

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

Running title: Crabs *Karstarma* from Reunion Island

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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.

Key Words: Crustacea, Sesarmidae, Indian Ocean, new species, endemic species, cave-dwelling species, taxonomy.

Introduction

On 15 November 2014, one of the authors (N. Crestey) discovered an unusual crab in the lava tube of ‘Brûlé des Citrons Galets’, near the south-eastern coast line of Réunion Island, Western Indian Ocean (WIO). This specimen was photographed but not captured (ACSP, 2014; Robert, 2014). It was distinct by its 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 similar P4 long legs, 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 in the lava tube ‘Brûlé des Citrons Galets’ supervised by the teacher A. Barrère. The crab, having apparently taken refuge in the backpack of A. Barrère, was retrieved the next day drowned in his pool. Although there is some doubt on exact place of collection for this specimen it was overall similar to that photographed in 2014 and was most probably from

backpack. During the school visit to the lava tube the 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 from where was described an endemic crab, *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 later 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.

Materials 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 × 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 × 16.9 mm (MNHN-IU-2013-7240), 1 female 13.1 × 16.5 mm (MHNH-IU-2013-7241), coll. N. Crestey and J.-P. Le Guelte, 16 November 2017.

Additional observations. *In situ* photographs (no specimens collected) lava tubes: ‘*Grotte au Trésor*’, photograph Christopher Lauret, 3 March 2016; ‘*Coulée de 2004*’, photograph F. Levener, 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 ~40°; 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.

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 13.05 × 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. (Fig. 4). All crabs were captured in the lava tube of '*Brûlé des Citrons Galets*'. 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 far from the shoreline at an altitude of about 50–60 m and its upper part is about 750 m far from the shoreline at an altitude of about 160–

170 m. 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 moister and muddy parts of the tunnels where it has been observed scraping the substrate for food.

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.

In Réunion Island more than 80 lava tubes or cavities, including about 15–20 near the coastline are listed by Audraa (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’ that are open to the public, thus explaining why the crabs were first observed there. Crab, however, is not often seen. It is not reported for example by Rochat *et al.* (2003) in the lava tube ‘Brûlé des Citrons Galets’ for a study on the Arthropoda of the tunnel, nor during several additional investigations conducted between 2003–2007 (J. Rochat, pers. comm. 16 November 2017). The only crab being 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 have been also prospected for cave-dwelling insects by Hoch *et al.* (2003) and Sendra *et al.* (2017), without mention of crab.

Distribution. So far known only from Réunion Island. This is the first record of a crab *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 god of fire, including fire of volcanoes to remind that the crab has been discovered in the lava tubes of the volcano ‘Piton de la Fournaise’, Réunion Island.

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, after the re-description of *K. jacksoni*. This relationship with *K. jacksoni* (Balss, 1934), the single *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 Ryukyu (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 1/4, unarmed on distal 3/4, 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).

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 ambulatory legged*’ species nested within *Karstarma* species and probably with distinct generic affinities: *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, fig. 5B–D), that cannot be recognized on the female examined from Réunion Island, probably because it is a juvenile. Collection of additional specimens, including adult males and females, are therefore needed before this species can be identified to species level. The presence of ‘*very long ambulatory 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 ambulatory legged*’ species living sympatrically with *K. vulcan* sp. nov. can be confirmed in the future in the lava tubes of Réunion Island, the situation will be then the same than that observed in the cave ‘*Gua Kalepale*’, Waigeo Island, where *K. ardea*, with ‘*very long legs*’ and preferring rocky parts, live sympatrically with *K. waigeo* Wowor & Ng, 2009, with ‘*normal*’ legs and preferring 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, $10^{\circ}25'29''S$, $105^{\circ}42'04.24''E$, 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.

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.

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.

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 CW ≥ 9.2 mm. The setation of propodi/dactyli of ambulatory legs is more sparse in specimens of *K. jacksoni* examined than in *K. vulcan* sp. nov., stiff setae being almost absent on the inner/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, somewhat like that observed for some ocypodid crabs of the genus *Ocypode* (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 sesarmid crabs stridulation performed by winners after fights, to reduce the chances of losers re-initiating another fight, has been observed by Chen *et al.* (2014, 2017).

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	3.3–3.9	3.8–4.1
leg 3 (P4) merus l/h	3.4–4.1	3.9–4.6
aspect of outer face	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

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 cave but has also been reported wandering outside this habitat (Gibson-Hill, 1947; Tweedie, 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 rubbles and vegetal debris in the same biotope than, for example, the land crab *Geograpsus grayi*. Orchard (2012: 215) indicate that the crab is observed from sea level to 50 m above sea level and that it may be observed out of cave when spawning, from November to April, eggs being released into the sea at night just after high tide.

Distribution. So far known from Christmas Island only.

Discussion

The discovery of two distinct species of *Karstarma*, *K. vulcan* sp. nov. and *K. sp.*, in the lava tube of 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, others *Karstarma* species living in karstic and/or anchialine caves. In others places of the world *Karstarma* species such as *K. balicum* and *K. emdi* have been recognized as ‘Critically Endangered’ species on IUCN Red List of threatened species (Whitten & Ng, 2015a, b). Most of the lava tubes of Réunion Island being situated in a protected national wildlife park the *Karstarma* discussed in the present contribution should probably appear too on the IUCN Red List.

With these two records from Réunion and *K. sp.* nov. from Java (Wowor & Ng, in press), the genus *Karstarma* appears to be a taxon increasingly more diverse than expected, counting currently 17 or 18 species. Wowor & Ng (2009, in press; 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. sp.* nov. Wowor & Ng (in press), more associated to freshwater and living in inland caves several kilometers away from the coast; group 2) species with very long legs, *K. ardea* Wowor & Ng, 2009, *K. ultrapes* (Ng, Guinot & Iliffe, 1994) and *K. philippinarum* Husana, Naruse & Kase, 2010, living in coastal caves and tolerating salt water; group 3) species with fully developed corneas and ambulatory legs not as long as in group 2, all other *Karstarma* species, excluding *K. novabritannia* (Ng, 1988) and *K. sulu* (Ng, 2002), inhabiting caves not far from the beach and tolerating brackish to salt water. The species newly discovered from Réunion Island belong to the group 2, for *K. sp.*, and to the group 3, for *K. vulcan* sp. nov.

Our results and those of Wowor & Ng (in press) 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, sometimes confused with each other’s before being recognized, are: *K. sp.* (first confused with *K. vulcan*) and *K. vulcan* sp. nov., in Réunion lava tubes; *K. ardea* Wowor & Ng, 2009 and *K. waigeo* Wowor & Ng, 2009, in Waigeo Island, cave ‘Gua Kalepale’; and *K. balicum* (Ng, 2002) (first confused with *K. emdi*, cf. Ng, 2002: 422) and *K. emdi* (Ng & Whitten, 1995) in Nusa Penida Island, cave ‘Giri Putri’. The morphological variations between the species being often very subtle, larger set 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 (in press).

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References

- ACSP (2014) Association Citoyenne de Saint Pierre, Ile de la Réunion. At <http://citoyennedestpierre.viabloga.com/news/une-nouvelle-espece-de-crabe-decouverte-dans-un-tunnel-de-lave>. Published 25/11/2014, consulted 2018.
- Audra, P. (1997) Inventaire préliminaire des cavernes de l’île de la Réunion (Océan Indien – France). *Spelunca*, 66: 23–38.
- Balss, H. (1934) Die Krabben der Reise J.W. Harms' nach der Christmas-Insel und dem Malaiischen Archipel. *Zoologischer Anzeiger*, 106(10): 225–237.
- Bullough, F. (2013) History and Geology of Christmas Island. *Geological Society of London blog*. At <https://blog.geolsoc.org.uk/2013/2012/2018/door-2018-history-and-geology-of-christmas-island/>. Consulted 2018.
- Cailhol, D. & Fulcrand, S. (2011) *Les tunnels de lave de l’île de la Réunion. Le milieu naturel, l’encadrement, la sécurité*. Rapport de mission d’expertise de la Fédération française de spéléologie, 1–61.
- Chen, P.Z., Carrasco, L.R. & Ng, P.K.L. (2014) Post-contest stridulation used exclusively as a victory display in mangrove crabs. *Ethology* 120(6): 532–539. <https://doi.org/10.1111/eth.12226>.
- Chen, P.Z., Carrasco, L.R. & Ng, P.K.L. (2017) Mangrove crab uses victory display to “browbeat” losers from re-initiating a new fight. *Ethology*, 123(12): 885–988. <https://doi.org/10.1111/eth.12696>.
- Crosnier, A. (1965) Crustacés Décapodes Grapsidae et Ocypodidae. *Faune de Madagascar*, 18: 1–143.

- Davie, P.J.F. (2002) *Crustacea: Malacostraca: Eucarida (Part 2): Decapoda - Anomura, Brachyura*. In: Wells, A. & Houston, W.W.K. (Eds) *Zoological Catalogue of Australia*. CSIRO Publishing, Melbourne, 19(3B): i–xiv, 1–641.
- Davie, P.J.F. & Ng, P.K.L. (2007) A new genus for cave-dwelling crabs previously assigned to *Sesarmoides* (Crustacea: Decapoda: Brachyura: Sesarmidae). *Raffles Bulletin of Zoology*, supplement 16: 227–231.
- Davie, P.J.F., Guinot, D. & Ng, P.K.L. (2015). *Anatomy and functional morphology of Brachyura*. Chapter 71-2, pp. 11–163. In: Castro, P., Davie, P.J.F., Guinot, D., Schram, F.R. & Von Vaupel Klein, J.C. (Eds), *Decapoda: Brachyura (Part 1)*. Treatise on Zoology — anatomy, taxonomy, biology. The Crustacea. Brill, Leiden & Boston. 9C-1, 1-638.
- Dez, J. (2018). Speleocanyon.re. At <https://www.facebook.com/juliendez.reunion/>. Consulted 2018.
- Emmerson, W.D. (2016) *A Guide to, and Checklist for, the Decapoda of Namibia, South Africa and Mozambique*. Cambridge Scholars Publishing: Volume 1: 1–590, Volume 2: 1–650, Volume 3: 1–720.
- Fujita, Y. & Naruse, T. (2016) *Karstarma boholano* (Ng, 2002) (Decapoda: Brachyura: Sesarmidae) from Tarama-jima Island, Ryukyu Islands, southwestern Japan. *Fauna Ryukyuana*, 28: 23–27.
- Gibson-Hill, C.A. (1947) Field notes on the terrestrial crabs. *Raffles Bulletin of Zoology*, 18: 43–52.
- Goursaud, J.P. (2018) Randopitons.re. Le tunnel de lave de Citrons Galets au Tremblet. At <https://randopitons.re/randonnee/1306-tunnel-lave-citrons-galets-tremblet>. Consulted 2018.
- Guinot, D., Tavares, M. & Castro, P. (2013) Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. *Zootaxa* 3665(1): 1–414.
- Hoch, H., Bonfils, J., Reynaud, B. & Attié, M. (2003) First record of troglobitic Hemiptera (Fulgoromorpha: Cixiidae) from La Réunion Island. *Annales de la Société Entomologique de France*, 39(3): 265–270.
- Husana, D.E.M., Naruse, T. & Kase, T. (2010) A new species of the genus *Karstarma* (Crustacea: Decapoda: Brachyura: Sesarmidae) from anchialines caves in the Philippines. *Raffles Bulletin of Zoology*, 58(1): 51–55.
- IGN (2018) Géoportail. Institut national de l'information géographique et forestière (IGN). At <https://www.geoportail.gouv.fr/>. Consulted 2018.
- Ihle, J.E.W. (1912) Ueber eine kleine Brachyuren-Sammlung aus unterirdischen Flüssen von Java. *Notes from the Leyden Museum*, 34(3–4): 177–182.
- Krauss, F. (1843) *Die Südafrikanischen Crustaceen, Eine Zusammenstellung aller bekannten Malacostraca, Bemerkungen über deren Lebensweise und geographische Verbreitung, nebst Beschreibung und Abbildung mehrer neuen Arten*. Stuttgart, Schweizerbartsche: 1–68, pl. 61–64.
- Lénat, J.-F., Gibert-Malengreau, B. & Galdéano, A. (2001) A new model for the evolution of the volcanic island of Réunion (Indian Ocean). *Journal of Geophysical Research*, 106(B5): 8645–8663.
- Michon, L. (2018) Tunnel de lave du Brûlé des Citrons Galets. In DEAL Réunion, Inventaire National du Patrimoine Géologique, Volcanisme (13 fiches), fiche n°12: 1–11. At <http://www.reunion.developpement-durable.gouv.fr/inventaire-national-du-patrimoine-geologique-r389.html>. Consulted 2018.

- Naruse, T. & Ng, P.K.L. (2007) On a new species of cavernicolous crab of the genus *Sesarmoides* Serène & Soh, 1970 (Crustacea: Decapoda: Brachyura: Sesarmidae) from Sulawesi, Indonesia. *Raffles Bulletin of Zoology*, 55(1): 127–130.
- Ng, P.K.L. (1988) A new sesarmine crab of the genus *Sesarmoides* Serène and Soh. 1970 (Crustacea Decapoda. Brachyura. Grapsidae) from Arawe Island, New Britain, Solomon Sea, with notes on the genus. *Micronesica*, 21: 181–187.
- Ng, P.K.L. (2002) New species of cavernicolous crabs of the genus *Sesarmoides* from the Western Pacific, with a key to the genus (Crustacea: Decapoda: Brachyura: Sesarmidae). *Raffles Bulletin of Zoology*, 50(2): 419–435.
- Ng, P.K.L. & Guinot, D. (2001) On the land crabs of the genus *Discoplax* A. Milne Edwards, 1867 (Crustacea: Decapoda: Brachyura: Gecarcinidae), with description of a new cavernicolous species from the Philippines. *Raffles Bulletin of Zoology* 49(2): 311–338.
- Ng, P.K.L., Guinot, D. & Iliffe, T.M. (1994) *Sesarmoides ultrapes* new species, a remarkable sesarmine crab from caves in the Solomon Islands (Decapoda: Brachyura: Grapsidae). *Crustacean Research*, 23: 12–22.
- Ng, P.K.L., Guinot, D. & Davie, P.J.F. (2008) *Systema Brachyurorum*: Part 1. An Annotated checklist of extant Brachyuran crabs of the world. *Raffles Bulletin of Zoology*, supplement series, 17: 1–286.
- Orchard, M. (2012). *Crabs of Christmas Island*. Christmas Island Natural History Association: 1–287.
- Orchard, M. (2018). Crabs of Christmas Island. At <https://www.christmasislandcrabs.com/>. Consulted 2018.
- Poupin, J. (2009) *Crustacés de la Réunion, Décapodes et Stomatopodes*. IRD Editions, Marseille: 140 pp.
- Robert, L. (2014) Une nouvelle espèce de crabe observée pour la première fois à la Réunion. *Le Journal de l'île de la Réunion*, édition du 17 novembre 2014, n°21118: 1, 17.
- Rochat, J., Blard, F., Gasnier, S. & Poussereau, J. (2003) Étude de la faune d'arthropodes de la caverne du Brûlé des Citrons Galets et de ses abords. *Rapport d'expertise, Insectarium of La Réunion/Cyathea*: 1–70.
- Sendra, A., Jiménez-Valverde, A., Rochat, J., Legros, V., Gasnier, S. & Cazanove, G. (2017) A new and remarkable troglobitic *Lepidocampa* Oudemans, 1890 species from La Réunion Island, with a discussion on troglobiomorphic adaptations in campodeids (Diplura). *Zoologischer Anzeiger*, 266: 95–104.
- Takakura, H. (2018) *Karstarma jacksoni* (Balss, 1934). At <http://www010.upp.so-net.ne.jp/uca/crab/crabxxxx/crab0269.html>. Consulted 2018.
- Tweedie, M.W.F. (1947) On the Brachyura of Christmas Island. *Raffles Bulletin of Zoology*, 18: 27–42.
- Whitten, T. & Ng, P.K.L. (2015a) *Karstarma balicum*. The IUCN Red List of Threatened Species 2015: e.T62082915A79816458. At <http://dx.doi.org/10.2305/IUCN.UK.2015-3.RLTS.T62082915A79816458.en>. Consulted 2018.
- Whitten, T. & Ng, P.K.L. (2015b). *Karstarma emdi*. The IUCN Red List of Threatened Species 2015: e.T62101765A79817417. <http://dx.doi.org/10.2305/IUCN.UK.2015-3.RLTS.T62101765A79817417.en>. Consulted 2018.
- Wowor, D. & Ng, P.K.L. (2009) Two new species of sesarmid crabs (Crustacea: Decapoda: Brachyura) associated with limestone formations in West Papua, Indonesia. *Zootaxa*, 2025: 21–31.
- Wowor, D. & Ng, P.K.L. (in press) A new sesarmid crab (Crustacea: Decapoda: Brachyura) associated with limestone formations in East Java, Indonesia. *Zootaxa*. in press.

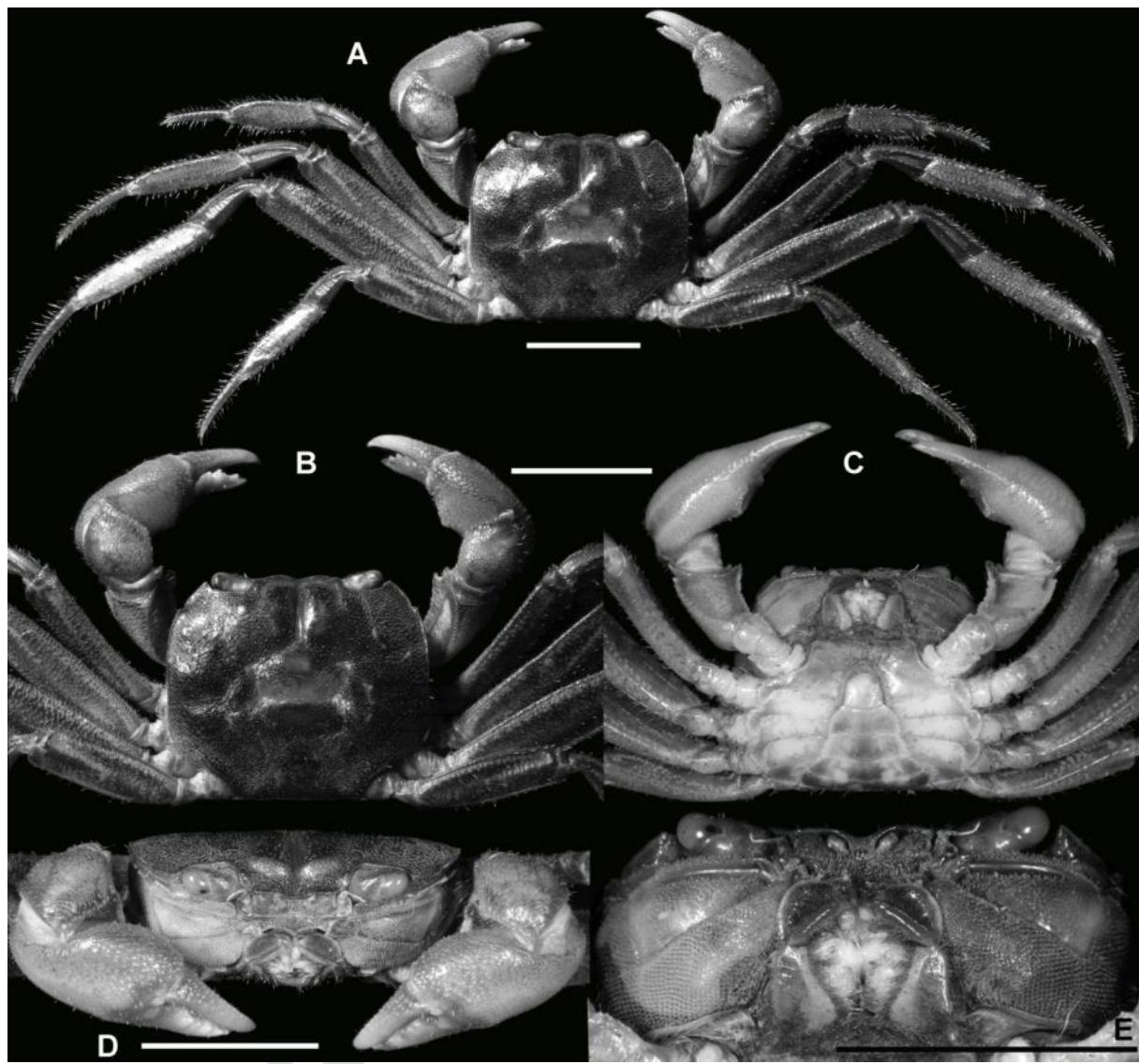
FIGURES

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).

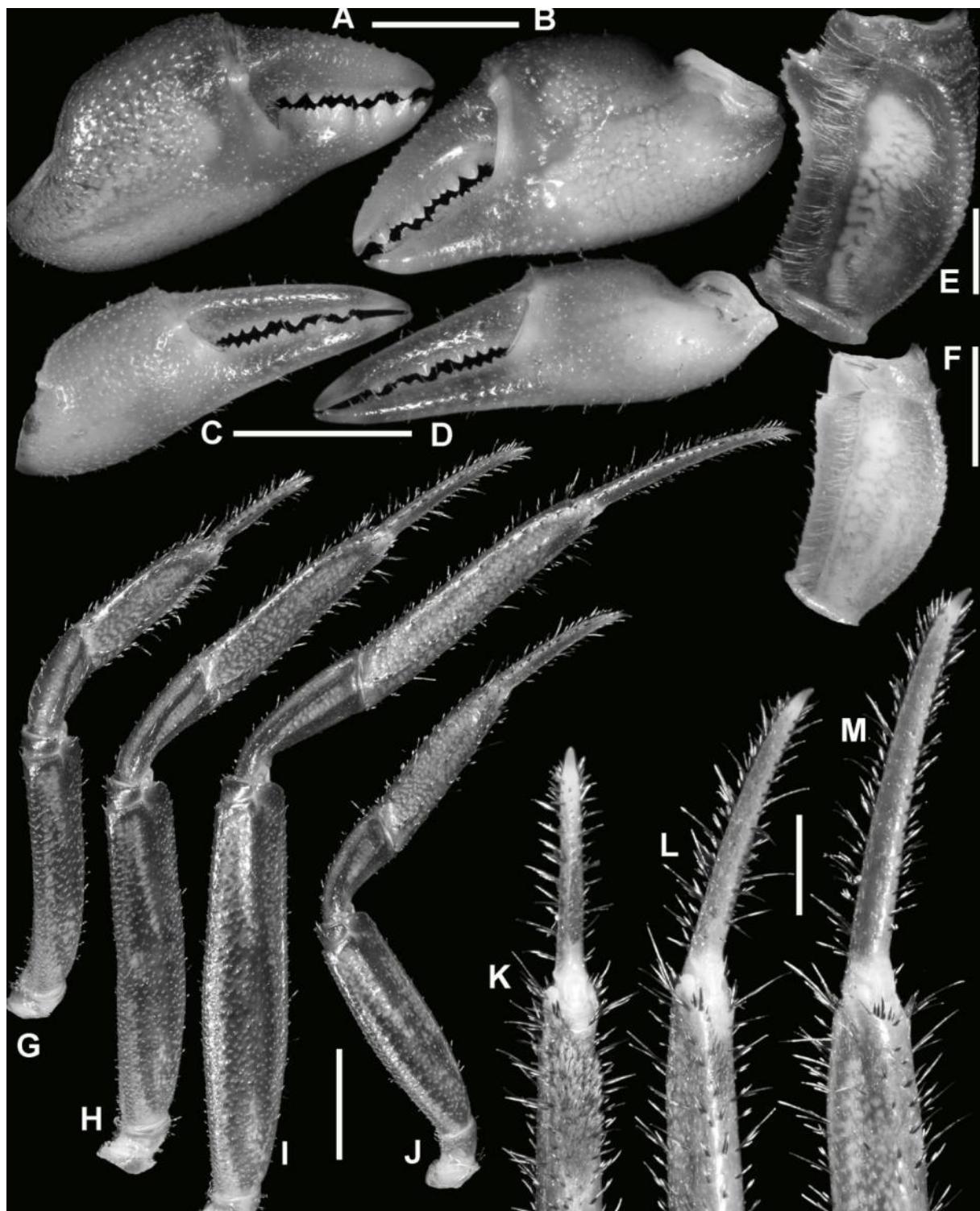


Figure 2. *Karstarma vulcan* sp. nov., holotype male, 16.2×18.9 mm MNHN-IU-2013-7243 (A, B, E, G, M); paratype female, 13.7×16.9 mm, MNHN-IU-2013-7240 (C, D, F). Right chela, outer (A, C) and inner views (B, D); merus of right cheliped, inner view (E, F); right ambulatory legs 1–4 (P2–P5), outer views (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).



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. Levener, 30/08/2014.

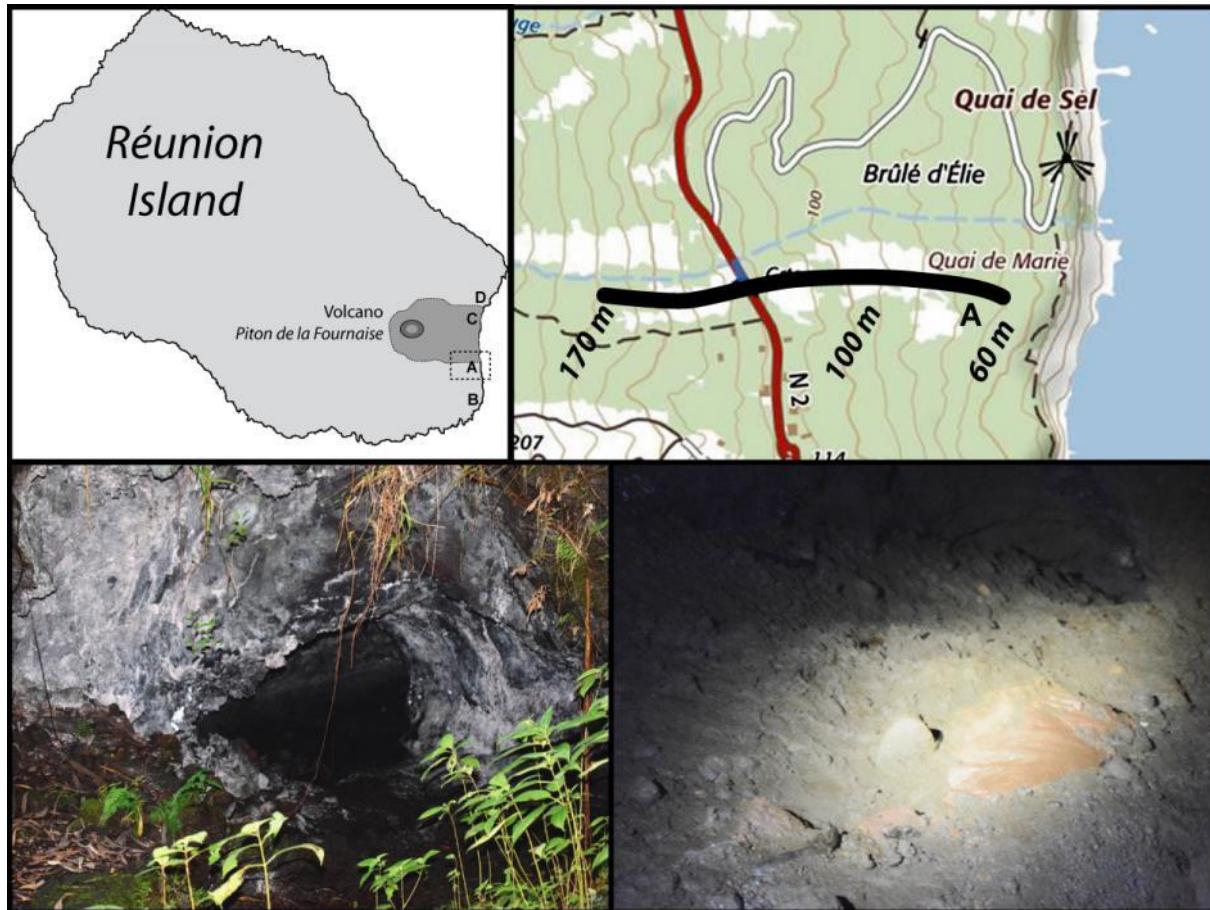


Figure 4. Habitat of *Karstarma vulcan* in Réunion Island. Upper raw, left: Réunion Island with indication of the volcano ‘Piton de la Fournaise’ and its ‘enclos’ (grey area) with places where crabs *Karstarma* were observed: A, ‘Brûlé des Citrons Galets’ (dotted rectangle enlarged on the right); B, ‘Grotte au Trésor’; C ‘Coulée de 2004’; D, ‘Grotte des Hirondelles’. Upper raw, 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).



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.

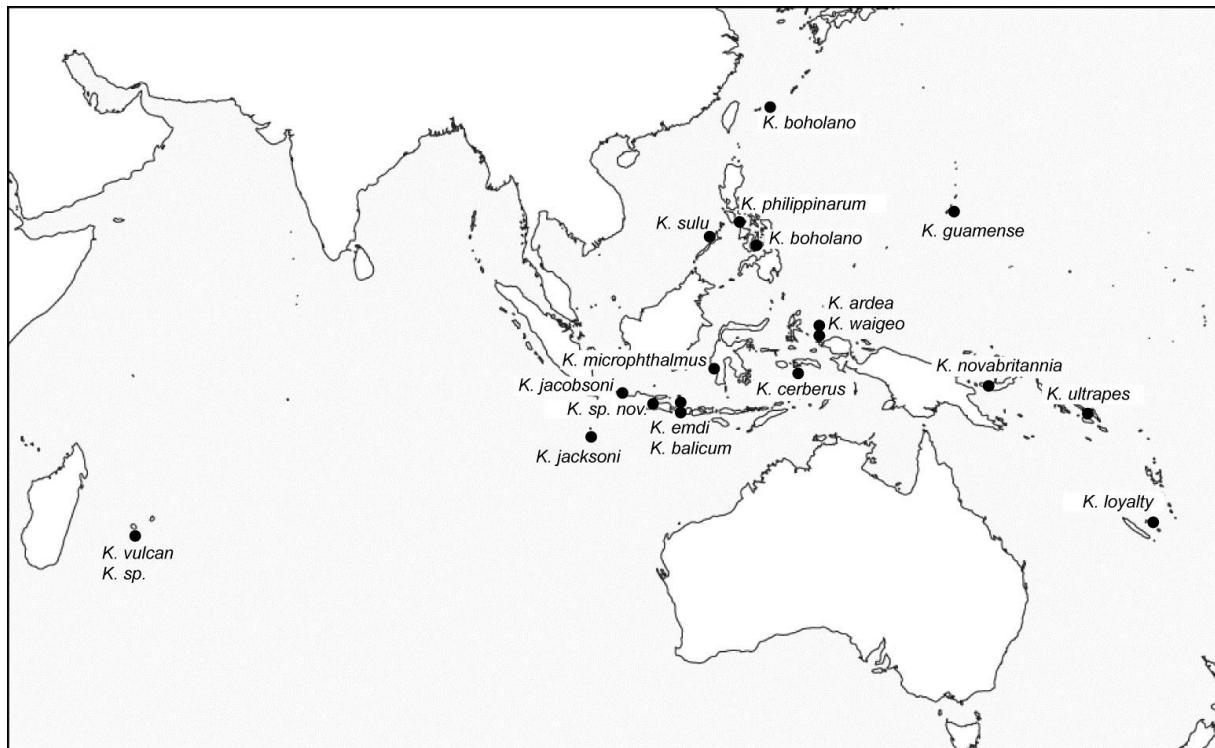


Figure 6. Geographic distribution of the 17 or 18 species of *Karstarma*, from west to east: *Karstarma vulcan* and *K. sp.* (Réunion); *K. jacksoni* (Christmas Island); *K. jacobsoni* (Central Java); *K. sp. nov.* (East Java, from Wowor & Ng, in press); *K. emdi* and *K. balicum* (Nusa Penida Island, 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).

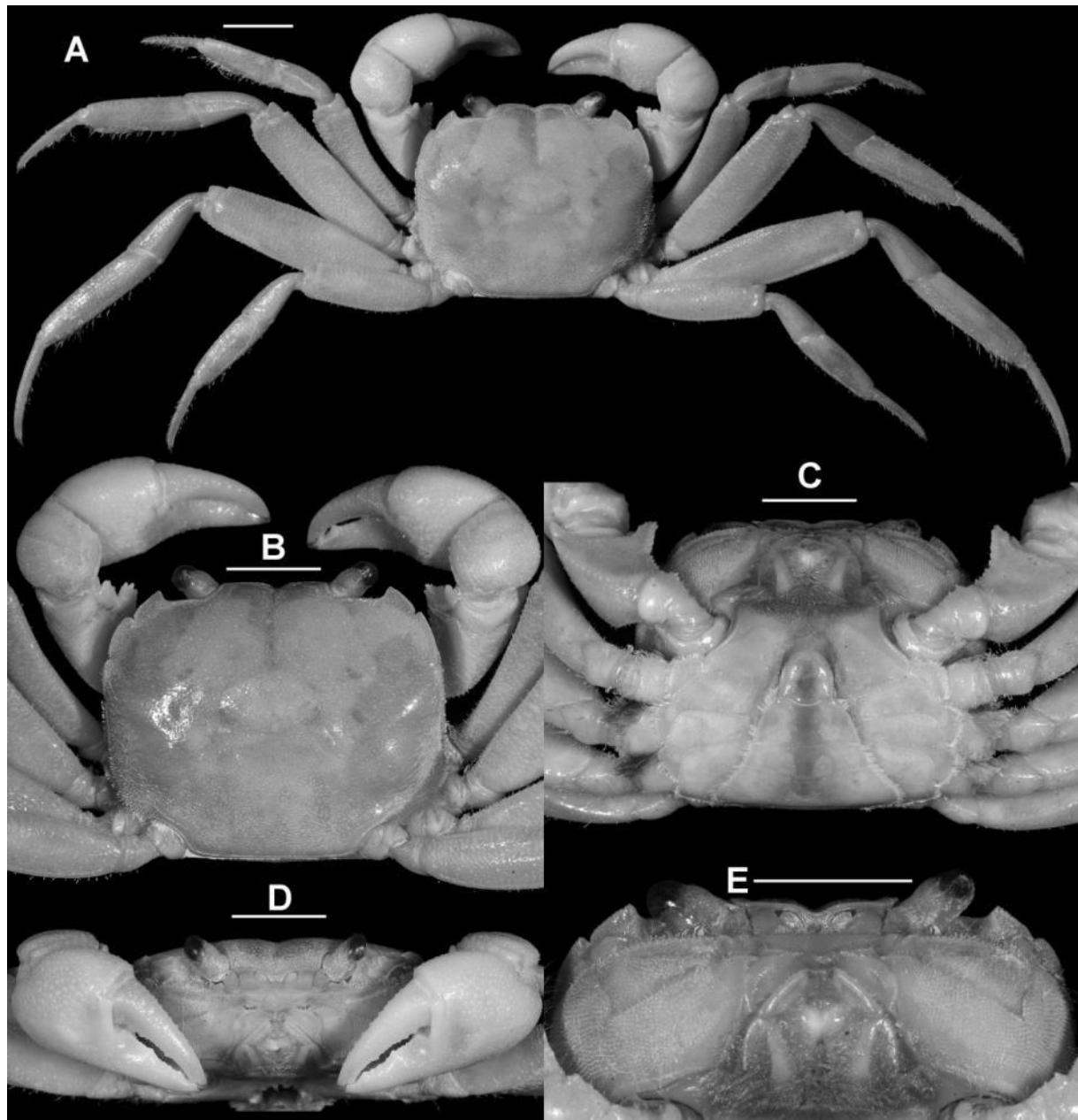


Figure 7. *Karstarma jacksoni* (Balss, 1934), 1 male 15.4 × 18.7 mm, Christmas Island, WAM C13968. A. dorsal habitus; B–D carapace and chelae, dorsal, ventral, frontal views, respectively; E. Front, orbits, buccal cavern and pterygostomian area (scales bars, 5 mm).

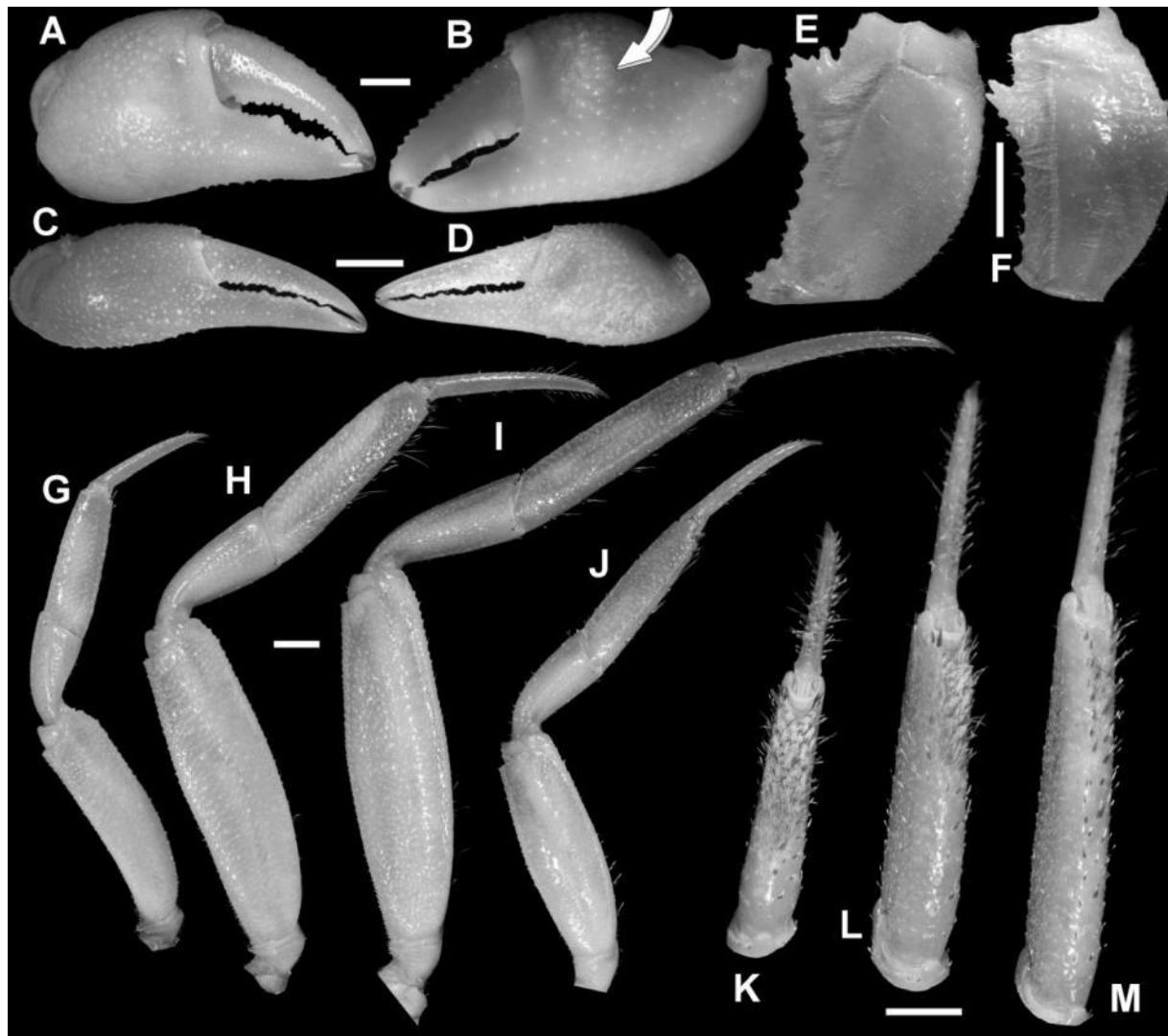


Figure 8. *Karstarma jacksoni* (Balss, 1934), Christmas Island, male 15.4×18.7 mm, Christmas Island, WAM C13968 (A, B, E, G–M), female 14.3×18.05 mm, WAM C13968 (C, D, F). Right chela, outer (A, C) and inner views (B, D), arrow indicate ‘stridulating’ ridge; merus of right cheliped, inner view (E, F); 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).

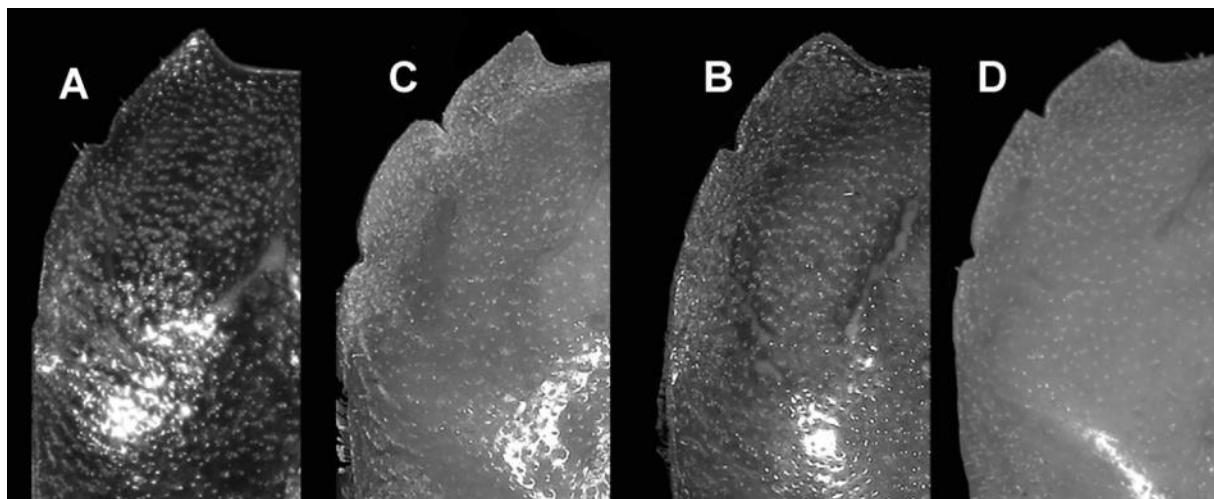


Figure 9. Comparison of anterolateral margins of carapace in *Karstarma vulcan* and *K. jacksoni* for specimens of approximately same size and sex. *Karstarma vulcan*, A) holotype male 16.2×18.9 mm, MNHN-IU-2013-7243; B) paratype female 13.7×16.9 mm, MNHN-IU-2013-7240. *Karstarma jacksoni*, C) male 15.4×18.7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

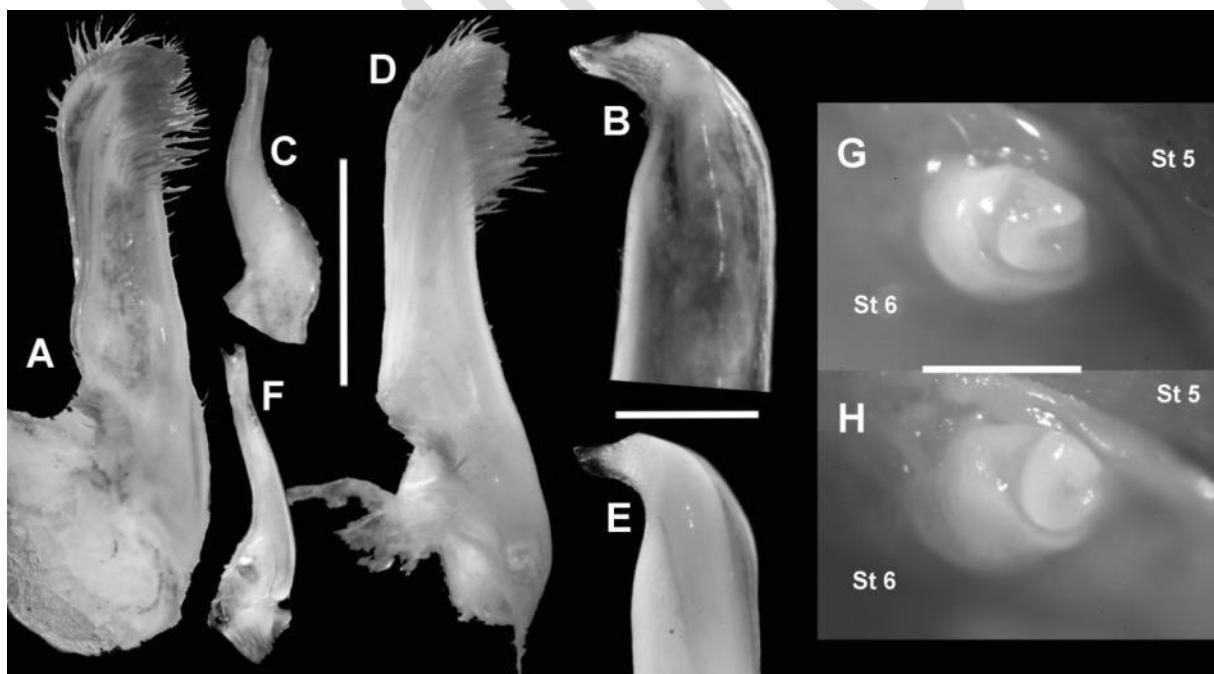


Figure 10. External genital organs in *Karstarma vulcan* sp. nov., A–C) holotype male 16.2×18.9 mm, MNHN-IU-2013-7243, G) paratype female 13.7×16.9 mm, MNHN-IU-2013-7240, and *K. jacksoni*, D–F) male 15.4×18.7 mm, WAM C13968, H) female 14.3×18.1 mm, WAM C13968. G1 sternal (A, D) and abdominal face (B, 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).

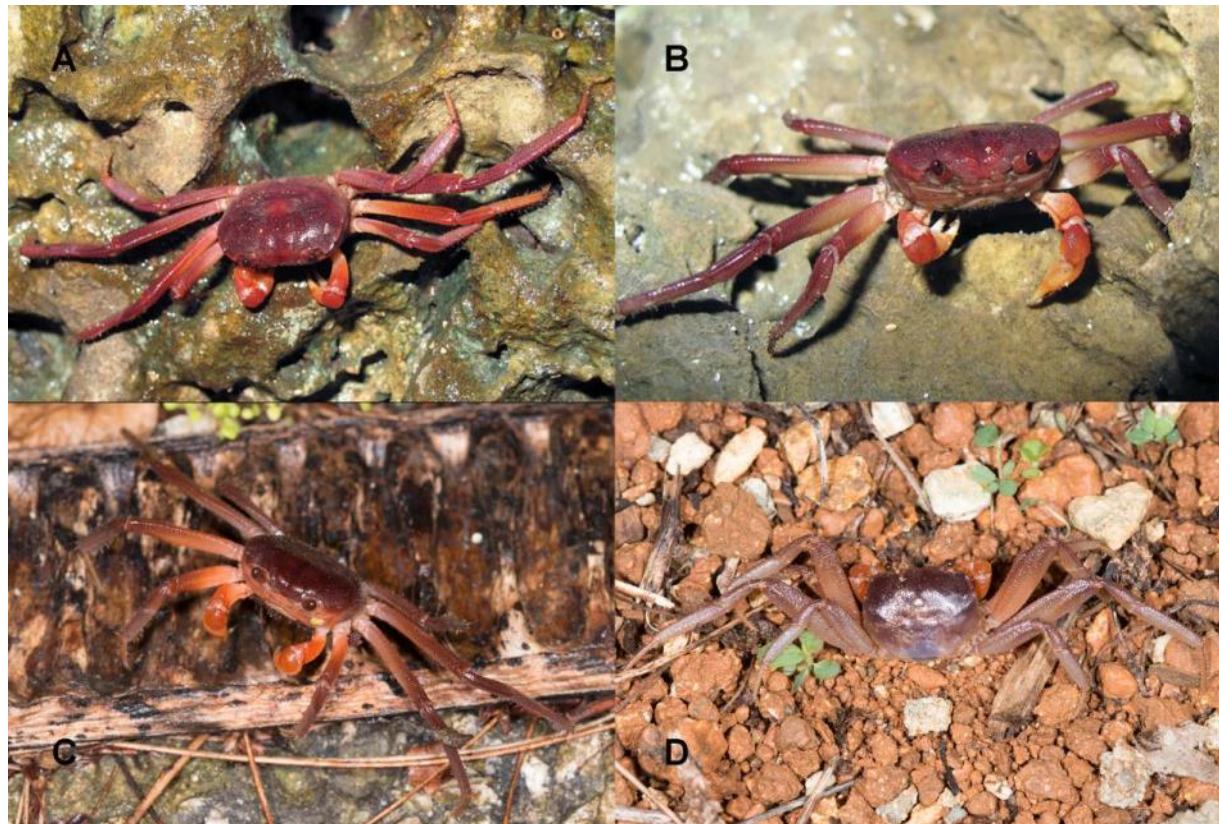


Figure 11. Live colour of *Karstarma jacksoni* (Balss, 1934), Christmas Island. A, B) in cave, photographs Max Orchard; C, D) outside cave, Photographs Hitoshi Takakura.