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On the identities of the highland vampire crabs, *Geosesarma foxi* (Kemp, 1918) and *G. serenei* Ng, 1986, with description of a new phytotelmic species from Penang, Peninsular Malaysia (Crustacea: Decapoda: Brachyura: Sesarmidae)

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Abstract. The identities of two poorly known semiterrestrial sesarmid crabs *Geosesarma foxi* (Kemp, 1918) and *G. serenei* Ng, 1986, from northern Peninsular Malaysia are clarified with the study of additional material. A new species associated with phytotelms in Penang, *G. faustum* n. sp., is described and distinguished from the two known species by various carapace, male pleon and gonopod characters. The taxonomy of the three species is discussed. All three are highland species, occurring only at altitudes higher than 700 m; and are characterised by their quadrate carapace, long and slender ambulatory legs, absence of a flagellum on the exopod of their third maxilliped, and relatively slender male first gonopod.

Key words. Phytotelmata, Southeast Asia, Sesarmidae, montane crabs, *Geosesarma*, taxonomy, new taxa

INTRODUCTION

In their survey of the freshwater crabs of Pulau Langkawi, a large island off the west coast of the state of Kedah in Peninsular Malaysia, Ng & Ng (1987) commented that they were unable to find the semiterrestrial sesarmid *Geosesarma foxi* (Kemp, 1918) which had been described from specimens found near the top of Gunung Raya, the highest peak there (see also Ng & Ng, 1989: 76). The types of *Geosesarma foxi* are deposited in the Zoological Survey of India (ZSI) in Calcutta, and the curator of the ZSI at that time, Maya Deb, kindly provided sketches of the male first gonopod and the exopod of the third maxilliped of the lectotype, which were published in Ng (1988: fig. 54C, D). Ng (1986a) had earlier referred specimens collected from Bukit Larut [= Maxwell Hills] in mainland Perak, identified as "*Sesarma foxi*" by Tweedie (1936) to a new species, *G. serenei*. During the Langkawi Scientific and Heritage Expedition of 2003 organised by the Malayan Nature Society, one of the participating scientists, Amirrudin Ahmad (now at the Universiti Malaysia Terengganu), sent the author a photograph of a red crab found badly crushed on a road going up Gunung Raya, which, judging by its carapace shape and colour was probably *G. foxi*. The condition of that specimen, however, was too poor for it to be useful for study.

In May 2014, Ji Tan and Chan Zi Yang, two students of Yong Hoi Sen in the University of Malaysia, collected several yellow crabs from among South American bromeliads which were being grown around a hotel at the top of Penang Hill in Penang Island in Peninsular Malaysia. Examination of these specimens indicated they were superficially close to *G. foxi* and *G. serenei*, but their precise identification would require fresh specimens of *G. foxi* being collected for detailed comparisons. By a remarkable coincidence, specimens of *G. foxi* were eventually collected from Langkawi on three separate occasions a few years later, just a few months apart. In July 2016, a Malaysian hiker found an intact dead male specimen on a hiking trail on the way to the summit of Gunung Raya. In December 2016, a Taiwanese biologist managed to collect several specimens while climbing the same trail down the mountain, and several weeks later in January 2017, a Singaporean visitor obtained more while he was staying at a resort at the summit of Gunung Raya.

In this paper, the identity of *Geosesarma foxi* (Kemp, 1918) is finally clarified on the basis of the good series of fresh specimens, and the species is diagnosed and figured. Detailed comparisons are now also made with the morphologically similar *G. serenei* Ng, 1986. The material from Penang Island is here shown to be a new species, and while resembling *G. foxi* and *G. serenei*, differs in a number of carapace, male pleon and first gonopod characters. This new species, *G. faustum*, is diagnosed in the present paper and compared with morphologically similar congeners.

The terminology used essentially follows that in Ng (1988) with recent amendments recommended by Davie et al. (2015). Measurements, in millimetres, are of the maximum carapace width and length, respectively. The abbreviations

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G1 and G2 are used for the male first and second gonopods, respectively. Specimens examined are deposited in the Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum, National University of Singapore.

TAXONOMY

Family Sesarmidae Dana, 1851

Geosesarma De Man, 1892

Type species. *Sesarma* (*Geosesarma*) *nodulifera* De Man, 1892, subsequent designation by Serène & Soh (1970).

Remarks. Members of *Geosesarma* De Man, 1892, are popularly known as "vampire crabs" because of the bright yellow eyes of a number of species (Rademacher & Mengedoht, 2011; Ng et al., 2015). The genus currently contains 58 species (cf. Ng et al., 2008; Schubart & Ng, 2014; Ng, 2015; Ng et al., 2015; Manuel-Santos et al., 2016; Ng & Lemaitre, 2017); almost all of which are semiterestrial in habits, living in and around freshwater habitats in Southeast Asia. They are regarded as secondary freshwater crabs by some authors (Yeo et al., 2008) although most species have large eggs and practice completely abbreviated larval development (cf. Ng, 1988).

Geosesarma foxi (Kemp, 1918) belongs to a group of *Geosesarma* species generally characterised by their quadrate carapaces, slender and relatively long ambulatory legs, with the exopod of the third maxilliped not possessing a flagellum, and that usually occur in highlands. Ng (1988) treated the two Malaysian species, *Geosesarma foxi (*Kemp, 1918) from Langkawi Island (Kedah), and *G. serenei* Ng, 1986, from Bukit Larut in Perak; commenting that the taxonomy of the material referred to "*G. foxi*" from southern Peninsular Thailand needed to be revised in the future. A third species, which may be allied to *G. foxi* and *G. serenei*, is *G. krathing* Ng & Naiyanetr, 1992, described from Krathing Waterfall in Chantaburi Province in eastern Thailand, near the Cambodian border. While this species shares the quadrate carapace and long slender ambulatory legs of *G. foxi* and *G. serenei* (and their male first gonopods are also superficially similar), the exopod of its third maxilliped has a well-developed flagellum (Ng & Naiyanetr, 1992: fig. 1B).

Geosesarma foxi (Kemp, 1918)
(Figs. 1–5, 7A–H)

Sesarma foxi Kemp, 1918: 238, figs. 3, 4.
Sesarma (*Geosesarma*) *foxi* – Serène, 1968: 107.
Geosesarma foxi – Serène & Soh, 1970: 407; Ng & Ng, 1987: 13; Ng, 1988: 122, fig. 54; Ng, 2004: 333 (list); Ng & Yeo, 2007: 115 (list); Ng et al., 2008: 220 (list).

Material examined. 1 male (11.4 × 11.0 mm) (ZRC 2016.0598), ca. mid-way Tangga Helang Seribu Kenangan hiking trail from base to just before summit of Gunung Raya, Langkawi Island, Peninsular Malaysia, coll. R.-M. Low, 16 July 2016; 3 males (11.5 × 11.4 mm, 9.6 × 9.7 mm, 7.8 × 7.7 mm), 3 females (11.8 × 11.9 mm, 7.5 × 7.3 mm, 6.8 × 6.7 mm) (ZRC 2016.619), near start of Tangga Helang Seribu Kenangan hiking trail from below summit of Gunung Raya, Langkawi Island, Peninsular Malaysia, ca. 780 m asl, coll. J.-J. Li, 31 December 2016; 4 males (10.9 × 10.9 mm, 9.9 × 10.0 mm, 8.0 × 7.9 mm, 6.6 × 6.7 mm), 1 ovigerous female (11.7 × 11.8 mm), 3 females (10.8 × 10.9 mm, 8.6 × 8.4 mm, 8.2 × 8.1 mm) (ZRC 2016.618), near start of Tangga Helang Seribu Kenangan hiking trail from below summit of Gunung Raya, Langkawi Island, Peninsular Malaysia, ca. 780 m asl, coll. P.Y.C. Ng, 12–13 January 2017.

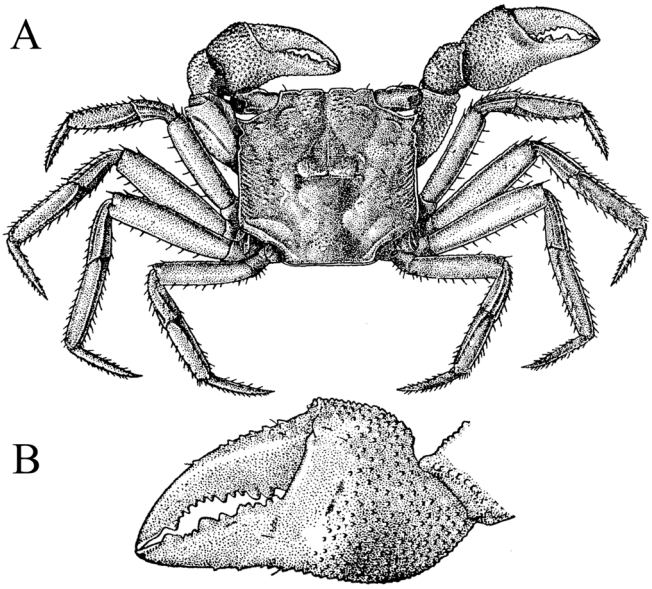

Fig. 1. *Geosesarma foxi* (Kemp, 1918), lectotype male (9.8 × 9.8 mm), Gunung Raya, Langkawi (after Kemp, 1918: figs. 3, 4). A, overall dorsal view; B, outer view of left chela.

Diagnosis. Carapace quadrate, slightly wider than long or subequal, adult width to length ratio 1.00–1.04, lateral margins parallel (Figs. 1A, 3A–C, 4); dorsal surface with regions just visible, anterior regions with small rounded granules on gastric regions (Figs. 3A–C, 4); front distinctly deflexed, frontal lobes broad with gently convex margins in dorsal view; postfrontal, postorbital cristae sharp, distinct (Figs. 3B–D, 4); external orbital tooth triangular, directed obliquely laterally, outer margin gently convex, tip not extending beyond lateral margin; second lateral tooth distinct, clearly separated from rest of margin by wide cleft (Figs. 3B, C, 4). Merus of third maxilliped subovate, shorter than ischium; exopod slender with no trace of flagellum (Fig. 7A). Outer surface of palm of adult male covered with small rounded granules and striae; inner surface granulated but without transverse ridge; dorsal margin of dactylus with 7 or 8 low, non-chitinous tubercles on proximal half (Figs. 1B, 3A, 4A, B, 5D). Ambulatory legs with long, slender merus, with sharp subdistal spine on dorsal margin, surfaces gently rugose (Figs. 1A, 3A, 4A, B). Male pleon broadly triangular; somite 6 wide, with convex lateral margins; telson almost semicircular, not recessed into distal margin of somite 6 (Fig. 5A–C). G1 slender; outer margin of subdistal part of

Fig. 2. *Geosesarma foxi* (Kemp, 1918), colour in life, Gunung Raya, Langkawi. A, B, male (10.9 × 10.9 mm) (ZRC 2016.618); C, male (9.9 × 10.0 mm) (ZRC 2016.618); D, female (10.8 × 10.9 mm) (ZRC 2016.618); E, juvenile male (8.0 × 7.9 mm) (ZRC 2016.618); F, male (11.5 × 11.4 mm) (ZRC 2016.619); G, probably male (9.6 × 9.7 mm) (ZRC 2016.619). Photo credits: A–E, Paul Y.C. Ng; F, G, J.-J. Li.

subterminal segment (in ventral view) with distinct shelf-like angle (Fig. 7B–E), distal chitinous part elongated, distal part gently curved, tip spatuliform (Fig. 7B–G).

Females. Females resemble males in all non-sexual characters, with the chelae equal, relatively slenderer and less inflated (Fig. 4B). The pleon is ovate, covering most of the thoracic sternum, with the telson broadly triangular with convex lateral margins and distinctly inserted into the distal margin of somite 6 (Fig. 5E). The vulvae on thoracic sternite 6 are large, positioned closer to suture with sternite 5, with an operculum and a large truncate vulvar process which arches over the opening (Fig. 5F). One female (11.7 × 11.8 mm, ZRC 2016.618) had several subovate eggs still under its pleon, with each measuring ca. 1.5 mm in diameter.

Variation. The carapace proportions vary slightly, with smaller males and females sometimes appearing slightly

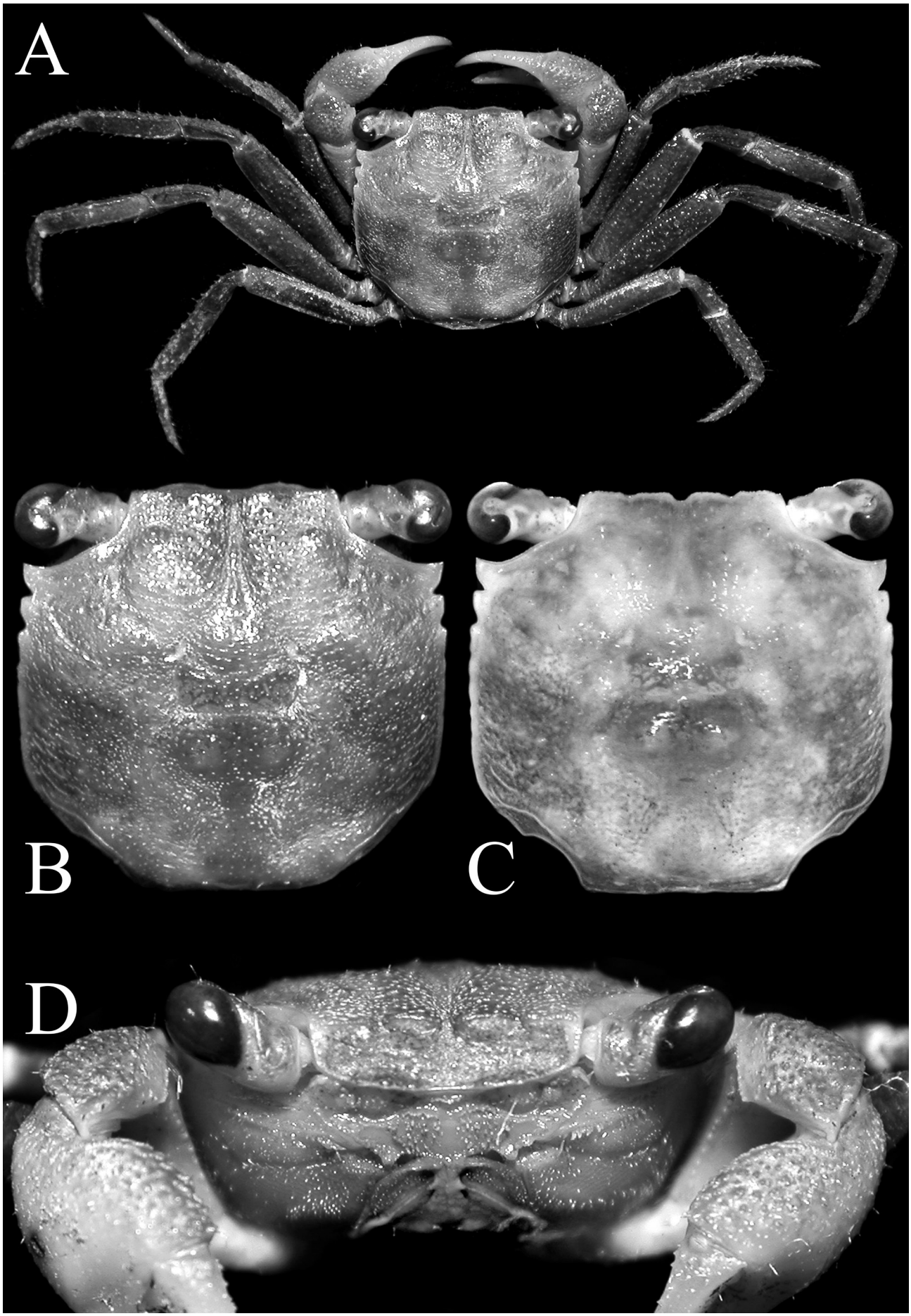

Fig. 3. *Geosesarma foxi* (Kemp, 1918), male (11.4 × 11.0 mm) (ZRC 2016.0598), Gunung Raya, Langkawi. A, overall dorsal view; B, C, dorsal view of carapace (viewed from slightly different angles); D, frontal view of cephalothorax.

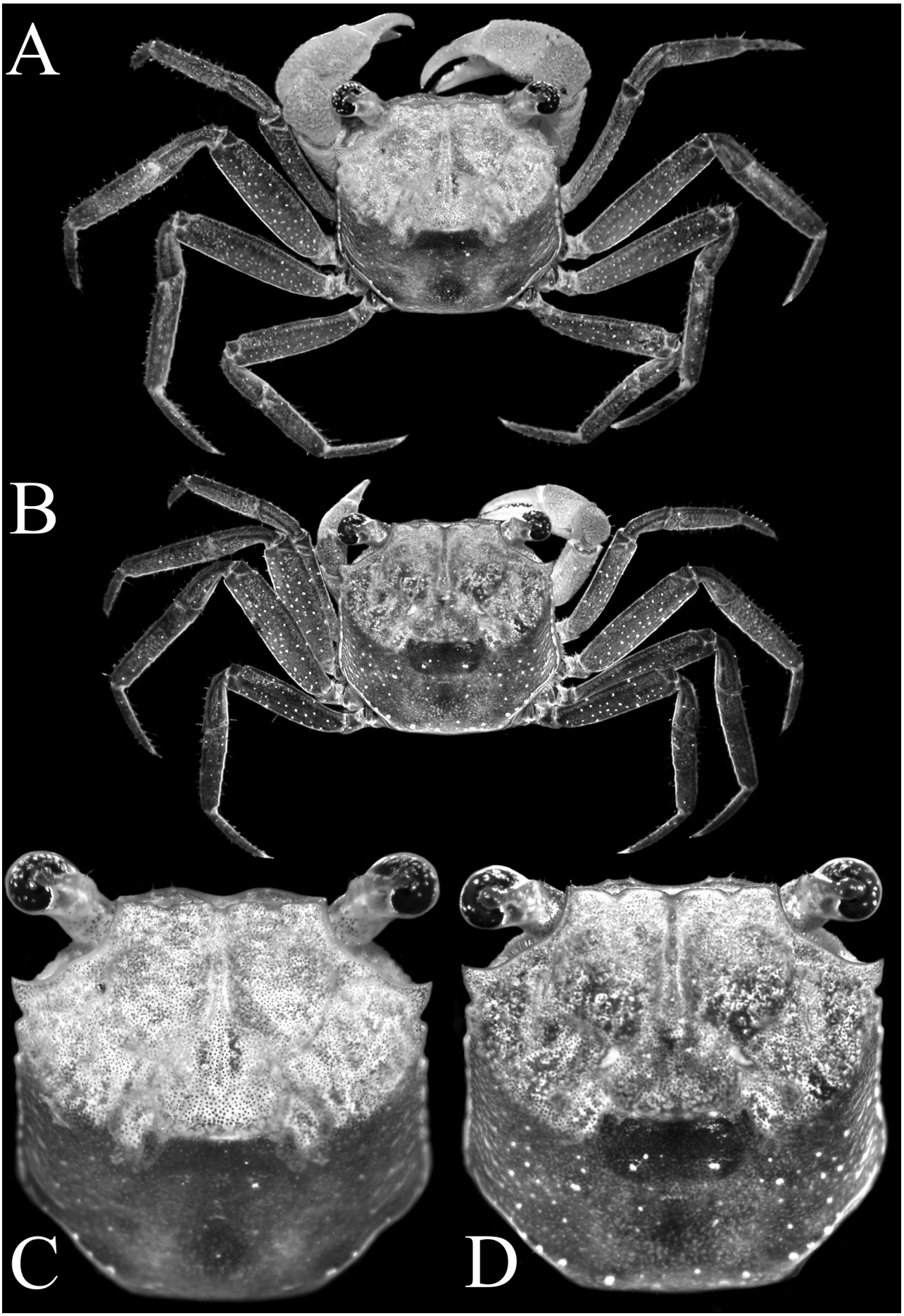

Fig. 4. *Geosesarma foxi* (Kemp, 1918). A, C, male (9.9 × 10.0 mm) (ZRC 2016.618); B, D, female (10.8 × 10.9 mm) (ZRC 2016.618). Both specimens from Gunung Raya, Langkawi. A, B, overall dorsal view; C, D, dorsal view of carapace.

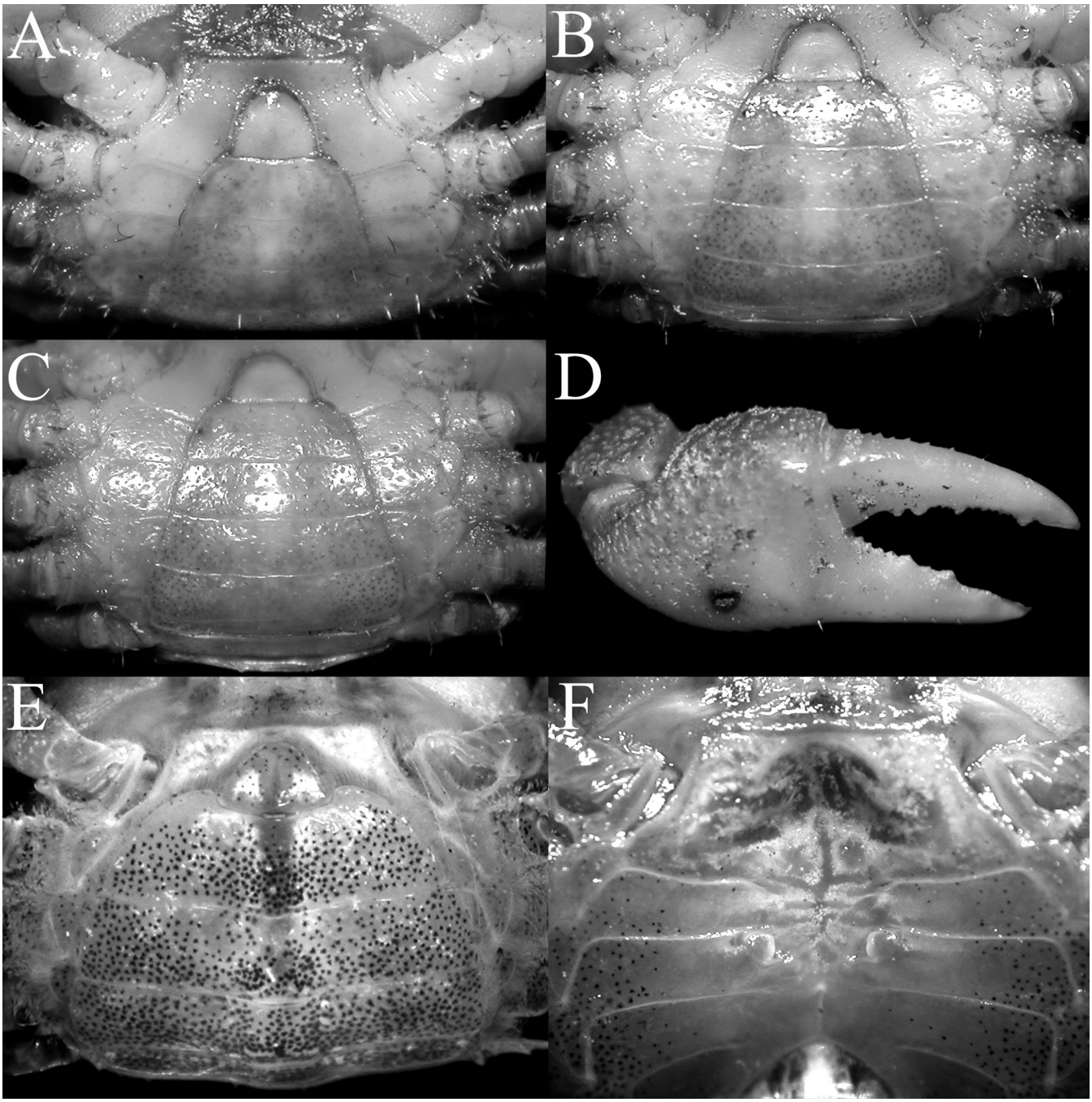

Fig. 5. *Geosesarma foxi* (Kemp, 1918). A–D, male (11.4 × 11.0 mm) (ZRC 2016.0598); E, F, female (10.8 × 10.9 mm) (ZRC 2016.618). Both specimens from Gunung Raya, Langkawi. A, anterior thoracic sternum, telson and pleonal somites 4–6; B, anterior thoracic sternum, telson and pleonal somites 3–6; C, posterior thoracic sternum, telson and pleonal somites 2–6; D, outer view of right chela; E, female pleon; F, female sternopleonal cavity showing vulvae.

more trapezoidal in shape, with the lateral margins slightly diverging (e.g., Fig. 4B). The second lateral tooth (after the external orbital tooth) is always distinct, although it may vary in size (Figs. 3B, C, 4C, D), and demarcated from the rest of the margin by a wide cleft. Smaller males (less than 7 mm carapace width) also have slender, equal chelae; and the G1, while resembling those of adults, are relatively straighter and poorly chitinised.

Colour. Kemp (1918: 240) described his fresh specimens of *G. foxi* as follows: "the carapace of the specimens is of a very dull reddish brown; the chelipedes are pale yellow suffused with pale red on the carpus and palm; the walking legs are deep brown with a fine mottling and dark chromatophores are thickly sprinkled on the abdomen." The series of specimens on hand essentially confirm his observations. In live specimens, the anterior half of the carapace (from the H-shaped gastro-cardiac groove) as well as the chelipeds are deep orange to almost red (Fig. 2). The intensity of the colour varies only slightly. The posterior half of the carapace and ambulatory legs vary from light brown to purplish black, and covered with numerous small white or light blue spots (Fig. 2). The frontal surfaces of the cephalothorax and thoracic sternum are deep orange (Fig. 2B), while the abdomen is orange with numerous small dark brown spots and mottling.

Taxonomic remarks. Kemp (1918: 240) described the species from two males measuring 9.8 × 9.8 mm and 9.7 × 9.8 mm, without specifying a holotype. Ng (1988: 122) designated the slightly larger male in the Zoological Survey of India in Calcutta as the lectotype of *Sesarma foxi* Kemp, 1918. For comparisons with *G. serenei* and *G. faustum* n sp., see remarks for the latter species.

Sympatric taxa. Three other species of freshwater crabs occur on Gunung Raya. The semiterrestrial potamid *Stoliczia bella* Ng & Ng, 1987, is found in or near permanent water bodies from near the base to about 700 m asl on Gunung Raya. At the base of Gunung Raya, the fully aquatic gecarcinucid *Siamthelphusa improvisa* (Lanchester, 1902) is common in shallow streams with vegetation. The gecarcinucid *Phricotelphusa gracilipes* Ng & Ng, 1987, is found in most of the streams and springs around the mountain, and even occurs in the forest floor and summit, sometimes far from permanent water sources. The author has also found it in piles of moist decaying leaves along the same trail where *G. foxi* was collected.

Geosesarma serenei Ng, 1986
(Figs. 6, 7I–P)

Sesarma ? *maculata* – Lanchester, 1902: 550 (not *Sesarma maculata* De Man, 1892)

Sesarma (*Sesarma*) *foxi* – Tweedie, 1936: 52 (not *Sesarma foxi* Kemp, 1918).

Sesarma foxi – Tweedie, 1940: 108, fig. 11 (not *Sesarma foxi* Kemp, 1918).

Geosesarma serenei Ng, 1986a: 6, fig. 2; Ng, 1988: 124, figs. 53A, 55; Ng, 2004: 333 (list); Ng & Yeo, 2007: 115 (list); Ng et al., 2008: 220 (list).

Material examined. Holotype: male (8.3 × 8.2 mm) (ZRC 1964.9.8.1), Bukit Larut, Maxwell Hill, 4°47′N 100°45′E, Perak, Peninsular Malaysia, ca. 1150 m, coll. H.M. Pendlebury, February 1932. Paratype: ovigerous female (10.4 × 9.7 mm) (ZRC 1964.9.8.2), same data as holotype. Others: 1 young male (7.0 × 6.9 mm), 1 female (7.4 × 7.1 mm) (ZRC 2003.64), Bukit Larut, Maxwell Hill, beyond Gunung Hijau Resthouse, 4°47′N 100°45′E, Perak, Peninsular Malaysia, ca. 1150 m, at night, coll. T.M. Leong & G. Lim, 27 March 2003.

Diagnosis. Carapace quadrate, slightly wider than long or subequal, adult width to length ratio 1.01–1.04, lateral margins parallel (Fig. 6A, B, F); dorsal surface with regions just visible, anterior regions with small rounded granules on gastric regions (Fig. 6A, B, E, F); front distinctly deflexed, frontal lobes broad with truncate margins in dorsal view; postfrontal, postorbital cristae sharp, distinct (Fig. 6B, F); external orbital tooth triangular, directed obliquely laterally, outer margin gently convex, tip not extending beyond lateral margin; second lateral tooth distinct, clearly separated from rest of margin by wide clef (Fig. 6B, F). Merus of third maxilliped subovate, shorter than ischium; exopod slender with no trace of flagellum (cf. Ng, 1988: fig. 55C). Outer surface of palm of adult male covered with small rounded granules and striae; inner surface granulated but without transverse ridge; dorsal margin of dactylus with 6 or 7 low, non-chitinous tubercles on proximal half (Fig. 6A, D). Ambulatory legs with long, slender merus, with sharp subdistal spine on dorsal margin, surfaces gently rugose (Fig. 6A, E). Male pleon broadly triangular; somite 6 wide, with convex lateral margins; telson almost semicircular, not recessed into distal margin of somite 6 (Fig. 6C). G1 slender; outer margin of subdistal part of subterminal segment (in ventral view) with gently sloping shelf-like area (Fig. 7I, J), distal chitinous part elongated, distal part almost straight, tip spatuliform (Fig. 7I–L).

Females. The adult female resembles the adult male in non-sexual characters, with the chelae equal, relatively slenderer and less inflated. The pleon is ovate, covering most of the thoracic sternum, with the telson broadly triangular with convex lateral margins and distinctly inserted into the distal margin of somite 6 (Fig. 6G). The vulvae on thoracic sternite 6 are relatively large, positioned closer to suture with sternite 5, with an operculum and a large truncate vulvar process which arches over the opening (Fig. 6H).

Variation. The few specimens on hand do not lend much for a discussion on their variation. Smaller specimens (7 mm carapace width, ZRC 2003.64) closely resemble the adult holotype male except that the second lateral tooth is relatively larger, the chelae are equal and slenderer (Fig. 6E, F). The G1 of this small male is weakly chitinised and clearly juvenile in form, and while it superficially resembles that of the adult, the distal part is almost straight and not chitinous (Fig. 7N–P).

Colour. The live colour of this species is not known, but probably similar to those of *G. foxi* and *G. faustum* n. sp. The small specimens of *G. serenei* (ZRC 2003.64) have the distinctive spots characteristic of the other two species.

Taxonomic remarks. In discussing differences with *G. serenei*, Ng (1988: 122) noted that the "subterminal segment of the G1 of *G. foxi* however, appears to be stouter and slightly shorter, and the terminal segment is also relatively shorter and the tip rounder. The two taxa may eventually prove conspecific when more specimens of both species become available, and the variations presently noted shown to be merely due to variation." This comparison was based on the sketch of the G1 provided to him by the Zoological Survey of India (Ng, 1988: fig. 54D). The present series of specimens of *G. foxi* show that this difference is not valid as it is now clear from examining the material that the G1 in Ng (1988) had been drawn with the structure tilted at a slight angle, making it appear stouter than it actually is. There are, however, other characters that can separate the two species. For detailed differences with *G. foxi* and *G. faustum* n sp., see remarks for the latter species.

In recording *G. serenei* (as *S. foxi*), Tweedie (1940: 108) commented that he had "two adult males, two females and two juveniles from Lacom, Peninsular Siam [present day Thailand], collected by the 'Skeat' Expedition of 1899–1900 and erroneously determined as *S. maculata* de

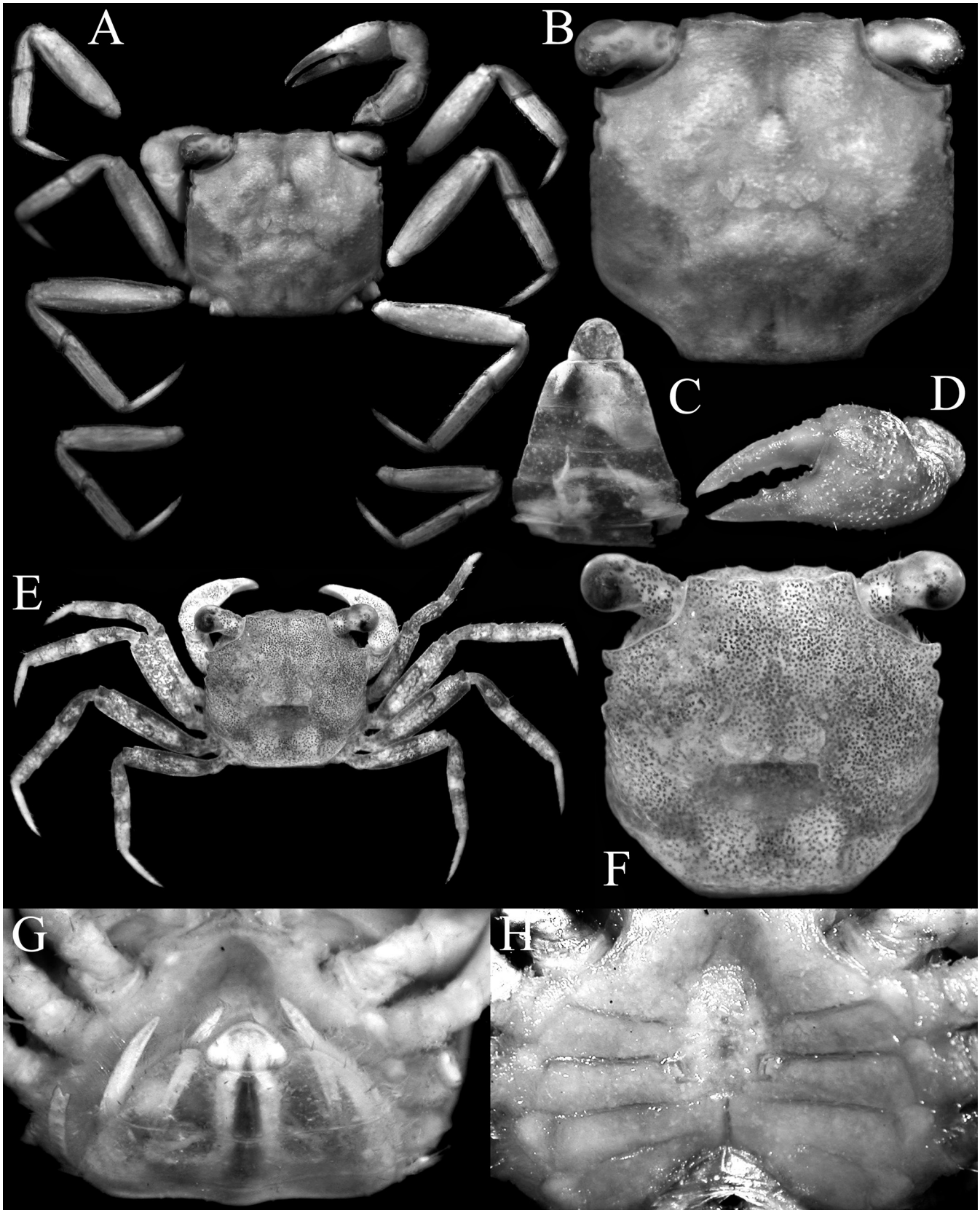

Fig. 6. *Geosesarma serenei* Ng, 1986. A–D, holotype male (8.3 × 8.2 mm) (ZRC 1964.9.8.1); E, F, young male (7.0 × 6.9 mm) (ZRC 2003.64); G, H, paratype ovigerous female (10.4 × 9.7 mm) (ZRC 1964.9.8.2). All specimens from Bukit Larut, Perak. A, E, overall dorsal view; B, F, dorsal view of carapace; C, male pleon; D, outer view of left chela; G, female pleon; H, female sternopleonal cavity showing vulvae.

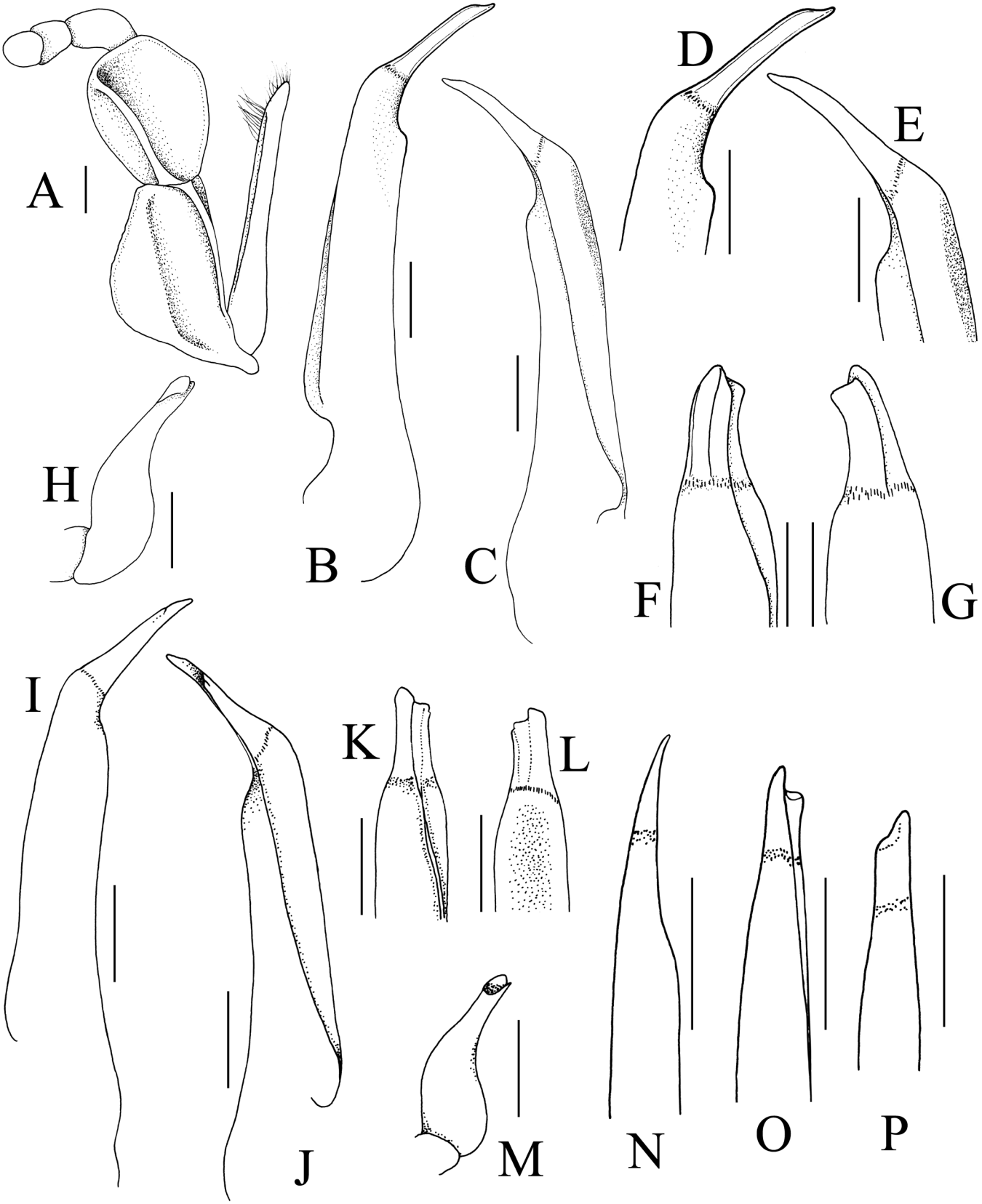

Fig. 7. A–H, *Geosesarma foxi* (Kemp, 1918), male (11.4 × 11.0 mm) (2016.0598), Gunung Raya, Langkawi; I–M, *G. serenei* Ng, 1986, holotype male (8.3 × 8.2 mm) (ZRC 1964.9.8.1), Bukit Larut, Perak; N–P, *G. serenei* Ng, 1986, young male (7.0 × 6.9 mm) (ZRC 2003.64), Bukit Larut. A, left third maxilliped (mostly denuded); B, I, N, left G1 (ventral view); C, J, left G1 (dorsal view); D, distal part of left G1 (ventral view); E, distal part of left G1 (dorsal view); F, K, O, distal part of left G1 (outer lateral view); G, L, P, distal part of left G1 (mesial view); H, M, left G2. Scales = 0.5 mm.

Man by Lanchester (l.c.). The two largest specimens of this series measure 11.7 (♂) and 11.0 (♀) mm. in anterior carapace breadth, and are the largest specimens of S. foxi so far recorded." In describing *G. serenei*, Ng (1986a: 36) placed Lanchester's (1902) and Tweedie's (1936) material from Peninsular Thailand under the synonymy of the new species with doubt. Tweedie (1940: 108–109) notes that the locality "Lacom" given by Lanchester is difficult to interpret precisely. It probably refers to Lakon, which is an alternative name for Nakon Si Thammarat. Other records indicate that the species is montane in habit and the 'Skeat' specimens probably came from the hills a short distance inland from Nakon Si Thammarat, which range up to a height of over 1500 metres. The present author agrees with this interpretation. Material from Nakon Si Thammarat will need to be examined to ascertain if the species there is actually *G. serenei* or another taxon.

Sympatric taxa. Another species of *Geosesarma*, *G. cataracta* Ng, 1986, also occurs on Bukit Larut, but lives at relatively lower altitudes among the mosses adjacent to waterfalls, possessing proportionately shorter and stouter ambulatory legs and a different G1 structure (see Ng, 1986a, 1988). Two species of potamids are present on Bukit Larut, *Stoliczia tweediei* (Roux, 1934) and *S. larutensis* Ng & Schubart, 2014. *Stoliczia tweediei* is a fully aquatic species and is present in the waterfalls at altitudes up to 900 m asl; while *S. larutensis* is semiterrestrial and lives in the damp forests of the summit, probably with *G. serenei* (see Ng, 1993; Ng & Schubart, 2014). One species of gecarcinucid, *Phricotelphusa hockingi* Ng, 1986, occurs in the streams and waterfalls but apparently does not reach the summit (Ng, 1986b, 1988).

Geosesarma faustum n. sp.
(Figs. 8–12)

Material examined. Holotype: male (10.6 × 10.5 mm) (ZRC 2016.617), Penang Hill, near Bellevue Hotel, Penang, 800 m, Peninsular Malaysia, inside introduced bromeliad *Neoregalia compacta* (Bromeliaceae), coll. J. Tan & Z.Y. Chan, June 2014. Paratypes: 2 males (10.6 × 10.5 mm, 8.9 × 8.7 mm), 4 females (12.0 × 11.5 mm, 11.1 × 10.7 mm, 11.0 × 10.7 mm, 10.6 × 10.6 mm), 2 ovigerous females (10.6 × 10.4 mm, 9.5 × 9.4 mm) (ZRC 2014.340), same data as holotype; 5 males (10.2 × 10.1 mm, 10.0 × 10.3 mm, 8.6 × 8.4 mm, 8.3 × 8.2 mm, 6.2 × 6.0 mm), 2 females (10.8 × 10.9 mm, 8.6 × 8.6 mm), 1 ovigerous female (9.2 × 9.3 mm), 1 young female (6.8 × 6.5 mm) (ZRC 2016.0599), in various bromeliads and *Pandanus* growing in shaded gardens at summit of Penang Hill, mostly near Bellevue Hotel, Penang, ca. 850 m, Peninsular Malaysia, coll. P.K.L. Ng & P.Y.C. Ng, 20 December 2016.

Diagnosis. Carapace quadrate, slightly wider than long or subequal, adult width to length ratio 0.97–1.04, lateral margins parallel (Figs. 9A–C, 10); dorsal surface with regions just visible, anterior regions with small rounded granules on gastric regions (Fig. 9B–D); front distinctly deflexed, frontal lobes broad, usually with truncate margins in dorsal view; postfrontal, postorbital cristae sharp, distinct (Figs. 9A–C, 10); external orbital tooth acutely triangular, directed obliquely laterally, outer margin gently convex, tip not extending beyond lateral margin; second lateral tooth low, barely discernible from rest of margin, often fused with rest of margin (Figs. 9B, C, 10). Merus of third maxilliped subovate, shorter than ischium; exopod slender with no trace of flagellum (Fig. 12A). Outer surface of palm of adult male covered with small rounded granules and striae; inner surface granulated but without transverse ridge; dorsal margin of dactylus with 7–9 low, non-chitinous tubercles on proximal half (Figs. 9A, 10, 11D). Ambulatory legs with long, slender merus, with sharp subdistal spine on dorsal margin, surfaces gently rugose (Figs. 9A, 10). Male pleon broadly triangular; somite 6 very wide, with convex lateral margins; telson relatively triangular, not recessed into distal margin of somite 6 (Figs. 11A–C, E). G1 slender; outer margin of subdistal part of subterminal segment (in ventral view) with sloping, subangular shelf-like area (Fig. 12B–E), distal chitinous part conspicuously elongated, distal part gently curved, tip spatuliform (Figs. 11F, 12B–G).

Females. Females resemble males in all non-sexual characters, with the chelae equal, relatively slenderer and less inflated (Figs. 8H, 10B). The pleon is ovate, covering most of the thoracic sternum, with the telson broadly triangular with convex lateral margins and distinctly inserted into the distal margin of somite 6 (Fig. 11G). The vulvae on thoracic sternite 6 are large, positioned closer to suture with sternite 5, with an operculum and a large truncate vulvar process which arches over the opening (Fig. 11H). The ovigerous females (10.6 × 10.4 mm, 9.5 × 9.4 mm, ZRC 2014.340) had large subovate eggs, each measuring about 1.5 mm in diameter (Fig. 8D).

Variation. The margins of the frontal lobes in *G. faustum* is usually subtruncate, but in several specimens, it appears more convex (Fig. 10A). As in *G. foxi*, the carapace shape varies slightly from just longer than broad to broader than long. The carapaces of many of the adult females and young males appear to be slightly more trapezoidal with the lateral margins gently diverging (Figs. 8H, 9C).

Colour. The colour and pattern of *G. faustum* n. sp. is very similar to *G. foxi*. The anterior half of the carapace, chelipeds, suborbital, subhepatic and pterygostomial regions are usually pale yellow to light orange (Fig. 8), never red. The posterior half of the carapace and ambulatory legs vary from brown to purplish black, with numerous small white or light blue spots (Fig. 8).

Etymology. The species name is derived from the Latin for fortunate and lucky; alluding to the circumstances leading to the discovery of the new species.

Taxonomic remarks. Kemp (1918: 240) reported on a "*Sesarma* sp." from an altitude of about 370 m on Penang Hill. Tweedie (1940) obtained more specimens from Penang Hill (no altitude provided), named the species *Sesarma penangensis*, and referred Kemp's (1918) record to his new

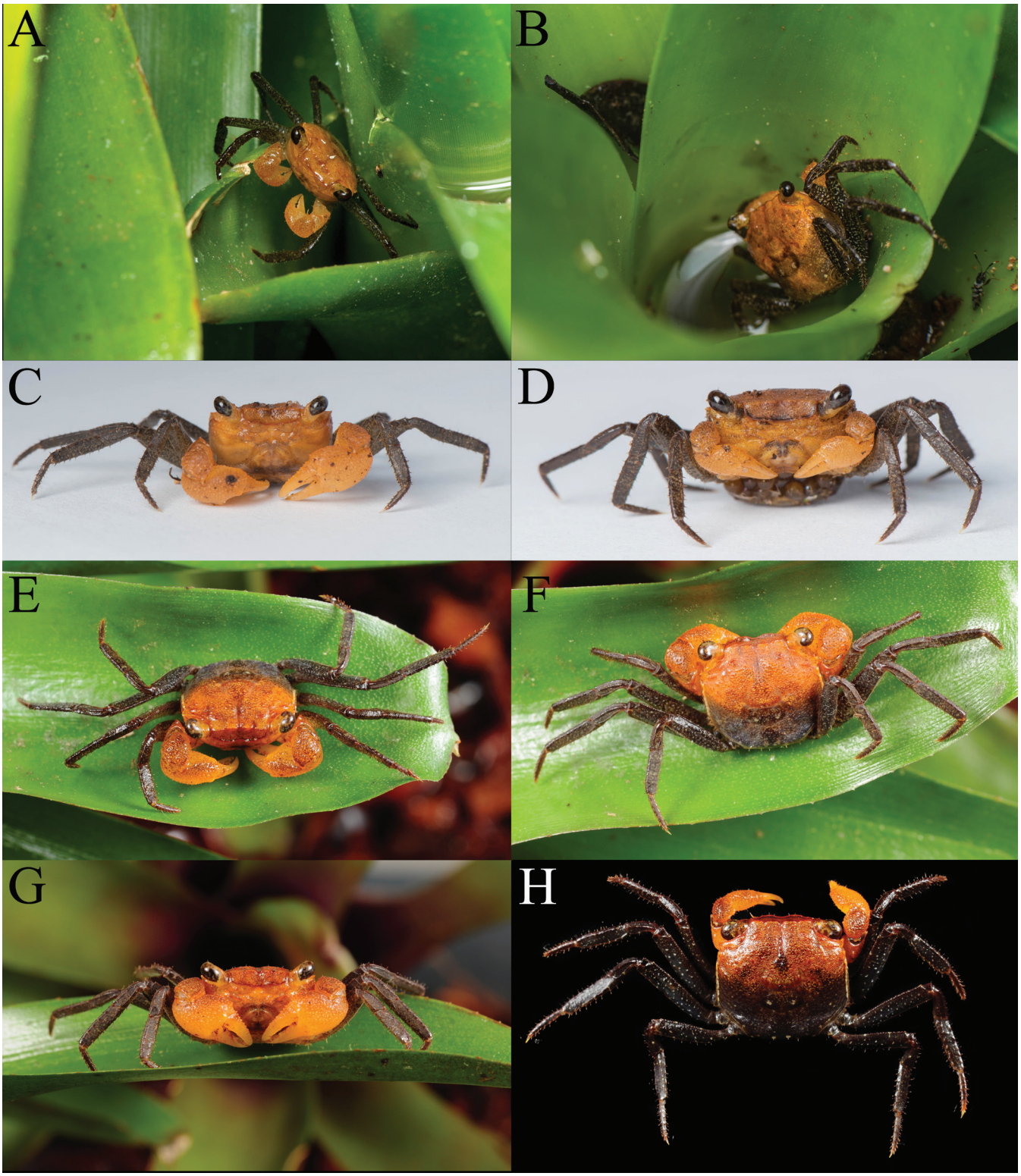

Fig. 8. *Geosesarma faustum* n. sp., colour in life, Penang Hill, Penang. A, B, specimens photographed in bromeliad in situ, part of type species; C, holotype male (10.6 × 10.5 mm) (ZRC 2016.617); D, paratype ovigerous female (10.6 × 10.4 mm) (ZRC 2014.340); E–G, paratype male (10.2 × 10.1 mm) (ZRC 2016.0599); H, paratype female (10.8 × 10.9 mm) (ZRC 2016.0599). Photo credits: A–D, Ji Tan; E–H, Paul Y. C. Ng.

taxon. From Kemp's (1918) description of his specimens, the author has little doubt that Tweedie is correct, and his specimens are not conspecific with what is here described as *G. faustum*. *Geosesarma faustum* is one of the highland *Geosesarma* species (see earlier; Ng, 1988), while *G. penangense* is a congener that is generally found at relatively lower altitudes; it is easily distinguished from *G. faustum* by its distinctly broader than long carapace, conspicuously shorter and stouter ambulatory legs, the exopod of the third maxilliped possessing a long flagellum and the G1 is proportionately stouter with short, spade-like chitinous distal part (cf. Ng, 1988: fig. 58A, C–E).

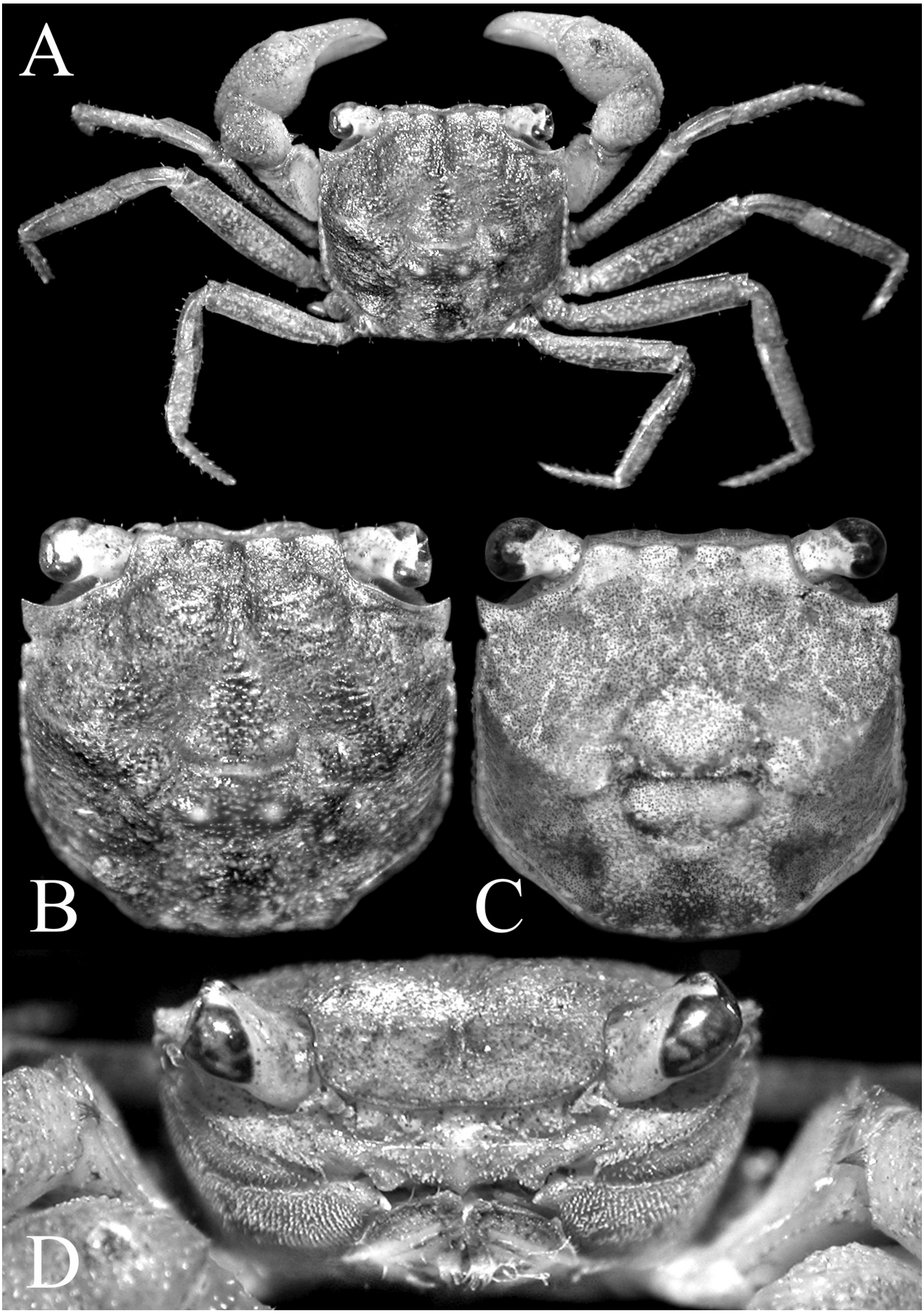

Fig. 9. *Geosesarma faustum* n. sp. A, B, D, holotype male (10.6 × 10.5 mm) (ZRC 2016.617), Penang Hill, Penang; C, paratype female (12.0 × 11.5 mm) (ZRC 2014.340), Penang Hill, Penang. A, overall dorsal view; B, C, dorsal view of carapace; D, frontal view of cephalothorax.

Geosesarma foxi and *G. faustum* n. sp. share a similar colour pattern, with the anterior half of the carapace and chelipeds bright yellow or orange, with the dark brown to almost black posterior half of the carapace and ambulatory legs covered with numerous small white dots. The same appears to be the case for *G. serenei*, with the more recent specimens showing traces of the small dots on the ambulatory legs.

While *G. foxi* s. str. is very similar to *G. faustum*, adults of *G. faustum* can easily be distinguished by the second lateral tooth on the carapace being poorly developed or almost undiscernible (Figs. 9B, C, 10) (distinct in *G. foxi*, Figs. 1A, 3B, C, 4); the male pleonal somite 6 is more subtruncate in shape (Fig. 11A–C, E) (margins distinctly more convex in *G. foxi*, Fig. 5A–C); the telson is more triangular in shape (Fig. 11A) (more semicircular in *G. foxi*, Fig. 5A); the outer margin of the subdistal part of the subterminal segment is gently sloping (Fig. 12B–E) (area forms a distinct angular shelf-like structure in *G. foxi*, Fig. 7B–E); and the chitinous distal part of the G1 is proportionately longer (Fig. 12B–E) (proportionately shorter in *G. foxi*, Fig. 7B–E). In addition, the external orbital tooth is usually relatively more acutely triangular (Figs. 9A–C, 10) (more broadly triangular in *G. foxi*, Figs. 3A–C, 4). The colour in life of the anterior half of the carapace and chelipeds of adult *G. foxi* s. str. is deep orange (Fig. 2A–D), sometimes becoming almost red (Fig. 2F, G). In contrast, the live colour of *G. faustum* tends to be pale yellow (Fig. 8A–D) to light orange (Fig. 8E–H). Although colour will probably vary slightly in a species, the good series of specimens of both species indicate that the orange of *G. foxi* generally tends to be darker.

Compared to *G. serenei*, the external orbital tooth of adult *G. faustum* is relatively more acutely triangular (Figs. 9A–C, 10) (more broadly triangular in *G. serenei*, Fig. 6A, B, E, F); the second lateral tooth on the carapace of *G. faustum* n. sp. is poorly developed or almost undiscernible (Figs. 9B, C, 10) (more distinct in *G. serenei*, Fig. 6A, B, E, F); the male pleonal somite 6 is more subtruncate in shape (Figs. 11A–C, E) (relatively less broad in *G. serenei*, Fig. 6C); the telson is more triangular in shape (Fig. 11A) (more semicircular in *G. serenei*, Fig. 6C); and the chitinous distal part of the G1 is proportionately longer (Fig. 12B–E) (proportionately shorter in *G. serenei*, Fig. 7I, J). The live colours of *G. serenei* are not known.

In its carapace shape, elongated ambulatory legs and color pattern, *G. faustum* bears a close resemblance to what has been reported in the aquarium trade as "*Geosesarma krathing*" (see Rademacher & Mengedoht, 2011). This material supposedly came from the type locality, Krathing Waterfalls in Thailand, but considering the general unreliability of aquarium records, it is quite possible that the specimens were from Penang or even Langkawi instead. While the colour (yellow) and pattern (the anterior half of the carapace and chelipeds are yellow) are very similar, these aquarium specimens do not appear to have the posterior part of the carapace and legs covered with fine spots like in true *G. faustum* (Fig. 8).

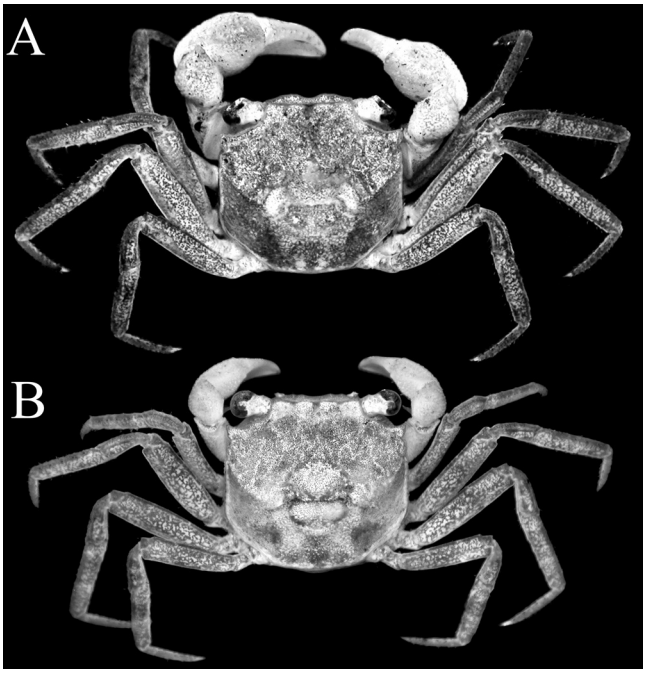

Fig. 10. *Geosesarma faustum* n. sp., overall dorsal view. A, paratype male (10.6 × 10.5 mm) (ZRC 2014.340), Penang Hill, Penang; B, paratype female (12.0 × 11.5 mm) (ZRC 2014.340), Penang Hill, Penang.

Sympatric taxa. A second species of *Geosesarma*, *G. penangense* (Tweedie, 1940) is present on Penang Hill, but has not been found higher than 370 m asl (see above). Living in the waterfalls and rocky streams is the fully aquatic potamid *Stoliczia stoliczkana* (Wood-Mason, 1871), but this species is not known from the summit (see Ng, 1992).

GENERAL DISCUSSION

Geosesarma foxi, *G. serenei* and *G. faustum* are high altitude species, occurring in montane habitats higher than 700 m asl. With regards to *G. foxi*, Kemp (1918: 240) recorded that the "specimens obtained by Mr. Buxton, the types of the species, were found on Gunong Raya in Langkawi I, at a height of 2000 ft. They were collected in moist places under stones or rotten wood at some distance from any stream." He also noted that "It appears probable that in these places the *Sesarma* have been able to adopt a strictly terrestrial mode of life and to ascend to considerable altitudes owing to the damp climate that prevails..." (Kemp, 1918: 238). The recent specimens of *G. foxi* were all found near the summit of Gunung Raya: "they were collected in the densely forested area near the top of the Gunung Raya hiking trail, at roughly 700 m plus asl. *Geosesarma foxi* is nocturnal, and the majority of specimens were collected late at night (after 10 pm) foraging among the plants, often ferns, along the side of the trail. The area is a considerable distance from any stream or permanent water source, but almost always moist due to cool temperatures of the high altitude and thick mist that blankets the area in the early morning and night. During the day, this species probably takes refuge in the moist leaf litter or in phytotelms such as between the leaves of *Pandanus* spp." (P.Y.C. Ng, personal communication).

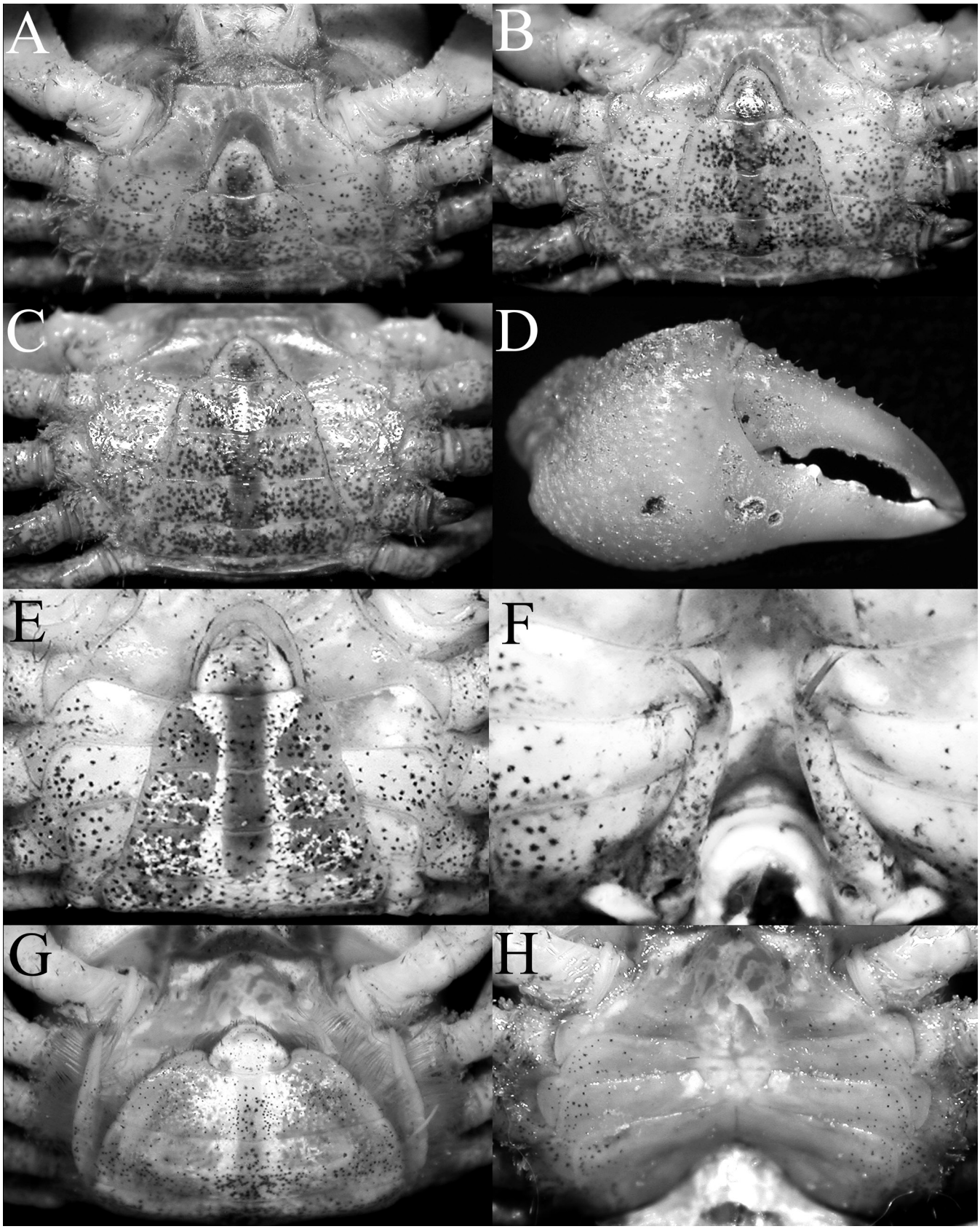

Fig. 11. *Geosesarma faustum* n. sp. A–D, holotype male (10.6 × 10.5 mm) (ZRC 2016.617); E, F, paratype male (10.6 × 10.5 mm) (ZRC 2014.340); G, H, paratype female (12.0 × 11.5 mm) (ZRC 2014.340). All specimens from Penang Hill, Penang. A, anterior thoracic sternum, telson and pleonal somites 5 and 6; B, anterior thoracic sternum, telson and pleonal somites 3–6; C, posterior thoracic sternum, telson and pleonal somites 2–6; D, outer view of right chela; E, posterior thoracic sternum, telson and pleonal somites 3–6; F, male sternopleonal cavity showing G1s; G, female pleon; H, female sternopleonal cavity showing vulvae.

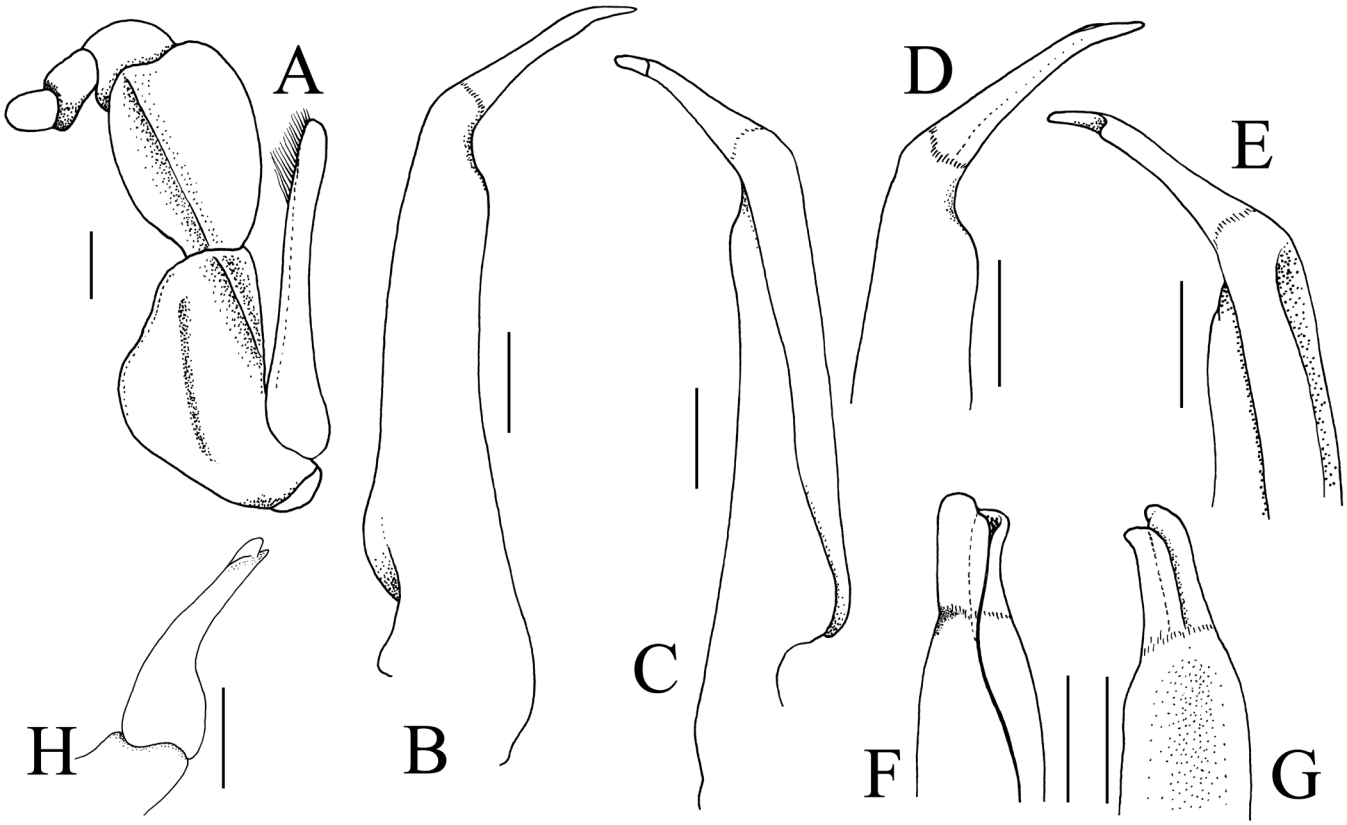

Fig. 12. A–H, *G. faustum* n. sp., holotype male (10.6 × 10.5 mm) (ZRC 2016.617), Penang Hill, Penang. A, left third maxilliped (mostly denuded); B, left G1 (ventral view); C, left G1 (dorsal view); D, distal part of left G1 (ventral view); E, distal part of left G1 (dorsal view); F, distal part of left G1 (outer lateral view); G, distal part of left G1 (mesial view); H, left G2. Scales = 0.5 mm.

Not much is known about the ecology of *G. serenei*, with the types collected at the summit of Bukit Larut, over 1000 m asl. As far as is known, they were found in the forest, with the recent material (ZRC 2003.64) collected at night.

The discovery of *G. faustum* in Penang is interesting because the species has never been reported in earlier publications despite the fact that Penang had been a major British bastion since 1786 and Penang Hill, the highest point on the island, has been inhabited for most of that time. This may not be surprising considering the biology of *G. foxi* and *G. serenei*. They are very cryptic species, hiding in the dense forest or among vegetation during the day, coming out to forage only late at night. Phytotelms are probably one of their major habitats or foraging sites. In natural forests or urban habitats where water may be scarcer, the crabs are rarely seen. Even for *G. foxi*, they have only been found recently, and not in large numbers. Since 2010, Penang Hill, especially the summit area, has been developed with the addition of new tourist facilities, hotels and natural attractions. These include many ecogardens and newly planted areas. Many areas are heavily planted with non-native bromeliads and *Pandanus*. The density of bromeliad plantings in and around the hotel area as well as the gardens means a new habitat has been created for species of *Geosesarma*, allowing them to flourish in good numbers so much so that they are now far more accessible for scientists to study. In the natural ecosystem, they are almost certainly more widely dispersed due to the more scattered distribution of suitable plants and the density of the vegetation on the forest floor.

Geosesarma faustum was observed to hide between the leaves of the bromeliads and *Pandanus*, scurrying into the water if disturbed (Fig. 8A, B). They were common during the day, especially in more shaded areas, and when there was cloud cover with light rain. Several females with eggs were seen, and numerous very small crabs were also seen around the plants, suggesting the crabs are breeding in the phytotelm. The large size of the eggs of all three species indicates that they practice direct development but it is not known if they carry the young crabs under their pleon, on the back of their carapaces (see Ng & Tan, 1995), or perhaps release the newly hatched crabs in the waters of the phytotelms.

Several species of *Geosesarma* are known to use various phytotelmata. *Geosesarma malayanum* Ng & Lim, in Ng, 1986, has been found in the cups of pitcher plants at high altitudes (Ng & Lim, 1987), while *G. peraccae* (Nobili, 1903) and *G. nemesis* Ng, 1986, from Singapore have been known to also frequent or use pitcher plants (notably *Nepenthes ampullaria*) (Tan & Ng, 2008; Ng & Court, 2010). In Sarawak (and Brunei), *G. gracillimum* (De Man, 1902) has been found in pitcher plants (unpublished data).

As to their conservation status, Ng & Yeo (2007: 115) listed *G. foxi* as "endangered", while *G. serenei* was regarded as "critically endangered"; the authors noting that the small known distribution range and possible threats to the forests were problems. While the present study has managed to get more specimens of *G. foxi* for study, the various environmental threats facing this species have not been

reduced. In fact, the threats may get worse in the years ahead as more parts of Gunung Raya (and Bukit Larut for *G. serenei*) are opened for increasing numbers of tourists. The same may be true for *G. faustum*, although the prolific planting of plants like bromeliads on the summit of Penang Hill has clearly helped the species, at least for the moment. Another potential problem is the aquarium trade. Ng et al. (2015: 12) noted that over-collecting is a serious threat for a species if it becomes popular in the trade as catching animals from the wild is not a sustainable practice. The ease by which *Geosesarma* crabs are kept and their often striking colours in life and habits, have made them much sought after terrarium subjects (see Rademacher & Mengedoht, 2011; Ng et al., 2015). The conservation status of primarily or wholly freshwater sesarmids like *Geosesarma*, however, have not been analysed following IUCN Red List guidelines, as had been done for primary freshwater crabs (see Cumberlidge et al., 2009).

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