

New genus and species of brachyuran crab from the southern East Pacific Rise (Crustacea Decapoda Brachyura Bythograeidae)

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Received 6 August 2002; accepted 24 September 2002

Presented by Philippe Taquet

Abstract – A new genus and species of a brachyuran crab, *Allograea tomentosa* n. gen. and n. sp., of the family Bythograeidae, collected at a hydrothermal vent locality south of the Easter Microplate (31°09'S) on the southern East Pacific Rise, is described. The genus *Allograea* is distinguished by lacking modifications of the fronto-orbital region, and by the absence of coloured fields and setal patches on the carapace and chelipeds. The body and legs are smooth but densely covered by a brown tomentum, the eyestalks are not reduced, but the cornea is unfaceted and unpigmented. Comparison of mitochondrial DNA sequences among all known bythograeid genera confirms the novelty of this taxon. **To cite this article:** *D. Guinot et al., C. R. Biologies 325 (2002) 1143–1152.* © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Bythograeidae / *Bythograea* / southern East Pacific Rise / Easter Microplate / hydrothermal crab / *mtCOI* DNA sequence divergence

Résumé – Nouveau genre et nouvelle espèce de Crabe dans le Sud de la dorsale du Pacifique oriental (Crustacea Decapoda Brachyura Bythograeidae). Un Crabe nouveau, appartenant à la famille des Bythograeidae, *Allograea tomentosa* n. gen. et n. sp., récolté à 31°09'S dans un site hydrothermal dans le Sud de la dorsale du Pacifique oriental, est décrit. *Allograea* diffère des quatre autres genres de Bythograeidae par l'absence de modifications de la région fronto-orbitaire et de plages colorées ou sétifères sur la carapace ou les chélicèdes. Le corps et les pattes sont lisses sous un dense tomentum brun, les pédoncules oculaires ne sont pas réduits, la cornée ne montre ni facettes ni pigment. La comparaison des séquences de l'ADN mitochondrial chez tous les genres connus de Bythograeidae confirme la nouveauté de ce taxon. **Pour citer cet article :** *D. Guinot et al., C. R. Biologies 325 (2002) 1143–1152.* © 2002 Académie des sciences / Éditions scientifiques et médicales Elsevier SAS

Bythograeidae / *Bythograea* / dorsale du Pacifique oriental / microplaque de l'île de Pâques / crabe hydrothermal / ADN mitochondrial / cytochrome oxydase 1

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Version abrégée

L'exploration de la partie méridionale de la dorsale du Pacifique oriental, au sud de la microplaque de l'île de Pâques, lors de la campagne américaine de l'*Alvin* en 1999, a révélé la présence d'un crabe de la famille des Bythograeidae Williams, 1980, représentant un nouveau genre et une nouvelle espèce, *Allograea tomentosa* n. gen. et n. sp. L'examen des enregistrements vidéos lors de la plongée 3337 du submersible *Alvin* révèle que les crabes de cette espèce sont présents sur un vaste champ de moules et sur des piliers de lave près des cheminées, et qu'ils sont associés à d'autres nombreux crabes (appartenant à une espèce nouvelle de *Bythograea* en cours de description), ainsi qu'à des anémones et de gros gastéropodes blancs buccinidés *Eosipho* sp.

Sur la dorsale du Pacifique oriental, la famille des Bythograeidae est représentée par deux genres : *Bythograea* Williams, 1980, avec quatre espèces (*B. thermydron* Williams, 1980, espèce type, *B. microps* de Saint Laurent, 1984, *B. intermedia* de Saint Laurent, 1988, et *B. laubieri* Guinot et Segonzac, 1997), et *Cyanagraea* de Saint Laurent, 1984, probablement monotypique, avec *C. praedator* de Saint Laurent, 1984 [1–5]. *Allograea* n. gen. est le cinquième genre connu de Bythograeidae, après *Bythograea* de la dorsale du Pacifique oriental et de la ride des Galapagos, *Cyanagraea* de la dorsale du Pacifique oriental, *Segonzacia* Guinot, 1989, de la ride médio-Atlantique, et *Austinograea* Hessler et Martin, 1989, du Pacifique occidental ainsi que de l'océan Indien occidental [6–13].

Malgré l'absence de spécimens mâles, l'établissement d'un genre nouveau est justifié par de remarquables caractères distinctifs, dont la combinaison n'a été rencontrée chez aucun autre Bythograeidae, à savoir : dense tomentum brun de soies plumeuses très courtes, recouvrant complètement le corps et les pattes ; carapace et appendices lisses ; bord antéro-latéral marqué par un bourrelet ; front large, presque droit ; orbites bien définies, fermées ; pédoncules oculaires épais,

cylindriques ; cornée non pigmentée ; yeux, antennules et antennes exposées, non enfoncées ; bord antérieur de l'épistome s'avancant peu dans la région buccale ; crête endostomienne presque complète, représentée antérieurement par un tubercule isolé, et formation d'un canal efférent bien délimité ; lacinie de mxp1 exclusivement localisée dans la partie latéro-externe de l'endostome et dépourvue de lobe mésial ; mxp3 avec mérus très proéminent à l'angle antéro-externe, palpe très court, propode non élargi, et dactyle petit, inséré dans le prolongement du propode ; pattes ambulatoires allongées et étroites ; pas de taches colorées ni de plages sétifères particulières (Figs 1–7).

Bythograea se distingue d'*Allograea* par les caractères ci-dessus mentionnés, notamment : région fronto-orbitaire, avec présence d'une grande plaque suborbitaire ; front saillant et défléchi, sous lequel sont abrités yeux, antennules et antennes ; orbites absentes ; pédoncules oculaires étroits et région cornéenne dilatée ; ornementation granuleuse des bords de la carapace ; bord antérieur de l'épistome divisé en lobes saillants ; crête endostomienne confinée postérieurement ; lacinie de mxp1 avec un lobe mésial développé ; mxp3 avec palpe très long et dactyle inséré sur le bord mésial du propode. *Allograea* est plus proche de *Cyanagraea*, aux orbites bien définies et aussi dépourvu de plaque suborbitaire. Mais *Cyanagraea* se distingue par sa très grande taille (130 mm de large, 25 mm pour *Allograea tomentosa*), par l'ornementation tuberculée des régions fronto-latérales, par les pédoncules oculaires élargis dans la zone cornéenne, par les pattes courtes, ainsi que par divers autres traits (épistome, endostome, maxillipèdes, pinces).

La comparaison des séquences de l'ADN mitochondrial [14–16] chez toutes les espèces connues de Bythograeidae a confirmé la nouveauté de ce taxon (Tableau 1). *Cyanagraea* est le plus proche parent d'*Allograea* (14% *mtCOI* de divergence génétique), ce qui corrobore les résultats des données morphologiques présentées ici.

1. Introduction

Members of the family Bythograeidae Williams, 1980, are a distinctive component of hydrothermal vent communities explored to date around the world's oceans. They are found along active mid-ocean ridges and in back-arc spreading centres. The family Bythograeidae is represented by four genera. *Bythograea* is found on the East Pacific Rise and Galapagos Rift; *Cyanagraea* is reported only on the EPR; *Segonzacia*, in the

Mid-Atlantic Ridge; and *Austinograea*, in the western Pacific and Indian Ocean.

The genus *Bythograea* Williams, 1980, is represented by four species. *B. thermydron* Williams, 1980 (type species), is the predominant crab species on most EPR vent sites between 21°N and 18°38'S, and on the Galapagos Rift. *B. microps* de Saint Laurent, 1984, has been observed at 21°N, 13°N and 9°50'N on the EPR and on the Galapagos Rift. *B. laubieri* Guinot and

Segonzac, 1997, has been collected in hydrothermal vents of the southern EPR between 11°S and 21°S. *B. intermedia* de Saint Laurent, 1988, is a poorly known species (description based on a single megalopa and six early crab stages), that has been observed only in the Galapagos Rift. The genus *Cyanagraea* de Saint Laurent, 1984, is probably monotypic, with *C. praedator* de Saint Laurent, 1984, distributed between 13°N and 18°S on the East Pacific Rise (although an uncertain species, *Cyanagraea* sp., is only known from video tapes at 18°S) [1–5]. The genus *Segonzacia* Guinot, 1989, is monotypic, with *Segonzacia mesatlantica* (Williams, 1988), distributed extensively at vents along the Mid-Atlantic Ridge [6–8]. The genus *Austinograea* Hessler and Martin, 1989, is represented by four species distributed in the western Pacific, as well as in Indian Ocean vents [6, 9–13]. *A. williamsi* Hessler and Martin, 1989, is known from the western Pacific. *A. yunohana* Takeda, Hashimoto and Ohta, 2000 is distributed at the Philippine Sea Plate. *A. alayseae* Guinot, 1990, is distributed in the southwestern Pacific at 22°S. *A. rodriguezensis* Tsuchida and Hashimoto, 2002, is found in the western Indian Ocean, at the Rodriguez Triple Junction site (25°19'S–70°E) [12, 13].

We describe herein a new genus and species of the family Bythograeidae, *Allograea tomentosa* n. gen. and n. sp. These are small and hairy crabs that were collected in a hydrothermal vent locality south of the Easter microplate (31°09'S) on the southern East Pacific Rise. We present a detailed morphological examination of the material and a comparison with other genera of the family Bythograeidae, which allowed us to recognise the taxonomic status of these crabs. Additionally, we present preliminary results on DNA sequence divergence for a mitochondrial gene among all known bythograeid genera, that confirm the novelty of this taxon. *Allograea* is thus the fifth known bythograeid genus, and the third one (in addition to *Bythograea* and *Cyanagraea*) found in the East Pacific Rise.

2. Material and method

Five mature bythograeid crabs, all females, were collected by the manned submersible *Alvin* in a hydrothermal vent site south of the Easter Microplate (31°09'S–111°56'W), at a depth of 2335 m. Three of the females were collected on 13 January 1999 (*Alvin* dive 3337), and two on 14 January 1999 (*Alvin* dive 3338). Examination of videos from *Alvin* dive 3337 revealed that these crabs were observed on a big mussel field and in lava pillar areas near vent chimneys, associated also to other bythograeid crabs (*Bythograea*

sp., description in preparation), which outnumbered the *Allograea* crabs, as well as anemones, unidentified small white worms, and big white buccinid gastropods *Eosipho* sp. Crab specimens were frozen whole at –60 °C soon after retrieval, for genetic analyses, and subsequently transferred to alcohol for morphological description.

We compared DNA sequence divergence among *Allograea* crabs and representatives of all bythograeid genera. These species included *B. thermydron*, *C. praedator*, *S. mesatlantica*, and *A. williamsi*. Total DNA of these samples was extracted from a claw muscle sample of each individual, following the manufacturer's protocol for the DNEASY kit (Qiagen, Inc., Valencia, CA). An approximately 710-bp fragment of a fragment of the mitochondrial Cytochrome c Oxydase Subunit I gene was amplified using published primers and PCR conditions [14]. Both strands of each PCR product were sequenced on an ABI 377 automated sequencer (Perkin-Elmer/ABI, Foster City, CA, USA). Sequences were proofread, aligned and assembled with Sequencher v. 4.1 (Gene Codes Corp., Ann Arbor, MI). Assembled sequences were truncated to 659-bp, a fragment that contained only clear and readable nucleotides. Kimura-2-parameter [15] sequence divergence among samples was estimated with PAUP* v. 4.0b8 [16].

Abbreviations: mxp1, first maxilliped, mxp3, third maxilliped. Measurements of carapace length × carapace width are given in millimetres (mm). Material used in this study is deposited at the 'Muséum national d'histoire naturelle', Paris (MNHN).

3. Systematic description

Family Bythograeidae Williams, 1980.

3.1. Genus *Allograea* n. gen.

Diagnosis (male unknown). Body not thick. Carapace transversely elliptical, flat; regions indistinct. Anterolateral margin marked by rounded edge. Front broad, not deflexed and not protruded from general outline of carapace, nearly truncated and straight. Eyes, antennules and antennae entirely exposed, not recessed under front. Interantennular septum extremely reduced. Antennules horizontally folded; basal article thick and entirely exposed. Antennae with proximal articles in same line and only slightly inclined. Suborbital plate absent. Orbits present, complete and closed, showing as clearly defined pockets. Eyestalks mobile, short and thick, cylindrical, completely located in orbits and easily visible; cornea present, not enlarged or reduced,

unpigmented, whitish, with facets obsolete. Endostomial (palatal) ridge that limits lateral efferent channel, interrupted and consisting in strong posterior crest and isolated prominent tubercule, close to anterior border of buccal frame; lacinia of mxp1 curved, not extended internolaterally and therefore restricting aperture of channel to form exhalant orifice; no mesial ('portunid') lobe. Mxp3 merus: surface without submarginal thickened zone and groove on margins; antero-external angle strongly produced; internal border with marked lobe. Mxp3 palp very short; propodus not particularly enlarged; dactylus markedly reduced and inserted at tip of propodus. Chelipeds short, somewhat asymmetrical;

fingers dimorphic, crossing at tip. Walking legs elongated and slender, meri and propodi narrow, dactyli thin (Figs 1–7).

Etymology. From the Greek 'graia' sea crab, and 'allos' other. The gender is feminine.

Type species. *Allograea tomentosa* n. gen. and n. sp.

3.2. *Allograea tomentosa* n. gen. and n. sp.

Description (male unknown). Body not thick. Body and legs completely covered by brown, dense tomentum, consisting of very short plumose setae, with sparse, longer simple setae; only white extremities of



Fig. 1. *Allograea tomentosa* n. gen. and n. sp., female: dorsal view. **A**, holotype, 16 × 25 mm (left side denuded) (MNHN-B28619); **B**, paratype, 16 × 25 mm (right side denuded) (MNHN-B28620). Scale bars: 1 cm.

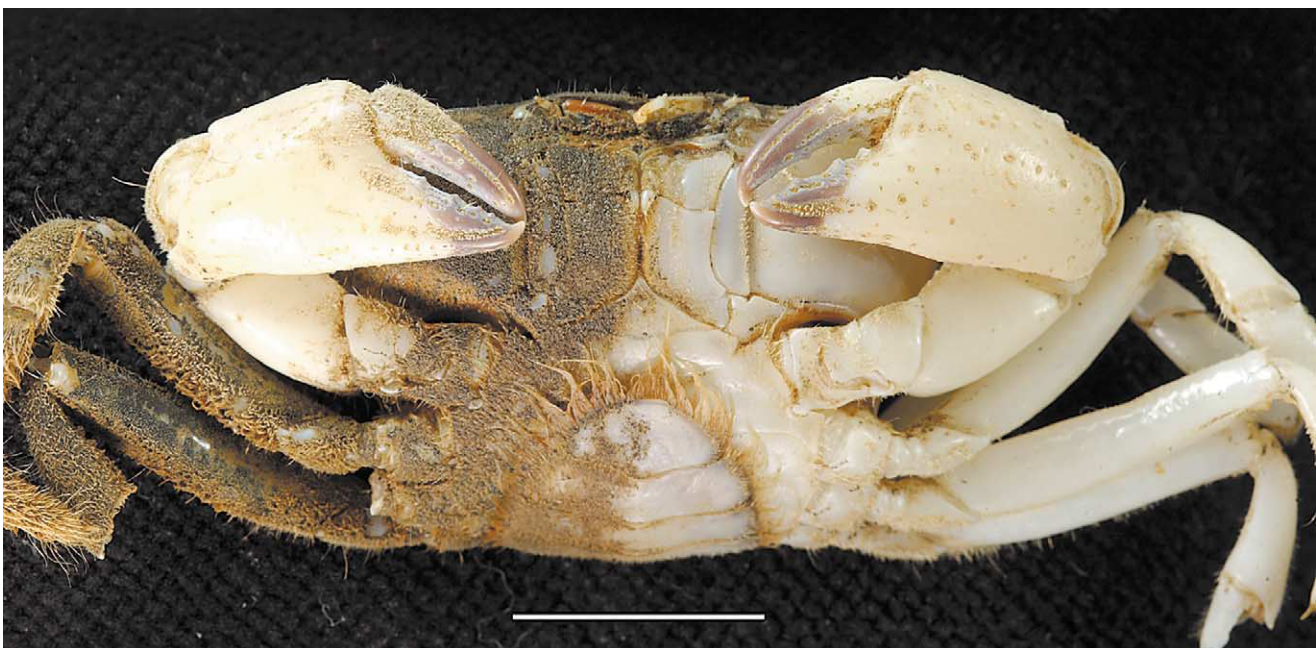


Fig. 2. *Allograea tomentosa* n. gen. and n. sp., female, holotype: ventral view. Scale bar: 1 cm.

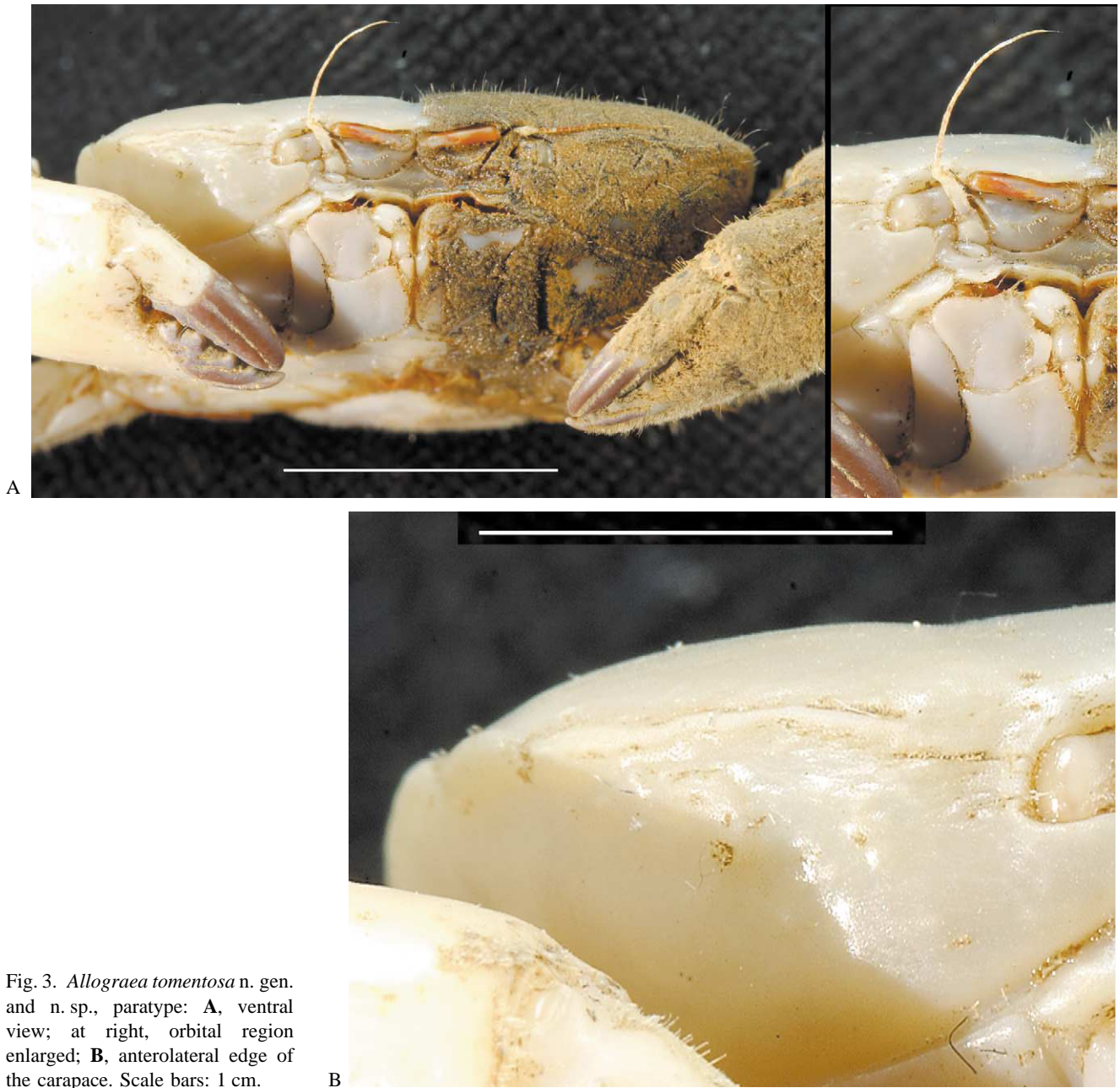


Fig. 3. *Allograea tomentosa* n. gen. and n. sp., paratype: **A**, ventral view; at right, orbital region enlarged; **B**, anterolateral edge of the carapace. Scale bars: 1 cm.

eyestalks, second antennular article and antennal flagellum (reddish-coloured by accumulation of metallic compounds) not covered by tomentum. Carapace transversely elliptical, flat; regions indistinct, surface entirely smooth, without transverse granulous rows, granules or ridges, but densely setose. Anterolateral margin marked by rounded edge, not joining exorbital angle, divided into three parts by two small notches. Front broad, not deflexed, nearly straight in outline, slightly sinuous, with small but marked external angles. Suborbital plate absent. Orbits well defined, rounded/ovate, entirely visible; orbital borders slightly thickened, smooth, without teeth or notches; external angle smooth, not

marked. Eyestalks short, cylindrical throughout length; cornea present, whitish, unfaceted. Eyes and two first pairs of cephalic appendages exposed, not recessed under front. Basal antennular article completely exposed, very thick. First article of antenna transversely elongated; basal article short; article 4 elongated, included into orbital hiatus; article 5 and flagellum nearly transversely inclined; flagellum very long. Mouth field not much divergent anteriorly. Anterior margin of epistome not much protruding ventrally into mouth field, divided into two parts: external part forming only small crescent-shape protrusion, internal part straight; medially, only a narrow projection. Floor

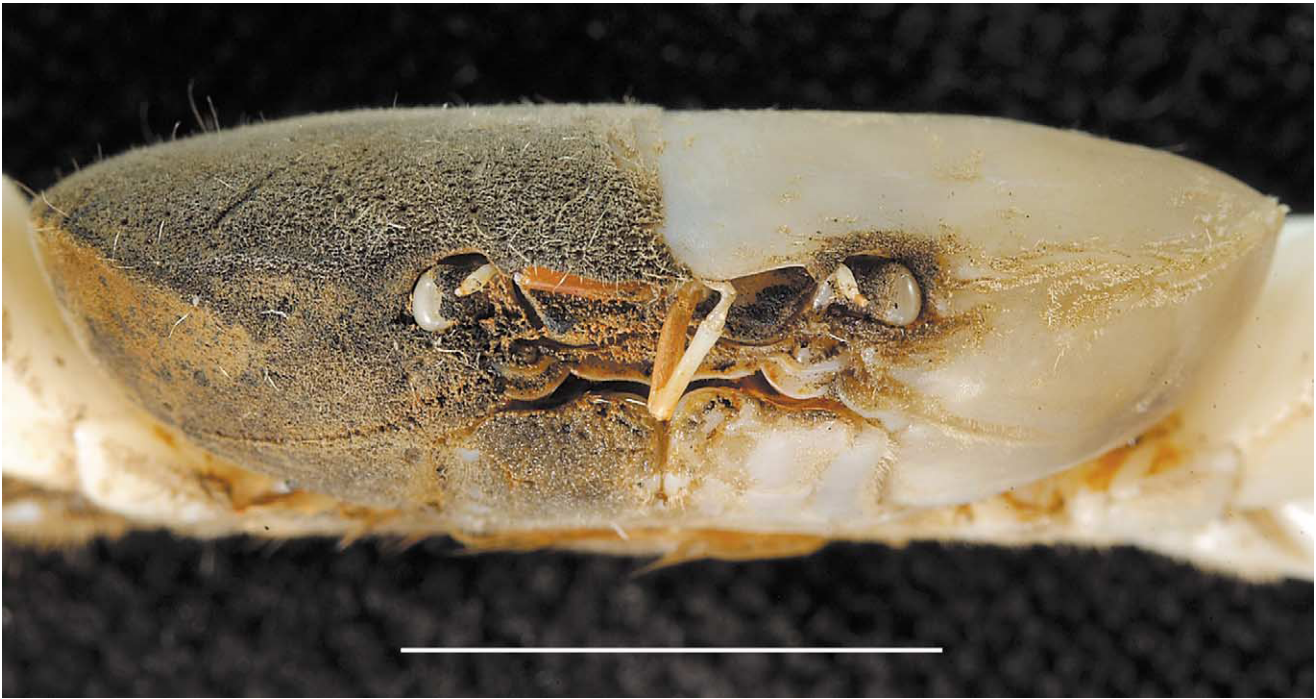


Fig. 4. *Allograea tomentosa* n. gen. and n. sp., holotype: frontal view. Scale bar: 1 cm.



Fig. 5. *Allograea tomentosa* n. gen. and n. sp., female, holotype: chelipeds (denuded). Scale bar: 1 cm.

of endostome with interrupted palatal ridge, formed by strong posterior crest continued by isolated prominent tubercule, not in contact with buccal frame, limiting lateral efferent channel; channel closed by lacinia of mxp1; internal half with velvety pubescence. Lacinia of mxp1 not extended laterally, without mesial lobe. Mxp3 filling mouth field, except for narrow gap between merus of endognath and epistome; exognath not overlapping sides of mouth frame; all surfaces smooth. Mxp3 endognath with antero-external angle of merus strongly produced, very close to epistome; internal

border of merus with marked mesial lobe; palp very short, small, tip only reaching proximal mesial margin of ischium; propodus not particularly enlarged, symmetrical in ventral view; dactylus extremely reduced, inserted at tip of propodus. Chelipeds short, somewhat asymmetrical; fingers dimorphic; both chelae covered on both sides by dense tomentum, and surfaces smooth when denuded; fingers grooved; occluding edge of dactylus on large chela (at right) with three blunt teeth, occluding edge of fixed finger with four marked teeth; tips of fingers on small chela pointed and crossing;



Fig. 6. *Allograea tomentosa* n. gen. and n. sp., female, holotype: cheliped with dense tomentum (not denuded). Scale bar: 1 cm.



Fig. 7. *Allograea tomentosa* n. gen. and n. sp., holotype: vulvae. Scale bar: 1 cm.

occluding edge of dactylus with very low, somewhat indistinct teeth, occluding edge of fixed finger with four acute teeth; dactyli dark-coloured on 3/4 length on both chelae, fixed fingers only in half distal part. Walking legs elongated and slender, all articles entirely covered with dense tomentum. Vulvae with large membranous area; anterior lunate slit.

Etymology. From the Latin *tomentosus*, covered with hair.

Type material. Southern East Pacific Rise, 31°09'S–111°56'W, *Alvin* dive 3337, 01–13–99, 2335 m: 1 female, 16 × 25 mm, holotype (left side denuded) (MNHN-B28619); 2 females, 16 × 25 mm (right side denuded), 14 × 22 mm, paratypes (MNHN-B28620). Southern East Pacific Rise, 31°09'S–111°56'W, *Alvin* dive 3338, 01–14–99, 2334 m: 1 female, 15 × 23.8 mm, paratype, 1 specimen with broken carapace (MNHN-B28621).

4. Position of *Allograea* n. gen. within the Bythograeidae

Despite the lack of male specimens, the establishment of the new genus is clear, due to the presence of distinctive characters. The female individuals are mature (developed vulvae). *Allograea* is undoubtedly a member of the family Bythograeidae. The overall resemblance to previously described species of *Bythograea*, *Cyanagraea*, *Segonzacia*, and *Austinograea* is obvious. However, no other bythograeid crab possesses the set of features that characterises *Allograea tomentosa*, which precludes placing the species in other genera. All other bythograeid genera have an anterolateral border of the carapace marked by granules; deflexed front; eyes, antennules and antennae greatly or at some extent recessed, more or less hidden under front; floor of endostome lacking anterior endostomial tubercle and without well-defined efferent channel; mxp3 with very long palp, propodus enlarged and asymmetrically ovate in ventral view, and dactylus half-ensiform and articulated on mesial side of propodus. All known bythograeid species show coloured spots on the carapace or chelipeds, dark-tipped tubercles on the carapace, or patches of setae in various parts of the carapace or chelae. *Allograea* lacks the coloured fields, which are probably sensory, and setose patches that are used at least partly for the entrapment of particulate food [1], since individuals are densely covered by a uniform tomentum (except for distal part of eyestalks and exposed part second article of antennule and antennal flagellum). The legs are generally shorter and thicker in most bythograeids.

Bythograea is easily distinguished from *Allograea* by the characters previously mentioned, but particularly by: dorsal surface of the carapace being ornamented with granules, sometimes arranged in rows, and glabrous, except for *B. microps* where yellowish setae are present (surface smooth and densely tomentose in *Allograea*); front markedly convex and deflexed (nearly straight and not deflexed in *Allograea*); orbits highly modified, almost non-existent, pockets not defined; presence of a broadened ocular area forming suborbital plate, delimited laterally by converging tubercle rows (closed orbits present, suborbital plate absent in *Allograea*); eyes and two first pairs of cephalic appendages deeply recessed (entirely exposed in *Allograea*); antennules only visible by folded second article, which surrounds eyestalk (basal antennular article exposed, second article not surrounding eyestalk in *Allograea*); antennae deeply recessed, strongly inclined and with proximal articles not in line (antennae visible, hardly inclined, all articles in same line in *Allograea*); eye-

stalks more or less slender (thick and cylindrical in *Allograea*); anterior margin of epistome strongly projecting forward and divided into unequal lobes: pointed external lobe and an irregular, bilobed internal part, the two mesial lobes of each side forming broad medial protrusion into mouth field [6] (not much projecting, external lobe only convex, internal part roughly straight, only a narrow medial protrusion in *Allograea*); mouth field anteriorly divergent (frame nearly quadrate in *Allograea*); floor of endostome with only posterior crest; mxp1 lacinia advanced laterally and with flattened mesial lobe [1] (endostomial ridge nearly complete, mxp1 lacinia occupying only external half of endostome and without mesial lobe in *Allograea*); a relatively large gap between mxp3 and borders of buccal frame (merus of mxp3 endognath anteroexternally close to buccal frame in *Allograea*); mxp3 endognath [6] with merus broadly rounded at anteroexternal angle and flanked on external and anterior margins by submarginal thickened zone and groove (angle strongly produced and surface smooth in *Allograea*); mxp3 with long palp, reaching about 1/2–2/3 length mesial margin of ischium (palp very short in *Allograea*); propodus broad and asymmetrically ovate in ventral view (not particularly enlarged and symmetrical in *Allograea*); mxp3 exognath overlapping sides of mouth frame (not overlapping in *Allograea*); ventral surface of carapace glabrous (densely tomentose in *Allograea*); except for the case of quite or completely white chelipeds in *B. thermydron*, colour extending onto palm of chelae or located on spots [5] (limited to fingers, and no spots in *Allograea*); chelipeds glabrous, apart from patches of setae at inner surfaces of chelae or proximally between fingers; but chelipeds hairy in *B. microps* (chelipeds completely covered with short, dense tomentum in *Allograea*); walking legs only with tufts of setae or sparse setae, only last articles setose (brownish, short and dense tomentum covering whole legs in *Allograea*); vulvae with lunate central slit in *B. thermydron* and *B. laubieri* (slit located more anteriorly in *Allograea*).

It is to be noted that the megalopa of *B. thermydron* shows fully formed normal orbits, well developed and exposed eyestalks; the cornea is faceted, not darkly pigmented. Drastic changes occur in the orbital region during development: the adult becomes completely specialised for life in the lightless environment, with modified and non-existent orbits and narrow, recessed eyestalks [1].

Allograea somewhat resembles *Cyanagraea*, which also lacks a suborbital plate [2, 4–6, 9]. *Cyanagraea* has eyes, antennules and antennae that are only slightly recessed (instead exposed in *Allograea*), and advanced and convex front (instead of nearly straight in

Allograea). *Cyanagraea* shares with *Allograea* antennae with proximal articles in line (except for first article that is placed laterally with regard to basal article in *Cyanagraea*); closed orbits (however, ovate in *Allograea*, rounded in *Cyanagraea*); well developed eyestalks; anterior margin of epistome without strong protrusions into mouth field (in *Cyanagraea* anterior margin forming continuous, not notched and regularly concave line, with rather marked medial protrusion into mouth field; in *Allograea*, each margin is notched and divided into two distinct parts; external part slightly protruding, internal part nearly straight, and medial protrusion weak); mouth field not much anteriorly divergent; mxp1 lacinia without mesial lobe (in *Cyanagraea* given as absent by [2], as acutely produced by [6]); mxp3 exognath not overlapping sides of mouth frame; mxp3 merus without thickened submarginal zone and groove on external and anterior margins; short chelipeds. *Allograea* and *Cyanagraea* differ by several characters: body size (130 mm width in *Cyanagraea*); carapace flat and smooth in *Allograea* (vaulted and with colour-tipped tubercles on frontolateral regions in *Cyanagraea*); antennules horizontally folded, basal article largely exposed in *Allograea* (obliquely folded, basal article not largely visible in *Cyanagraea*); eyestalks cylindrical, without enlargement of cornea in *Allograea* (cornea enlarged and amber-coloured in *Cyanagraea*); lacinia of mxp1 not extended and efferent channel well-defined in *Allograea* (lacinia occupying most part of endostome, no defined efferent channel in *Cyanagraea*).

Allograea shares with *Segonzacia* the general shape of the carapace and smooth dorsal surface (but anterolateral border is granulous in *Segonzacia*, bounded by rounded edge in *Allograea*), cylindrical eyestalks, lacinia of mxp1 not extended laterally. The two genera differ by several characters, including the location of eyestalks, antennules and antennae (recessed in *Segonzacia*, entirely exposed in *Allograea*); suborbital plate (present but not delimited by rows of tubercles in *Segonzacia*, absent in *Allograea*); anterior margin of epistome (not notched laterally and regularly concave in *Segonzacia*; notched, internal part nearly straight in *Allograea*); endostomial ridges (more complete in *Allograea*); presence of oval, coloured suborbital spots (absent in *Allograea*), and characters of mxp3 merus and palp [6–8].

Allograea shares with *Austinograea* a transversely elliptical carapace, dorsal surface without transverse granulous rows, and mxp1 lacinia not extended laterally. But the three known species of *Austinograea* have no moveable eyestalks, and the eyes are more or less degenerated. There are additional differences, including

the location of eyestalks, antennules, and antennae, which are recessed in *Austinograea* (exposed in *Allograea*), suborbital plate present in *Austinograea* (absent in *Allograea*), anterior margin of epistome continuous, not notched, and regularly concave in *Austinograea*, such as in *Cyanagraea* (notched, divided into two distinct parts in *Allograea*); endostomial ridge short and only posterior in *Austinograea* (developed in *Allograea*), mxp3 coxa partly covered in *Austinograea* (more visible in other genera), mxp3 merus with antero-external margin oblique in *Austinograea* (strongly produced in *Allograea*), shape of mxp3 palp, and other characters [6, 10–13].

In conclusion, *Allograea* appears to be closer to *Cyanagraea* than to *Bythograea*, most obviously because of the shape of the fronto-orbital region, location of the eyestalks and two first pairs of cephalic appendages, well-defined orbits, relative development of the eyes, and shapes of the epistomial margin and mouth field. But *A. tomentosa* is distinguished by a very short mxp3 palp, without specially enlarged propodus, and dactylus which is small and normally inserted at the tip of the propodus.

By lacking modifications of the fronto-orbital region, a recession of the eyes and first cephalic appendages under front, specialised features of third maxillipeds, and setose or coloured fields on body or chelipeds, *Allograea* seems to be the less modified member of the family Bythograeidae. However, it is a unique bythograeid, with rather complete endostomial ridge (instead more or less confined to posterior part of buccal cavity in other genera), allowing a rather closed efferent channel and well-defined exhalant orifice to direct efferent branchial water current. Well developed endostomial ridges that reach the anterior buccal frame are present in several brachyuran families, either marine such as the Oziidae Dana, 1851 (= Menippidae Ortmann, 1893), Eriphiidae Macleay, 1838, and Carcinoplacidae H. Milne Edwards, 1852, or freshwater such as the Pseudothelphusidae Rathbun, 1893. According to its few modified characters, *Allograea* appears to be the bythograeid member that is closest to non-hydrothermal Brachyura. These characters are somewhat suggestive of affinities with the Carcinoplacidae, which have a reduced interantennular septum, wide front and similar location of eyes, antennules and antennae, complete endostomial ridges limiting well-defined efferent channel, mxp1 lacinia with mesial lobe, and wide thoracic sternum.

5. Comparison of DNA sequences

Comparison of DNA sequences of a fragment of the mitochondrial Cytochrome c Oxydase Subunit I gene

Table 1. Percentage Kimura-2-parameter DNA sequence divergence of a 659-bp fragment of the mitochondrial Cytochrome c Oxydase Subunit I gene among bythograeid genera.

	<i>Allograea tomentosa</i>	<i>Cyanagraea praedator</i>	<i>Bythograea thermydron</i>	<i>Segonzacia mesatlantica</i>
<i>C. praedator</i>	14%			
<i>B. thermydron</i>	21%	17.2%		
<i>S. mesatlantica</i>	18.2%	15.5%	21.5%	
<i>A. williamsi</i>	19.2%	18.9%	18.8%	17.7%

among all bythograeid genera confirms the novelty of *Allograea* n. gen. (Table 1). Average percentage sequence divergence between *Allograea* and the other bythograeid genera (18.1%) is very similar to the average percentage sequence divergence values among the other genera (18.3%). Therefore, molecular data support the separation of *Allograea* as a different genus. Based on percentage sequence divergence alone, *Cyanagraea* appears to be the closest relative of *Allograea* (14%

mtCOI sequence divergence), which is also suggested by the morphological data presented here. However, molecular phylogenetic analyses, including additional DNA markers, are needed to infer the true relationships among bythograeid genera (Hurtado et al.; work in progress). In conclusion, based on both morphological and molecular data, *Allograea* is the fifth known bythograeid genus, and the third one found in the East Pacific Rise, in addition to *Bythograea* and *Cyanagraea*.

Acknowledgements. Thanks to D. Geffard, P. Loubry and D. Serette for assistance in the illustration, to M. Segonzac for information and comments, to P. Castro, R. Brusca and M. Mateos for reviewing the manuscript. We thank the pilots and crew of DSV *Alvin* and R/V *Atlantis* for their hospitality and assistance. Research was supported by the Monterey Bay Aquarium Research Institute (project # 200104) and grants from NSF (OCE9633131 and OCE9910799).

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