Karstarma umbra, a new species of cavernicolous crab (Brachyura: Sesarmidae) from Vanuatu, with a key to the genus

Peter K. L. Ng

Abstract.—A new species of cavernicolous sesarmid crab is described from Vanuatu. Karstarma umbra sp. nov. belongs to a group of three species that has the chitinous distal part of the male first gonopod slender and elongate. The new species can easily be distinguished from K. balicum (from Bali, Indonesia) and K. loyalty (from Loyalty Islands) by its distinctly longer ambulatory legs and its relatively more slender male first gonopod. Karstarma umbra is morphologically closest to K. waigeo (from Indonesian Papua) but has proportionately longer legs and the outer margin of the male first gonopod is distinctly concave. The taxonomy of the genus is discussed and a revised key to the 18 species is provided.

Key words: Taxonomy, Grapsoidea, South Pacific, new species, key, Karstarma, species-groups

Introduction

Seventeen species of the cave sesarmid genus Karstarma Davie & Ng, 2007, are known from the Indian Ocean and western Pacific (Ng et al., 2008; Wowor & Ng, 2009, 2018; Husana et al., 2010; Poupin et al., 2018) (Table 1). A new species is here described from caves in Santo Island in Vanuatu. The taxonomy of the genus is discussed and a revised key is constructed to help identify the species.

Specimens are deposited in the Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum, National University of Singapore; and the Naturalis Biodiversity Centre (ex Rijksmuseum van Natuurlijke Historie, RMNH), Leiden, The Netherlands.

The terminology used follows Davie et al. (2015). Measurements provided, in millimetres, are of the maximum carapace width and length, respectively. The ambulatory merus is measured with the structure positioned horizontally on a level surface; the length being taken from the proximal angle with the basisischium to the distalmost margin where it articulates with the carpus; while the width is obtained at the widest point, which is usually at the median point (cf. Maenosono & Naruse, 2016). The following abbreviations are used: G1 = male first gonopod; G2 = male second gonopod; P2–P5 = pereopods 2–5 (ambulatory legs 1–4, respectively).

Taxonomy

Family Sesarmidae Dana, 1851

Karstarma Davie & Ng, 2007

Type species

Sesarmoides boholano Ng, 2002, by original designation.

Remarks

Although Wowor & Ng (2009) recognised
two groups of *Karstarma* which they defined by the shape of the carapace, proportions of the P3 and P4, as well as structures of the G1 and vulva; three groups are actually discernible. Wowor & Ng (2018) noted that the three species of *Karstarma* from Java and Sulawesi appeared to be closer to species of *Geosesarma* De Man, 1892 (see Ng & Wowor, 2019) and they form a third group (see also Poupin et al., 2018).

Members of the *K. ultrapes* species-group are the most distinctive, possessing a carapace

Table 1. List of known *Karstarma* species

| Species                  | Distribution                                      | References                                                      |
|--------------------------|---------------------------------------------------|-----------------------------------------------------------------|
| *Karstarma ardea*        | Wowor & Ng, 2009                                  | Wowor & Ng (2009)                                               |
| *Karstarma balicum*      | Nusa Penida, Bali, Indonesia                      | Ng (2002)                                                      |
| *Karstarma boholano*     | Bohol, Philippines; Ishigaki Island, Ryukyu, Japan; Green Island, Taiwan | Ng (2002), Naruse *et al.* (2005), Husana *et al.* (2010), Li *et al.* (2019) |
| *Karstarma cerberus*     | Nusa Lain, west of Ambon, Indonesia               | Holthuis (1964), Fransen *et al.* (1997), present study        |
| *Karstarma emdi*         | Nusa Penida, Bali, Indonesia                      | Ng & Whitten (1995), Ng (2002)                                 |
| *Karstarma guamense*     | Tumon Bay, Guam                                   | Ng (2002)                                                      |
| *Karstarma jacksoni*     | Christmas Island, Australian Indian Ocean Territory | Balss (1934), Orchard (2012), Poupin *et al.* (2018)           |
| *Karstarma jacobsoni*    | Gunung Sewu, Central Java, Indonesia              | Ihle (1912), Holthuis (1964), Naruse & Ng (2007), Wowor & Ng (2018) |
| *Karstarma loyalty*      | Lifou Island, Loyalty Islands, New Caledonia      | Ng (2002)                                                      |
| *Karstarma malang*       | Malang, East Java, Indonesia                      | Wowor & Ng (2018)                                              |
| *Karstarma microphthalmus* | Gua Marapetang, south Sulawesi, Indonesia      | Naruse & Ng (2007)                                             |
| *Karstarma novabritannia* | Arawe Island, New Britain                         | Ng (1988), present study                                       |
| *Karstarma philippinarum* | Boracay and Samal Islands, Philippines            | Husana *et al.* (2010)                                        |
| *Karstarma sulia*        | Palawan, Philippines                              | Ng (2002)                                                      |
| *Karstarma ultrapes*     | Florida and Malaita Islands, Solomon Islands      | Ng *et al.* (1994), Wowor & Ng (2009), Husana *et al.* (2010) |
| *Karstarma umbra* sp. nov. | Santo, Vanuatu                                   | Present study                                                  |
| *Karstarma vulcan*       | Réunion Island                                    | Poupin *et al.* (2018)                                         |
| *Karstarma waigeo*       | Raja Ampat, Indonesian Papua                      | Wowor & Ng (2009)                                              |
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which is clearly trapezoidal in shape with the posterior part very wide; the epigastric and protogastric cristae are fused, forming a large swelling that protrudes anteriorly, intruding to the level of the frontal margin, with the frontal region just or barely visible in dorsal view; the cornea of the eye is not reduced; the P4 is very elongate (more than four times the carapace length); there are no prominent long tufts of setae between the coxae of P2–P4; the G1 has the chitinous distal part straight, cylindrical and gently bent outwards at an angle of about 30–40° along the longitudinal axis; and the vulva is formed by a large U-shaped posterior sternal vulval cover with a prominent anterior cover, with both projections partially covering the prominent rounded operculum. Three species are in this group: K. ardea, K. philippinarum and K. ultrapes. No ovigerous females are known but on the basis of their small vulvae, their eggs are probably small and less than a millimetre in diameter.

Members of the K. jacobsoni species-group also have a trapezoidal carapace but the posterior part is proportionately less wide and the carapace appears more subquadrate; the epigastric and protogastric cristae are lower, with the sharp epigastric crista protruding anteriorly to some degree but not completely obscuring the frontal region in dorsal view; the cornea of the eye is distinctly reduced; the P4 is elongate (less than four times the carapace length); there are prominent tufts of dense, long setae between the coxae of P2–P4; the G1 has the chitinous distal part straight, cylindrical and sharply bent outwards at an angle of about 90° along the longitudinal axis; and the vulva has a prominent posterior sternal vulval cover with a small anterior one, the whole structure being distinctly elevated. Eleven species are in this group: K. balicum, K. boholano (type species), K. cerberus, K. emdi, K. guamense, K. jacksoni, K. loyalty, K. novabritannia, K. sulu, K. vulcan, and K. waigeo. The egg size of several species are known and they are all small, less than a millimetre in diameter (see Ng, 2002; Orchard, 2012; Poupin et al., 2018; unpublished data), with Li et al. (2019) recently obtaining planktonic zoeae for K. boholano. Most of the species have a short and truncate chitinous distal part of the G1; only in three species is the chitinous distal part elongate and tapering—K. balicum, K. loyalty and K. waigeo, like in K. umbra sp. nov.

The figures of K. cerberus and K. novabritannia appear to depict the two species possessing epigastric cristae which are directed anteriorly and reaching the frontal margin (Holthuis 1964: fig. 1, 2a; Ng 1988: pl. 1) like those in the K. ultrapes species-group (Fig. 6A, B). This is, however, not accurate as the cara-
pace had been slightly tilted anteriorly when the structure was originally drawn or photographed. Both species actually have normal epigastric cristae that do not protrude anteriorly (Fig. 5A–D). These two species also have setae between the coxae of P2–P4 but the setae are concentrated on the sides of these coxae, relatively shorter and less dense than those of the other species in the group and when viewed ventrally, less obvious (Fig. 5F, G). This is like the condition in species of the *K. ultrapes* species-group (Fig. 6C, D). In all the other species in the *K. boholano* species-group, these tufts of setae are dense, long and prominent in ventral view (e.g., Fig. 3A, B). In the holotype of *K. novabritannia*, the specimen has been denuded so there are no more setae at the base of the legs (Fig. 5E) but these remain visible in the female paratype (Fig. 5F, G). The vulvae of these two species have not been described or figured before but they are similar to the condition in other members of the group (see Fig. 5H).

*Karstarma* as it now understood (sensu Davie & Ng, 2007) is therefore likely to be polyphyletic, with the species resembling each other only because they live in caves. That being said, members of the *K. boholano* and *K. ultrapes* species-groups live in coastal or anchialine cave systems while those of the *K. jacobsoni* group live in inland limestone caves. When a full revision can be done, new genera can then be established. The *K. jacobsoni* species-group would probably be the most difficult one to determine because it is close to *Geosesarma* which is a large polyphyletic genus (see Ng & Wowor, 2019).

It is well known that cavernicolous taxa often possess long ambulatory legs and paler body coloration, but true stygobites invariably lose all their coloration and their eyes are reduced (see Holthuis, 1986; Guinot, 1988, 1994). In the case of *Karstarma*, only the three species now known from Java and Sulawesi (*K. jacobsoni*, *K. microphthalmus* and *K. malang*) can be regarded as stygobites. All the other species, including *K. umbra*, are best described as stygophiles or stygoxenes, and while mainly found in caves, are probably found in habitats outside the caves as well (see Ng, 2013; Ng & Guinot, 2014). Most of these species in fact, are well pigmented or even dark coloured. *Karstarma jacksoni*, for example, has a dark brown carapace and bright orange chelae (Orchard, 2012) and has been collected in caves as well as nearby limestone formations, hiding in crevices during the day and coming to forage only at night (unpublished data). These habitats are often densely vegetated so observing and collecting the crabs is difficult.

**Karstarma umbra sp. nov.**
(Figs. 1–4)
LSIDurn:lsid:zoobank.org:act:BFCB8970-64A9-4551-B8FA-353EB6E82265

**Material examined**
Holotype: male (15.0 × 12.7 mm) (ZRC 2019.1834), sample SK05-Lips32, vial 2044, in single gallery, 60 m long, Dhevathar Cave, near Port Olry, 15°02.091′S 167°3.894′E, northeastern Santo, Vanuatu, coll. J Lips, 17 August 2005. Paratypes: 1 male (14.0 × 11.7 mm), 1 female (17.5 × 14.2 mm) (ZRC 2019.1835), same data as holotype; 1 female (11.6 × 10.0 mm) (ZRC 2018.45), Loren Cave, 14°58.850′S 167°03.553′E, east coast of Cape Queiros, northeastern Santo, Vanuatu, coll. F. Bréhier, 8 September 2006.

**Comparative material**
*Karstarma jacksoni* (Balss, 1934): 1 male (ZRC 2009.824), The Settlement, Christmas Island, coll. 7 December 2007; 2 males (ZRC 2019.1126), on wall of Cocos Padang Lodge, Christmas Island, coll. 15–20 December 2000; 1 female (ZRC 2019.1128), Cocos Padang Lodge, Christmas Island, coll. 15–20 December 2000; 1 male (ZRC 2019.1127), Cocos Padang Lodge, Christmas Island, vicinity, coll.
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H. H. Tan, 16 December 2014; 1 male (ZRC 2019.416), Captain’s Retreat, in bathroom, Christmas Island, coll. 5 February 2012; 1 male (ZRC 2017.720), Retreat, Christmas Island, coll. 26 March 2011; 1 female (ZRC 2017.717), Runaway Cave, Waterfall Road,

Fig. 1. Karstarma umbra sp. nov. A, C, holotype male (15.0 × 12.7 mm) (ZRC 2019.1834), Vanuatu; B, D, paratype female (17.5 × 14.2 mm) (ZRC 2019.1835), Vanuatu. A, B, overall dorsal view; C, D, dorsal view of carapace.
Fig. 2. *Karstarma umbra* sp. nov., holotype male (15.0 × 12.7 mm) (ZRC 2019.1834), Vanuatu. A, frontal view of cephalothorax; B, left third maxilliped; C, outer view of left chela; D, inner view of left chela; E, G–I, right P2–P5 (all to same scale); F, propodus and dactylus of P2 showing setal brush on ventral margins; J, anterior thoracic sternum and sternopleonal cavity; K, pleon.
**Fig. 3.** *Karstarma umbra* sp. nov. A, holotype male (15.0 × 12.7 mm) (ZRC 2019.1834), Vanuatu; B–D, paratype female (17.5 × 14.2 mm) (ZRC 2019.1835), Vanuatu. A, B, anterior thoracic sternum and pleon; C, sternopleonal cavity and vulvae; D, left vulva; E, outer view of left chela.

**Fig. 4.** *Karstarma umbra* sp. nov., holotype male (15.0 × 12.7 mm) (ZRC 2019.1834), Vanuatu. A, left G1 (dorsal view); B, distal part of left G1 (ventral view); C, distal part of left G1 (submesial view); D, E, (ventral view at different angles); F, left G2 (dorsal view). All structures demuded. Scales: A, F = 0.5 mm; B–E = 0.2 mm.
Fig. 5. *Karstarma novabritannia* (Ng, 1988). A, C, E, holotype male (23.9 × 20.0 mm) (ZRC 1965.7.29.66), New Britain; B, D, F–H, paratype female (26.7 × 24.9 mm) (ZRC 1965.7.29.67). A, B, overall dorsal view; C, D, dorsal view of carapace; E, F, anterior thoracic sternum and pleon; G, tufts of setae between coxae of P2 and P3; H, sternopleonal cavity and vulvae.
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Christmas Island, coll. 30 January 2010; 1 male (ZRC 2017.716), Runaway Cave, Waterfall Road, Christmas Island, coll. 28 January 2010; 5 males, 5 females (ZRC 2017.779), Runaway Cave, Waterfall Road, coll. 26 January 2010; 1 female (ZRC 2019.719), Freshwater Cave, Waterfall Road, Christmas Island, coll. 21 March 2011; 2 ovigerous females (ZRC 2017.715), Whip Cave, Waterfall Road, coll. 30 January 2010; 1 female ZRC 2013.1853), in 10–15 m airpocket, in submarine cave, Thundercliff Cave, 10°27.964′S 105°36.404′E, Christmas Island, coll. 30 January 2010; 1 female (ZRC 2019.718), in 10–15 m airpocket, in submarine cave, Thundercliff Cave, 10°27.964′S 105°36.404′E, Christmas Island, coll. 29 January 2010; 1 female (ZRC 2019.354), in 10–15 m airpocket, in submarine cave, Thundercliff Cave, 10°27.964′S 105°36.404′E, Christmas Island, coll. 16 February 2012. Karstarma cerberus (Holthuis, 1964): Holotype male (34.0 × 30.0 mm) (RMNH D19488), in complete darkness, cave on Nusa Lain island, just west of Ambon, Moluccas, Indonesia, coll. F. Kopstein, 21 March 1923; paratypes: 2 males, 5 females (RMNH D19489); Indonesia, same data as holotype. Karstarma novabritannia (Ng, 1988): Holotype male (23.9 × 20.0 mm) (ZRC 1965.7.29.66), Arawe Island, New Britain, Sol-
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omon Sea, ca. 6°8′53″S 149°2′13″E, leg. P. H. Hediger, 1933; paratype: 1 female (26.7 × 24.9 mm) (ZRC 1965.7.29.67), same data as holotype. *Karstarma emdi* (Ng & Whitten, 1995): 2 males, 2 females (ZRC 2004.99), in cave, Nusa Penida, Bali, Indonesia, coll. A. J. Whitten, August 2003. *Karstarma boholano* (Ng, 2002): 2 females (ZRC 2011.1039), Panglao, Bohol, Philippines, coll. P. K. L. Ng, December 2010. In addition, see material of other *Karstarma* species in Ng et al. (1994), Ng (2002), Naruse & Ng (2007), Wowor & Ng (2009, 2018) and Husana et al. (2010).

**Diagnosis**

Carapace trapezoidal in shape, widest between P3 and P4 bases (Fig. 1A–D); dorsal surface mostly smooth except for low striae on branchial region, with small, short tufts of setae evenly distributed on anterior half; external orbital tooth, when visible, separated from first anterolateral tooth by small but distinct V-shaped cleft, outer margin gently convex, ca. 3 times length of inner margin, sometimes with small shallow cleft behind first one; rest of anterolateral margin gently convex (Figs. 1C, D, 2A); posterolateral margin gently diverging (Fig. 1C, D); frontal margin distinctly bilobed, with shallow, wide, median notch, margin of each lobe convex; epigastric crista distinct, 4-lobed; postorbital crista very low, just visible as slight bulges (Fig. 1C, D); gastric region well defined, median longitudinal groove present along epi- and protogastric regions, diverging on meso- and metagastric regions and surrounding gastro-cardiac groove, cervical groove distinct (Fig. 1C, D); eyes well developed filling orbit, with large, pigmented cornea (Figs. 1C, D, 2A). Third maxilliped with ischiium much longer than merus; slender exopod with long flagellum (Fig. 2B). Thoracic sternites 2 and 3 fused, suture indistinct; suture between 3 and 4 visible as low ridge (Figs. 2J, 3A, B); sternopleonal cavity deep, without male pleonal locking tubercle, rim of sternople-
**Etymology**

The name is derived from the Latin for spirits in shadows, alluding to the cave habitat of the species. The name is used as a noun.

**Remarks**

The G1 structure of *K. umbra* has the distal chitinous part elongate and slender, and is a condition shared with *K. balicum*, *K. loyalty* and *K. waigeo*. *Karstarma umbra* can easily be distinguished from *K. balicum* and *K. loyalty* by its proportionately longer ambulatory legs and the G1 being relatively more slender with the chitinous distal part subtruncate. *Karstarma umbra* most closely resembles *K. waigeo* but the ambulatory legs are notably longer than *K. waigeo*, the meri of P3 and P4 being 3.8 and 4.2 times, respectively (Fig. 2G, H) (versus meri of P3 and P4 being 3.5 and 4.0 times longer than wide, respectively; cf. Wowor & Ng, 2009: figs. 2A, 3A). Even more significant are the differences in proportions of the propodus of P3 and P4; in *K. umbra*, the length to width proportion of the P4 propodus is 5.4 (Fig. 2H) whereas in *K. waigeo* and *K. umbra* are superficially similar and both have the tip of the chitinous distal part bifurcate, that of *K. umbra* is proportionately more slender and the outer margin is distinctly more concave (Fig. 4A–E).

**Biology**

Like other *Karstarma* species, *K. umbra* is almost certainly a semiterrestrial species, hiding in crevices during the day and foraging on karst walls at night (see Ng & Whitten, 1995; Ng, 2002). The types of *K. umbra* were all collected from the karst systems on the northeastern part of Santo. Three of specimens were from Dhevathar Cave near Port Olry (15°02.091'S 167°3.894'E) and were obtained during a preliminary survey of the karst systems on Santo Island (L. Deharveng, personal communication; see also Lips et al., 2011). One paratype female was collected from Loren Cave, which is an anchialine system about 30 m from the coastline (see Bréhier et al., 2011) and is only about 6 km to the north of Dhevathar Cave. In these cave systems, two other crabs were found: the sesarmid *Labuani um trapezoideum* (H. Milne Edwards, 1837) (as “*Laubanium trapezoideum*”) and the varunid *Orcovita cf. meneiceae* Ng & Ng, 2002 (as “*Orcovita sp.*”) (Bréhier et al., 2011: 311). *Labuani um trapezoideum* is a semiterrestrial species not normally found in caves but has a preference for vertical walls with fast flowing waters and the Loren specimen probably entered the cave while foraging (see Jeng et al., 2003; Naruse & Ng, 2020). The completely aquatic genus *Orcovita* is known to be a wholly anchialine species and has been found in cave systems (see Ng et al., 1996; Davie & Ng, 2012).

**Key to species of Karstarma**

1a. Ocular peduncle short, cornea reduced, small, eyes occupying only part of orbit

......................................................-2

1b. Ocular peduncle and cornea normal size, entirely occupying orbit...........................4

2a. Lateral margin of carapace distinctly convex; P4 merus 2.5–2.7 times longer than broad; G1 chitinous distal part relatively shorter, directed outwards at an angle of about 30° [Sulawesi, Indonesia] ...........................................-K. microphthalmus

2b. Lateral margin of carapace gently divergent, appears almost straight; P4 merus 3.5 times longer than broad or more; G1 chitinous distal part relatively long, directed outwards at angle of about 45°..............................................................3

3a. Ocular peduncle distinctly more swollen with distinct median ridge; P4 proportionately longer ratio of total leg
length to carapace width 2.5–2.7; G1 relatively more robust, chitinous distal part with tip relatively wider, more than half that of main stem [Central Java, Indonesia] – K. jacobsoni

3b. Ocular peduncle relatively less swollen, surface smooth; P4 proportionately shorter, ratio of total leg length to carapace width 2.1–2.6; G1 relatively more slender, width of chitinous distal part tapering more sharply, less than half that of main stem [East Java, Indonesia] – K. malang

4a. Carapace shape distinctly trapezoidal, posterior part much wider than anterior part; epigastric and protogastric cristae fused, swollen protruding anteriorly, intruding to level of frontal margin with frontal region not visible in dorsal view; G1 chitinous distal part relatively long, directed outwards at angle of about 45° – K. malang

4b. Carapace shape approximately sub-quadrate, slightly trapezoidal in shape, posterior part slightly wider than anterior part; epigastric and protogastric cristae lower, separate, not protruding anteriorly, not intruding to level of frontal margin with frontal region clearly visible in dorsal view; G1 chitinous distal part relatively long, directed outwards at angle of about 90°, may be slightly bent upwards or downwards – K. novabritannia

5a. Ambulatory legs relatively shorter, P3 merus 3.3–5.1 times longer than broad [Philippines] – K. philippinarum

5b. Ambulatory legs extremely long, P3 merus 5.4–5.5 times longer than broad – K. philippinarum

6a. Outer margin of external orbital tooth almost straight; posterior part of sternal vulval cover relatively more narrow, forming wider C-shaped bracket around vulva [Solomon Islands] – K. ultrapes

6b. Outer margin of external orbital tooth convex; posterior part of sternal vulval cover broad, forming U-shaped bracket around vulva [Indonesian Papua] – K. ardea

7a. Setae between coxae of P2–P4 in both sexes, not dense or long, at most with setae on sides of coxae – K. ardea

7b. With prominent dense tufts of long setae between coxae of P2–P4 in both sexes – K. ardea

8a. Tip of external orbital tooth reaching just beyond level of frontal margin; male telson equal in length to pleonal somite 6 [Ambon, Indonesia] – K. cerberus

8b. Tip of external orbital tooth not reaching level of frontal margin; male telson shorter than pleonal somite 6 [New Britain, Papua New Guinea] – K. novabritannia

9a. G1 with elongate, slender chitinous distal part – K. ardea

9b. G1 with relatively short, truncate chitinous distal part – K. ardea

10a. P4 merus 3.5–3.6 times longer than wide; tip of G1 chitinous distal part subtruncate – K. ardea

10b. P4 merus 4.0–4.2 times longer than wide; tip of G1 chitinous distal part bifurcate – K. ardea

11a. Outer margin of G1 stem with gentle submedian hump [Loyalty Islands] – K. loyalty

11b. Outer margin of G1 stem almost straight. [Bali, Indonesia] – K. balicus

12a. P4 merus 4.0 times longer than wide; P4 propodus 4.4 times longer than wide;
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G1 proportionately stouter, outer margin gently concave [Indonesian Papua]......................K. waigeo

12b. P4 merus 4.2 times longer than wide; P4 propodus 5.4 times longer than wide; proportionately more slender, outer margin distinctly concave [Vanuatu]..........................K. umbra

13a. Clefts between external orbital tooth and anterolateral teeth shallow, second tooth absent or almost undiscernible [Réunion Island, Indian Ocean]..................K. vulcan

13b. Clefts between external orbital tooth and anterolateral teeth distinct, second tooth low but often visible..................14

14a. Dorsal margin of P2–P4 meri with sharp subdistal spine [Palawan, Philippines]..........................K. sulu

14b. Dorsal margin of P2–P4 meri with subdistal angle, dentiform but not spiniform, sometimes undiscernible................15

15a. External orbital tooth usually truncate, outer margin straight to gently concave, separated from first anterolateral tooth by prominent, deep V-shaped notch; P4 merus 3.7 times longer than wide; G1 chitinous distal part relatively short, subconical in shape [Bohol, Philippines; southern Ryukyu Islands, Japan; Taiwan]..........................K. boholano

15b. External orbital tooth not truncate, outer margin almost straight to gently convex, separated from first anterolateral tooth by narrow cleft or relatively shallower notch; P4 merus 3.4–4.1 times longer than wide; G1 chitinous distal part relatively more elongate, beak like................16

16a. P4 propodus 4.5 times longer than wide; G1 chitinous distal part bent downwards [Bali: Indonesia]..........................K. emdi

16b. P4 propodus 4.2–4.8 times longer than wide; G1 chitinous distal part bent at right angles or slightly upwards......................17

17a. P4 merus 4.1 times longer than wide; P4 propodus 4.2 times longer than wide; G1 chitinous distal part bent at right angles [Guam]..........................K. guamensis

17b. P4 merus 3.4–4.1 times longer than wide; P4 propodus 4.6–4.8 times longer than wide; G1 chitinous distal part slightly turned upwards [Christmas Island, Indian Ocean]..........................S. jacksoni

Acknowledgements

The author is most grateful to Louis Deharveng and Josiane Lips (Muséum national d’Histoire Naturelle, Paris) for passing the specimens to him for study. Thanks are also due to Louis Deharveng and Frank Bréhier for habitat information. Charles Fransen (RMNH) kindly allowed the author access to the specimens in RMNH used for the comparative work. Various suggestions from two anonymous referees are also much appreciated.

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