Description of two new species of the genus *Heterochelamon* Türkay & Dai, 1997 (Crustacea: Decapoda: Brachyura: Potamidae), from southern China

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This study describes two new species of freshwater crab of the genus *Heterochelamon* Türkay & Dai, 1997 from southern China, *H. huidongense* from Guangdong Province and *H. jinxiuense* from Guangxi Zhuang Autonomous Region. The two new species can be differentiated from congeners by characters derived from the shape of the epibranchial tooth, external orbital angle, cheliped proportions and structure of the male first gonopod. The present study brings the number of *Heterochelamon* species to seven. We used the mitochondrial 16S rRNA gene for a molecular analysis and the results are consistent with the morphological features that support the recognition of two new taxa.

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Abstract

This study describes two new species of freshwater crab of the genus *Heterochelamon* Türkay & Dai, 1997 from southern China, *H. huidongense* from Guangdong Province and *H. jinxiuense* from Guangxi Zhuang Autonomous Region. The two new species can be differentiated from congeners by characters derived from the shape of the epibranchial tooth, external orbital angle, cheliped proportions and structure of the male first gonopod. The present study brings the number of *Heterochelamon* species to seven. We used the mitochondrial 16S rRNA gene for a molecular analysis and the results are consistent with the morphological features that support the recognition of two new taxa.

Introduction

The brachyuran crabs belong to the order Decapoda and currently include more than 7000 living species; it is the most diverse group of extant crustaceans (Ng, Guinot & Davie, 2008). Freshwater crabs originated about 136 million years ago (Tsang et al., 2014). With changes in geography over time, some brachyuran crabs adapted to freshwater, eventually forming more than 1300 species of semi-terrestrial or aquatic freshwater crabs (Cumberlidge & Ng, 2009). The rapid divergent evolution of freshwater crabs may be due to the co-evolution between the male and female external genitalia (Yao et al., 2019).

Freshwater crabs are found in the tropics and subtropics in most parts of the world, occurring in aquatic habitats ranging from clear montane streams to lowland rivers and even in

39 caves or tree holes (Dai, 1999; Ng, Guinot & Davie, 2008). Southern China, where mountains
40 and rivers are abundant, provides a multitude of habitats for a large number of species and the
41 large numbers of new taxa reported in recent years indicate that research on this group remains in
42 a "discovery" phase (Yeo et al., 2008; Zhu, Naruse & Zhou, 2010; Naruse, Zhu & Zhou,
43 2013; Huang, Mao & Huang, 2014; Shih & Do, 2014; Huang, Shih & Mao, 2016; Huang, Shih
44 & Ng, 2017; Huang, Ahyong & Shih, 2017; Ng, 2017; Huang, 2018; Huang, Shih & Ahyong,
45 2018; Huang, Wong & Ahyong, 2018; Wang, Huang & Zou, 2019; Wang, Zhou & Zou, 2019).
46   Currently, the freshwater crabs distributed in China are represented by 49 genera in the
47 families Potamidae Ortmann, 1896 and Gecarcinucidae Alcock, 1910 (Chu et al., 2018; Chu,
48 Wang & Sun, 2018; Huang, Shih & Ahyong, 2018; Huang, Huang & Shen, 2020). The potamid
49 genus *Heterochelamon* was established by Türkay & Dai (1997) to accommodate *Potamon*
50 *(Geothelphusa) purpureomanualis* Wu, 1934 (type species), theretofore assigned to
51 *Malayapotamon*, and two new species, *H. guangxiense* and *H. yangshuoense*. Naruse, Zhu &
52 Zhou (2013) further described two new species, *H. tessellatum* and *H. castanea*. The five known
53 species exclusively occur in Guangxi Zhuang Autonomous Region (Türkay & Dai, 1997;
54 Naruse, Zhu & Zhou, 2013).
55   In 2011, we collected specimens of a *Heterchelamon* species from Jinxiu, Guangxi, but the
56 crabs were not identified at the time. It was not until 2018 that our research team identified the
57 specimens as belonging to an undescribed species. In 2019, freshwater crab enthusiast Jia-Ming
58 Tian collected some dark colored freshwater crabs from Huidong, Guangdong. We collected
59 specimens too and identified the crabs to be another new species of the genus *Heterochelamon*.
60 As such, we herein describe two new species of the genus *Heterochelamon*, including one from
61 Guangdong Province, representing the first species of the genus known from outside of Guangxi.
62   To study the phylogenetic relationships of species within *Heterochelamon*, we used the
63 mitochondrial 16S rRNA gene data of four species from this genus, including the two new
64 species reported in this paper. Molecular data supports the recognition of the two new species
65 and their assignment to *Heterochelamon*.
66

Material & Methods

68 Specimens were collected by Song-Bo Wang, Yi-Yang Xu, Jia-Ming Tian and Xi-Jiao Wei;
69 preserved in 95% ethanol and deposited in the Department of Parasitology of the Medical
70 College of Nanchang University, Jiangxi, China (NCU MCP), National Tropical Disease
71 Research Center, Shanghai, China (TDRC). The abbreviations G1 and G2 are used for the male
72 first gonopod and second gonopod, respectively. Carapace width and length are reported in
73 millimeters. The terminology used primarily follows that of Dai (1999), Naruse, Zhu & Zhou
74 (2013) and Davie et al. (2015).
75   Muscle tissue was extracted from the ambulatory legs and chelipeds, and total genomic
76 DNA was extracted from the tissues using the Omega Tissue Kit following the manufacturer's
77 protocol. Mitochondrial 16S rRNA gene sequences were obtained by PCR amplification with the
78 primers 1471 (5'-CCTGTTTANCAAAAACAT-3') and 1472 (5'-

79 AGATAGAAACCAACCTGG-3') (Shih et al., 2004). The PCR procedure was as follows: 33
80 cycles of denaturation for 50 s at 94°C, annealing for 40 s at 52°C, and extension for 1 min at
81 72°C, followed by a final extension for 10 min at 72°C. Sequences were obtained by automated
82 sequencing (ABI3730 automatic sequencer).
83   Sequences were aligned using MAFFT vers.7.355 (Nakamura et al., 2018) based on the G-
84 INS-I method and the selection of conserved regions with Gblocks 0.91b (Castresana, 2000).
85 GTR+I+G was the best fit model for the sequence evolution of the 16S dataset, as determined
86 with MrModeltest vers.2.2 (Nylander, 2005) and then selected based on the Akaike information
87 criterion (AIC). MrBayes vers.3.2.6 (Ronquist et al., 2012) was used to construct a Bayesian
88 inference (BI) tree. Four Markov chain Monte Carlo (MCMC) chains were run for 2,000,000
89 generations, with samples stored once every 1000 generations, discarding the first 25% as burn-
90 in. Tracer vers.1.6 (Rambaut et al., 2014) was used to check effective sample size (ESS) values
91 (all of greater than 200). Simultaneously with the BI analysis, we used MEGA vers.X.0 (Kumar
92 et al., 2018) to select the best evolutionary model for maximum likelihood (ML) analysis, which
93 was the HKY+I+G model based on the Bayesian information criterion (BIC). The ML tree was
94 built after 1000 bootstrap replicates by using MEGA vers.X.0 (Kumar et al., 2018).
95   The electronic version of this article in portable document format will represent a published
96 work according to the International Commission on Zoological Nomenclature (ICZN), and hence
97 the new names contained in the electronic version are effectively published under that Code from
98 the electronic edition alone. This published work and the nomenclatural acts it contains have
99 been registered in ZooBank, the online registration system for the ICZN. The ZooBank LSIDs
100 (Life Science Identifiers) can be resolved and the associated information viewed through any
101 standard web browser by appending the LSID to the prefix http://zoobank.org/. The LSID for
102 this publication is: urn:lsid:zoobank.org:pub: F680C21E-0BED-4724-BA62-1174336F433F. The
103 online version of this work is archived and available from the following digital repositories: Peer
104 J, PubMed Central, and CLOCKSS.
105
106 **Results**
107 **Systematics**
108
109 **Family Potamidae Ortmann, 1896**
110 *Heterochelamon* **Türkay & Dai, 1997**
111
112 *Heterochelamon huidongense* **n. sp. (Figs. 1-4)**
113 urn:lsid:zoobank.org: act: 0F67FA91-6734-4800-9C03-76668635A1E2
114
115 **Material examined.** Holotype: male (25.8 × 23.1 mm) (NCU MCP 423601), Xinaobei Village
116 (22°55'14.59''N 114°33'51.85''E, 47 m asl.), Baihua Town, Huidong County, Huizhou City,
117 Guangdong Province, coll. Song-Bo Wang, Yi-Yang Xu and Jia-Ming Tian, 6th Jul. 2019.
118 Paratypes: 3 males (30.0 × 25.8 mm, 26.2 × 23.1 mm, 21.3 × 18.6 mm) (NCU MCP 423602,

119 TDRC 002005, TDRC 002006) and 2 females (26.1 × 23.5 mm, 20.6 × 18.5 mm) (NCU MCP
120 423603, TDRC 002007), same data as holotype. Others: 5 males (29.6 × 25.4 mm, 26.4 × 23.5
121 mm, 25.1 × 22.3 mm, 28.4 × 24.5 mm, 21.3 × 18.9mm; NCU MCP 423606, NCU MCP 423607,
122 NCU MCP 423608, NCU MCP 423609, NCU MCP 423610) and 2 females (21.1 × 19.1 mm,
123 14.5 × 12.5 mm; NCU MCP 423612, NCU MCP 423613), same data as holotype.
124

125 **Comparative material.** *Heterochelamon yangshuoense* Türkay & Dai, 1997: Holotype, male,
126 IZCAS CB 05102, Yangshuo County, Guilin City, Guangxi Zhuang Autonomous Region, 8th
127 May 1975. *H. guangxiense* Türkay & Dai, 1993: Holotype, male, IZCAS CB 01336, Guangxi
128 Zhuang Autonomous Region, May 1974. *H. purpureomanualis* Türkay & Dai, 1997: not
129 holotype, male, IZCAS CB, Yao Mountain, Xiuren Town, Lipu County, Guilin City, Guangxi
130 Zhuang Autonomous Region, 1938. *H. tessellatum* Naruse, Zhu & Zhou, 2013: Holotype, male,
131 NCU MCP 2012.0003, Dong Men Zhuang, Shuangluo Village, Sanli Town, Shanglin County,
132 Guangxi Zhuang Autonomous Region, 14th Aug. 2006, Paratypes, 1 male, NCU MCP
133 2012.0004, 1 female, NCHUZOOL 13572, same data as holotype. *H. castanea* Naruse, Zhu &
134 Zhou, 2013: Holotype: male, NCU MCP 2012.0001, Lituan Village, Baiming Town, Liujiang
135 County, Liuzhou City, Guangxi Zhuang Autonomous Region, Aug. 2006, Paratype: 1 female,
136 NCU MCP 2012. 0002, same data as holotype.
137

138 **Diagnosis.** Carapace subquadrate, dorsal surface generally smooth, regions not clearly
139 demarcated. External orbital angle triangular, sharp; postorbital cristae inconspicuous.
140 Epibranchial tooth very sharp, distinct. Anterolateral margin cristae. Suborbital, pterygostomial
141 regions smooth. Median lobe of epistome posterior margin protruded slightly. Third maxilliped
142 exopod exceeding posterior margin of merus, with long slender flagellum. Chelipeds unequal,
143 cutting edges of finger of larger cheliped with blunt teeth, with narrow gap when fingers closed.
144 Ambulatory legs slender. Male telson triangular, lateral margins slightly concave. Female vulva
145 located at middle of sternite 6. G1 terminal segment flat and medially bent, not tapered distally,
146 apex rounded, reaching pleonal locking tubercle on mid length of sternite 5 but not exceeding
147 sternites 4/5 suture.
148

149 **Description.** Carapace subquadrate, width about 1.1 times as length (n = 13), regions not clearly
150 demarcated; dorsal surface convex longitudinally, smooth (Figs. 1A, 3A). External orbital angle
151 triangular, generally sharp, separated from anterolateral margin by U-shaped notch; postorbital
152 cristae inconspicuous, postfrontal lobe slightly convex, separated from each other; cervical
153 groove indistinct; H-shaped gastric groove indiscernible (Figs. 1A and 3A). Epibranchial tooth
154 very sharp, distinct; anterolateral margin cristae, straight, lined 7-8 granules, shorter than
155 posterolateral margin; posterolateral surface equally smooth (Figs. 1A, 3A). Frontal, supra-,
156 infraorbital margins cristate, lined with indistinct granules; suborbital, pterygostomial regions
157 smooth, with a few round granules (Fig. 1B). Epistome posterior margin distinctly cristate,
158 median lobe low, triangular, lateral margins slightly sinuous (Fig. 1B).

159   Third maxilliped exopod exceeding posterior margin of merus, with long slender flagellum;
160   merus about 1.2 times as broad as long, slightly depressed medially; ischium about 1.4 times as
161   long as broad, with distinct median sulcus (Fig. 2B).
162   Male Chelipeds unequal (Fig. 1A). Merus surface smooth without any pits; carpus with
163   inner angle produced into strong spine, surface sparsely covered with pits (Figs. 1A). Cutting
164   edges of larger cheliped fingers with row of large round blunt teeth, with narrow gap when
165   fingers closed (Fig. 2A). Ambulatory legs slender; third legs longest when stretched laterally,
166   fourth ambulatory leg propodus about 1.6 times as long as broad, slightly shorter than dactylus,
167   with scattered thorn-like setae (Fig. 2E).
168   Male thoracic sternites 2/3 demarcated by distinct suture, sternites 3/4 fused by shallow
169   groove (Fig. 2C). Male sterno-pleonal cavity deep, reaching anteriorly to mid-length of thoracic
170   sternite 4; median groove between sternites 7/8 long (Fig. 2E). Male pleon triangular, third
171   somite widest; telson triangular with rounded apex, lateral margin slightly concave (Fig. 2C);
172   somite 6 trapezoidal, margins slightly oblique; somites 3–6 gradually decreasing in width,
173   increasing in length in males (Figs. 2D). Female pleon broadly ovate (Fig. 3B); vulva small,
174   ovate, located at middle of sternite 6, opening inwards, posterior margin slightly bulged (Fig.
175   3C).
176   G1 slender; terminal segment flat, bent medially, not tapered distally, distal part rounded;
177   exceeding pleonal locking tubercle on mid length of sternite 5, not reaching suture between
178   sternites 4/5 (Figs. 4A-D, 2F). Distinct boundary between terminal segment and subterminal
179   segment, latter length about 2.5 times as former, groove for G2 in ventral surface; G2 basal
180   segment triangular, length about 2.1 times distal segment (Fig. 4).
181
182   **Etymology.** The species is named after the type locality, Huidong County, Huizhou City,
183   Guangdong Province.
184
185   **Distribution.** The new species is known only from type locality presently, Huidong County,
186   Huizhou City, Guangdong Province, southern China.
187
188   **Ecology.** This new species was collected at three sites along a river using fish cages or by hand
189   (Figs. 5B, 5C). The water of the river is relatively clear, and the water flow is slow. The width of
190   the river is approximately 1-3 meters and the depth is approximately 0.2-0.3 meters. The river
191   bed is mainly sand and soil (Fig. 5E). There are many shrubs and low hills around the river,
192   many households located dozens of meters away from the river and some vegetable gardens
193   along the river (Fig. 5A). At one of the collection points, we also collected specimens of the
194   gecarcinucid *Somanniathelphusa sinensis* H. Milne-Edwards, 1853 (Fig. 5D), which we believe
195   coexists with the new species in the river.
196
197   **Remarks.** Compared to congeners, *Heterochelamon huidongense* n. sp. can easily be separated
198   by its G1 not reaching sternites 4/5 suture *in situ* and terminal segment being medially bent
199   (Figs. 2E and 4A, Table 1) (versus reaching sternites 4/5 suture and straight in congeners, except

200 *H. tessellatum* which has G1 that also does not reach the sternites 4/5 suture but is strongly bent
201 proximally), as well as a combination of characters: very sharp epibranchial tooth , triangular
202 external orbital angle, slightly convex anterolateral margins (Fig. 1A), triangular male telson
203 (Fig. 2C), inward opening female vulva (Fig. 3C). For detailed differences between this new
204 species and congeners, see Table 1.

205

206 ***Heterochelamon jinxiuense* n. sp. (Figs. 5-8)**
207 urn:lsid:zoobank.org:act:5D34B999-78C7-4522-9F74-E872A34B7462

208

209 **Material examined.** Holotype: 1 male (24.6 × 19.8 mm) (NCU MCP 342001), from Tongfu
210 Village (24°17'10.89''N 115°5'17.28''E, 267 m asl.), Toupai Town, Jinxiu Yao Autonomous
211 County, Laibin City, Guangxi Zhuang Autonomous Region, coll. Xi-Jiao Wei, 8th Jul. 2011.
212 Paratypes: 3 males (20.3 × 15.8 mm, 15.8 × 12.6 mm, 17.8 × 14.8 mm) (NCU MCP 342002,
213 TDRC 002008, TDRC 002009) and 1 female (12.9 × 10.4 mm) (NCU MCP 342003), same data
214 as holotype. Other: 1 male (14.1 × 11.4 mm) (NCU MCP 342006), same data as holotype.

215

216 **Comparative material.** See for *Heterochelamon huidongense* n. sp.

217

218 **Diagnosis.** Carapace trapezoidal, flat, surface very smooth. External orbital angle blunt,
219 postorbital cristae, postfrontal lobe indiscernible. Epibranchial tooth blunt, distinct; anterolateral
220 margin cristae, slightly convex. Suborbital, pterygostomial regions very smooth. Median lobe of
221 epistome posterior margin distinctly protruding. Third maxilliped exopod with long flagellum,
222 ischium longitudinal median sulcus almost indistinct. Chelipeds strongly unequal in male adults,
223 surface smooth, lower cutting edge of major cheliped finger with very large, blunt teeth, with
224 medium gap when fingers closed. Ambulatory legs slender. Thoracic sternites 2/3 demarcated by
225 distinct deep suture, anterior part of sternite 3 convex. Male sterno-pleonal cavity deep, narrow.
226 Male telson triangular, lateral margin straight. Female vulva reaching sternites 5/6 suture. Male
227 G1 terminal segment rod-like, decreasing in diameter, subdistal segment suddenly inwardly bent,
228 reaching sternites 4/5 suture.

229

230 **Description.** Carapace trapezoidal, flat, width about 1.3 times as length (n = 6), regions not
231 clearly demarcated; dorsal surface slightly convex, covered with inconspicuous pits (Figs. 6A,
232 8A). External orbital angle blunt, separated from anterolateral margin by shallow notch;
233 postorbital cristae inconspicuous, postfrontal lobe indistinct; cervical groove indistinct; H-shaped
234 gastric groove indiscernible (Figs. 6A, 8A). Epibranchial tooth blunt, distinct; anterolateral
235 margin cristae, slightly convex, lined with several granules, shorter than posterolateral margin;
236 posterolateral surface smooth (Figs. 6A, 8A). Frontal and orbital margins cristate, lined with
237 indistinct granules, supra-, infraorbital margins glazed; suborbital, pterygostomial regions very
238 smooth, not covered with granules (Fig. 6B). Epistome posterior margin distinctly cristate,
239 median lobe triangular, distinctly protruding, lateral margins almost straight (Fig. 6B).

240   Third maxilliped exopod exceeding posterior margin of merus, with slender flagellum;
241   merus about 1.2 times as broad as long, with median depression; ischium about 1.4 times as long
242   as broad, longitudinal median sulcus distinct (Fig. 7B).
243   Chelipeds strongly unequal in adult males (Fig. 7A). Merus surface smooth without any
244   pits; carpus inner angle forming stout spine, surface not covered with pits (Fig. 1A). Cutting edge
245   of larger cheliped fixed finger with large rounded teeth, movable finger cutting edge lined with
246   several small teeth, with medium gap when fingers closed (Fig. 7A). Ambulatory legs slender;
247   third legs longest, the fourth ambulatory leg propodus about 2.0 times as long as broad, equal to
248   dactylus in length (Figs. 6A, 7F).
249   Male thoracic sternites 2/3 demarcated by distinct deep suture, anterior part of sternite 3
250   convex, sternites 3/4 suture discernible as shallow groove, abdominal cavity reaching imaginary
251   line joining posterior third of cheliped coxae (Fig. 7C). Male sterno-pleonal cavity deep, narrow;
252   median longitudinal groove between sternites 7/8 medium-length (Fig. 7E). Male pleon
253   triangular, third somite widest; telson triangular with round apex, lateral margin slightly convex;
254   somite 6 trapezoidal; somite 3–6 gradually decreasing in width (Fig. 7D). Female vulva very
255   small, ovate, reaching sternites 5/6 suture, located at upper of sternite 6 (Fig. 8B).
256   Male G1 slender; terminal segment rod-like, almost straight, tapered distally; apex sharp,
257   abruptly bent inwards subdistally; reaching beyond pleonal locking tubercle on mid length of
258   sternite 5, to suture between sternites 4/5 (Figs. 7E, 9). Boundary between terminal segment and
259   subterminal segment clear, latter length about 2.4 times as former, groove for G2 in ventral
260   surface, G2 destroyed during dissection (Fig. 9).
261
262   **Etymology.** The species is named after the type locality, Jinxiu Yao Autonomous County, Laibin
263   City, Guangxi Zhuang Autonomous Region.
264
265   **Distribution.** The new species is known only from type locality presently, Jinxiu Yao
266   Autonomous County, Laibin City, Guangxi Zhuang Autonomous Region, southern China.
267
268   **Ecology.** The collection site is a small river running behind Tongfu village. The river is mostly
269   surrounded by dwarf mountains and many kinds of fruit trees. The river is approximately 2
270   meters in width, the water depth is approximately 0.4 meters, the riverbed mainly consists of
271   sand and gravel and the water quality is good.
272
273   **Remarks.**
274   *Heterochelamon jinxiuense* n. sp. can easily be differentiated from its congeners by its distally
275   tapered G1 (Fig. 9, Table 1) (versus widening distally or not tapered distally in congeners), blunt
276   external orbital angle (Fig. 6A, Table 1) (versus triangular or acutely triangular in congeners,
277   except that of *H. guangxiense* which is also blunt), strongly unequal chelipeds in adult males and
278   medium gap when male major chela fingers closed (Fig. 7A, Table 1) (versus strongly unequal in
279   *H. tessellatum, H. purpureomanualis* and *H. yangshuoense,* but fingers with very broad and

280 oblong gap when closed; other species unequal with narrow gap when closed). The detailed
281 differences between this new species and congeners are also presented in Table 1.
282   The new species was collected in 2011, of which the material consisted of five male (one
283 adult and four immature) and one female. The G2 of the only mature male had been destroyed by
284 the time we examined the specimens. We were also unable to find this species in a subsequent
285 collection trip. As of such, the G2 is not described here.
286
287 **Phylogenetic analyses**
288 We obtained the mitochondrial 16S rRNA gene molecular data from four species of
289 *Heterochelamon* for the first time. Other sequences used were downloaded from GenBank. To
290 show where these two new species fit within the Asian freshwater crab phylogeny, 60 species of
291 47 genera in the family Potamidae Ortmann, 1896, were used (Table 2). The trees were
292 constructed via the BI and ML methods and showed a high degree of consistency, and the
293 topological structure was determined from BI with support values from both methods (Fig. 10).
294 The phylogenetic results support the recognition of the two new *Heterochelamon* species, *H.*
295 *tessellatum* and *H. castanea* cluster with the two new species to form an independent branch in
296 the "China-East Asia Islands" clade (Shih, Yeo & Ng, 2009).
297

Discussion

299   The genetic analysis supports the recognition of four species of *Heterochelamon* which can
300 also be differentiated morphologically. These four species form a monophyletic group with
301 relatively high support values. Due to the lack of specimens of the other three species of
302 *Heterochelamon*, we were unable to obtain their molecular data for analysis and therefore unable
303 to determine the phylogenetic relationships of these species with the above four species.
304   Türkay & Dai (1997) established *Heterochelamon* with *Potamon (Geothelphusa)*
305 *pupureomanualis* Wu, 1934 as a type species. However, the real identity of the specimens
306 examined by Türkay & Dai (1997) is questionable, because their specimens are different from
307 the original description by Wu (1934) in the following particulars. Although we could not
308 examine type material or topotypic material from Luocheng Country, Guangxi Zhuang
309 Autonomous Region: the shape of the external orbital tooth is acutely triangular in Wu (1934)
310 versus triangular in Türkay & Dai (1997), the epibranchial tooth is very sharp in Wu (1934)
311 versus blunt in Türkay & Dai (1997), and the G1 terminal segment has a bent tip in Wu (1934)
312 versus straight terminal segment in Türkay & Dai (1997). These differences are also presented in
313 Table 1. Furthermore, the specimens examined by Türkay & Dai (1997) were said to be collected
314 from Xiushui County, Guangxi. The locality record seems to be incorrect, because Xiushui
315 County is in Jiangxi, not in Guangxi. Dai (1999) corrected the locality of *H.* cf.
316 *purpureomanualis* to Xiuren County, Guangxi, and we believe that this is correct locality for it.
317 We concur Naruse, Zhu & Zhou (2013) that the specimens referred to *H.* cf. *pupureomanualis* by
318 Türkay & Dai (1997) could actually represent an undescribed species.

319   With a few exceptions, most Chinese freshwater crab genera have restricted distributional
320 ranges. The geographical distribution pattern of many freshwater crabs is caused by geographical
321 isolation, which is due to the limited dispersal abilities of freshwater crabs and low fertility (Yeo
322 et al., 2008; Ji et al., 2016; Jia et al., 2018). The distribution pattern of freshwater crabs in
323 mainland China is closely related to the regional differentiation of China's natural geographical
324 environment. This genus was reported to be mainly distributed in northern Guangxi (Türkay &
325 Dai, 1997; Naruse, Zhu & Zhou, 2013). However, this paper describes a new species from
326 southern Guangdong, which is not in accord with our previous understanding of the distribution
327 of the genus, suggesting that the genus presents a wider distribution pattern than previously
328 thought. Although widened, the distribution of *Heterochelamon* is still within the Huanan
329 freshwater zoogeographical province, which mainly consists of Guangxi, Guangdong and Hainan
330 (Huang, Ebach & Ahyong, 2020). Within this zoogeographical province, there are relatively few
331 abiotic factors such has high mountains and rivers that may obstruct the dispersal of freshwater
332 crabs. We therefore speculate that there may be other new species of *Heterochelamon* in this
333 zoogeographical province that have not yet been discovered.
334

Conclusions

336 This study describes two new species of freshwater potamid crabs, referred to the genus
337 *Heterochelamon*. We obtained sequence data of the mitochondrial 16S rRNA gene from the two
338 new species and two other congeneric species for genetic analysis. The analysis supports the
339 recognition of the two new species and the monophyly of the genus. The known distribution of
340 this genus has been heretofore restricted to northern Guangxi, but our study now shows that the
341 genus also occurs in southern Guangdong.
342

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348 other two anonymous reviewers for greatly improving our manuscript.
349

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Figure 1

Heterochelamon huidongense n. sp. Holotype male (25.8 × 23.1 mm) (NCU MCP 423601).

(A) overall habitus; (B) frontal view of the cephalothorax. Scales = 1 cm. Photo credit: Song-Bo Wang.
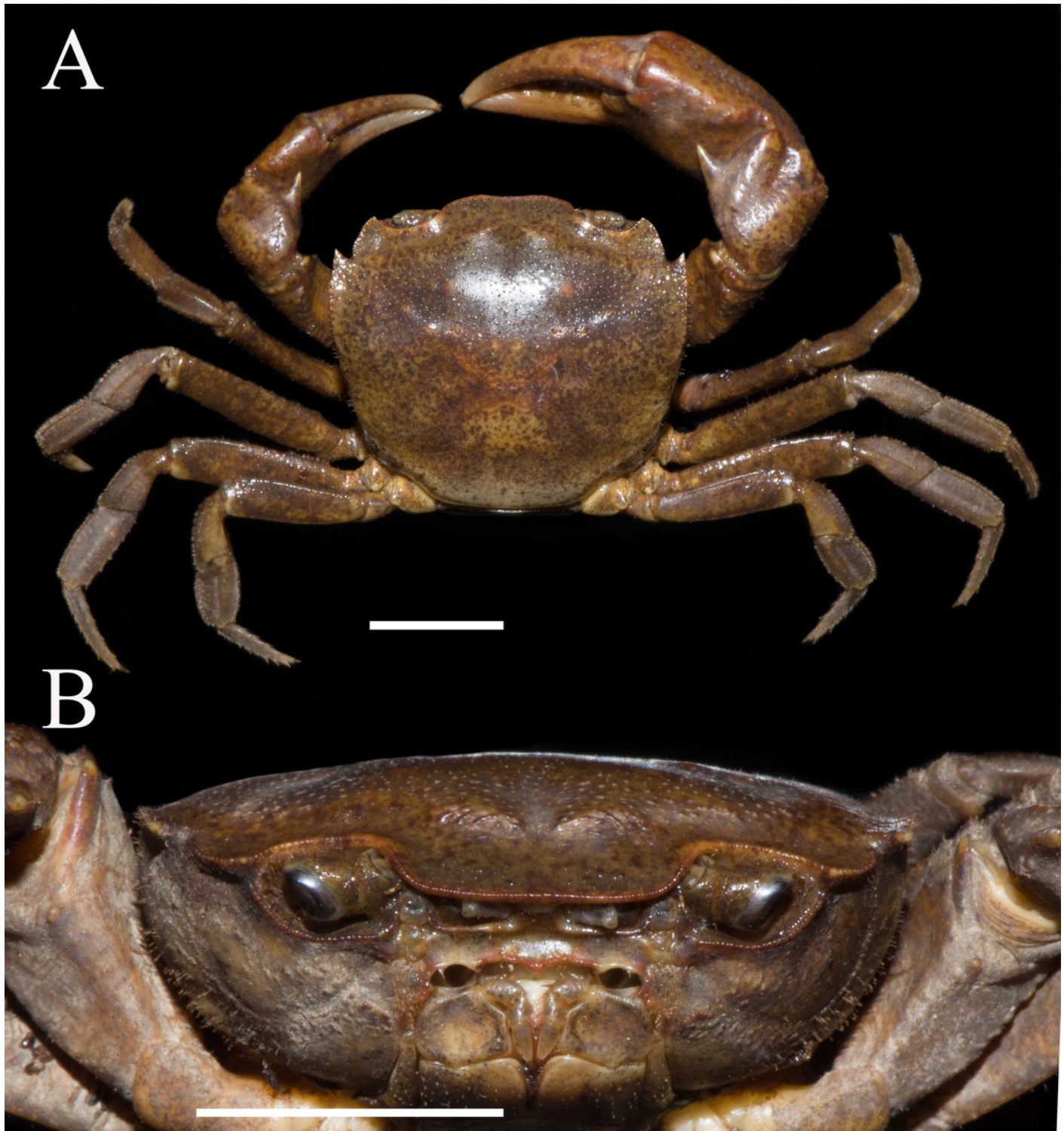
Figure 2

Heterochelamon huidongense n. sp. Holotype male (25.8 × 23.1 mm) (NCU MCP 423601).

(A) outer view of larger cheliped; (B) left third maxilliped; (C) ventral view of anterior thoracic sternum; (D) ventral view of pleon; (E) ventral view of sterno-pleonal cavity with right G1 *in situ*; (F) right fourth ambulatory leg . Scales = 0.5 cm. Photo credit: Song-Bo Wang.
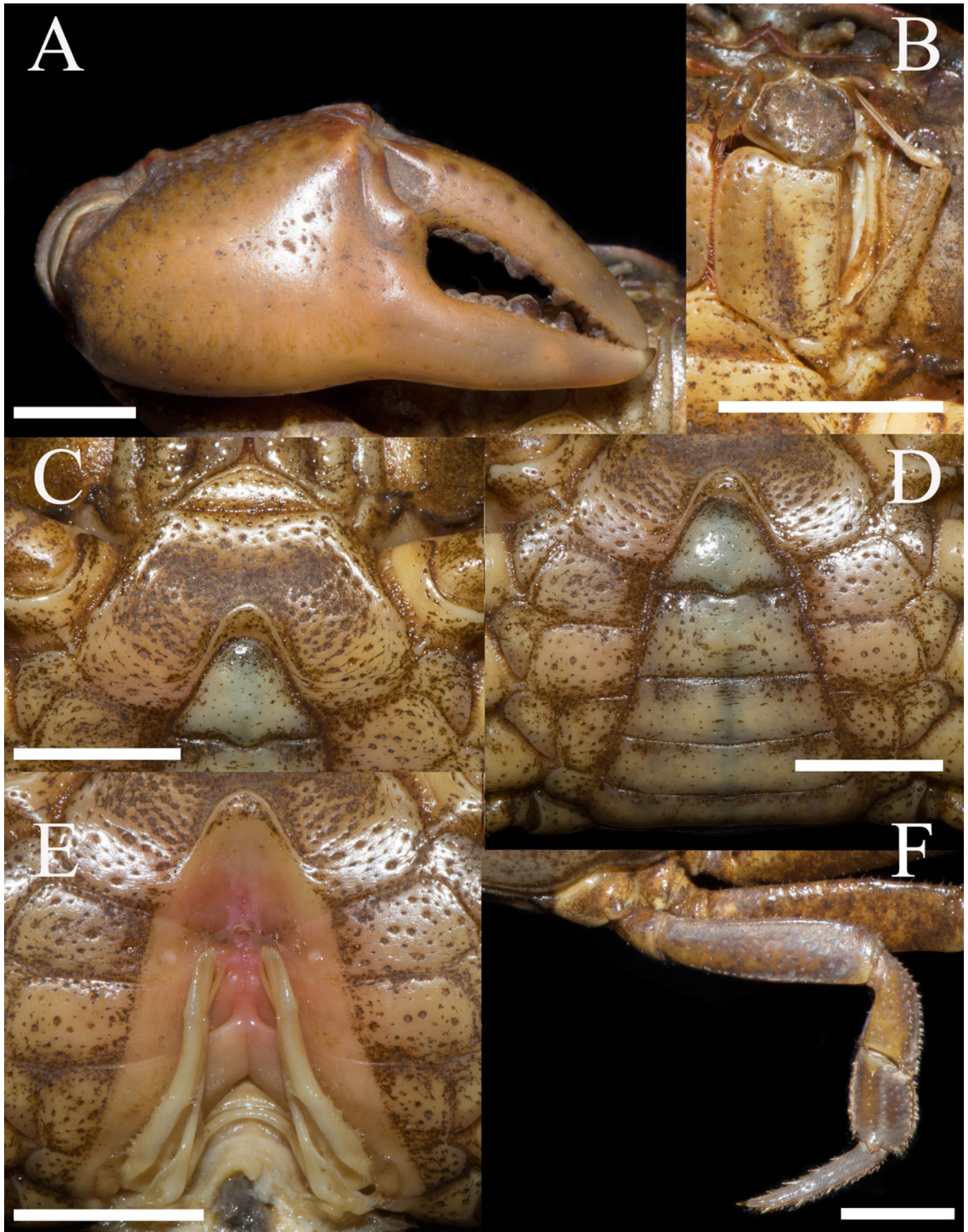
Figure 3

Heterochelamon huidongense n. sp. Paratype female (26.1 × 23.5 mm) (NCU MCP 423603).

(A) overall habitus; (B) ventral view of pleon; (C) vulvae. Scales = 1 cm. Photo credit: Song-Bo Wang.
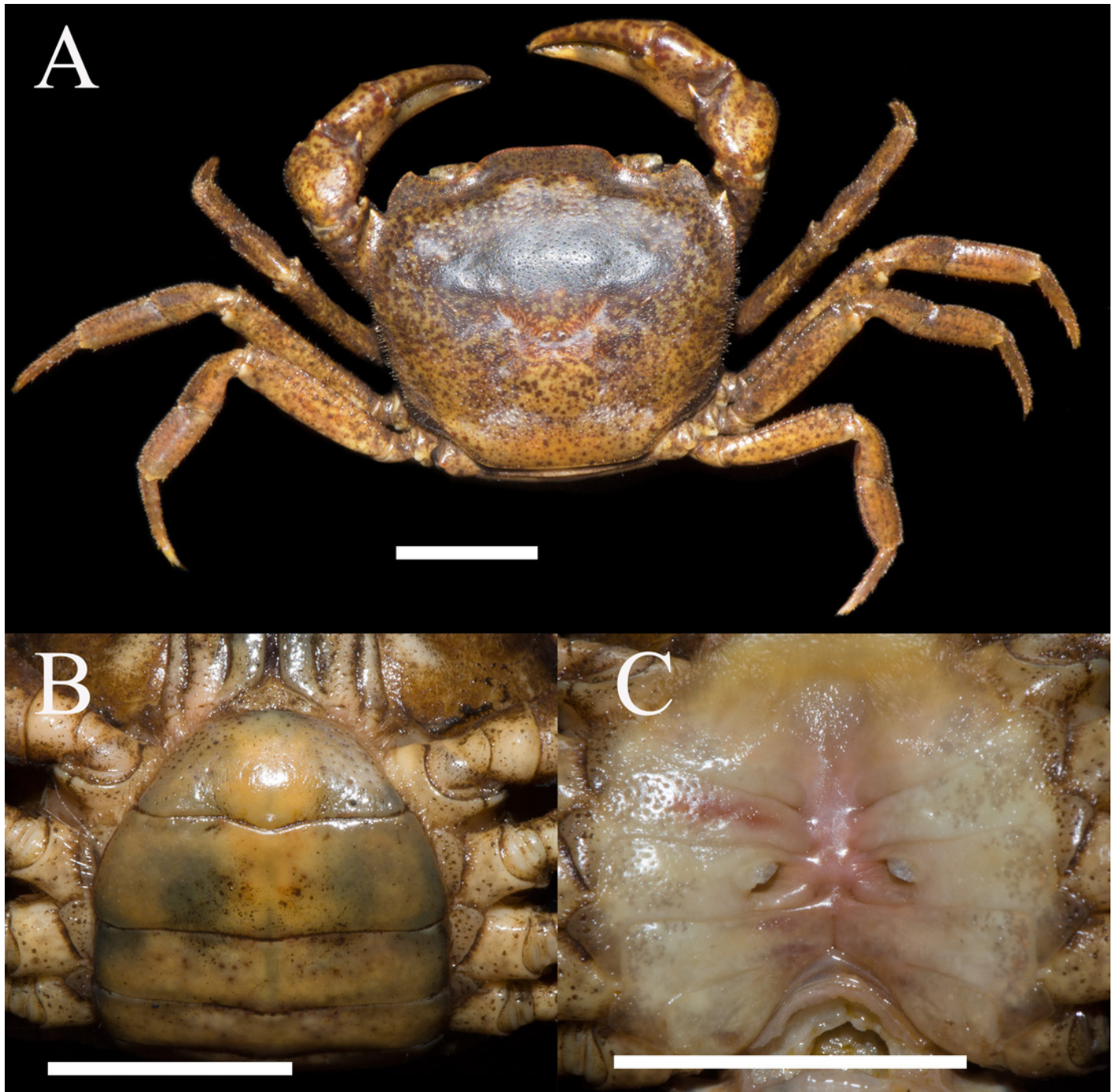
Figure 4

Gonopods of holotype of *Heterochelamon huidongense* n. sp.

(A) ventral view of the left G1; (B) ventral view of the terminal segment of left G1; (C) dorsal view of the left G1; (D) dorsal view of the terminal segment of left G1; (E) ventral view of the left G2. Scales = 1 mm. Photo credit: Song-Bo Wang.
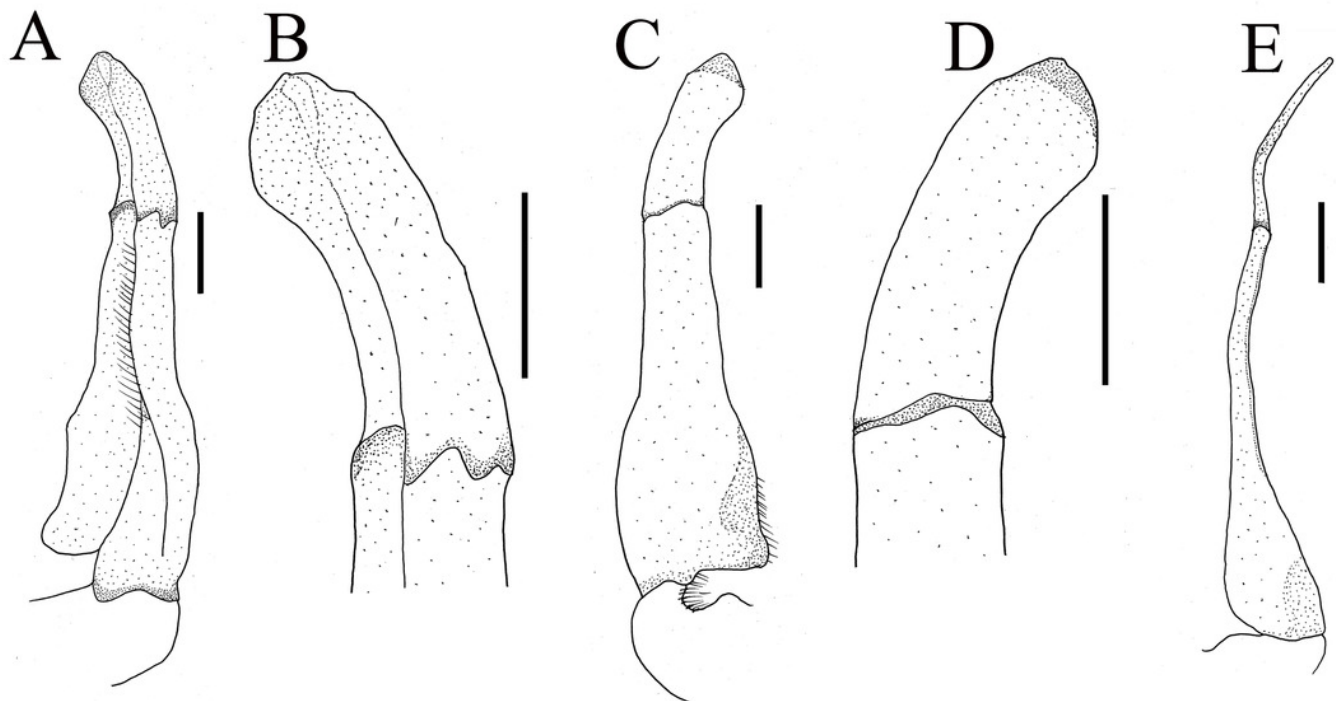
Figure 5

Habitat Environment of *Heterochelamon huidongense* n. sp.

(A) Surrounding environment of the collection point; (B) living specimen of *H. huidongense* n. sp. collected with a fish cage; (C) *H. huidongense* n. sp. in the water; (D) living specimen of *Somanniathelphusa* Bott, 1968, collected with a fish cage; (E) collection point. Photo credit: A, B, D, E from Song-Bo Wang and C from Chao Huang.
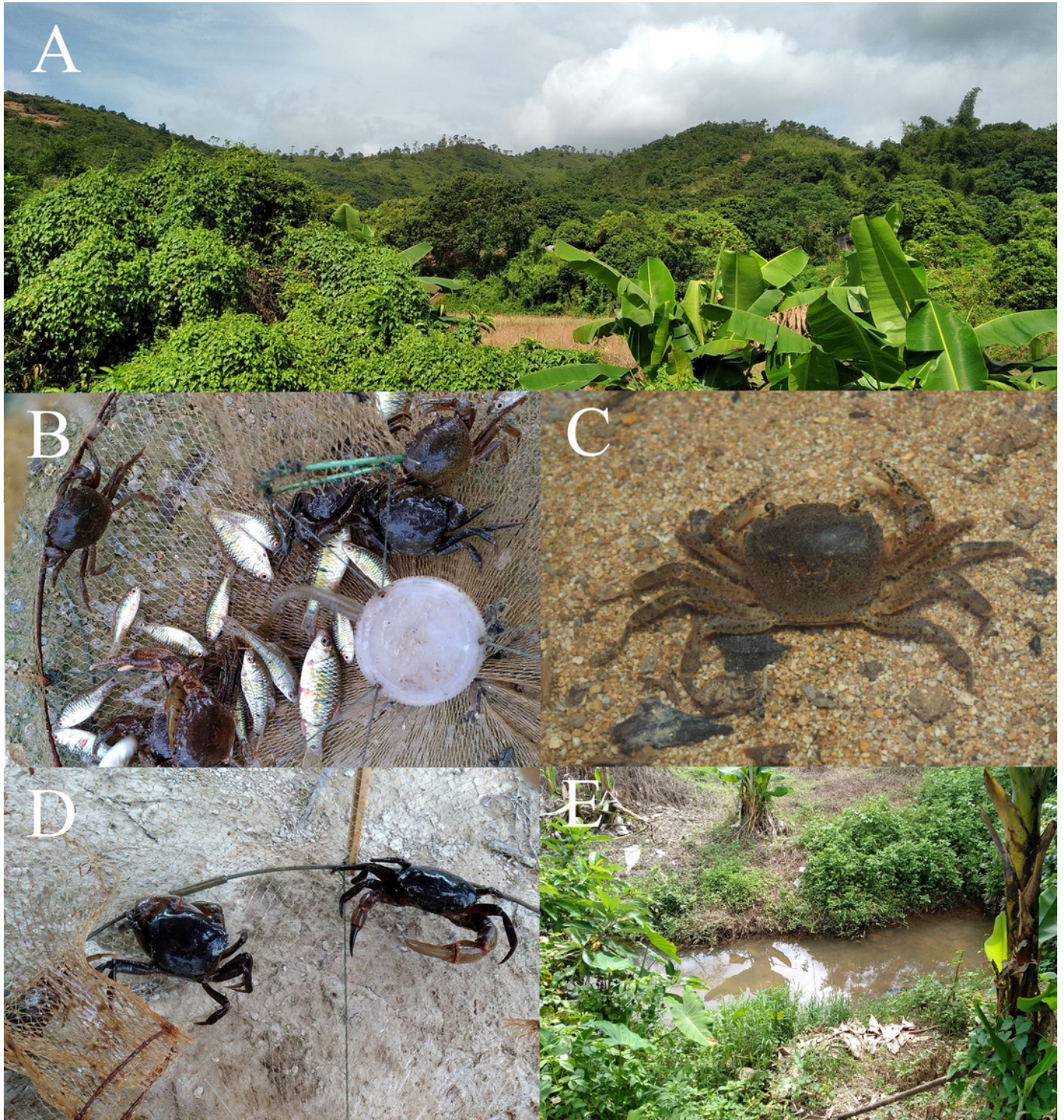
Figure 6

Heterochelamon jinxiuense n. sp. Holotype male (24.6 × 19.8 mm) (NCU MCP 342001).

(A) overall habitus; (B) frontal view of the cephalothorax. Scales = 1 cm. Photo credit: Song-Bo Wang.

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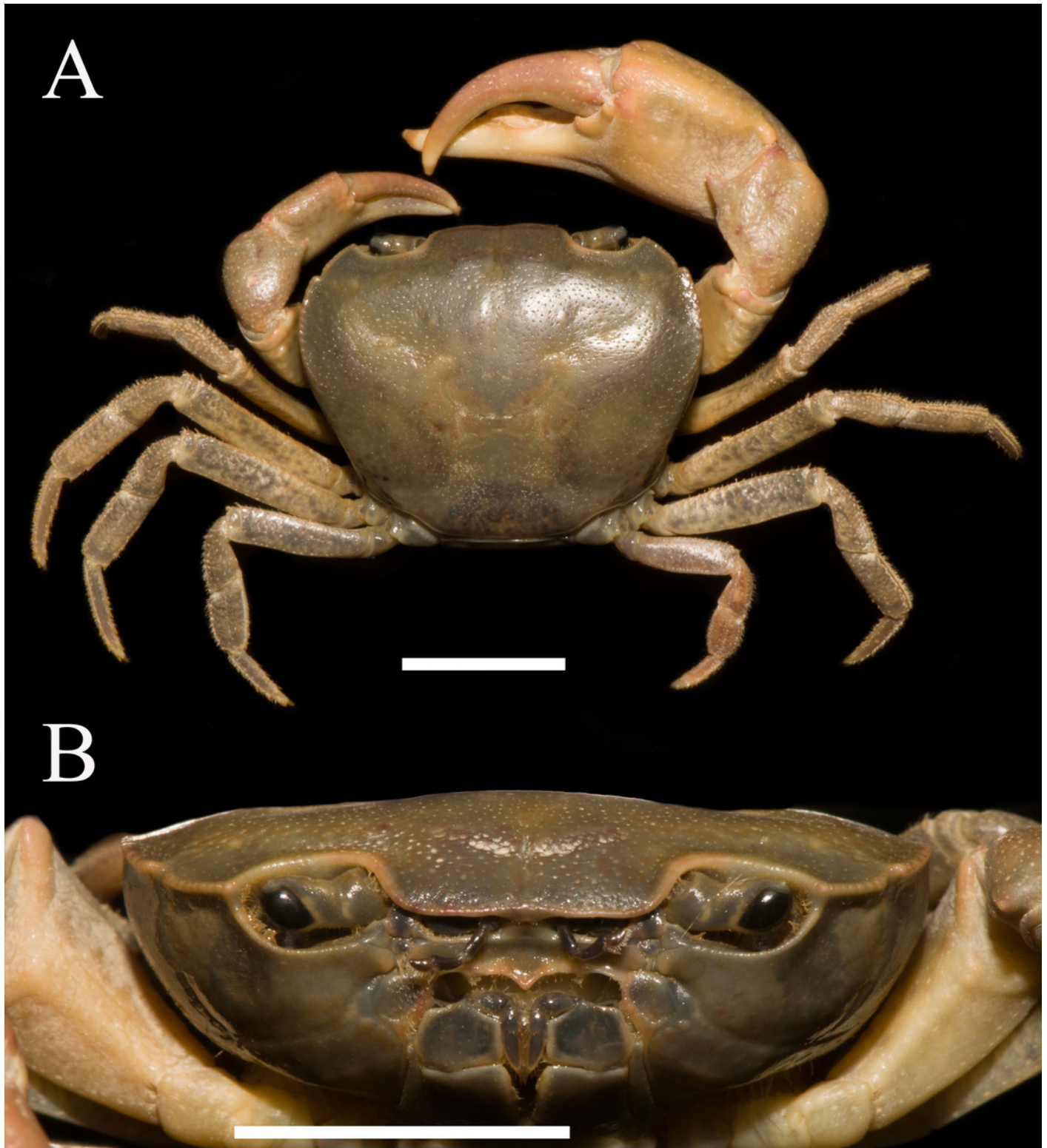


Figure 7

Heterochelamon jinxiuense n. sp. Holotype male (24.6 × 19.8 mm) (NCU MCP 342001).

(A) outer view of larger cheliped; (B) left third maxilliped; (C) ventral view of anterior thoracic sternum; (D) ventral view of pleon; (E) ventral view of sterno-pleonal cavity with right G1 *in situ*; (F) right fourth ambulatory leg. Scales = 0.5 cm. Photo credit: Song-Bo Wang.

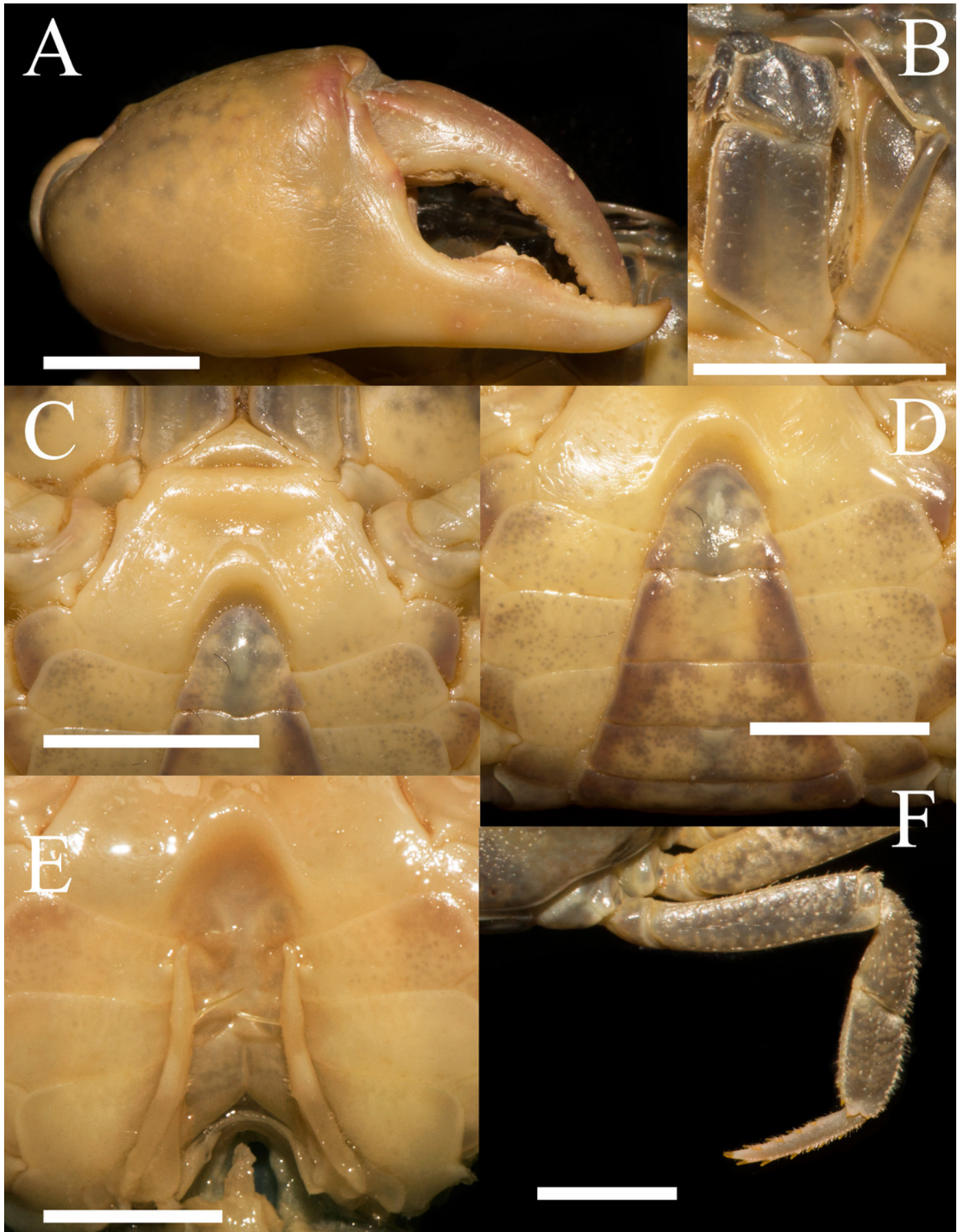



Figure 8

Heterochelamon jinxiuense n. sp. Paratype female (12.9 × 10.4 mm) (NCU MCP 342003).

(A) overall habitus; (B) ventral view of vulvae. Scales = 1 cm. Photo credit: Song-Bo Wang.

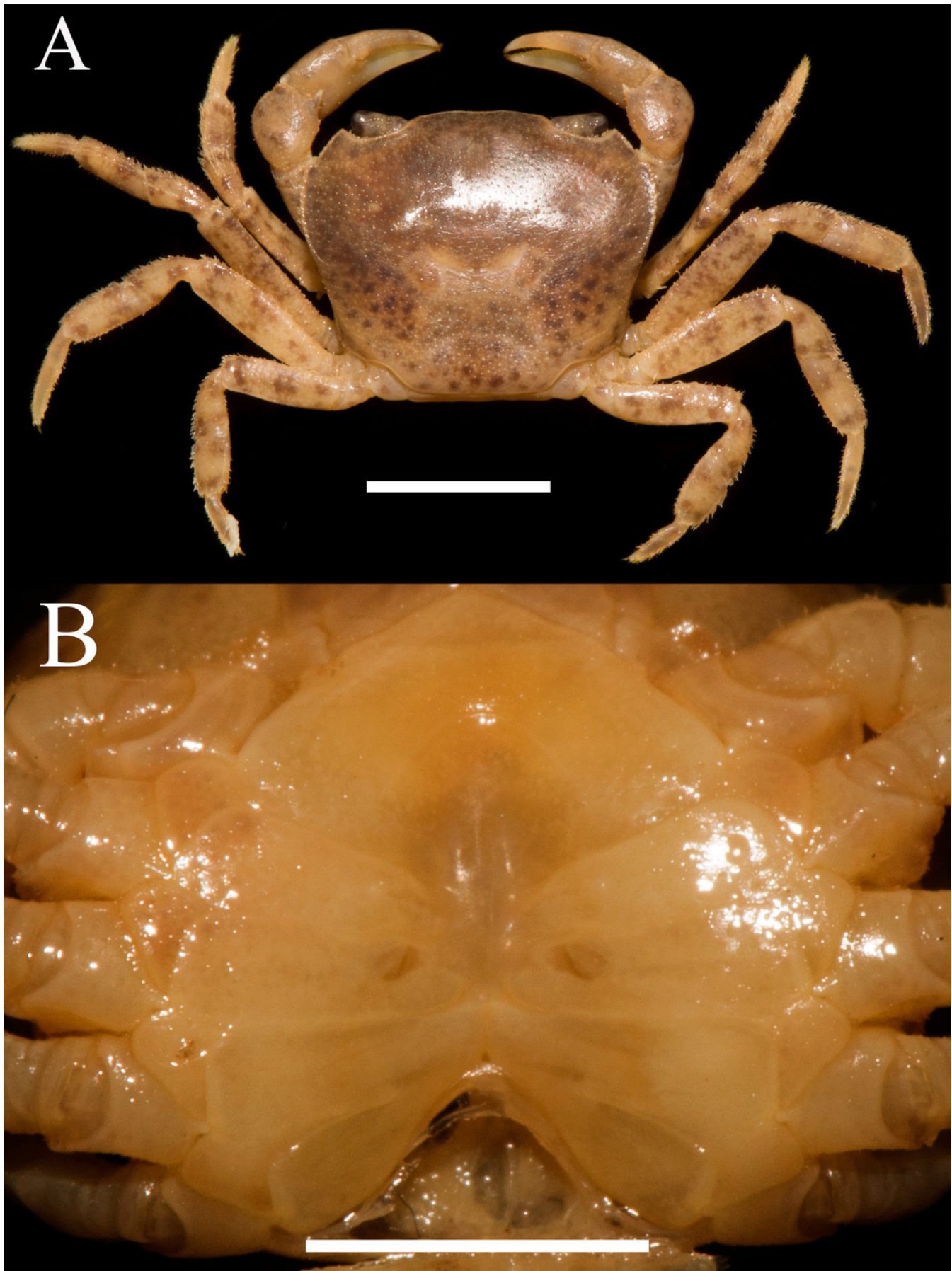



Figure 9

The first gonopods of holotype of *Heterochelamon jinxiuense* n. sp.

(A) ventral view of the right G1; (B) ventral view of the terminal segment of right G1; (C) dorsal view of the right G1; (D) dorsal view of the terminal segment of right G1; (E) side view of the right G1. Scales = 1 mm. Photo credit: Song-Bo Wang.

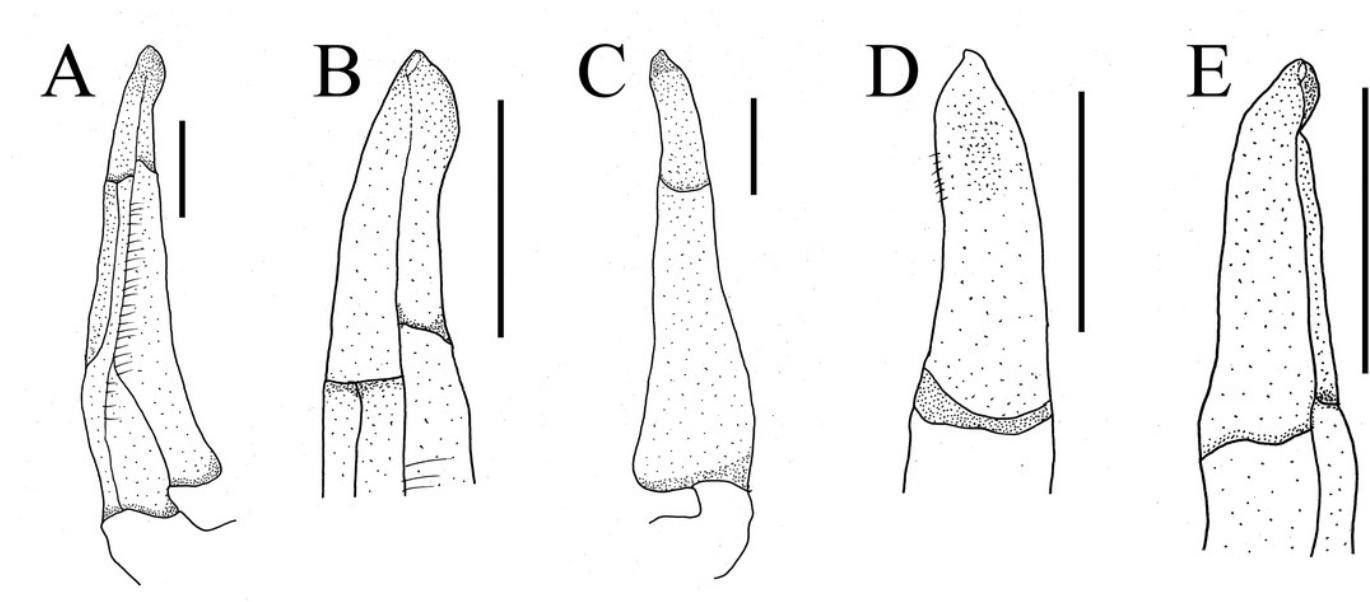
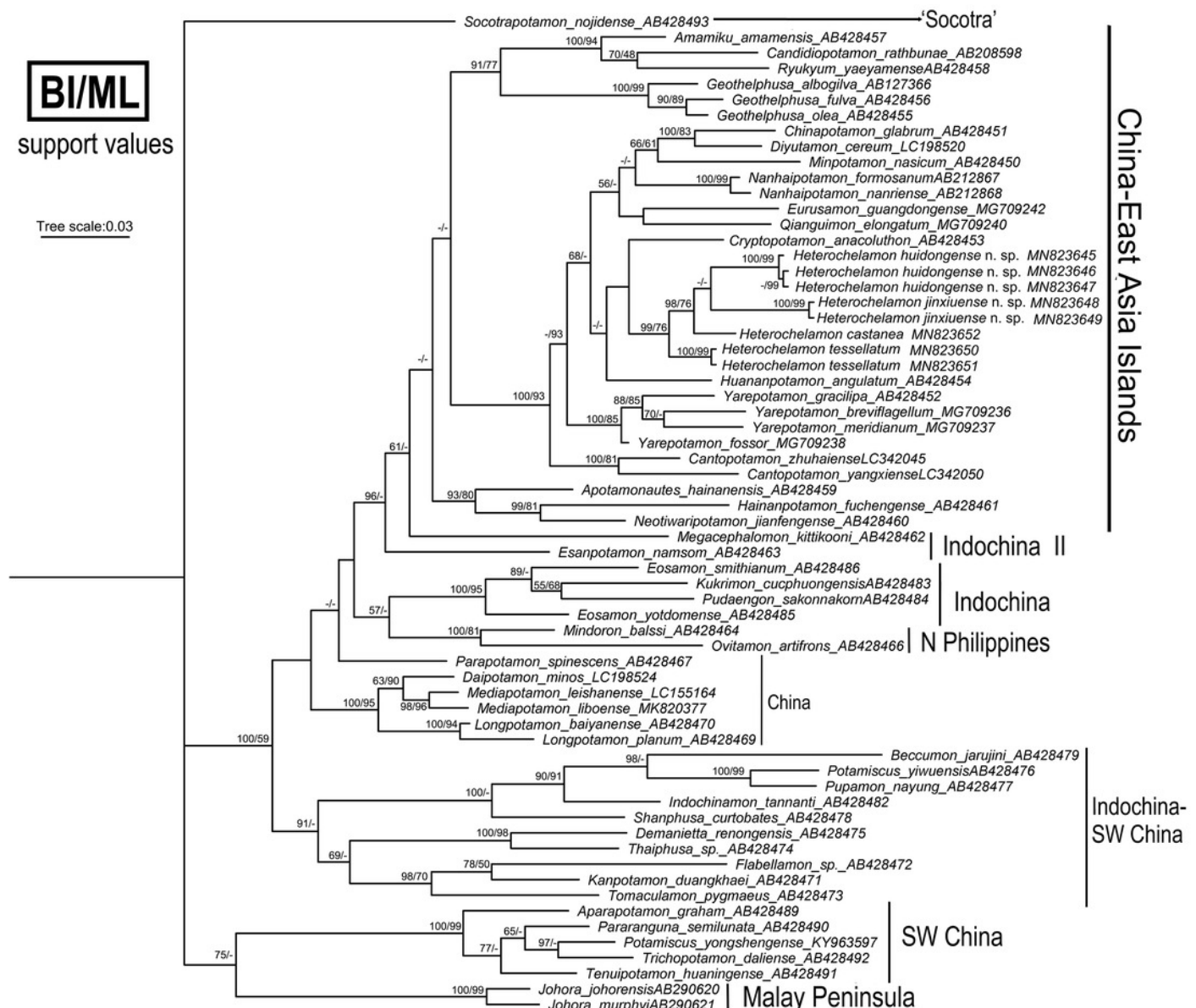



Figure 10

Phylogenetic tree.

Reconstructed base on the 16S rRNA genes of *Heterochelamon* and some species of Asian potamids sampled for comparison. Branch lengths and topologies were obtained from BI analysis. Probability values at the nodes represent support values for BI and ML. Only values > 50% are shown. Photo credit: Song-Bo Wang.

Differences between the species of *Heterochelamon* Türkay & Dai, 1997.

	H. huidongense	*H. jinxiuense*	*H. tessellatum*	*H. castanea*	*H. purpureomanualis*[1]	*H. cf. purpureomanualis*[2]	*H. guangxiense*	*H. yangshuoense*
External orbital angle	Triangular (Fig. 1A)	Blunt (Fig. 6A)	Acutely triangular (cf. Naruse, Zhu & Zhou, 2013: Fig. 1A)	Triangular (cf. Naruse, Zhu & Zhou, 2013: Fig. 4A)	Acutely triangular (cf. Wu, 1934: Fig. 2)	Triangular (cf. Türkay & Dai, 1997)	Blunt (cf. Türkay & Dai, 1997)	Triangular (cf. Türkay & Dai, 1997)
Epibranchial tooth	Very sharp, separated from external orbital angle by broad notch (Fig. 1A)	Blunt, separated from external orbital angle by narrow notch (Fig. 6A)	Very sharp, separated from external orbital angle by broad notch (cf. Naruse, Zhu & Zhou, 2013: Fig. 1A)	Very sharp, separated from external orbital angle by narrow notch (cf. Naruse, Zhu & Zhou, 2013: Fig. 4A)	Very sharp, separated from external orbital angle by narrow notch (cf. Wu, 1934: Fig. 2)	Blunt, separated from external orbital angle by narrow notch (cf. Türkay & Dai, 1997)	Very sharp, separated from external orbital angle by broad notch (cf. Türkay & Dai, 1997)	Very sharp, separated from external orbital angle by broad notch (cf. Türkay & Dai, 1997)
Adult male chelipeds	Unequal (Fig. 1A)	Strongly unequal (Fig. 6A)	Strongly unequal (cf. Naruse, Zhu & Zhou, 2013: Fig. 1A)	Unequal (cf. Naruse, Zhu & Zhou, 2013: Fig. 4A)	Strongly unequal (cf. Wu, 1934: Fig. 2)	Strongly unequal (cf. Türkay & Dai, 1997)	Unequal (cf. Türkay & Dai, 1997)	Strongly unequal (cf. Türkay & Dai, 1997)
Gap of adult male major chela fingers when closed	Narrow, wedge-shaped (Fig. 2A)	Medium, teardrop-shaped (Fig. 7A)	Very broad, oblong (cf. Naruse, Zhu & Zhou, 2013: Fig. 2B)	Narrow, wedge-shaped (cf. Naruse, Zhu & Zhou, 2013: Fig. 5B)	Very broad, oblong (cf. Wu, 1934: Fig. 2)	Very broad, oblong (cf. Türkay & Dai, 1997)	Narrow, wedge-shaped (cf. Türkay & Dai, 1997)	Very broad, oblong (cf. Türkay & Dai, 1997: fig. 6-2)

G1 *in situ*	Not reaching sternites 4/5 suture (Fig. 2E)	Reaching sternites 4/5 suture (Fig. 8E)	Not reaching sternites 4/5 suture (cf. Naruse, Zhu & Zhou, 2013: Fig. 2A)	Reaching sternites 4/5 suture (cf. Naruse, Zhu & Zhou, 2013)	No information	Reaching sternites 4/5 suture (cf. Türkay & Dai, 1997: fig. 4-3)	Reaching sternites 4/5 suture (cf. Türkay & Dai, 1997: fig. 5-3)	Reaching sternites 4/5 suture (cf. Türkay & Dai, 1997: fig. 6-4)
Terminal segment of G1	Flat, bent in middle, not tapered distally, distal part rounded (Fig. 4)	Rod-like, straight, tapered distally, distal part sharp, bent slightly at distal (Fig. 9)	Knuckle-shaped, strongly bent proximally, widening distally, widest part more than twice as wide as base (cf. Naruse, Zhu & Zhou, 2013: Fig. 3A)	Rod-like, straight, not tapered distally, distal part rounded and bent slightly (cf. Naruse, Zhu & Zhou, 2013: Fig. 6A)	No information	Rod-like, straight, not tapered distally, distal part protruding slightly in inner edge (cf. Türkay & Dai, 1997: fig. 4-4)	Rod-like, slightly bent, not tapered distally, distal part protruding in inner edge (cf. Türkay & Dai, 1997: fig. 5-4)	Knuckle-shaped, straight, widening distally, widest part more than twice as wide as base (cf. Türkay & Dai, 1997: fig. 6-5)

1 [1]Recorded by Wu, 1934 from Luocheng County, Guangxi Zhuang Autonomous Region, China.

2 [2]Recorded by Türkay & Dai, 1997 cf. Wu, 1934 from Xiuren County, Guangxi Zhuang Autonomous Region, China.

GenBank accession number of the species used for phylogenetic analysis.

The 16S rRNA gene of 60 species belonging to 47 genera of the family Potamidae.

Species	Museum Catalogue No.	Locality	GenBank No.
Heterochelamon huidongense n. sp.	NCU MCP 423604	Guangdong, China	MN823645
Heterochelamon huidongense n. sp.	NCU MCP 423605	Guangdong, China	MN823646
Heterochelamon huidongense n. sp.	NCU MCP 423606	Guangdong, China	MN823647
Heterochelamon jinxiuense n. sp.	NCU MCP 342004	Guangdong, China	MN823648
Heterochelamon jinxiuense n. sp.	NCU MCP 342005	Guangdong, China	MN823649
Heterochelamon tessellatum Naruse, Zhu & Zhou, 2013	NCU MCP 153601	Guangxi, China	MN823650
Heterochelamon tessellatum Naruse, Zhu & Zhou, 2013	NCU MCP 153602	Guangxi, China	MN823651
Heterochelamon castanea Naruse, Zhu & Zhou, 2013	NCU MCP 341901	Guangxi, China	MN823652
Amamiku amamense (Minei, 1973)	NCHUZOOL 13125	Amami, the Ryukyus	AB428457
Aparapotamon grahami (Rathbun, 1929)	ZRC YCM 0334(II)	Yunnan, China	AB428489
Apotamonautes hainanensis (Parisi, 1916)	ZRC	Hainan, China	AB428459
Beccumon jarujini (Ng & Naiyanetr, 1993)	ZRC 1991.1865 (paratype)	Chiangma, Thailand	AB428479
Candidiopotamon rathbunae (De Man, 1914)	NCHUZOOL	Nantou, Taiwan	AB208598
Cantopotamon yangxiense Chao, Ahyong & Shih, 2017	SYSBM 001564	Guangdong, China	LC342050
Cantopotamon zhuhaiense Chao, Ahyong & Shih, 2017	SYSBM 001439	Guangdong, China	LC342045
Chinapotamon glabrum (Dai, Song, Li & Liang, 1980)	CAS CB	Guangxi, China	AB428451
Cryptopotamon anacoluthon (Kemp, 1918)	NCHUZOOL 13122	Hong Kong	AB428453
Daipotamon minos Ng & Trontelj	ZRC 1996.1045	Guizhou, China	LC198524
Demanietta renongensis (Rathbun, 1905)	ZRC 1998.146	Ranong, Thailand	AB428475
Diyutamon cereum Huang, Shih & Ng	SYSBM	Guizhou, China	LC198520
Eosamon smithianum (Kemp, 1923)	ZRC	Chantaburi, Thailand	AB428486
Eosamon yotdomense (Naiyanetr, 1984)	ZRC 1991.1851	Ubon Ratchathani, Thailand	AB428485
Esanpotamon namsom Naiyanetr & Ng, 1997	ZRC 1997.776 (paratype)	Udon Thani, Thailand	AB428463
Eurusanm guangdongense Huang, 2018	SYSBM 001408	Guangxi, China	MG709242
Flabellamon sp.	ZRC	Mae Sot, Thailand	AB428472
Geothelphusa albogilva Shy, Ng & Yu, 1994	NCHUZOOL	Pingtung, Taiwan	AB127366
Geothelphusa marginata fulva Naruse, Shokita & Shy, 2004	NCHUZOOL 13124	Iriomote, the Ryukyus	AB428456
Geothelphusa olea Shy, Ng & Yu, 1994	NCHUZOOL 13123	Taichung, Taiwan	AB428455
Hainanpotamon fuchengense Dai, 1995	NCHUZOOL 13128	Hainan, China	AB428461
Huananpotamon angulatum (Dai & Lin, 1979)	ZRC	Fujian, China	AB428454
Indochinamon tannanti (Rathbun, 1904)	ZRC 1998.264	Yunnan, China	AB428482
Johora johorensis (Roux, 1936)	ZRC 1990.576	Gunung Pulai,	AB290620

		Johor, Malaysia	
Johora murphyi Ng, 1986	ZRC 2001.2267	Kota Tinggi, Johor, Malaysia	AB290621
Kanpotamon duangkhaei Ng & Naiyanetr, 1993	ZRC	Kanchanaburi, Thailand	AB428471
Kukrimon cucphuongense (Dang, 1975)	ZRC NHH9729 160997	Ninh Binh, Vietnam	AB428483
Longpotamon baiyanense Ng & Dai, 1997	ZRC	Hunan, China	AB428470
Longpotamon planum Dai, 1992	ZRC 1998.1178	Anhui, China	AB428469
Mediapotamon leishanense Dai, 1995	SYSBM 001094	Guizhou, China	LC155164
Mediapotamon liboense Wang, Zhou & Zou, 2019	NCU MCP 343004	Guizhou, China	MK820377
Megacephalomon kittikooni (Yeo & Naiyanetr, 1999)	ZRC 1998.22 (holotype)	Xieng Khuang, Laos	AB428462
Mindoron balssi (Bott, 1968)	ZRC	Mindoro, the Philippines	AB428464
Minpotamon nasicum (Dai & Chen, 1979)	NCHUZOOL 13121	Fujian, China	AB428450
Nanhaipotamon formosensis (Parisi, 1916)	NCHUZOOL 13144	Tainan, Taiwan	AB212867
Nanhaipotamon nanriense Dai, 1997	CAS CB05103	Fujian, China	AB212868
Neotiwaripotamon jianfengense Dai & Naiyanetr, 1994	NCHUZOOL 13127	Hainan, China	AB428460
Ovitamon artifrons (Bürger, 1894)	ZRC	Luzon, the Philippines	AB428466
Parapotamon spinescens (Calman, 1905)	NCU MCP	Yunnan, China	AB428467
Pararanguna semilunatum Dai & Chen, 1985	ZRC	Yunnan, China	AB428490
Potamiscus yiwuensis Dai & Cai, 1998	ZRC	Yunnan, China	AB428476
Potamiscus yongshengense Dai & Chen, 1985	NNU150951	Yunnan, China	KY963597
Pudaengon sakonnakorn Ng & Naiyanetr, 1995	ZRC	Thailand	AB428484
Pupamon nayung (Naiyanetr, 1993)	ZRC 1995.558 (paratype)	Udon Thani, Thailand	AB428477
Qianguimon elongatum Huang, 2018	SYSBM 001424	Guangdong, China	MG709240
Ryukyum yaeyamense (Minei, 1973)	NCHUZOOL 13126	Iriomote, the Ryukyus	AB428458
Shanphusa curtobates (Kemp, 1918)	NRM 13920	Taunggyi, Shan State, Myanmar	AB428478
Socotrapotamon nojidensis Apel & Brandis, 2000	ZRC 2000.2232	Socotra, Yemen	AB428493
Tenuipotamon huaningense Dai & Bo, 1994	CAS CB05175	Yunnan, China	AB428491
Thaiphusa sp.	ZRC 1997.656	Thailand	AB428474
Tomaculamon pygmaeus Yeo & Ng, 1997	ZRC 1997.326-330 (paratype)	Phitsanulok, Thailand	AB428473
Trichopotamon daliense Dai & Chen, 1985	NCHUZOOL 13130	Yunnan, China	AB428492
Yarepotamon breviflagellum Huang, 2018	SYSBM 001442	Guangdong, China	MG709236
Yarepotamon fossor Huang, 2018	SYSBM 001417	Guangxi, China	MG709238

| *Yarepotamon gracilipa* (Dai, Song, Li & Liang, 1980) | ZRC | Guangxi, China | AB428452 |
| *Yarepotamon meridianum* Huang, 2018 | SYSBM 001581 | Guangdong, China | MG709237 |

1 CAS CB, Chinese Academy of Sciences, Beijing, China; NCHUZOOL, Zoological Collections
2 of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan; NCU
3 MCP, Department of Parasitology of the Medical College of Nanchang University, Jiangxi,
4 China; NNU, College of Life Sciences, Nanjing Normal University, Nanjing, China; NRM,
5 Swedish Museum of Natural History, Stockholm, Sweden; SYSBM, Sun Yat-sen Museum of
6 Biology, Sun Yat-Sen University, Guangzhou, China; ZRC, Zoological Reference Collection of
7 the Raffles Museum of Biodiversity Research, National University of Singapore, Singapore.