



Two new freshwater crab species of the genus *Nanhaipotamon* Bott, 1968 (Crustacea, Decapoda, Potamidae) from Huizhou, Guangdong Province, southern China

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Abstract

Two morphologically distinct new species of *Nanhaipotamon* Bott, 1968, are described from Huizhou, Guangdong Province, southern China. The smooth carapace and lack of flagellum on the third maxilliped exopod immediately separate *N. incendium* n. sp. from all other known *Nanhaipotamon*. It is also the first species of this genus to be recorded from a relatively high altitude of 700 m a.s.l. *Nanhaipotamon aureomarginatum* n. sp. is externally much more typical of species of its genus but can be distinguished from congeners by its unique male first gonopod. The two new species are more or less sympatric with a morphological disparate congener, which we tentatively assign as *N. aff. aculatum* Dai, 1997 and *N. aff. hongkongense* (Shen, 1940), respectively, but with different habitats. A genetic analysis using the mitochondrial cytochrome oxidase subunit I shows that while the two new species are sufficiently distinct from other known species of *Nanhaipotamon*, they have extraordinarily close relationships with their respective sympatric congeners, which calls for further investigation. The ecology of these two new species are also noted.

Key words: cytochrome oxidase subunit I (COI), hillstream, new species, sympatric, systematics

Introduction

Guangdong Province in southern China is rich in freshwater crab species with some areas such as Huizhou City yet to be scientifically surveyed for them. New species from this province continue to be discovered at a fast rate (e.g. Huang *et al.* 2012, 2016, 2017, 2018a, b). The potamid genus *Nanhaipotamon* Bott, 1968, so far with 18 species, mainly occurs in the subtropical rainforests and agricultural lands of southern and eastern continental China, but is also present in the Taiwan main island and surrounding islands (Dai 1999, Shih *et al.* 2005, Huang *et al.* 2012, Huang *et al.* 2018b). Crabs of *Nanhaipotamon* are typically lowland species, usually found below 500 m a.s.l., that excavate burrows in the soft mud close to hillstreams (Dai 1999; Shih & Ng 2011; Shih *et al.* 2011; Huang *et al.* 2012, 2018b; Lin *et al.* 2012, 2013). The name of the genus is derived from its main distribution, which is along the coastal areas of China facing the South China Sea (“Nanhai”). All known species of this genus share a similar bauplan: a bulging and generally smooth carapace typical of semiterrestrial potamids. The genus is pending revision as some “species” are indistinguishable externally and have very similar gonopodal morphology, while intraspecific variations are not well documented, causing problems in species identification (Huang *et al.* 2018b). Multiple insufficiently described species further compact this problem.

A few years ago, the first author (Chao Huang) noticed photos of a bright red freshwater crab from Huizhou on a social media post. The crab superficially resembled *Nanhaipotamon*, but its unique frontal regions of carapace were void of granules as typically seen in this genus (cf. Dai 1999). Several subsequent attempts to track down this animal were not successful. It was not until 2017, that we were able to obtain a few specimens that were donated to us by

Wei-Hang Wang, a researcher on jumping spiders, who had managed to find these crabs in dry shallow burrows at a relatively high altitude in Boluo County, Huizhou. After we collected additional material, this bright red crab was promptly identified as a new *Nanhaipotamon* species and is described here as *Nanhaipotamon incendium* **n. sp.** On our second collection trip to Huizhou, we stumbled upon some mud holes next to a creek in another locality, from which we dug out some peculiar-looking crabs of *Nanhaipotamon* whose anterolateral margins and granules of the carapace front were strikingly bright golden. A series of specimens were thus collected for study. The unique morphology of the male first gonopods of these specimens indicates they belong to yet another undescribed species, which is described herein as *Nanhaipotamon aureomarginatum* **n. sp.**

Notably, *Nanhaipotamon incendium* **n. sp.** is sympatric with *N. aff. aculatum* Dai, 1997, whereas *Nanhaipotamon aureomarginatum* **n. sp.** is sympatric with *N. aff. hongkongense* (Shen, 1940). In both cases, the sympatric congeners occupy different habitats and are also morphologically distinct from each other. Genetic evidence shows that while the two new species are sufficiently distinct from other known species of *Nanhaipotamon*, they cannot be separated from their respective congeners using the mitochondrial cytochrome oxidase subunit I (COI). We speculate that strong divergent selection forces (“anti-cryptic speciation”) are the main cause of this striking disparity between morphology and genetics (Bickford *et al.* 2007). This intriguing phenomenon calls for further genetic investigation which is regrettably inaccessible for us at the moment. The abovementioned *N. aff. aculatum* and *N. aff. hongkongense*, while morphologically similar, are genetically distinct and also come from different localities than the real *N. aculatum* and *N. hongkongense* and as such could not be identified with certainty.

Material and methods

Specimens were collected by hand from southern China and preserved in 75% ethanol since 2017. These (type material) are now deposited in the Australian Museum, Sydney, Australia (AM); the Zoological Collection of the National Chung Hsing University, Taichung, Taiwan (NCHUZOO); the Sun Yat-sen Museum of Biology, Sun Yat-sen University, Guangzhou, China (SYSBM); and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore, Singapore (ZRC). Measurements, in millimetres, are of the carapace width and carapace length, respectively. Other abbreviations are as follows: G1, male first gonopod; G2, male second gonopod. The terminology used primarily follows that of Dai (1999) and Davie *et al.* (2015).

A portion of the COI gene, with 616–658 basepairs (bp), was amplified following Shih & Poupin (2020), using the primers LCO1490, COL14, HCO2198 and COH6 (Folmer *et al.* 1994; Roman & Palumbi 2004; Schubart & Huber 2006), as well as a new designed internal primer ICOUB (5'-CCYCTTTCTACYATACTTCT-3'). Sequences of the different haplotypes were deposited into GenBank (accession numbers given in Table 1). *Nanhaipotamon aculatum* is only known from a single male specimen from Hong Kong. There is no precise locality data and also no DNA from the holotype to confirm the identity of this species. Our specimens from neighboring Shenzhen, however, show similar morphology to the illustrations in Dai (1997). We tentatively treat these Shenzhen specimens as belonging to this species. The case of *Nanhaipotamon guangdongense* Dai, 1997, is similar to the above, except the only male specimen is from Guangdong. We used a specimen from Gujing, Jiangmen of Guangdong Province to represent the species as that is where the holotype most likely came from (Huang *et al.* 2018b). Other COI sequences of *Nanhaipotamon* from southern China were also downloaded from GenBank for comparison, including *N. macau* Huang, Wong & Ahyong, 2018 (MK226142) and *N. wupingense* Cheng, Yang, Zhong & Li, 2003 (AB433569, AB470510, AB470511). Pairwise estimates of the Kimura (1980) 2-parameter distances for genetic diversities between specimens were calculated in MEGA (vers. 10.0.5, Kumar *et al.* 2018).

TABLE 1. Specimens and the haplotypes of the COI gene from *Nanhaipotamon* species collected from southern China used in this study. See “Material and Methods” for abbreviations of museums and universities.

Species	Locality	Catalogue no. of SYSUM (unless indicated)	Sample size	GenBank access. no. COI	
<i>N. incendium</i> n. sp.	Guangdong: Huizhou	001806	2	MZ662832, MZ662833	
	Guangdong: Huizhou	001803	1	MZ662834	
	Guangdong: Huizhou	001804	1	MZ662835	
	Guangdong: Huizhou	001802	1	MZ662836	
	Guangdong: Huizhou	001805	1	MZ662837	
<i>N. aff. aculatum</i>	Guangdong: Huizhou	001779	1	MZ662838	
	Guangdong: Huizhou	001778	1	MZ662839	
	Guangdong: Huizhou	001776	1	MZ662840	
<i>N. aureomarginatum</i> n. sp.	Guangdong: Huizhou	001812	1	MZ662841	
	Guangdong: Huizhou	001815	1	MZ662842	
	Guangdong: Huizhou	001813	1	MZ662843	
	Guangdong: Huizhou	NCHUZOOL 17036	1	MZ662844	
	Guangdong: Huizhou	AM P.105615	1	MZ662845	
<i>N. aff. hongkongense</i>	Guangdong: Huizhou	001992	1	MZ662846	
	Guangdong: Huizhou	001993	1	MZ662847	
	Guangdong: Huizhou	001998	1	MZ662848	
	Guangdong: Huizhou	001999	1	MZ662849	
	Guangdong: Shenzhen	002001	1	MZ662850	
	Guangdong: Shenzhen	002002	1	MZ662851	
	<i>N. hongkongense</i>	Hong Kong: New Territory: Nai Chung stream	ZRC 1991.1776 (neotype)	1	MZ662852 ^a
		Hong Kong: Hong Kong Island: Wan Chai Gap; Tin Wan	NCHUZOOL 17037, 17038	2	MZ662853, MZ662854
Hong Kong: Hong Kong Island: Tin Wan		NCHUZOOL 17039	1	MZ662855	
Hong Kong: Hong Kong Island: Tin Wan		NCHUZOOL 17040	1	MZ662856	
<i>N. aculatum</i>		Guangdong: Shenzhen	001303	1	MZ662857
	Guangdong: Shenzhen	001028, 001179	2	MZ662858, MZ662859	
<i>N. guangdongense</i>	Guangdong: Dongguan	NCHUZOOL 13138	1	AB433575	
	Guangdong: Jiangmen	001141	1	MZ662860	
<i>N. zhuhaiense</i> Huang, Huang & Ng, 2012	Guangdong: Zhuhai	001001	1	MZ662861	
	Guangdong: Zhuhai	001249	1	MZ662862	
	Guangdong: Zhuhai	001023	1	MZ662863	
	Guangdong: Zhuhai	001015	1	MZ662864	

^a sequences are shorter and not included for further analyses (see DNA analyses and discussion).

Taxonomy

Family Potamidae Ortmann, 1896

Subfamily Potamiscinae Bott, 1970

Genus *Nanhaipotamon* Bott, 1968

Type species. *Potamon (Potamon) formosanum* Parisi, 1916, by original designation; gender neuter.

Nanhaipotamon incendium n. sp.

(Figs. 1–3, 7I, J, 8A)

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Type material. Holotype: SYSBM 001799, male (31.3 × 25.0 mm), Boluo County [ca. 23.3°N, 114.3°E], Huizhou City, Guangdong Province, China, shallow mud burrow, 700 m a.s.l., coll. C. Huang, August 2018.

Paratypes: SYSBM 001801, 001803, 001804, 3 males (27.0 × 21.6 mm, 25.4 × 20.5 mm, 18.7 × 15.3 mm), same data as for holotype; SYSBM 001800, 001802, 2 females (32.0 × 25.0 mm, 29.4 × 23.6 mm), same data as for holotype; SYSBM 001805, male (25.2 × 20.2 mm), Boluo County, Huizhou City, Guangdong Province, China, shallow mud burrow, 700 m a.s.l., coll. W.H. Wang, August 2017; SYSBM 001806, female (27.9 × 21.6 mm), same data as above; NCHUZOOL 17034, male (31.3 × 25.0 mm), Boluo County, Huizhou City, Guangdong Province, China, deep mud burrow with water at bottom, 700 m a.s.l., coll. C. Huang, November 2018; AM P.105614, male (29.1 × 23.8 mm), Boluo County, Huizhou City, Guangdong Province, China, shallow mud burrow, 700 m a.s.l. coll., C. Huang, August 2018; AM P.105614, female (32.7 × 26.6 mm), same data as above; ZRC 2021.0415, male (25.8 × 20.5 mm), same data as above; ZRC 2021.0416, female (25.6 × 21.0 mm), same data as above.

Diagnosis. Carapace broader than long, regions indistinct (Fig. 1). Dorsal surface smooth, finely pitted, convex (Fig. 1). Anterolateral margins smooth, lined with numerous indistinct granules (Fig. 1). Posterolateral surfaces smooth (Fig. 1). Sub-orbital, sub-hepatic and pterygostomial regions clearly divided by sutures, with smooth and pitted surface (Fig. 2A). Maxilliped III exopod reaching to proximal one-fifth of merus, flagellum absent (Fig. 3A). G1 slender, reaching beyond pleonal locking tubercle almost up to suture between sternites IV/V *in situ* (Fig. 2D). G1 subterminal segment 2.6–2.7 × as long as terminal segment, tapering distally. G1 terminal segment relatively small, inverted foot-shaped; inner proximal margin strongly concave; inner distal margin almost straight to gently convex; apex acute, directed outward, orientation oblique to longitudinal axis of G1 (Figs. 3C–E, 7I, J). G2 subterminal segment 2.0–2.1 × as long as flagellum-like terminal segment (n = 3) (Fig. 3B).

Description. Carapace broader than long, width 1.2–1.3 × length (n = 13), regions indistinct (Fig. 1). Dorsal surface smooth, finely pitted, convex (Fig. 1). Front deflexed, margin ridged in dorsal view (Fig. 1). Epigastric cristae smooth, very low and almost indistinct, separated from each other by narrow gap (Figs. 1, 2A). Postorbital cristae smooth, very low, laterally extended, almost fused with epigastric cristae and epibranchial teeth (Fig. 1). Branchial regions inflated; cervical grooves very shallow, inconspicuous; mesogastric region convex (Fig. 1). External orbital teeth blunt, triangular with gently convex outer margins, each separated from anterolateral margin by small gap (Figs. 1, 2A). Epibranchial teeth very small and inconspicuous (Figs. 1, 2A). Anterolateral margins smooth, lined with numerous indistinct granules (Fig. 1). Posterolateral surfaces smooth (Fig. 1). Orbits large, supraorbital and infraorbital margins ridged (Figs. 1, 2A). Sub-orbital, sub-hepatic and pterygostomial regions clearly divided by sutures, with smooth and pitted surface (Fig. 2A). Epistome median lobe broadly triangular, lateral margins almost straight (Fig. 2A).

Maxilliped III with merus subtrapezoidal, about as wide as long, median depression distinct; ischium subtrapezoidal, width about 0.9 × length, with distinct median sulcus, with anterior mesial margin rounded; exopod reaching to proximal one-fifth of merus, flagellum absent (Fig. 3A).

Chelipeds (pereiopod I) unequal, relatively less inflated in females (Figs. 1, 3F–I). Merus trigonal in cross section, margins weakly crenulated, surfaces generally smooth (Figs. 1, 2A). Carpus with long, acute spine at inner-distal angle, spinule at base, surfaces generally smooth (Fig. 1). Major cheliped palm length about 1.1–1.2 × height in males (n = 5), 1.2–1.3 × in females (n = 5); dactylus 1.0–1.1 × palm length in males (n = 5) and females (n = 5)

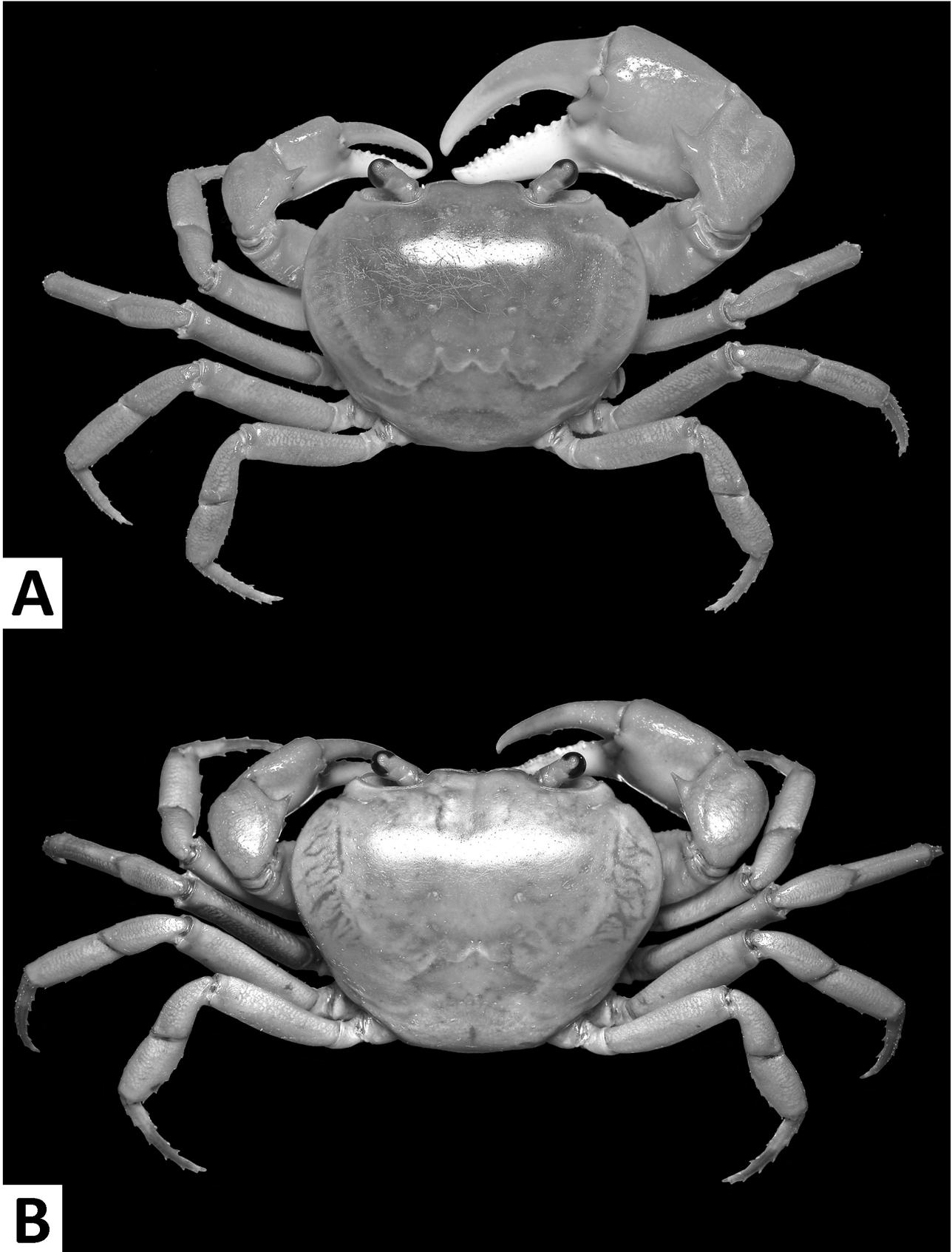


FIGURE 1. Dorsal habitus of *Nanhaipotamon incendium* n. sp. (A) male holotype (31.3 × 25.0 mm), SYSBM 001799; (B) female paratype (32.0 × 25.0 mm), SYSBM 001800.

(Fig. 3F–I). Palm surface generally smooth, pitted, inner posterior region slightly granulated. Dactylus curved, as long as pollex. Occlusal margin of fingers lined with blunt, round teeth; small gape when finger tips in contact (Fig. 3F–I).

Ambulatory legs (pereiopods II–V) slender, with short and sparse setae. Pereiopod III merus $0.6\text{--}0.7 \times$ carapace length in males ($n = 5$), $0.6\text{--}0.7$ in females ($n = 5$). Pereiopods V propodus $2.3\text{--}2.4 \times$ as long as broad in males ($n = 5$), $2.3\text{--}2.5$ in female ($n = 5$), shorter than dactylus (Fig. 1).

Male thoracic sternum generally smooth, pitted; sternites I–IV relatively narrow, width $1.6 \times$ as length (Fig. 2B, C). Sternites I, II separated by ridge, fused as broadly triangular structure; sternites II, III separated by conspicuous transverse sulcus, reaching edge of sternum; sternites III, IV fused, without visible demarcation (Fig. 2B, C). Male sterno-pleonal cavity reaching anteriorly beyond level of posterior articular condyle of cheliped coxa (Fig. 2B–D); median longitudinal groove separating sternites VII, VIII deep (Fig. 2D). Male pleonal locking tubercles positioned at mid-length of sternite V (Fig. 2D). Adult female vulvae ovate, relatively large but not reaching sternites V or VII, positioned closely to one another, orientation oblique to longitudinal axis of sterno-pleonal cavity (Fig. 2F).

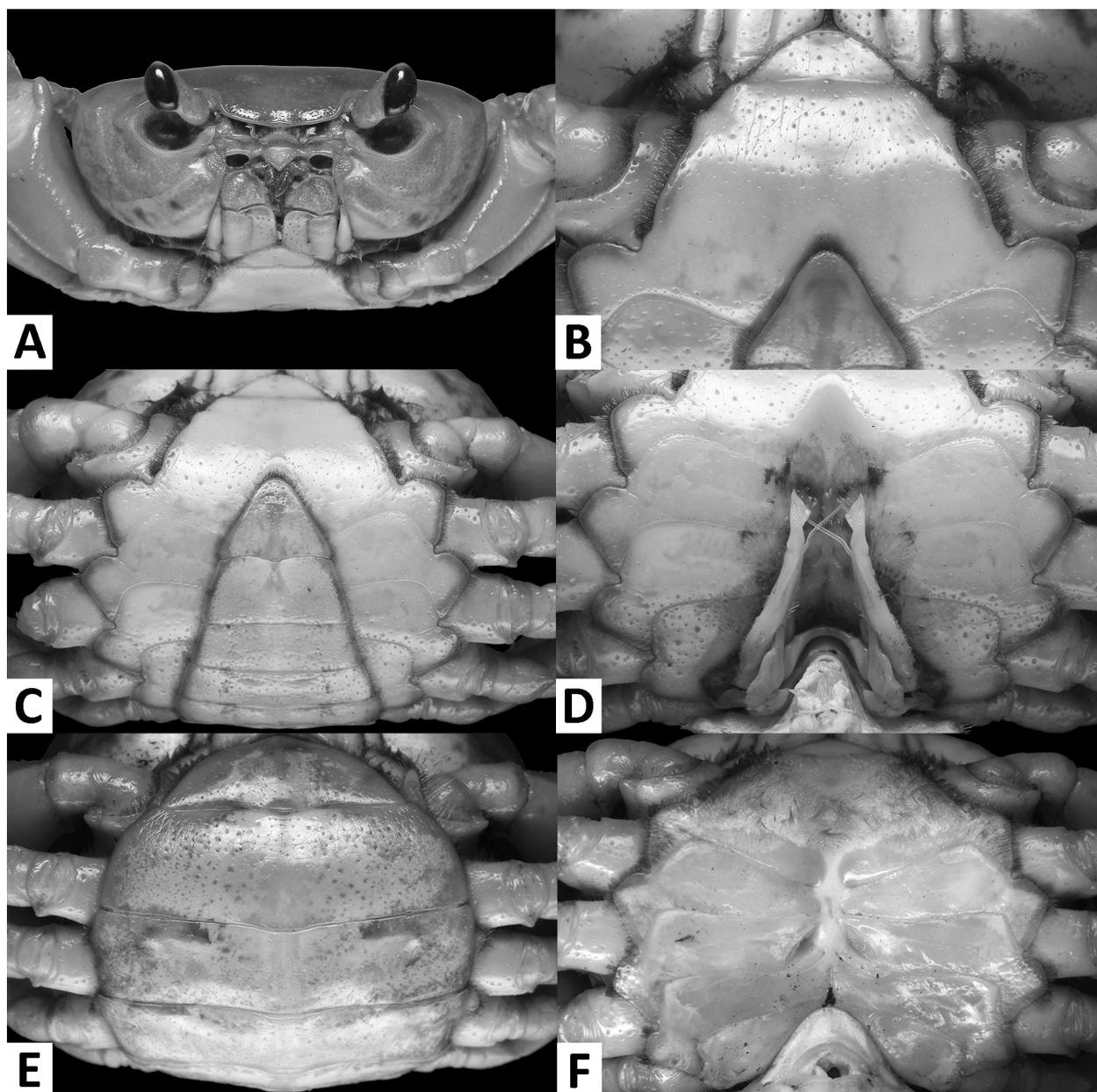


FIGURE 2. *Nanhaiopotamon incendium* n. sp.: male holotype (31.3 × 25.0 mm), SYSBM 001799 (A–D); female paratype (32.0 × 25.0 mm), SYSBM 001800 (E, F). (A) cephalothorax, frontal view; (B) anterior thoracic sternum; (C) thoracic sternum, pleonites III–VI and telson; (D) sterno-pleonal cavity with G1 *in situ*, ventral view; (E) pleonites III–VI and telson; (F) sternum showing vulvae.

Pleon and telson triangular in males (Fig. 2C) and broadly ovate in females (Fig. 2E). Male pleonites III–VI progressively narrower, lateral margins nearly straight; pleonite VI $2.2 \times$ as broad as long. Male telson $1.3 \times$ as broad as long, with blunt apex (Fig. 2C).

G1 slender, reaching beyond pleonal locking tubercle almost up to suture between sternites IV/V *in situ* (Fig. 2D). G1 subterminal segment $2.6\text{--}2.7 \times$ as long as terminal segment ($n=3$), tapering distally. G1 terminal segment relatively small, inverted foot-shaped; inner proximal margin strongly concave; inner distal margin almost straight to gently convex; apex acute, directed outward, orientation oblique to longitudinal axis of G1 (Figs. 3C–E, 7I, J). G2 subterminal segment $2.0\text{--}2.1 \times$ as long as flagellum-like terminal segment ($n=3$) (Fig. 3B).

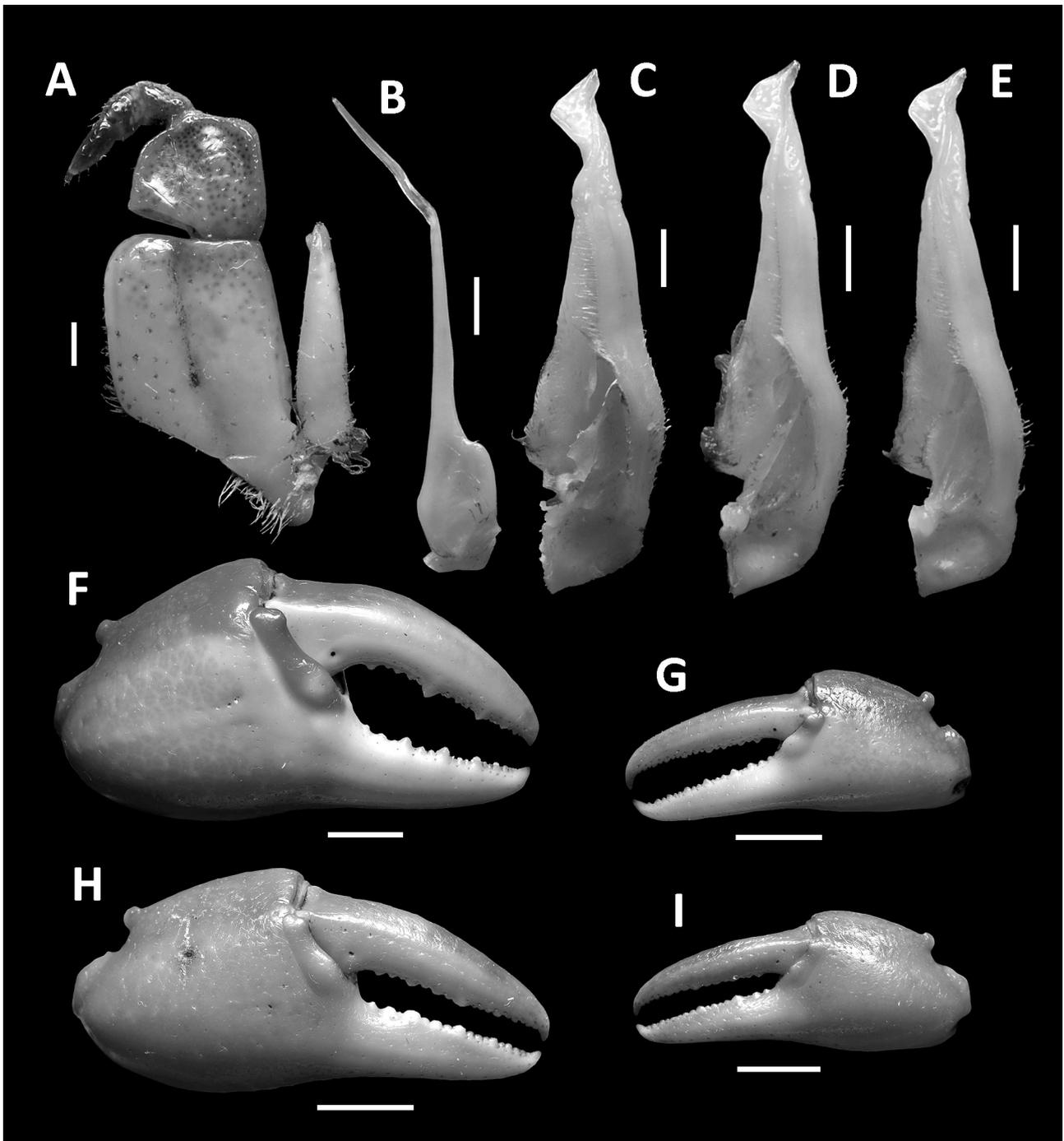


FIGURE 3. *Nanhaipotamon incendium* n. sp.: male holotype (31.3×25.0 mm), SYSBM 001799 (A–C, F, G); male paratype (27.0×21.6 mm), SYSBM 001801 (D); male paratype (25.4×20.5 mm), SYSBM 001803 (E); female paratype (32.0×25.0 mm), SYSBM 001800 (H, I). (A) left maxilliped III; (B) left G2, ventral view; (C–E) left G1, ventral view; (F, H) major cheliped; (G, I) minor cheliped. Scale bars: A–E = 1.0 mm; F–I = 5.0 mm.

Etymology. The specific name “incendium” means fire in Latin, which describes the live colouration of the species. The name thus is to be conceived as a noun in the nominative singular standing in apposition to the generic name.

Colour in life. Carapace, ambulatory legs and upper half of chelipeds generally bright red to orange, lower half of chelipeds white.

Habitat. *Nanhaipotamon incendium* n. sp. is a semiterrestrial species that burrows in the forest floor of relatively high-altitude rainforests at around 700 m a.s.l., which is the highest recorded for this genus (Dai 1997, 1999). During summer, the rainforest not only receives a lot of rain but also abundant mist, which enables the crabs to freely roam on the forest floor. Crabs were collected from moist shallow burrows that do not reach the water table up to 50 m away from the nearest hillstream. In the winter when it is drier, however, the crabs burrow deep until they reach the water table. The once occupied shallow holes were found to be abandoned. Holes with fresh wet mud near the entrance were inaccessible to us due to the presence of roots and rocks, which made excavation nearly impossible. Immediately next to the hillstream, however, we found a few juveniles and a freshly molted adult male in mud holes under rocks. *Longpotamon anyuanense* (Dai, Zhou & Peng, 1995) is a large aquatic species, which lives under rocks in the hillstreams and is sympatric with the new species. *Nanhaipotamon* aff. *aculatum* were found from the same mountain, but at lower altitudes typically around 100 m a.s.l. Only on one instance, the habitats of the two species seemed to overlap to some extent as they were found side by side in 500 m a.s.l. (W.-H. Wang, pers. comm.).

Remarks. The overall intraspecific morphological variation is low. Larger specimens of *N. incendium* n. sp. tend to have a relatively wider carapace. The general shape of the G1 terminal segment in the new species seems to be stable, however, the inner distal margin varies from almost straight to gently convex (Fig. 3C–E). *Nanhaipotamon incendium* n. sp. is a unique species within this genus in that it has smooth sub-orbital, sub-hepatic and pterygostomial regions (Fig. 2A) [vs. granulated or striated in all other congeners (Fig. 5A; Huang *et al.* 2018b: figs. 3B, 8B)], and the exopod of the maxilliped III is relatively shorter and completely lacks a flagellum (Fig. 3A) [vs. relatively longer exopod with flagellum in all other congeners (Fig. 6A; Huang *et al.* 2018b: fig. 5A)]. The relatively small G1 terminal segment of the new species is also unique within the genus (Figs. 3C–E, 7I, J) [vs. G1 terminal segment relatively large to very large in congeners (Figs. 6C–E, 7A–H; Huang *et al.* 2018b: figs. 5C–E, 7)]. The G1 of the new species is very distinct from the sympatric *Nanhaipotamon* aff. *aculatum* due to the same reason (Fig. 7D). In the field, the new species can readily be distinguished from the sympatric congener by its bright red to orange colouration (Fig. 8A) (vs. blue or light brown carapace in *N. aff. aculatum*; Fig. 8B). *Nanhaipotamon* cf. *hongkongense* from neighboring Shenzhen (Fig. 7E–G) can also be bright orange to red and may look similar to the new species, but the smoothness of the carapace frontal regions immediately separates the two species apart.

Conservation status. *Nanhaipotamon incendium* n. sp. is only known from a single collection point and is likely highly endemic. We do not know of any current threats to this species, though its bright colours make it a prime target for the pet trade. As the collection of freshwater crabs are not yet regulated by law in China, we choose to remain discreet about the exact locality of the new species.

Nanhaipotamon aureomarginatum n. sp.

(Figs. 4–6, 7K, L, 8C)

urn:lsid:zoobank.org:act:441A93FB-91A0-4FF3-9945-2EE9885B81BB

Type material. Holotype: SYSBM 001807, male (37.7 × 30.7 mm), Huidong County [ca. 23.0°N, 114.7°E], Huizhou City, Guangdong Province, China, burrow in soft mud near hillstream, 100 m a.s.l., coll. C. Huang, November 2018.

Paratypes: SYSBM 001809–001812, 4 males (30.9 × 25.3 mm, 29.1 × 23.2 mm, 27.4 × 22.3 mm, 24.7 × 20.5 mm), same data as holotype; SYSBM 001808, 001813–001815, 4 females (33.9 × 28.4 mm, 29.6 × 24.9 mm, 19.24 × 16.1 mm, 13.5 × 11.1 mm), same data as holotype; NCHUZOOL 17035, male (26.5 × 21.5 mm), same data as holotype; NCHUZOOL 17036, female (25.5 × 20.8 mm), same data as holotype; AM P.105615, male (28.9 × 23.2 mm), same data as holotype; AM P.105615, female (17.9 × 15.0 mm), same data as holotype.

Diagnosis. Carapace broader than long, regions indistinct (Fig. 4). Dorsal surface generally smooth, pitted, convex, slightly rugose on anterolateral regions in smaller specimens (Fig. 4). Anterolateral margins cristate with fused granules, bent inward posteriorly (Fig. 4). Posterolateral surfaces with low, oblique striae converging posteriorly; granules scattered among striae, some merged together (Fig. 4). Sub-orbital, pterygostomial regions covered with

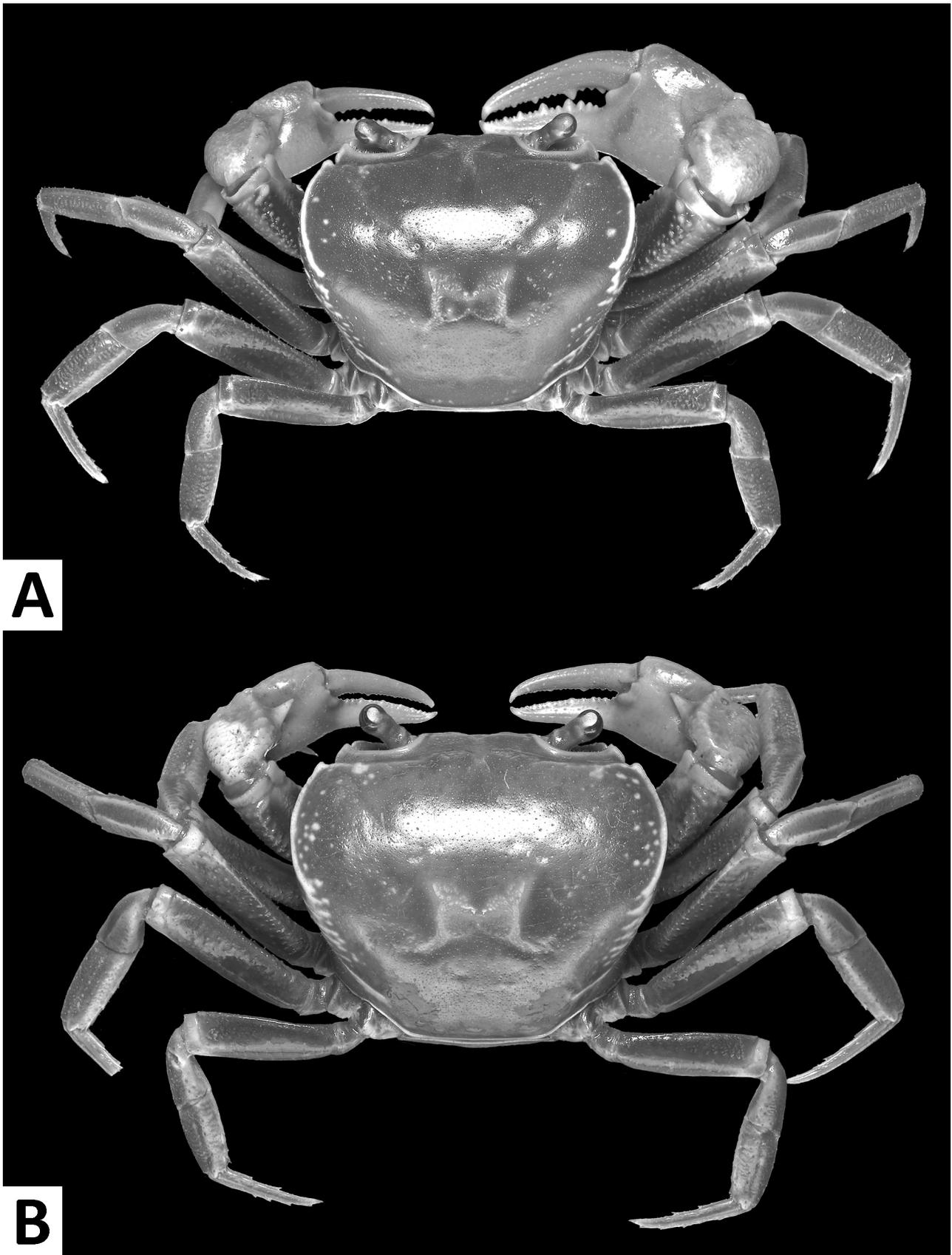


FIGURE 4. Dorsal habitus of *Nanhaipotamon aureomarginatum* n. sp.: (A) male holotype (37.7 × 30.7 mm), SYSBM 001807; (B) female paratype (33.9 × 28.4 mm), SYSBM 001808.

large round granules; sub-hepatic region with lines of fused smaller granules (Fig. 5A). Maxilliped III exopod reaching to proximal one-third of merus, with flagellum (Fig. 6A). G1 slender, reaching beyond suture between sternites IV/V *in situ* (Fig. 5D). G1 subterminal segment $2.1\text{--}2.2 \times$ as long as terminal segment. G1 terminal segment large, duck head-shaped; mesial margin strongly convex; outer margin strongly concave; anterior margin almost straight, oblique to longitudinal axis of G1; apex pointing outwards (Figs. 6C–E, 7K, L). G2 subterminal segment $1.7\text{--}1.8 \times$ as long as flagellum-like terminal segment (Fig. 6B).

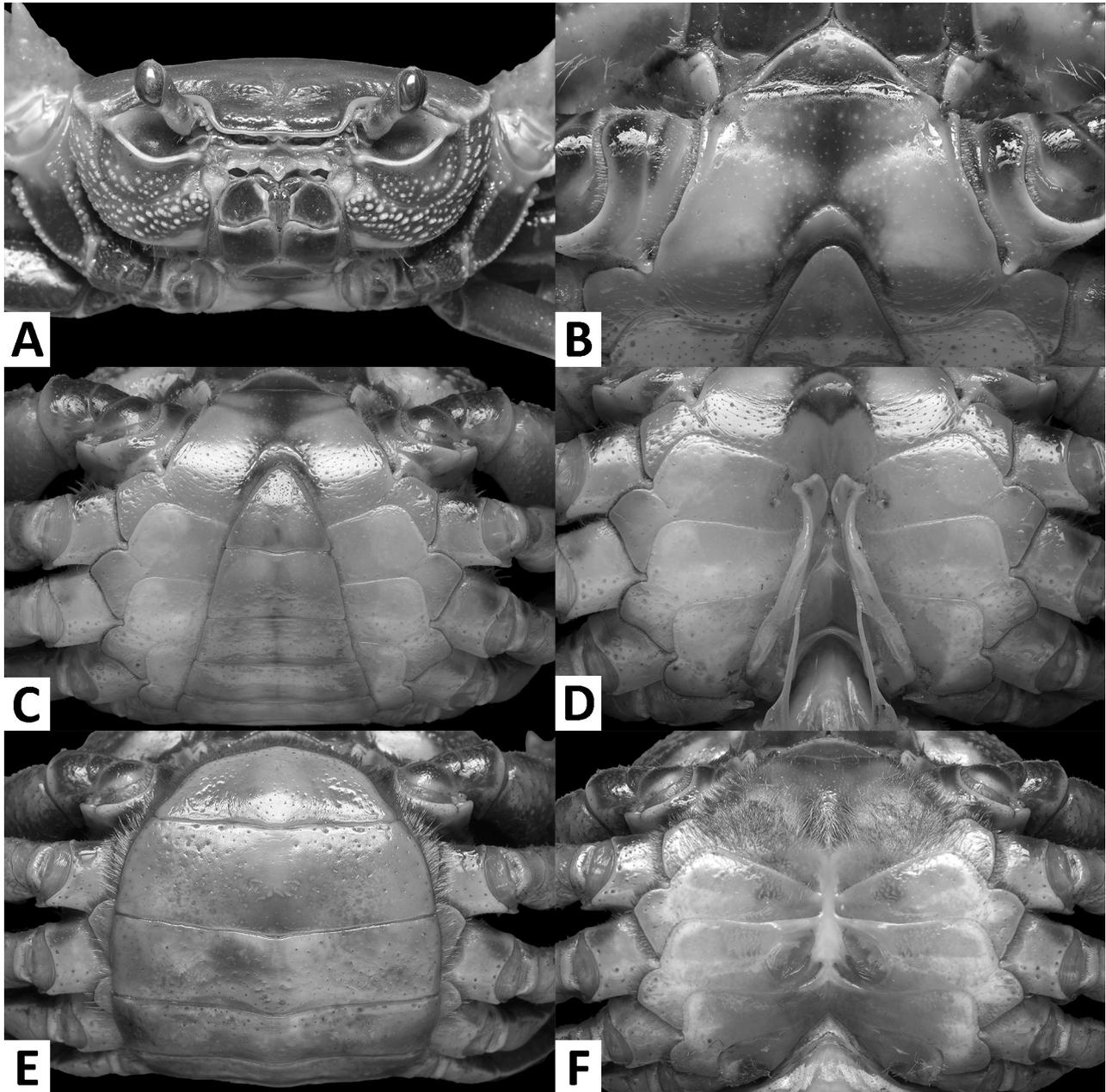


FIGURE 5. *Nanhaipotamon aureomarginatum* n. sp.: male holotype (37.7 × 30.7 mm), SYSBM 001807 (A–D); female paratype (33.9 × 28.4 mm), SYSBM 001808 (E, F). (A) cephalothorax, frontal view; (B) anterior thoracic sternum; (C) thoracic sternum, pleonites III–VI and telson; (D) sterno-pleonal cavity with G1 *in situ*, ventral view; (E) pleonites III–VI and telson; (F) sternum showing vulvae.

Description. Carapace broader than long, width $1.2\text{--}1.3 \times$ length ($n = 13$), regions indistinct (Fig. 1). Dorsal surface generally smooth, pitted, convex, slightly rugose on anterolateral regions in smaller specimens (Fig. 4). Front deflexed, margin slightly ridged in dorsal view (Fig. 4). Epigastric cristae low, separated by a narrow gap (Fig. 4). Postorbital cristae prominent, laterally extended, almost fused with epigastric cristae and epibranchial teeth (Fig. 4). Branchial regions inflated; cervical grooves shallow; mesogastric region convex (Fig. 4). External orbital

teeth blunt, triangular with gently convex outer margins, each separated from anterolateral margin by small gap (Figs. 4, 5A). Epibranchial teeth small, granular (Figs. 4, 5A). Anterolateral margins cristate with fused granules, bent inward posteriorly (Fig. 4). Posterolateral surfaces with low, oblique striae converging posteriorly; granules scattered among striae, some merged together (Fig. 4). Orbits large; supraorbital and infraorbital margins cristate (Figs. 4, 5A). Sub-orbital, pterygostomial regions covered with large round granules; sub-hepatic region with lines of fused smaller granules (Fig. 5A). Epistome median lobe broadly triangular, lateral margins sinuous (Fig. 5A).

Maxilliped III with merus subtrapezoidal, about as wide as long, median depression distinct; ischium; ischium subtrapezoidal, width about $0.7 \times$ length with distinct median sulcus, with anterior mesial margin rounded; exopod reaching to proximal one-third of merus, with flagellum (Fig. 6A).

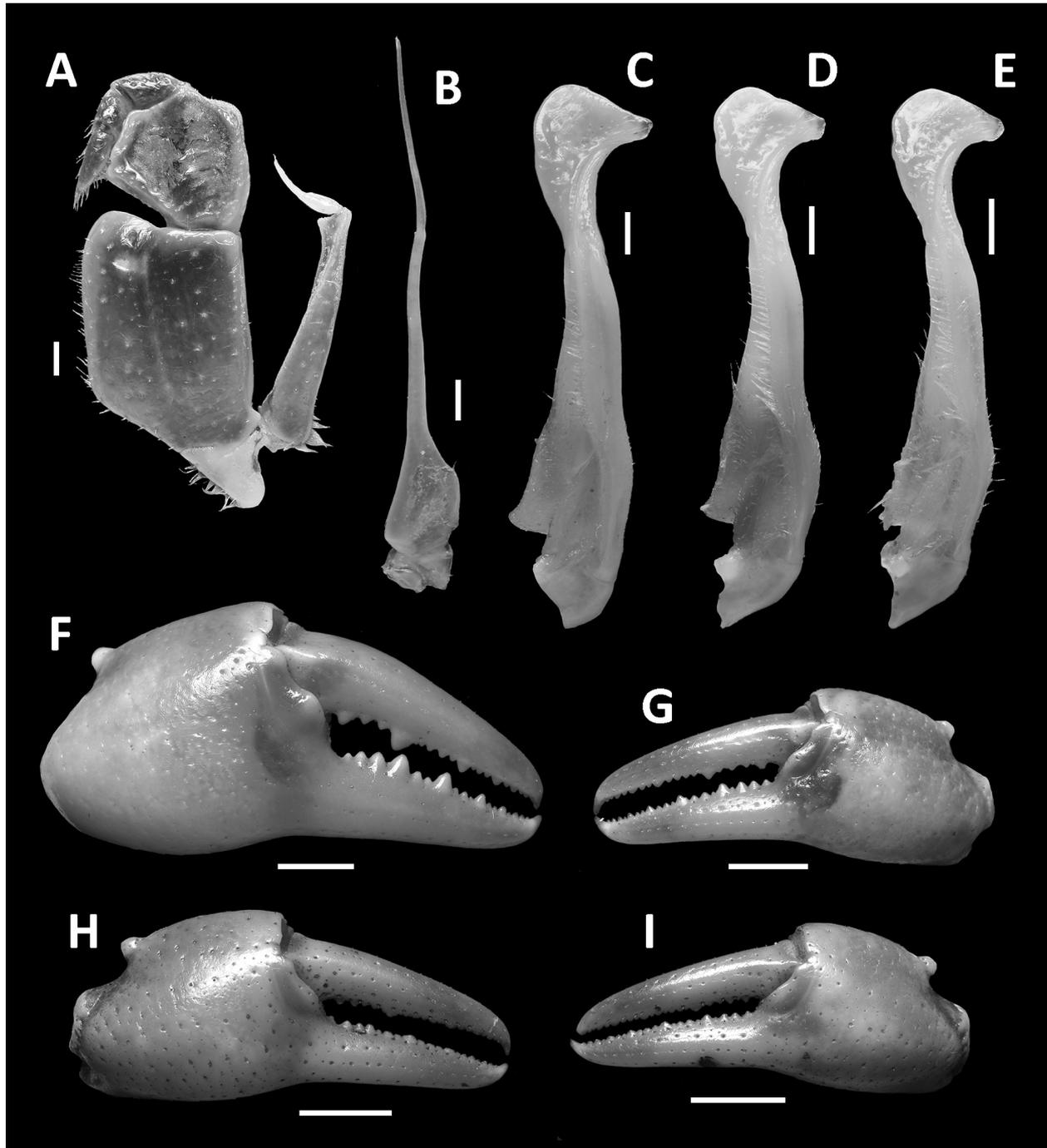


FIGURE 6. *Nanhaipotamon aureomarginatum* n. sp.: male holotype (37.7 × 30.7 mm), SYSBM 001807 (A–C, F, G); male paratype (30.9 × 25.3), SYSBM 001809 (D); male paratype (28.9 × 23.2 mm), AM (E); female paratype (33.9 × 28.4 mm), SYSBM 001808 (H, I). (A) left maxilliped III; (B) left G2, ventral view; (C–E) left G1, ventral view; (F, H) major cheliped; (G, I) minor cheliped. Scale bars: A–E = 1.0 mm; F–I = 5.0 mm.

Chelipeds (pereopod I) unequal, relatively less inflated in females (Figs. 4, 6F–I). Merus trigonal in cross section, margins lined with granules, outer-dorsal surface rugose (Figs. 4, 5A). Carpus with long, acute spine at inner-distal angle, spinule at base, dorsal surface rugose (Fig. 4). Major cheliped palm length about 1.3–1.4 × height in males (n = 6), 1.4 × in females (n = 3); dactylus about 1.0–1.1 × palm length in both males (n = 6) and females (n = 3) (Fig. 6F–I). Palm surface pitted, dorsal surface rugose. Dactylus as long as pollex. Occlusal margin of fingers lined with irregular blunt teeth, slight gape when finger tips in contact (Fig. 6F–I).

Ambulatory legs (pereopods II–V) slender, with short and sparse setae. Pereopods III merus 0.7 × carapace length in males (n = 6), 0.6–0.7 × in females (n = 3). Pereopods V propodus 2.0–2.4 × as long as broad in males (n = 6), 2.2–2.3 × in females (n = 3) (Fig. 4).

Male thoracic sternum generally smooth, pitted; sternites I–IV relatively narrow, width 1.4 × as length (Fig. 5B, C). Sternites I, II fused, appearing broadly triangular; sternites II, III separated by shallow transverse sulcus, reaching edge of sternum; sternites III, IV fused, with barely visible demarcation (Fig. 5B, C). Male sterno-pleonal cavity reaching anteriorly to level of mid-length of cheliped coxa (Fig. 5B–D); median longitudinal groove separating sternites VII, VIII deep (Fig. 5D). Male pleonal locking tubercles positioned at mid-length of sternites V (Fig. 5D). Adult female vulvae ovate, relatively large but not reaching sternites V or VII; positioned closely to one another, orientation oblique to longitudinal axis of sterno-pleonal cavity (Fig. 5F).

Pleon and telson triangular in males (Fig. 5C) and broadly ovate in females (Fig. 5E). Male pleonites III–VI progressively narrower, lateral margins nearly straight; pleonite VI 1.9 × as broad as long. Male telson 1.2 × as broad as long, with blunt apex (Fig. 5C).

G1 slender, reaching beyond suture between sternites IV/V *in situ* (Fig. 5D). G1 subterminal segment 2.1–2.2 × as long as terminal segment (n = 3). G1 terminal segment large, duck head-shaped; mesial margin strongly convex; outer margin strongly concave; anterior margin almost straight, oblique to longitudinal axis of G1; apex pointing outwards (Figs. 6C–E, 7K, L). G2 subterminal segment 1.7–1.8 × as long as flagellum-like terminal segment (n = 3) (Fig. 6B).

Etymology. The specific name “*aureomarginatum*” alludes to the new species’ golden-coloured anterolateral margins of the carapace. The name thus is to be conceived as an adjective in the nominative singular.

Colour in life. Colour variable. Carapace generally brown to dark purple; anterolateral margins, orbital margins, and granules and striae on frontal and lateral regions of carapace golden to bright orange. Ambulatory legs olive yellow to dark purple. Chelipeds light bluish grey to orange. Juveniles usually completely brown.

Habitat. *Nanhaipotamon aureomarginatum* n. sp. is a lowland semi-terrestrial species found at around 100 m a.s.l. While it is sympatric with *Nanhaipotamon* aff. *hongkongense* at the type locality, the two species seem to be ecologically distinct. The smaller sized *N.* aff. *hongkongense* digs in the gravelly soil at the water’s edge next to the larger and fast flowing streams, whereas *N. aureomarginatum* n. sp. is more terrestrial and prefers to burrow in soft mud near the smaller branches of the hillstream or seeps.

Remarks. The overall intraspecific morphological variation is low. The general shape of the G1 in *N. aureomarginatum* n. sp. seems to be quite stable (Fig. 6C–E). While externally a typical *Nanhaipotamon*, the proportionately large G1 terminal segment of *N. aureomarginatum* n. sp. (Figs. 6C–E, 7K, L) is unique amongst all congeners, with only the exceptions of *N. macau* and *N. wupingense* (Figs. 3C–E, 7I, J; Huang *et al.* 2018b). *Nanhaipotamon aureomarginatum* n. sp. can be nevertheless differentiated from the latter two species by the higher and rounded inner distal margin of the G1 terminal segment (Fig. 6C–E, 7K, L) [vs. G1 terminal segment with inner distal margin lower and sinuous in *N. macau* (Huang *et al.* 2018b: fig. 6C) and *N. wupingense* (Huang *et al.* 2018b: fig. 6D)]. In the field, the new species can easily be separated with the sympatric *N.* aff. *hongkongense* by the live colouration (see “colour in life”; Fig. 8C) (vs. dark red to red in *N.* aff. *hongkongense*; Fig. 8D).

Conservation status. *Nanhaipotamon aureomarginatum* n. sp. is likely highly endemic. Its bright colours make it a prime target for collection for the pet trade. With this consideration, we choose to remain discreet about the exact locality of the new species.

DNA analyses and discussion

The pairwise nucleotide divergences with K2P distance for the first main clade are given in Table 2. The divergences within the “*N. incendium* + *N. aff. aculatum*” and “*N. aureomarginatum* + *N. aff. hongkongense*” clades are 0.43% (0–0.92%) and 0.85% (0–1.82%), respectively. The minimum interspecific divergences of the above two clades with other species/clades are 1.86% and 2.17%, respectively. The sequence of the neotype of *N. hongkongense* (ZRC 1991.1776) obtained is short (295 bp), but it is still enough to confirm specimens from Hong Kong Island are conspecific (Table 2).

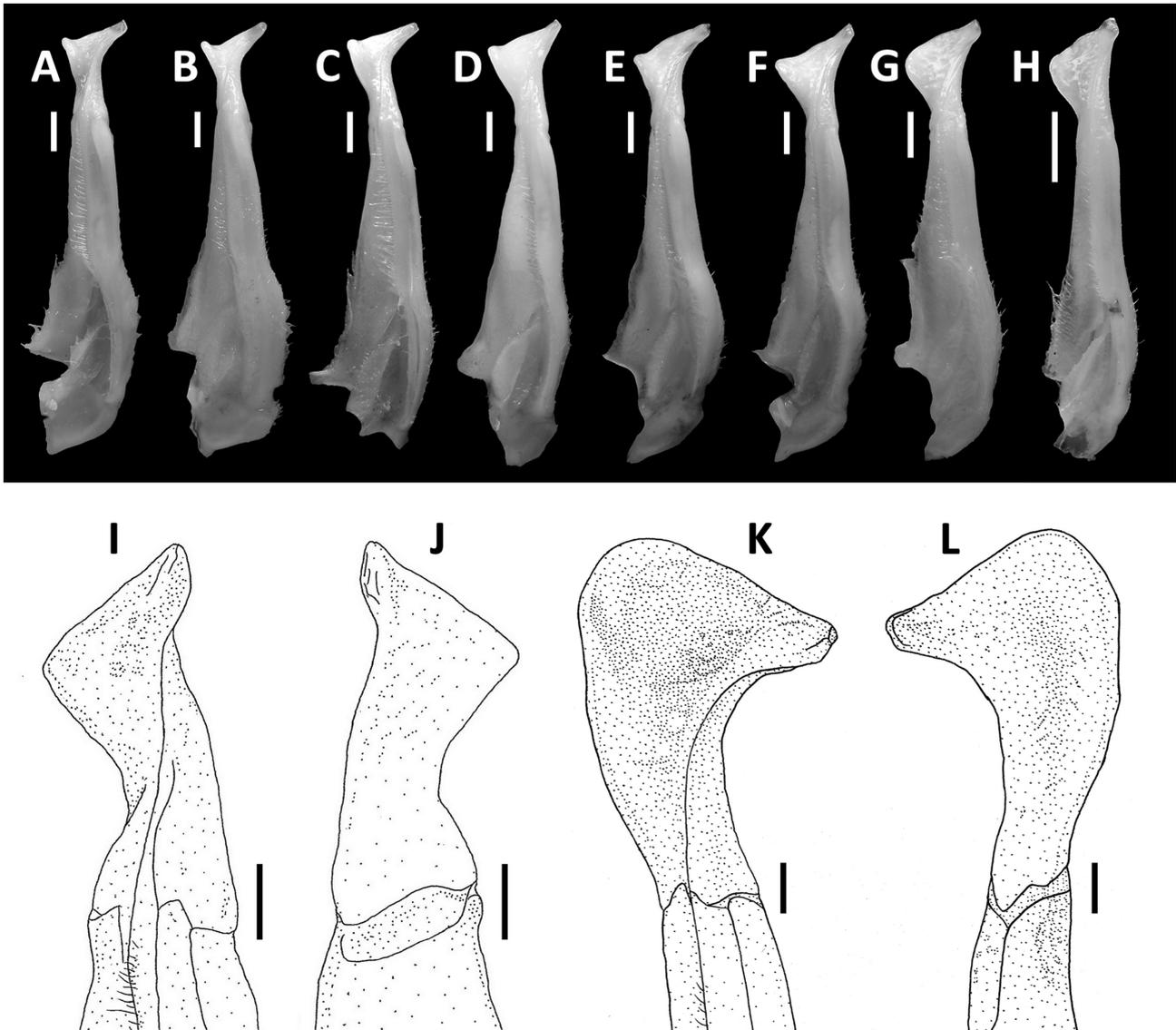


FIGURE 7. G1s of species of *Nanhaipotamon* compared in this study: *Nanhaipotamon aculatum* Dai, 1997, male (34.9 × 28.3 mm), SYSBM 001176, Bao'an, Shenzhen (A); *Nanhaipotamon aculatum*, male (40.4 × 31.5 mm), SYSBM 001179, Bao'an, Shenzhen (B); *Nanhaipotamon aculatum*, male (37.5 × 30.0 mm), SYSBM 001179, Shenzhen (C); *Nanhaipotamon* aff. *aculatum*, male (39.7 × 31.9 mm), SYSBM 001776, Boluo, Huizhou (D); *Nanhaipotamon* cf. *hongkongense* (Shen, 1940), male (32.0 × 25.4 mm), SYSBM 001780, Yantian, Shenzhen (E); *Nanhaipotamon* cf. *hongkongense*, male (31.0 × 25.4 mm), SYSBM 001781, Yantian, Shenzhen (F); *Nanhaipotamon* cf. *hongkongense*, male (28.0 × 22.5 mm), SYSBM 001782, Yantian, Shenzhen (G); *Nanhaipotamon* aff. *hongkongense*, male (20.5 × 16.2 mm), SYSBM, Huidong, Huizhou (H); *Nanhaipotamon incendium* n. sp., male holotype (31.3 × 25.0 mm), SYSBM 001799 (I, J); *Nanhaipotamon aureomarginatum* n. sp., male holotype (37.7 × 30.7 mm), SYSBM 001807 (K, L). (A–H) left G1, ventral view; (I, K) left G1 terminal segment, ventral view; (J, L) left G1 terminal segment, dorsal view. Scale bars: A–H = 1.0 mm; I–L = 0.5 mm.

TABLE 2. Matrix of percentage pairwise nucleotide divergences with K2P distance based on COI within and between clade/species of *Nanhaipotamon* related with the two new species from southern China (see Table 1). Values of range are given in parentheses.

	Within clade/ species		Between clades/ species					
	Nucleotide divergence	<i>N. incendum</i> +	<i>N. aureomarginatum</i> +	<i>N. hongkongense</i> +	<i>N. aculatum</i> +	<i>N. zhuhaiense</i> +	<i>N. macau</i> +	<i>N. wupingense</i> +
<i>N. incendum</i>	0.43 (0–0.92)							
<i>N. aff. aculatum</i>								
<i>N. aureomarginatum</i>	0.85 (0–1.82)	2.58 (2.01–2.83)						
<i>N. aff. hongkongense</i>								
<i>N. hongkongense</i>	0.49 (0–0.92)	2.49 (1.86–2.97)	2.75 (2.17–3.14)					
<i>N. aculatum</i>	0.33 (0–0.61)	2.78 (2.49–3.13)	2.90 (2.49–3.14)	2.41 (2.17–2.65)				
<i>N. zhuhaiense</i>	0.82 (0.46–1.23)	8.77 (8.16–9.41)	9.39 (8.36–10.17)	9.08 (8.54–9.8)	8.36 (8–8.71)			
<i>N. macau</i>	—	9.66 (9.32–9.93)	9.86 (9.05–10.33)	9.37 (9.23–9.59)	9.18 (9.05–9.23)	4.02 (3.94–4.1)		
<i>N. guangdongense</i>	—	9.44 (9.35–9.54)	10.18 (9.57–10.56)	9.72 (9.57–9.97)	9.23 (8.99–9.38)	2.88 (2.5–3.36)	3.69 (3.69–3.69)	
<i>N. wupingense</i>	0.92 (0.15–1.39)	9.17 (8.23–9.81)	9.67 (8.59–10.58)	9.22 (8.94–9.65)	9.13 (8.59–9.47)	12.15 (11.81–12.56)	13.64 (13.51–13.71)	12.72 (12.31–13.33)

Based on the COI analyses, the clades “*N. incendium* + *N. aff. aculatum*” and “*N. aureomarginatum* + *N. aff. hongkongense*” are sufficiently divergent from other related congeners (Table 2; Shih *et al.* 2011: table 2) and other potamid genera (e.g., Chu *et al.* 2015: table 1; Huang *et al.* 2020: table 1) to be considered distinct lineages within *Nanhaipotamon*. The sympatric congeners *N. aff. aculatum* and *N. aff. hongkongense* are likely cryptic species but their exact identity and relationship with the two new species remain elusive. Nonetheless, the two new species can be genetically separated from all other related congeners included in the analysis. *Nanhaipotamon aff. hongkongense* is most similar with *N. hongkongense* from Hong Kong and *N. cf. hongkongense* from Shenzhen in morphology and colouration, but it is considerably smaller in size (Figs. 7H, 8D). It is nearly impossible to compare the G1 of different populations of the “*hongkongense* group” with any degree of confidence as the intraspecific variation between individuals from the same locality can be very large (Fig. 7E–G). In addition, a preliminary COI analysis (not shown) using a larger data set could not find monophyly in the different populations of *N. hongkongense* as identified by morphology from Hong Kong and Shenzhen, indicating the presence of cryptic speciation. On the other hand, *N. aff. aculatum* closely resembles *N. aculatum* in external and gonopodal morphology and colouration (Figs. 7D, 8B). Although *N. aff. aculatum* seems to have a slightly broader G1 terminal segment (Fig. 7D), there is also considerable intraspecific variation amongst *N. aculatum* to account for (Fig. 7A–C).

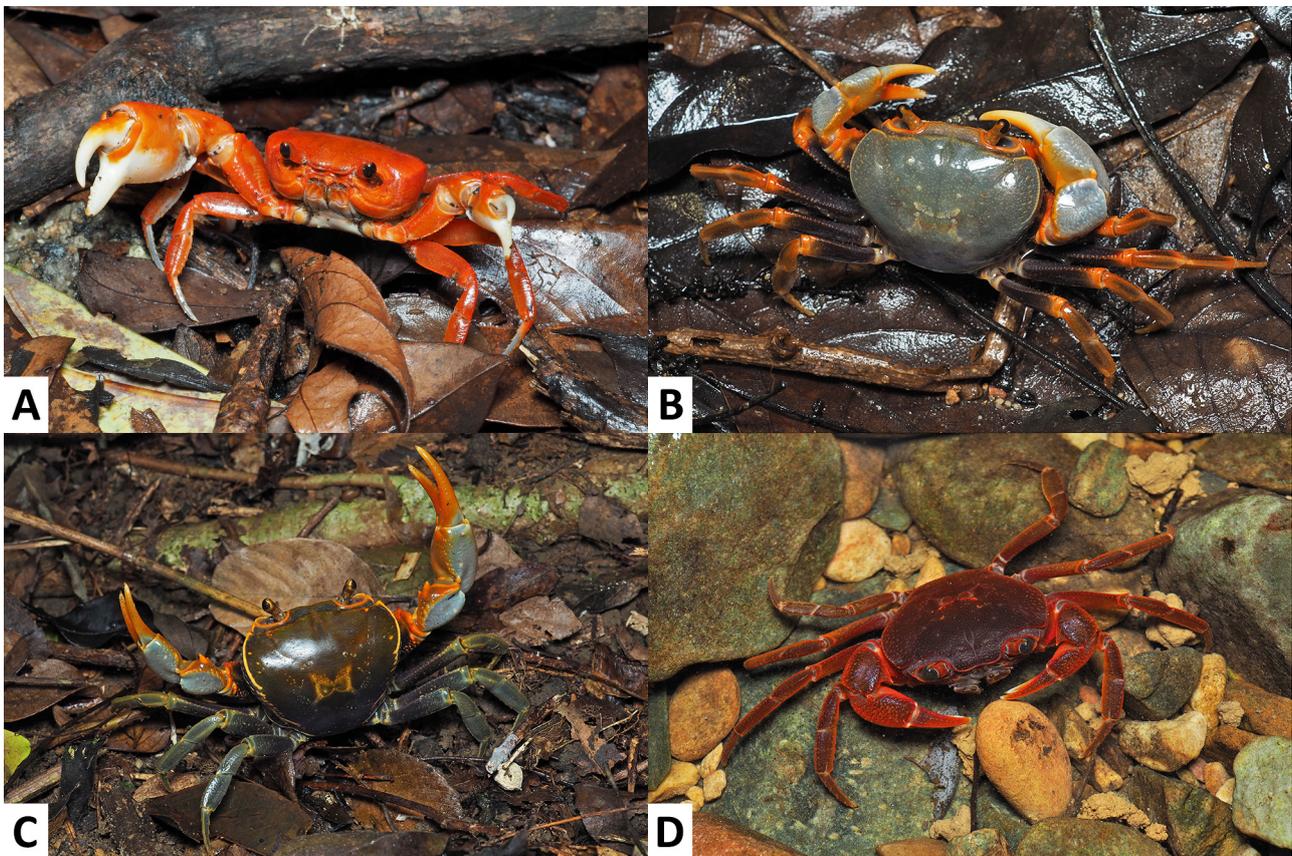


FIGURE 8. Colour in life. (A) *Nanhaipotamon incendium* **n. sp.**, male, from type locality, specimen not collected; (B) *Nanhaipotamon aff. aculatum* Dai, 1997, male, from type locality of *Nanhaipotamon incendium* **n. sp.**, specimen not collected; (C) *Nanhaipotamon aureomarginatum* **n. sp.**, male holotype (37.7 × 30.7 mm), SYSBM 001807, from type locality; (D) *Nanhaipotamon aff. hongkongense* (Shen, 1940), male, from type locality of *Nanhaipotamon aureomarginatum* **n. sp.**, specimen not collected.

According to the present DNA analysis, the two new species are genetically indistinct from their respective sympatric congeners (Table 2). This intriguing result drastically conflicts the morphological evidence, which clearly separates the two new species from their respective sympatric congeners. This phenomenon is most likely caused by “anti-cryptic” speciation, where strong divergent selection forces caused rapid morphological divergence (Bickford *et al.* 2007; Chapple *et al.* 2011). Other cases that resemble “anti-cryptic” speciation can be found in other freshwater crabs, e.g., *Geothelphusa* Stimpson, 1858 from Taiwan (the *G. olea* Shy, Ng & Yu, 1994 complex; Shih *et al.* 2007a), *Somanniathelphusa* Bott, 1968 (including *S. amoyensis* Naiyanetr & Dai, 1997, *S. taiwanensis* Bott, 1968,

and *S. zhangpuensis* Naiyanetr & Dai, 1997) (Shih *et al.* 2007b, and *Sundathelphusa* Bott, 1969 from the Philippines [including *S. boex* Ng & Sket, 1996, *S. cavernicola* (Takeda, 1983), and *S. urichi* Ng & Sket, 1996] (Klaus *et al.* 2013); as well as marine crabs, e.g., *Eriocheir* De Haan, 1835 [in De Haan, 1833–1850] [between *E. hepuensis* Dai, 1991 and *E. japonica* (De Haan, 1835 [in De Haan, 1833–1850]) from Taiwan]) (J.-W. Xu *et al.* 2009; Ng *et al.* 2017); *Helice* De Haan, 1833 [in De Haan, 1833–1850] (including *H. formosensis* Rathbun, 1931, *H. latimera* Parisi, 1918, and *H. tientsinensis* Rathbun, 1931) (Shih & Suzuki 2008; N.K. Ng *et al.* 2018), *Gelasimus* Latreille, 1817 [including *G. borealis* (Crane, 1975), *G. dampieri* (Crane, 1975), *G. vocans* (Linnaeus, 1758), and *G. vomeris* (McNeill, 1920)] (Shih *et al.* 2010), and *Paraleptuca* Bott, 1973 [between *P. boninensis* (Shih, Komai & Liu, 2013) and *P. crassipes* (White, 1847), if only based on COI; Shih *et al.* 2013]. In the case of *Helice formosensis*, *H. latimera* and *H. tientsinensis*, the three species can not be separated by mitochondrial and nuclear markers (12S, 16S, COI, ITS-2 and 28S); and the intermediate morphological form of the latter two species has been found (J.-M. Xu *et al.* 2010), which suggests that, at least for *H. latimera* and *H. tientsinensis*, the observed morphological differences among them may only be intraspecific variation (N.K. Ng *et al.* 2018). In contrast, using an additional control region marker, *Paraleptuca boninensis* and *P. crassipes* can be genetically separated, supporting the morphological evidence (Shih *et al.* 2013). Similarly, using nuclear ITS-1 sequences, at least some species in the *Geothelphusa olea* complex and the *Gelasimus vocans* complex can be successfully separated (Chu *et al.* 2015; H.-T. Shih, unpublished data). Further studies using higher resolution of markers (e.g., control marker, ITS-1, ITS-2, etc.) are needed to reveal the genetic relations within the “*N. incendium* + *N. aff. aculatum*” and “*N. aureomarginatum* + *N. aff. hongkongense*” clades. Collections should also be carried out to further confirm whether any morphologically intermediate forms exist. As we can see, with cryptic speciation, “anti-cryptic” speciation, limited usable morphological characters and large intra-population and intra-species morphological variation, the genus *Nanhaipotamon* presents a challenge to conventional taxonomy and opportunity to better understand speciation and evolution.

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