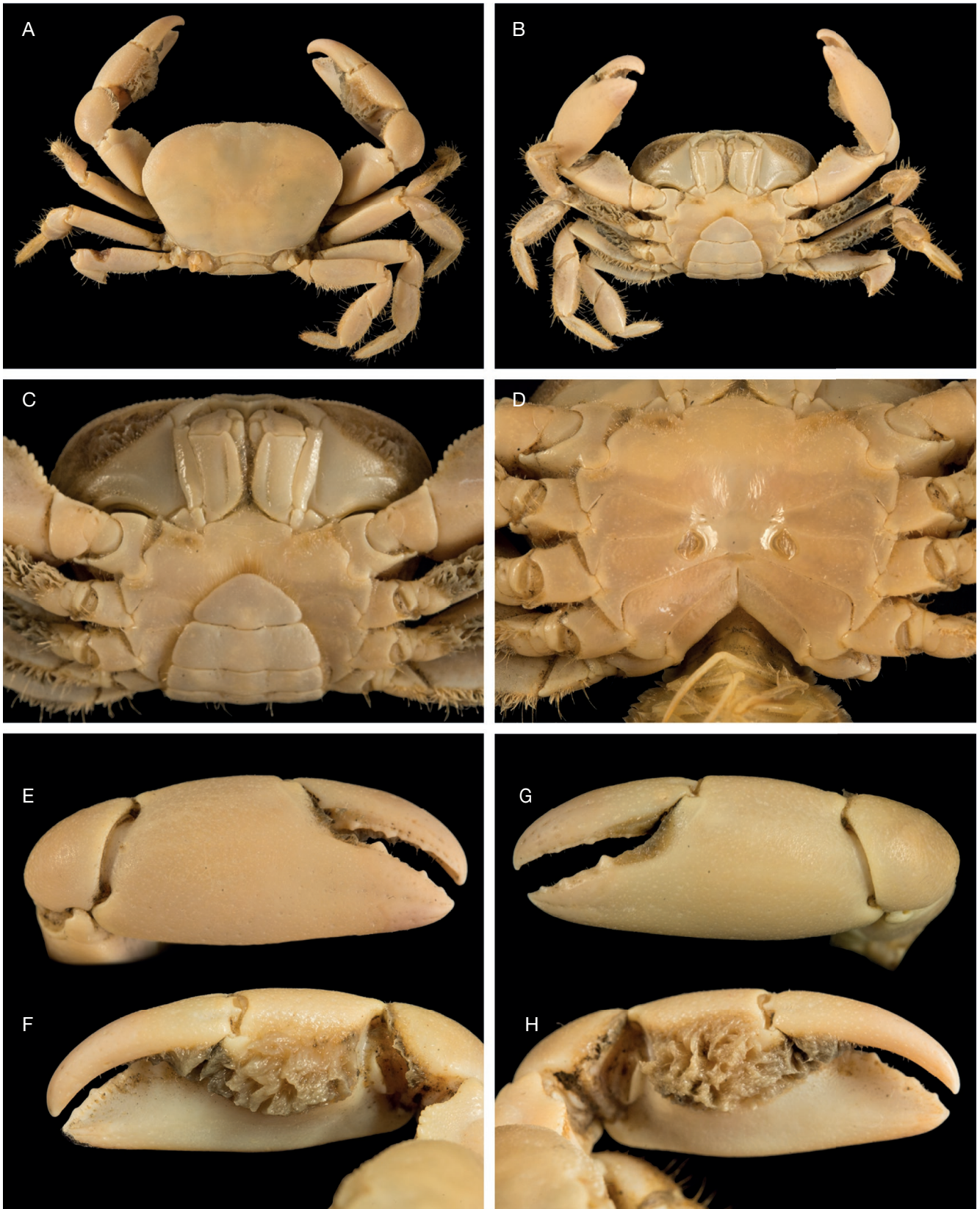
FıG. 7. — *Austinograea hourdezi* n. sp., paratype, ♀ 18.3 × 28.4 mm (right-handed), Lau Back-Arc Basin, BIOLAU cruise, BL 12, Vai Lili site, 23°13'S, 176°38'W, 1750 m, MNHN-IU-2016-10745 (= MNHN-B24060): **A**, dorsal view; **B**, **C**, ventral views, with pleon; **D**, thoracic sternum and vulvae; **E**, **G**, both chelae without spots on outer surface; **F**, **H**, both chelae with patches of setae on inner surface; **E**, **F**, right crusher; **G**, **H**, left cutter.
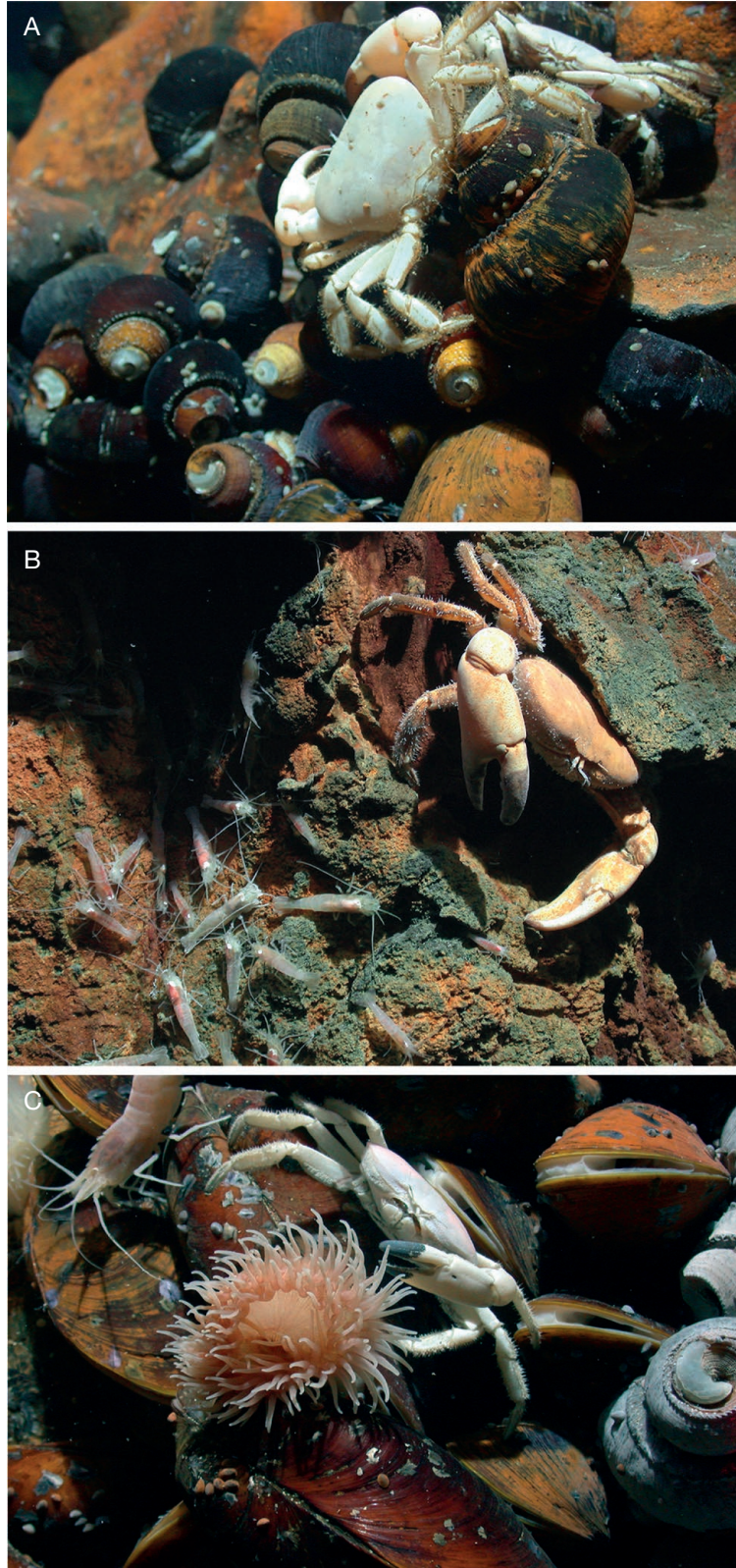
Fig. 8. — **A**, **B**, *Austinograea alayseae* Guinot, 1990, photographed *in situ*: see absence of patches of setae on inner surface of chelae: **A**, crab with white carapace, Lau Basin 2009 cruise, Kilo Moana site, 20°03.23'S, 176°08.01'W, 2621 m, among mussels *Bathymodiolus brevior* Cosel, Métivier & Hashimoto, 1994 and snails *Ifremeria nautilei* Bouchet & Warén, 1991; **B**, crab with carapace stained orange due to iron or manganese oxide deposits, and cluster of alvinocaridid shrimps, Lau Basin, TUIM07MV, Kilo Moana site, 20°03.23'S, 176°08.01'W, 2621 m; **C**, *Austinograea hourdezi* n. sp. (presumed identification, see p. 89), Lau Basin, Lau Basin 2009 cruise, Kilo Moana site, among mussels *Bathymodiolus brevior*, gastropods *Ifremeria nautilei*, sea anemone probably *Cyananthea hourdezi* Zelnio, Rodríguez & Daly, 2009, and alvinocaridid shrimp, *Alvinocaris komaii* Zelnio & Hourdez, 2009. This invidual with palm of preserved left cheliped (regenerated?) bearing only a single dark spot is atypical such as many *Austinograea* species showing regenerated chelipeds; patches of setae discernible just above on inner surface of chela and on right subhepatic region. Photographies courtesy of C. R. Fisher (Penn State University, USA).

they are left-handed, which means that one chela was regenerated. These females that bear a spot on each cheliped, crusher and cutter, are:

MNHN-IU-2016-10744, 1 ♀ 27.1 × 44.6 mm (left-handed), Lau Back-Arc Basin, Lau Basin 2009 cruise, dive 427, ABE site, 20°45.65'S, 176°11.45'W, 2130 m, 28.V.2009 (preserved in ethanol 85%). It belongs to the same sample that contains two typical females devoid of spots on chelae palm;

MNHN-IU-2016-10768 (= MNHN-B27834), 1 ♀ 22.7 × 36.5 mm, North Fiji Basin, STARMER II cruise, dive PL 18, Mussel Valley, 18°50'S, 173°29'E, 2750 m, 13.VII.1989 (was found with a typical male of *A. alayseae*).

A large, right-handed ♀ 30.0 × 48.5 mm (MNHN-IU-2016-10752) from the Lau Back-Arc Basin, MGLN07MV cruise, dive 230, Kilo Moana site, 20°03.23'S, 176°08.01'W, 2623 m, 07.IX.2006, and identified as *A. hourdezi* n. sp. on the basis of other characters, has the right chela of a crusher type with one marked spot plus a second spot only as a yellow trace, and the cutter with two yellowish spots (Fig. 4D, E), This male chela pattern is unusual for female *A. hourdezi* n. sp., which are generally devoid of any spot (Fig. 7E, G).

A bythograeid that bears only a left cheliped, photographed *in situ* (Fig. 8C) at the site Kilo Moana during the Lau Basin 2009 cruise and with a single dark spot on the chela could be *A. hourdezi* n. sp., based on the patches of setae discernible just at the suface of the inner chela palm and on setose patches on the right subhepatic region. This could be an atypical specimen of *A. hourdezi* n. sp., with a regenerated cheliped. It was found associated with mussels *Bathymodiolus brevior* Cosel, Métivier & Hashimoto, 1994 (see Cosel *et al.* 1994), gastropods *Ifremeria nautilei* Bouchet & Warén, 1991, sea anemone *Cyananthea hourdezi* Zelnio, Rodríguez & Daly, 2009 (see Zelnio *et al.* 2009; E. Rodríguez, pers. comm. 2017). Due to the same features, the seemingly right-handed crab collected at Tow Cam site, dive 240, and photographed *in situ* (Zelnio *et al.* 2009: fig. 14B) associated with an unidentifiable actiniarian zoanthidean, could be also identified to *A. hourdezi* n. sp., but it is difficult to discern the presence of spots on the chelae.

All of these specimens with atypical spot(s) on the chelae exhibit all other morphological traits of *A. hourdezi* n. sp., and are not *A. williamsi* nor *A. rodriguezensis*, both of which are characterised by one spot on the outer chela palm, near the dactylus base. We assume that most of these atypical crabs were initially right-handed and that left-handers represent individuals whose asymmetry has been reversed following autotomy and regeneration of the lost cheliped (see *Chelae: crusher and cutter. Regenerated chelae*). This reversion of chelipeds, which causes a dramatic rearrangement and triggers a new allometric growth, is thought to have induced a novel implantation of the spots on the chelae, mainly when autotomy or loss occurs at a large size of crabs. These atypical individuals, without other equivocal morphological evidence and presumably not genetically cryptic, are here treated as *A. hourdezi* n. sp. subject to their recognition by molecular sequences (in study).

MOLECULAR ANALYSIS

In the early 2000s fragments of *Austinograea* from the Lau Back-Arc Basin, Valu Fa Ridge, recognised by Guinot (1990) as "*Austinograea* aff. *williamsi*" and here described as *A. hourdezi* n. sp. were sent by D. Guinot to L. A. Hurtado (Texas A&M University, USA) and V. Leignel (Université du Maine, Le Mans, France) for molecular analyses. Genetic divergence warranted recognition of a new species. The sequences obtained for the 16S rDNA, Cytb, and 28S rDNA recovered that the uncorrected nucleotide divergence for the mitochondrial 16S rDNA gene was 5.5% between *A. hourdezi* n. sp. and *A. williamsi*; 7% between *A. hourdezi* n. sp. and *A. alayseae*; and 5.9% between *A. williamsi* and *A. alayseae* (Mateos *et al.* 2012: 1, 3, 5, 6, 10, fig. 2, table 1, as *Austinograea* aff. *williamsi*).

Austinograea jolliveti n. sp.
(Figs 9A-H; 10A-E; 11A-E)

TYPE MATERIAL. — **Holotype**. ♂ 12.8 × 20.0 mm (right-handed), western Pacific, North Fiji Basin, STARMER II cruise, dive 18 (PL 18), Mussel Valley site, 18°50'S, 173°29'E, 2750 m, 13.VII.1989 (MNHN-IU-2016-10769) (Figs 9A-H; 11A-E). **Paratypes**. 1 ♂ 14.7 × 25.4 mm, 1 ♀ 12.4 × 21.6 mm (Fig. 10A-E), same data (MNHN-IU-2016-10770).

OTHER MATERIAL EXAMINED. — 1 ♀ 13.6 × 22.0 mm (left-handed), western Pacific, 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 (preserved in ethanol 85%).

TYPE LOCALITY. — Western Pacific, North Fiji Basin, Mussel Valley site, 2750 m.

ETYMOLOGY. — Dedicated to Didier Jollivet (CNRS, Station biologique de Roscoff, France), in recognition of his pioneering work on the ecology of the southwestern Back-Arc Basin hydrothermal communities in 1989 and for his valuable contribution to deciphering the delicate interplay of physical and biological factors in shaping the evolutionary history of hydrothermal vent fauna.

DISTRIBUTION. — Southwestern Pacific; only collected from one site in the Lau Basin (ABE site) and one site in the North Fiji Basin (Mussel Valley site).

DESCRIPTION (MALE)
Carapace
Carapace transversely elliptical, flat; regions indistinct. Dorsal surface nearly smooth, except for rare small granules on frontal region and tubercles on orbital region; numerous small pits. Anterolateral margin marked by rounded edge, slightly granulous. Posterolateral margins convergent; posterior margin slightly concave. Subhepatic region with dense setae mainly only at lateral edge. Front broad, not protruded, bluntly pointed medially and with two slightly convex lobes. Eyes, antennules and antennae recessed under front. Suborbital plate absent. Outer side of orbital region tuberculated. Proepistome incomplete. Orbital region deeply concave and open laterally, containing antennules, antennae and possible

eye remnants. Eyestalk absent, podophthalmite fused to floor of orbital region; cornea absent, no visible pigment. Antennules folded horizontally, filling most of orbit. Antenna inserted in wide supraorbital notch; urinary article fixed, broad, recessed, basal article (2 + 3) cylindrical, moveable; article 4 elongated shorter, inclined. Margin of epistome projecting medially and formed of two markedly concave lobes, marked by row of low granules. Pterygostomial lobe granulous; pterygostomial region mostly smooth.

Thoracopods

Third maxillipeds completely closing buccal cavity. Ischium long, with marked longitudinal internal groove. Merus about half as long as ischium, narrow; external margin regularly curved, oblique, without marked angle; half distal part markedly narrow and much produced; half proximal internal margin with prominent median lobe. Carpus inserted in notch of anterointernal margin of merus; propodus thick; dactylus about as long as merus; inner margins of propodus and dactylus with brush-like setae. Exopod longer than endopod ischium. Wide mxp3 coxa with only proximal portion visible, its lateral projection hidden by junction of thoracic sternum (sternite 4) with pterygostome. Chelipeds long, heteromorphic. Palm of both chelipeds with inner surface bearing medially thick patches of setae, densely extending along occluding margins of both fingers, thus well dorsally visible along half of fingers. Dark colour extending on about whole fixed finger (the dark coloured of half posterior portion joins the coloured spot), and on two-thirds of dactylus of both crusher and cutter. Major cheliped (crusher) stouter than minor ones (cutter); merus notably elongated, largely extending beyond margin of carapace, narrow, anterior border entirely straight, with regular, small, distally reduced teeth; both fingers thick, blunt-tipped. Crusher: palm rather long, dorsal surface slightly convex, pitted; a conspicuous but hollow depression near base of fixed finger, appearing as pigmented spot, more or less in continuity with black area of fixed finger; dactylus elongate, thick, with only one blunt median tooth; fixed finger thick, with only one blunt proximal tooth on occluding margin; fingers thick, gaping, with blunt tips. Male cutter: palm elongate, nearly flat, smooth, with a conspicuous dark spot near base of fixed finger similar to that of the crusher; both fingers thick, more elongate, occluding, with blunt tips; dactylus with occluding margin smooth; occluding border of fixed finger with one proximal small tooth, and another one small more distally. P2-P5 shorter than chelipeds; P4 longest. Meri of P2, P3 with patch of dense setae on ventral margins, the patch being dense, thicker on inferior margin; meri of P4 and P5 and carpi, propodi of P2-P5 fringed on dorsal and ventral margins with short, stiff setae, mixed with longer setae. Dactyli elongate, with patches of short setae on anterior and posterior margins.

Thoracic sternum

Thoracic sternum with sutures 4/5-7/8 incomplete. Median line along sternite 8 and hardly continuying along sternite 7. Junction of sternite 4 with pterygostome via rather long juxtaposition; no patch of setae. Press-button of locking mechanism acute, close to suture 5/6, lacking on a side in holotype.

Pleon

Pleon of six free somites and telson, regularly triangular, third somite widest; telson short, bluntly triangular, rounded distally; pleonal somite 6 longest. G1: straight, with sparse, small and short setae, arranged in two rows along mid-part only. G2: about less than half G1's length; flagellum very short, straight, flattened.

Description (female)

Subhepatic region without patches of dense setae. Chelipeds slightly dimorphic, both as cutters, major cheliped being hardly longer than minor cheliped; merus not elongated; chelae not markedly dissimilar; as in males, a pigmented spot near base of fixed finger on both propodi; both fingers not gaping, with acute tips. No pleonal locking mechanism. Pleon with margins densely fringed with setae. Vulvae rounded, closed by soft membrane.

Comparative diagnosis

The description of *Austinograea jolliveti* n. sp. is based on four, rather small specimens, from two vent sites. The species can be, however, distinguished from all other known *Austinograea* species by: 1) small size (to be checked on additional material); 2) subhepatic region with dense setae only at lateral edge (this feature needs to be checked on additional male material); 3) merus of male cheliped long, markedly extending beyond carapace margin, narrow on its whole length, regularly toothed on dorsal margin; 4) dorsal surface of propodus of both chelae in both sexes (Figs 9E, G; 10A, C) with a differently pigmented spot at the limit of the fixed finger (versus only one spot in male *A. williamsi*, and two spots in male *A. hourdezi* n. sp., moreover located on the anterior portion of the palm in both species, instead at the basis of fixed finger in *A. jolliveti* n. sp.); and 5) G2 much shorter than G1 and with a very reduced, straight flagellum (Figs 9D; 11E) (compare with fig. 8 of Tsuchida & Hashimoto 2002, showing the two pairs of gonopods in *A. alayseae*, *A. williamsi*, and *A. rodriguezensis*).

The unique spot near the base of dactylus on dorsal surface of both chelae in both sexes of *A. jolliveti* n. sp. (Figs 9E, G; 10A, C) is of a different nature from the two depressions of *A. hourdezi* n. sp. It shows as a differently pigmented "pustule" and is similar to the violaceous spot of *Bythograea microps* Saint Laurent, 1984 (from the East Pacific Rise) in about the same location, i.e., at the base of the palm of the male minor chela and of both female chelae (Guinot & Segonzac 1997: figs 7C, 9D-F; 2006c: 468, fig. 5; Guinot & Hurtado 2003). This pigmented spot, supposedly sensory, easily allows distinguishing male and female *A. jolliveti* n. sp. from all other *Austinograea* species, and also from *Gandalfus*.

FIG. 9. — *Austinograea jolliveti* n. sp., holotype, ♂ 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, MNHN-IU-2016-10769: **A**, dorsal view; **B**, **C**, ventral views; **D**, thoracic sternum with G1 and G2 *in situ*; **E**, **G**, both chelae with one coloured spot at fixed finger base and patch of setae at occluding margins of fingers; **F**, **H**, both chelae with patches of setae on inner surface and extending along occluding margins of fingers; **E**, **F**, right crusher; **G**, **H**, left cutter. Note the long merus.

Fɪɢ. 10. — *Austinograea jolliveti* n. sp., paratype, ♀ 12.4 × 21.6 mm (right-handed), North Fiji Basin, STARMER II cruise, dive 18 (PL 18), Mussel Valley site, 18°50'S, 173°29'E, 2750 m, MNHN-IU-2016-10770: **A**, **C**, both chelae with one coloured spot at fixed finger base and patches of setae extending proximally between fingers; **B**, **D**, both chelae with patches of setae extending between fingers; **A**, **B**, right crusher; **C**, **D**, left cutter; **E**, ventral surface with vulvae.
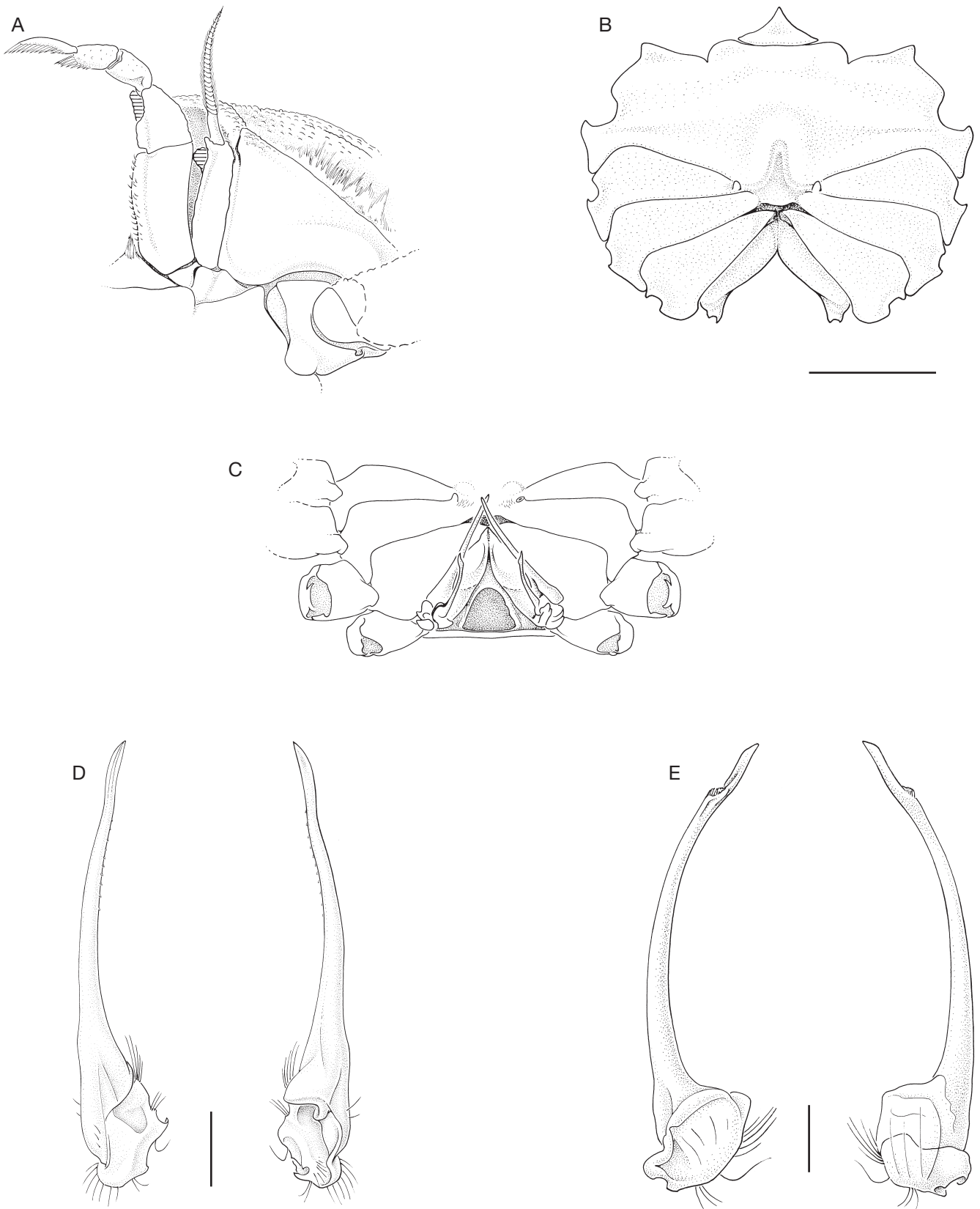
Fig. 11. — *Austinograea jolliveti* n. sp., holotype, ♂ 12.8 × 20.0 mm (right-handed), North Fiji Basin, STARMER II cruise, dive 18 (PL 18), Mussel Valley site, 18°50'S, 173°29'E, 2750 m, MNHN-IU-2016-10769: **A**, mxp3; **B**, thoracic sternum; **C**, G1 and G2 *in situ* (reconstructed); **D**, G1, two views; **E**, G2, two views. Scale bars: B, 5 mm; D, 1 mm; E, 0.5 mm (note the scale bars of the two gonopods, the G2 being about half-length of G1); A, C, without scale.

GENERAL DISCUSSION

Geological and biogeographical settings

The complex geomorphology of the southwestern Pacific is considered the result of the interaction between the Pacific and Australia plates. Western Pacific Back-Arc Basins constitute a series of biogeographic entities relatively isolated one from each other, which remain hydrothermally active for a few millions years. This complicated system of fragmented ridges originated from the clockwise rotation of the South Carolina and Melanesian Arcs and the collision of the Ontong-Java Plateau about 25 Ma (Hall 2002). The ongoing collision between these two plates occupies a very large area due to the formation of two opposing subduction zones (Vanuatu and Solomon) with active island arcs that contributed to the emergence of back-arc basin spreading centres (Pearce & Stern 2006) (Figs 1; 2). The collision of the Melanesian Arc and the Ontong Java Plateau about 18 Ma resulted in the clockwise rotation of the South Fiji Basin and the emergence of the present-day basins, starting with the westward reorientation of Woodlark Ridge System (presently subducting under the Solomon Islands Arc) and the expansion of the North Fiji Basin about 6-10 Ma and, ultimately, the southern spreading of the Lau Basin about 2 Ma. In the southeastern part, the Pacific plate is subducting westward at the Tonga-Kermadec trench, whereas the Australia plate is subducting eastward and northward in the western area at the Vanuatu, San Cristobal and New Britain trenches (Ruellan & Lagabrielle 2005).

The tectonic history (and associated hydrographic patterns) of this region likely had a major impact on the vent fauna distribution and may explain some of the patterns of population differentiation and phylogenetic groups admixture presently observed, at least in the Manus and Lau Basins (Thaler et al. 2011, 2014; Plouviez et al. 2013; D. Jollivet, pers. comm. 2017). This system of disconnected ridges that expands over more than 6000 km² displays quite similar vent communities dominated by deep-sea mussels and symbiotic provannid gastropods that undeniably share a common phylogeographic origin. The separate geologic evolution of the basins since their opening and hydrological barriers can severely impede along-axis dispersal, thus allowing allopatric speciation for species with a short pelagic phase over the bottom (Desbruyères et al. 2006a: fig. 1, table 1) but not necessarily for species with planktotrophic larvae able to feed from the water column and reach the surface waters. Vent-endemic species have an ephemeral lifespan (Van Dover et al. 2002), so they must be able to effectively disperse and colonise new vents after locations become inactive. As bythograeid crabs are benthic, they must disperse through the water column during their larval stages. The strong-swimming larvae of brachyuran crabs may disperse high in the water column (Mitarai et al. 2016), such as larvae of the sea snail or false limpet Shinkailepas Okutani, Saito & Hashimoto, 1989 that show a vertical migration and long-distance dispersal potential (Yahagi et al. 2017). Thus, although evidence for long-distance dispersal events may occur between basins, taxa of most vent fields are presently evolving separately, with recent speciation events in allopatry possibly linked to the step-by-step colonisation of the ridge system that has been taking place since the opening of the basins about 5-6 Ma (Taylor & Karner 1983; Auzende et al. 1988, 1997; Taylor 1995; Jollivet 1996; Thaler et al. 2014).

Distribution of Bythograeidae in the back-arc basins of the western Pacific

In the western Pacific, instead being linearly distributed along the mid-oceanic ridges, the vent fields occur patchily throughout spreading centers associated with back-arc basins; this non-linear distribution results in complicated connectivity among vent sites and more complex patterns of population differentiation, speciation processes and genetic deviation (Thaler 2012). This non-linear distribution of vent sites can be exploited to test hypotheses on larval and microbial transport, genetic isolation, and speciation.

From south to north, the two opposing subduction zones are associated with a series of small back-arc basins (marginal basins), as follows: Havre Trough behind the Kermadec Arc, Lau Basin behind the Tonga Arc, the North Fiji Basin between the Vanuatu Arc and Fiji Islands, Coriolis, Woodlark Basins, and the Manus Basin behind the New Britain Arc; Mariana Trough; Bonin Arc; and Okinawa Trough (Fig. 1). The junction between the two subduction zones consists of a number of interconnected active spreading centres in the North Fiji and Lau Basins (Desbruyères et al. 1994, 2006a; Taylor 1995; Ruellan & Lagabrielle 2005). Species of Austinograea are distributed all along these spreading centres, whereas Gandalfus puia McLay, 2007 is only reported further south.

Gandalfus puia, which belongs to the closest genus to Austinograea, occurs only on the Kermadec Arc (26°S-36°20'S). It is mainly associated with venting along the Kermadec subduction system, which includes 12 volcanoes (Desbruyères et al. 2006a). The southernmost record for a bythograeid crab is reported near New Zealand with G. puia (McLay 2007). Austinograea hourdezi n. sp. and A. alayseae are found on hydrothermal sites of the Lau and North Fiji Basins, ranging at depths ranging from 1700 to 2700 m (Fig. 2), located at the boundary between the Pacific and Indo-Australasian plates, and about 1000 km apart (Auzende et al. 1988; Desbruyères et al. 1994). Austinograea jolliveti n. sp. is also known from the Fiji and Lau Basins, from 2130 to 2750 m.

The Lau Basin, the first back-arc basin to be recognised as a young ocean basin formed by splitting of a volcanic island arc, is an active back-arc basin flanked to the west by the fossil Lau Ridge and to the east by the Tofua Volcanic Arc (Karig 1970; Fouquet et al. 1991). The Valu Fa Ridge, situated at the southern end of the East Lau Spreading Center, is located at the vicinity of the Tofua Volcanic Arc. The vent fields Kilo Moana and Tow Cam are dominated by pillows and lobate basalts with broad, flat domes that are cut by faults and fissures, while the southern vent fields ABE, Tu'i Malila and Vai Lili are characterised by more complex volcanic morphology, with pillows, distinct flow fronts, and larger domes (Ferrini et al. 2008). At the Vai Lili site (Lau Basin), in which many specimens of A. hourdezi n. sp. have been

collected, there are numerous active smokers of two types: black smokers with temperatures ranging from 330° to 400°C and white smokers with temperatures ranging from 250° to 320°C. The chemical composition of the fluid is similar to that of other back-arc basin vent systems (Ishibashi *et al.* 1994; Desbruyères *et al.* 2006a), with the exception of a very low pH of 2 and a high content of metallic ions. Animal communities associated with the crabs are generally located around the chimneys, where fluids are percolating at temperatures between 5° and 33°C; water temperature remote from the chimneys has been measured at 1.7°C (Desbruyères *et al.* 1994: pl. 1A, B; 2006a). In the Hine Hina site the fluid mixing temperature is generally lesser than 20°C, and the fluid is released through a dome of highly vesiculated and brecciated andesite; the near-surface rocks are impregnated with sulfides (Chevaldonné *et al.* 1991: table 2; Desbruyères *et al.* 1994: pl. 1F; 2006a). The biological community from the Lau Basin figured by Fisher *et al.* (2007: fig. 1), consisting of light-coloured snails (*Alviniconcha hessleri* Okutani & Ohta, 1988 *sensu lato* (see Denis *et al.* 1993), black snails (*Ifremeria nautilei*) and brown mussels (*Bathymodiolus brevior* see Cosel *et al.* 1994; Breusing *et al.* 2015), includes an unnamed white crab without spots on the chelae: it could be *A. alayseae*. Our Figure 8A shows gastropods and mussels at Kilo Moana site photographed *in situ* associated with an *Austinograea* that is probably *A. alayseae* due to the chelae devoid of setose patches.

Austinograea hourdezi n. sp. has also been found at the active White Lady vent site of the North Fiji Basin. This site is one of the components of a complex hydrothermal field, which comprises both diffuse fluids (31°C) and active chimneys with high temperatures (91°C and 296°C as maximum measured in two different chimneys) (Chevaldonné *et al.* 1991: table 3; Desbruyères *et al.* 1994; 2006a). *Austinograea jolliveti* n. sp. was observed on mussel beds at the Mussel Valley site, located northward on the North Fiji Basin. The diffuse venting site is on a flat volcanic dome framed by a group of collapsed lava lakes with a great number of pillars. Venting shows no oxide or sulfide accumulation, but fresh formations of basaltic glass; the limpid fluid was expelled through a series of low temperature vents (maximum 8.5°C) (Desbruyères *et al.* 1994; 2006a; Hashimoto *et al.* 1999).

After the description in 1989 of the first *Austinograea*, *A. williamsi*, then of *A. alayseae* in 1990, and today of two new species, *A. hourdezi* n. sp. (as *Austinograea* sp. aff. *williamsi* in Guinot 1990) and *A. jolliveti* n. sp., the study of the rich collection deposited in the MNHN and of a material sent in loan by C. H. Fisher shows that *A. alayseae*, *A. hourdezi* n. sp. and *A. jolliveti* n. sp. are found together in the southwestern Pacific.

Austinograea species are also found in the Manus Basin vent communities. Vents occur at a fast spreading centre on three disjunct and successive ridge segments (Auzende *et al.* 1996). In the PACMANUS complex (03°43.50'S, 151°40.50'E, 1700 m) venting occurs either through fissures zones or diffuse areas with warm fluids 45°-63°C, or through 10-15 m high smokers expelling acidic fluids with temperatures up

to 268°C, high chlorinity, and high metallic content (Hashimoto *et al.* 1999; Desbruyères *et al.* 2006a). There are at least two distinct bythograeid species in the Manus Basin, one with heterochelous, heterodotous and sexually dimorphic chelae (Fig. 12) being apparently different from *A. alayseae*, *A. hourdezi* n. sp. and *A. jolliveti* n. sp, see below "*The Austinograea from the Manus Basin*".

In the Mariana Trough inhabits another *Austinograea* that is distinct from the three congeneric species found in the Lau and North Fiji Basins. In fact, *A. williamsi* appears to be an endemic species to the Mariana Trough, which is a back-arc basin occupying a central position in hydrothermal areas in the northwestern Pacific, being surrounded by the Okinawa Trough, the Izu-Ogasawara Arc, the Mariana Arc, and the Manus Basin. Situated from 19°45'N to 14°N between the remnant volcanic arc of the West Mariana Ridge and the volcanic front of the Mariana Arc, it corresponds to a wide linear rift valley of an axial volcanic ridge. Maximum measured temperatures of vents was 284°C in the Alice Springs field, the first discovered vent, in which 30 species from the chemosynthetic communities were reported, the *Alviniconcha* snails and the *Austinograea* crabs being the dominant animals. *Austinograea williamsi* is found in abundance in snail beds filling the vent openings (Hessler & Lonsdale 1991; Desbruyères *et al.* 2006a; Kojima & Watanabe 2015: figs 25.1, 25.2, table 1).

At the northern end, the Mariana Arc connects with the Izu-Ogasawara arc system that extends south from Tokyo to the Island of Guam, with many submarine volcanoes, and in which rifting plays an important role. Here, *Austinograea* is replaced by its sister genus *Gandalfus*, with the species *G. yunohana* that lives at comparatively shallower depths, 420-1380 m (Takeda *et al.* 2000: fig. 1, as *Austinograea yunohana*; McLay 2007; Fujikura *et al.* 2008; Yang *et al.* 2010; Kojima & Watanabe 2015: figs 25.1, 25.2; Yamanaka *et al.* 2015: fig. 10.1, tables 10.1, 10.2).

The Okinawa Trough is a back-arc basin located between the Eurasian continent and the Ryukyu Island Arc. Among the 109 species reported in the Okinawa Trough hydrothermal vent fields, the bythograeid crab *Gandalfus yunohana* has been found in a single field, the Minami-Ensei Knoll site, together with a geryonid, *Geryon* aff. *granulatus* Sakai, 1978 (Watanabe & Kojima 2015: fig. 34.1, table 34.1; Yamanaka *et al.* 2015: figs 10.1, 10.2)

The distribution of bythograeids in the western Pacific supports the analysis by Desbruyères *et al.* (2006a: figs 2-5, table 1) on global faunal affinities among extant basins and ridges in this vast system. The Lau and North Fiji Basins communities display a strong faunal alliance. *Austinograea alayseae* and *A. hourdezi* n. sp. co-occur in the Lau Basin, probably at Tow Cam, Hine Hina, Vai Lili, Kilo Moana, Tu'i Malila, ABE sites (see Figs 3; 8), and in the North Fiji Basin; *A. jolliveti* n. sp., apparently more uncommon, cohabits with *A. hourdezi* n. sp. at the ABE site. As *A. alayseae* was likely not always properly identified in classified material and in the unsorted collections, it is likely that it has been confused with the two new species described here. Mariana Basin communities

display a low similarity with the three southwestern Pacific Basin communities, with endemic *A. williamsi*. The Okinawa Basin and Izu-Ogasawara Arc faunal communities, which are clearly distinct from those of the other back-arc basins, host a distinct genus, *Gandalfus* that, puzzlingly, is also found on the Kermadec Arc, near New Zealand. It is noteworthy that we have never found *A. williamsi* in the vent fields of the southwestern Pacific.

The bythograeid vent fauna of the southwestern and north-western Pacific (Fig. 1) proves to be still richer than previously suspected, with presently a total of five species: four *Austinograea* species, of which two are here described as new, and *Gandalfus puia*. Another *Austinograea* species, *A. rodriguezensis*, inhabits the Central Indian Ridge, and the second species of *Gandalfus*, *G. yunohana*, is found off Central Japan (see Yang *et al.* 2010; 2013: fig. 1 map). The separation between the four *Austinograea* species needs a careful examination, based on a sufficiently representative material of all taxa, which fortunately is the case for the MNHN collection. There are no apparent differences in the overall size and shape of the carapace in males and females of *Austinograea* species, thus the chela morphology is the best diagnostic character (see Key to the species).

THE *AUSTINOGRAEA* FROM THE MANUS BASIN

Austinograea alayseae has been often reported from the Manus Basin (Galkin 1992, 1997; Hashimoto *et al.* 1998: fig. 7; 1999; López-González *et al.* 2005; Guinot & Segonzac 2006b). According to Galkin (1997: fig. 1), the scavenger and carnivore *A. alayseae* dominates the fauna at the Manus Basin (PACMANUS site), being abundant at vent openings crawling actively on the snail thickets, and also ranges into non-vent terrain. It is reported from active (Kowalczyk) as well as inactive (Binns) (Erickson *et al.* 2009) sites. Genetic differences between individuals (supposed to be *A. alayseae*) from the Manus Basin and from the Tofua Volcanic Arc at the east of the Lau Basin, located about 3000 km apart in the southwestern Pacific, have been found (Kim *et al.* 2014, 2016), suggesting the existence of a separate species, distinct from *A. alayseae*.

Crabs collected in the Manus Basin at the PACMANUS site by the *Shinkai 2000* were identified as *A. alayseae* by Tsuchida & Hashimoto (2002). We have examined two large specimens from this site (a right-handed ♂ 31.3 × 48.8 mm and a left-handed ♀ 29.6 × 44.8 mm, 3°43.60'S, 151°40.32'E, field E, 1676 m, 17.XI.1998) deposited in the MNHN (MNHN-IU-2016-10750 [= MNHN-B28761]) (Fig. 12). With the outer surface of chelae devoid of any spot, males correspond neither to *A. hourdezi* n. sp. nor to *A. jolliveti* n. sp.; they are closer to *A. alayseae* due to the shape of mxp3 merus, the setose G1, the glabrous chelae at inner surface, and the glabrous subhepatic regions. Nevertheless, owing to some observed differences (male crusher more elongated, especially the fingers that are markedly gaping; male cutter with the dark colour extending beyond the extreme tip until the two-thirds of the fingers), these two individuals are here separated from *A. alayseae* in waiting more material from the Manus Basin and genetic data (in study). This crab, with the male and female chelae figured Fig. 12A, B, respectively, is preliminarily considered *Austinograea* sp. aff. *A. alayseae*.

We discuss below (see *Genetic data*) the genetic sequences of *A. alayseae* from the Manus Basin provided by Yang *et al.* (2013) and Kim *et al.* (2014: table 1): the results show its separation into two branches and suggest some mitogenomic differences, likely supporting the presence of two lineages that could be treated as two species, of which one, hypothetically, could be *A. alayseae* or *A. hourdezi* n. sp., even *A. jolliveti* n. sp., and, in addition, an unnamed species with the chelae as in Fig. 12. Recently, the first transcriptome for a hydrothermal crab was based on two individuals of a vent crab collected from the Manus Basin and identified to *A. alayseae* (Hui *et al.* 2017), but, as always, illustration of the sequenced specimens was not provided so that the identity of the sequenced brachyuran remains in doubt. A genetic study using mitochondrial DNA and microsatellite markers revealed that populations of the vent-restricted gastropod *Ifremeria nautilei* from the Manus Basin did not show genetic subdivisions but were genetically distinct from those of the North Fiji and Lau Basins in which populations were undif-

KEY TO SPECIES OF *AUSTINOGRAEA* HESSLER & MARTIN, 1989

A key to the five species of *Austinograea* is provided, based on chelae, in order to potentially identify the crabs photographed *in situ* by evaluating the videos of the dives on board or later by examining the photographs.

1. Palm chela with outer surface devoid of coloured spot and inner surface without patches of setae. Subhepatic region of carapace glabrous .... *Austinograea alayseae* Guinot, 1990
— Palm chela with outer surface bearing one spot 2
— Palm chela with outer surface bearing two coloured spots in males, inner surface with patches of setae. Subhepatic region of carapace with patches of setae .... *Austinograea hourdezi* n. sp.

2. One spot near base of fixed finger .... *Austinograea jolliveti* n. sp.
— One spot near base of dactylus 3

3. Palm chela with inner surface covered by patches of setae; small patch of setae on thoracic sternum at level of P1, especially in females .... *Austinograea williamsi* Hessler & Martin, 1989
— Palm chela with inner surface only setose on dactylus near occluding margin and on propodus near base of dactylus; no setae on thoracic sternum at level of P1 in both sexes ....
.... *Austinograea rodriguezensis* Tsuchida & Hashimoto, 2002

FIG. 12. — *Austinograea* sp. aff. *A. alayseae* Guinot, 1990, ♂ 31.3 × 48.8 mm (right-handed), ♀ 29.6 × 44.8 mm (left-handed), Manus Basin, *Shinkai 2000*, 3°43.60'S, 151°40.32'E, PACMANUS site, field E, 1676 m (see Tsuchida & Hashimoto 2002), MNHN-IU-2016-10750 (= MNHN-B28761): **A**, male chelae, crusher and cutter, outer surfaces of palms; **B**, female chelae, cutter and crusher, outer surfaces of palms.

ferentiated. The phylogeographic break between the Manus and North Fiji/Lau populations was not interpreted as the result of a colonisation event, but likely due to a vicariant process isolating the existing single population spanning Manus, North Fiji, and Lau Basins into two populations. The process that restricts contemporary gene flow and isolates the Manus Basin population of *I. nautilei* from widespread populations that occupy the North Fiji and Lau Basins is unknown (Kojima *et al.* 2000; Thaler *et al.* 2011). Estimates of gene flow implied migration from the Lau to North Fiji Basin with a splitting time of tens of thousands of generations and genetic isolation between those two basins and the Manus Basin for several hundred thousand generations; for *I. nautilei* the rather weak gene flow from Lau to North Fiji and the genetic barrier between Manus and North Fiji may be explained by the ocean circulation (Mitarai *et al.* 2016). Accordingly, the presence of a potential distinct *Austinograea* in the Manus Basin through similar phylogeographic isolation remains to be detected by morphological examination of specimens from populations sampled in various vent sites and/or by genetic analyses.

It was shown that, in the western Pacific, variable dispersal filters exist, which isolate populations of some, but not all, vent-occurring species from Manus Basin (Thaler 2012), and it would be interesting to determine if *Austinograea* exhibits strong population isolation between Manus Basin and southern oceanic basins, as exemplified by some other organisms.

CHELAE: CRUSHER AND CUTTER. REGENERATED CHELAE

In many decapod crustaceans growth of chelipeds is isometric until the time of puberty moult, with the same trend continuing in adult females, whereas in males the marked spurt in the level of allometry is accompanied by a sudden increase in the relative size of chelae. Chelipeds differentiate morphologically into major (crusher) and minor (cutter) chelae, based on morphologically and functionally different dentition patterns (handedness) so that they become heterochelous, heterodontous, and sexually dimorphic. This corroborates the constatation that, of the five pairs of pereopods, the decapod chelae are versatile organs of attack and defence that make them the most vulnerable for autotomy (self-amputation) (Mariappan *et al.* 2000). The

loss of the right chela is the result of autotomy during inter- and intraspecific competition for limited resources like food, shelter, mate, and as a strategy to avoid predation and wound limitation as well as establishment and maintenance of dominance hierarchies. Thus, the possession of a new major claw is essential for acquisition of limited resources and agonistic and aggressive interactions. With the loss of the right chela, which is a serious problem for many decapods, handedness transitions from the right to left chela, leading to left-handed individuals; after handedness reversal, dentition on the left dactylus of the newly-converted crusher is close to that of the original right crusher without generally attaining the same shape, even after many moults (Masunari *et al.* 2015). The regenerated major cheliped is more slender than the original, less robust and weaker than previously. Rapid regeneration of the major cheliped over several moults appears to be an appropriate strategy that is beneficial for the injuried crab.

In populations of *Austinograea* right-handed crabs are predominant, so that the "normal" morphology is observed in males with right crusher and left cutter. Usually, the male crusher is relatively larger and more inflated than the cutter of both sexes, and the male cutter is larger than that of the females. Chela asymmetry is variously developed from species to species. For example, in *A. williamsi*, which live in high densities near active sites of the Mariana Trough, right-handed male individuals were characterised by strong heterochely and heterodonty, and the sexual dimorphism was pronounced; heterochely was observed only in males, with the exception of only one large female (in 36 females) that was reported with heterochely (Tsuchida & Fujikura 2000: fig. 3). Among the *A. williamsi* analysed, 60% of males had a right crusher and a left cutter ("normal" type) and the other 40% had two cutters; and 5% of females had a right cutter and a left crusher; the remaining 95% have two cutters; additionally, numerous males and females had small regenerated chelae or were lacking either left or right chela. Because approximately half of the males of *A. williamsi* did not exhibit heterochely, being also as large as those that did, Tsuchida & Fujikura (2000: figs 2-4) suggested the crusher may not be related to reproduction. This is not the case of most crabs, in which the major chela of males is used in reproductive behaviour (courtship, copulatory guarding, mating) together for feeding, protection from predators, competing over territory.

The relatively high proportion of left-handed vent crabs with atypical chelae that are found in nature is likely due to the accidental loss of the major cheliped and seems clearly related to the presence of regenerated chelae and handedness reversal: the right crusher being lost, the left cutter is converted to the new crusher. The chelae of these individuals do not share size and morphology of those of their congeners having an original right crusher. Accordingly, there are male specimens that possess two cutter chelae. For investigation of development of chela asymmetry and its use as taxonomical character in vent crabs, this parameter must be taken into account. An additional factor is the presence of numerous individuals lacking the two chelae or only one.

Guinot (1990) reported in *A. alayseae* the presence of male left-handed individuals, with homomorphic chelae close to the cutter type. We have re-examined the sample of paratypes from the Lau basin, Vai Lili site, i.e., 35 ♂ and 52 ♀, MNHN-IU-2008-11309 (= MNHN-B24055): it contains typical right-handed males and females, with crusher and cutter, but also left-handed males and females with two cutters, which seemingly corresponds to regenerated chelae. Curiously, we have also found large right-handed female *A. alayseae* (the largest 34.3 × 55.0 mm; 33.4 × 53.0 mm) that have heteromorphic and heterodont chelae, with an heterochely as pronounced as in the males.

Typical males of *A. hourdezi* n. sp. (Figs 4A, B; 5E-H) and, to a less extent, of *A. jolliveti* n. sp. (Fig. 9E-H) show heteromorphic chelipeds, with specific differences and probably also variation in growth pattern. Typically, only large females have a right crusher and a left cutter, and youngest show the cutter type in both chelae. A large number of females of *A. hourdezi* n. sp. with two cutters correspond to individuals bearing regenerated chelae; these individuals, instead of bearing two marked spots on the chelae, exhibit a single marked spot and a second one, faint or indiscernible (Fig. 9E-H). At most, we can understand that males regenerate their chelae with only one spot or not at all spot, but it is puzzling that females, typically devoid of spots on the chelae, regenerate chelae with a spot, as certain males. By contrast, the regeneration of chelae does not affect the presence or absence of setose patches of setae on the inner chela palm, always absent in both sexes of *A. alayseae* and present in both sexes of *A. hourdezi* n. sp. and *A. williamsi*.

Comparative morphometric and statistical analyses of the chelae conducted in populations of all *Austinograea* species, as Tsuchida & Fujikura (2000) for *A. williamsi*, should provide precise information on the percentage of left-handed individuals. The large number of left-handed crabs with regenerated chelae in populations of *Austinograea* is an issue yet to be resolved. There is very limited knowledge on species' behaviour in vent populations and on hydrothermal communities interactions such as predation or competition that significantly affect community structure. But direct *in situ* observations with the use of cameras deployed on deep sea observatories have shown that vent species strongly respond to food source, often leading to aggressive behaviour, involving claw attacks (Matabos *et al.* 2015).

According to environmental data from seven diffuse flow hydrothermal vent sites along the Eastern Lau Spreading Center provided by Podowski *et al.* (2010: 27, 34, 42, figs 1, 2, 7, 8, tables 3, 5), *Austinograea* crabs occupied areas with the greatest exposure to vent flow showing a considerable tolerance; they consistently demonstrated a preference for biological substrata in the most hydrothermally active areas, and were likely to be predator-free, without potential predators on adults, since few metazoans are able to tolerate the conditions present in the areas of highest productivity at vents.

Three species of *Austinograea* were reported as including *A. alayseae*, *A. williamsi*, and *Austinograea* spp. when the two species could not be differentiated: only about 15% of the

crabs could confidently be identified to the species level, the remaining was separated into these three categories. Presence of sympatric species could explain an aggressive intraspecific behaviour during feeding time in absence of food supply, development of territoriality, and sexual competition.

It has been shown that in stone crabs *Menippe* spp. declawed crabs were less mobile or less motivated to feed (Duermit *et al.* 2017), but comparisons with vent crabs are risky.

IDENTIFICATION OF *AUSTINOGRAEA* SPECIES IN FAUNAL ASSEMBLAGES

Identification of faunal assemblages that have colonised the extreme hydrothermal environments is a difficult task. In publishing reports of the cruises, a challenge is to give a name to the collected organisms, generally very poorly known and often new to science.

In a series of papers on animal communities of the Eastern Lau Spreading Center and Valu Fa Ridge, a difficulty was encountered in identifying the crabs. Sen *et al.* (2013: fig. 3A, tables 2-4) reported that the bythograeid crabs could be identified as *Austinograea williamsi* or *A. alayseae* only if the inside of the cheliped was visible. Although the species were identified when possible, they were grouped as *Austinograea* spp. for the purpose of statistical analyses. It is clear that these authors were dealing either with the true *A. alayseae*, which has glabrous chelae, or with the species here described as new, *A. hourdezi* n. sp., with patches of dense setae on the inner surface of chelae in both sexes (Figs 5A, F, H; 7A, B, F, H), or *A. jolliveti* n. sp. (Figs 9A-H; 10A-E; 11A-E), but without the probability of *A. williamsi* (also with patches of setae on chelae) that is apparently confined to the nortwestern Pacific. According to Sen *et al.* (2014), in a paper analysing the progression of Lau Basin hydrothermal sites over time and characterising the different stages of succession of the vent communities, as *Austinograea williamsi* and *A. alayseae* could not be reliably distinguished, they were again regarded as *Austinograea* spp. Lau vent crabs were referred to as solitary fauna (non-aggregated) that were found only in early and mid-successional stages of vent, and seemed well-adapted to take advantage of the high levels of primary production associated with venting, but largely disappeared when active venting decreased below a certain level. Similarly, Sen *et al.* (2016: 602, 610, tables 2, 5) stated that from dorsal images the *Austinograea* species inhabiting the Lau vents could not be reliably distinguished as *A. alayseae* or *A. williamsi*. Thus, they were grouped together as *Austinograea* spp. in the comparison between peripheral and near-vent communities: crabs, along with shrimps, were present in higher abundances in the active sites than the peripheral sites. The genetic divergence for the mitochondrial 16S rDNA gene reported between the three species *A. williamsi*, *A. alayseae* and *A. hourdezi* n. sp. (Mateos *et al.* 2012: 10, fig. 2, as *Austinograea* aff. *williamsi*) were not considered.

Zelnio & Hourdez (2009), by studying the alvinocaridid shrimps from hydrothermal vents (sites Kilo Moana, Tow Cam, ABE) collected by the TUIM07MV cruise at the Lau Basin, mentioned the presence of crabs living in association with shrimps, mussels and snails (see Fig. 3A). They have recognised two bythograeid species, *Austinograea alayseae* and *A. williamsi*. As these explored sites are the same where *A. hourdezi* n. sp. occurs in abundance and from where *A. williamsi* seems lacking, it is likely that these authors were dealing with *A. alayseae* and *A. hourdezi* n. sp., or perhaps *A. jolliveti* n. sp.

GENETIC DATA

According to Kim *et al.* (2013: 1, 6) identification of bythograeids based on morphological characteristics "often leads to incorrect species recognition due to a lack of taxonomic factors and the existence of sibling (or cryptic) species" (but these authors do not give any specific example), and "systematics based on morphological identification is not only time-consuming, but it is also difficult due to a lack of taxonomists for vent organisms". Kim *et al.* (2013) considered inevitable the use of DNA barcoding for vent organisms using mitochondrial cytochrome c oxidase subunit 1 (CO1). As existence of pseudogenes has been recorded in *Austinograea alayseae*, Kim *et al.* (2013) performed long PCR for the amplification of CO1 in this species. Based on a phylogeny with other COI sequences from other vent crabs, they concluded about the presence of Numts in *A. alayseae*, but all the reported substitutions were synonymous and sequences were devoid of stop codons or indels (see Chu *et al.* 2015).

To establish the mitochondrial genome of *A. alayseae*, Kim *et al.* (2014: 251, table 1) used specimens collected from two geographically distinct hydrothermal vents, the Tofua Arc Basin (accession no. KC851803) and the Manus Basin (accession no. JQ035660) respectively, located about 3000 km apart in the southwestern Pacific. Their genomes were found identical except for the mitochondrial control region (a marker whose resolution is higher than that of COI and useful for comparisons at the population level), which showed about 17.5% of nucleotide divergence. Moreover, Kim *et al.* (2013) previously found several highly divergent COI in a series of *A. alayseae* specimens from the Tonga Arc. The observed genetic differences in the mitochondrial control region, which cannot be attributed to gene polymorphism, indicated a clear separation of *A. alayseae* into two distinct OTUs, suggesting a "putative sub-species level". They likely correspond to the presence of two closely-related but different geographic taxa, perhaps the true *A. alayseae* and the species here described as new, *A. hourdezi* n. sp., which co-occur in several sites, perhaps also *A. jolliveti* n. sp. that seems to be uncommon. It is not unlikely that such various results could be based on misidentified specimens. Analyses of the genome are fully required to compare the populations of *Austinograea* species from different vents, contributing significantly to our knowledge on the diversity and improving taxonomic research base on morphology. But fully exploiting reciprocal benefits requires that the recovered genetic data are based on a correct identification of the species, with, at the very least, a traceable origin of the sequenced individuals useable by non-specialists.

The complete mitogenome of *Gandalfus yunohana* has been obtained from one crab collected at the Nikko Seamount, 472 m, on the Izu-Ogasawara Ridge (Yang *et al.* 2010),

in order to esteem its phylogenetic relationships with the closest relative brachyurans. For the phylogenetic study of complete mitochondrial genome of another deep-sea vent crab *G. puia* from the Tonga Arc vent field and for comparison with the genome of *A. alayseae*, Kim *et al.* (2016) used the same material than previously in 2014 (Kim *et al.* 2014: table 1), i.e., specimens (JQ035660 and KC851803) from two remote regions, the Tofua Arc and the Manus Basins. In the resulting phylogenetic tree, mitogenomic differences were expressed as a bifurcation in two distinct branches for *A. alayseae*, as precedingly. As a consequence, without a clear morphological diagnosis of analysed individuals, there is a possibility that such a sequence diversity reflects a species admixture as it is the case in the Lau and North Fiji Basins with the possible sympatric co-occurrence of *A. alayseae*, *A. hourdezi* n. sp. and *A. jolliveti* n. sp. Possibility of a separate species in the Manus Basin should not be rejected, see Fig. 12A, B.

Austinograea alayseae was similarly separated into two branches in the tree of brachyuran phylogenetic relationships based on the alignment of concatenated 13 mitochondrial coding genes by Mandon *et al.* (2017: fig. 1) in a study of the mitogenome of *Segonzacia mesatlantica* Williams, 1988. The GenBank number KC851803 corresponds, as precedingly, to *Austinograea* from the Manus Basin (Kim *et al.* 2014: table 1), and NC_020314 is a reference sequence identical to KC851803 (P. Mandon, pers. comm. June 2017) and thus corresponds to the same sequence of the same crab that was collected in the Manus Basin from the Vienna Woods site, 2484 m (Yang *et al.* 2013: supplementary material). The Vienna Woods site is an important field of active and fossil chimneys about 300 m in diameter, with the associated fauna essentially constituted by gastropods *Alviniconcha hessleri* sensu lato, *Ifremeria nautilei*, galatheids, shrimps, cirripeds, and bythograeids (Auzende *et al.* 1996: fig. 7).

In a series of papers on the complete mitogenome of brachyuran species, the genomes of *A. alayseae*, *A. rodriguezensis*, *Gandalfus yunohana* and *G. puia* were downloaded from GenBank and included in reconstructed phylogenetic trees, all showing occurrence of T and A nucleotides that differed from that all of other studied Brachyura (Xin *et al.* 2017a: 309; 2017b; Tang *et al.* 2017).

Molecular basis of adaptive evolution by a transcriptome analysis performed in *A. alayseae* collected from the Manus Basin revealed that candidate genes related to harsh condition adaptation and in order to facilitate inhabiting the extreme environment were identified, namely genes related to sensory, circadian rhythm, hormone, hypoxia stress, metal detoxification, high osmotic pressure and pathogens; in the degenerated eyestalk, transcription of phototransduction related genes, important for retinal function, was greatly reduced (Hui *et al.* 2017).

MAIN CHARACTERS OF *AUSTINOGRAEA*

The family Bythograeidae (ranked to superfamily level, Bythograeoidea Williams, 1980, see diagnosis in Davie *et al.* 2015c) is endemic to deep-sea hydrothermal vents, with a combination of characters that is not known in other brachyuran families.

The thoracic sternum is rather wide, all sutures are widely interrupted, and the median line extends along sternite 8 and practically not or variously along sternite 7 (Figs 4C; 6C; 7C, D; 9B-D; 10E; 11B; Guinot 1990: fig. 2C).

As stated by Hessler & Martin (1989), a junction sternum/pterygostome characterises the genus *Austinograea*, without modifying the location of the branchial afferent openings (Milne Edwards openings) but with, however, an implication on the shape and embayment of the mxp3 coxa. Junction is well visible in *A. williamsi* (Hessler & Martin 1989: 645, 657, figs 6a, 7a, 8b), in *A. alayseae* (Guinot 1990: 882, fig. 2A, pl. 1, fig. B), in *A. rodriguezensis* (see Tsuchida & Hashimoto 2002: figs 4, 7). The same pattern occurs in *Gandalfus yunohana* (Takeda *et al.* 2000: fig. 2B), and probably also in *G. puia*, although not mentioned or figured by McLay (2007). Such a junction is absent in the other bythograeids (Hessler & Martin 1989: figs 1b, 6b, c, 8a, c, 15b), where there are only various stages of extension of sternite 4 towards the pterygostome, resulting in different shapes of the mxp3 coxa and branchial afferent openings: *Cyanagraea* Saint Laurent, 1984 and *Allograea* Guinot, Hurtado & Vrijenhoek, 2002 with a wide gap between the sternite 4 and the pterygostome, thus mxp3 coxa largely exposed; *Bythograea* Williams, 1980 with a narrower gap between the sternite 4 and the pterygostome, a larger portion of the elongated mxp3 coxa being intercalated; *Segonzacia* Guinot, 1989 with the sternite 4 rather close to the pterygostome but not completely separating the mxp3 coxa from the cheliped. The *Austinograea*/*Gandalfus* group is thus distinguished by a complete junction, so that the mxp3 coxa is completely separated from the cheliped, and its distal portion deeply recessed. The junction thoracic sternum/pterygostome does not significantly vary along *Austinograea* species: *A. hourdezi* n. sp. (Figs 5C, D; 7C, D); *A. jolliveti* n. sp. (Figs 9B, C; 10E); *A. alayseae* (Guinot 1990: fig. 2A).

The modality of protection of the penis, i.e., the external, muscular projection of the ejaculatory duct that is inserted into the G1 during mating, shows in Brachyura a regular pattern that is practically constant at familial and even suprafamilial levels. Bythograeidae shows a condylar protection, i.e., the penis is enclosed inside the condyle of the P5 coxa, but in exhibiting two distinct patterns. The male gonopore opening, from which emerges the penis, is either located on the anterior margin of the coxo-sternal condyle (most bythograeids: *Bythograea*, *Cyanagraea*, *Segonzacia*, see Guinot *et al.* 2013: 84, fig. 8H, table 4), or it is partially located on the coxa itself (*Austinograea* and *Gandalfus*).

In Brachyura the two pairs of gonopods are conservative features, and the G2 morphology has a phylogenetic significance, its reduction implying a functional change of the female copulatory system. Guinot (1979) hypothetised that a long G2 could be regarded as plesiomorphic, the shortness of the complete G2 (with reduction of the flagellum) apomorphic, and medium length G2 represented an intermediate state (see also Guinot & Hurtado 2003; Guinot *et al.* 2013). In some rare heterotremes the G2 shape shows several character

states within a family, e.g. in Calappidae De Haan, 1833, even within a genus, e.g. *Calappa* Weber, 1795, and a molecular multi-locus phylogeny of this family supported the long G2 as the ancestral state (Ewers-Saucedo *et al.* 2015, 2017). The Bythograeidae displays this gonopodal diversity (Guinot *et al.* 2013): in most bythograeids, *Bythograea*, *Cyanagraea* and *Segonzacia*, the G2 is longer than G1 or equal to the G1 length (Hessler & Martin 1989: fig. 14; McLay 2007: table 2). McLay (2007: table 2) distinguished *Gandalfus* from *Austinograea* notably on the basis of a long G2 (equal to or greater than G1), with the flagellum much longer that the peduncle (G2 peduncle about one third of overall length in *G. yunohana*; about one half of overall length in *G. puia*). In *Austinograea* the G2 is distinctly shorter than the G1, with remarkable variation along species (especially in the flagellum size), but, however, remains rather short (see comparative figures in Tsuchida & Hashimoto 2002: fig. 8). The G2 is about half the length of G1 in *A. alayseae* (Guinot 1990: fig. 3) and *A. rodriguezensis* (see Tsuchida & Hashimoto 2002: fig. 8), about less than half the G1 length in *A. williamsi* (Hessler & Martin 1989: fig. 14a-e; Tsuchida & Fujikura 2000: figs 6-8), *A. hourdezi* n. sp. (Figs 4C; 6D, E) and *A. jolliveti* n. sp. that, moreover, has a very reduced flagellum (Figs 9C, D; 11D, E). McLay (2007) considered the long bythograeid G2 was the ancestral condition and, compared to the long G2 of other bythograeids, the short G2 of the *Austinograea*/*Gandalfus* group was interpreted as the derived condition in the family, also supported by the eye regression pattern (see Davie *et al.* 2015a).

The rows of spines on the G1 dorsal surface of *Austinograea williamsi* were postulated to be used to keep the position of the G1 "by hooking the female gonopore", and the short setae on the G1 ventral surface "to sense" the female seminal receptacle (Tsuchida & Fujikura 2000: 413, fig. 7). Micromorphological studies seem to show that in *A. williamsi* the G1 proximal foramen is too small for the G2 insertion, suggesting that the G2 acts "as a sensor" guiding the G1, i.e., the typical intromittent, inseminating structure, into the female seminal receptacle (Tsuchida & Fujikura 2000: 413, fig. 8). According to McLay (2007), however, it is likely that the bythograeid G2 has a role in sperm transfer and, when it is long, may have a role in disrupting sperm from previous matings.

The ocular regression, to variable degrees, is a main characteristic of the family Bythograeidae (Williams 1980), the *Austinograea*/*Gandalfus* group having the most drastic reduction of eyes. In *Austinograea* the eyestalks are reduced, the eyes are fixed, and the cornea is vestigial or absent, unpigmented, without facets (Hessler & Martin 1989: figs 4, 5a; Guinot 1990: figs 1, 4; Tsuchida & Hashimoto 2002: fig. 3). Similarly, in *Gandalfus* eyes are fixed, with the stalks embedded in the orbital wall, and a vestigial cornea (Takeda *et al.* 2000: fig. 4A-C; McLay 2007: figs 2A, 3, 4, table 3). As *Austinograea* and *Gandalfus* are not the deepest living of bythograeids and *Gandalfus* is even the shallowest occurring bythograeid genus (from 270-239 to 1647 m), McLay (2007) noted that the pattern of eye development was not strictly correlated with depth.

A study of the locomotor activity in 'eyeless crabs' under different lighting conditions by Kabasawa (1992: 21) presumably used *G. yunohana*, as the specimens were collected from the Kaikata Seamount by the *Shinkai 2000* at 470 m. Experimental observations have shown that crabs had photo-sensivity, became active in the dark and the circadian rhythmicity did not occur under continuous darkness.

As the vent crabs have reduced eyestalks and vestigial cornea, they evolve alternatives in adapting to constant darkness, thus chemical communication should be the predominant mode of their behaviour, such as predation and mating. Hui *et al.* (2017) discovered that, in the eyestalk of the practically blind *A. alayseae*, immune related genes were highly expressed, indicating the eyestalks might be involved in the crab immune responses, thus their important roles in the environment adaptation; in the degraded eyestalk, 10 olfactory receptor and three gustatory receptor genes were identified; and, although eyestalks of *A. alayseae* are degraded, three transcripts encoding important eyestalk prohormone and hormone were characterised.

Many questions remain to understand the evolutionary mechanisms underlying adaptation to life in the dark of bythograeids. The colourless body (except for the pigmented areas on carapace or spots on chelae, with different texture, in some species) and the ocular regression of vent crabs, to a greater extent in the *Austinograea*/*Gandalfus* group, allowed a comparison with cavernicolous/troglobitic brachyurans (Guinot 1990: fig. 6). In contrast to adults, larval stages of bythograeids are bright red and have pigmented compound eyes. As megalopae and postlarvae of brachyuran crabs are benthic and with a limited dispersal ability, the dispersion is only possible via planktonic larval stages. And, in fact, zoeae of *Bythograea thermydron* Williams, 1980 were reported as possessing image-forming compound eyes, with a visual pigment sensitive to the blue light of mesopelagic waters; when larvae begin to descend to vents and settle at the vents, they lose their image-forming optics, resulting in benthic megalopae that possess high-sensitivity naked-retina (Jinks *et al.* 2002). The newly hatched larvae of *Gandalfus yunohana* have pigmented compound eyes and are phototactic (Miyake *et al.* 2007; Hamasaki *et al.* 2010: fig. 2)

The female reproductive system described in *Austinograea williamsi* by Köhnk *et al.* (2017: fig. 7) is characterised by the remarkable size of the ovary, the shape and orientation of the seminal receptacle that consists of a single chamber, the lack of a cuticular chamber, the vagina of concave type connected to the rotated seminal receptacle by the most dorsal part, all features interpreted as distinctive from other brachyurans. This configuration could not be checked in other *Austinograea* species, but we presume it is uniform in the whole genus.

In *Austinograea williamsi* setal patches are found on the inner surface of the chelae (in both sexes), on subhepatic regions (in both sexes), and on the thoracic sternum close to the chelipeds (generally more in females than in males) (Hessler & Martin 1989: figs 1, 2, 4A, 6a, 10c). These setose areas harbor large numbers of bacteria, which are well known to be the main primary producers in hydrothermal vent communities

(Van Dover 2000). It should be noted, however, that patches of setae on chelae, subhepatic and thoracic regions are not evenly distributed in all species of *Austinograea*, *A. alayseae* being the most glabrous (no setae on chelae and carapace), in contrast to *A. hourdezi* n. sp. and *A. jolliveti* n. sp.

The gastric mill of bythograeids, extensively studied in *A. williamsi*, known to be an opportunistic scavenger and with gut contents including portion of small bivalve shells, shows characteristic features; but nothing about the non-specialised nature of the foregut of the vent crabs was considered indicative of their unique habitat (Martin *et al.* 1998).

According to Tudge *et al.* (1998), who examined the spermatozoal ultrastructure in three species of bythograeids, *Bythograea thermydron*, *Segonsacia mesatlantica* (Williams, 1988), and *Austinograea alayseae*, spermatozoal evidence suggested a relationship between the bythograeids and the deep-water but not hydrothermal crab *Calocarcinus africanus* Calman, 1909 and wider relationships with the Xanthoidea MacLeay, 1838. They concluded that either *C. africanus* could be assigned to the Bythograeidae or that a separate own group could be erected for *Calocarcinus* Calman, 1909, which resulted in the establishment of Calocarcininae Števčić, 2005 within the Trapezoidea Miers, 1886. Mateos *et al.* (2012) did not found any indication of *C. africanus* being the closest relative to Bythograeidae. The relationships of Bythograeidae with other Brachyura is still debated (Davie *et al.* 2015b; Leignel *et al.* 2017).

Studies on the early life history of bythograeids are crucial to elucidate the mechanism of population maintenance at the hydrothermal vents, which are generally active for no more than a decade (Van Dover *et al.* 2002). The larval development of *Gandalfus yunohana* consists of fifth or sixth zoeal stages and a megalopa (Hamasaki *et al.* 2010; Nakajima *et al.* 2010); Tsuchida *et al.* (1998) reported moulting and growth of adults reared in tanks for more than six years. Thirty-three larval morphological characters of the first stage zoea were compared by Nakajima *et al.* (2010) to those of various brachyuran families. *Gandalfus yunohana* shared 22 characters with the first zoeal stage of *Calocarcinus*, which may support affinities of Bythograeidae with *C. africanus*, as proposed by Tudge *et al.* (1998). It is likely that the larval development of *Austinograea* species is roughly similar to that of *Gandalfus*. More work on larval descriptions and molecular phylogenetics are required to resolve the relationships between these crabs.

CONCLUSION

In conclusion, in the western Pacific six evolutionary brachyuran lineages can be distinguished based on external morphology for the two genera *Austinograea* and *Gandalfus* in view of their sister group relationship. Single distinct species inhabit vent fields along the Central Indian Ridge (*A. rodriguezensis*), the Mariana Back-Arc Basin (*A. williamsi*), the Tonga-Kermadec Arc (*G. puia*), and along the Izu-Ogasawara Arc (*G. yunohana*). In contrast, vents in North Fiji and Lau Back-Arc Basins may host at least three *Austinograea* species; if an additional *Austinograea* species is later recognised in the Manus Basin (in study), four bythograeid species would inhabit the southwestern Pacific. Within the snail complex *Alviniconcha* Okutani & Ohta, 1988, the dominant inhabitant of hydrothermal vents throughout southwestern Pacific and Indian oceans, DNA sequences for mitochondrial genes have revealed six distinct evolutionary lineages, five cryptic species having been previously confused under the previously monotypic genus *Alviniconcha hessleri*; the oldest dates of speciation events in the *Alviniconcha* complex of species is presumed to have been initiated about 60 Ma before the emergence of the western Pacific Ridge (Kojima *et al.* 2001; Hidaka *et al.* 2015; Johnson *et al.* 2015; D. Jollivet, pers. comm. 2017). We can draw a parallel between the western Pacific brachyuran lineages (morphologically recognisable) and the allopatric/sympatric gastropod lineages, which, however, could not be distinguished by their external morphology.

Our findings of these two new bythograeid species belonging to a genus until now known only by two species in the hydrothermal fields of the western Pacific provide important insights into the biodiversity and biogeography of vent endemic ecosystems. There is no convincing evidence of what is responsible for much of this brachyuran diversity in the western Pacific: speciation without geographic isolation, i.e., sympatric speciation, or allopatric speciation due to secondary contact zones between species with entirely separate geographical ranges but subjected to population dispersal and to subsequent recolonisation of habitats. Is this success related to the non-linear distribution of vents in this vast area and oceanic circulation patterns? Detection of cryptic species in hydrothermal systems is a phenomenon that is rapidly increasing mainly through genetic approaches in various groups, including annelids, sea anemones, mussels, gastropods, and crustaceans. Genetic analyses of the western-Pacific bythograeids, which have not yet resulted in the identification of extensive cryptic diversity, will perhaps recover a more complex biodiversity pattern of brachyuran crabs than previously recognised in this vast area. The ChuBacArc campaign scheduled in 2019 by Didier Jollivet and Stéphane Hourdez (Roscoff) in several back-arc basins of the western Pacific will undoubtedly provide a better understanding of the evolutionary biology of hydrothermal species, including *Austinograea* crabs.

Increasing attention needs to be paid to detrimental impacts of commercial activities, especially mineral extraction, and to a lesser extent the disruptive removal of specimens from their natural environments and scientific over-sampling as well as unintentional and intentional damage sampling on vent ecosystems (Vrijenhoek 2010; Van Dover 2011, 2014; Keaveney *et al.* 2016; Van Dover *et al.* 2016). Protection and future preservation of biological communities of the unique hydrothermal environments require knowledge of the biodiversity and connectivity of associated species, together with cooperation, effective deep-sea resource management and policy at national and international levels.

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