



Cave-dwelling crabs of the genus *Karstarma* from lava tubes of the volcano ‘Piton de la Fournaise’, in Réunion Island, with description of a new species and redescription of *Karstarma jacksoni* (Balss, 1934) from Christmas Island (Decapoda, Brachyura, Sesarmidae)

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Abstract

Sesarmid crabs of the genus *Karstarma* Davie & Ng, 2007 are reported for the first time in the Western Indian Ocean: they were discovered in the lava tubes of the volcano ‘Piton de la Fournaise’, Réunion Island. A new species, morphologically similar to *Karstarma jacksoni* (Balss, 1934) from Christmas Island, Eastern Indian Ocean, is recognized and described. A redescription of *K. jacksoni* is also provided. A second species is recognized, but being represented in the collection by a single juvenile, it cannot be identified to species level until more collections are made in the lava tubes. [Zoobank: <http://zoobank.org/NomenclaturalActs/C70A95B2-D667-491D-BD35-5DF32E3FFB08>]

Key words: Crustacea, Grapsoidea, Indian Ocean, endemic species, cave-dwelling species, taxonomy

Introduction

On 15 November 2014, one of the authors (N.C.) discovered an unusual crab in a lava tube, named ‘Brûlé des Citrons Galets’, situated near the south-eastern coast line of Réunion Island, in the Western Indian Ocean (WIO). The specimen was photographed but not captured (ACSP 2014; Robert 2014). It had a distinctively long third ambulatory leg (P4), a character unknown for any of the land crabs previously reported from Réunion Island (Poupin 2009). This crab was provisionally identified as *Sesarmoides ?longipes* (Krauss, 1843), a species with similarly long P4, common in WIO but living in a different habitat, being found in mangroves and not caves (Emmerson 2016). This first observation and a request for additional reports and/or captures have resulted in several reports of the crab between 2014–2018, in four distinct lava tubes (‘Brûlé des Citrons Galets’, ‘Coulée de 2004’, ‘Grotte au Trésor’, and ‘Grotte des Hirondelles’).

On 19 February 2016 a juvenile specimen was obtained by chance after a school trip to the lava tube, ‘Brûlé des Citrons Galets’, supervised by the teacher A. Barrère. The crab, having apparently hitchhiked in the backpack of A. Barrère, was retrieved the next day, drowned in his home swimming pool. Although there is some doubt on exact place of collection for this specimen, it was similar to the specimen photographed in 2014. During the school visit to the lava tube, similar crabs were actually seen by the students (A. Barrère, pers. comm.).

Nicole Crestey, travelling to Bali on 12 October 2017, had the opportunity to visit the ‘Giri Putri’ cave, type locality of the endemic, *Karstarma balicum* (Ng 2002). She was struck by the resemblance between this crab and the one that she had photographed in the lava tube of ‘Brûlé des Citrons Galets’ and became convinced that the latter belonged to *Karstarma*. To identify the specimen captured on 19 February 2016, it was sent to the first author for study. Its examination plus a review of the literature on the cave-dwelling crabs confirmed that it was not a *Sesarmoides* because the typical stridulating apparatus of these species, described in Davie & Ng (2007), was absent. Instead, the crab belonged to *Karstarma* Davie & Ng, 2007, a genus with 15 species until now.

Three more crabs were finally caught by two of us (N. Crestey, J.-P. Le Guelte) in the lava tube of ‘Brûlé des Citrons Galets’, two adult females on 16 November 2017 and one male on 16 March 2018. These three specimens proved to be related to *Karstarma jacksoni* (Balss, 1934), the only other species of the genus already reported in the Indian Ocean, being endemic to Christmas Island. A set of specimens of *Karstarma jacksoni* from Christmas Island was loaned from the Western Australian Museum, Perth (WAM) for comparison between Réunion and Christmas Island crabs. The three adult specimens from Réunion Island differed from *K. jacksoni* by a series of subtle morphological differences. These differences, added to the great distance between Réunion and Christmas Island, ~5500 km apart, seemed sufficient to consider that the *Karstarma* from Réunion Island belonged to a new species. This new species is described herein accompanied by a redescription of *Karstarma jacksoni* (Balss, 1934), poorly illustrated in previous taxonomic contributions.

Careful re-examination of the first crab, a juvenile, captured in 2016 demonstrated it was not conspecific with the three adult specimens captured in 2017 and 2018. It may belong to another *Karstarma* species, unidentifiable to species level until adult specimens are collected. A diagnosis is provided, however, for this juvenile treated as *Karstarma* sp., and its relationships in *Karstarma* discussed.

Material and methods

The specimens collected have been preserved in 75% alcohol and deposited in the Muséum national d’Histoire naturelle (MNHN), Paris. The terminology follows previous contributions on *Karstarma* species (Ng 1988, 2002; Davie & Ng 2007; Wowor & Ng 2009; Husana *et al.* 2010). Terminology for female vulvae is from Guinot *et al.* (2013). The terms ‘pleon’ and ‘somite’ have been used instead of ‘abdomen’ and ‘segment’ following Davie *et al.* (2015). The measurements have been made using a digital calliper to the ± 0.1 mm. Size of specimens is expressed as carapace length (CL) by carapace width (CW). Measurements of ambulatory legs 1–4, corresponding to pereopods P2–P5, have been measured in a straight line along the upper margin of each article, total length of each ambulatory leg being calculated as the sum of lengths for merus, carpus, propodus and dactyl (excluding the coxa). Other abbreviations used are: ACSP, Association Citoyenne de Saint Pierre, Ile de la Réunion; h, height, Is., Island; juv., juvenile; l, length, MNHN, Muséum national d’Histoire naturelle, Paris; Myr, million year; ov., ovigerous; pers. comm., personal communication; St, sternite; WAM, Western Australian Museum, Perth.

Systematic account

Family Sesarmidae Dana, 1851

Genus *Karstarma* Davie & Ng, 2007

Karstarma vulcan sp. nov.

(Figs. 1A–E, 2A–M, 3A–F, 6, 9A, B, 10A–C, G)

Sesarmoides ?longipes—ACSP 2014: webpage (Réunion, colour photograph).—Robert 2014: 1, 17 (same color photograph as ACSP). Not *Sesarmoides longipes* (Krauss, 1843).

Material examined. Holotype: male 16.2 \times 18.9 mm (MNHN-IU-2013-7243), lava tube ‘Brûlé des Citrons Galets’, Le Tremblet, Saint Philippe, Réunion Island, coll. N. Crestey and J.-P. Le Guelte, 16 March 2018. Paratypes (same data as holotype): 1 female 13.7 \times 16.9 mm (MNHN-IU-2013-7240), 1 female 13.1 \times 16.5 mm (MNHN-IU-2013-7241), coll. N. Crestey and J.-P. Le Guelte, 16 November 2017.

Additional observations. *In situ* photographs (no specimens collected) from lava tubes: ‘Grotte au Trésor’, photograph Christopher Lauret, 3 March 2016; ‘Coulée de 2004’, photograph F. Leveneur, 30 August 2014 and Julien Dez, 14 February 2018; ‘Grotte des Hirondelles’, photograph François Martel-Asselin, 2 May 2010.

Type locality. Lava tube ‘Brûlé des Citrons Galets’, Le Tremblet, Saint Philippe, Réunion Island.

Diagnosis. Carapace (Fig. 1A–C) approximately trapezoidal, maximum width across base of second and third ambulatory legs, width 1.2 times length; dorsal surface gently convex, slightly uneven, minutely pitted, not setose

with only scattered short setae more abundant on posterolateral regions, regions poorly marked except for epigastric and urogastric grooves, posterolateral regions with a few faint oblique striae. Lateral margins of carapace sub-parallel, diverging weakly posteriorly. Anterolateral margin with 2 main teeth including external orbital angle (Fig. 9A, B); first tooth (external orbital angle) blunt, directed inwards at angle of $\sim 40^\circ$; second tooth with blunt tip separated from former tooth by shallow cleft; third tooth poorly marked, separated from second tooth by minute notch, or absent, tip of second tooth placed closer to tip of first tooth than third.



FIGURE 1. *Karstarma vulcan* sp. nov., holotype, male, 16.2 × 18.9 mm (MNHN-IU-2013-7243). A) dorsal habitus; B–D) carapace and chelae, dorsal, ventral, frontal views respectively; E) buccal cavern, third maxilliped and pterygostomian area (scale bars 10 mm).

Front (Fig. 1D) deflected at almost 90° , 0.4 times fronto-orbital width (measured between tip of anterolateral teeth), 2.2–2.4 wider than high, frontal margin minutely granulated, slightly sinuous with a large median V-shaped notch, postfrontal cristae composed of two large protuberances placed transversely between base of ocular peduncles on each side of epigastric groove. Supraorbital margin widely U-shaped, eyes well developed, cornea pigmented as wide as ocular peduncle; infraorbital margin composed of strong ridge with transverse granulation ventrally and line of short curved setae dorsally. Epistome obtusely triangular on upper side, lower side with 1 median, 2 lateral triangular projections. Branchiostegite (Fig. 1D, E) covered with reticulate uniform network of

short setae. Third maxilliped ischium (Fig. 1E) slightly longer than merus, median groove with row of setae, merus with oblique crest adjacent to inner margin, exopod with flagellum as long as width of merus.

Chelipeds of male (Figs. 1A–D, 2A, B, E) symmetrical; merus triangular in cross-section, all margins denticulated, inner face (Fig. 2E) with longitudinal row of pubescence, inner ventral margin with about 10 denticles on proximal $\frac{3}{4}$ and a denticulated flange on distal $\frac{1}{4}$, outer face with transverse striae furnished with short setae; carpus rounded, unarmed, dorsal face with short setiferous striae; chela much higher than in female, 2 times as long as high, inner and outer faces of palm inflated, coarsely granulated, larger granules of inner face disposed on a salient transverse ridge that rubs against the infraorbital margin ('stridulating' mechanism; see remarks under *K. jacksoni*), upper and lower margins rounded, unarmed, cutting edges of fingers not gaping when fingers closed, with 8–12 large sub-triangular teeth of unequal sizes all along margin; tip of fingers corneous, hoof-like; movable finger 1.2 as long as palm, dorsal margin with granules. Chelipeds of female symmetrical; inner ventral margin of merus minutely denticulated, without distal flange (Fig. 2F); chela (Fig. 2 C, D) much elongated than in male, 2.8–3.0 as long as high, inner and outer face of palm moderately inflated sparsely pitted, upper and lower margins rounded, unarmed, cutting edges of fingers not gaping when fingers closed, with minute sub-equal triangular teeth on proximal $\frac{3}{4}$, unarmed on distal $\frac{1}{4}$, tip of fingers corneous, hoof-like, incurved, movable finger 1.4 as long as palm.

Ambulatory legs 1–4 (P2–P5) (Fig. 2G–M) long, third leg longest 3.1–3.4 and 2.6–2.8 as long as CL and CW, respectively, tufts of setae present between coxae of ambulatory legs 1, 2 and 2, 3 (Fig. 1C); outer faces of meri with short striae (reduced in females), with median rounded carina in distal half separating dorsal and ventral sulci (more pronounced in leg 3), upper and lower margins carinated, unarmed, length to width ratios of meri of legs 2, 3, 3.8–4.1, 3.9–4.6, respectively; carpi 0.4–0.6 meri length, unarmed, outer faces with 2 longitudinal carinae, lower one finely granulated; propodi 0.6–0.7 meri length, unarmed, furnished with longitudinal rows of long stiff setae on upper and lower margins and on inner/outer faces (1 or 2 rows on each face), outer faces flat and smooth, mat of setae (Fig. 1 K, L) present on distal lower margin of legs 1, 2 in males only; dactyli sub-cylindrical, unarmed, as long or slightly longer (1.1) than propodi, gently curved in distal third, with similar longitudinal rows of setae than on propodi, terminating in corneous claws.

Male pleon (Fig. 1C), sub-triangular, telson rounded at tip, as high as wide; 6th somite the highest, trapezoidal, anterior margin sinuous lateral margins convex; somites 3–5 elongated, somite 5 3.5 as long as high, somites 1–3 the longest, somite 3 not reaching base of P5 coxae. G1 (Fig. 10A, C), stout, distal part directed outward at an angle of about 90°, terminating in chitinous tip. G2 (Fig. 10B) approximately half as long as G1, barely curved, with U-shaped corneous extremity.

Female pleon rounded, about 1.5–1.6 as wide as long, lateral margins markedly convex, maximum width between somites 4, 5, telson sub-triangular, rounded at tip, somite 6 the highest, somites 4, 5 largest of similar height. Vulva (Fig. 10G) on sternite 6, with broad sternal rim covered with folded central operculum.

Size. From 13.0 × 16.5 mm to 16.2 × 18.9 mm.

Live coloration (Fig. 3A–F). Carapace and ambulatory legs brown or purple. Male chelipeds light brown to brown orange or yellow on chelae. Female chelipeds paler brown to white on chelae. Male pleon white with brown at junctions of somites, female pleon white. Overall live coloration similar to *K. boholano* (Ng, 2002) in colour in Ng (2002: fig. 17) and Fujita & Naruse (2016: fig. 1A–D), *K. jacksoni* in colour herein (Fig. 11) and Orchard (2012: 215–217), and *K. waigeo* Wowor & Ng, 2009 in colour in Wowor & Ng (2009: fig. 7C, D).

Habitat. All crabs were captured in the lava tube of 'Brûlé des Citrons Galets' (Fig. 4). This tunnel is discussed in Audra (2009) and Michon (2018). Its total length is about 700 m and it is perpendicular to the coast. Its lower part is 120 m from the shoreline at an altitude of about 50–60 m above sea level and its upper part is about 750 m far from the shoreline at an altitude of about 160–170 m above sea level. It has several openings allowing the crabs to enter or leave the tunnel easily. The crabs were all collected near the sea in the lower part of the tunnel (point 'A' on Fig. 4). During heavy rains, this section receives sediments and vegetal debris from the gutter of the road (N2 in red on Fig. 4) where the main entrance is situated. The crab apparently prefers the moist and muddy parts of the tunnels where it has been observed scraping the substrate for food.

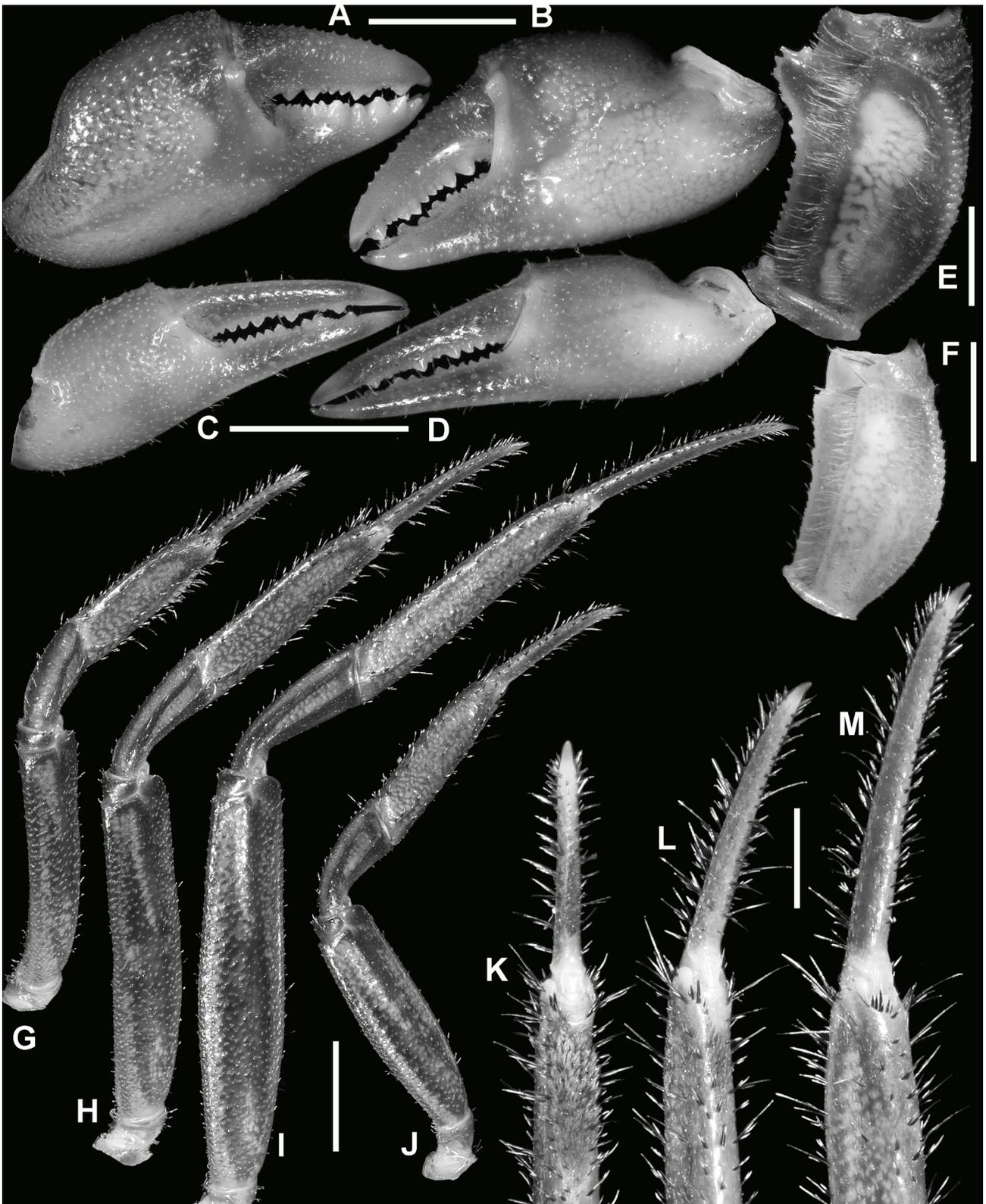


FIGURE 2. *Karstarma vulcan* sp. nov., holotype, male, 16.2 × 18.9 mm (MNHN-IU-2013-7243) (A, B, E, G, M); paratype, female, 13.7 × 16.9 mm (MNHN-IU-2013-7240) (C, D, F). Right chela, outer (A, C) and inner views (B, D); merus of right cheliped, inner view (E, F); right ambulatory legs 1–4 (P2–P5), outer views (G–J); distal part of propodi and dactyli of right ambulatory legs 1–3 (P2–P4), ventral views (K–M) (Scale bars: A, B, G–J, 5 mm; C–F, K–M, 2.5 mm).

Photographs of probably the same species have been obtained from three other tunnels, ‘Grotte au Trésor’, ‘Coulée de 2004’, and ‘Grotte des Hirondelles’, respectively points B, C, D (Fig. 4). The crab seems therefore

distributed only along the south-eastern coast of Réunion Island where are situated the lava tubes coming out near the coastline suggesting that it is perhaps closely associated to this kind of cave.



FIGURE 3. Live colour of *Karstarma vulcan* sp. nov. A, B, lava tube ‘Brûlé des Citrons Galets’ photographs J.-P. Le Guelte, 16/03/2018, holotype, male 16.2 × 18.9 mm (MNHN-IU-2013-7243) (specimen captured in the lava tube but brought outside the cave for photograph); C, D) lava tube ‘Brûlé des Citrons Galets’ photographs N. Crestey, 16/11/2017, C) female, 13.05 × 16.5 mm (MHNH-IU-2013-7241) (left cornea injured); D) top: ventral view, female, paratype 13.7 × 16.9 mm (MNHN-IU-2013-7240); bottom: dorsal view, female, paratype 13.05 × 16.5 mm (MHNH-IU-2013-7241). Live specimens, not collected, in the lava tube of ‘Coulée de 2004’: E) photograph J. Dez, 14/02/2018 from (Dez, 2018); and F) photograph F. Leveneur, 30/08/2014.

In Réunion Island more than 80 lava tubes or cavities, including about 15–20 near the coastline, are listed by Audra (1997) and Cailhol & Fulcrand (2011). A lot of them need official authorization to be visited, which is not the case for the lava tubes of ‘Brûlé des Citrons Galets’ and ‘Coulée de 2004’, which are open to the public, thus explaining why the crabs were first observed there. *Karstarma vulcan* sp. nov., however, is not often seen. It was not reported by Rochat *et al.* (2003) in their study on the arthropods of ‘Brûlé des Citrons Galets’, nor during several additional investigations conducted between 2003–2007 (J. Rochat, pers. comm. 16 November 2017). The only crab seen at that time, in the lower part of the tunnel, was *Geograpsus grayi* (H. Milne Edwards, 1853), common along the littoral of Réunion Island, apparently having fallen from one of the numerous manholes present

in that section. Lava tubes situated higher in the mountain at an altitude of >250–1000+ m above sea level have been also explored for cave-dwelling insects by Hoch *et al.* (2003) and Sendra *et al.* (2017), without mention of *K. vulcan*.

Distribution. Known only from Réunion Island. This is the first record of *Karstarma* in the WIO (Fig. 6). This is a cryptic species that has remained unnoticed in Réunion for a long time despite numerous studies of wildlife in the Island in the past. It is probably most active at night and is potentially present in all lava tubes allowing an easy access to the shoreline where the crab is likely to lay its eggs. In WIO it is perhaps also present in the Islands of Madagascar, Mauritius and/or Rodrigues in similar cave biotopes. In Rodrigues Island (~ 820 km east to Réunion Island), for example, karstic caves are known in the wildlife park, ‘François Leguat Giant Tortoise and Cave Reserve’ where more investigations for *Karstarma* crabs would be interesting.

Etymology. This new species is named after ‘Vulcan’ (used as an appositive noun) the ancient Roman god of fire, including fire of volcanoes, in allusion to the crab’s being discovered in the lava tubes of the volcano ‘Piton de la Fournaise’.

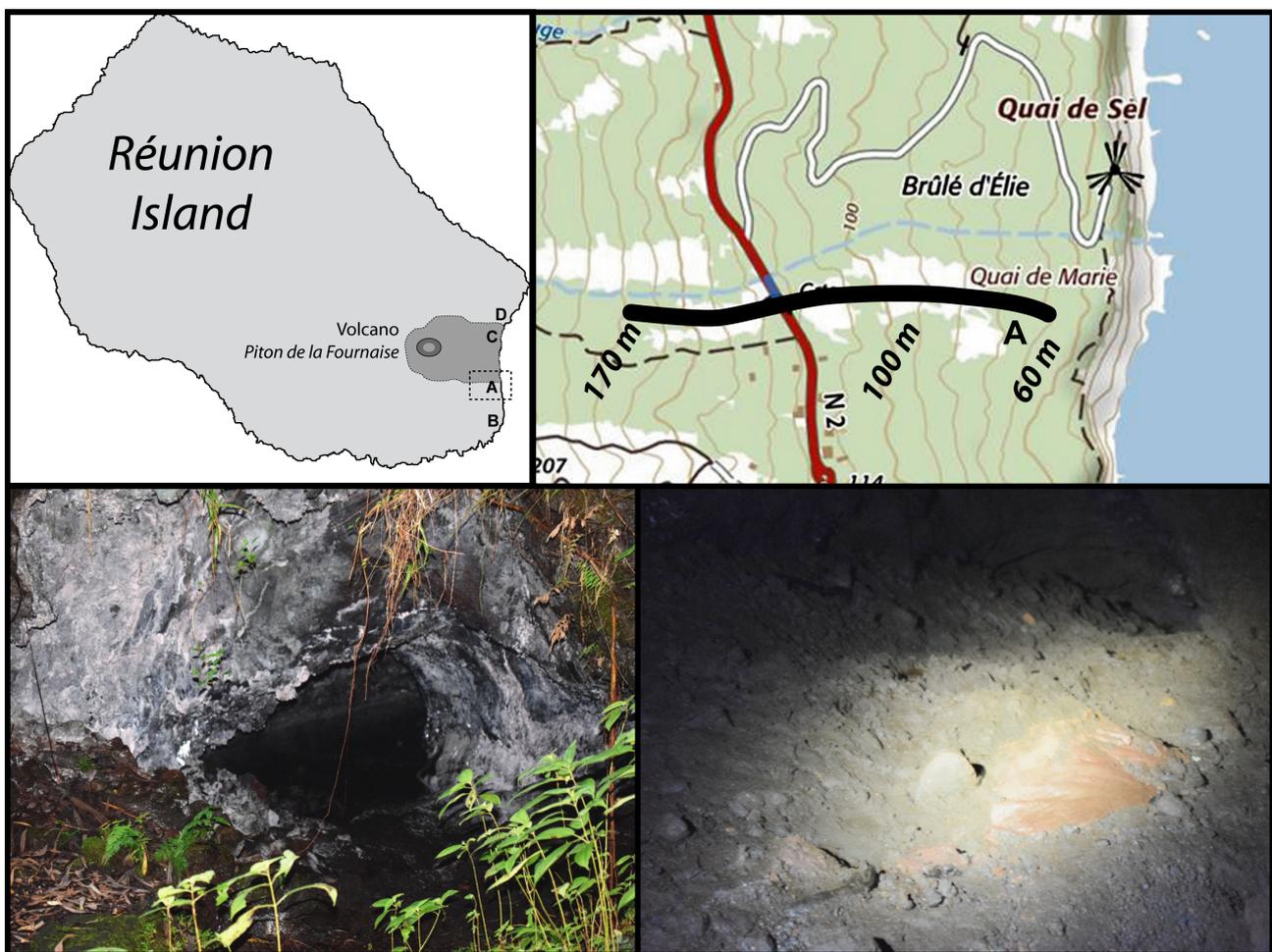


FIGURE 4. Habitat of *Karstarma vulcan* in Réunion Island. Upper row, left: Réunion Island with indication of the volcano ‘Piton de la Fournaise’ and its ‘enclos’ (grey area) with places where crabs *Karstarma* were observed: A, ‘Brûlé des Citrons Galets’ (dotted rectangle enlarged on the right); B, ‘Grotte au Trésor’; C ‘Coulée de 2004’; D, ‘Grotte des Hirondelles’. Upper row, right: position of the lava tube ‘Brûlé des Citrons Galets’ in the south-western part of the Island, point A is the place where crabs were collected, altitudes indicated for 60, 100, 170 m (GPX trace of tunnel in black, from Goursaud, 2018; background map from IGN, 2018). Bottom row, left: entrance of lava tube ‘Brûlé des Citrons Galets’, near road ‘N2’ (in red on IGN map). Bottom row, right: place of collection of the crabs, at the end of the tunnel, showing sediment left after heavy rains. (Photographs J.-P. Le Guelte).

Remarks. *Karstarma vulcan* sp. nov. is most closely related to *K. jacksoni* (Balss, 1934). The differences between the two species are presented in Table 1. This relationship with *K. jacksoni*, the only *Karstarma* species previously reported in the Indian Ocean, suggests that they have perhaps a common ancestor. Christmas Island is a

much older geomorphological unit (~ 60–10 Myr; Bullough 2013) than Réunion Island (~ 2.1 Myr; Lénat *et al.* 2001). The South Equatorial current carries to the west of the tropical Indian Ocean, from Christmas Island to Réunion Island. This suggests that the ancestors of *K. jacksoni* may have colonized Réunion Island by marine dispersal of their larvae.

Karstarma vulcan **sp. nov.** is also related to *K. waigeo* Wowor & Ng, 2009, with similar aspect of carapace and ambulatory legs (compare Fig. 1A, B with Wowor & Ng 2009: fig. 2A, B). In *K. waigeo*, however, the first anterolateral tooth is more curved inwards, the notch between the first and second anterolateral teeth is deeper, the oblique striae on posterolateral carapace are better marked, the meri of ambulatory are proportionately less elongated with length to width ratios of second, third legs 3.5, 4.0, respectively (instead of 3.8–4.1 and 3.9–4.6 in *K. vulcan* **sp. nov.**), the cutting edges of the fingers of the male chela (Fig. 2 A, B) have relatively much lower teeth (Wowor & Ng 2009: fig. 3C), the lateral margins of the 6th male somite (Fig. 1C) are more convex (Wowor & Ng, 2009: fig. 3B), and the vulva (Fig. 10G) has a different shape, lacking broad sternal rim (Wowor & Ng 2009: fig. 6E).

In the form of the vulva (Fig. 10G) and live colour (Fig. 3), *Karstarma vulcan* **sp. nov.** also resembles *K. boholano* (Ng, 2002) from Bohol (Philippines) and the Ryukyu Islands (Japan), being the single species of the genus found in two caves that are very distant geographically (~1700 km apart). *Karstarma boholano* is distinguished by: possessing a deep V-shaped tooth between the first and second anterolateral teeth of carapace (compare Fig. 1B, 9A, B with Ng 2002: fig. 12A), having oblique striae on posterolateral carapace better marked, the meri of the ambulatory legs less elongated, length to width ratios of meri of second, third legs being 3.4, 3.7, respectively (versus 3.8–4.1 and 3.9–4.6 in *K. vulcan* **sp. nov.**), and with a much shorter chitinous distal part of G1 in male (compare Fig. 10B with Ng 2002: fig. 12E–G).

***Karstarma* sp.**

(Fig. 5A–D)

Material examined. 1 female juvenile 8.6 × 9.8 mm (MNHN-IU-2013-7242), lava tube ‘Brûlé des Citrons Galets’, Le Tremblet, Saint Philippe, Réunion Island, coll. A. Barrère, Lucie Lavaud, Agnès Lavaud, Justine Sehedic, 19 February 2016.

Additional observation. *In situ* photographs (no specimens collected) lava tube ‘Coulée de 2004’, lower section, near end of tunnel, Matthieu Balanger, 13 August 2017.

Diagnosis (juvenile aspect). Carapace trapezoidal, 1.1 as wide as long; dorsal surface gently convex with epigastric and urogastric grooves poorly marked. Lateral margins of carapace diverging posteriorly. Anterolateral margin with 2 main teeth including external orbital angle; first tooth (external orbital angle) blunt, directed inwards at an angle of ~ 30°; second tooth with blunt tip separated from former tooth by deep V-shaped notch; third tooth poorly marked separated from second tooth by minute notch.

Front 0.45 times fronto-orbital width (measured between tip of anterolateral teeth), 2.7 wider than high. Supraorbital margin widely U-shaped, eyes with cornea pigmented as wide as ocular peduncle. Cheliped symmetrical, chela 3.3 as long as high, inner and outer surfaces of palm slightly inflated, upper and lower margin rounded, unarmed; cutting edges of fingers slightly gaping when fingers closed, with minute triangular teeth on proximal ¼, unarmed on distal ¾, tip of fingers corneous, hoof-like, incurved, movable finger 1.2 as long as palm.

Ambulatory legs 1–4 long, third leg (P4) longest 3.8 and 3.4 as long as CL and CW, respectively, tufts of setae present between coxae of ambulatory legs 1, 2 (P2, 3) and 2, 3 (P3, 4); outer faces of meri with sparse short transverse striae, upper and lower margins carinated, unarmed, length to width ratio of meri of legs 2, 3 (P3, 4), 4.6, 5.0, respectively; carpi 0.5 meri length, unarmed, outer faces with 2 longitudinal carinae; propodi 0.6 meri length, unarmed, furnished with longitudinal rows of long stiff setae on upper and lower margins; dactyli sub-cylindrical, unarmed, 1.0–1.1 propodi length, gently curved in distal third, with similar longitudinal rows of setae than on propodi, terminating in corneous claws. Female pleon and vulva juvenile.

Live coloration. (Fig. 5A–D) carapace purple or orange, chelipeds orange with white on fingers of chelae, ambulatory legs bright orange on meri and carpi, white on propodi and dactyli.

Habitat. Lava tubes of ‘Brûlé des Citrons Galets’ and ‘Coulée de 2004’. This species seems to prefer the rocky parts of the lava tubes (see Fig. 5 C, D).

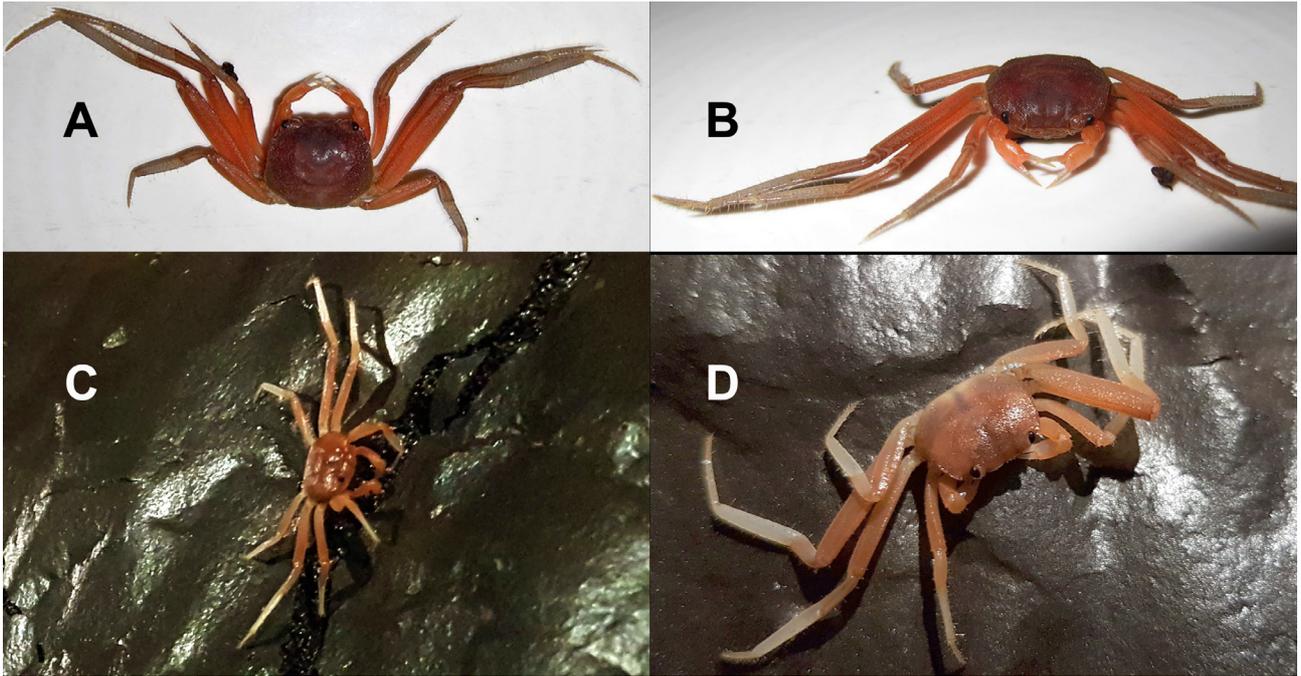


FIGURE 5. Live colour of *Karstarma* sp. A, B) female juv. 8.6×9.8 mm (MNHN-IU-2013-7242), probably from lava tube 'Brûlé des Citrons Galets', photographs A. Barrère, 19 February 2016; C, D) specimen not collected, from lava tube 'Coulée de 2004', lower entrance near the shore, photographs Matthieu Balanger, 13 August 2017.

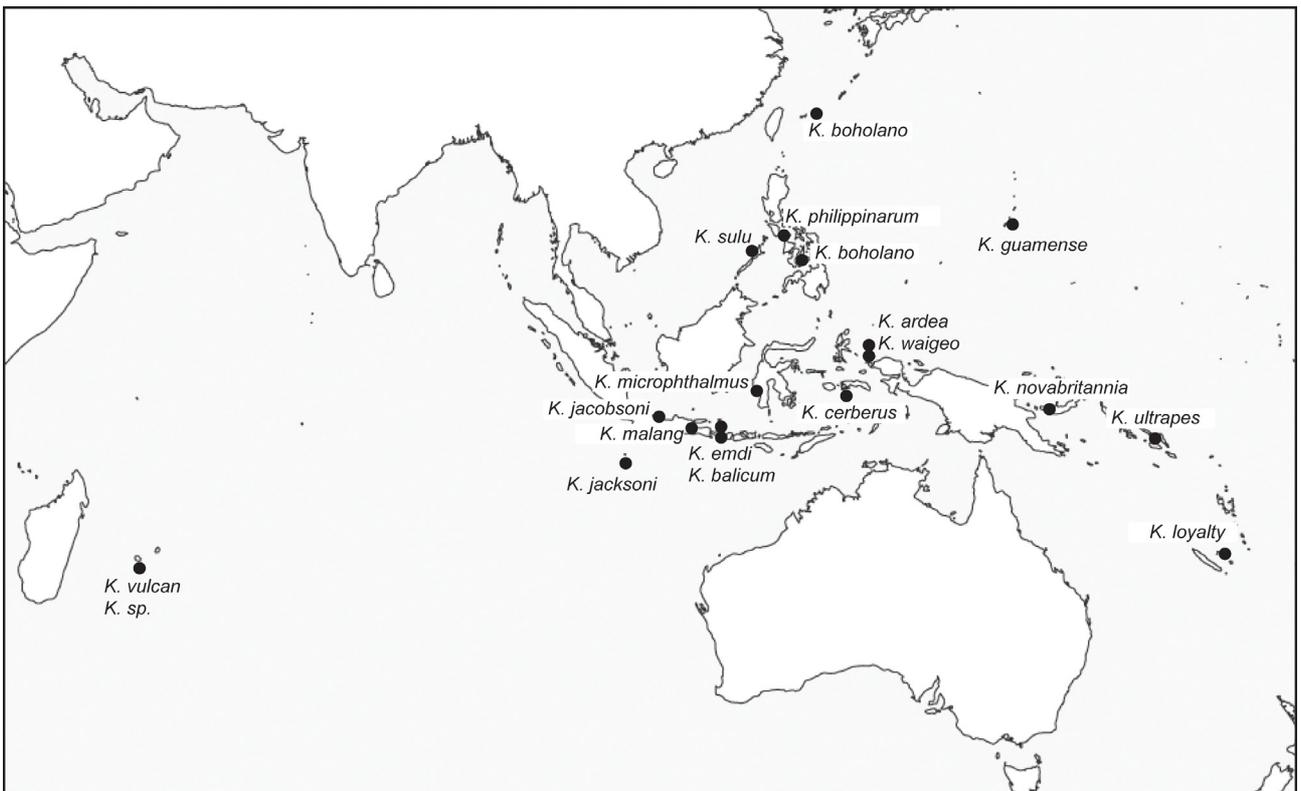


FIGURE 6. Geographic distribution of the 17 or 18 species of *Karstarma*, from west to east: *Karstarma vulcan* and *K. sp.* (Réunion); *K. jacksoni* (Christmas Island); *K. jacobsoni* (Central Java); *K. malang* (East Java, from Wowor & Ng 2018); *K. emdi* and *K. balicum* (Nusa Penida Island, sympatric in same cave); *K. microphthalmus* (South Sulawesi); *K. sulu* (Palawan Island); *K. philippinarum* (Boracay Island); *K. boholano* (Bohol and Tarama Islands); *K. cerberus* (Ambon Island); *K. ardea* and *K. waigeo* (Waigeo Island; sympatric in same cave but in rocky parts for *K. ardea* and muddy substrates for *K. waigeo*); *K. guamense* (Guam Island); *K. novabritannia* (New Britain Island); *K. ultrapes* (Nggela Pile Island); *K. loyalty* (Lifou Island).

Distribution. Réunion Island.

Remarks. This juvenile specimen, probably collected in the same lava tube than *Karstarma vulcan* **sp. nov.**, was first thought to be a juvenile of that species. After careful examination it appears that it is distinct from *K. vulcan* **sp. nov.** by at least three characters: a) carapace trapezoidal (instead of approximately trapezoidal); b) relatively longer legs, leg 3 being 3.8 and 3.4 times CL and CW, respectively (instead of 3.1–3.4 and 2.6–2.8, respectively) with a merus more elongated having a length to width ratio of 5.0 (instead of 3.9–4.6); c) live colour of ambulatory legs, orange on meri and carpi and white on propodi and dactyli (instead of brown or purple). All these characters are shared by three species identified by Wowor & Ng (2009) as a group of very long-legged species nested within *Karstarma*, and probably with distinct generic affinities: viz. *K. ardea* Wowor & Ng, 2009, *K. ultrapes* (Ng, Guinot & Iliffe, 1994), and *K. philippinarum* Husana, Naruse & Kase, 2010. The vulvae of females in this group has a typical “large U-shaped posterior projection and a prominent anterior projection, with both projections partially covering the prominent rounded operculum” (Wowor & Ng 2009: 29, fig. 5B–D), but this was not observed on the female examined from Réunion Island, probably because it is a juvenile. Collection of additional specimens, including adult males and females, is therefore needed before this species can be identified to species level. The presence of ‘very long-legged’ species, however, cannot be confirmed with certainty in the Indian Ocean with the present observations because characters such as the shape of the carapace and proportion of the legs vary in the juveniles as observed for the gecarcinid *Discoplax gracilipes* Ng & Guinot 2001 (see variation: 325) and the sesarmid *Karstarma boholano* (P.K.L. Ng. pers. comm.) If the presence of a ‘very long-legged’ species living sympatrically with *K. vulcan* **sp. nov.** can be confirmed in the future, the situation will be similar to that observed in the cave ‘Gua Kalepale’, Waigeo Island, where *K. ardea*, which has ‘very long legs’ and prefers rocky parts, lives sympatrically with *K. waigeo* Wowor & Ng, 2009, which has ‘normal’ legs and prefers muddy substrates.

***Karstarma jacksoni* (Balss, 1934)**

(Figs. 7A–E, 8A–M, 9C, D, 10D–F, H, 11A–D)

Sesarma (*Sesarma*) *jacksoni* Balss, 1934: 230, fig. 3 (Type locality Grimes Cave, Christmas Is., 10°26'32"S, 105°39'37"E).

Sesarma jacksoni—Gibson-Hill 1947: 43 (Christmas Is.).—Tweedie 1947: 33 (Christmas Is.).

Sesarmoides jacksoni—Ng 1998: 186 (Christmas Is.).—Davie 2002: 226 (catalogue).—Ng 2002: 433 (discussion and key).

Karstarma jacksoni—Davie & Ng 2007: 229 (New genus and key).—Ng *et al.* 2008: 221 (Checklist).—Orchard 2012: 215 (Field guide) 2018: webpage (colour photograph).—Takakura 2018: webpage (colour photographs).

Material examined. Christmas Island, Australia, Eastern Indian Ocean. 1 male 10.9 × 12.8 mm, 1 female ov. 13.7 × 16.8 mm, 1 female juv. 7.5 × 9.2 mm, 1 juv. 6.0 × 7.0 mm (WAM C13970; ex. WA 531-85), Daniel Roux Cave, 30 feet below entrance, coll. and det. R.W. George, 21/02/78; 1 male 15.4 × 18.7 mm, ‘Golf Course’, 19/11/78, det. R.W. George, 1 female 14.3 × 18.05 mm, Silver City, ‘House 640 on porch during rain’ coll. D. Morton, 12/11/78, det. R.W. George (WAM C13968, ex. WA 529-85a-b); 1 juv. 3.2 × 3.6 mm, 19th Hole Cave, 10°25'29"S, 105°42'04.24"E, coll. J. Anderson, 30/03/2004, det. P. Davie (WAM C54757); 1 juv. 2.1 × 2.3 mm, no data, Christmas Island, det. P. Davie (WAM C54747); 1 juv. 2.5 × 2.8 mm, no data, Christmas Island, det. P. Davie (WAM C54752); 1 juv. 4.5 × 5.3 mm, no data, Christmas Island, det. P. Davie (WAM C54748).

Diagnosis. Carapace (Fig. 7A, B) approximately trapezoidal, maximum width across base of second, third ambulatory legs (P3, 4), width 1.2–1.3 times length. Lateral margins of carapace sub-parallel, diverging very weakly posteriorly; dorsal surface gently convex, regions poorly marked, epigastric and urogastric grooves shallow, posterolateral regions with a few faint oblique striae. Lateral margins of carapace sub-parallel, diverging weakly posteriorly; anterolateral margin with 3 teeth including external orbital angle, first tooth (external orbital angle) acute, curved anteriorly at an angle of 50° (Fig. 9C, D); second tooth with blunt tip separated from former tooth by V-shaped cleft; third tooth smallest poorly marked, separated from second tooth by clearly cut notch, tip of second tooth placed closer to first tooth than third.

Front (Fig. 7E) similar to *K. vulcan* **sp. nov.**, 0.4–0.5 times fronto-orbital width (measured between tip of anterolateral teeth), 2.3–2.6 wider than high. Frontal margin, supraorbital margin, eyes, cornea, infraorbital margin, epistome, branchiostegite, and third maxilliped (Fig. 7E, F) similar to *K. vulcan* **sp. nov.**

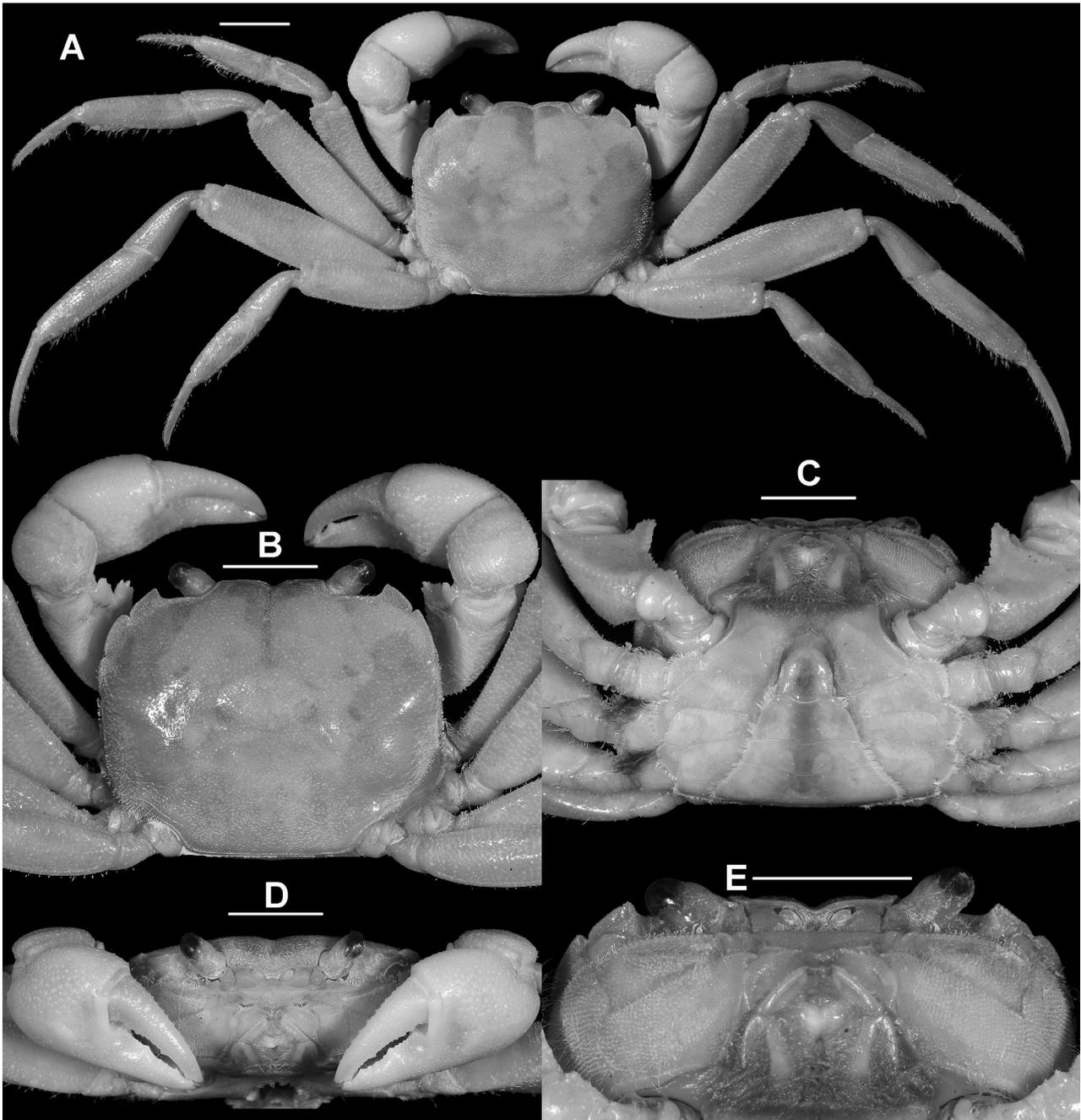


FIGURE 7. *Karstarma jacksoni* (Bals, 1934), 1 male 15.4 × 18.7 mm, Christmas Island, WAM C13968. A. dorsal habitus; B–D carapace and chelae, dorsal, ventral, frontal views, respectively; E. Front, orbits, buccal cavern and pterygostomian area (scales bars, 5 mm).

Cheliped of male (Fig. 8A, B) symmetrical, merus triangular in cross-section, outer ventral margin and dorsal margin denticulated, inner ventral margin with a few sharp teeth on proximal half and strong flange (Fig. 8E) on distal half, inner face with a longitudinal line of pubescence, outer face with short transverse striae; carpus rounded unarmed, dorsal surface smooth with a few sparse granules, inner dorsal margin with line of low granules; chela higher than in females, 2.0–2.2 as long as high, inner and outer faces inflated, coarsely granulated, larger granules on inner face disposed on a salient transverse ridge forming a ‘stridulating’ ridge (Fig. 8B; see remarks); fingers of chela with small sub-triangular teeth of unequal sizes all along cutting margins, with slight gape when fingers closed; tip of fingers corneous, hoof-like; movable finger 1.4–1.5 as long as palm, dorsal margin with granules. Cheliped of female with same flange on distal half of inner ventral margin of merus than in male, but reduced in size (Fig. 8F); chela more elongated than in male, 2.3–3.1 as long as high, overall similar to that of *K. vulcan* **sp. nov.**, movable finger 1.3–1.6 as long as palm.

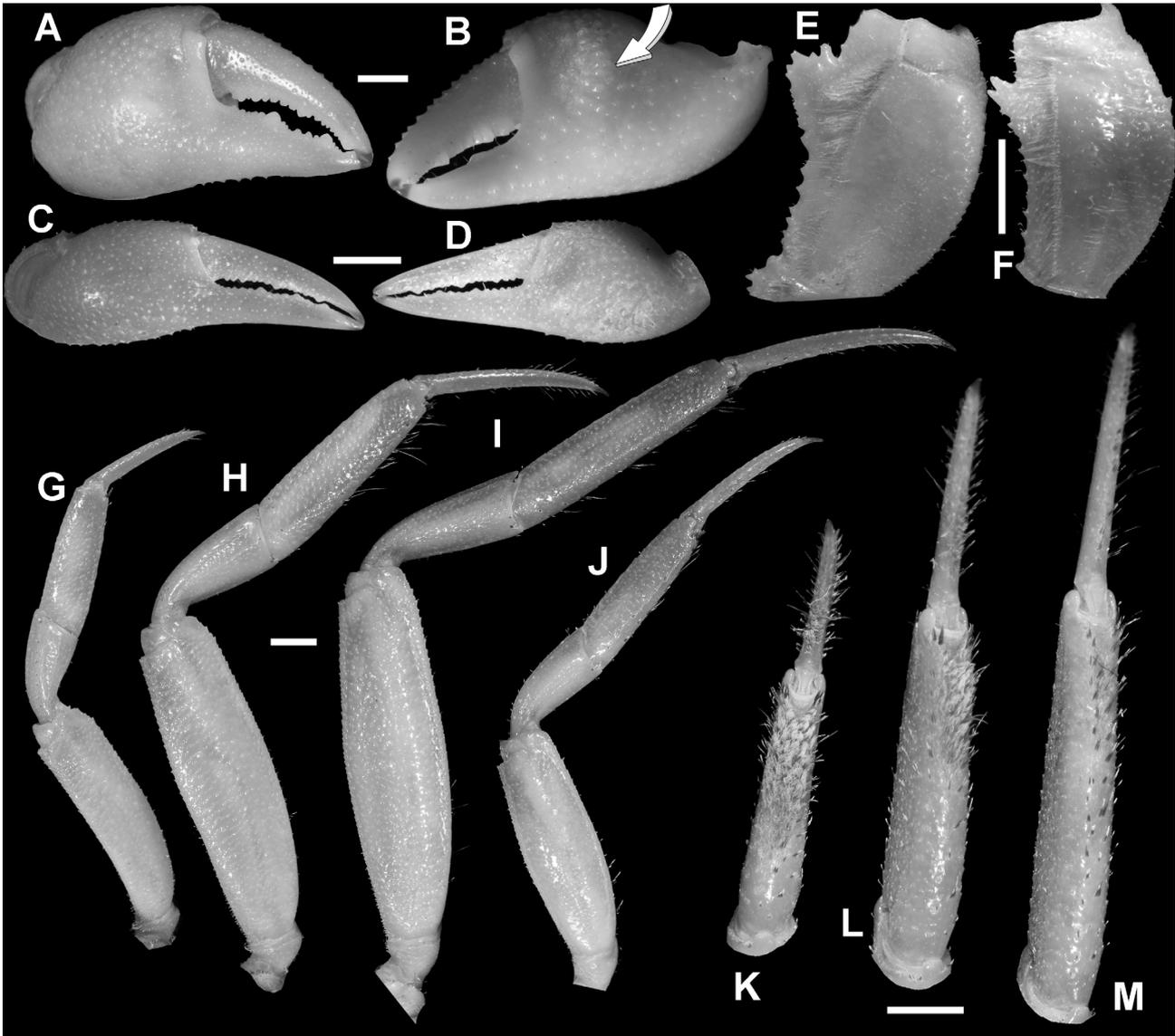


FIGURE 8. *Karstarma jacksoni* (Balss, 1934), Christmas Island, male 15.4 × 18.7 mm, Christmas Island, WAM C13968 (A, B, E, G–M), female 14.3 × 18.05 mm, WAM C13968 (C, D, F). Right chela, outer (A, C) and inner views (B, D), arrow indicate ‘stridulating’ ridge; merus of right cheliped, inner view (E, F); right ambulatory legs 1–4 (P2–P5), outer view (G–J); distal part of propodi and dactyli of right ambulatory legs 1–3, ventral view (K–M) (scale bars, 2 mm).

Ambulatory legs 1–4 (P2–P5) (Fig. 8G–M) of similar proportions in males and females, longest leg (leg 3, P4) 2.3–2.6 (male) and 2.4–2.8 (female) as long as CW, and 2.8–3.1 (male), 2.9–3.4 (female), as long as CL. Prominent tufts of setae present between coxae of legs 1, 2 (P3, 4) and legs 2, 3 (P3, 4) in male and female. Meri unarmed, dorsal and inner ventral margins with faint carina, outer faces convex with short transverse striae, inner faces smooth, length to width ratios of meri of legs 2, 3 (P3, 4) between 3.3–3.9 and 3.4–4.1, respectively. Carpi as in *K. vulcan sp. nov.* Propodi and dactyli with fewer stiff setae on upper margins and outer faces than in *K. vulcan sp. nov.*, probably an artefact due to cleaning the specimens (see remarks), outer faces of propodi convex with granules, mat of setae present on distal half of inner faces of legs 1–3 (P2–4), in male only (Fig. 8K–M). Dactyli as in *K. vulcan sp. nov.*

Male pleon (Fig. 7C) triangular, telson rounded at tip, as high as wide; 6th somite the highest, trapezoidal, anterior margin sinuous, lateral margins feebly convex; somites 3–5 elongated, somite 5 4.0 as long as high, somites 1–3 the longest, somite 3 not reaching base of P5 coxae. Female pleon similar in shape than in *K. vulcan sp. nov.*, about 1.5–1.6 as wide as long. G1, G2 (Fig. 10D–F) and vulva (Fig. 10H) as in *K. vulcan sp. nov.*

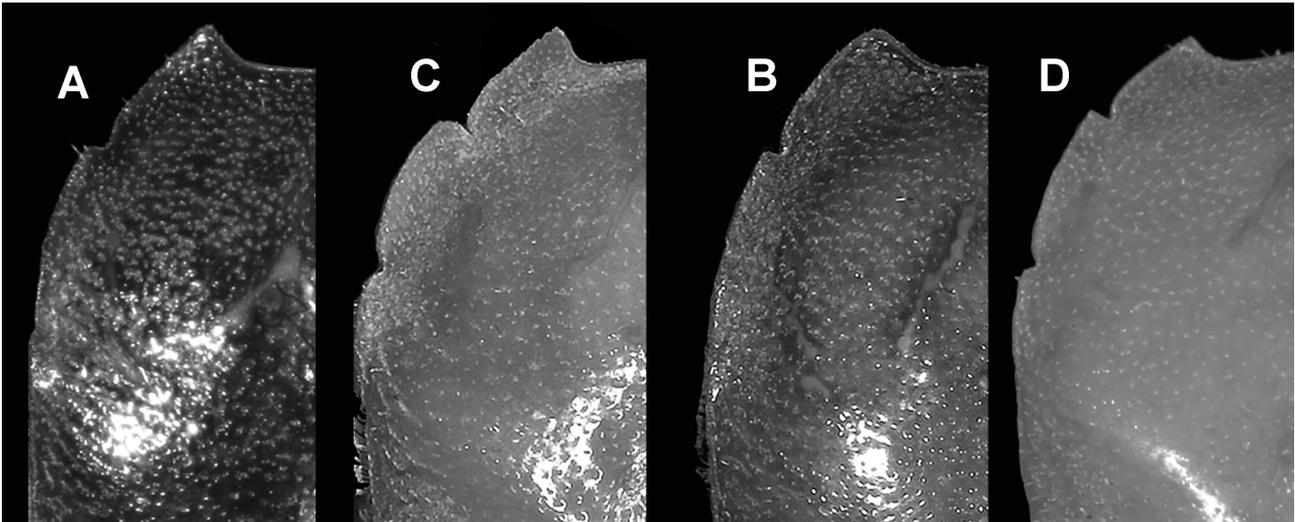


FIGURE 9. Comparison of anterolateral margins of carapace in *Karstarma vulcan* and *K. jacksoni* for specimens of approximately same size and sex. *Karstarma vulcan*, A) holotype male 16.2 × 18.9 mm, MNHN-IU-2013-7243; B) paratype female 13.7 × 16.9 mm, MNHN-IU-2013-7240. *Karstarma jacksoni*, C) male 15.4 × 18.7 mm, WAM C13968; D) female 14.3 × 18.1 mm, WAM C13968.

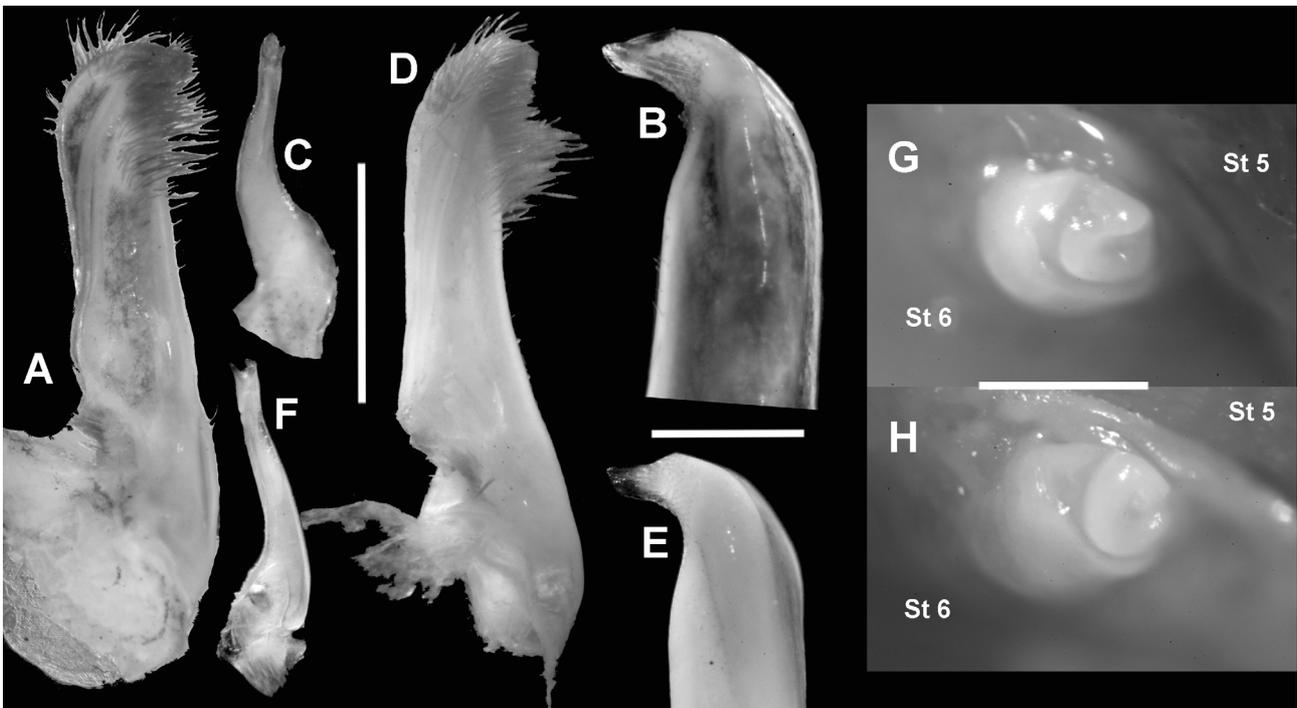


FIGURE 10. External genital organs in *Karstarma vulcan* **sp. nov.**, A–C) holotype male 16.2 × 18.9 mm, MNHN-IU-2013-7243, G) paratype female 13.7 × 16.9 mm, MNHN-IU-2013-7240, and *K. jacksoni*, D–F) male 15.4 × 18.7 mm, WAM C13968, H) female 14.3 × 18.1 mm, WAM C13968. G1 sternal (A, D) and abdominal face (B, E; setae removed); G2 sternal face (C, F); female right vulva (G, H; St 5, 6 indicate sternites 5, 6) (scale bars A, C, D, F, 2 mm; B, E, G, H, 1 mm).

Remarks. *Karstarma jacksoni* is morphologically similar to *K. vulcan* **sp. nov.** but can be separated by a series of characters that are presented in Table 1. In the set of five juveniles of *K. jacksoni* examined (CW <7.0 mm), the anterolateral armature of the carapace can still be used to separate this species from *K. vulcan* **sp. nov.** but the aspect of the meral flange on cheliped is not present and cannot be used, this structure being noticed only for individuals with CW ≥ 9.2 mm. The setation of the ambulatory propodi and dactyli is more sparse in *K. jacksoni* than in *K. vulcan* **sp. nov.**, stiff setae being almost absent on the inner and outer surfaces and on the upper margins. This seems to be an artefact due to brushing the specimens for observation because these setae were seen on photographs of live specimens examined for this work (Fig. 11).

In the largest male examined the inner face of the chela has a salient ‘stridulating’ ridge with prominent granules, similar to that observed for some ocyropodid crabs of the genus *Ocyropode* (e.g. *O. pauliani* Crosnier, 1965). This ridge is also observed in *K. vulcan* **sp. nov.** but in that species it rubs against the infraorbital margin, while in *K. jacksoni* it rubs against the flange of the merus, much more developed in that species. These structures, not present in females, are perhaps used by the males to produce sounds, for example during mating or fighting behaviour. In sesarimid crabs stridulation is performed by winners after fights, to reduce the chances of losers re-initiating another fight (Chen *et al.* 2014, 2017).

Size. Specimens examined and measured for biometry range in size from 7.5 × 9.2 mm to 15.4 × 18.7 mm. A set of small specimens in poor condition (legs broken or missing) was also examined but not retained for biometry, ranging in size from 2.1 × 2.3 mm to 6.0 × 7.0 mm.

Live coloration (Fig. 11A–D) Carapace and legs purple-red with paler areas at bases of ambulatory legs; cornea black-red; cheliped orange with fingers of chela paler or white.

Habitat and ecology. This crab is found in karstic caves but has also been reported wandering outside this habitat (Gibson-Hill 1947; Tweedi 1947; Ng 1988; Orchard 2012). In the material examined a female (14.3 × 18.05 mm, WAM C13968) is labelled as being collected in urban habitat at “House 640 on porch during rain” and photographs by Takakura (2018) (reproduced on Fig. 11C, D) show the crab feeding outside between rubble and vegetal debris in the same biotope as the land crab *Geograpsus grayi*. Orchard (2012: 215) indicated that the crab is observed from sea level to 50 m above sea level and that it may be observed outside caves when spawning, from November to April, with the eggs being released into the sea at night just after high tide.

Distribution. Known from Christmas Island only.

TABLE 1. Differences between *Karstarma jacksoni* (Balss, 1934) and *K. vulcan* **sp. nov.** (n is the number of specimens examined and measured; anterolateral angle of carapace measured along longitudinal axis).

	<i>K. jacksoni</i> (n=5)	<i>K. vulcan</i> (n=3)
Anterolateral angle of carapace	strongly curved inward (~ 50°), acute at tip	slightly curved inward (~ 40°), blunt at tip
Notch between 1 st and 2 nd anterolateral teeth	deep, V-shaped	shallow, U-shaped
Notch between 2 nd and 3 rd anterolateral teeth	deeply cut	absent or poorly marked
Distal flange on inner ventral margin of merus of cheliped	strong in male (CW ≥ 12.8 mm), moderate in female (CW ≥ 9.2 mm)	moderate in male (CW = 18.9 mm), absent in female (CW 16.5–16.9 mm)
Chela of male	cutting edge of fingers with small triangular teeth	cutting edge of fingers with large triangular teeth
Meri of ambulatory legs	Less elongated	More elongated
leg 2 (P3) merus l/h ratio	3.3–3.9	3.8–4.1
leg 3 (P4) merus l/h ratio	3.4–4.1	3.9–4.6
aspect of outer surface	median carina in distal half separating dorsal, ventral sulci	regularly convex
Propodi of ambulatory legs outer face	slightly convex, with short striae	flat, smooth
Sixth somite of male pleon, lateral margins	weakly convex	markedly convex

Discussion

The discovery of two distinct species of *Karstarma*, *K. vulcan* **sp. nov.** and *K. sp.*, in the lava tubes on Réunion Island constitutes the first WIO records for this genus. This appears to be the first observation of crabs living in caves of an active volcano, other *Karstarma* species live only in karstic and/or anchialine caves. In others places of the world *Karstarma* species such as *K. balicum* and *K. emdi* (Ng & Whitten, 1995) have been recognized as ‘Critically Endangered’ species on IUCN Red List of threatened species (Whitten & Ng 2015a, b). With most of

the lava tubes of Réunion Island situated in a protected national wildlife park, the *Karstarma* species found therein should probably be on the IUCN Red List as well.

With these two records from Réunion and another new species from Java (Wowor & Ng 2018), the genus *Karstarma* appears to be a taxon increasingly more diverse than expected, counting currently 17 or 18 species. Wowor & Ng (2009, 2018, pers. comm.) have identified three distinct groups in the genus: Group 1, species with reduced corneas, including *K. jacobsoni* (Ihle, 1912), *K. microphthalmus* (Naruse & Ng, 2007) and *K. malang* Wowor & Ng, 2018, which are associated with freshwater and live in inland caves several kilometers away from the coast; Group 2, species with very long legs, such as *K. ardea*, *K. ultrapes*, and *K. philippinarum*, which live in coastal caves and tolerate salt water; Group 3, species with fully developed corneas and with ambulatory legs not as long as in Group 2, all other *Karstarma* species inhabiting caves not far from the beach and tolerating brackish to salt water, excluding *K. novabritannia* (Ng, 1988) and *K. sulu* (Ng, 2002). For the species newly discovered from Réunion Island, *K. vulcan* sp. nov. can be classified in Group 3, while *K. sp.* can be classified in Group 2.

Our results and those of Wowor & Ng (2018) indicate that still more investigations are needed for *Karstarma* in tropical caves because these are cryptic species that can live sympatrically in same caves, and probably more new species will be discovered in the future. Sympatric species currently identified, and sometimes confused with each other before being recognized, are: *K. sp.* (first confused with *K. vulcan*) and *K. vulcan* sp. nov., in Réunion lava tubes; *K. ardea* and *K. waigeo* in Waigeo Island, cave 'Gua Kalepale' (Wowor & Ng 2009); and *K. balicum* (first confused with *K. emdi*) and *K. emdi* in Nusa Penida Island, cave 'Giri Putri' (Ng & Whitten 1995; Ng 2002). The morphological variations between the species being often very subtle, larger sets of specimens are required for each species to better appreciate intraspecific variations. DNA studies including all the species will be also of primary importance in further contributions to better understand the relationships between the species and will probably confirm that *Karstarma* as presently recognized must be split in at least three distinct genera corresponding to groups 1 to 3 identified by Wowor & Ng (2018).

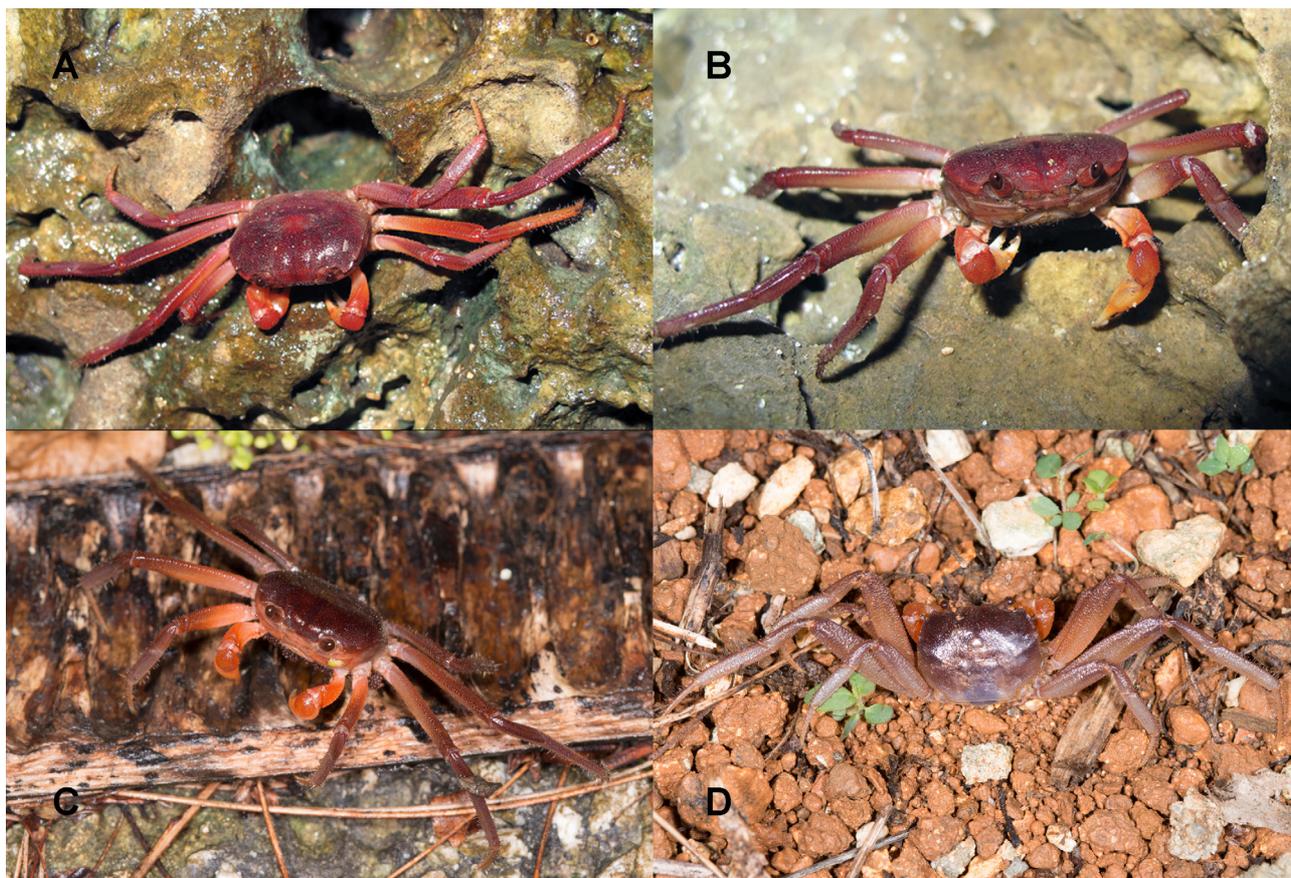


FIGURE 11. Live colour of *Karstarma jacksoni* (Balss, 1934), Christmas Island. A, B) in cave, photographs Max Orchard; C, D) outside cave, Photographs Hitoshi Takakura.

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