Zoological Studies **56:** 41 (2017)
doi:10.6620/ZS.2017.56-41

Zoological Studies

Open Access

Cantopotamon, A New Genus of Freshwater Crabs from Guangdong, China, with Descriptions of Four New Species (Crustacea: Decapoda: Brachyura: Potamidae)

Chao Huang[1,2,3], Shane T. Ahyong[1,2], and Hsi-Te Shih[4,*]

[1]*Palaeontology, Geobiology and Earth Archives Research Centre, School of Biological, Earth and Environmental Sciences, UNSW, Kensington, NSW 2052, Australia*

[2]*Australian Museum, 1 William St, Sydney NSW 2010, Australia*

[3]*School of Life Sciences, Sun Yat-sen University, Guangzhou 510275, China*

[4]*Department of Life Science and Research Center for Global Change Biology, National Chung Hsing University, 250, Kuo Kuang Road, Taichung 40227, Taiwan*

(Received 25 September 2017; Accepted 7 December 2017; Published 20 December 2017; Communicated by Benny K.K. Chan)
urn:lsid:zoobank.org:pub:E8D372CC-CB92-40CE-A61B-A1E8AFAC230B

Chao Huang, Shane T. Ahyong, and Hsi-Te Shih (2017) A new genus and four new species of freshwater crab, *Cantopotamon zhuhaiense* n. gen., n. sp., *C. shangchuanense* n. gen., n. sp., *C. hengqinense* n. gen., n. sp. and *C. yangxiense* n. gen., n. sp. are described from Guangdong, China, based on morphology and two mitochondrial markers (16S rDNA and cytochrome oxidase subunit I). Species of *Cantopotamon* closely resemble species of *Yarepotamon* Dai & Türkay, 1997, but differ by the combination of carapace, third maxilliped, male pleon, male first gonopod and female vulva characters. Molecular data derived from the mitochondrial 16S rDNA also supports the establishment of the new genus.

Key words: Potamidae, *Cantopotamon*, New genus, New species, Freshwater crab, Morphology, 16S rDNA, Cytochrome oxidase subunit I.

BACKGROUND

The discovery of new taxa of freshwater crabs continues at a significant rate, especially in China and India (*e.g.*, Cumberlidge et al. 2011; Pati and Devi 2015; Shih et al. 2016; Huang et al. 2017; Mitra and Valarmathi 2017). China has the highest species richness of freshwater crabs globally (Cumberlidge et al. 2011). South China, the region comprising Guangdong, Guangxi, Hainan, Hong Kong and Macau, has a high diversity of potamid crabs (Dai 1999; Shih and Ng 2011), but many parts, including the southern coastline of Guangdong, remain largely unexplored for freshwater crabs. This monsoon subtropical coastline consists of a complex topography of lowlands, estuaries, islands and low mountains and hills.

Recent surveys have revealed the presence of four closely allied new species in coastal regions west of the Pearl River, Guangdong, which could not be morphologically assigned to any existing genus. These crabs seem to be mainly aquatic, found in small and oligotrophic low-altitude hillstreams. Although they are similar to some species of *Yarepotamon* Dai & Türkay, 1997 in external appearance, the confluence of the postorbital cristae and the epigastric cristae, the distinctly twisted terminal segment of the male first gonopod and the distinctly smaller female vulvae clearly set them apart. Molecular analyses using mitochondrial 16S rRNA and cytochrome

*Correspondence: Tel/Fax: 886-4-22856496. E-mail: htshih@dragon.nchu.edu.tw

oxidase subunit I (COI) sequences corroborate the monophyly of these four new taxa and their separation from other genera. Therefore, we recognize *Cantopotamon* as a new genus for these four new species.

MATERIALS AND METHODS

Specimens were collected by hand, preserved in 75% ethanol and deposited in the Sun Yat-sen Museum of Biology, Sun Yat-sen University, Guangzhou, China (SYSBM); Chinese Academy of Science, Beijing, China (CAS); and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore, Singapore (ZRC). Measurements, in millimeters, are of the carapace width and length, respectively. The following abbreviations are used: G1 - male first gonopod; G2 - male second gonopod.

Sequences of 16S were obtained following Shih et al. (2016), using the primers 16H10 and 16L29 (Schubart 2009), and aligned with the aid of ClustalW (vers. 1.4, Thompson et al. 1994), after verification with the complementary strand. To confirm the systematic position of this species, the 16S sequences of genera from the eastern Asian continent in Shih et al. (2009) and Huang et al. (2017) are included for comparison; *Socotrapotamon nojidensis* Apel & Brandis, 2000 is used as an outgroup. We followed Shih et al. (2009) to exclude the variable regions in loop regions of the 16S that could not be aligned adequately for phylogenetic analyses. The best-fitting model for sequence evolution of the 16S dataset was determined by MrModeltest (vers. 2.2, Nylander 2005), selected by the Akaike information criterion (AIC). The best model obtained was HKY+I+G, which was subsequently applied for Bayesian inference (BI) analysis. The BI analysis was performed with MrBayes (vers. 3.2.2, Ronquist et al. 2012) and the search was run with four chains for 10 million generations, with trees sampled every 1000 generations. The convergence of chains was determined by the average standard deviation of split frequency values below the recommended 0.01 (Ronquist et al. 2005) and the first 1050 trees were discarded as the burnin accordingly. ML analysis was conducted in RAxML (vers. 7.2.6, Stamatakis 2006). The model GTR + G (*i.e.* GTRGAMMA) was used for all subsets with 100 runs, and found the best ML tree by comparing likelihood scores. The robustness of the ML tree was evaluated by 1000 bootstrap pseudoreplicates under the model GTRGAMMA. Additional sequences of COI for the species of the new genus, also obtained following the method described by Shih et al. (2016), were combined with 16S and analyzed by the BI and ML

Table 1. The haplotypes of 16S rRNA and COI genes of the new genus *Cantopotamon* from China

Species identified	Localities of China	Museum catalogue no.
C. zhuhaiense	Xiangzhou, Zhuhai City, Guangdong	SYSBM 001439 (paratype)
	Xiangzhou, Zhuhai City, Guangdong	SYSBM 001440, 001441 (paratypes)
	Xiangzhou, Zhuhai City, Guangdong	ZRC
C. hengqinense	Hengqin Island, Zhuhai City, Guangdong	SYSBM 001559 (paratype)
	Hengqin Island, Zhuhai City, Guangdong	SYSBM 001561 (paratype)
C. shangchuanense	Shangchuan island, Taishan City, Guangdong	SYSBM 001428 (paratype)
	Shangchuan island, Taishan City, Guangdong	SYSBM 001429 (paratype)
C. yangxiense	E'huang Ridge, Yangxi, Yangjiang City, Guangdong	SYSBM 001564

Species identified	sp. no.	16S haplotypes	acces. no. 16S	COI haplotypes	acces. no. COI
C. zhuhaiense	1	Cz1	LC342045	Cz-C	LC342051
	2	Cz2	LC342046	Cz-C	LC342051
	1	Cz2	LC342046	Cz-C	LC342051
C. hengqinense	1	Ch	LC342047	Ch-Ca	LC342052
	1	Ch	LC342047	Ch-Cb	LC342053
C. shangchuanense	1	Cs1	LC342048	Cs-C1	LC342054
	1	Cs2	LC342049	Cs-C2	LC342055
C. yangxiense	1	Cy	LC342050	Cy-C	LC342056

methods mentioned above. GTR + I was the best model for both 16S and COI datasets. Sequences of the different haplotypes of 16S and COI have been deposited in the DNA Data Bank of Japan (DDBJ) database (accession numbers in Table 1). Basepair (bp) differences, as well as the pairwise estimates of Kimura 2-parameter (K2P) distance (Kimura 1980) and the uncorrected p-distance for genetic diversities between haplotypes, were also calculated by MEGA (vers. 7.0, Kumar et al. 2016).

RESULTS
Taxonomy

Family Potamidae Ortmann, 1896
Subfamily Potamiscinae Bott, 1970

Genus *Cantopotamon* n. gen.
urn:lsid:zoobank.org:act:6CBDB48E-9199-4D62-B3B9-928B999057A9

Type species *Cantopotamon zhuhaiense* n. gen., n. sp., by present designation.

Diagnosis: Carapace broader than long; dorsal surface slightly convex, branchial regions relatively flat (Fig. 1A); postorbital and epigastric cristae visible, confluent (Fig. 1A); external orbital angle bluntly triangular, separated from anterolateral margin by gap (Figs. 1A, B); median lobe of posterior margin of epistome triangular (Fig. 1B). Third maxilliped ischium relatively broad; exopod reaching beyond anterior margin of ischium, with flagellum (Fig. 2D). Male pleon triangular, reaching anteriorly almost to level of posterior margins of cheliped coxae (Fig. 1C). G1 slender, inner proximal section of sub-terminal segment curved dorsally, terminal segment relatively short, sinistrally twisted on left G1 (Figs. 1D, 2B, C, 9). G2 basal segment subovate (Fig. 2A). Vulva small, ovate, not reaching suture of sternites 5/ 6 (Fig. 11).

Etymology: The genus name is a combination of *Canton*, synonym for Guangdong, the province in which this genus occurs, and the generic name *Potamon.* Gender: neuter.

Remarks: Although superficially similar to some species of *Yarepotamon*, *Cantopotamon* n. gen. can easily be distinguished by its confluent postorbital cristae and epigastric cristae (Fig. 1A) (versus separate in *Yarepotamon*, cf. Dai & Türkay, 1997: pl. II, fig. 2), twisted terminal segment of the G1 (Fig. 2C) (versus not twisted in *Yarepotamon*, cf. Dai & Türkay, 1997: fig. 6, 4) and relatively small female vulvae that do not reach the suture of sternites 5/6 (Fig. 11A) (versus female vulvae reaching suture of sternites 5/6 in *Yarepotamon*, cf. Dai & Türkay, 1997: fig. 6, 7). *Yarepotamon* is currently being revised by the first author. Specimen details of comparative material are given in Appendix I.

Key to the species of *Cantopotamon*:

1. G1 relatively short, tip of terminal segment not reaching male pleonal locking tubercle ..... *C. zhuhaiense*
- G1 relatively long, tip of terminal segment exceeding male pleonal locking tubercle 2
2. Tip of G1 terminal segment horn-shaped .... *C. hengqinense*
- Tip of G1 terminal segment blunt 3
3. Inner margin of G1 terminal segment with blunt projection ..... *C. yangxiense*
- Inner margin of G1 terminal segment convex .... *C. shangchuanense*

Cantopotamon zhuhaiense n. sp.
(Figs. 1-2, 9A, 10A, 11A, 12A)
urn:lsid:zoobank.org:act:003D5AB3-EBF6-4BB1-80AA-F77A7A1415F9

Type material: Holotype: SYSBM 001438, male (29.1 × 22.9 mm), Xiangzhou (22.25°N, 113.56°E), Zhuhai City, Guangdong, small hillstreams, under rocks, coll. C. Huang, July, 2013. Paratypes: SYSBM 001440, 1 female (24.6 × 20.0 mm), same data as holotype. SYSBM 001439, 1 male (24.1 × 20.1 mm), same data as holotype, SYSBM 001441, 1 female (22.3 × 17.3 mm), same data as holotype.

Other material examined: SYSBM 001425, 1 male (30.2 × 24.0 mm), Xiangzhou, Zhuhai City, Guangdong, small hillstreams, under rocks, coll. C. Huang, March, 2012. SYSBM 001426, 1 female (17.8 × 14.5 mm), same as above male; ZRC, 1 male, 2 females, Xiangzhou, Zhuhai City, Guangdong, June 2011.

Etymology: This species is named after the type locality, Zhuhai City, Guangdong Province, China.

Diagnosis: Third maxilliped merus width about 1.2 × length; ischium width about 0.77 × length (Figs. 1B, 2D). Major cheliped palm length about 1.3 × height (Fig. 1A). Male pleonite 6 width about 2.2 × length; telson width about 1.2 × length (Fig. 1C). Tip of G1 terminal segment not reaching tubercle forming pleonal locking structure, scarcely exceeding sternite 5/6 suture (Fig. 1D); subterminal segment length about 2.2 × length of terminal segment, inner proximal section curved

dorsally; terminal segment inner margin broadly triangular, tip cone-shaped (Figs. 1D, 2B, C, 9A, B). G2 about 2.6 × length of flagelliform distal segment (Fig. 2A).

Description of male: Carapace broader than long, regions indistinct; dorsal surface slightly convex transversely and longitudinally; surface generally smooth with fused rugae on anterolateral region (Fig. 1A). Front slightly deflexed, margin slightly ridged on dorsal view (Fig. 1A). Epigastric cristae distinct, separated by narrow gap (Figs. 1A, B). Postorbital cristae sharp, laterally expanded, fused with epigastric cristae and epibranchial teeth (Figs. 1A, B). Branchial regions relatively flat (Fig. 1A). Cervical groove shallow, inconspicuous (Fig. 1A). Mesogastric region slightly convex (Fig. 1A). External orbital angle triangular (Fig. 1A). Epibranchial tooth small, granular, but distinct (Fig. 1A, B). Anterolateral margin distinctly cristate, lined with approximately 16-18 granules; lateral part bent inward (Fig. 1A). Posterolateral margin comparatively smooth, lined with oblique striae, converging towards posterior carapace margin (Fig. 1A). Orbits small; supraorbital and infraorbital margins cristate, lined with numerous inconspicuous granules (Fig. 1B). Sub-orbital and upper parts of pterygostomial regions covered with large rounded granules; sub-hepatic region lined with oblique striae (Fig. 1B).

Epistome posterior margin narrow; median lobe sharply triangular, lateral margins almost straight (Fig. 1B).

Third maxilliped merus width about 1.2 × length; ischium width about 0.8 × length; merus trapezoidal, with median depression; ischium trapezoidal, with distinct median sulcus. Exopod reaching to proximal one-third of merus; flagellum long; dorsomesial margin of ischium subauriculiform (Figs. 1B, 2D).

Chelipeds (pereopod 1) unequal (Fig. 1A). Merus cross-section trigonal; margins crenulated (Fig. 1B). Carpus with sharp distomesial spine and spinule at base; dorsal surface with curved striae (Fig. 1A). Major cheliped palm length about 1.3 ×

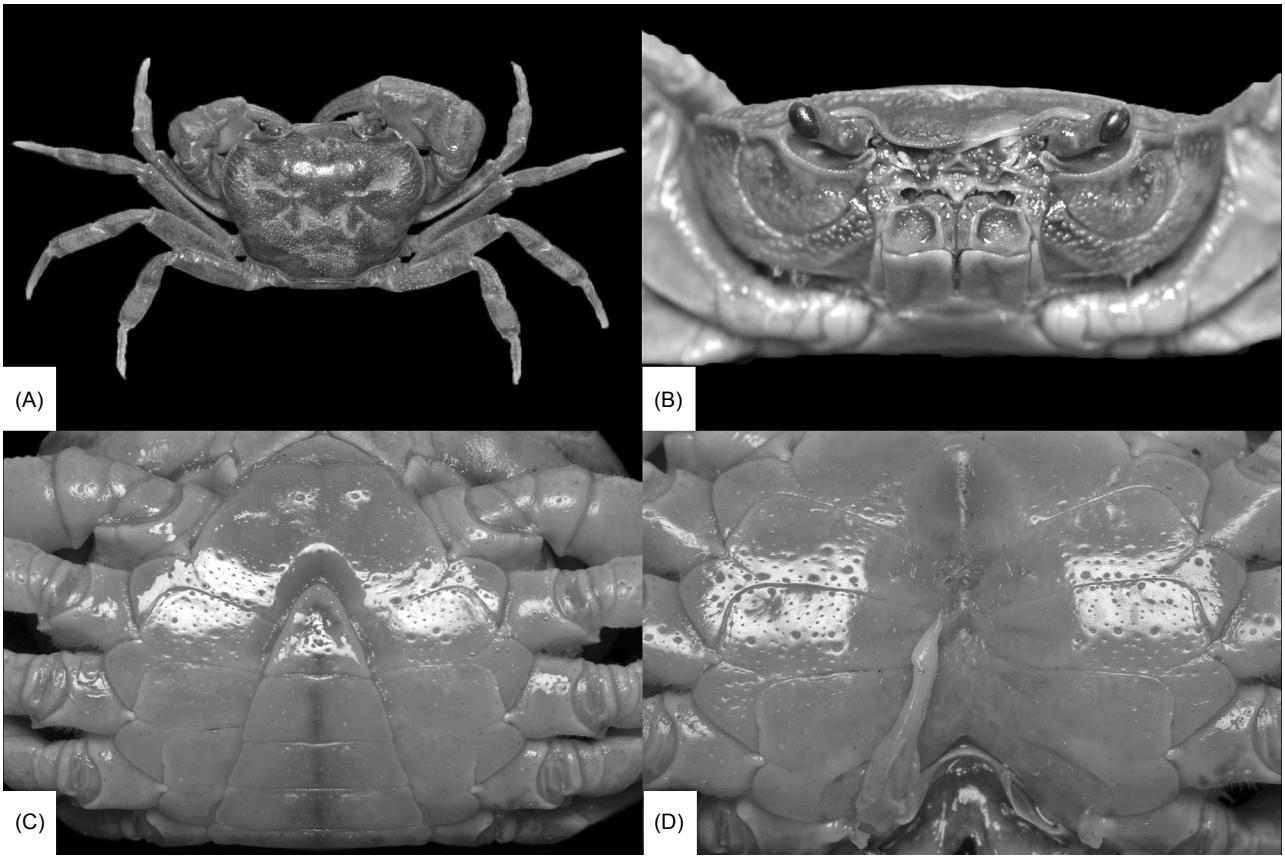

Fig. 1. *Cantopotamon zhuhaiense* n. gen., n. sp., male holotype (29.1 × 22.9 mm) (SYSBM 001038). (A) dorsal overall view; (B) frontal view of cephalothorax; (C) ventral view showing anterior thoracic sternum and pleon; (D) ventral view showing sterno-pleonal cavity with right G1 *in situ* (left G1 removed).

height (Fig. 1A). Movable finger as long as fixed finger (Fig. 1A). Occlusal margin of fingers with rounded, blunt teeth; with gape when closed (Fig. 1A).

Ambulatory legs slender (pereopods 2-5); dactylus with dense, short setae; propodus, carpus and merus with relatively sparse, short, setae (Fig. 1A). Pereopod 5 propodus about 2 times as long as broad, about as long as dactylus (Fig. 1A).

Thoracic sternum generally smooth, weakly pitted; sternites 1, 2 completely fused, triangular; sternites 3, 4 fused without obvious median suture (Figs. 1C, 10A). Male sterno-pleonal cavity reaching anteriorly to level of midlength of cheliped coxae; deep median longitudinal groove between sternites 7, 8 (Fig. 1D). Pleonal locking tubercle slightly posterior to mid-length of sternite 5 (Fig. 1D).

Male pleon triangular, almost reaching anteriorly to level of posterior margin of cheliped coxae; somites 3-6 progressively broader longitudinally, lateral margins straight; somite 6 width about 2.2 × length; telson width about 1.2 × length; apex rounded (Fig. 1C).

Fig. 2. *Cantopotamon zhuhaiense* n. gen., n. sp., male (29.1 × 22.9 mm) (SYSBM 001038). (A) left G2; (B) left G1 (ventral view); (C) G1 terminal segment (ventral view); (D) right third maxilliped. Scale bar = 1.0 mm.

G1 generally slender, relatively short, tip of terminal segment not reaching tubercle forming pleonal locking structure, barely exceeding sternite 5/6 suture (Fig. 1D); subterminal segment length about 2.2 × length of terminal segment, inner proximal section curved dorsally; terminal segment relatively short, sinistrally twisted (on left G1), curved inwards and pointing anteriorly, inner margin broadly triangular, tip cone-shaped (Figs. 1D, 2B, C, 9A, B). G2 basal segment subovate, about 2.6 × length of flagelliform distal segment (Fig. 2A).

Size range: Male (*n* = 3) 24.1 × 20.1 to 30.2 × 24.0 mm; female (*n* = 3) 17.8 × 14.5 to 24.6 × 20.0 mm.

Remarks: *Cantopotamon zhuhaiense* n. sp. is closest to *C. shangchuanense* n. sp. and *C. hengqinense* n. sp. in overall external morphology, but can be distinguished by its shorter G1 that does not the reach tubercle of the pleonal locking structure *in situ* (Fig. 1D) [versus long G1 that reaches beyond in both *C. shangchuanense* n. sp. (Fig. 3D) and *C. hengqinense* n. sp. (Fig. 5D)]; broadly triangular inner margin of G1 terminal segment (Fig. 2C) [versus convex in *C. shangchuanense* n. sp. (Fig. 4C) and sinuous in *C. hengqinense* n. sp. (6C)]; and other characters as shown in table 2.

Colour in life: Mottled brown overall (Fig. 12A).

Ecology: This species is mainly aquatic, living under rocks in small hillstreams. At its type locality, *C. zhuhaiense* is sympatric with *Nanhaipotamon* cf. *guangdongense* Dai, 1997 and *Nanhaipotamon zhuhaiense* Huang, Huang & Ng, 2012. One individual, still moving, was observed within the grasp of a *Nanhaipotamon* cf. *guangdongense* in the latter's mud burrow, suggesting they are at least occasional prey items of *Nanhaipotamon*.

Distribution: Xiangzhou, Zhuhai, Guangdong.

***Cantopotamon shangchuanense* n. sp.**

(Figs. 3-4, 9B, 10B, 11B, 12B)

urn:lsid:zoobank.org:act:214D7745-AB4C-4A3D-862B-9C1D57BA4301

Type material: Holotype: SYSBM 001427, male (24.1 × 19.5 mm), Shangchuan island (21.63°N, 112.78°E), Taishan City, Guangdong, small hillstreams, under rocks, coll. C. Huang, March, 2015. Paratypes: SYSBM 001429, 1 female (17.3 × 14.1 mm), same data as holotype. SYSBM 001428, 1 male (21.0 × 17.2 mm), same data as holotype, SYSBM 001430, 1 female (14.8 × 11.9 mm), same data as holotype.

Etymology: This species is named after the type locality, Shangchuan Island, Taishan City, Guangdong Province, China.

Diagnosis: Third maxilliped merus width about 1.2 × length; ischium width about 0.71 × length (Figs. 3B, 4D). Major cheliped palm length about 1.2 × height (Fig. 3A). Male pleonite 6 width about 2.3 × length; telson width about 1.4 × length (Fig. 3C). Tip of G1 terminal segment reaching well beyond tubercle forming pleonal locking structure, exceeding sternite 4/5 suture (Fig. 3D); subterminal segment about 2.5 times as long as terminal segment, inner proximal section curved dorsally; terminal segment inner distal margin

Table 2. Morphological differences among *Cantopotamon zhuhaiense* n. sp., *C. shangchuanense* n. sp., *C. hengqinense* n. sp. and *C. yangxiense* n. sp.

Characters	*C. zhuhaiense*	*C. shangchuanense*	*C. hengqinense*	*C. yangxiense*
Male pleonite 6 (width/length)	2.2 (Fig. 1C)	2.3 (Fig. 3C)	2.5 (Fig. 5C)	2 (Fig. 7C)
Male telson (width/length)	1.2 (Fig. 1C)	1.4 (Fig. 3C)	1.6 (Fig. 5C)	1.4 (Fig. 7C)
G1 *in situ*	not reaching tubercle forming pleonal locking structure (Fig. 1D)	reaching well beyond tubercle forming pleonal locking structure (Fig. 3D)	reaching beyond tubercle forming pleonal locking structure (Fig. 5D)	reaching well beyond tubercle forming pleonal locking structure (Fig. 7D)
G1 subterminal segment length relative to terminal segment	2.2 (Fig. 2B)	2.5 (Fig. 4B)	2.3 (Fig. 6B)	2.3 (Fig. 8B)
Inner margin of G1 terminal segment	broadly triangular (Figs. 2C, 9A, B)	convex (Figs. 4C, 9C, D)	sinuous (Figs. 6C, 9E, F)	with blunt projection (Figs. 8C, 9G, H)
Tip of G1	cone-shaped (Figs. 2C, 9A, B)	blunt (Figs. 4C, 9C, D)	horn-shaped (Figs. 6C, 9E, F)	blunt (Figs. 8C, 9G, H)

strongly convex, tip blunt (Figs. 3D, 4B, C, 9C, D). G2 basal segment subovate, about 2.6 times length of flagelliform distal segment (Fig. 4A).

Description of male: Carapace broader than long, regions indistinct; dorsal surface slightly convex transversely and longitudinally; surface generally smooth with fused rugae on anterolateral region (Fig. 3A). Front slightly deflexed, margin slightly ridged on dorsal view (Fig. 3A). Epigastric cristae distinct, separated by narrow gap (Figs. 3A, B). Postorbital cristae sharp, laterally expanded, fused with epigastric cristae and epibranchial teeth (Figs. 3A, B). Branchial regions slightly swollen (Fig. 3A). Cervical groove shallow, inconspicuous (Fig. 3A). Mesogastric region slightly convex (Fig. 3A). External orbital angle triangular (Fig. 3A). Epibranchial tooth small, granular, but distinct (Figs. 3A, B). Anterolateral margin distinctly cristate, lined with approximately 17-19 granules; lateral part bent inward (Fig. 3A).

Posterolateral margin comparatively smooth, lined with oblique striae, converging towards posterior carapace margin (Fig. 3A). Orbits small; supraorbital and infraorbital margins cristate, lined with numerous inconspicuous granules (Fig. 3B). Sub-orbital and upper parts of pterygostomial regions covered with large rounded granules, sub-hepatic region lined with oblique striae (Fig. 3B).

Epistome posterior margin narrow; median lobe sharply triangular, lateral margins almost straight (Fig. 3B).

Third maxilliped merus width about 1.2 × length; ischium width about 0.7 × length; merus trapezoidal, with median depression; ischium trapezoidal, with distinct median sulcus; exopod reaching to proximal one-third of merus, flagellum long; dorsomesial margin of ischium subauriculiform (Figs. 3B, 4D).

Chelipeds (pereopod 1) unequal (Fig. 3A). Merus cross-section trigonal; margins crenulated (Fig. 3B). Carpus with sharp distomesial spine and spinule at base, dorsal surface with curved striae (Fig. 3A). Major cheliped palm length about 1.2 × height (Fig. 3A). Movable finger as long as fixed finger (Fig. 3A). Occlusal margin of fingers with rounded, blunt teeth; with very small gape when

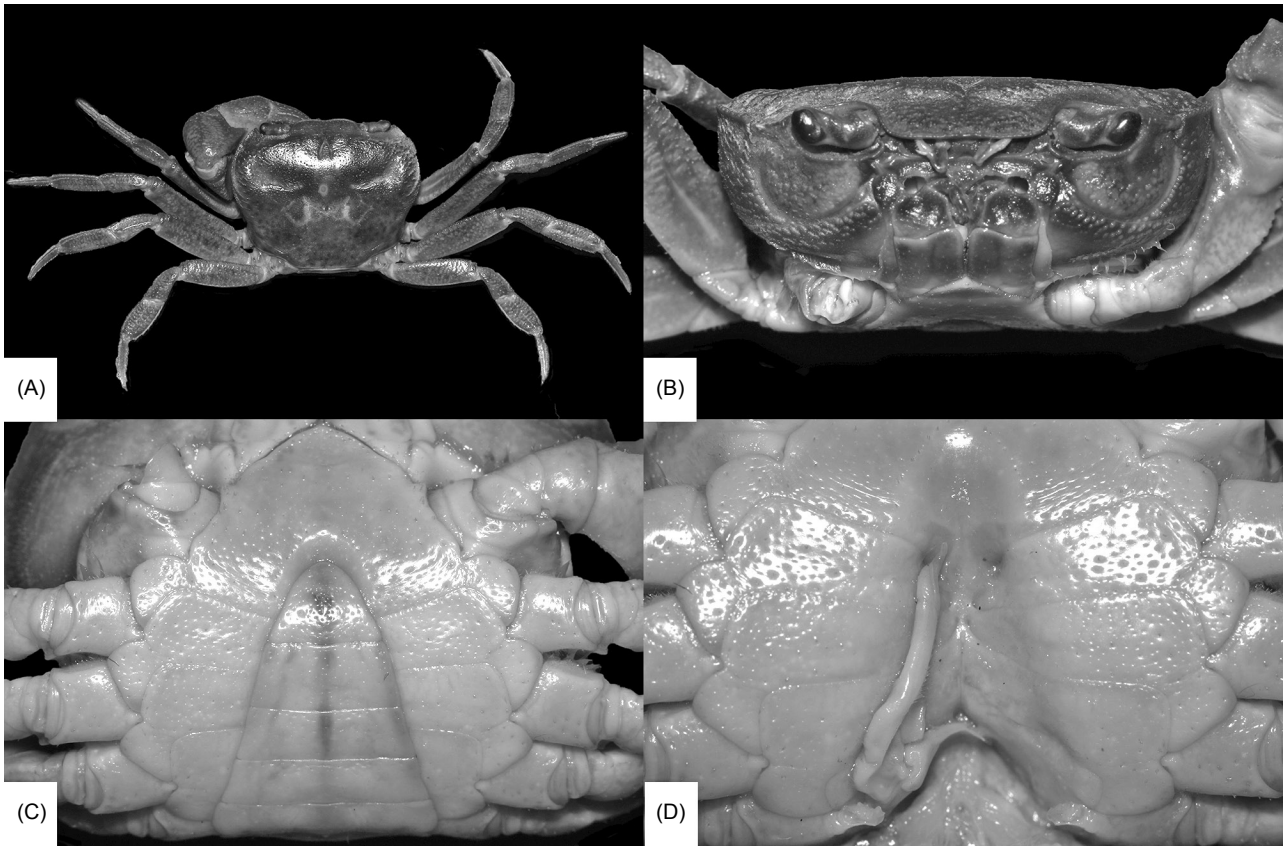

Fig. 3. *Cantopotamon shangchuanense* n. gen., n. sp., male (24.1 × 19.5 mm) (SYSBM 001427). (A) dorsal overall view; (B) frontal view of cephalothorax; (C) ventral view showing anterior thoracic sternum and pleon; (D) ventral view showing sterno-pleonal cavity with right G1 *in situ* (left G1 removed).

closed (Fig. 3A).

Ambulatory legs (pereopods 2-5) slender, with dense short setae on dactylus, relatively sparse short setae on the propodus, carpus and merus (Fig. 3A). Pereopod 5 with propodus about 2 times as long as board, subequal to dactylus (Fig. 3A).

Thoracic sternum generally smooth, weakly pitted; sternites 1, 2 completely fused, triangular; sternites 3, 4 fused without obvious median suture (Figs. 3C, 10B). Male sterno-pleonal cavity reaching anteriorly to midlength of cheliped coxae; median longitudinal groove between sternites 7/8 deep (Fig. 3D). Pleonal locking tubercle slightly posterior to mid-length of sternite 5 (Fig. 3D).

Male pleon triangular, almost reaching anteriorly to level of posterior margin of cheliped coxae; pleonites 3-6 progressively broader longitudinally, lateral margins straight; somite 6 width about 2.3 × length; telson width about 1.4 × length, apex rounded (Fig. 3C).

Fig. 4. *Cantopotamon shangchuanense* n. gen., n. sp., male (24.1 × 19.5 mm) (SYSBM 001427). (A) left G2; (B) left G1 (ventral view); (C) G1 terminal segment (ventral view); (D) left third maxilliped. Scale bar = 1.0 mm.

G1 tip of terminal segment reaching well beyond tubercle forming pleonal locking structure, exceeding sternite 4/5 suture (Fig. 3D); subterminal segment about 2.5 times as long as terminal segment, inner proximal section curved dorsally; terminal segment relatively short, sinistrally twisted (on left G1), curved inwards and pointing anteriorly, inner distal margin strongly convex, tip blunt (Figs. 3D, 4B, C, 9C, D). G2 basal segment subovate, about 2.6 times length of flagelliform distal segment (Fig. 4A).

Size range: Male (*n* = 2) 21.0 × 17.2 to 24.1 × 19.5 mm; female (*n* = 2) 14.8 × 11.9 to 17.3 × 14.1 mm.

Remarks: *Cantopotamon shangchuanense* n. sp. is close to *C. zhuhaiense* n. sp., in overall external morphology, but can be separated by a unique combination of characters as shown in the Remarks section for *C. zhuhaiense* n. sp. and table 2.

Colour in life: Mottled brown overall (Fig. 12B).

Ecology: This species is mainly aquatic, living under rocks in small hillstreams. The hillstream in which it was found drains directly to the sea, with *Eriocheir* sp. also inhabiting the lower reaches. The species of *Eriocheir* was not confirmed, but given the location, it was probably *E. hepuensis* (see Naser et al. 2012). No other potamids where found at the type locality.

Distribution: Shangchuan Island, Taishan, Guangdong.

***Cantopotamon hengqinense* n. sp.**

(Figs. 5-6, 9C, 10C, 11C, 12C)

urn:lsid:zoobank.org:act:9520E984-450A-4058-B298-6B1C86FA0B85

Type material: Holotype: SYSBM 001558, male (19.9 × 16.0 mm), Dahengqin Mountain (22.11°N, 113.50°E), Hengqin Island, Zhuhai City, Guangdong, small hillstream, under rocks, coll. C. Huang, Feb, 2016. Paratypes: SYSBM 001559, 1 female (13.0 × 10.6 mm), same data as holotype. SYSBM 001560-001561, 2 males (15.5 × 12.4 mm, 13.2 × 10.7 mm), same data as holotype.

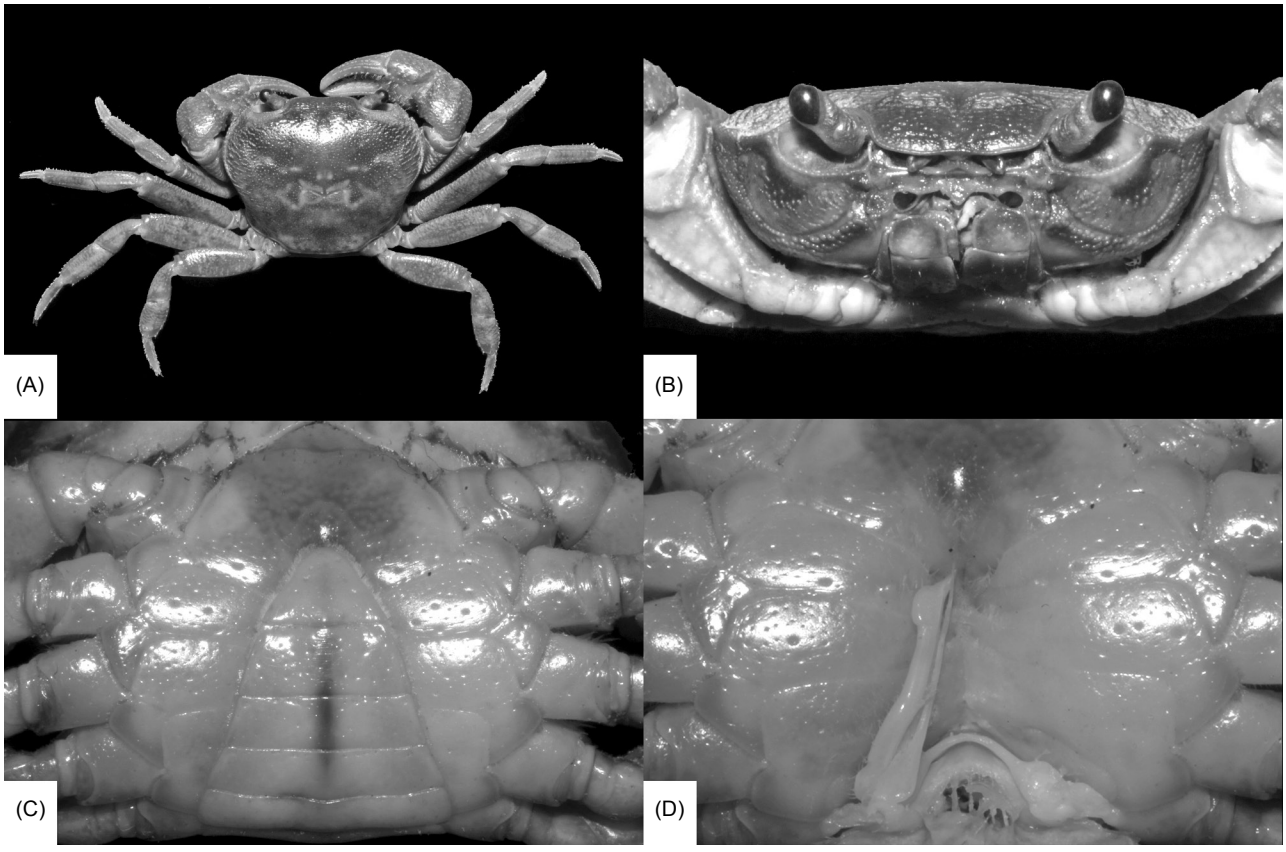

Fig. 5. *Cantopotamon hengqinense* n. gen., n. sp., male (19.9 × 16.0 mm) (SYSBM 001558). (A) dorsal overall view; (B) frontal view of cephalothorax; (C) ventral view showing anterior thoracic sternum and pleon; (D) ventral view showing sterno-pleonal cavity with right G1 *in situ* (left G1 removed).

Other material examined: SYSBM 001640, 1 male (17.5 × 13.6 mm), Hengqin Island, Zhuhai City, Guangdong, small hillstream, under rocks, coll. C. Huang, Aug, 2017. SYSBM 001641-1644, 4 females (20.5 × 16.0 mm, 15.1 × 11.8 mm, 14.1 × 10.8 mm, 12.3 × 10.0 mm), same as above male.

Etymology: This species is named after the type locality, Hengqin Island (also known as Ilha de Montanha in Portuguese), Zhuhai City, Guangdong Province, China.

Diagnosis: Third maxilliped merus width about 1.1 × length; ischium width about 0.71 × length (Figs. 5B, 6D). Major cheliped palm length about 1.3 × height (Fig. 5A). Male pleonite 6 width about 2.5 × length; telson width about 1.6 × length (Fig. 5C). Tip of G1 terminal segment (*in situ*) reaching well beyond tubercle forming pleonal locking structure, exceeding sternal suture 4/5 (Fig. 5D); subterminal segment about 2.3 times as

Fig. 6. *Cantopotamon hengqinense* n. gen., n. sp., male holotype (19.9 × 16.0 mm) (SYSBM 001558). (A) left G2; (B) left G1 (ventral view); (C) G1 terminal segment (ventral view); (D) left third maxilliped. Scale bar = 1.0 mm.

long as terminal segment, inner proximal section curved dorsally; terminal segment curved inwards and pointing anteriorly, outer proximal region swollen, with strongly convex margins, tip horn-shaped (Figs. 5D, 6B, C, 9E, F). G2 basal segment subovate, about 2.6 times length of flagelliform distal segment (Fig. 6A).

Description of male: Carapace broader than long, regions indistinct; dorsal surface slightly convex transversely and longitudinally; surface generally smooth with fused rugae on anterolateral region (Fig. 5A). Front slightly deflexed, margin slightly ridged on dorsal view (Fig. 5A). Epigastric cristae distinct, separated by narrow gap (Figs. 5A, B). Postorbital cristae sharp, laterally expanded, fused with epigastric cristae and epibranchial teeth (Figs. 5A, B). Branchial regions relatively flat (Fig. 5A). Cervical groove shallow, inconspicuous (Fig. 5A). Mesogastric region slightly convex (Fig. 5A). External orbital angle triangular (Fig. 5A). Epibranchial tooth small, granular, but distinct (Figs. 5A. B). Anterolateral margin distinctly cristate, lined with approximately 19-21 granules; lateral part bent inward (Fig. 5A). Posterolateral margin comparatively smooth, lined with oblique striae, converging towards posterior carapace margin (Fig. 5A). Orbits small; supraorbital and infraorbital margins cristate, lined with numerous inconspicuous (Fig. 5B). Sub-orbital and upper parts of pterygostomial regions covered with large rounded granules, sub-hepatic region lined with oblique striae (Fig. 5B).

Epistome posterior margin narrow; median lobe sharply triangular, lateral margins almost straight (Fig. 5B).

Third maxilliped merus width about 1.1 × length; ischium width about 0.7 × length; merus trapezoidal, with median depression; ischium trapezoidal, with distinct median sulcus; exopod reaching to proximal third of merus, flagellum long; dorsomesial margin of ischium subauriculiform (Figs. 5B, 6D).

Chelipeds (pereopod 1) unequal (Fig. 5A). Merus cross-section trigonal; margins crenulated (Fig. 5B). Carpus with sharp distomesial spine and spinule at base, dorsal surface with curved striae (Fig. 5A). Major cheliped palm length about 1.3 × height (Fig. 5A). Movable finger as long as fixed finger (Fig. 5A). Occlusal margin of fingers with rounded, blunt teeth; with very slight gape when closed (Fig. 5A).

Ambulatory legs (pereopods 2-5) slender; dactylus with dense short setae; propodus, carpus and merus with relatively sparse short setae (Fig. 5A). Pereopod 5 with propodus length about 2 × width, subequal to dactylus (Fig. 5A).

Thoracic sternum generally smooth, weakly pitted; sternites 1, 2 completely fused, triangular; sternites 3, 4 fused without obvious median suture (Figs. 5C, 10C). Male sterno-pleonal cavity reaching anteriorly to midlength of chelipeds coxae; median longitudinal groove between sternites 7, 8 deep (Fig. 5D). Pleonal locking tubercle slightly posterior to mid-length of sternite 5 (Fig. 5D).

Male pleon triangular, almost reaching anteriorly to level of posterior margin of cheliped coxae; pleonites 3-6 progressively broader longitudinally, lateral margins straight; somite 6 width about 2.5 × length; telson width about 1.6 × length, apex rounded (Fig. 5C).

G1 tip of terminal segment reaching well beyond tubercle forming pleonal locking structure *in situ*, exceeding sternal suture 4/5 (Fig. 5D); subterminal segment about 2.3 times as long as terminal segment, inner proximal section curved dorsally; terminal segment relatively short, sinistrally twisted on the left G1, curved inwards and pointing anteriorly, outer proximal region swollen, with strongly convex margins, tip horn-shaped (Figs. 5D, 6B, C, 9E, F). G2 basal segment subovate, about 2.6 times length of flagelliform distal segment (Fig. 6A).

Size range: Male (n = 4) 13.2 × 10.7 to 19.9 × 16.0 mm; female (n = 5) 12.3 × 10.0 to 20.5 × 16.0 mm.

Remarks: *Cantopotamon hengqinense* n. sp. is closest to *C. zhuhaiense* n. sp., in overall external morphology, but can be separated by a unique combination of characters as outlined under the Remarks section of *C. zhuhaiense* n. sp. and table 2.

Colour in life: Mottled brown overall (Fig. 12C).

Ecology: This species is mainly aquatic, living under rocks in small hillstreams.

Conservation status: Currently, only 8% of Chinese freshwater crabs are assessed as threatened according to IUCN criteria, though the true percentage is likely much higher due to the high proportion of data deficient species (Cumberlidge 2016). Situated south of Zhuhai City and adjacent to Macau, Hengqin Island is the largest of the 146 islands in Zhuhai. It was formerly composed of two islands: Xiaohengqin and Dahengqin, but was joined as one through land reclamation. It has seen rapid economic development in recent years with a significant

degree of urbanization. The human population of the island was less than 8,000 in 2008, but this number is expected to rise to 280,000 by 2020. Dahengqin Mountain is situated at the far south of Hengqin Island and covers an area of around 25 km^2. The mountain is isolated, surrounded by sea to the east, west and south, and by residential areas to the north. Surveys conducted around the region indicate that *C. hengqinense* likely has an area of occupancy of only around 15 km^2, being only known from three hillstreams in close proximity on Dahengqin Mountain. This extremely restricted distribution makes this species highly vulnerable to habitat degradation and destruction. According to the official development plans for Hengqin Island, an ecological park is to be built for tourism on Dahengqin Mountain. Although the plan does state conservation as a priority, the alteration of the original habitat coupled by the significant increase in human activity in the area will no doubt impact the habitat. Given the limited area of occurrence and expected rise in the island's human population, the area of occupancy and quality of the habitat of *C. hengqinense* can be reasonably projected to decline. Therefore, the conservation status of *C. hengqinense* under IUCN Red List criteria corresponds to Endangered B2(a)(b).

Distribution: Hengqin Island, Zhuhai, Guangdong.

***Cantopotamon yangxiense* n. sp.**

(Figs. 7-8, 9D, 10D, 11D, 12D)
urn:lsid:zoobank.org:act:FD44220C-7E73-49A2-9E89-2874964EA328

Type material: Holotype: SYSBM 001562, male (19.3 × 16.0 mm), E'huang Ridge (21.82°N, 111.44°E), Yangxi, Yangjiang City, Guangdong, small hillstreams, under rocks, coll. C. Huang, May, 2015. Paratypes: SYSBM 001563, 1 female (18.5 × 14.9 mm), same data as holotype. ZRC, 1 male (17.0 × 14.1 mm), same data as holotype. ZRC, 1 female (19.8 × 16.0 mm), same data as holotype.

Other material examined: 1 male (20.5 × 17.0 mm) (SYSBM 001564), same data as

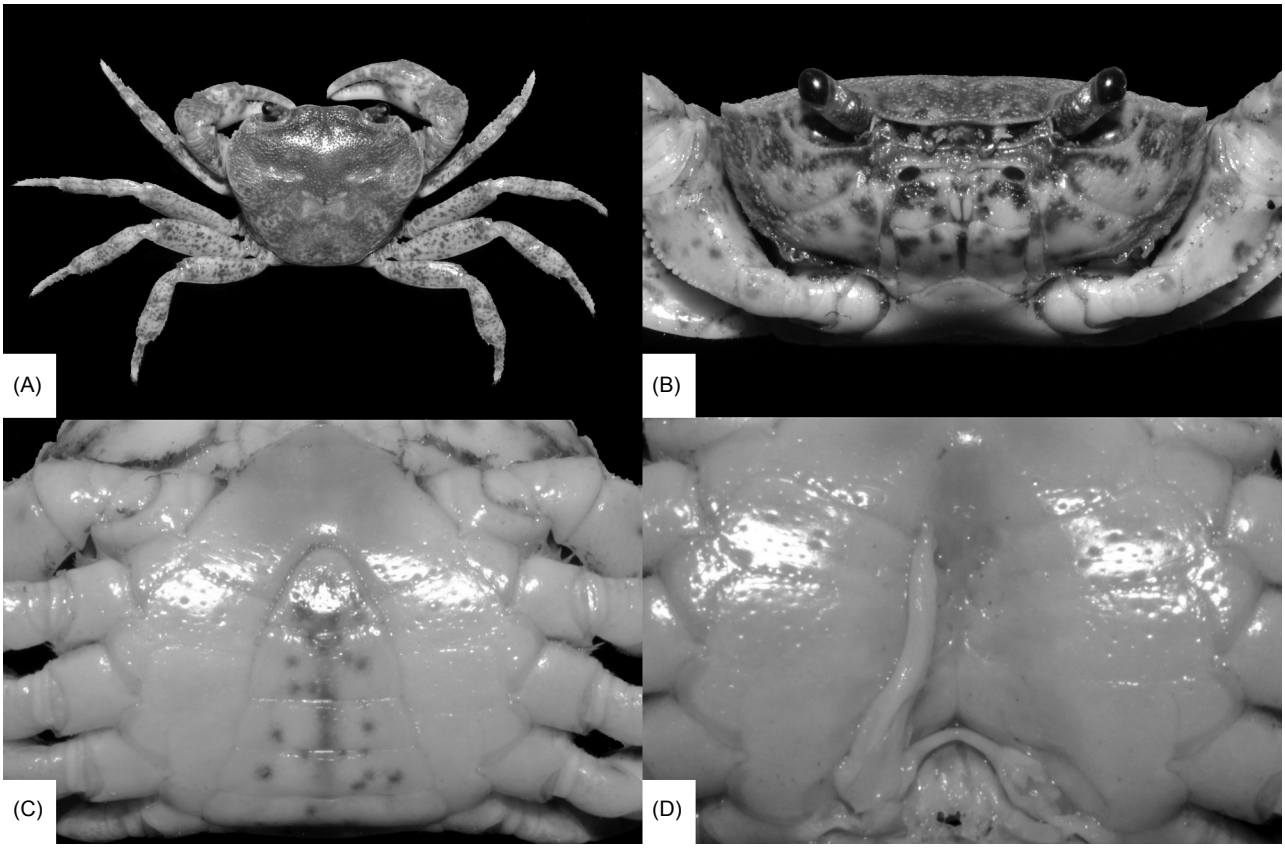

Fig. 7. *Cantopotamon yangxiense* n. gen., n. sp., male holotype (19.3 × 16.0 mm) (SYSBM 001562). (A) dorsal overall view; (B) frontal view of cephalothorax; (C) ventral view showing anterior thoracic sternum and pleon; (D) ventral view showing sterno-pleonal cavity with right G1 *in situ* (left G1 removed).

holotype. 2 females (18.3 × 15.1 mm, 16.9 × 13.8 mm) (SYSBM 001565-001566), same data as holotype. 2 males (16.7 × 13.9 mm, 16.4 × 13.4 mm) (SYSBM 001567-001568), Longgao Mountain (21.67°N, 111.67°E), Yangxi, Yangjiang City, Guangdong, small hillstreams, under rocks, coll. C. Huang, May, 2015. 2 females (15.4 × 12.4 mm, 13.6 × 11.4 mm) (SYSBM 001569-001570), same data as above.

Etymology: This species is named after the type locality Yangxi, Yangjiang, Guangdong Province.

Diagnosis: Third maxilliped merus width about 1.1 × length; ischium width about 0.7 × length (Figs. 7B, 8D). Major cheliped palm length about 1.3 × height (Fig. 7A). Male pleonite 6 width about 2 × length; telson width about 1.4 × length, apex rounded (Fig. 7C). Tip of G1 terminal segment reaching well beyond tubercle forming pleonal locking structure *in situ*, exceeding sternal

Fig. 8. *Cantopotamon yangxiense* n. gen., n. sp., male holotype (19.3 × 16.0 mm) (SYSBM 001562). (A) left G2; (B) left G1 (ventral view); (C) G1 terminal segment (ventral view); (D) left third maxilliped. Scale bar = 1.0 mm.

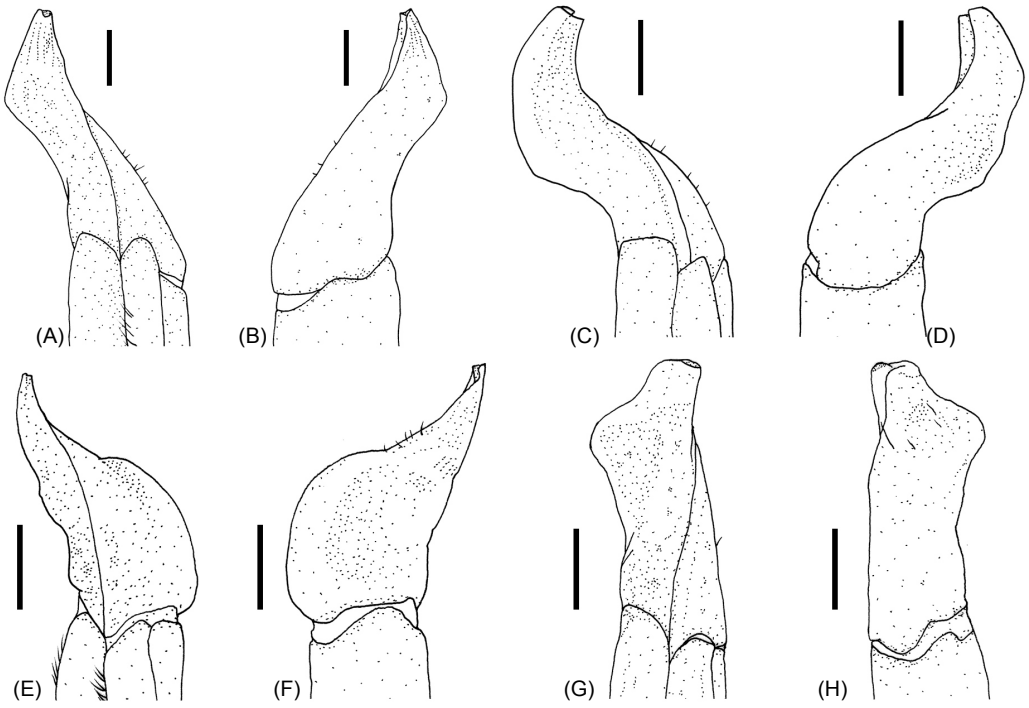

Fig. 9. G1 terminal segment. (A) *Cantopotamon zhuhaiense* n. gen., n. sp., male holotype, ventral view; (B) *C. zhuhaiense*, male holotype, dorsal view; (C) *C. shangchuanense* n. gen., n. sp., male holotype, ventral view; (D) *C. shangchuanense*, male holotype, dorsal view; (E) *C. hengqinense* n. gen., n. sp., male holotype, ventral view; (F) *C. hengqinense*, male holotype, dorsal view; (G) *C. yangxiense* n. gen., n. sp., male holotype, ventral view; (H) *C. yangxiense*, male holotype, dorsal view. Scale bar = 0.5 mm.

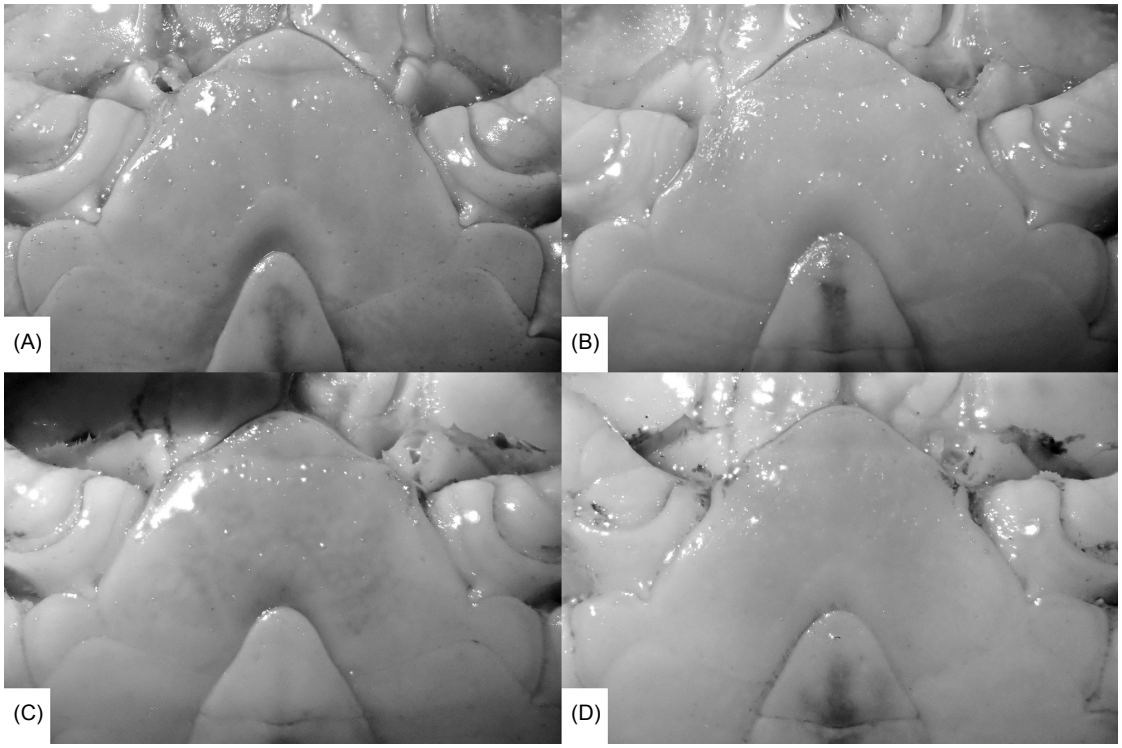

Fig. 10. Male thoracic sternum. (A) *Cantopotamon zhuhaiense* n. gen., n. sp., male holotype (29.1 × 22.9 mm) (SYSBM 001038); (B) *C. shangchuanense* n. gen., n. sp., male holotype (24.1 × 19.5 mm) (SYSBM 001427); (C) *C. hengqinense* n. gen., n. sp., male holotype (19.9 × 16.0 mm) (SYSBM 001558); (D) *C. yangxiense* n. gen., n. sp., male holotype (19.3 × 16.0 mm) (SYSBM 001562).

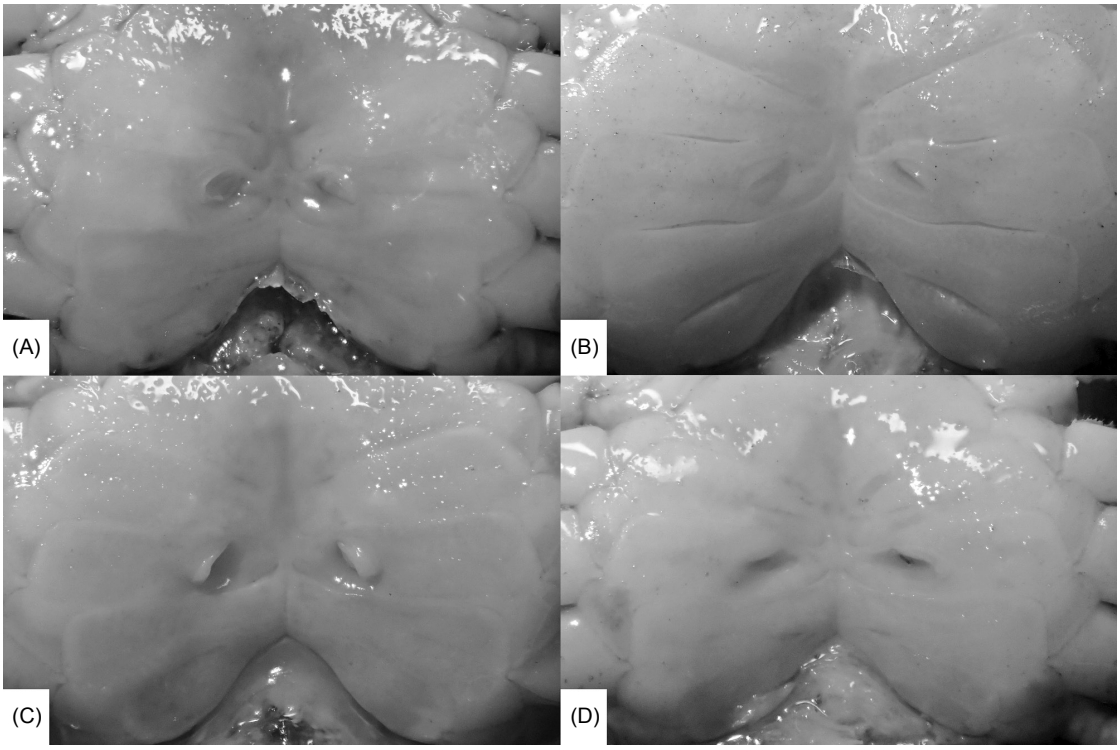

Fig. 11. Female vulvae. (A) *Cantopotamon zhuhaiense* n. gen., n. sp., female paratype (24.6 × 20.0 mm) (SYSBM 001440); (B) *C. shangchuanense* n. gen., n. sp., female paratype (17.3 × 14.1 mm) (SYSBM 001429); (C) *C. hengqinense* n. gen., n. sp., female paratype (13.0 × 10.6 mm) (SYSBM 001559); (D) *C. yangxiense* n. gen., n. sp., female paratype (18.5 × 14.9 mm) (SYSBM 001563).

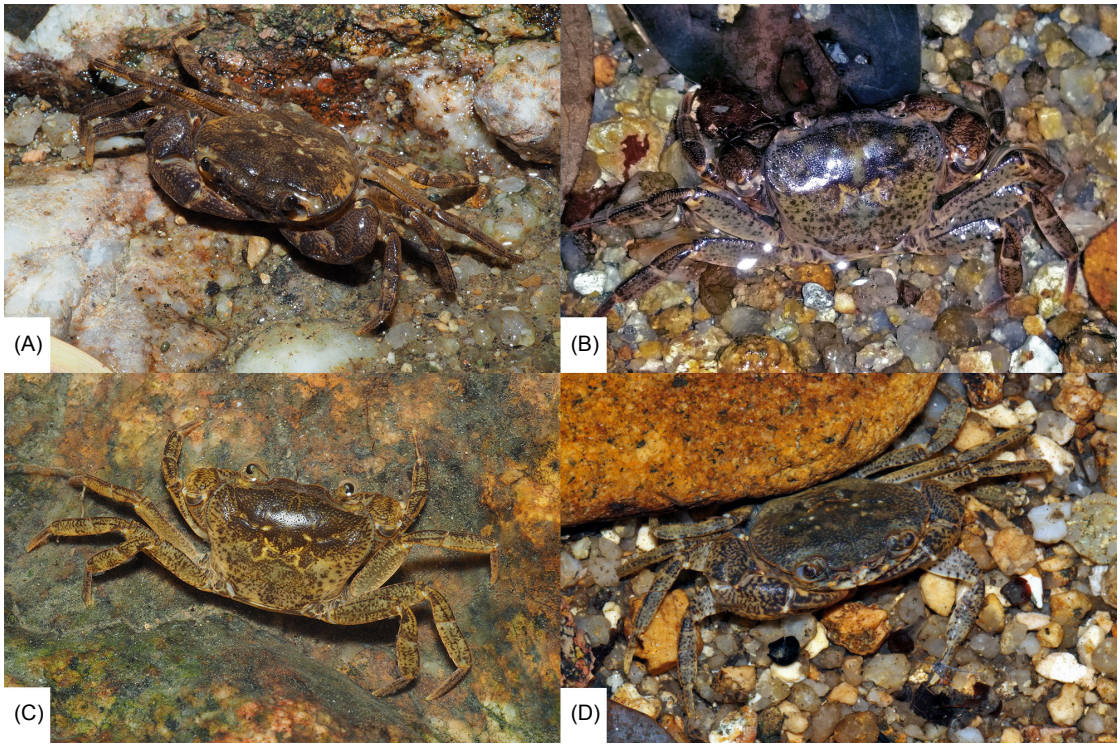

Fig. 12. Colour in life. (A) *Cantopotamon zhuhaiense* n. gen., n. sp., not collected; (B) *C. shangchuanense* n. gen., n. sp., male paratype (21.0 × 17.2 mm) (SYSBM 001428); (C) *C. hengqinense* n. gen., n. sp., male holotype (19.9 × 16.0 mm) (SYSBM 001558); (D) *C. yangxiense* n. gen., n. sp., female paratype (18.5 × 14.9 mm) (SYSBM 001563).

suture 4/5 (Fig. 7D); subterminal segment about 2.3 times as long as terminal segment, inner proximal section curved dorsally; terminal segment inner margin with sub-distal blunt projection, tip blunt (Figs. 7D, 8B, C, 9G, H). G2 basal segment subovate, about 2.6 times length of flagelliform distal segment (Fig. 8A).

Description of male: Carapace broader than long, regions indistinct; dorsal surface slightly convex transversely and longitudinally; surface generally smooth with fused rugae on anterolateral region (Fig. 7A). Front slightly deflexed, margin slightly ridged on dorsal view (Fig. 7A). Epigastric cristae distinct, separated by narrow gap (Figs. 7A, B). Postorbital cristae sharp, laterally expanded, fused with epigastric cristae and epibranchial teeth (Figs. 7A, B). Branchial regions relatively flat (Fig. 7A). Cervical groove shallow, inconspicuous (Fig. 7A). Mesogastric region slightly convex (Fig. 7A). External orbital angle triangular (Fig. 7A). Epibranchial tooth small, granular, but distinct (Figs. 7A, B). Anterolateral margin distinctly cristate, lined with approximately 20-24 granules; lateral part bent inward (Fig. 7A). Posterolateral margin comparatively smooth, lined with oblique striae, converging towards posterior carapace margin (Fig. 7A). Orbits small; supraorbital and infraorbital margins cristate, lined with numerous inconspicuous granules (Fig. 7B). Sub-orbital and upper parts of pterygostomial regions covered with large rounded granules, sub-hepatic region lined with oblique striae (Fig. 7B).

Third maxilliped merus width about 1.1 × length; ischium width about 0.67 × length; merus trapezoidal, with median depression; ischium trapezoidal, with distinct median sulcus; exopod reaching to proximal third of merus, flagellum long; dorsomesial margin of ischium subauriculiform (Figs. 7B, 8D). Posterior margin of epistome narrow; median lobe sharply triangular, lateral margins almost straight (Fig. 7B).

Chelipeds (pereopod 1) unequal (Fig. 7A). Merus cross-section trigonal; margins crenulated (Fig. 7B). Carpus with sharp distomesial spine and spinule at base, dorsal surface with curved striae (Fig. 7A). Major cheliped palm length about 1.3 × height (Fig. 7A). Movable finger as long as fixed finger (Fig. 7A). Occlusal margin of fingers with rounded, blunt teeth; with small gape when closed (Fig. 7A).

Ambulatory legs (pereopods 2-5) slender; dactylus with dense short setae; propodus, carpus and merus with relatively sparse, short setae (Fig. 7A). Pereopod 5 propodus length about 1.9 × width, subequal to dactylus (Fig. 7A).

Thoracic sternum generally smooth, weakly pitted; sternites 1, 2 completely fused, triangular; sternites 3, 4 fused, without obvious median suture (Figs. 7C, 10D). Male sterno-pleonal cavity reaching anteriorly to level of midlength of cheliped coxae; median longitudinal groove between sternites 7/8 deep (Fig. 7D). Pleonal locking tubercle slightly posterior to mid-length of sternite 5 (Fig. 7D).

Male pleon triangular, almost reaching anteriorly to level of posterior margins of cheliped coxae; pleonites 3-6 progressively broader longitudinally, lateral margins straight; somite 6 width about 2 × length; telson width about 1.4 × length, apex rounded (Fig. 7C).

G1 straight, tip of terminal segment reaching well beyond tubercle forming pleonal locking structure *in situ*, exceeding sternal suture 4/5 (Fig. 7D); subterminal segment about 2.3 times as long as terminal segment, inner proximal section curved dorsally; terminal segment relatively short, sinistrally twisted on the left G1, pointing anteriorly, inner margin with sub-distal blunt projection, tip blunt (Figs. 7D, 8B, C, 9G, H). G2 basal segment subovate, about 2.6 times length of flagelliform distal segment (Fig. 8A).

Size range: Male (*n* = 5) 16.4 × 13.4 to 20.5 × 17.0 mm; female (*n* = 6) 13.6 × 11.4 to 19.8 × 16.0 mm.

Remarks: *Cantopotamon yangxiense* n. sp. is closest to *C. zhuhaiense* n. sp. in overall external morphology, but can be separated by its longer G1, which reaches *in situ* well beyond the tubercle forming the pleonal locking structure (Fig. 7D) [versus not reaching in *C. zhuhaiense* n. sp. (Fig. 1D)]; the blunt projection on the inner margin of the G1 terminal segment (Fig. 8C) [versus broadly triangular margin in *C. zhuhaiense* n. sp. (Fig. 2C)]; and other characters as shown in table 2.

Colour in life: Generally mottled brown (Fig. 12D).

Ecology: This species is mainly aquatic, living under rocks in small hillstreams.

Distribution: Yangxi, Yangjiang, Guangdong.

Phylogenetic relationships

In the present phylogenetic analyses, 65 species from 49 potamid genera were included. A 502 bp segment, excluding the variable regions, of the 16S rDNA was amplified and aligned. The BI and ML analyses based on 16S sequences resulted in similar topologies (Fig. 13). Monophyly

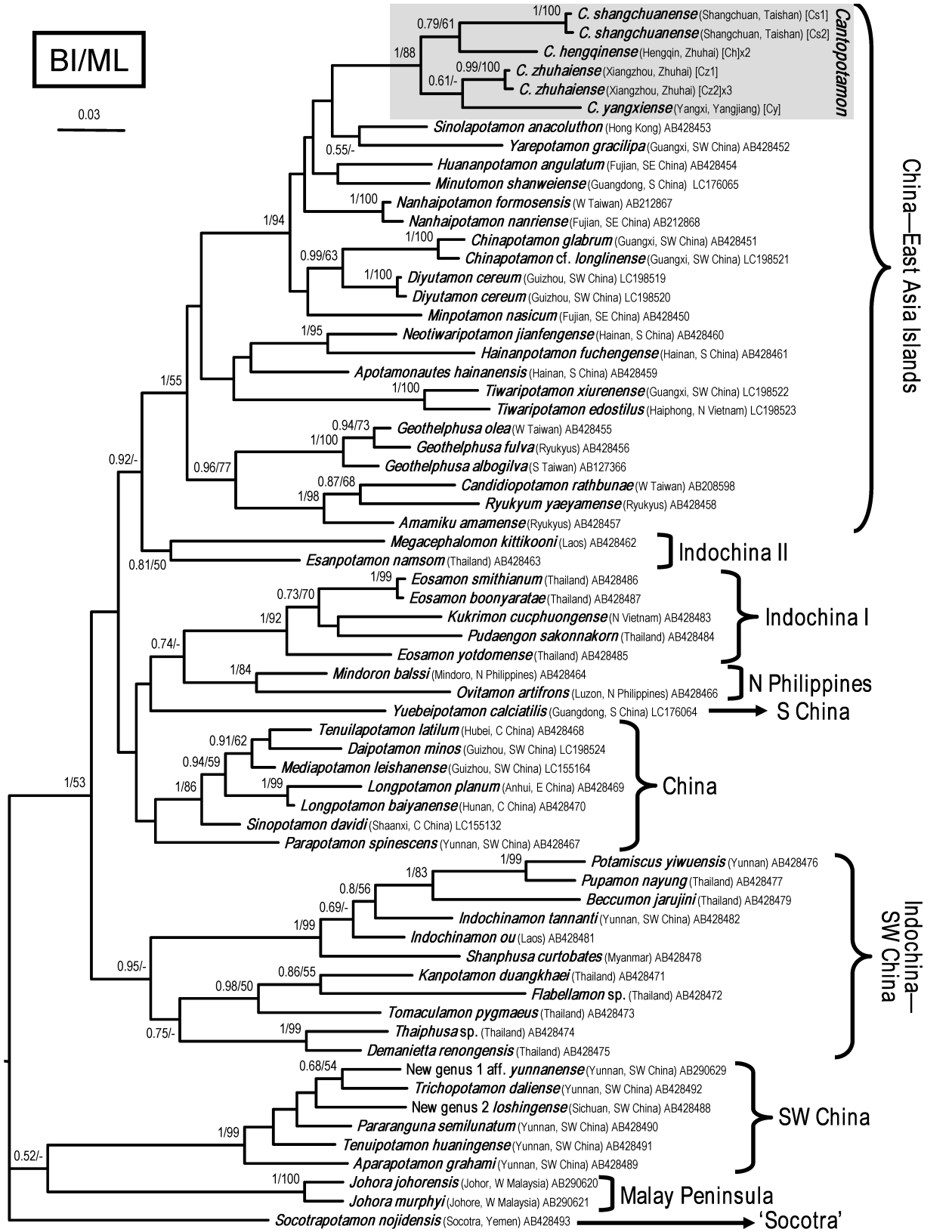

Fig. 13. Bayesian inference (BI) tree of 16S rDNA for the subfamily Potamiscinae, with the sequences and accession numbers in Shih et al. (2009), as well as some additional species (see Material and methods). *Cantopotamon* is highlighted in gray. Bayesian (BI) posterior probabilites and maximum likelihood (ML) bootstrap proportions are indicated at nodes. Only values > 50% are shown.

of *Cantopotamon* is well supported as part of the "China-East Asia Islands" clade (Shih et al. 2009), although its position among these genera is ambiguous based on present data. Combined analysis of the 16S and COI data also supports the validity of the four new species (Fig. 14), with two pairs of sister species, *C. zhuhaiense* + *C. hengqinense*, and *C. shangchuanense* + *C. yangxiense*. Minimum interspecific K2P and p-distance divergences in COI between the four new species is 7.73% and 7.29%, respectively, with bp difference of 48 bp between *C. zhuhaiense* and *C. hengqinense*.

DISCUSSION

The distances estimated between K2P and the p-distance (recommended in Srivathsana and Meier 2011) are close (see above), so the K2P distance was chosen to allow a consistent comparison with most barcoding studies. Minimum interspecific K2P divergence within *Cantopotamon* (7.73%) exceeds that of most other species of freshwater crabs: 6.89% between *Geothelphusa albogilva* Shy, Ng & Yu, 1994 and *G. tawu* Shy, Ng & Yu, 1994; 5.54% between *G. marginata* Naruse, Shokita & Shy, 2004 & *G. fulva* Naruse, Shokita & Shy, 2004; 6.22% between *Tiwaripotamon pluviosum* Do, Shih & Huang, 2016 and *T. pingguoense* Dai & Naiyanetr, 1994; 3% between *Sayamia germani* (Rathbun, 1902) and *S. sexpunctata* (Lanchester, 1906) (reviewed by Chu et al. 2015; Do et al. 2016). Both island species *C. hengqinense* and *C. shangchuanense* are more closely related to their respective adjacent mainland species than they are to each other, suggesting vicariant speciation has occurred. This is consistent with the fact that both Shangchuan Island and Hengqin Island are inshore islands less than 10 km away from the mainland.

Application of both morphological and molecular evidence supports recognition of the new genus *Cantopotamon*, comprising four new species. *Cantopotamon* is most closely related to other genera from South China as part of the "China-East Asia Islands" clade (Shih et al. 2009), although present data do not allow robust determination of its phylogenetic position among these genera; further research using other DNA markers will be required. Future collections on the other islands of southern Guangdong may reveal even more island-bound species of *Cantopotamon*. Their phylogenetic relations may provide us some insights into the processes that formed these islands.

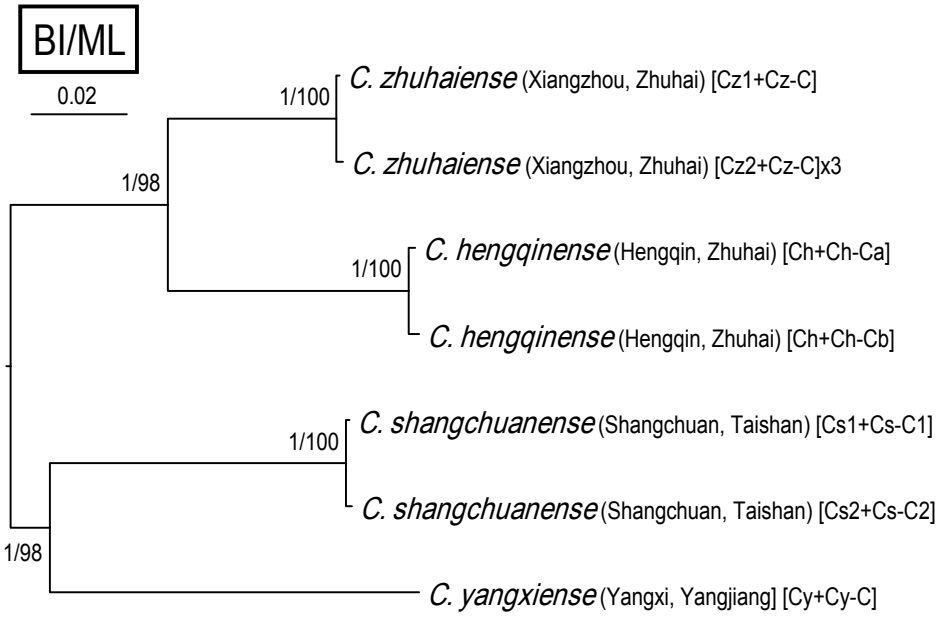

Fig. 14. Bayesian inference (BI) tree of the combined 16S rDNA and COI for the four species of *Cantopotamon*. Bayesian (BI) posterior probabilites and maximum likelihood (ML) bootstrap proportions are indicated at nodes. Only values > 50% are shown.

Acknowledgements: This work, the new genus name and new species names have been registered with ZooBank under urn:lsid:zoobank.org:pub:E8D372CC-CB92-40CE-A61B-A1E8AFAC230B. This study was supported by a grant from the BEES Student Research Funding scheme and PANGEA Small Research Grants (UNSW) to CH; and a grant from the Ministry of Science and Technology (MOST 105-2621-B-005-002-MY3), Executive Yuan, Taiwan, to HTS. We acknowledge two anonymous referees who greatly improved this manuscript. This is a contribution from the Australian Museum Research Institute.

Authors' contributions: CH did field collections and initiated the manuscript; STA tutored CH in morphological methods and scientific illustration; HTS performed the DNA analyses. All authors contributed to drafting and revising the manuscript. All authors read and approved the final manuscript.

Competing interests: CH, STA and HTS declare that they have no conflict of interest.

Availability of data and materials: Sequences generated in the study have been deposited in the DNA Data Bank of Japan (DDBJ) database (accession numbers in Table 1 in manuscript).

Consent for publication: Not applicable.

Ethics approval consent to participate: Not applicable.

REFERENCES

Chu KH, Schubart CD, Shih HT, Tsang LM. 2015. Genetic diversity and evolution of Brachyura. *In*: Castro P, Davie PJF, Guinot D, Schram FR, von Vaupel Klein JC (ed) Treatise on zoology - anatomy, taxonomy, biology - the Crustacea, complementary to the volumes translated from the French of the Traité de Zoologie. Brill, Leiden, **9**(C)(I), Decapoda: Brachyura (Part 1)**:**775-820.

Cumberlidge N. 2016. Global Diversity and Conservation of Freshwater Crabs (Crustacea: Decapoda: Brachyura). A Global Overview of the Conservation of Freshwater Decapod Crustaceans, Springer International Publishing, pp. 1-22.

Cumberlidge N, Ng PKL, Yeo, DCJ, Naruse T, Meyer KS, Esser LJ. 2011. Diversity, endemism and conservation of the freshwater crabs of China (Brachyura: Potamidae and Gecarcinucidae). Integr Zool **6:**45-55.

Dai AY, Türkay M. 1997. Revision of the Chinese freshwater crabs previously placed in the genus *Isolapotamon* Bott, 1968 (Crustacea: Decapoda: Brachyura: Potamidae). Raffles B Zool **45:**237-264.

Dai AY. 1999. Fauna Sinica: Arthropoda Crustacea Malacostraca Decapoda Parathelphusidae Potamidae. Science Press, Beijing, China, 501 pp. (in Chinese with English summary)

Do VT, Shih HT, Huang C. 2016. A new species of freshwater crab of the genus *Tiwaripotamon* Bott, 1970 (Crustacea, Brachyura, Potamidae) from northern Vietnam and southern China. Raffles B Zool **64:**213-219.

Huang C, Shih HT, Ng PKL. 2017. A new genus and new species of Potamidae (Crustacea: Decapoda: Brachyura: Potamoidea), the first stygomorphic cave crab known from China and East Asia. Zootaxa **4232:**71-84, **4250:**600.

Kimura M. 1980. A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. J Mol Evol **16:**111-120.

Kumar S, Stecher G, Tamura K. 2016. MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. Mol Biol Evol **33:**1870-1874.

Mitra S, Valarmathi K. 2017. *Himalayapotamon chambaensis*, a new species of freshwater crab (Crustacea: Brachyura: Potamidae) from Himachal Pradesh, India. Zootaxa **4324:**482-490.

Naser MD, Page TJ, Ng NK, Apel M, Yasser AG, Bishop JM, Ng PKL, Clark PF. 2012. Invasive records of *Eriocheir hepuensis* Dai, 1991 (Crustacea: Brachyura: Grapsoidea: Varunidae): Implications and taxonomic considerations. Bioinvasions Rec **1:**71-86.

Nylander JAA. 2005. MrModeltest vers. 2.2. Evolutionary Biology Centre, Uppsala Univ., Uppsala, Sweden.

Pati SK, Devi ARS. 2015. Description of a new genus and new species of freshwater crab (Brachyura: Gecarcinucidae) from the Western Ghats, Keral, India. Zool Stud **54:**35. doi:10.1186/s40555-015-0112-0.

Ronquist F, Huelsenbeck JP, van der Mark P. 2005. MrBayes 3.1 manual. Available at http://mrbayes.csit.fsu.edu/manual.php.

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MRBAYES 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst Biol **61:**539-542.

Schubart CD. 2009. Mitochondrial DNA and decapod phylogenies: the importance of pseudogenes and primer optimization. Decapod Crustacean Phylogenetics. Crustacean Iss **18:**47-65.

Shih HT, Huang C, Ng PKL. 2016. A re-appraisal of the widely-distributed freshwater crab genus *Sinopotamon* Bott, 1967, from China, with establishment of a new genus (Crustacea: Decapoda: Potamidae). Zootaxa **4138:**309-331.

Shih HT, Ng PKL. 2011. Diversity and biogeography of freshwater crabs (Crustacea: Brachyura: Potamidae, Gecarcinucidae) from East Asia. Syst Biodivers **9:**1-16.

Shih HT, Ng PKL, Davie PJF, Schubart CD, Türkay M, Naderloo R, Jones D, Liu MY. 2016. Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea: Brachyura), based on phylogenetic relationships, with a reorganization of subfamily rankings and a review of the taxonomic status of *Uca* Leach, 1814, sensu lato and its subgenera. Raffles B Zool **64:**139-175.

Shih HT, Yeo DCJ, Ng PKL. 2009. The collision of the Indian plate with Asia: molecular evidence for its impact on the phylogeny of freshwater crabs (Brachyura: Potamidae). J Biogeogr **36:**703-719.

Stamatakis A. 2006. RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. Bioinformatics **22:**2688-2690.

Thompson JD, Higgins DG, Gibson TJ. 1994. CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic Acids Res **22:**4673-4680.

Appendix I. Comparative material from China. (download)