



New crabs from hydrothermal vents of the Kermadec Ridge submarine volcanoes, New Zealand: *Gandalfus* gen. nov. (Bythograeidae) and *Xenograpsus* (Varunidae) (Decapoda: Brachyura)

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Abstract

Gandalfus puia gen. et sp. nov. (Bythograeidae) is reported from submarine volcanoes near the Kermadec Islands. The genus *Austinograea* is revised with the result that *A. yunohana* Takeda, Hashimoto & Ohta, 2000 is transferred to the new genus. Both of these species occur in relatively shallow waters (240–1650 m) compared to other bythograeids. A sister group hypothesis of the modern genera, *Allograea* + (*Segonzacia* + (*Cyanagraea* + (*Bythograea* + (*Gandalfus* + *Austinograea*)))) is presented to provide an interpretation of variation in eye regression and male gonopods; *Austinograea* and *Gandalfus* are the most derived genera. The pattern of eye regression with depth is discussed. A varunid, *Xenograpsus ngatama* sp. nov., also collected from these volcanoes, is the first record of this genus from the southern hemisphere. Keys to all known species of the family Bythograeidae (13 species 6 genera) and to the genus *Xenograpsus* (3 species) are presented.

Key words: *Austinograea*, Kermadec Islands, South Pacific, identification key, eye regression, evolution

Introduction

In a recent review of vent decapods, Martin & Haney (2005) listed 125 species belonging to 33 families. In addition, Desbruyères & Segonzac (1997) have provided a useful handbook to hydrothermal vent faunas. Studies of hydrothermal vents and seamounts in recent years have resulted in the discovery of many new species of unusual crabs, particularly of the families Bythograeidae Williams, 1980 and Varunidae H. Milne Edwards, 1853. These animals are important predators in hydrothermal vent communities because they are often very numerous (Martin *et al.* 1998; Jeng *et al.* 2004; Martin & Haney 2005). Sampling of the Kermadec underwater volcanoes by NIWA biologists has brought to light two new crabs belonging to these families. New anomurans of the genera *Munida* and *Agononida* (see Vereshchaka 2005) and *Munidopsis* (see Schnabel & Bruce 2006) have also recently been reported. Webber (2004) reported a new species of prawns of the genus *Alvinocaris* and *Chorocaris* from this area. Other animals discovered from these active volcanoes, at a depth of 216–460 m, include a large mussel, *Gigantidas gladius* Cosel & Marshall, 2003 (Cosel & Marshall 2003). The Kermadec volcanoes are associated with Pacific–Australian plate convergence at the Kermadec Trench. “Rumble III” is an active volcanic site that shoals to 220 m and last erupted in 1986 as observed by a Japanese fishing trawler at the time (Ian Wright, pers. comm.). Recent geological reports on this site can be found in de Ronde *et al.* (2001), Wright (2001) and Wright *et al.* (2002).

The Bythograeidae includes 12 species in 5 genera (assuming that *Bythograea intermedia* Saint Laurent, 1988 is a synonym of *B. thermydron* Williams, 1980; see Guinot & Hurtado 2003: 431). Most of these are known from the Eastern Pacific Rise with only 4 species of *Austinograea* Hessler & Martin, 1989 known from

the Western Pacific and Indian Ocean: *Austinograea williamsi* Hessler & Martin, 1989 (type species), *Austinograea rodriguezensis* Tsuchida & Hashimoto, 2002, *Austinograea alayseae* Guinot, 1990 and *Austinograea yunohana* Takeda, Hashimoto & Ohta, 2000. One species, *A. alayseae*, from 1900 m depth in the Lau back-arc Basin, West of Tonga, occurs closest to New Zealand. A new bythograeid crab from the Brothers Seamount near the Kermadec Islands provides the first record of this family from the New Zealand region, and considerably extends the distribution of the family southwards. As its closest affinities appear to be with *Austinograea*, it has also been necessary to review the constitution and diagnostic characters of this genus.

Another group of crabs found around hydrothermal vents belong to the genus *Xenograpsus* Takeda & Kurata, 1977, the first of which, *X. novaeinsularis* Takeda & Kurata, 1977, was discovered at a new volcanic island in the Ogasawara Islands, Japan. This species also occurs at the Mariana Islands, part of the same volcanic arc (Türkay & Sakai 1995). A second species, *X. testudinatus* Ng, Huang & Ho, 2000 was discovered at shallow water hydrothermal vents off the east coast of Taiwan. Recently collected specimens from the Macaulley Caldera, near the Kermadec Islands, add a new third species and the first record of this genus in the southern hemisphere.

The only vent-associated brachyuran previously reported from New Zealand waters is the macrophthalmid crab *Macrophthalmus (Hemiplax) hirtipes* (Jacquinot, in Hombron & Jacquinot, 1843) (see Kamenev *et al.* 1993) from a site near Whale Island off the east coast of the North Island. Large numbers were found at a depth of 42 m, apparently at high temperatures (17–81°C). This is a curious association, because, prior to this record, *M. hirtipes* was regarded as an estuarine crab of the lower intertidal area (McLay 1988). The identification of this species has been independently verified. Less surprising was the record of *Pinnotheres novaezelandiae*, which was found inside the mussel *Perna canaliculus* attached to the bottom near the gaseous hydrothermal vents.

All the specimens listed in this paper are deposited in the National Institute of Water and Atmosphere Invertebrate Collection at Greta Point, Wellington, New Zealand. Specimen size is reported as carapace width x carapace length, measured in millimeters (mm). The abbreviations P2–P5 are used for pereopods and G1 and G2 are used for the male first and second gonopods. In the collection data, the National Institute of Water and Atmosphere is abbreviated to NIWA and the New Zealand Oceanographic Institute is abbreviated to NZOI.

Bythograeidae Williams, 1980

Bythograeidae Williams, 1980: 444.

Type genus. *Bythograea* Williams, 1980.

***Gandalfus* gen. nov.**

Diagnosis. Carapace wider than long, transversely elliptical, flat; front broad, lateral margins rounded. Orbits elongate transversely, incomplete; eyestalks fixed; suborbital plate trapezoidal, not visible dorsally. Interantennular septum reduced to small dorsal and ventral keel. Epistome not projecting, gently sinuous in frontal view. Merus of third maxilliped almost as long as entire medial margin of endopod. Walking legs (P2–P5) shorter than chelipeds. Proximal portion of lateral projection of third maxilliped coxa not visible ventrally. G2 equal to or greater than G1. Male and female abdominal segments freely articulating.

Type species. *Gandalfus puia* sp. nov., by present designation.

Other species. *Austinograea yunohana* Takeda, Hashimoto & Ohta, 2000.

Etymology. *Gandalfus* is derived from the name of the omnipotent “Gandalf”, a character in J. R. Tolkien’s “Lord of the Rings”, which was made into a film by Peter Jackson, in New Zealand, the home of the type species. Gender is masculine.

Discussion. The first bythograeid genus to be found and described was *Bythograea* Williams, 1980 for *B. thermydron* Williams, 1980 from the Galapagos Rift area. Then de Saint Laurent (1984) added a second genus for *Cyanagraea praedator* de Saint Laurent, 1984 collected from the East Pacific Rise. Later *Austinograea williamsi* Hessler & Martin, 1989 from the Mariana Basin was added, and in the same year *Segonzacia* Guinot, 1989 was introduced to receive *Bythograea mesatlantica* Williams, 1988 from the mid-Atlantic Ridge. This had the effect of restricting *Bythograea* to the Pacific Ocean. The last genus to be established was for *Allograea tomentosa* Guinot, Hurtado & Vrijenhoek, 2002 from the Southeast Pacific Rise. Since that time, new species have been added to one or other of these five genera (although 3 genera remain monotypic) so that we now recognise 12 previously described species (Table 1) from all the major oceans: Pacific, Indian and Atlantic. These crabs are restricted to areas of submarine volcanic activity.

TABLE 1. Species List of Bythograeidae Williams, 1980..

Allograea Guinot, Hurtado & Vrijenhoek, 2002 (type species *Allograea tomentosa* Guinot, Hurtado & Vrijenhoek, 2002)
 **Allograea tomentosa* Guinot, Hurtado & Vrijenhoek, 2002

Austinograea Hessler & Martin, 1989 (type species *Austinograea williamsi* Hessler & Martin, 1989)
 **Austinograea alayseae* Guinot, 1990
 **Austinograea rodriguezensis* Tsuchida & Hashimoto, 2002
 **Austinograea williamsi* Hessler & Martin, 1989

Bythograea Williams, 1980 (type species *Bythograea thermydron* Williams, 1980)
 **Bythograea galapagensis* Guinot & Hurtado, 2003
 **Bythograea intermedia* de Saint Laurent, 1988 (maybe the same as *B. thermydron* Williams, 1980)
 **Bythograea laubieri* Guinot & Segonzac, 1997
 **Bythograea microps* de Saint Laurent, 1984
 **Bythograea thermydron* Williams, 1980
 **Bythograea vrijenhoeki* Guinot & Hurtado, 2003

Cyanagraea de Saint Laurent, 1984 (type species *Cyanagraea praedator* Saint Laurent, 1984)
 **Cyanagraea praedator* de Saint Laurent, 1984

Gandalfus **gen. nov.** (type species *Gandalfus puia* **sp. nov.**)
 * *Gandalfus puia* **sp. nov.**
 * *Gandalfus yunohana* (Takeda, Hashimoto & Ohta, 2000)

Segonzacia Guinot, 1989 (type species *Bythograea mesatlantica* Williams, 1988).
 **Segonzacia mesatlantica* (Williams, 1988)

The main characters that have been used as the basis of these genera include features of the carapace surface, tubercles and tomentum, development of the orbits, mobility and size of the eyestalks, recession of cephalic appendages under the front, ventral exposure of the third maxilliped coxa, and other aspects of the third maxilliped, and the gonopods.

Amongst the Brachyura the G1 is a conservative feature (Guinot & Hurtado 2003: 436) but the G2 size shows considerable variation. In bythograeids several features of the gonopods show variation (Table 2). The G1 in this family is usually stoutly constructed, curved, not twisted and largely unornamented except in *Austinograea* where it is slender, curved and ornamented with a longitudinal row of spines. The G1 usually narrows to a pointed tip with a terminal aperture. The G2 consists of a peduncle that is separated mid-way from the apical flagella by a notch. The length of the G2 is normally much greater than the G1 so that it can protrude from the terminal aperture and presumably enter the female gonopore. Tsuchida & Fujikura (2000) suggested that the bythograeid G2 does not have a pumping role in sperm transfer, but is instead a sensory device guiding the G1 into the female gonopore. However, this hypothesis ignores the setose notch mid-way along

the G2, which seems to act as a valve so that, with the pumping action of the G2, sperm is impelled into the narrowing bore of the G1, forcing it out of the G1 tip and into the female spermatheca. This mechanism is widespread in other brachyuran crabs. It is likely that the G2 has a role in sperm transfer in all bythograeids regardless of its size and in species with length of G2 \gg G1, it may have a role in disrupting sperm from previous matings.

TABLE 2. male pleopods and body size of bythograeid crabs.

Species	First Male Gonopod	Second Male Gonopod	Maximum CW (mm)
<i>Segonzacia mesatlantica</i> (Williams, 1988)	Stout straight, covered with short setae, not twisted, tip bilobed with two dense clumps of long setae.	Peduncle straight separated from flagella by notch around mid-way, flagella thinner, coiled. G2 exceeds length of G1.	Male: 39.0 x 22.0 mm Female: 35.0 x 21.0 mm
<i>Cyanograea praedator</i> de Saint Laurent, 1984	Stout slightly curved, not twisted, covered in short setae, tip pointed.	Peduncle nearly straight, notched around mid-way, flagella thinner, flattened and curved. G2 equal to or longer than G1.	Male: 81.2 x 45.8 mm Female: 123.0 x 74.8 mm
<i>Allograea tomentosa</i> Guinot, Hurtado & Vrijenhoek, 2002	Unknown	Unknown	Male: unknown Female: 25.0 x 16.0 mm
<i>Bythograea galapagensis</i> Guinot & Hurtado, 2003	Stout, strongly curved, twisted, many minute spinules on distal part (except the tip), dense row of long setae sub-distally, tip pointed.	Peduncle almost straight, notched mid-way, flagella straight. G2 much longer than G1.	Male: 52.3 x 29.6 mm Female: 44.6 x 24.8 mm
<i>Bythograea intermedia</i> de Saint Laurent, 1988	Unknown maybe the same as <i>B. thermydron</i> Williams, 1980.	Unknown maybe the same as <i>B. thermydron</i> Williams, 1980.	Based on early crab stages and megalopa. Recorded only once.
<i>Bythograea laubieri</i> Guinot & Segonzac, 1997	Stout, slightly curved apex, not twisted, distal third with field of short setae, lateral apical flap present, tip pointed.	Peduncle curved, notched mid-way, flagella thinner, sinuous. G2 longer than G1.	Male: 33.0 x 19.0 mm Female: 42.6 x 24.0 mm
<i>Bythograea microps</i> de Saint Laurent, 1984	Stout, strongly curved, weakly twisted, tip pointed.	Peduncle curved notched mid-way, flagella thinner sinuous. G2 longer than G1.	Male: 31.0 x 24.0 mm Female: 7.0 x 4.8 mm
<i>Bythograea thermydron</i> Williams, 1980	Stout, strongly curved, markedly twisted, apex covered in short setae, tip rounded.	Peduncle almost straight, notched mid-way, flagella thinner, curved. G2 much longer than G1.	Male: 73.0 x 39.5 mm Female: 64.0 x 33.0 mm.
<i>Bythograea vrijenhoeki</i> Guinot & Hurtado, 2003	Stout, curved, not twisted, without setae, tip pointed.	Peduncle curved, notched mid-way, flagella thinner, sinuous. G2 longer than G1.	Male: 42.4 x 24.2 mm Female: 42.3 x 24.1 mm
<i>Austinograea alayseae</i> Guinot, 1990	Slender, curved, numerous, prominent acute spines along most of length except near apex, slightly twisted, tip flattened, blunt.	Peduncle curved, notched at distal 2/3 length, flagella thinner, short flattened. G2 about half G1.	Male: 55.0 x 35.0 mm Female: 63.0 x 38.0 mm

TABLE 2. (continued)

Species	First Male Gonopod	Second Male Gonopod	Maximum CW (mm)
<i>Austinograea rodriguezensis</i> Tsuchida & Hashimoto, 2002	Slender, almost straight, 4 small stout spines in sub-terminal dorsal row, slightly twisted, tip pointed.	Peduncle curved, notched at distal 2/3 length, flagella thinner, flattened. G2 half length of G1	Male: 14.1 x 9.1 mm Female: 24.2 x 15.4 mm
<i>Austinograea williamsi</i> Hessler & Martin, 1989	Slender slightly curved and twisted, short spines distributed along proximal 80%, tip pointed. .	Peduncle curved, notched at distal 2/3 length, flagella thinner, flattened. G2 less than half length of G1.	Male: 39.0 x 24.5 mm Female: 41.0 x 25.8 mm
<i>Gandalfus yunohana</i> (Takeda, Hashimoto & Ohta, 2000)	Slender curved, not twisted, 8 small spines along middle region, tip pointed.	Peduncle short, notched at 1/3 rd of length, curved, flagella thinner, flattened, curved, G2 ~ G1.	Male: 41.9x 26.9 mm Female: 50.5 x 32.5 mm
<i>Gandalfus puia</i> sp. nov.	Slender curved, not twisted, approx. 15 small spines along whole length, tip pointed.	Peduncle about 1/2 of length, curved, notched mid-way, flagella thinner, curved, flattened towards tip. G2 ~ G1.	Male: 36.7 x 22.6 mm Female: 41.1 x 26.2 mm

The genus *Austinograea*, however, shows remarkable variation in G2 length: in *A. alayseae*, *A. rodriguezensis* the G2 is about half the length of the G1 while in *A. williamsi* it is less than half the length of G1. In *A. yunohana*, the G1 and G2 are about equal. Takeda *et al.* (2000) pointed out that this feature of *A. yunohana* did not fit the generic definition given by Hessler & Martin (1989). Therefore, to accommodate their new species, Takeda *et al.* (2000) modified the generic definition of *Austinograea* from “second male pleopod distinctly shorter than the first” to “male second pleopod as long as or longer than half the length of the first”. Like *A. yunohana* the present new species from New Zealand also has a G2 that is as long as the G1. However, now that we have another species it seems preferable to group these two species in a new genus. This change returns *Austinograea* to its original definition, wherein the G2 is distinctly shorter than the G1, and restricted to *A. williamsi* Hessler & Martin, 1989 (type species), *A. rodriguezensis* Tsuchida & Hashimoto, 2002 and *A. alayseae* Guinot, 1990.

This rearrangement of bythograeid species (see Table 1) establishes a consistent pattern in the G1 vs G2 character: in *Segonzacia*, *Cyanagraea*, and *Bythograea* the G2 is longer than or equal to the length of G1, while in *Austinograea* the G2 is only about half the length of G1, and in the closely related *Gandalfus* the G2 is approximately equal to the G1. A plausible hypothesis would be that the G2 > G1 is the ancestral condition for bythograeids. Evidence that *Austinograea* and *Gandalfus* are the most derived genera is also supported by regression of their eyes so that these species lack functional eyes and are effectively blind. A parallel trend seems to be a tendency towards reduction in body size (see Table 2).

***Gandalfus puia* sp. nov.**

(Figs. 1A–F, 2A–G, 3A–B, 4A–B, 5A–D)

Type material. *Holotype*: male, 24.3 x 15.5 mm, Rumble III, 35°44.22–44.04'S, 178°29.72–29.63'E, 270–239 m, stn TAN0107/128, 21.05.2001, NZOI Z10782 (NIWA 27855); *Paratypes*: 1 female 41.1 x 26.2 mm, Brothers Seamount, 34°51.56'W, 179°03.53'E, 1604 m, JAMSTEC, stn Z15262, 26.10.2004 (NIWA 27407); 1 female, 36.5 x 22.1 mm, Brothers Seamount, 34°51.70'S, 179°3.58'E, 1647 m, stn KOK0506/32,

02.05.2005 (NIWA 18019); 1 male, 33.4 x 21.9 mm, Macauley Caldera, Kermadec Islands, 30°12.78'S, 181°33.04'E, 337 m, 12.04.2005 (NIWA 18017).

Other material. 1 male, 36.7 x 22.6 mm (damaged), 1 male, 18.0 x 11.6 mm, Macauley Caldera, Kermadec Islands, 30°12.78'S, 181°33.04'E, 337 m, stn KOK0505/22, 12.04.2005 (NIWA 18018).

Etymology. The specific name "*puia*" is the Maori word for volcano or geothermal spring, in reference to the fact that the type locality is on top of an underwater volcano near the Kermadec Islands, New Zealand; used as a noun in apposition.

Description. Carapace 1.53–1.65 times wider than long (length/width = 0.61–0.64), elliptical in outline, surface flat, coarsely granular especially on anterior half, convex along anterior-posterior axis, more steeply sloped in front than behind. Regions not well defined; cardiac-gastric regions marked by shallow U-shaped groove. Dorsal frontal margin almost straight, 0.19CW; small median lobe slightly prominent, adorned with 3 small granules; lateral margin granulate, concave, forming supra-orbital notch before merging with frontal region of carapace. Shallow median groove extending posteriorly from frontal margin. Anterolateral margins curved, convex, bearing granules that continue onto sub-branchial surface. Posterolateral margins convergent, posterior carapace margin sinuous, adorned by granular ridge. Sub-hepatic region without setae, Epimeral line well marked.

Front not projecting from anterior margin; orbits not visible dorsally; sub-orbital areas only slightly visible. Orbital region smooth, elongate, 0.4CW; interantennular septum incomplete, left-right division marked by small dorsal and ventral keels; posterior wall formed by immovable eyestalk, cornea vestigial, unpigmented, without facets and mostly concealed by lateral wall of orbit and overlying third article of antenna; floor of orbit formed by basal articles of antennule and antenna and lobe from carapace edge. All articles of antennule mobile; first (urinal) article of antenna fixed, second article with limited mobility, third and fourth articles mobile. Antennules and antennae folded horizontally; antennule filling most of orbit, almost meeting antennal peduncle; antenna filling supraorbital notch. Mesial antennular flagellum shorter than lateral flagellum. Antennal flagellum 0.8 length of dorsal frontal margin.

Epistome dorsal surface marked by ridge at lower border of orbit, almost vanishing at midline, edge not projecting, marked by row of granules, gently sinuous about midline; pterygostomial areas of mouth-field granulate.

Third maxilliped endopod ischia not touching when closed, 1.6 times longer than wide, strongly marked groove running alongside medial border; merus about as long as wide, half as long as ischium, medial border sinuous to accommodate palp which is inserted at tip of merus; carpus and propodus slightly longer than merus; dactyl slightly longer than ischium, inner margins of propodus and dactyl bearing a dense fringe of setae. Exopod longer than endopod ischium, terminating in small medial exterior lobe and hidden cristate lobe beside insertion of palp. On ventral surface, proximal surfaces of pereopods densely setose, especially in female, extending onto sternal surface. Margins of female abdomen densely fringed with setae.

Chelipeds distinctly longer than walking legs; merus triangular in cross section, corners granulate granules larger on anterior border. Chelipeds dimorphic, right (crusher) stouter than left (cutter); fingers excavated, gaping on right (touching only at tips), occluding on left; both fingers armed with several proximal teeth of variable size including one larger tooth at midlength of fixed fingers. Both left and right dactyli close behind tip of fixed finger. Ratio of propodus depth/length always greater on right (0.43–0.50) than on left (0.41–0.44) cheliped. Ratio of male cheliped propodus length/carapace width greater in male (0.92) than similar sized female (0.65).

Walking legs (P2-P5) shorter than chelipeds; second pair longest; carpi, propodi and dactyli fringed with long setae with a felt of short stiff setae on dorsal and ventral margins. Dactyli stout, terminating in sharp claw.

Abdomen of six free segments, third segment widest (0.3CW in male; 0.4CW in mature female); locking mechanism in male consisting of tubercle on sternite 5, near confluence of sutures 4/5 and 5/6, fitting into pit on posterolateral corners of last abdominal segment. Mature female without abdominal locking mechanism.

Male telson 1.4 x as wide as long, female 1.67, posterior border rounded. Sternal sutures from 4/5 to 7/8 not meeting in mid-line.

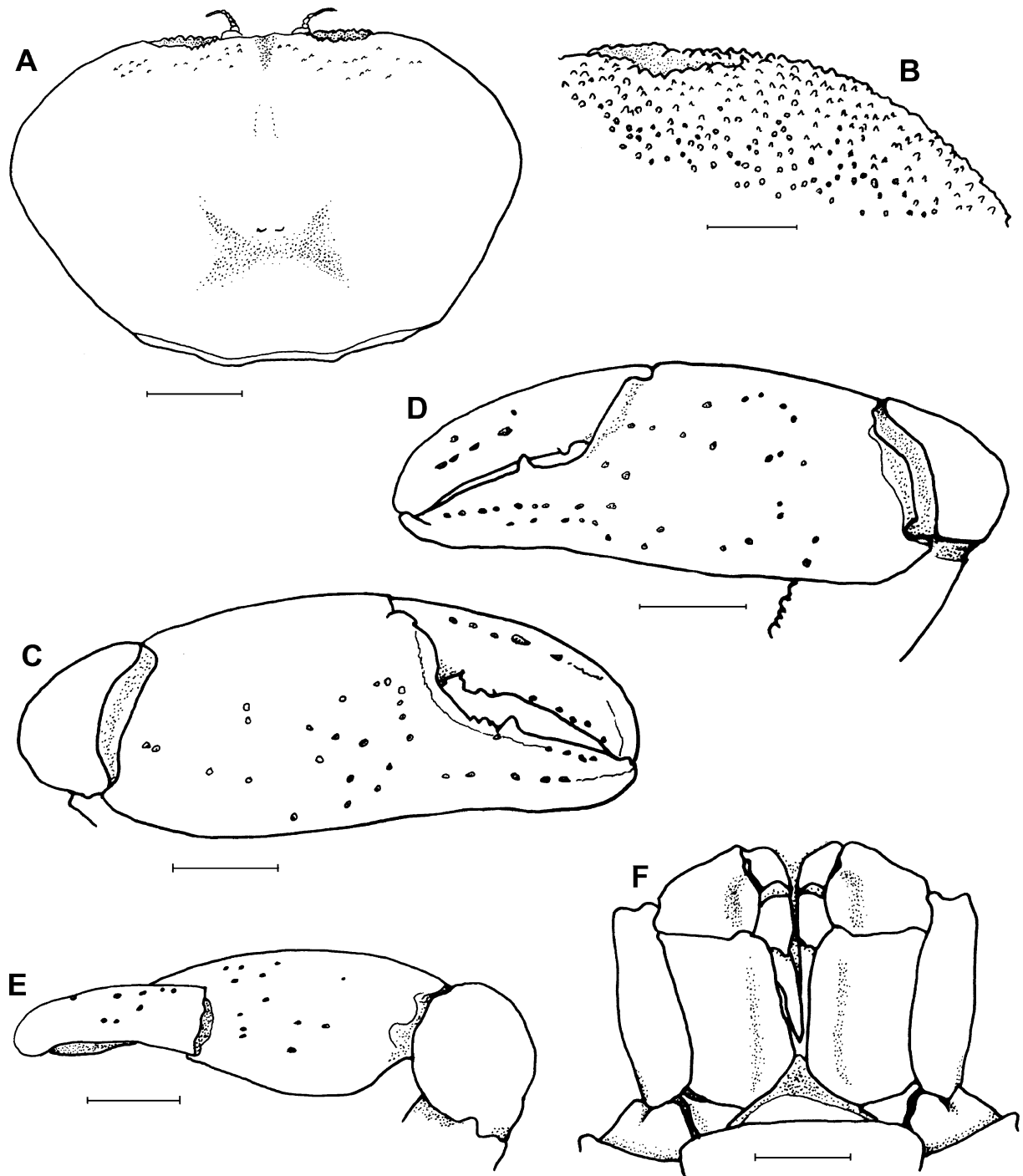


FIGURE 1. *Gandalfus puia* sp. nov., holotype male, 24.3 x 15.5 mm, Rumble III (NZOI stn Z10782). A, Dorsal view carapace (scale bar = 4 mm). B, magnified right anterolateral margin (scale bar = 2 mm). C, outer face right cheliped (scale bar = 4 mm). D, outer face left cheliped (scale bar = 4 mm). E, dorsal view right cheliped (scale bar = 4 mm). F, third maxillipeds (scale bar = 2 mm).

First male gonopod slender, stout, curved; with approximately 15 small spines and reaching anterior edge of abdominal cavity. Second male gonopod as long as first with notch at midlength and 15–20 small, marginal spines; tip flattened. Female gonopore slit-like 0.4 x 0.3 mm (female CW = 36.5 mm), oriented along anterior-posterior body axis, not operculate.

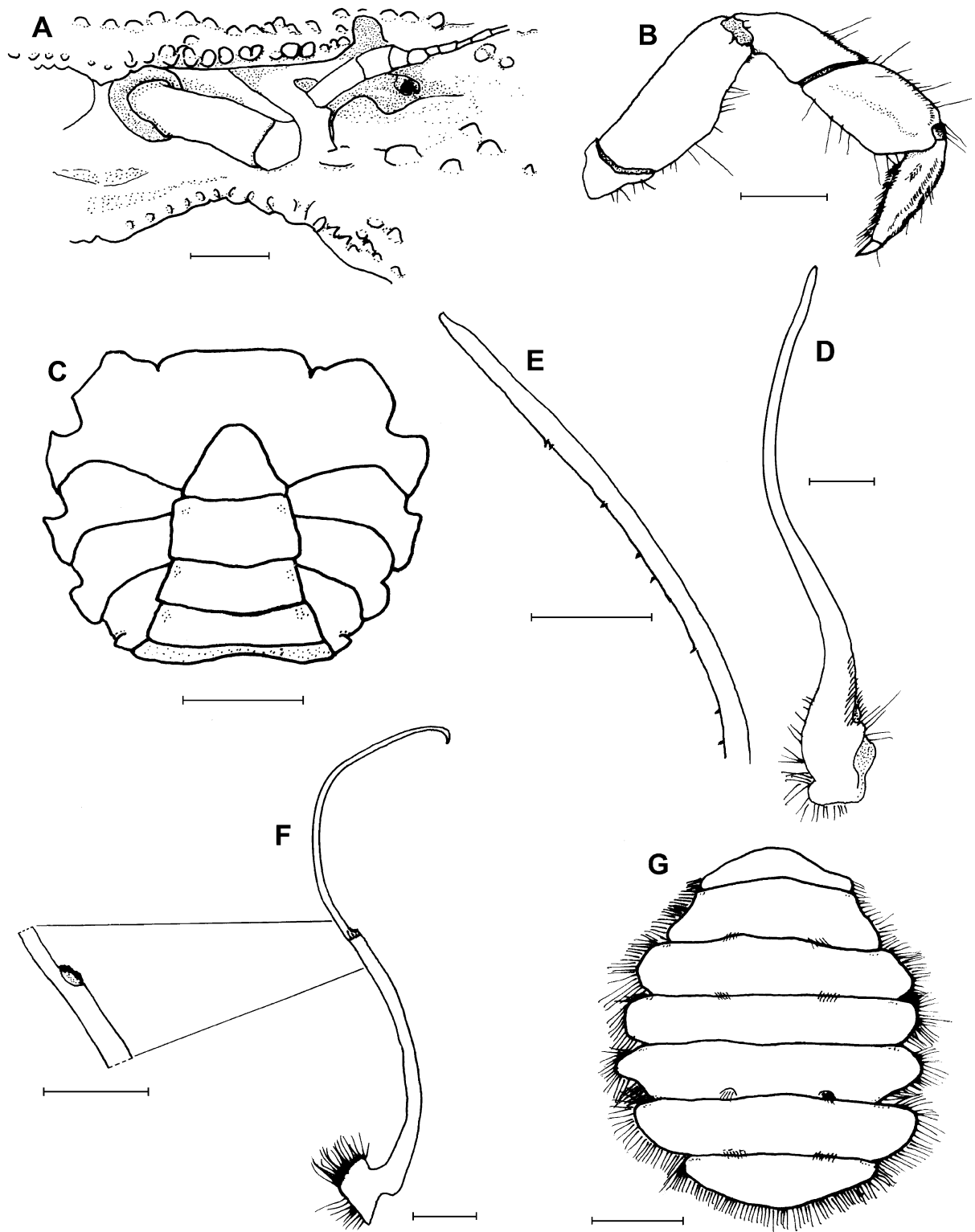


FIGURE 2. *Gandalfus puia* sp. nov., A–F: holotype male, 24.3 x 15.5 mm, Rumble III (NZOI stn Z10782). G, female, 36.5 x 22.1 mm Brothers Seamount (KOKO0506/32). A, frontal view left orbit (scale bar = 1 mm). B, posterior view right P5 (scale bar = 4 mm). C, male abdomen (scale bar = 4 mm). D, right G1 (scale bar = 1 mm). E, magnified distal part of right G1 (scale bar = 1 mm). F, right G2 with middle region magnified (both scale bars = 1 mm). G, female abdomen (scale bar = 5 mm).

Colour. The male, 18.0 x 11.6 mm, is either recently moulted or lived at some distance from the vent: it is pale yellow/cream ground colour, fingers pale brown, setae on legs a darker brown. Other specimens are

coated with a brown ferric precipitate. These colours were observed on the specimens examined and in photos taken at the time of collection.

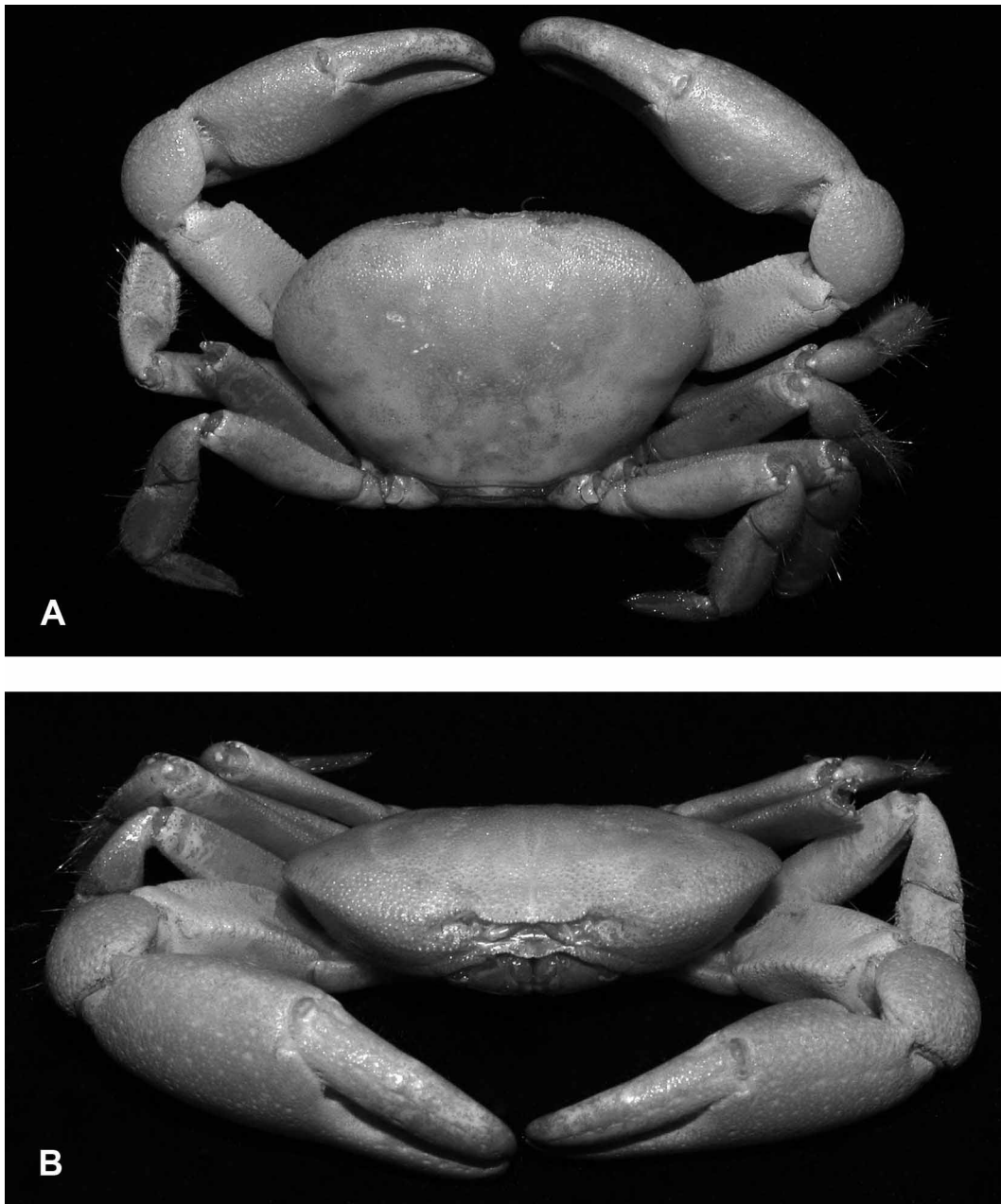


FIGURE 3. *Gandalfus puia* sp. nov., holotype male, 24.3 x 15.5 mm, Rumble III (NZOI stn Z10782). A, dorsal view. B, frontal view.

Discussion

Six specimens, four males and two female of *G. puia* have been collected from three sites between 30°12'S–35°44'S and 181°33'E–178°29'E. Male size ranges from 24.3 x 15.5 to 36.7 x 22.6 (est.) mm and female size ranges from 36.5 x 22.1 to 41.1 x 26.2 mm. Both sexes probably reach a similar size, as is typical for other species in the family (see Table 2). The females collected in October 2004 and in May 2005 both carried empty egg cases, indicating recent release of the larvae. As in other bythograeids the female gonopore is not operculate. Bythograeid crabs span a large size range with *Cyanograea praedator* being by far the largest at

123.0 x 74.8 mm. In *Austinograea*, *A. alayseae* reaches 63.0 x 38.0 mm while in the new genus *Gandalfus*, *G. yunohana* reaches 50.5 x 32.5 mm. Heterochely was evident in all *G. puia* specimens examined, with the right cheliped being a crusher and the left a cutter. In the only other bythograeid studied in detail, *Austinograea williamsi*, only males exhibited heterochely, although 40 % had two cutters (Tsuchida & Fujikura 2000). All females (except for one large female) had two cutters. With only six *G. puia* specimens available, it is unclear whether the two species are different with respect to heterochely. However, *Bythograea vrijenhoeki* seem to show both heterochely and heterodonty (Guinot & Hurtado 2003).

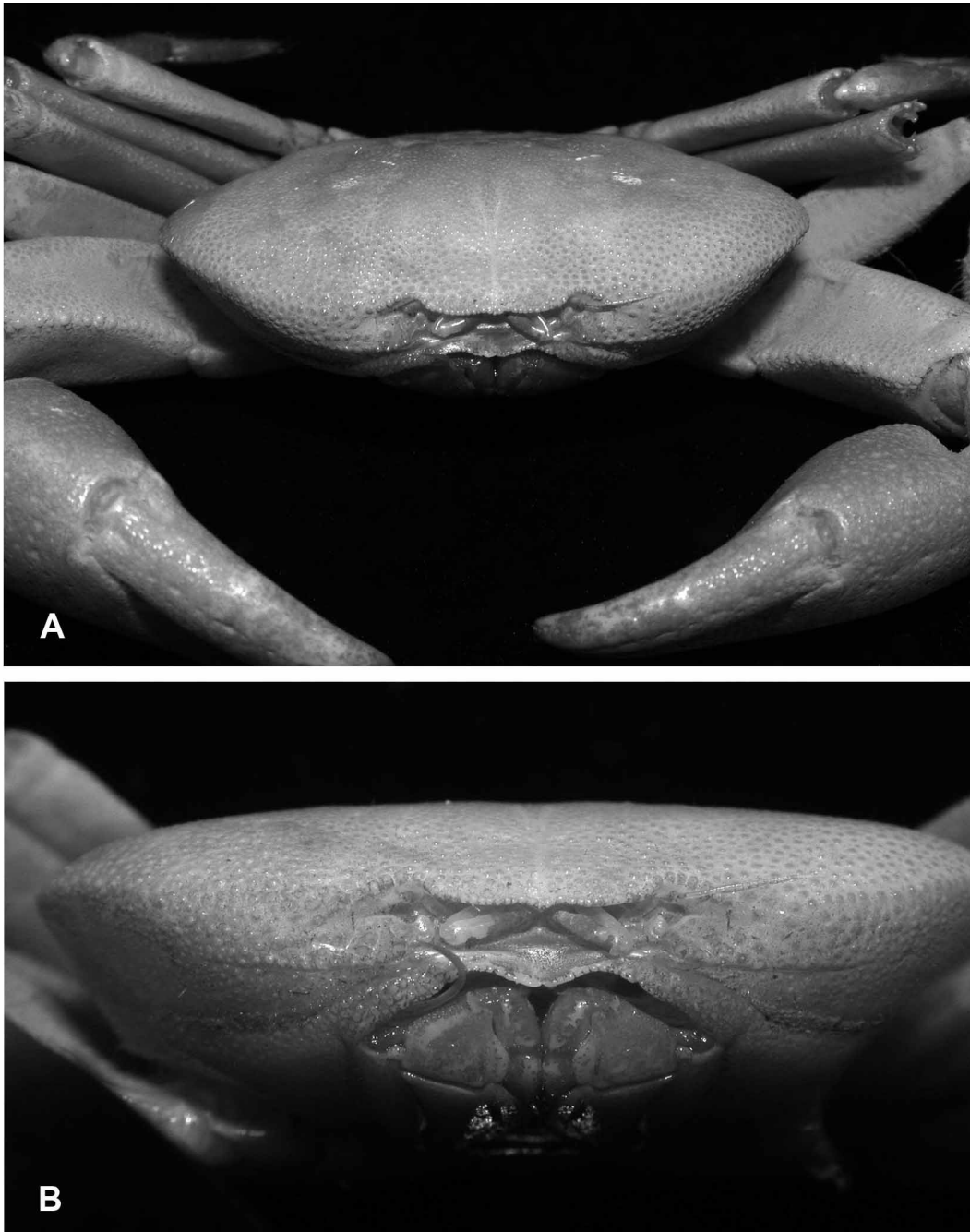


FIGURE 4. *Gandalfus puia* **sp. nov.**, holotype male, 24.3 x 15.5 mm, Rumble III (NZOI stn Z10782). A, oblique frontal view. B, orbital region.

Several *G. puia* were a rusty-red colour, coated with what is probably an iron precipitate (see Discussion under *Xenograpsus*) suggesting that they lived close to the vent and/or had not moulted recently. All bythograeids are obligate members of vent faunas and adapted to life in a toxic environment at high tempera-

tures. Tsuchida *et al.* (1998) kept several *G. yunohana* captive for up to six years at 15°C during which they moulted and grew. Molt increments ranged from 12.4% for males and 9.3% for females with intermolt intervals from 360 to 1350 days. This bythograeid crab is evidently slow growing and long lived, but *in situ* growth rates may well be higher.

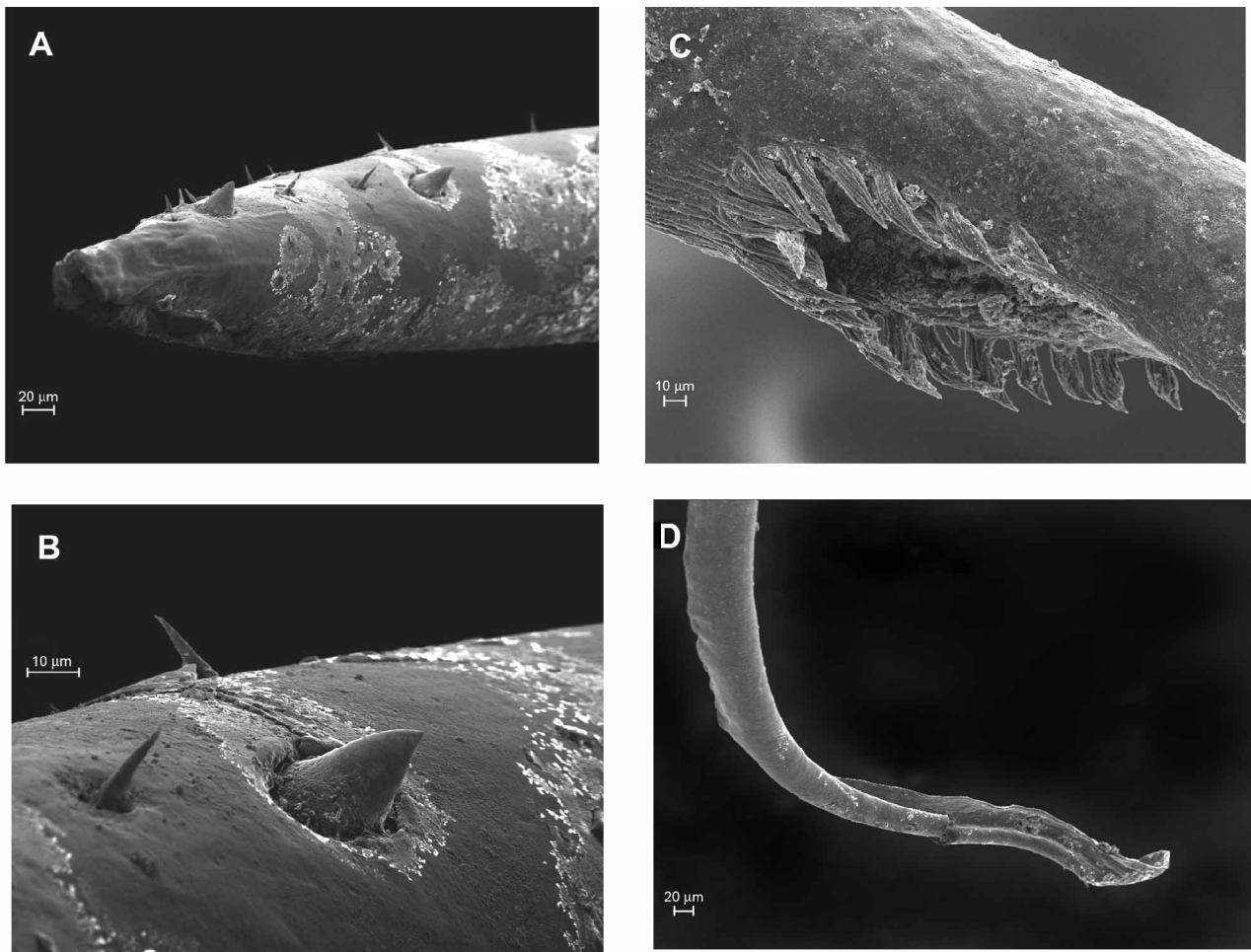


FIGURE 5. *Gandalfus puia* sp. nov., male 36.7 x 22.6 mm, Macauley Caldera. A, first gonopod tip. B, spines on surface of first gonopod. C, second gonopod notch. D, second gonopod tip.

Bythograeid crabs are typically found at great depths, from more than 1000 to 3660 m, but *G. puia* has been recorded from depths of 239 m to 1647 m. It is by far the shallowest bythograeid recorded. The other species, *G. yunohana*, also lives at comparatively shallow depths, 420–1380 m.

Bythograeids are well known in the East Pacific, both north and south of the equator (southernmost species *Allograea tomentosa* at 31°09'S), but until now the only reports from the Indo-West Pacific have been 4 species of *Austinograea*: *A. rodriguezensis* from the Indian Ocean (at 25°19.2'S), *A. williamsi* from the Mariana Basin (at 18°12.8'N), *A. yunohana* south of Japan (at 32°06.19'N) and *A. alayseae* southwest of Tonga (at 22°13'S). The new species *G. puia* was collected from the Kermadec Ridge (southern-most site 35°44'S) thereby considerably extending the range of the family to the south. Transferring *A. yunohana* from *Austinograea* to *Gandalfus* means that the new genus is represented in both the northern and southern hemispheres. The record from near New Zealand is the southernmost for a bythograeid crab, exceeding that of *Allograea tomentosa*.

Regression of eyes in relation to depth in bythograeids (Table 2)

In the new species, *G. puia*, the eyestalk is fixed, the cornea is vestigial, unpigmented, without facets, and mostly obscured from view by the orbital walls. In effect it forms the rear wall of the orbit. Similarly in *G. yunohana* the eyestalk is also fixed and cornea unpigmented. Eyes in crabs that are covered with a coating of red oxide cannot be functional because the cornea (such as it is) is concealed.

Bythograeids show ontogenetic optical regression: for example in *Bythograea thermydron* the eyes of the megalopa (settled on mussels or tube worms) are large, exceeding the size of the orbit, the cornea is faceted and clearly functional. This remains true for early crab stages as well, but in later stages the eyes do not fill the entire orbit, the eyestalk is short and cornea reduced, though mobile. The adult condition is achieved, at most, over 5 or 6 post-megalopa moults (Williams 1980). During development, relative growth of the eye is clearly negative. This evidence supports the view that bythograeid ancestors had well-developed eyes. Loss of pigmented corneas in adults seems to be an adaptation for life around vents (Guinot & Hurtado 2003), but larval stages presumably still need well-developed eyes for dispersal and location of settlement sites (Epifanio *et al.* 1999).

Most of the better known bythograeids appear to have broad depth ranges (Table 3): the sole Atlantic species, *Segonzacia mesatlantica*, has the greatest depth range 2628 m and for *Austinograea williamsi* the depth range is 1450–3660 m (range 2210 m). Although not known to be common, the two species of *Gandalfus* have depth ranges of 420–1380 m (range 960 m) for *G. yunohana* and 239–1647 m (range 1207 m) for *G. puia*. *Austinograea alayseae* has been collected within 1750–2630 m (range 880 m). The remaining species have much narrower ranges, less than 500 m: *Cyanograea praedator* 2535–2630 m (range 105 m), *Bythograea laubieri* 2334–2832 m (range 498 m), *B. microps* 2450–2684 m (range 198 m), *B. vrijenhoeki* 2333–2338 m (range 5 m) and *A. rodriguezensis* 2420–2450 m (range 30 m) while *Allograea tomentosa* is only known from 2335 m, *B. galapagensis* from 2461 m, and *B. intermedia* from 2488 m. This may well be a reflection of the paucity of records, but in the case of *B. thermydron*, which has been frequently collected, all specimens came from 2430–2673 m (range 243 m). Ranking the bythograeid genera from deepest to shallowest, on the basis of mean depth, we have *Cyanograea*, *Bythograea*, *Austinograea*, *Allograea*, *Segonzacia*, and *Gandalfus*.

In deep-sea animals we expect that their eyes become less and less useful with increasing depth because of reduced or absent ambient light. Therefore, we might predict that with increasing depth, eye development and function would be decreased. In *Cyanograea* the eyes are restricted, the stalk is short, cornea reduced, orbits almost non-existent. In *Bythograea* the eyes are mobile, although the stalk is often reduced, with cornea reduced and unpigmented. In *Austinograea* the eyes are fixed, stalks reduced, and cornea vestigial or absent. In *Allograea* the eyes are mobile, filling entire orbit, cornea large but without facets. In *Segonzacia* the eyes are mobile, stalk short in adults, and cornea large although unpigmented in adults. Lastly, in *Gandalfus*, eyes are fixed, with the stalks embedded in orbital wall and cornea vestigial. While all bythograeids have eyes modified to some extent, the pattern of eye development with depth does not conform to the prediction: the genera with the most derived (most highly reduced) eyes, *Austinograea* and *Gandalfus*, are not the deepest living. In fact *Gandalfus* is the shallowest occurring genus, although we need to note that the species with the deepest record is *Austinograea williamsi*. Explanation of the eye condition in bythograeids is evidently more complex. Given that bythograeids are endemic to hydrothermal vents the eye versus depth prediction may not be relevant because the depth zone of each species/genus may be determined by the extent of submarine volcano building so that the crabs simply occupy whatever habitat is available regardless of depth. Reduction of optical abilities may well have been originally associated with deep-sea colonisation, but now the crabs disperse to colonise vent areas at other depths. On the Kermadec Ridge we have the situation of *G. puia*, without eyes, alongside a species of *Xenograpsus*, which has well-developed eyes. This may well be a reflection of the more recent colonisation of hydrothermal vents by *Xenograpsus*.

TABLE 3. Depth distribution and condition of eyes in bythograeid crabs. Depth data from Martin & Haney (2005) and other literature.

Species	Condition of Eyes	Distribution and Depth Range (m)
<i>Segonzacia mesatlantica</i> (Williams, 1988)	Eyes mobile, stalk normal in small crabs, short in adults. Corneal area large, unpigmented in adults, but without facets	Mid-Atlantic, 850–3478 m
<i>Cyanograea praedator</i> de Saint Laurent, 1984	Eyestalk movement restricted, short. Cornea pigmented but reduced and without facets. Orbits almost non-existent.	East Pacific Rise, 2535–2630 m
<i>Allograea tomentosa</i> Guinot, Hurtado & Vrijenhoek, 2002	Eyestalk mobile. Cornea large, without facets and unpigmented. Eye fills entire orbit.	Southern East Pacific Rise, 2335 m
<i>Bythograea galapagensis</i> Guinot & Hurtado, 2003	Eyestalk short, not filling entire orbit, mobile, narrow. Cornea in juveniles pigmented, fringed with soft setae, tip more fusiform in adult female	East Pacific Rise, Galapagos Rift, 2461 m
<i>Bythograea intermedia</i> de Saint Laurent, 1988	Could be the same as preceding species.	East Pacific Rise, 2488 m
<i>Bythograea laubieri</i> Guinot & Segonzac, 1997	Eyestalk short, not filling entire orbit, mobile. Cornea reduced, eyes recessed.	Southern East Pacific Rise, 2334–2832 m
<i>Bythograea microps</i> de Saint Laurent, 1984	Eyestalk short, not filling entire orbit, mobile. Cornea without facets and reduced, more so in adults	East Pacific Rise, 2450–2648 m
<i>Bythograea thermydron</i> Williams, 1980	Eyestalk short, not filling entire orbit, mobile. Cornea without facets, reduced, more so in adults.	East Pacific Rise, Galapagos Rift, 2430–2673 m
<i>Bythograea vrijenhoeki</i> Guinot & Hurtado, 2003	Eyestalks short, not filling entire orbit, mobile. Cornea unpigmented or with small dark remnant, fringed with soft setae.	Southern East Pacific Rise, 2333–2338 m
<i>Austinograea alayseae</i> Guinot, 1990	Eyestalk reduced, fixed. Cornea vestigial, without facets and pigment.	Lau back-arc Basin, West of Tonga, and Manus back arc Basin, 1750–2630 m
<i>Austinograea rodriguezensis</i> Tsuchida & Hashimoto, 2002	Eyestalk reduced, fixed. Cornea absent.	Indian Ocean, 2420–2454 m
<i>Austinograea williamsi</i> Hessler & Martin, 1989	Eyestalk reduced, fixed. Cornea absent.	Mariana back arc Basin, 1450–3660 m
<i>Gandalfus yunohana</i> (Takeda, Hashimoto & Ohta, 2000)	Eyestalk reduced, fixed. Cornea unpigmented, not obscured from frontal view by orbital walls.	Philippine Plate off Japan, 420/450–1380 m
<i>Gandalfus puia</i> sp. nov.	Eyestalk reduced, fixed. Cornea vestigial, unpigmented, without facets and mostly obscured from view by orbital walls.	Kermadec Ridge, 239/270–1647 m

What is the most likely evolutionary history of bythograeid crabs? Clearly the ancestor must have been a crab with well-developed eyes, and with G1 armed with setae and G2 as long as or longer than G1. Guinot (1990) has shown that possession of similar sized G1 and G2 is the primitive state for the Brachyura. A possible sister group hypothesis of the modern genera is *Allograea* + (*Segonzacia* + (*Cyanagraea* + (*Bythograea* + (*Gandalfus* + *Austinograea*))))). According to this view, the very short G2 would be an apomorphy of *Austinograea*, with all other bythograeids retaining the ancestral state. Great reduction of the eyes and the eyestalk forming part of the orbit would be an apomorphy of *Gandalfus* + *Austinograea*. Note that *Segonzacia* only occurs in the Atlantic Ocean, so perhaps it should be set aside so as not to obscure the relationships between the Indo-Pacific genera. This would in effect require the assumption that *Segonzacia* shared a common ancestor with *Allograea*, which then gave rise to the Indo-Pacific genera. Guinot *et al.* (2002) consider that *Allograea* is the least modified species and perhaps closest to the ancestor. It is more similar to *Cyanagraea* than to *Bythograea*. Unfortunately no male *Allograea* have been collected. Mitochondrial sequence data seem to confirm the hypothesis that *Allograea* is closest to the ancestor and suggest that *Cyanagraea* is its closest relative (Guinot *et al.* 2002). Similarly, monophyletic status of the genus *Bythograea* with *Cyanagraea* as out-group is confirmed (Guinot & Hurtado 2003). Comparison of antennal and orbital characters suggest that the Bythograeidae and Goneplacinae, another deep-sea group, may be sister taxa (Guinot *et al.* 2002). The only known zoeal stage attributable to the Bythograeidae was collected from the Galapagos Rift and is so bizarre that it resembles no other brachyuran zoea (Van Dover *et al.* 1984). When a full set of molecular data is available for all the bythograeids it can be analysed with respect to possible ancestral groups to construct a better hypothesis about their evolutionary origins

Key to the bythograeidae

(Modified after Guinot & Segonzac 1997; Hessler & Martin 1989; Tsuchida & Hashimoto 2002)

1. Eyes, antennules and antennae not deeply recessed. Orbits well circumscribed (complete). Frontal border of carapace in dorsal view nearly straight 2
 - Eyes, antennules and antennae deeply recessed under front. Orbits open and not well circumscribed (incomplete). Frontal border of carapace rounded in dorsal view 3
2. Cornea present but unpigmented and without facets. Orbits ovate. Body covered by uniformly short tomentum, carapace flat and smooth. Widest point of carapace at about one third of carapace length *Allograea tomentosa* Guinot, Hurtado & Vrijenhoek, 2002.
 - Cornea well-developed, pigmented but without facets. Orbits rounded. Carapace vaulted and with colour-tipped tubercles on fronto-lateral region; tomentum confined to patches. Widest point of carapace just posterior to frontal border *Cyanagraea praedator* de Saint Laurent, 1984
3. Eyes mobile, peduncle well developed. Coxa of third maxilliped not obscured in ventral view, lateral extension visible, not hidden by ventral pterygostomial margin of carapace, sternum and cheliped coxa. 4
 - Eyes immobile, peduncle vestigial and embedded in orbit wall. Coxa of third maxilliped partially obscured in ventral view, lateral extension hidden by juxtaposition of ventral margin of carapace in pterygostomial region with anterolateral sternal border and cheliped coxa 9
4. Shallow concavity ventrolateral to orbit, filled with soft setae *Segonzacia mesatlantica* (Williams, 1988).
 - Area ventrolateral to orbit finely punctate, without cavity or dense patch of setae 5
5. Ocular peduncles dilated at their extremity; corneal region clearly visible. P2–5 thin, lengthened, with propodi clearly longer than wide especially P4 6
 - Ocular peduncles slender and almost cylindrical for their entire length except for marked dilation of the cornea, which is deeply seated. P2–5 short and thick, with propodi only slightly longer than wide 7
6. Tuft of plumose setae on internal face of cheliped propodus in female and occasionally in male. Thicker

- eyestalks and broad cornea in both sexes. Corneal region hoof-shaped. G1 Stout, strongly curved, markedly twisted, apex covered in short setae, tip rounded, glabrous. P5 merus length 3 times width in male...
..... *Bythograea thermydron* Williams, 1980
- No tufts of setae on cheliped. Thinner eyestalks, with fusiform cornea. G1 stout, strongly curved, twisted, many minute spinules on distal part (except the tip), dense row of long setae sub-distally, tip acute. P5 merus length 2.5 times width..... *Bythograea galapagensis* Guinot & Hurtado, 2003
7. Setae on internal face of cheliped propodus not arranged in a tuft. Chelipeds of female not dimorphic, propodus narrow, granulose and setose on both faces with the exception of a swollen smooth non-setose area near the inferior border. Chelipeds of male dimorphic in size and ornamentation: propodus of crusher cheliped stout, smooth and non-setose; cutter cheliped the same as in female. G1 strongly curved, weakly twisted..... *Bythograea microps* de Saint Laurent, 1984
- Setae on internal face of cheliped propodus arranged in a tuft. Chelipeds dimorphic in both sexes, weakly granulose. G1 slightly curved, not twisted. 8
8. Pale brown areas on chelae. Carapace granules white tipped. G1 without setae; without lateral apical flap. Suborbital plate smooth. Walking legs longer thinner; P5 merus length 2.9 times width in male; P5 propodus length 2.3 times width in male..... *Bythograea vrijenhoeki* Guinot & Hurtado, 2003.
- Pale violet areas on chelae. Carapace granules red or brown tipped. G1 distal third with field of short setae, lateral apical flap present. Suborbital plate granular. Walking legs shorter and thicker; P5 merus 2.2 times width in male. P5 propodus length 1.3 times width in male.....
..... *Bythograea laubieri* Guinot & Segonzac, 1997
9. Epistome strongly sinuous in frontal view. Male G2 distinctly shorter than G1 10
- Epistome gently sinuous in frontal view. Male G2 approximately as long as G1 12
10. Dense patch of setae covering subhepatic region of carapace. Chelae with inner occluding margins of dactylus and mid-central section of propodus with dense patch of setae. Eyestalks deeply buried in orbital wall, scarcely visible. G1 with few spines..... 11
- No patch of setae covering subhepatic region of carapace or chelae. Eyestalks fused to orbital wall, just visible, with unpigmented cornea. G1 with dense long spines scattered continuously along its length
..... *Austinograea alayseae* Guinot, 1990
11. G1 with approximately four small spines arranged in a row on dorsal surface. Cutter cheliped fingers deeply dished, with occluding margins almost straight; teeth on fingers of similar size
..... *Austinograea rodriguezensis* Tsuchida & Hashimoto, 2002
- G1 with many spines arranged in double or triple rows. Cutter cheliped deeply dished, with occluding margins slightly curved; several larger teeth especially on fixed finger
..... *Austinograea williamsi* Hessler & Martin, 1989
12. Carapace finely granular. Cornea of eye visible in frontal view. Peduncle of G2 about one third of overall length *Gandalfus yunohana* (Takeda, Hashimoto & Ohta, 2000
- Carapace coarsely granular. Cornea of eye almost totally obscured in frontal view by orbital wall. Peduncle of G2 about one half of overall length *Gandalfus puia* sp. nov.

Varunidae H. Milne Edwards, 1853

Xenograpsus Takeda & Kurata, 1977

Xenograpsus ngatama sp. nov.

(Figs. 6A–F, 7A–E, 8A–B, 9A–B)

Type material. *Holotype*: male, 16.0 x 15.6 mm, Macauley Caldera, 30°2.06'S, 181°17.36'E, 161 m, stn KOK0505/43, 15.04.2005 (NIWA 18013). *Paratypes*: 1 male, 19.7 x 19.0 mm, Macauley Caldera, 30°2.16'S,

181°17.63'E, 109 m, stn KOK0505/45, 16.04.2005 (NIWA 18022); 1 female, 12.8 x 11.7 mm, Macauley Caldera, 30°2.01'S, 181°17.37'E, 156 m, stn KOK0505/49, 17.04.2005 (NIWA 18021).

Other material. 5 males, 11.0 x 10.5, 11.4 x 11.0, 13.0 x 12.1, 14.0 x 13.5, 15.2 x 14.4 mm, Macauley Caldera, 30°2.01'S, 181°17.37'E, 156 m, stn KOK0505/49, 17.04.2005 (NIWA 18020); 1 male, 27.1 x 25.8 mm, 1 male, missing carapace 44.1 x 42.0 (estimated), 1 female damaged, 34.8 x 33.1 mm, Brothers Seamount, 35°44.22–44.04'S, 178°29.72–29.63'E, 270–239 m, 21.05.2001 (NIWA); 2 males 16.8 x 15.3, 17.8 x 16.5 mm, Northwest of Kermadec Ridge, 25°53.4153.61'S, 177°11.10–11.07'E, 139–236 m, stn TAN0411/10, 04.10.2004 (NIWA 18014).

Etymology. The specific name “*ngatama*” is the Maori word for “brother”, in reference to the fact that the new species occurs on a local oceanic feature, the Brothers Seamount. For pronunciation, the “g” is silent but the combination “nga” gives the name a long “aa” sound at the beginning.

Description. Carapace quadrate, wider than long, surface strongly convex, punctate with some areas of coarse granules. Cervical and gastro-cardiac grooves well marked. Epigastric cristae weakly defined, other epigastric and protogastric granules of variable size tending to be arranged in oblique lines; row of granules behind cervical groove and short diagonal granulated ridge near posterolateral corner of carapace. Frontal margin convex on each side of central notch, minutely granulated. Orbital margin granulate, deeply concave, exposing most of orbit to dorsal view; tuberculate swelling above inner orbital angle. External orbital angle continuing as finely granulate anterolateral margin to a small tooth at widest point. Lateral margins parallel until corner where it angles across base of P5 to straight posterior margin. Branchial area with finely granulated oblique striae near posterolateral corner.

Front 0.34CW; interantennular septum complete. Orbit divided in half by angled keel that meets antenna. Antennules folding horizontally; first article filling most of antennal fossa; second and third articles elongate, of similar length; mesial and lateral flagella of similar length. Antenna of five articles plus flagellum; first two articles fixed against strong suborbital projection; distal margin of second article with projecting granulate rim; third to fifth articles mobile, decreasing in size followed by flagellum; length of flagellum and mobile part length 0.1CW.

Eyestalk short, thick, cornea well developed occupying whole of ventro-distal area. Sub-orbital margin begins at postorbital corner, granulate, concave to deep incision terminating in strong suborbital projection, visible dorsally, whose edge is also granulate. Shelf-like granulate ridge beneath suborbital margin, beginning under suborbital projection and extending for short distance beyond postorbital corner beneath anterolateral carapace margin.

Endostome concave; granulated dorsal margin scalloped to form ventral floor of antennal fossa; narrow suture marking attachment to epistome; granulated posterior margin of epistome concave, divided in two by median keel. Epimeral line well-marked; strong granulated shelf at anterior corner of buccal frame. Third maxillipeds closing without median gap, but not reaching epistome anteriorly; ischium smooth, longer than wide ratio 1.35, merus concave cristate granulate especially along distal margin, slightly wider than long, covering end of exopod laterally; palp inserted near disto-lateral corner of merus carpus running across most of distal margin of merus, palp just reaching ischiomerus joint.

Chelipeds well developed, left and right similar size. Anterior margin of basis-ischium cristate. Merus triangular in cross section; borders granulate; outer and upper surface of carpus granulate; propodus granulate, upper borders marked by row of granules; some granules on outer face of propodus arranged in 3 or 4 rows which can extend on to the fixed finger; granules on upper surface of dactyl arranged as 3 rows converging distally. Fingers curved inward and downward, hollowed out mesially, gaping mid-way but meeting at tips; proximal two-thirds with 8 or 9 granular teeth; distal third margins scissor-like. Tips of fingers horny and covered in dense brush of fine setae.

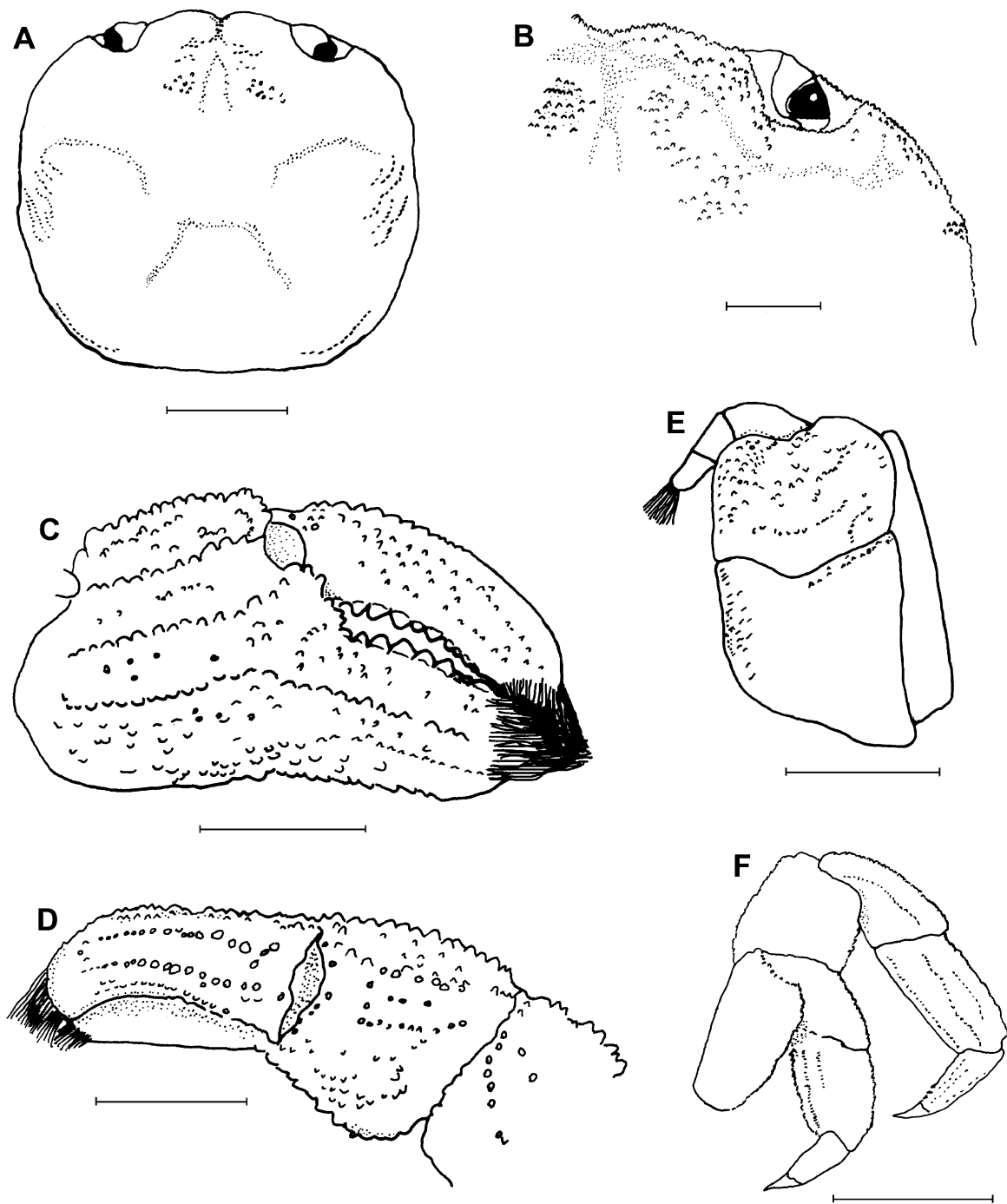


FIGURE 6. *Xenograpsus ngatama* sp. nov., holotype male, 16.0 x 15.6 mm, Macauley Caldera (NIWA 18013). A, dorsal view whole carapace (scale bar = 5 mm). B, magnified right anterolateral margin (scale bar = 2 mm). C, outer face right cheliped (scale bar = 2 mm). D, dorsal view right cheliped (scale bar = 2 mm). E, left third maxilliped (scale bar = 2 mm). F, posterior view right P4 and P5 (scale bar = 5 mm);

Walking legs (P2-P5) stout, depressed, margins granulate, without setae; third pair longest. Meri widening distally, surface marked by transverse striae of minute granules; P5 merus length 2.3 times width; carpi, propodi and dactyli with longitudinal rows of larger granules, especially on upper and lower margins. Dactyli short, ending in stout horny claw.

Male abdomen surface smooth, narrow, length 1.3 times width; segments narrowing and becoming longer posteriorly; telson length 1.5 times width, tip narrow, rounded. Abdominal locking mechanism of sternal tubercle on sternite 5 fitting into pit on posterolateral corners of last abdominal segment functional in holotype

male, but not functional in smaller male (CW = 17.3 mm) (in this animal the sternal tubercles are present but do not engage with the last abdominal segment). Abdominal cavity extending across two-thirds of cheliped sternite, but abdomen not extending as far. Proximal margin of abdominal cavity raised as finely granulated ridge. Sternal surface minutely punctate, smooth, sutures 4/5 to 7/8 not meeting in midline.

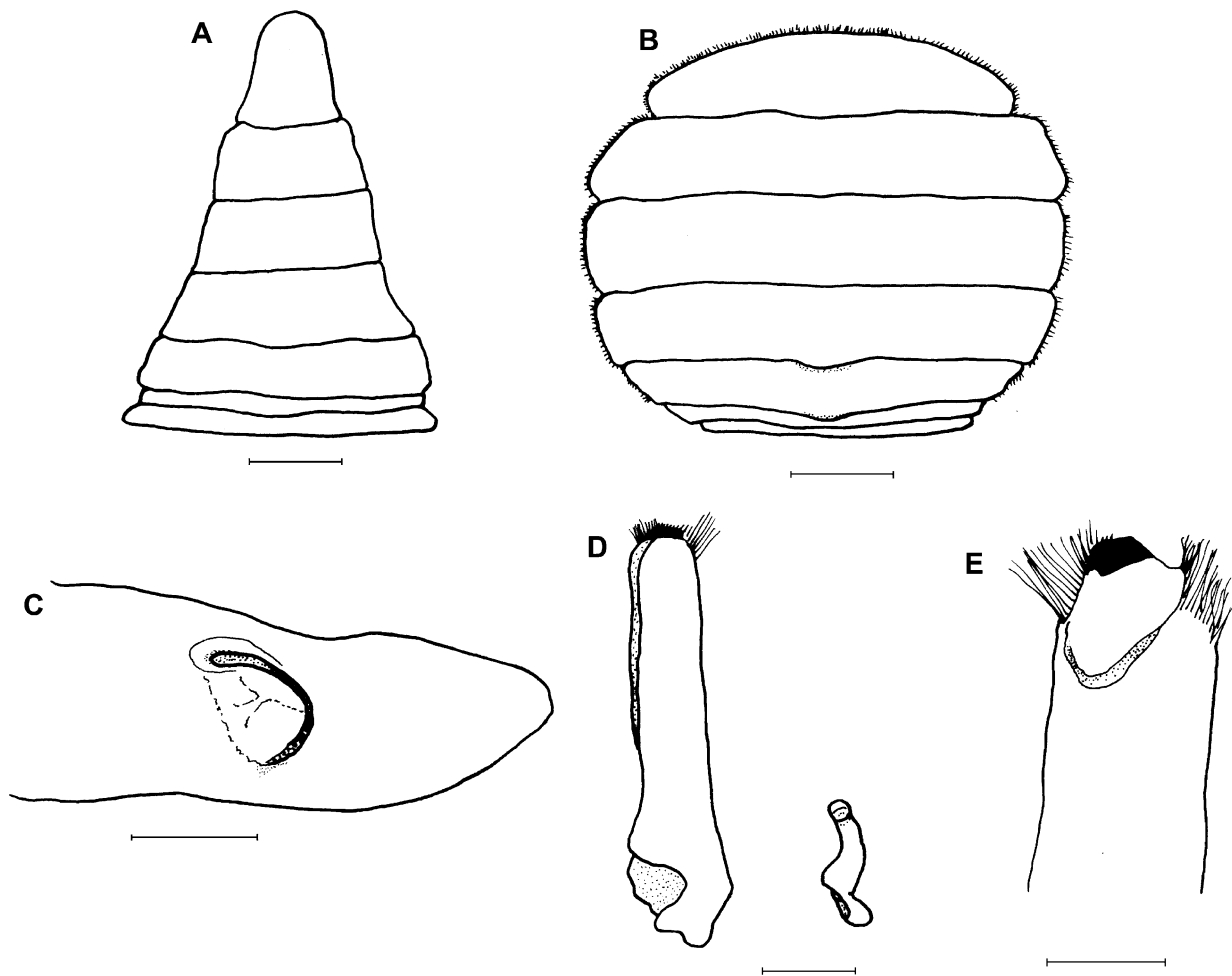


FIGURE 7. *Xenograpsus ngatama* sp nov. A, holotype male, 16.0 x 15.6 mm, Macauley Caldera (NIWA 18013). B–C, female, 34.8 x 33.1 mm Brothers Seamount (NZOI stn Z10782). D–E, male, 44.1 x 42.0 mm, Brothers Seamount (NZOI stn Z10782). A, male abdomen (scale bar = 2 mm). B, female abdomen (scale bar = 4 mm). C, left gonopore female (scale bar = 1 mm). D, G1 and G2 (scale bar = 2 mm), E, tip of G1 from opposite side (scale bar = 1 mm).

Mature female abdomen covering entire sternal surface; length 0.87 times width; segments becoming longer posteriorly; fifth segment widest, margins fringed with soft setae. Telson length 0.3 times width, tip evenly rounded. Gonopore large, standing out from sternal surface entrance closed by calcified operculum, hinge line not flexible in paratype female. Three well-developed pairs of biramous pleopods.

Male first gonopod stout, almost straight, not twisted, length 5.3 times width; aperture terminal, tip horny concealed by soft setae. Second gonopod curved, much shorter than first (ratio 0.3), length 4.2 times width, tip soft and blunt.

Colour. Pale green-grey ground colour with brown bands on pereopods and brown patches on the carapace. These colours were observed on specimens examined and in photos taken at the time of collection.

Discussion. The three species of *Xenograpsus* are quite distinct from each other. *Xenograpsus novaeinsularis* from Japan and Marianas has well developed epigastric cristae, one prominent protogastric tubercle, anterolateral tooth present, oblique granulate crista absent on carapace above base of P5 and cervical groove prominent. *Xenograpsus testudinatus* Ng, Huang & Ho, 2000 from Taiwan has the epigastric cristae well

developed, one prominent protogastric tubercle, anterolateral tooth absent, oblique granulate crista present on carapace above base of P5 and cervical groove not prominent; while *X. ngatama* from New Zealand has epigastric tubercles not arranged in cristae, many large protogastric tubercles, anterolateral tooth present, oblique granulate crista present on carapace above base of P5 and a prominent cervical groove.

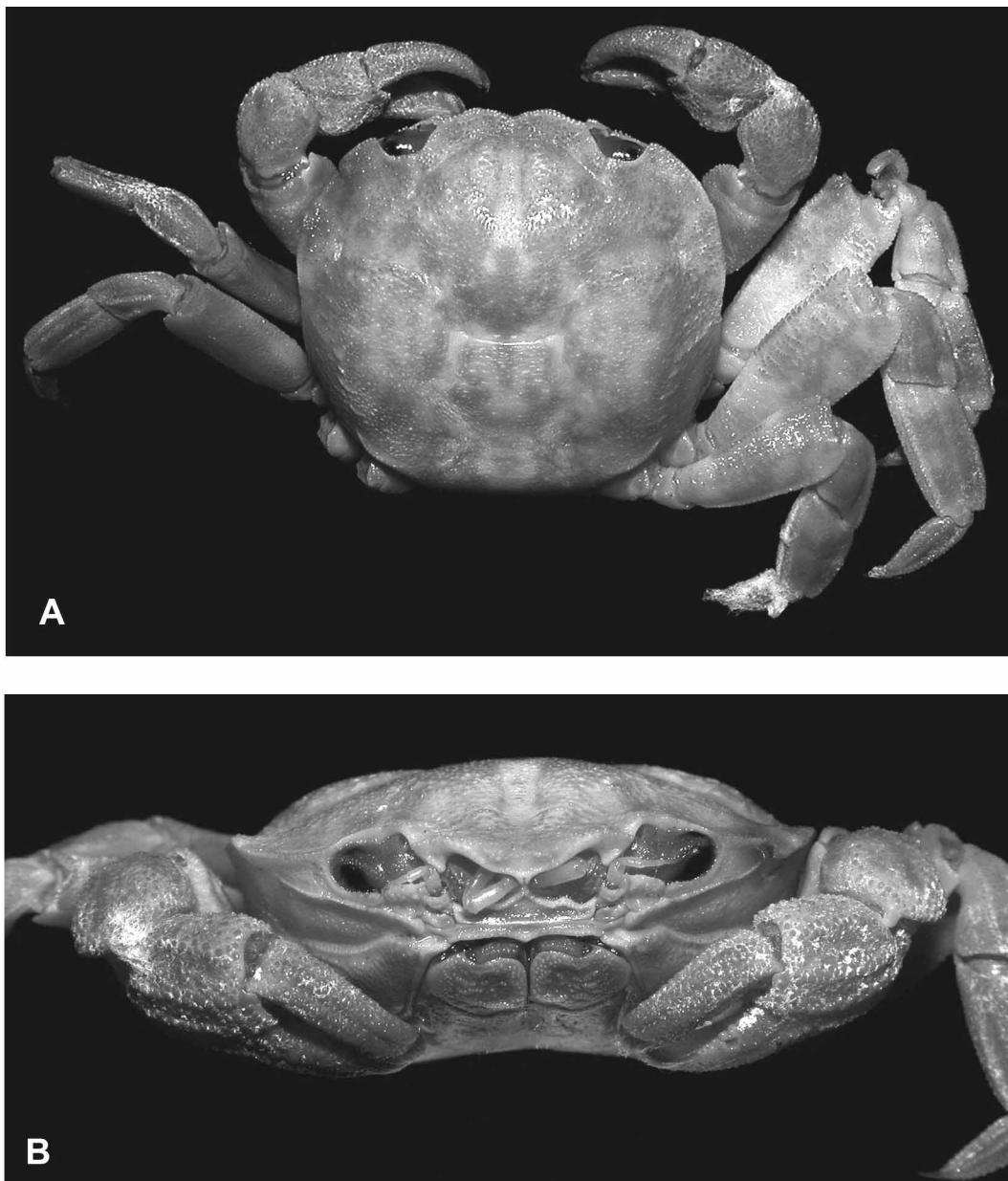


FIGURE 8. *Xenograpsus ngatama* sp nov., holotype male 16.0 x 15.6 mm, Macauley Caldera (NIWA 18013). A, dorsal view. B, frontal view.

Xenograpsus ngatama has been recorded from five sites on the Kermadec Ridge between 25°53'S–35°44'S and 181°17'E–177°11'E. The maximum size for males is 44.1 x 42.0 mm and for females 34.8 x 33.1 mm. The depth range is 109–270 m. Videos taken at the time of sampling showed *X. ngatama* crawling over and around the mussels, *Gigantidas gladius* (Ashley Rowden, pers. com.). Some of the specimens were completely covered with a rusty brown coating. A spectral EDAX analysis in an SEM showed that this coating is mostly composed of iron oxides. Evidently this crab can live very close to actively venting areas, but others, lacking this coating, live further away. *Xenograpsus novaeinsularis* can live at temperatures around 30°C, much higher than the surrounding water (Takeda, Takeuchi & Suganuma 1993; Türkay & Sakai 1995). Jeng *et al.* (2004) described the peculiar method of feeding by *X. testudinatus* whereby they swarm near vents, con-

suming the zooplankton “rain” killed by toxic effluent, catching their prey using their setose chelipeds. These crabs are evidently obligate vent dwellers capable of living in this inimical environment. In contrast to bythograeids these crabs still have fully developed eyes, presumably because they are more recent colonists. Unique larval characters of *X. testudinatus* suggest that the genus *Xenograpsus* will probably need to be placed in a separate family or subfamily (Jeng, Clark & Ng 2004).

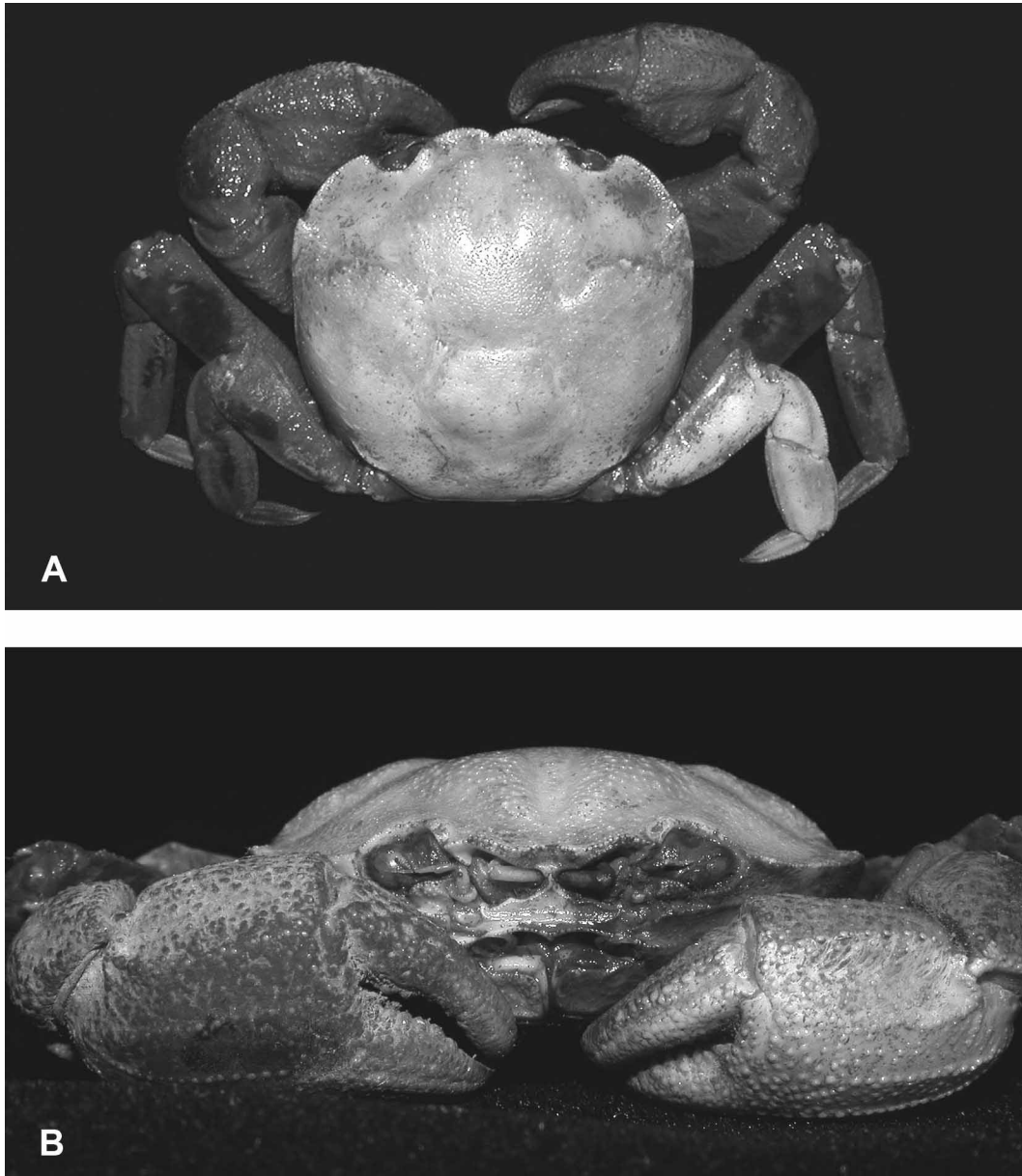


FIGURE 9. *Xenograpsus ngatama* **sp nov.**, male, 27.1 x 25.8 mm, Brothers Seamount (NZOI Z10782). A, dorsal view. B, frontal view.

Key to species of *Xenograpsus*

- 1. Epigastric tubercles not arranged in cristae; many large protogastric tubercles..... *X. ngatama* **sp. nov.**
- Epigastric cristae well developed; single prominent protogastric tubercle 2
- 2. Single anterolateral tooth; cervical groove well marked *X. novaeinsularis* Takeda & Kurata, 1977 (Japan)
- No anterolateral teeth; cervical groove not well marked.....
.....*X. testudinatus* Ng, Huang & Ho, 2000 (Taiwan)

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