

Molecular evidence and differences in gonopod morphology lead to the recognition of a new species of the freshwater crab genus *Candidiopotamon* Bott, 1967 (Crustacea, Brachyura, Potamidae) from eastern Taiwan

Hsi-Te Shih¹, Tohru Naruse², Christoph D. Schubart^{3†}

¹ Department of Life Science and Global Change Biology Research Center, National Chung Hsing University, 250, Kuo Kuang Road, Taichung 402, Taiwan

² Tropical Biosphere Research Center, Iriomote Station, University of the Ryukyus, 870 Uehara, Taketomi, Okinawa 907-1541, Japan

³ Zoology & Evolution, University of Regensburg, 93040 Regensburg, Germany

Corresponding author: Hsi-Te Shih (htshih@dragon.nchu.edu.tw)



Academic editor: Sameer Pati

Received: 21 May 2023

Accepted: 19 August 2023

Published: 11 September 2023

ZooBank: <https://zoobank.org/D5B5FB43-D492-45CD-B571-017D1014ED6F>

Citation: Shih H-T, Naruse T, Schubart CD (2023) Molecular evidence and differences in gonopod morphology lead to the recognition of a new species of the freshwater crab genus *Candidiopotamon* Bott, 1967 (Crustacea, Brachyura, Potamidae) from eastern Taiwan. ZooKeys 1179: 169–196. <https://doi.org/10.3897/zookeys.1179.106718>

Copyright: © Hsi-Te Shih et al.
This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International – CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).

Abstract

A new freshwater crab of the potamid genus *Candidiopotamon* Bott, 1967, is described from eastern Taiwan. *Candidiopotamon penglai* sp. nov. is morphologically similar to *C. rathbuni* (De Man, 1914) from western Taiwan, but can be distinguished by the morphology of the male first gonopod (G1), as well as by their mitochondrial DNA (16S rRNA and COI genes). In the G1 of *C. rathbuni*, the subterminal segment shows a cline from robust in northern populations to slender in southern populations. In the G1 of *C. penglai* sp. nov., a distinctly larger and more distally directed keel-like projection is found on the distal inner edge of the terminal segment, with northern populations having an inward-curving subterminal segment and southern populations a straight subterminal segment. The genetic differentiation of the two species of *Candidiopotamon* within Taiwan is discussed, and morphological differences are compared. A key to the species of *Candidiopotamon* is also provided.

Key words: 16S rDNA, *Candidiopotamon penglai*, *Candidiopotamon rathbuni*, cytochrome oxidase subunit I, Decapoda, morphology, new species, taxonomy

Introduction

Taiwanese freshwater systems are populated by three genera of potamid freshwater crabs, viz., *Candidiopotamon* Bott, 1967, *Geothelphusa* Stimpson, 1858, and *Nanhaipotamon* Bott, 1968, with the former two often occurring in sympatry. Recent molecular studies suggested that the colonization of *Candidiopotamon* and *Geothelphusa* to Taiwan took place shortly after Taiwan was geologically shaped as an island, ca 5–6 mya (Shih et al. 2006, 2011). Subsequent geological uplifts of mountain chains have resulted in parallel separation processes in both genera of crabs, with similar time estimates based on mitochondrial DNA (Shih et al. 2004, 2006, 2007, 2011).

[†] Deceased.

Despite sharing the same evolutionary history and the same habitat, the taxonomic situation of these two genera is quite different. In the case of *Geothelphusa*, nearly 40 species have been described from Taiwan, many of them recently (Shih and Ng 2011; Shy et al. 2014, 2020, 2021), and new species descriptions are still underway (cf. Shy et al. 2020), although a few of them have been synonymized (Shih and Shy 2009; Shih and Ng 2011; Shy et al. 2020, 2021) or at least suggested to be conspecific (Shih et al. 2023). In contrast, *Candidiopotamon* has only one described species in Taiwan, i.e., *Candidiopotamon rathbuni* (De Man, 1914), occurring throughout the island. Shih et al. (2006), however, showed that *C. rathbuni* in Taiwan is not homogeneous and consists of several (5 or 6) evolutionary significant units (ESU sensu Ryder 1986; Waples 1991; Chu et al. 2015) that can be identified genetically, appear to be reproductively isolated, geographically defined, and whose evolution can be explained by tectonic events that date back hundreds of thousands to several million years.

In the present study, we describe a new pseudocryptic species, *C. penglai* sp. nov., for the eastern populations of Taiwanese *Candidiopotamon*. We also conduct detailed morphological examinations, and molecular analyses using 16S rDNA and cytochrome oxidase subunit I (COI), with additional samples of Taiwanese representatives of *Candidiopotamon*, to test whether external characters related to reproduction correspond to genetic differences. The two Taiwanese species of *Candidiopotamon* are also compared with three congeners from the Ryukyu Islands in Japan, viz., *C. kumejimense* Minei, 1973, *C. okinawense* Minei, 1973, and *C. tokashikense* Naruse, Segawa & Aotsuka, 2007.

Materials and methods

Taxon sampling and morphological characters

Specimens of the Taiwanese *Candidiopotamon* species were collected from mountain streams and coastal plains (Fig. 1, Table 1) and were preserved in 75–95% ethanol. Specimens of the following congeners were used as comparative material: *Candidiopotamon kumejimense* Minei, 1973: 1 male, 32.6 × 36.5 mm, RUMF-ZC-2596, Gima River, Kumejima Island, Ryukyu Islands, Japan, coll. Y. Fujita, 6 Aug. 2010. *Candidiopotamon okinawense* Minei, 1973: 1 male, 37.6 × 41.6 mm, RUMF-ZC-547, Mt. Nishime, Okinawa Island, Ryukyu Islands, Japan, coll. N. Kawauchi, 20 Jun. 1999. *Candidiopotamon tokashikense* Naruse, Segawa & Aotsuka, 2007: 1 male, 36.4 × 41.7 mm, RUMF-ZC-220, stream on southeastern side of mountain located between Tokashiki and Tokashiku, Tokashiki Island, Ryukyu Islands, Japan, coll. Ryoko D. Segawa and T. Aotsuka, 15 Apr. 1997.

We used the following abbreviations for morphological description: **CW**, carapace width; **CL**, carapace length; **G1**, male first gonopod; and **G2**, male second gonopod. The terminology follows Ng (1988), Dai (1999), Naruse et al. (2007), and Davie et al. (2015). Characters of G1 and G2 were measured using an eyepiece micrometer and a stereomicroscope (Nikon SMZ-10). To reduce the effect of allometric growth on measurements, only adult specimens were used for ratio characters. In the present study, minimum adult sizes were defined by estimating the inflection point of the major chela's height for males; and by searching for the smallest individual whose pleonal 5th somite width was equal to or wider than the 3rd somite width for females. As a result, puberty sizes were

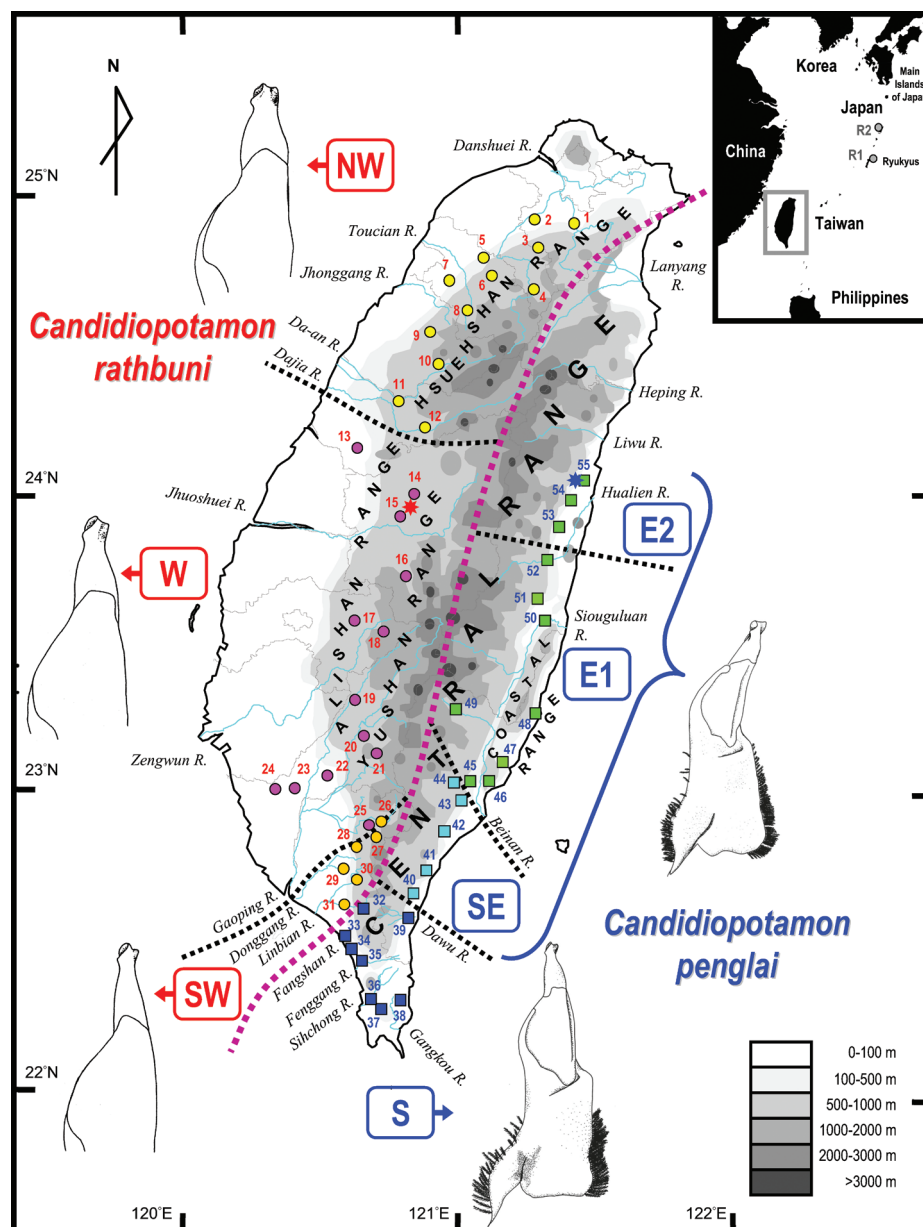


Figure 1. Collection sites for *Candidiopotamon rathbuni* (De Man, 1914) (circles) and *Candidiopotamon penglai* sp. nov. (squares) in Taiwan, as well as other congeners from the Ryukyus, Japan. Different colors indicate sampling sites of clades. Dotted lines indicate the possible biogeographic boundaries between clades NW, W, SW, S, SE, E1, and E2, corresponding to the color in Fig. 2; as well as species. The red star and blue star indicate the type localities of *C. rathbuni* and *C. penglai* sp. nov., respectively. Three forms of male left G1 are shown for clades in *C. rathbuni* and two forms for clades in *C. penglai* sp. nov.

provisionally defined as follows: *C. rathbuni*, male, 25.0 mm CW or 21.8 mm CL, female, 25.0 mm CW or 23.8 mm CL; *C. penglai*, male, 28.2 mm CW or 23.3 mm CL, female, 27.6 mm CW or 23.5 mm CL. Specimens examined are deposited in the Department of Life Science, National Chung Hsing University, Taiwan (**NCHUZOO**), the National Science Museum, Tokyo, Japan (**NSMT**), the Ryukyu University Museum, Fujikan, Japan (**RUMF**), and the Zoological Reference Collection, the Lee Kong Chian Natural History Museum, National University of Singapore (**ZRC**).

Table 1. Haplotypes of 16S and COI of *Candidiopotamon rathbuni* (De Man, 1914) and *Candidiopotamon penglai* sp. nov. collected from different populations of Taiwan, as well as the outgroups from the Ryukyus. Numbers within square brackets correspond to localities in Fig. 1. R., river; Co., county.

Species and clades	Localities	Catalog no. of NCHUZOL (unless indicated)	Sample size	16S	Access. nos.	COI	Access. nos.
<i>C. rathbuni</i>							
NW clade							
	New Taipei City (Wulai [1])	13146	1	NW1	AB208590	NW1-C	AB625764
	New Taipei City (Wulai [1])	15189	1	NW2	AB208589	NW2-C	OR344947
	New Taipei City (Sansia [2])	12956	2	NW3	OR346841, OR346842	NW3-C	OR344948, OR344949
	New Taipei City (Wulai [1]); Hsinchu Co. (Guansi [5]; Jianshih [6]; Wufong [8])	13146; 12927; 12915; 12914	5	NW4	AB208591, AB208591, AB208591, AB208591, AB208591	NW4-C1	OR344950, OR344951, AB433579, OR344952, OR344953
	Taoyuan (Dongyanshan, Fusing [3])	12955	2	NW4	OR346843, OR346844	NW4-C2	OR344954, OR344955
	Taoyuan (Baling, Fusing [4])	12954	1	NW4	OR346845	NW4-C3	OR344956
	Hsinchu Co. (Beipu [7]); Miaoli (Baguali, Tai-an [9])	12917; 12916	2	NW4	AB208591, AB208591	NW4-C4	OR344957, OR344958
	Hsinchu Co. (Beipu [7])	12917	1	NW4	AB208591	NW4-C5	OR344959
	Miaoli (Erbensong [10])	15193	1	NW4	AB208591	NW4-C6	OR344960
	Hsinchu Co. (Jianshih [6])	12904	1	NW5	AB208592	NW5-C	OR344961
	Miaoli (Baguali, Tai-an [9])	12916	1	NW6	AB208593	NW4-6	OR344962
	Taichung (Dongshih [11])	12918	1	NW7	AB208594	NW7-C1	OR344963
	Taichung (Dongshih [11])	12918	1	NW7	AB208595	NW7-C2	OR344964
	Taichung (Dongshih [11])	12918	1	NW7	AB208596	NW7-C3	OR344965
	Taichung (Guguan [12])	12941	1	NW8	AB208597	NW8-C	OR344966
W clade							
	Taichung (Caohu, Dali [13]; Taiping [13]); Nantou (Shueili [15])	12944; 12924; 12902	3	W1	AB208598, AB208598	W1-C	OR344967, OR344968, OR344969
	Nantou (Shueili [15])	17185	2	W2	OR346846, OR346847	W2-C	OR344970, OR344971
	Nantou (Shueili [15])	12902	1	W3	AB208599	W3-C1	OR344972
	Nantou (Lianhua Pond, Yuchih [14])	12903	1	W3	AB208599	W3-C2	OR344973
	Nantou (Lianhua Pond, Yuchih [14])	12903	1	W3	AB208599	W3-C3	OR344974
	Nantou (Shueili [15])	15187	1	W4	AB208600	W4-C	OR344975
	Nantou (Yapingshan, Sinyi [16])	12393	1	W5	OR346848	W5-C	OR344976
	Chiayi Co. (Guanhua, Jhuci [17])	12942	1	W6	AB208601	W6-C1	OR344977
	Chiayi Co. (Dabang, Alishan [18])	13609	1	W6	AB208601	W6-C2	OR344978
	Kaohsiung (Mincyuan, Sanmin [19])	12921	2	W6	AB208601, AB208601	W6-C3	OR344979, OR344980
	Kaohsiung (Baolai, Liouguei [20])	12920	1	W6	AB208601	W6-C4	OR344981
	Kaohsiung (Baolai, Liouguei [20])	12920	1	W6	AB208601	W6-C5	OR344982
	Kaohsiung (Daganshan, Alian [24])	12919	2	W6	AB208601, AB208601	W6-C6	OR344983, OR344984
	Kaohsiung (Tianliao [23])	12923	1	W6	AB208601	W6-C7	OR344985
	Kaohsiung (Tianliao [23])	12923	1	W6	AB208601	W6-C8	OR344986
	Kaohsiung (Chuyunshan, Taoyuan [21])	12922	1	W7	AB208602	W7-C	OR344987
	Kaohsiung (Meinong [22])	13368	1	W8	AB208603	W8-C	OR344988
	Pingtung (Ila, Wutai [25]; Jiamu, Wutai [25])	12928; 12949	2	W9	AB208604	W9-C	OR344989, OR344990

Species and clades	Localities	Catalog no. of NCHUZ00L (unless indicated)	Sample size	16S	Access. nos.	COI	Access. nos.
SW clade							
	Pingtung (Wutai [26])	12945	1	SW1	AB208607	SW1-C1	OR344991
	Pingtung (Haocha, Sandimen [27])	12947	1	SW1	AB208607	SW1-C2	OR344992
	Pingtung (Haocha, Sandimen [27])	15201	1	SW2	AB208606	SW2-C	OR344993
	Pingtung (Haocha, Sandimen [27])	15200	1	SW3	AB208608	SW3-C1	OR344994
	Pingtung (Liangshan, Majia [28])	17184	1	SW3	OR346849	SW3-C2	OR344995
	Pingtung (Taiwu [29])	12907	1	SW4	AB208605	SW4-C1	OR344996
	Pingtung (Taiwu [29])	15219	1	SW4	AB208605	SW4-C2	OR344997
	Pingtung (Taiwu [29])	15219	1	SW4	AB208605	SW4-C3	OR344998
	Pingtung (Laiyi [30])	12925	3	SW4	AB208605, AB208605, AB208605	SW4-C4	OR344999, OR345000, OR345001
	Pingtung (Lili, Chunrih [31])	12908	1	SW4	AB208605	SW4-C5	OR345002
<i>C. penglai</i>							
S clade							
	Pingtung (Jiucijia, Chunrih [32])	13074	1	S1	AB208609	S1-C1	OR345003
	Pingtung (Jiucijia, Chunrih [32])	13074	1	S1	AB208609	S1-C2	AB290649
	Pingtung (Nanshihu R., Shihzih [33]; Cili R., Shihzih [33])	12939; 12948	2	S1	AB208610, AB208609	S1-C3	OR345005, OR345006
	Pingtung (Fangshan R., Shihzih [34])	12910	1	S1	AB208611	S1-C4	OR345007
	Pingtung (Maozaikengnei, Hengchun [37])	RUMF-ZC-57	1	S1	AB208615	S1-C5	OR345008
	Pingtung (Nanrenshan, Manjhou [38])	12940	1	S1	AB208615	S1-C6	OR345009
	Taitung (Dawu [39])	15220; 12943	2	S1	AB208616, AB208616	S1-C7	OR345010, OR345011
	Pingtung (Jiucijia, Chunrih [32])	13074	1	S2	AB208613	S2-C3	OR345012
	Pingtung (Fangshan R., Shihzih [34])	12910	1	S3	AB208612	S1-C3	OR345013
	Pingtung (Nanshihu R., Shihzih [33])	12939	1	S4	AB208614	S4-C1	OR345014
	Pingtung (Danlu, Shihzih [35])	12912	1	S4	AB208614	S4-C2	OR345015
	Pingtung (Danlu, Shihzih [35])	15207	1	S4	AB208614	S4-C3	OR345016
	Pingtung (Sihchong R., Checheng [36])	NCHUZ00L	1	S4	AB208614	S4-C4	OR345017
	Pingtung (Nanrenshan, Manjhou [38])	NCHUZ00L	1	S4	AB208614	S4-C5	OR345018
	Pingtung (Nanrenshan, Manjhou [38])	15215	1	S4	OR346850	S4-C6	OR345019
SE clade							
	Taitung (Taiban, Daren [40])	NCHUZ00L	1	SE1	AB208617	SE1-C1	OR345020
	Taitung (Taiban, Daren [40])	15218	1	SE1	AB208617	SE1-C2	AB551394
	Taitung (Taiban, Daren [40])	15218	1	SE1	AB208617	SE1-C3	OR345022
	Taitung (Jihben [42]; Taimali [41])	12929; 12931	2	SE1	AB208617, AB208617	SE1-C4	OR345023, OR345024
	Taitung (Taimali [41])	12953	2	SE1	OR346851, OR346852	SE1-C5	OR345025, OR345026
	Taitung (Jihben [42])	12929	1	SE1	AB208617	SE1-C6	OR345027
	Taitung (Lijia, Beinan [43])	15160	1	SE1	AB208617	SE1-C7	OR345028
	Taitung (Lijia, Beinan [43])	12933	1	SE1	AB208617	SE1-C8	OR345029
	Taitung (Jihben [42])	12986	1	SE2	OR346853	SE2-C	OR345030
	Taitung (Taimali [41])	12931	1	SE3	AB208618	SE3-C1	OR345031
	Taitung (Taimali [41])	12931	1	SE3	AB208618	SE3-C2	OR345032
	Taitung (Taimali [41])	12931	1	SE3	AB208618	SE3-C3	OR345033
	Taitung (Taimali [41])	12931	1	SE3	AB208618	SE3-C4	OR345034
	Taitung (Hongye, Yanping [44])	12937	1	SE4	AB208619	SE4-C	OR345035
	Taitung (Hongye, Yanping [44])	12937	1	SE5	AB208620	SE5-C	OR345036

Species and clades	Localities	Catalog no. of NCHUZ00L (unless indicated)	Sample size	16S	Access. nos.	COI	Access. nos.
	Taitung (Hongye, Yanping [44])	12937	1	SE6	AB208621	SE6-C	OR345037
E1 clade							
	Taitung (Luming R., Yanping [45]); Hualien (Jingpu, Fengbin [50])	12934; 12909	3	E1	AB208626 , AB208626 , AB208622	E1-C1	OR345038 , OR345039 , OR345040
	Taitung (Taiyuan, Donghe [48])	12936	1	E1	AB208622	E1-C3	OR345041
	Taitung (Luanshan, Yanping [47])	15212	1	E1	AB208624	E1-C4	OR345042
	Taitung (Chenggong, Sansian [49])	17183	1	E1	OR346854	E1-C5	OR345043
	Taitung (Jiafeng, Beinan [45])	NCHUZ00L	1	E2	AB208625	E2-C	OR345044
	Taitung (Chenggong, Sansian [49])	15206	1	E3	AB208623	E3-C	OR345045
	Taitung (Wulu, Haiduan [50])	12950	1	E4	OR346855	E4-C	OR345046
	Hualien (Fuyuan, Rueishuei [51])	12935	1	E1	AB208622	E1-C2	OR345047
	Hualien (Jili Lake, Guangfu [52])	15228	1	E1	OR346856	E1-C6	OR345048
	Hualien (Jili Lake, Guangfu [52])	15227	1	E1	OR346857	E1-C7	OR345049
E2 clade							
	Hualien (Shueiyuandi, Shoufeng [53]; Liyu Lake, Shoufeng [54]; Ji-an [55])	RUMF-ZC-8165 (paratype); 12952 (paratype); 15213 (paratype); 12932 (paratype); RUMF-ZC-8164 (paratype); 12951 (holotype)	6	E5	OR346858 , OR346859 , OR346860 , OR346861 , OR346862 , OR346863 , OR346864	E4-C	OR345050 , OR345051 , OR345052 , OR345053 , OR345054 , OR345055 , OR345056
All localities			112				
Outgroups							
<i>C. okinawense</i>	Ryukyus, Japan (Okinawa [R1])		1	Co	AB208627	Co-C	OR345057
<i>Amamiku amamense</i>	Ryukyus, Japan (Amami [R2])		1	Aa	AB428457	Aa-C1	OR345058
Naruse, Segawa & Shokita, 2004	Ryukyus, Japan (Amami [R2])		1	Aa	OR346865	Aa-C2	OR345059

Genetic analyses

Genomic DNA was isolated from the muscle tissue of the legs by using the Sigma mammalian genomic DNA miniprep kit (Sigma-Aldrich, St. Louis, MO, USA) or the GeneMark tissue and cell genomic DNA purification kit (Taichung, Taiwan). A region of approximately 510 to 550 basepairs (bp) of the 5'-end of the mitochondrial large ribosomal subunit (16S rRNA) gene was selected for amplification with polymerase chain reaction (PCR) using the primers 1471, 1472 (Crandall and Fitzpatrick 1996), 16Sar, 16Sbr (Palumbi et al. 1991), 16L29 and 16H10 (Schubart 2009). A portion of the mitochondrial cytochrome oxidase subunit I (COI) gene was amplified with the primers LCO1490 and HCO2198 (Folmer et al. 1994), and LCOB (5'-CAAAYCATAAAGAYATYGG-3'), HCOex3 (5'-GCTCANACTACRAATCCTA-3') (Shih et al. 2022), and the newly designed primers LCOex2 (5'-ACACATCTTTAGAYTTGCAATCTAA-3'), LCOex3 (5'-ACACATCTTYARAYTTGCAATYTAA-3'), HCOs (5'-ACTTCDGGRTGDCCAAARAAYCA-3') and HCOex0 (5'-GAYTCTTTTTTDCDDGAYTC-3'). The PCR conditions for the above primers were 50s 94 °C / 70s 45 °C / 60s 72 °C (denaturation/annealing/extension for 40 cycles), followed by 72 °C extension for 10 min. Sequences were obtained by automated sequencing (Applied Biosystems 3730) and were aligned with the aid of the MUSCLE function of MEGA (v. 11, Tamura et al. 2021), after verification with the complimentary strand. Sequences have been deposited into NCBI GenBank (accession numbers. shown in Table 1).

Previously generated 16S sequences of *Candidiopotamon* from Taiwan (Shih et al. 2006) were also used for the construction of the phylogenetic tree.

For the combined 16S and COI dataset, the best-fitting models for sequence evolution of individual datasets were determined by PartitionFinder (v. 2.1.1, Lanfear et al. 2017), selected by the Bayesian information criterion (BIC). The best model, HKY+I+G, was subsequently applied for Bayesian inference (BI) analysis. The BI was performed with MrBayes (v. 3.2.6, Ronquist et al. 2012). The search was run with four chains for 10 million generations and four independent runs, 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. 2020), and the first 1100 trees were discarded as the burn in. The maximum likelihood (ML) analysis was conducted in RAxML (v. 7.2.6, Stamatakis 2006). The model GTR + G (i.e., GTRGAMMA) was used for all subsets with 100 runs to find the best ML tree by comparing likelihood scores. The robustness of the ML tree was evaluated by 1,000 bootstrap pseudoreplicates using the model GTRGAMMA. Basepair (bp) differences and pairwise estimates of Kimura 2-parameter (K2P) distances (Kimura 1980) for genetic diversities between specimens were calculated with MEGA.

Results

Genetic analyses

A 553 bp segment of the 16S rDNA and a 658 bp segment of COI from 112 specimens of *C. rathbuni* and *C. penglai* sp. nov. were amplified and aligned. A total of 36 haplotypes of the 16S gene and 83 haplotypes of COI were found (Table 1). The phylogenetic tree constructed from BI analysis, with the respective confidence values from the ML analysis, is shown in Fig. 2. Only confidence values larger than 50% are shown. Based on Fig. 2 of the combined dataset, all *Candidiopotamon* from Taiwan are monophyletic, supported by BI and ML methods. Both the populations from western Taiwan (representing *C. rathbuni*) and eastern Taiwan (representing *C. penglai* sp. nov.) form two distinct major clades with high supports. In *C. rathbuni*, the SW clade was first isolated, and the other two clades (W and NW) form a larger clade. All three clades are highly supported, except for the ML method of the W clade. In *C. penglai* sp. nov., the SE clade diverged firstly, and the other three clades (S, E1, and E2) form a larger clade with E2 clade with a single haplotype ("E5+E5-C") from northern Hualien. Three clades (SE, S, and E1) are highly supported, except for the ML method of S clade.

The pairwise nucleotide divergences and the total bp number differences of COI within and between clades and species are shown in Table 2. The genetic distances (and bp differences) within most clades are from 0 to 2.17% (0–14 bp), except the W clade with a larger value, 0–3.93% (0–25 bp). The genetic distances (bp differences) between clades are 3.92%–7.45% (25–46 bp) in *C. rathbuni*; and 1.7%–4.41% (11–28 bp) in *C. penglai* sp. nov. The intraspecific distances (bp differences) of *C. rathbuni* and *C. penglai* sp. nov. are 0–7.45% (0–46 bp) and 0–4.41% (0–28 bp), respectively. The interspecific distance (and bp difference) is 10.72%–13.65% (65–81 bp).



Figure 2. A Bayesian inference (BI) tree for *Candidiopotamon rathbuni* (De Man, 1914) and *Candidiopotamon penglai* sp. nov., as well as outgroups, based on the combined 16S rDNA and cytochrome oxidase I. Probability values at the nodes represent support values for BI and maximum likelihood (ML). For haplotype names, see Table 1. The color of clades corresponds to the color of collection sites in Fig. 1, which are also shown as the numbers in parenthesis after the haplotype names.

Table 2. Matrix of percentage pairwise nucleotide divergences with K2P distance and the number of bp differences based on COI within and between clades of *Candidiopotamon* species from Taiwan (see Table 1). In the right half, lower-left values are K2P distance and upper-right ones are bp differences. Values of the range are given in parentheses.

		Within clade		Between clades								
		Nucleotide divergence	bp difference	<i>C. rathbuni</i>			<i>C. penglai</i>				<i>C. rathbuni</i>	<i>C. penglai</i>
				NW	W	SW	S	SE	E1	E2		
<i>C. rathbuni</i>	NW	0.59 (0–1.54)	3.85 (0–10)		33.86 (25–43)	38.64 (35–44)	73.55 (69–80)	74.67 (72–81)	72.4 (69–78)	72.73 (71–76)		
	W	1.96 (0–3.93)	12.6 (0–25)	5.37 (3.92–6.92)		37.17 (29–46)	70.93 (65–76)	72.1 (66–79)	69.75 (67–75)	70.63 (68–73)		
	SW	0.89 (0–1.85)	5.83 (0–12)	6.16 (5.54–7.07)	5.95 (4.58–7.45)		73.05 (66–79)	73.22 (68–78)	71.62 (69–75)	72.58 (70–74)		
<i>C. penglai</i>	S	1.36 (0–2.16)	8.81 (0–14)	12.25 (11.41–13.48)	11.83 (10.72–12.79)	12.19 (10.89–13.34)		22.14 (18–28)	18.19 (15–21)	12.81 (11–15)		
	SE	1.12 (0–2.17)	7.25 (0–14)	12.45 (11.93–13.65)	12.05 (10.9–13.32)	12.23 (11.26–13.13)	3.46 (2.79–4.41)		22.18 (17–27)	21.83 (20–25)		
	E1	0.54 (0–1.07)	3.55 (0–7)	12.04 (11.41–13.09)	11.61 (11.1–12.6)	11.93 (11.44–12.57)	2.83 (2.32–3.28)	3.47 (2.64–4.24)		13.83 (12–16)		
	E2	0	0	12.11 (11.79–12.72)	11.79 (11.3–12.24)	12.11 (11.62–12.38)	2.06 (1.7–3.28)	3.41 (3.12–3.92)	2.15 (1.86–2.49)			
<i>C. rathbuni</i>		4.18 (0–7.45)	26.34 (0–46)									72.34 (65–81)
<i>C. penglai</i>		2.53 (0–4.41)	16.26 (0–28)								12.06 (10.72–13.65)	

Taxonomy

Family Potamidae Ortmann, 1896

Subfamily Potamiscinae Ortmann, 1896 (sensu Yeo and Ng 2004)

Genus *Candidiopotamon* Bott, 1967

Candidiopotamon Bott, 1967: 210; Bott 1970: 189; Minei 1974: 245; Dai 1999: 154; Shy and Yu 1999: 95; Ng et al. 2008: 161; Sasaki 2019: 11551; Shy et al. 2020: 1.

Type species. *Potamon* (*Potamon*) *rathbuni* De Man, 1914.

Distribution. Taiwan and the Ryukyu Islands (Okinawa, Kumejima, and Tokashiki islands) of Japan.

Remarks. The genus *Candidiopotamon* was erected by Bott (1967) with the type species, *Potamon* (*Potamon*) *rathbuni* De Man, 1914, and the genus was named from the type locality of the type species, Candidius-See (= Sun Moon Lake, Rihyuetan) in Nantou Co. (= County), central-western Taiwan. *Candidiopotamon* was placed in the family Sinopotamidae Bott, 1970, by Bott (1970), but the Sinopotamidae was synonymized under the Potamidae by Yeo and Ng (2004), and this has been supported by genetic data (Shih et al. 2009). Following this study, there are now two species in Taiwan (*C. rathbuni* in the west and *C. penglai* sp. nov. in the east) and three from the Ryukyu Islands of Japan (*C. okinawense* in Okinawa Island, *C. kumejimense* in Kumejima Island, and *C. tokashikense* in Tokashiki Island). *Candidiopotamon guangdongense* Dai,

1999, claimed to be found in Guangdong, China, but this is a junior synonym of *C. rathbuni* and was based on incorrect locality labels (Shih and Ng 2011; Ng et al. 2017; Shy et al. 2020).

Key to the species of *Candidiopotamon* Bott, 1967

- 1 Distal part of G1 opening outwards, terminal segment relatively slender..... **2**
- Distal part of G1 opening distally, terminal segment relatively stout **3**
- 2 Subterminal segment of G1 straight or curving inwards; distal inner edge of terminal segment of G1 with proportionally larger keel-like projection directed more distally..... ***C. penglai* sp. nov. (eastern Taiwan)**
- Subterminal segment of G1 straight; distal inner part of terminal segment of G1 with proportionally smaller keel-like projection directed more laterally ***C. rathbuni* (De Man, 1914) (western Taiwan)**
- 3 Outer angle of frontal margin of carapace not touching first segment of endopod of antenna ***C. okinawense* Minei, 1973 (Okinawa Island, Japan)**
- Outer angle of frontal margin of carapace touching first segment of endopod of antenna **4**
- 4 Outer dorsal margin of second ambulatory propodus with 1 row of spines; subdistal carina of G1 directed dorsally ***C. tokashikense* Naruse, Segawa & Aotsuka, 2007 (Tokashiki Island, Japan)**
- Outer dorsal margin of second ambulatory propodus without spines; subdistal carina of G1 directed inwards ***C. kumejimense* Minei, 1973 (Kumejima Island, Japan)**

Candidiopotamon rathbuni (De Man, 1914)

Figs 3, 4A, B, 5A–D

Potamon (*Potamon*) *rathbuni* De Man, 1914: 128, pl. 3(4–4d) [type locality: Sun Moon [Rihyuetan], Nantou, Taiwan]; Parisi 1916: 153; Oshima 1921: 123; Balss 1922: 134; Maki and Tsuchiya 1923: 153, pl. 19(2); Balss 1937: 162, fig. 21; Sakai 1939: 580, pl. 128(1); Sakai 1940: 57; Lin 1949: 25; Chiu 1962a: 425. *Thelphusa rubra* Nakagawai Nakagawa, 1915a: 1036 (nomen nudum); 1915b: 322. *Potamon* (*Geothelphusa*) *obtusipes* – Terao 1915: 503, 1 unnumbered fig.; Nakagawa 1917: 303, fig. 21 (non *Geothelphusa obtusipes* Stimpson, 1858). *Potamon obtusipes* – Nakagawa 1916: 137, pl. 2(1) (non *Geothelphusa obtusipes* Stimpson, 1858). *Potamon rathbuni* – Koba 1936a: 166, fig. 1; Koba 1936b: 202, text-fig.; Horikawa 1940: 27; Iwata 1940: 2; Chiu 1962b: 58; Chiu 1964: 67 (part); Pretzmann 1963: 365, fig. 15. *Candidiopotamon rathbuni* – Bott 1967: 210, fig. 10; Bott 1970: 189, pls 40(74), 55(75); Minei 1974: 246, figs 7–9 (part); Sakai 1976: 564, text-fig. 307; Dai et al. 1984: 115, fig. 69; Hwang and Mizue 1985: 10, fig. 7, pl. IIA (part); Shy et al. 1996: 239, fig. 17; CH Jeng et al. 1998: 70, 2 unnumbered figs; Dai 1999: 154, fig. 80, pl. 9(7) (part); Shy and Yu 1999: 94, 3 unnumbered figs, “fig. 31” on p. 106 (part); Lee and Tung 2000: 70; Ng 2000: 249 (part); Jeng et al. 2010: 80, 7 unnumbered figs; Ng et al. 2017: 76; Shy et al. 2020: 2, figs 11A, 13, 14, 16, 17 (part).

Candidiopotamon sp. – Jeng et al. 1994: 56; Jeng et al. 1996: 51; Jeng et al. 1997: 62; MS Jeng et al. 1998: 60.

Candidiopotamon guangdongense Dai, 1999: 156, fig. 81, pl. 19(8).

Candidiopotamon rathbunae – Liu and Li 2000: 90; Ng 2000: 249 (part); Chen et al. 2001: 43, 2 unnumbered figs on p. 43, 46 (part); Lee 2001: 145, 2 unnumbered figs (part); Ng et al. 2001: 49 (part); Chen et al. 2003: 29, 5 unnumbered figs (part); Naruse et al. 2004: 7, fig. 2Bd, Bv.; Shih et al. 2006: 983 (part); Ng et al. 2008: 161 (part); Shih et al. 2009: 706; Shy and Lee 2009: 207, 10 unnumbered figs (part); Chiu et al. 2015: 202, 227, 1 unnumbered fig. on p. 202 (part); Ho 2015: 141, 2 unnumbered figs (part); Liu and Hartnoll 2017: 227; Sasaki 2019: 11552 (part).

Material examined. TAIWAN – 3 males, CW 25.6 × CL 22.6–28.6 × 25.6 mm, 1 female, 38.0 × 32.8 mm, NCHUZOO 15191, Sinsian, Wulai, New Taipei City, coll. C. A. Chen, 20 Aug. 2001; 1 male, 40.0 × 35.8 mm, NCHUZOO 15189, Sinsian, Wulai, New Taipei City, coll. H.-T. Shih, 29 Apr. 1994; 1 male, 30.2 × 27.4 mm, 1 female, 35.1 × 30.7 mm, NCHUZOO 12915, Jianshih, Hsinchu Co., coll. H.-T. Shih, 25 May 2001; 1 female, 40.0 × 34.0 mm, NCHUZOO 15184, Hengshan, Hsinchu Co., coll. H.-C. Liu, 24 Sep. 1995; 2 males, 33.4 × 29.1–32.8 × 29.0 mm, 1 female, 33.9 × 29.0 mm, RUMF-ZC-53, Cingcyuan, Wufeng, Hsinchu Co., coll. C.A. Chen, 28 Aug. 2001; 1 male, 30.9 × 27.0 mm, NCHUZOO 15192, Shuei-weiping, Dahu, Miaoli, coll. H.-D. Zhu, 7 Mar. 2001; 3 males, 25.7 × 22.6–35.4 × 31.2 mm, 1 female, 26.7 × 23.9 mm, NCHUZOO 15194, Baguali, Tai-an, Miaoli, coll. H.-T. Shih, 25 Jan. 2002; 1 male, 34.5 × 30.6 mm, NCHUZOO 15211, 2 males, 19.1 × 16.5, 19.8 × 17.6 mm, 5 females, 17.9 × 15.9–31.0 × 26.9 mm, NCHUZOO 12918, 1 male, 31.6 × 27.5 mm, 1 female, 27.9 × 23.8 mm, RUMF-ZC-54, Sihjiaolin, Dongshih, Taichung, coll. H.-T. Shih, 28 Dec. 2001; 1 male, 23.3 × 20.3 mm, NCHUZOO 12944, Caohu, Taichung, coll. H.-C. Liu, 23 Apr. 1993; 1 male, 30.4 × 26.1 mm, NCHUZOO 12924, Taiping, Taichung, coll. students of Tunghai Univ., 8 Jun. 2001; 2 males, 26.4 × 23.2, 27.7 × 24.2 mm, NCHUZOO 15214, Lianhuachih, Wucheng, Yuchi, Nantou, coll. H.-T. Shih, 22 Jun. 2001; 1 male, 28.0 × 23.9, 1 female, 29.7 × 25.4 mm, NCHUZOO 15181, Rihyuetan, Nantou (type locality), coll. H.-T. Shih and H.-T. Hung, 4 Mar. 2003; 1 male, 38.6 × 32.4 mm, NCHUZOO 15187, Sinshan, Shueili, Nantou, coll. H.-C. Liu, 8 Aug. 1995; 1 male, 36.3 × 30.9, 1 female, 24.2 × 21.0 mm, NCHUZOO 15185, Jiji, Shueili, Nantou, coll. H.-C. Liu, 8 Aug. 1995; 3 males, 32.3 × 27.6–36.7 × 31.1 mm, 2 females, 26.4 × 22.5, 33.0 × 28.7 mm, NCHUZOO 15205, Chukou, Fanlu, Chiayi Co., coll. H.-C. Liu, 21–22 Mar. 1996; 1 male, 44.6 × 36.8 mm, 1 female, 40.9 × 34.4 mm, RUMF-ZC-86, Guanyin Waterfall, Chiayi Co., coll. J.-Y. Shy, 6 Dec. 1990; 1 male, 35.2 × 29.3 mm, NCHUZOO 12946, Alishan, Chiayi Co., coll. C.-H. Wang, 26 May 2002; 1 male, 21.2 × 19.1 mm, NCHUZOO 15182, Dakeng, Dongyuan, Dongshan, Tainan, coll. H.-T. Shih, 20 Oct. 2000; 5 males, 19.7 × 16.8–29.6 × 25.6 mm, 1 female, 24.9 × 20.9 mm, NCHUZOO 15186, Gaoyuan, Dongshan, Tainan, coll. H.-C. Liu, 16 Aug. 1997; 1 male, 26.6 × 22.6 mm, NCHUZOO 15196, Gueidan, Nansi, Tainan, coll. H.-T. Shih, 20 Oct. 2000; 1 male, 28.8 × 24.9 mm, NCHUZOO 15198, Mincyuan, Sanmin, Kaohsiung, coll. C.-B. Wu, 17 Aug. 2000; 1 male, 30.6 × 26.0 mm, 1 female, 25.0 × 21.8 mm, NCHUZOO 15195, Baolai, Liouguei, Kaohsiung, coll. H.-T. Shih, 14 Dec. 2001; 1 male, 31.5 × 26.6 mm, NCHUZOO 12922, Chuyunshan, Taoyuan, Kaohsiung, coll. C.-S.

Chen, 6 May 2000; 1 male, 34.3 × 29.0 mm, NCHUZOO 15188, Guanglin, Meinong, Kaohsiung, coll. C.-S. Chen, 15 Dec. 2000; 3 females, 33.7 × 29.7–40.4 × 35.0 mm, NCHUZOO 15183, Guanglin, Meinong, Kaohsiung, coll. H.-C. Liu, 4 Aug. 1995; 1 male, 37.3 × 32.3 mm, 1 female, 26.7 × 23.2 mm, NCHUZOO 15190, Jiasian, Kaohsiung, coll. H.-C. Liu, 5 Aug. 1995; 3 males, 30.5 × 26.2–38.8 × 34.0 mm, 1 female, 27.8 × 23.8 mm, NCHUZOO 15197, Tianliao, Kaohsiung, coll. H.-T. Shih, 16 Nov. 2001; 1 male, 24.2 × 20.5 mm, 1 female, 26.2 × 22.3 mm, NCHUZOO 15202, Shandimen, Pingtung, coll. H.-C. Liu, 16 Aug. 1997; 1 male, 34.4 × 29.4 mm, NCHUZOO 15201, Haocha, Pingtung, coll. H.-T. Shih, 31 May 2000; 2 males, 36.3 × 30.7, 37.7 × 32.3 mm, 1 female, 32.9 × 27.3 mm, NCHUZOO 15199, Taiwu, Pingtung, coll. C.-C. Huang and C.-K. Yang, 29 Jul. 1999; 1 male, 34.5 × 29.0 mm, 1 female, 37.4 × 30.9 mm, RUMF-ZC-55, Taiwu, Pingtung, coll. H.-T. Shih, 12 Nov. 2000; 2 males, 33.4 × 28.3, 37.5 × 31.7 mm, NCHUZOO 15203, Wutan, Taiwu, Pingtung, coll. H.-C. Liu, 18 Jul. 1997; 3 females, 13.2 × 11.3–29.5 × 24.9 mm, NCHUZOO 12925, Laiyi, Pingtung, coll. H.-C. Liu, 16 Jul. 1996.

Diagnosis. Carapace subtrapezoidal, CW 1.10–1.21× CL (mean 1.16, $n = 5$), dorsal surface almost flat, relatively rough, epigastric and postfrontal cristae distinct, both cristae represented by 1–3 oblique lines of granules, lateral end of postfrontal cristae far apart from epibranchial tooth; external orbital and epibranchial teeth distinct, sharp, directed anteriorly. G1 terminal segment proportionally longer, more slender, distal opening directed laterally, distal inner edge with keel-like projection in dorsal view, projection proportionally small, directed more laterally; G1 subterminal segment straight.

Description. Carapace (Figs 3A, B, 4A) subtrapezoidal in dorsal view, CW 1.10–1.21× CL (mean 1.16, $n = 5$), dorsal surface almost flat, relatively rough, somewhat pilose. Epigastric cristae distinct; postorbital crista, represented by 1–3 oblique lines of granules, not reaching epibranchial tooth. External orbital angle acute, directed anteriorly; ridge between external orbital angle and distinct epibranchial tooth cristate and granulated; anterolateral margin distinctly cristate, lined with large, elongated granules.

Antenna (Fig. 3B) short, reaching ~ 1/2 length of basal segment of antenna when antenna folded backwards.

Eye (Fig. 3B) developed; maximal width of cornea wider than base of peduncle in frontal view.

Chelae of large males unequal, females or young specimens with subequal chelae; palm of major chela (Fig. 3C) ~ 2/3× as high as minor chela, outer surface with scattered granules; cutting edges of both fingers with regularly arranged large and small teeth, gape almost absent when fingers closed.

Ambulatory legs moderately long; propodus cross-section oblong, each of 2 inner and 1 ventral outer longitudinal margins with 1 spine-row.

Male pleonal somites elongate trapezoidal, sixth pleonal somite length ~ 1/2 of its width; telson obtusely triangular, length ~ 1/2 of its width, distal end reaching imaginary line joining lower hinges of cheliped coxae. Female pleon of adult wide, covering ventral surface of thoracic sternum except for part of thoracic sternites 1 and 2.

G1 (Fig. 3D, F) straight in dorsal view when dorso-proximal margin of subterminal segment set parallel to observer's eyes. Ventral side of subterminal

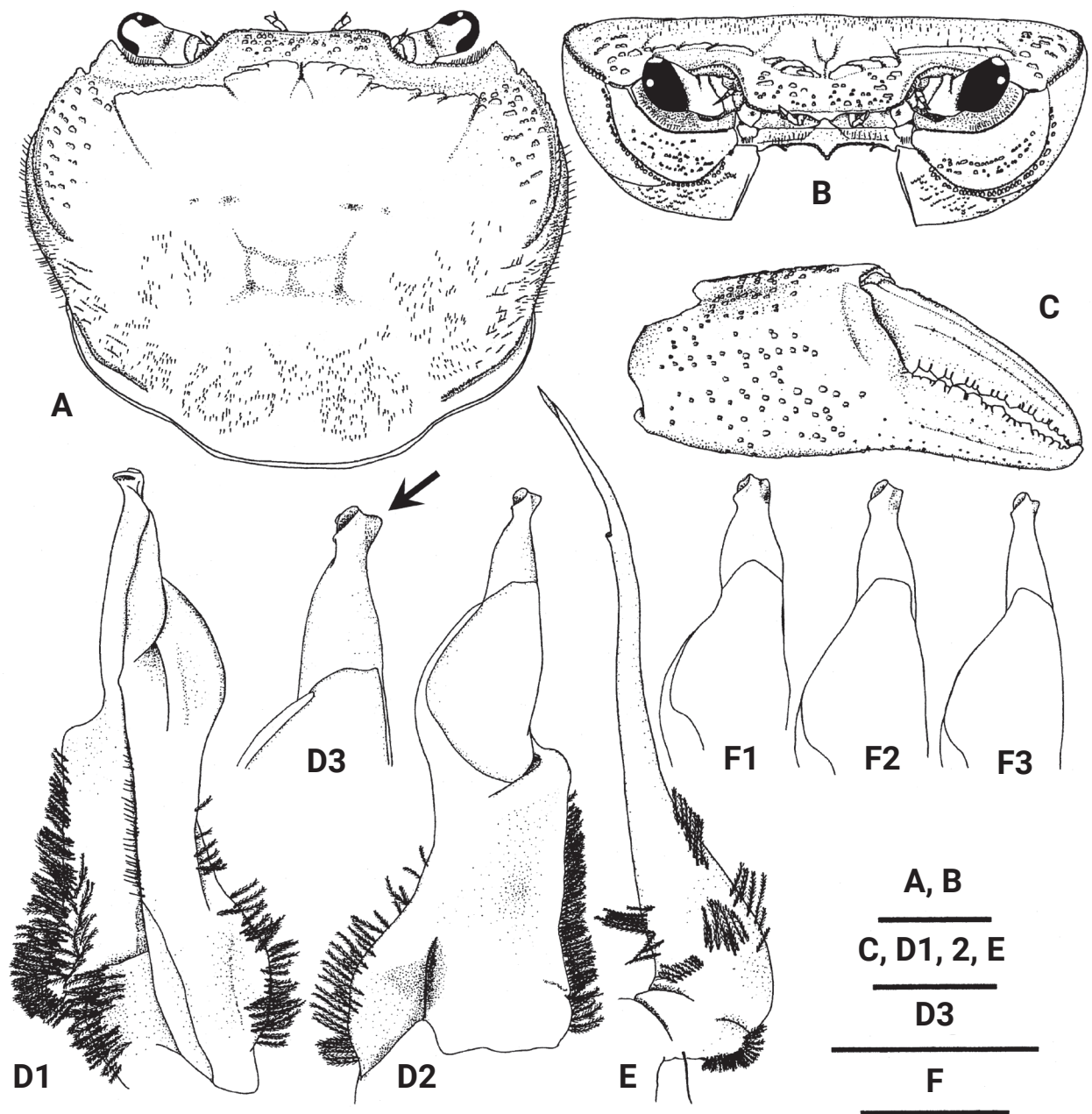


Figure 3. *Candidiopotamon rathbuni* (De Man, 1914): male (44.6 × 36.8 mm) from Chiayi, western Taiwan (RUMF-ZC-86) (A–E); male (35.4 × 31.2 mm) from Miaoli, northwestern Taiwan (NCHUZ00L 15194) (F1); male (36.7 × 31.1 mm) from Chiayi, western Taiwan (NCHUZ00L 15205) (F2); male (36.3 × 30.7 mm) from Taiwu, Pingtung, southwestern Taiwan (NCHUZ00L 15199) (F3). **A** carapace, dorsal view **B** carapace, frontal view **C** male major chela, outer view **D1** left G1, ventral view **D2** left G1, dorsal view **D3** left G1 terminal segment, dorsal view **E** left G2 **F1–3** left G1s terminal segment, dorsal view. Scale bars: 10 mm (A–C); 2 mm (D–F). Arrow indicates the keel-like projection on the distal inner edge of the terminal segment.

segment with median seam extending to subproximal part of terminal segment. Synovial membrane long, wide, occupying distal ~ 2/5 of subterminal segment in dorsal view. Terminal segment bottle-necked, relative width gradually narrowed from northwestern (Fig. 3F1) to southwestern populations (Fig. 3F3), but no clear gap between them (Fig. 3F); distal opening directed outwards, with

relatively small, laterally directed keel-like projection on opposite side of opening. G2 slightly shorter than G1; G2 flagellum $\sim 1/4$ length of G2 total length.

Vulvae close to each other, obliquely oblong, occupying proximal two-thirds of thoracic sternite 6.

Coloration (Figs 4A, B, 5A–D). Most large specimens are dark red, but sometimes dark purple or orange individuals can be found. Small individuals are generally dark brown with black spots.

Distribution (Fig. 1). *Candidiopotamon rathbuni* is distributed along the western side of the Central Range, i.e., New Taipei City, Taoyuan, Hsinchu Co., Miaoli, Taichung, Changhua, Yunlin, Chiayi Co., Tainan, Kaohsiung, and the northwestern part of Pingtung. The type locality of *C. rathbuni* is Rihyuetan (= Sun Moon Lake, or the Candidus Sea), Nantou, west of the Central Range of Taiwan.

Habitat. Most large specimens were found under large stones within streams. Sometimes adults move outside the water at night.

Remarks. Based on one male (31.4×26 mm) and one female (37×31.3 mm) specimens, De Man (1914) described the morphology of *Candidiopotamon rathbuni* in great detail except for the gonopods. The lack of a description of G1 makes it difficult to ascertain which species is the real *C. rathbuni*. The topotypic specimens of *C. rathbuni* (NCHUZ00L 15187, 15185, 15214) possess the laterally directed subdistal keel and straight subterminal segment of G1. Furthermore, the type locality of *C. rathbuni*, Sun Moon Lake (= Rihyuetan), is located in west-central Taiwan (i.e., west of the Central Range, < 1000 m, a.s.l), which suggests that the species distributed in western Taiwan keeps the name *C. rathbuni*, and that of eastern Taiwan is herewith described as a new species.

In his papers on the life history of *Paragonimus westermani*, Nakagawa (1915a, 1915b) used “*Thelphusa rubra Nakagawai*” for the specimens collected by himself from Hsinchu (including Miaoli), northwestern Taiwan as the second intermediate host of the species, without further information on the specimens he observed. We have examined the specimens from Hsinchu (NCHUZ00L 12915, 15184, RUMF-ZC-53) and Miaoli (NCHUZ00L 15192, 15194), which belong to *C. rathbuni* from western Taiwan in morphology and genetics. Regarding the brick-red coloration from the name “*rubra*”, the coloration of *C. rathbuni* is variable from dark purple and dark red to orange (see “Coloration” of this species).

Subsequently, Terao (1915) referred Nakagawa’s specimens of “*Thelphusa rubra Nakagawai*” to *Potamon* (*Geothelphusa*) *obtusipes* (Stimpson, 1858). However, the real *P. obtusipes* is only distributed in Amami Islands, the Ryukyus and does not show the red coloration (Shih 2008: figs 51, 52). Terao’s (1915: 508) drawing of *P. (G.) obtusipes* clearly showed that his specimen represented a species of *Candidiopotamon*, and Ng et al. (2001) also doubted that “*Thelphusa rubra Nakagawai*” was actually *C. rathbuni*. In addition to the above history, Nakagawa stated that “As a matter of convenience, the crab, which has been described as *Thelphusa* sp., is provisory treated here (as *Thelphusa rubra Nakagawai*) temporarily”. Because Nakagawa collected the specimens from Hsinchu and Miaoli, northwestern Taiwan where *C. rathbuni* is distributed, “*Thelphusa rubra Nakagawai*” sensu Nakagawa (1915a, 1915b) and *Potamon* (*Geothelphusa*) *obtusipes* sensu Terao (1915) are considered here as junior synonyms of *C. rathbuni*.

***Candidiopotamon penglai* sp. nov.**

<https://zoobank.org/3AC24730-7610-4C20-8F55-963FE8C56D6A>

Figs 4C–F, 5E–H, 6, 7

Potamon rathbuni – Chiu 1964: 67 (part).

Candidiopotamon rathbuni – Minei 1974: 246, figs 7–9 (part); CH Wang 1984: 41; Yu et al. 1996: 9, 29, fig. 10; MS Jeng 1998: 86, 1 unnumbered fig.; Shy and Yu 1999: 94, 3 unnumbered figs, “fig. 31” on p. 106 (part); Ng 2000: 249 (part); Ng et al. 2017: 76; Shy et al. 2020: 2, figs 11A, 13, 14, 16, 17 (part); Li and Chiu 2019a: 103, 3 unnumbered figs; Li and Chiu 2019b: 2 unnumbered figs on p. 56; Shy et al. 2020: 2, figs 2E, 14E (part); SW Wang et al. 2021: 32, pl. 3E.

Candidiopotamon rathbunae – Ng 2000: 249 (part); Chen et al. 2001: 43, 2 unnumbered figs on p. 43, 46 (part); Lee 2001: 145, 2 unnumbered figs (part); Ng et al. 2001: 49 (part); Chen et al. 2003: 29, 5 unnumbered figs (part); Shih et al. 2006: 983 (part); Ng et al. 2008: 161 (part); Shy and Lee 2009: 207, 10 unnumbered figs (part); Li and Chiu 2013: 70, 3 unnumbered figs; Chiu et al. 2015: 202, 227, 1 unnumbered fig. on p. 202 (part); Ho 2015: 141, 2 unnumbered figs (part); Sasaki 2019: 11552 (part).

Type material. TAIWAN – **Holotype:** male, 38.4 × 33.4 mm, NCHUZOO 12951, Ji-an, Hualien, coll. H.-C. Liu, 4 May 2000. – **Paratypes:** 1 male, 35.6 × 30.5 mm, RUMF-ZC-8164, 1 female, 18.0 × 15.8 mm, NCHUZOO 12932, collection data same as for holotype; 1 female, 34.3 × 29.6 mm, RUMF-ZC-8165, Shueiyuandi, Shoufeng, Hualien, coll. N.-H. Jang-Liaw, 5 Mar. 2002; 1 male, 23.4 × 20.0 .5 mm, NCHUZOO 12952, Liyu Lake, Shoufeng, Hualien, coll. H.-T. Shih, 26 Jan. 2007; 1 male, 27.5 × 24.2 mm, NCHUZOO 15213, Liyu Lake, Shoufeng, Hualien, coll. H.-T. Shih, 28 Jan. 2007; 1 male, 36.4 × 30.9 mm, NCHUZOO 15224, 1 male, 27.0 × 23.8, NCHUZOO 15226, 1 female, 36.5 × 31.4, NCHUZOO 15225, Liyu Lake, Shoufeng, Hualien, coll. HTS’s lab students, 13 Apr. 2023; 1 male, 28.3 × 24.8 mm, 1 female, 35.2 × 31.6 mm, ZRC 2023.0309, Liyu Lake, Shoufeng, Hualien, coll. HTS’s lab students, 13 Apr. 2023.

Other material. TAIWAN – 1 male, 23.9 × 20.1 mm, NCHUZOO 15227, 1 male, 29.3 × 27.6 mm, NCHUZOO 15228, 1 male, 33.1 × 29.7 mm, NCHUZOO 15229, Jili Lake, Guangfu, Hualien, coll. HTS’s lab students, 12 Apr. 2023; 1 female, 37.7 × 33.6 mm, NCHUZOO 15230, Luoshan, Fuli, Hualien, coll. HTS’s lab students, 11 Apr. 2023; 2 males, 35.9 × 30.6, 37.0 × 31.9 mm, 2 females, 27.6 × 23.5, 36.7 × 31.9 mm, RUMF-ZC-56, Jingpu, Hualien, coll. M.-Y. Liu, 18 Jun. 2001; 2 males, 33.0 × 28.9, 30.4 × 26.5 mm, NSMT-Cr 15170, Jingpu, Hualien, coll. M.-Y. Liu, Jan. 2001; 1 male, 31.7 × 26.7 mm, NCHUZOO 15221, Chenggong, Taitung, coll. N.-H. Jang-Liaw, 6 Mar. 2002; 3 males, 28.2 × 23.3–34.0 × 28.8 mm, 2 females, 16.4 × 13.6, 38.3 × 31.0 mm, NCHUZOO 12931, Taimali, Taitung, coll. H.-C. Liu, 22 Aug. 1997; 4 males, 28.6 × 24.8–33.7 × 29.1 mm, 1 female, 32.5 × 27.0 mm, NCHUZOO 15206, Sansiantai, Chenggong, Taitung, coll. H.-C. Liu and H.-L. Hsu, 5 Sep. 1997; 2 males, 31.4 × 25.9, 27.0 × 23.3 mm, NCHUZOO 12933, Lijia, Beinan, Taitung, 1250 m a.s.l, coll. S.-P. Wu, 22 Aug. 2001; 1 male, 28.4 × 24.6, NCHUZOO 12938, 32.9 × 28.7 mm, ZRC 2003.0036, Luanshan, Yanping, Taitung, coll. H.-T. Shih, 10 Jan. 2001; 4 males, 29.0 × 24.6–

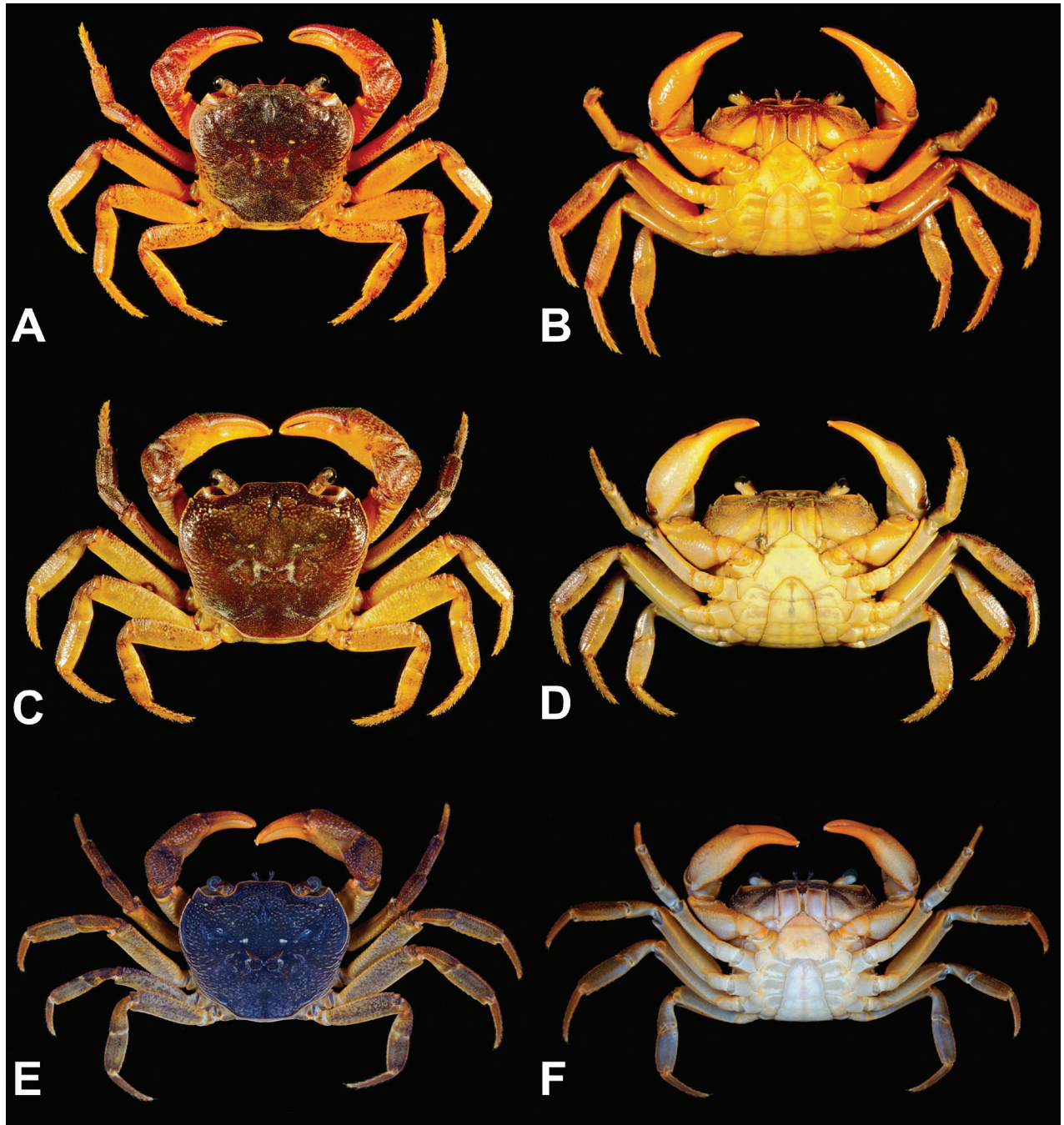


Figure 4. Color in life of *Candidiopotamon rathbuni* (De Man, 1914) (**A, B**) and *Candidiopotamon penglai* sp. nov. (**C–F**). **A, C, E** overall dorsal view **B, D, F** overall ventral view **A, B** NCHUZOL 15181 (male, 28.0 × 23.9 mm, Rihyuetan, Nantou, western Taiwan) **C, D** NCHUZOL 15204 (male, 39.7 × 34.4 mm, Nanrenshan, Pingtung, southern Taiwan); NCHUZOL 15224 (paratype male, 36.4 × 30.9 mm, Liyu Lake, Shoufeng, Hualien, eastern Taiwan).

35.6 × 29.3 mm, 1 female, 21.9 × 18.4 mm, NCHUZOL 15218, Taiban, Daren, Taitung, coll. H.-C. Liu, 22 Apr. 1995; 1 female, 44.7 × 35.9 mm, NCHUZOL 15210, Dawu, Taitung, coll. H.-C. Liu and C.-H. Wang, 22 Aug. 1997; 1 male, 28.9 × 24.1 mm, 1 female, 29.8 × 25.0 mm, NCHUZOL 12943, Dawu, Taitung, coll. H.-T. Shih, 9 Jan. 2001; 2 males, 40.1 × 33.6, 42.9 × 36.2 mm, 1 female, 38.4 × 31.5 mm, NCHUZOL 15207, Danlu, Shihzih, Pingtung, coll. H.-T. Shih, 12 Mar. 1999; 1 male, 28.0 × 23.3 mm, NCHUZOL 15208, Wangsha, Hengchun, Pingtung, coll. H.-T. Shih, 5 Mar. 2000; 1 male, 31.0 × 25.2 mm, RUMF-



Figure 5. Color in life of *Candidiopotamon rathbuni* (De Man, 1914) (**A–D**) and *Candidiopotamon penglai* sp. nov. (**E–H**). **A, B** NCHUZ00L 15194 (male, 35.4 × 31.2 mm, Tai-an, Miaoli, northwestern Taiwan) **C** NCHUZ00L 15211 (male, 24.8 × 22.1 mm, Dongshih, Taichung, western Taiwan) **D** NCHUZ00L 15181 (male, 28.0 × 23.9 mm, Rihyuetan, Nantou, western Taiwan) **E, F** NCHUZ00L 15204 (2 males, 39.7 × 34.4 mm, 40.6 × 34.3 mm, Nanrenshan, Pingtung, southern Taiwan) **G** NCHUZ00L 15224 (paratype male, 36.4 × 30.9 mm, Liyu Lake, Shoufeng, Hualien, eastern Taiwan) **H** NCHUZ00L 15229 (male, 33.1 × 29.7 mm, Jili Lake, Guangfu, Hualien, eastern Taiwan).

ZC-57, Wangsha, Hengchun, Pingtung, coll. H.-T. Shih, 31 Mar. 1999; 2 males, 41.7 × 35.0, 41.9 × 35.0 mm, 1 female, 35.7 × 29.8 mm, NCHUZ00L 15217, Nanrenshan, Manjhoul, Pingtung, coll. H.-T. Shih, 19 Oct. 1996; 3 males, 37.0 × 30.8–40.6 × 34.7 mm, NCHUZ00L 15204, Nanrenshan, Manjhoul, Pingtung, coll. R.-H. Lee, 8 Feb. 2003; 1 male, 44.3 × 37.0 mm, ZRC 2003.0037, Nanrenshan, Manjhoul, Pingtung, coll. H.-T. Shih, 24 Feb. 1999; 1 male, 43.8 × 36.7 mm, RUMF-ZC-58, Kenting, Hengchun, Pingtung, coll. H.-T. Shih, 6 Jan. 2000; 1 male, 30.6 × 26.2 mm, 1 female, 35.2 × 29.3 mm, NSMT-Cr 15171, Sihchong R., Mudan, Pingtung, coll. H.-T. Shih, 10 Mar. 1999; 1 male, 38.7 × 32.4 mm, 3 females, 38.3 × 33.5–43.6 × 35.9 mm, NCHUZ00L 15209, Nanshih, Shihzih, Pingtung, coll. H.-C. Liu, 22 Jul. 1997.

Diagnosis. Carapace subtrapezoidal, CW 1.14–1.24× CL (mean 1.18, $n = 45$), dorsal surface almost flat, relatively rough, epigastric and postfrontal cristae distinct, both cristae represented by 1–3 oblique lines of granules, lateral end of postfrontal cristae far apart from epibranchial tooth; external orbital and epibranchial teeth distinct, sharp, directed anteriorly. G1 terminal segment proportionally longer and slender, distal opening directed laterally, distal inner edge with keel-like projection in dorsal view, projection proportionally large, directed more distally; G1 subterminal segment curving inwards (in eastern to southeastern Taiwan populations) or straight (in southern Taiwan populations).

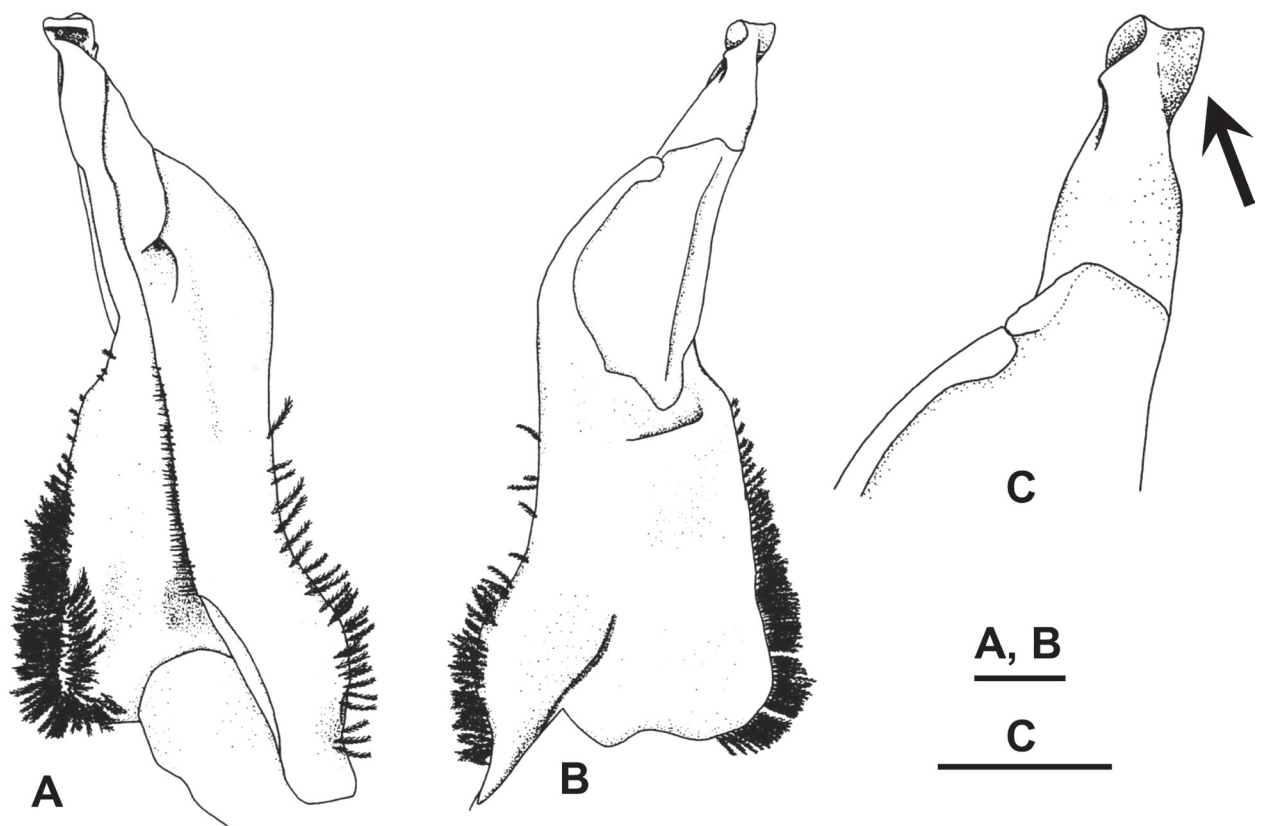


Figure 6. *Candidiopotamon penglai* sp. nov., holotype male (38.4 × 33.4 mm) from Ji-an, Hualien (NCHUZ00L 12951), G1 in bent form **A** left G1, ventral view **B** left G1, dorsal view **C** left G1 terminal segment, dorsal view. Scale bars: 1 mm. Arrow indicates the keel-like projection on the distal inner edge of the terminal segment.

Etymology. The new species is named after Penglai, the ancient name of Taiwan. It also refers to the fact that the island of Taiwan was formed by the Penglai Orogeny (ca 5 million years ago) (Teng 1990; Liu et al. 2000), and the ancestral *Candidiopotamon* most likely colonized Taiwan at that time (Shih et al. 2006). The species name is used as a noun in apposition.

Coloration (Figs 4C–F, 5E–H). Same as *C. rathbuni*, but young individuals tend to be reddish (e.g. Fig. 5H).

Distribution (Fig. 1). *Candidiopotamon penglai* sp. nov. is distributed along the eastern side of the Central Range of Taiwan (except for the northeastern area), i.e., Hualien and Taitung in eastern Taiwan, as well as Hengchun Peninsula (the southern part of Pingtung and the southern tip of Taitung) in southern Taiwan. The type locality of *C. penglai* sp. nov. is Ji-an, Hualien (Fig. 1: no. 55).

Habitat. Same as *C. rathbuni*.

Remarks. A detailed morphological comparison reveals that specimens of *C. rathbuni* from western Taiwan and *C. penglai* sp. nov. from eastern Taiwan show differences in G1 structure. *Candidiopotamon rathbuni* has a smaller and more laterally directed keel-like projection on the distal inner part of the terminal segment (Fig. 3D3) [vs larger and more distally directed structure in *C. penglai* (Figs 5C, 6C)]. Furthermore, *C. rathbuni* show almost straight subterminal segment of G1 (Fig. 3D2), whereas those of *C. penglai* are varied either straight (S clade, Fig. 7) or bent (E1, E2 and SE clades, Fig. 6) (Figs 1, 5B, 6B; see Discussion).

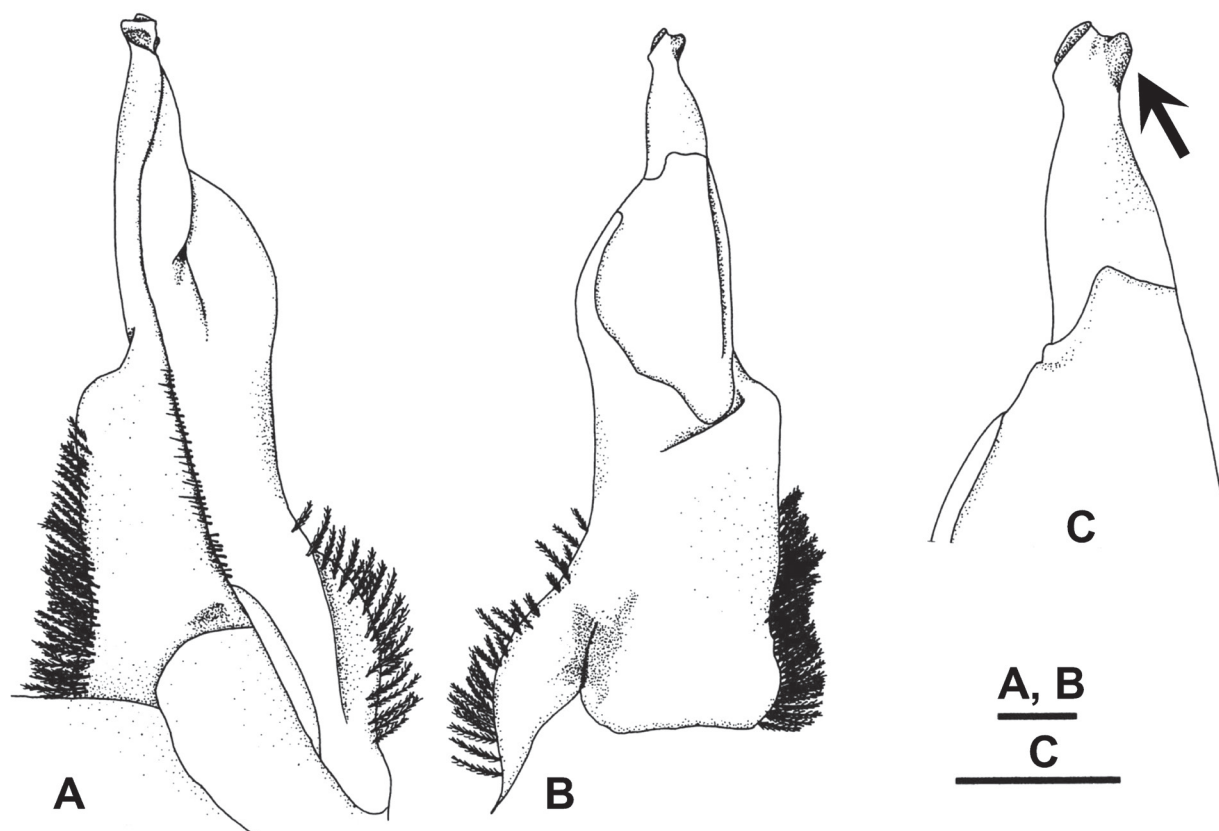


Figure 7. *Candidiopotamon penglai* sp. nov., male (42.9 × 36.2 mm) from Shihzih, Pingtung (NCHUZ00L 15207), G1 in straight form **A** left G1, ventral view **B** left G1, dorsal view **C** left G1 terminal joint, dorsal view. Scale bars: 1 mm. Arrow indicates the keel-like projection on the distal inner edge of the terminal segment.

This new species includes clades from eastern Taiwan (E1, E2, SE and S, see Fig. 1) that are genetically distinct from *C. rathbuni* from western Taiwan (NW, W and SW) (Table 2, Fig. 2), with a reliable character of G1 also separating the two species (see above). Within *C. penglai* sp. nov., there are two forms of the curvature in G1, with the bent form found in the E1, E2 and SE clades, and the straight form in the S clade (Fig. 1; see Discussion).

Discussion

The phylogenetic pattern of *Candidiopotamon* in Taiwan inferred by the combined 16S and COI (Fig. 2) agrees with the phylogeny exclusively based on 16S (Shih et al. 2006). But with the inclusion of the COI marker and specimens from more sites in NW and E2 clades (Fig. 1), the tree in this study obtains higher nodal supports, and more distinct clades can be observed (Fig. 2). The separation of the eastern and western clades was proposed to be caused by the isolating effect of the Taiwan Central Range during 5.7 ± 1.1 million years ago (Shih et al. 2006).

The genetic distance between these two major clades from eastern and western Taiwan is $\geq 10.72\%$ (K2P distance) (Table 2), which is much higher than most recognized species within the Potamidae, e.g., the minimum interspecific distances are between 1.31%–3.17% in *Geothelphusa* spp.; 6.7% in *Johora* spp.; 9.97% in *Lacunipotamon*; 2.17% in *Nanhaipotamon* spp.; 1.8% in *Longpotamon yangtsekiense* complex; and 6.22%–7.59% in *Tiwaripotamon* (see Chu et al. 2015; Do et al. 2016; Huang et al. 2020; Shy et al. 2021). Representatives of the two major clades are very similar in general morphology but can still be usually distinguished by the structure of the G1 (Fig. 1; see Remarks under *C. rathbuni*). As a result, we establish a new species, *Candidiopotamon penglai* sp. nov., for the eastern major clade. *Candidiopotamon penglai* sp. nov. can be considered a pseudocryptic species (i.e., minor morphological difference, and only receiving species status after other methods have been deployed to strengthen the case; as introduced by Ragionieri et al. 2012 and defined by Chu et al. 2015). Similar cases have been reported in several other brachyuran crabs (e.g., Ragionieri et al. 2012; Shih et al. 2013, 2018; Ng and Shih 2014, 2015, 2023; Lai et al. 2017; Fratini et al. 2019; Prema et al. 2022).

The maximum intraspecific distances within the Taiwanese species of *Candidiopotamon* are large, with 7.45% in *C. rathbuni* and 4.41% in *C. penglai* sp. nov. (Table 2). The large maximum intraspecific distances in some species of freshwater crabs have been proposed to be caused by the wide distribution with different degrees of geographical barriers, e.g., 3.33% in *Geothelphusa takuan* Shy, Ng & Yu, 1994 in northwestern Taiwan (Shy et al. 2021) and 5.25% in *Tiwaripotamon pluviosum* Do, Shih & Huang, 2016 in the boundary region between Vietnam and China (Do et al. 2016).

In *C. rathbuni*, three clades are recognizable, NW, W and SW (Fig. 2), with NW and W being closely related. In the present study, we found morphological variations in the G1 of *C. rathbuni*: the width of the subterminal segment gradually becomes stouter from northwestern to southwestern clades (Fig. 1). The morphological differences, however, are too subtle to recognize each clade consistently. In *C. penglai* sp. nov., both S and SE clades are monophyletic, but two clades are found in the eastern region between Beinan R. and Liwu R. (Figs 1, 2). The morphological study shows that the E1, E2 and SE clades have bent G1, but the G1 in the S clade is straighter (Fig. 1). The curvature or sinuosity

of the G1 has been often used as an important character in taxonomic work on freshwater crabs. It is known that the shape of G1 can be variable. Brandis et al. (1999) showed that the terminal segment of G1 can be passively bent in its flexible zone, and that the shape of the flexible zone is responsible for the direction of deflection of the terminal segment. In the case of the E1, E2 and SE clades of *C. penglai* sp. nov., since the subterminal segment of the G1 is bent sideward direction (mesially) constantly from the synovial membrane, it is difficult to attribute the curvature to the passive bent of the flexible zone.

In a paper dealing with the freshwater decapod fauna of Yunlin, Chiayi, and Tainan counties of western Taiwan, Shy et al. (1996) diagnosed G1 of *C. rathbuni* as “curving inwards”, and the drawing of G1 showed a bent shape as well (Shy et al. 1996: fig. 17c, d). This description and figure were followed by Shy and Yu (1999: 97, “fig. 31” on p. 106) and Shy et al. (2020: 5, fig. 16). This specimen used, NTOU F10129 (Department of Environmental Biology and Fisheries Science, National Taiwan Ocean University, Keelung, Taiwan), was collected from Meishan, Chiayi Co., but the G1 was dried before (Jhy-Yun Shy personal communication), which may explain, why the G1 is more sinuous, unlike those from western clades.

Conclusions

In this study, a new pseudocryptic species, *Candidiopotamon penglai* sp. nov., from eastern Taiwan is established based on minor morphological differences of the G1 and pronounced differences in mitochondrial 16S and COI sequences. Morphological variation of the G1 was found in both *C. rathbuni* and *C. penglai* sp. nov. In *C. rathbuni*, a tendency from robust G1 in the northwestern population to slender G1 in southwestern populations was observed. In *C. penglai* sp. nov., northern and southern populations show the bent and straight form in the subterminal segment of G1, respectively.

Acknowledgements

The authors thank Hsueh-Wen Chang (National Sun Yat-sen University, Taiwan), Shigemitsu Shokita (University of the Ryukyus, Japan), Chia-Hsiang Wang (National Taiwan Museum, Taiwan), Hung-Chang Liu (Taiwan Academy of Ecology, Taiwan), Peter K. L. Ng and Ngan-Kee Ng (National University of Singapore, Singapore), Hisakatsu Minei (Kyushu University, Japan), Jhy-Yun Shy (National Penghu University, Taiwan), and Dark Brandis (Senckenberg Research Institute, Germany) for their help on various work and suggestions, and Min-Wan Chen for measuring specimens and performing part of the molecular work. We acknowledge Peter K. L. Ng (ZRC) and Chao Huang (Australian Museum Research Institute), as well as the subject editor Sameer Kumar Pati, who greatly improved the manuscript.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was supported by a grant from the National Science and Technology Council (NSTC 112-2313-B-005-051-MY3), Executive Yuan, Taiwan, to HTS. TN was supported by the 21st Century COE program of the University of the Ryukyus.

Author contributions

HTS conceived this study, performed the molecular analysis, and drafted the manuscript. TN performed the morphological description, participated in the discussion and drafted the manuscript. CDS participated in the discussion and final touches to the manuscript. All authors read and approved the final manuscript.

Author ORCIDs

Hsi-Te Shih  <https://orcid.org/0000-0003-1317-8783>

Tohru Naruse  <https://orcid.org/0000-0001-9212-5246>

Data availability

All of the data that support the findings of this study are available in the main text.

References

- Balss H (1922) Ostasiatische Decapoden. IV. Die Brachyrrhynchen (Cancridea). Archiv für Naturgeschichte 88A(11): 4–166.
- Balss H (1937) Potamoniden (Decapoda Brachyura) der Philippinen und des Malayischen Archipels. Internationale Revue der Gesamten Hydrobiologie 34(1–6): 143–197. <https://doi.org/10.1002/iroh.19370340111>
- Bott R (1967) Potamiden aus Ost-Asien (*Parapotamon* De Man, *Sinopotamon* n. gen., *Candidiopotamon* n. gen., *Geothelphusa* Stimpson) (Crustacea, Decapoda). Senckenbergiana Biologica 48: 203–215.
- Bott R (1970) Die Süßwasserkrabben von Europa, Asien, Australien und ihre Stammesgeschichte. Eine Revision der Potamoidea und der Parathelphusoidea. (Crustacea, Decapoda). Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 526: 1–338.
- Brandis D, Storch V, Türkay M (1999) Morphology and function of the copulatory system in freshwater crabs of the genus *Potamon*. Journal of Morphology 239: 157–166. [https://doi.org/10.1002/\(SICI\)1097-4687\(199902\)239:2<157::AID-JMOR4>3.0.CO;2-E](https://doi.org/10.1002/(SICI)1097-4687(199902)239:2<157::AID-JMOR4>3.0.CO;2-E)
- Chen WJ, Shy JY, Cheng JH, Hsu MJ (2001) Freshwater crabs in the water systems of Kaohsiung and Pingtung areas. Nature Conservation Quarterly 36: 42–47. [In Chinese]
- Chen WJ, Tsai SH, Hsu MJ, Cheng JH (2003) Freshwater Crab Fauna in Southern Taiwan. Kaohsiung County Government, Kaohsiung, Taiwan, 125 pp. [In Chinese]
- Chiu JK (1962a) Intermediate hosts of *Paragonimus westermanii* at Shen-Keng District of Taipei County, Taiwan (Formosa). The Journal of Parasitology 48(3): 421–426. <https://doi.org/10.2307/3275206>
- Chiu JK (1962b) Two species of *Paragonimus* occurring at Alilao Village of Taipei County, Taiwan (Formosa). Kyushu Journal of Medical Science 13: 51–66.
- Chiu JK (1964) Prevalence of *Paragonimus* infection in crab hosts in Taiwan. Bulletin of the Institute of Zoology, Academia Sinica 3: 63–73.
- Chiu YW, Liang SH, Hsieh BS, Huang DJ, Gan YC (2015) 50 selected springs of Taiwan. Forestry Bureau, Council of Agriculture, Executive Yuan, Taipei, 231 pp. [In Chinese]

- 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 (Eds) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea. Volume 9C-II. Decapoda: Brachyura (Part 2). Brill, Leiden, 775–820. https://doi.org/10.1163/9789004190832_016
- Crandall KA, Fitzpatrick Jr JFJ (1996) Crayfish molecular systematics: Using a combination of procedures to estimate phylogeny. Systematic Biology 45(1): 1–26. <https://doi.org/10.1093/sysbio/45.1.1>
- Dai AY (1999) Fauna Sinica. Arthropoda: Crustacea: Malacostraca: Decapoda: Parathelphusidae, Potamidae. Science Press, Beijing, 501 pp. [30 pls] [In Chinese]
- Dai AY, Feng ZQ, Chen GX, Song YZ (1984) Medical Crustaceans in China. Science Press, Beijing, 146 pp. [In Chinese]
- Davie PJF, Guinot D, Ng PKL (2015) Anatomy and functional morphology of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FR, von Vaupel Klein JC (Eds) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea. Volume 9C-I. Decapoda: Brachyura (Part 1). Brill, Leiden, 11–163. https://doi.org/10.1163/9789004190832_004
- De Man JG (1914) Note sur quelques Crustacés Décapodes Brachyures terrestres et d’eau douce appartenant au Musée Civique de Gènes. Annali del Museo Civico di Storia Naturale di Genova 46: 122–138. [pls I–III]
- 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. The Raffles Bulletin of Zoology 64: 213–219.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. Molecular Marine Biology and Biotechnology 3: 294–299.
- Fratini S, Cannicci S, Porri F, Innocenti G (2019) Revision of the *Parasesarma guttatum* species complex reveals a new pseudocryptic species in south-east African mangroves. Invertebrate Systematics 33: 208–224. <https://doi.org/10.1071/IS18028>
- Ho PH (2015) Arthropoda: crabs. In: Shao KT, Chang JS, Jeng MS, Tu TH, Ho CW, Chiu YW, Chan TY, Ho PH, Chao SM, Joung SJ, Lin PL (Eds) A Guide Book of Common Economic Aquatic Animals and Plants in Taiwan. Fisheries Agency, Council of Agriculture, R.O.C., Taipei, 136–159. [In Chinese]
- Horikawa Y (1940) A list of Formosan crabs. Scientific Taiwan 8(1): 21–31. [In Japanese]
- Huang C, Shih HT, Ahyong ST (2020) The freshwater crab genus *Lacunipotamon* Dai, Song, He, Cao, Xu & Zhong, 1975 (Decapoda, Brachyura, Potamidae), with descriptions of two new species from southwestern China. Crustaceana 93(11–12): 1361–1379. <https://doi.org/10.1163/15685403-bja10067>
- Hwang JJ, Mizue K (1985) Fresh-water crabs of Taiwan. Nagasaki Daigaku Suisangakubu Kenkyu Hokoku 57: 1–21.
- Iwata M (1940) Observations on the localities of the red crab and *Katayama formosana*. Journal of Kansai Medical Affairs 500: 1–4. [In Japanese]
- Jeng CH, Lin HJ, Wang MF, Jan CP (1998) Common Seashore Crabs of Taichung. Yung-An Elementary School, Taichung County, Taiwan, 92 pp. [In Chinese]
- Jeng CH, Wang MF, Lai SL, Hsu HL (2010) Ecological Notes of Crabs. Asian University, Taichung, Taiwan, 127 pp. [In Chinese]
- Jeng MS (1998) The Prawns and Crabs of Kenting National Park. Kenting National Park, Pingtung, Taiwan, 133 pp. [In Chinese]
- Jeng MS, Shao KT, Fung HR, Tzeng CS (1997) Northeast Coast Area. Investigations into ecological resources and monitoring (III). Ministry of Transport and Tourism, Taipei County, Taiwan, [x+]194 pp. [In Chinese]

- Jeng MS, Shao KT, Fung HR, Tzeng CS, Wu SH (1998) Northeast Coast Area. Investigations into ecological resources and monitoring (IV). Ministry of Transport and Tourism, Taipei County, Taiwan, [xiii+]182 pp. [24 figs] [In Chinese]
- Jeng MS, Shao KT, Fung HR, Tzeng CS, Yang JT (1994) Northeast Coast Area. Investigations into ecological resources and monitoring (I). Ministry of Transport and Tourism, Taipei County, Taiwan, vii+206 pp. [In Chinese]
- Jeng MS, Shao KT, Fung HR, Tzeng CS, Yang JT (1996) Northeast Coast Area. Investigations into ecological resources and monitoring (II). Ministry of Transport and Tourism, Taipei County, Taiwan, [ix+]184 pp. [In Chinese]
- Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution* 16(2): 111–120. <https://doi.org/10.1007/BF01731581>
- Koba K (1936a) Studies on the Japanese Potamonidae (I): Notes on *Potamon rathbuni* de Man as a second intermediate host of *Paragonimus westermani* (Kerbert) in Formosa. *Transactions of the Natural History Society of Formosa* 26: 164–174. [In Japanese]
- Koba K (1936b) Revision of the specific name of a crab as a second intermediate host of *Paragonimus westermani* in Formosa. *Science Reports of the Tokyo Bunrika Daigaku. Section B* 29: 201–207.
- Lai JCY, Shih HT, Ng PKL (2017) The systematics of land crabs of the genus *Gecarcoidea* H. Milne Edwards, 1837, and recognition of a pseudocryptic species, *G. humei* (Wood-Mason, 1874) from the eastern Indian Ocean (Crustacea: Decapoda: Gecarcinidae). *Invertebrate Systematics* 31: 406–426. <https://doi.org/10.1071/IS16052>
- Lanfear R, Frandsen PB, Wright AM, Senfeld T, Calcott B (2017) PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution* 34: 772–773. <https://doi.org/10.1093/molbev/msw260>
- Lee JH (2001) A Field Guide to Crabs in Taiwan. Bigtrees Co., Taipei, 174 pp. [In Chinese]
- Lee JH, Tung SC (2000) Crabs of Tainan County Coast. Tainan County Government and Kung San Institute of Technology, Tainan, Taiwan, 72 pp. [In Chinese]
- Li JJ, Chiu YW (2013) Land Crabs of Hengchun Peninsula. National Museum of Marine Biology & Aquarium, Pingtung, Taiwan, 91 pp. [In Chinese]
- Li JJ, Chiu YW (2019a) An Atlas of Land Crabs on Hengchun Peninsula 2.0. National Museum of Marine Biology & Aquarium, Pingtung, Taiwan, 136 pp. [In Chinese]
- Li JJ, Chiu YW (2019b) A Field Guide of Land Crabs on Hengchun Peninsula 2.0. National Museum of Marine Biology & Aquarium, Pingtung, Taiwan, 64 pp. [In Chinese]
- Lin CC (1949) A catalogue of brachyurous Crustacea of Taiwan. *Quarterly Journal of the Taiwan Museum* 2: 10–33.
- Liu HC, Hartnoll RG (2017) Precocious mating in the freshwater crab *Candidiopotamon rathbunae* (De Man, 1914). *Crustaceana* 90(2): 225–233. <https://doi.org/10.1163/15685403-00003644>
- Liu HC, Li CW (2000) Reproduction of the freshwater crab, *Candidiopotamon rathbuni* De Man (Brachyura: Potamidae) in Taiwan. *Journal of Crustacean Biology* 20(1): 89–99. <https://doi.org/10.1163/20021975-99990019>
- Liu TK, Chen YG, Chen WS, Jiang SH (2000) Rates of cooling and denudation of the early Penglai Orogeny, Taiwan, as assessed by fission-track constraints. *Tectonophysics* 320(1): 69–82. [https://doi.org/10.1016/S0040-1951\(00\)00028-7](https://doi.org/10.1016/S0040-1951(00)00028-7)
- Maki M, Tsuchiya K (1923) A monograph of the Decapoda Crustacea of Formosa. Report, Department of Agriculture, Government Research Institute, Taihoku 3: 1–11, 1–215, 1–4. [pls 1–24] [In Japanese]

- Minei H (1974) Potamoid crabs of Taiwan, with description of one new species (Crustacea, Decapoda). *Journal of the Faculty of Agriculture, Kyushu University* 18(4): 239–251. <https://doi.org/10.5109/22860>
- Nakagawa K (1915a) Research on the development of *Paragonimus* (No. 3). I. The intermediate host of *Paragonimus*: An opinion on their entry and release. II. *Paragonimus* larval behavior and resistance. *Chugai-Iji-Shinpo* 850: 1035–1043. [In Japanese]
- Nakagawa K (1915b) Research on the development of *Paragonimus*: On the intermediate host. *Zyuzenkai-Zasshi* 20: 311–329. [In Japanese]
- Nakagawa K (1916) The mode of infection in pulmonary distomiasis: Certain freshwater crabs as intermediate hosts of *Paragonimus westermanii*. *The Journal of Infectious Diseases* 18(2): 131–142. <https://doi.org/10.1093/infdis/18.2.131>
- Nakagawa K (1917) Human pulmonary distomiasis caused by *Paragonimus westermani*. *The Journal of Experimental Medicine* 26(3): 297–323. <https://doi.org/10.1084/jem.26.3.297>
- Naruse T, Segawa RD, Aotsuka T (2007) Two new species of freshwater crab (Crustacea: Decapoda: Potamidae) from Tokashiki Island, central Ryukyu Islands, Japan. *Systematics and Biodiversity* 5(4): 409–415. <https://doi.org/10.1017/S1477200007002551>
- Naruse T, Segawa R, Shokita S (2004) *Amamiku*, a new genus for the true freshwater crab, *Candidiopotamon amamense* Minei, 1973 (Decapoda: Brachyura: Potamidae), from the Central Ryukyu Islands, Japan. *Zootaxa* 653(1): 1–8. <https://doi.org/10.11646/zootaxa.653.1.1>
- Ng PKL (1988) *The Freshwater Crabs of Peninsular Malaysia and Singapore*. Shinglee Press, Singapore, 156 pp.
- Ng PKL (2000) Book review: A.-Y. Dai. 1999. *Fauna Sinica. Crustacea: Decapoda: Parathelphusidae, Potamidae*: 1–501., pls. 1–30. (Science Press, 16 Donghuangchenggen, Bei Jie, Beijing 100717, People's Republic of China). [In Chinese with English abstract.] [ISBN 7-03-006407-0] Hard cover. *Crustaceana* 73: 249–251.
- Ng PKL, Shih HT (2014) The systematics of the land crabs of the *Discoplax hirtipes* (Dana, 1851) species-group (Crustacea: Decapoda: Brachyura: Gecarcinidae), with description of a new species from the eastern Indian Ocean. *The Raffles Bulletin of Zoology (Supplement 30)*: 109–135.
- Ng PKL, Shih HT (2015) The land crabs of the *Discoplax longipes* A. Milne-Edwards, 1867 species group, with description of a new species from Guam (Crustacea: Decapoda: Brachyura: Gecarcinidae). *Zootaxa* 3980: 379–405. <https://doi.org/10.11646/zootaxa.3980.3.3>
- Ng PKL, Shih HT (2023) *Tuerkayana latens*, a new species of land crab from French Polynesia, with a discussion on the phylogeny of the genus (Crustacea: Decapoda: Brachyura: Gecarcinidae). *Zoological Studies (Taipei, Taiwan)* 62: 10. <https://doi.org/10.6620/ZS.2023.62-10>
- Ng PKL, Guinot D, Davie PJF (2008) *Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world*. *The Raffles Bulletin of Zoology (Supplement 17)*: 1–296.
- Ng PKL, Shih HT, Ho PH, Wang CH (2017) An updated annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *Journal of the National Taiwan Museum* 70(3/4): 1–208. [https://doi.org/10.6532/JNTM.201712_70\(3;4\).01](https://doi.org/10.6532/JNTM.201712_70(3;4).01)
- Ng PKL, Wang CH, Ho PH, Shih HT (2001) An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum Special Publication Series 11*: 1–86.

- Oshima M (1921) Supplement of the species list of the crabs and shrimps of the decapod crustaceans from Formosa. Zoological Magazine, Tokyo 33: 122–124. [In Japanese]
- Palumbi SR, Martin A, Romano S, Mcmillan WO, Stice L, Grabowski G (1991) The Simple Fool's Guide to PCR. A Collection of PCR Protocols, version 2. Honolulu, Hawaii, University of Hawaii, 45 pp.
- Parisi B (1916) I Decapodi Giapponesi del Museo di Milano IV. Cyclometopa. Atti della Società italiana di scienze naturali e del Museo civico di storia naturale di Milano 55: 153–190.
- Prema M, Hsu JW, Shih HT, Ravichandran S (2022) First record of the genus *Pseudohelice* Sakai, Türkey & Yang, 2006 from India and description of a new pseudocryptic species (Crustacea: Brachyura: Varunidae). Zoological Studies (Taipei, Taiwan) 61: 56. <https://doi.org/10.6620/ZS.2022.61-56>
- Pretzmann G (1963) Über einige süd-und ostasiatische Potamoniden. Annalen des Naturhistorischen Museums in Wien 66: 361–372.
- Ragionieri L, Fratini S, Schubart CD (2012) Revision of the *Neosarmatium meinerti* species complex (Decapoda: Brachyura: Sesarmidae), with descriptions of three pseudocryptic Indo-West Pacific species. The Raffles Bulletin of Zoology 60: 71–87.
- Ronquist F, Huelsenbeck JP, Teslenko M, Nylander JAA (2020) MrBayes 3.2 manual. <https://nbisweden.github.io/MrBayes/manual.html> [Accessed 2 Feb. 2023]
- 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. Systematic Biology 61(3): 539–542. <https://doi.org/10.1093/sysbio/sys029>
- Ryder OA (1986) Species conservation and systematics: The dilemma of subspecies. Trends in Ecology & Evolution 1(1): 9–10. [https://doi.org/10.1016/0169-5347\(86\)90059-5](https://doi.org/10.1016/0169-5347(86)90059-5)
- Sakai T (1939) Studies on the Crabs of Japan. IV. Brachygnatha, Brachyrhyncha. Yoken-do, Tokyo, 365–741 + 1–23 [=index]. [pls 42–111]
- Sakai T (1940) Bio-geographic review on the distribution of crabs in Japanese waters. Records of Oceanographic Works in Japan 11: 27–63.
- Sakai T (1976) Crabs of Japan and the Adjacent Seas. Kodansha, Tokyo, 773 pp. [251 pls]
- Sasaki J (2019) The Species List of Decapoda, Euphausiacea, and Stomatopoda, all of the World, version 03-3.1. Local Independent Administrative Agency Hokkaido Research Organization, Resources Management and Enhancement Division, Abashiri Fisheries Research Institute, Fisheries Research Department, Hokkaido, Japan, 14644 pp. <https://doi.org/10.13140/RG.2.2.22353.89446>
- Schubart CD (2009) Mitochondrial DNA and decapod phylogenies: the importance of pseudogenes and primer optimization. In: Martin JW, Crandall KA, Felder DL (Eds) Decapod Crustacean Phylogenetics. Crustacean Issues. CRC Press, Taylor & Francis Group, Boca Raton, London, New York 18: 47–65. <https://doi.org/10.1201/9781420092592-c4>
- Shih HT (2008) Diversity of the freshwater crabs from the Ryukyus and Japan. Wetlands Taiwan 68: 2–23. [In Chinese]
- Shih HT, Ng PKL (2011) Diversity and biogeography of freshwater crabs (Crustacea: Brachyura: Potamidae, Gecarcinucidae) from East Asia. Systematics and Biodiversity 9(1): 1–16. <https://doi.org/10.1080/14772000.2011.554457>
- Shih HT, Shy JY (2009) *Geothelphusa makatao* sp. nov. (Crustacea: Brachyura: Potamidae), a new freshwater crab from an uplifted Pleistocene reef in Taiwan. Zootaxa 2106(1): 51–60. <https://doi.org/10.11646/zootaxa.2106.1.4>

- Shih HT, Chan BKK, Ng PKL (2018) *Tubuca alcocki*, a new pseudocryptic species of fiddler crab from the Indian Ocean, sister to the southeastern African *T. urvillei* (H. Milne Edwards, 1852) (Crustacea, Decapoda, Brachyura, Ocypodidae). *ZooKeys* 747: 41–62. <https://doi.org/10.3897/zookeys.747.23468>
- Shih HT, Komai T, Liu MY (2013) A new species of fiddler crab from the Ogasawara (Bonin) Islands, Japan, separated from the widely-distributed sister species *Uca (Paraleptuca) crassipes* (White, 1847) (Crustacea: Decapoda: Brachyura: Ocypodidae). *Zootaxa* 3746(1): 175–193. <https://doi.org/10.11646/zootaxa.3746.1.8>
- Shih HT, Ng PKL, Chang HW (2004) Systematics of the genus *Geothelphusa* (Crustacea, Decapoda, Brachyura, Potamidae) from southern Taiwan: A molecular appraisal. *Zoological Studies (Taipei, Taiwan)* 43: 561–570.
- 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). *Journal of Biogeography* 36(4): 703–719. <https://doi.org/10.1111/j.1365-2699.2008.02024.x>
- Shih HT, Hsu JW, Chang K, Chen MW (2023) Taxonomy and phylogeography of the freshwater crab *Geothelphusa tawu* species complex (Crustacea: Decapoda: Potamidae) from southern Taiwan and offshore islets. *Zoological Studies (Taipei, Taiwan)* 62: 37. <https://doi.org/10.6620/ZS.2023.62-37>
- Shih HT, Ng PKL, Schubart CD, Chang HW (2007) Phylogeny and phylogeography of the genus *Geothelphusa* (Crustacea: Decapoda, Brachyura, Potamidae) in southwestern Taiwan based on two mitochondrial genes. *Zoological Science* 24(1): 57–66. <https://doi.org/10.2108/zsj.24.57>
- Shih HT, Hung HC, Schubart CD, Chen CA, Chang HW (2006) Intraspecific genetic diversity of the endemic freshwater crab *Candidiopotamon rathbunae* (Decapoda, Brachyura, Potamidae) reflects five million years of geological history of Taiwan. *Journal of Biogeography* 33(6): 980–989. <https://doi.org/10.1111/j.1365-2699.2006.01472.x>
- Shih HT, Ng PKL, Naruse T, Shokita S, Liu MY (2011) Pleistocene speciation of freshwater crabs (Crustacea: Potamidae: *Geothelphusa*) from northern Taiwan and southern Ryukyus, as revealed by phylogenetic relationships. *Zoologischer Anzeiger* 250(4): 457–471. <https://doi.org/10.1016/j.jcz.2011.07.004>
- Shih HT, Prema M, Kumar AAJ, Saher NU, Ravichandran S, Odhano S, Paulay G (2022) Diversity and distribution of fiddler crabs (Crustacea: Brachyura: Ocypodidae) around the Arabian Sea. *Zoological Studies (Taipei, Taiwan)* 61: 65. <https://doi.org/10.6620/ZS.2022.61-65>
- Shy JY, Lee PW (2009) Guide to the Taiwanese Freshwater Crabs. Morning Star Publishing, Taipei, 221 pp. [In Chinese]
- Shy JY, Yu HP (1999) Freshwater crabs of Taiwan. National Museum of Marine Biology and Aquarium, Pingtung, Taiwan, 114 pp. [In Chinese]
- Shy JY, Lai HT, Yu HP (1996) On the freshwater shrimps and crabs from the three southwestern counties Yunlin, Chiayi and Tainan of Taiwan. *Annual of Taiwan Museum* 39: 201–247. [In Chinese]
- Shy JY, Shih HT, Mao JJ (2014) Description of a new montane freshwater crab (Crustacea: Potamidae: *Geothelphusa*) from northern Taiwan. *Zootaxa* 3869(5): 565–572. <https://doi.org/10.11646/zootaxa.3869.5.6>
- Shy JY, Shih HT, Mao JJ (2021) *Geothelphusa boreas*, a new montane freshwater crab (Crustacea: Potamidae: *Geothelphusa*) from northeastern Taiwan, and the identity of *G. hirsuta* Tan & Liu, 1998. *Zootaxa* 5061(1): 93–104. <https://doi.org/10.11646/zootaxa.5060.1.4>

- Shy JY, Shih HT, Ng PKL (2020) Crustacean Fauna of Taiwan: Brachyuran Crabs, Vol. III - Freshwater Crabs - Potamidae, Gecarcinucidae. National Penghu University of Science and Technology, Penghu, Taiwan, [26+]232 pp.
- Stamatakis A (2006) RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* (Oxford, England) 22(21): 2688–2690. <https://doi.org/10.1093/bioinformatics/btl446>
- Tamura K, Stecher G, Kumar S (2021) MEGA11: Molecular Evolutionary Genetics Analysis version 11. *Molecular Biology and Evolution* 38(7): 3022–3027. <https://doi.org/10.1093/molbev/msab120>
- Teng LS (1990) Geotectonic evolution of late Cenozoic arc-continent collision in Taiwan. *Tectonophysics* 183(1–4): 57–76. [https://doi.org/10.1016/0040-1951\(90\)90188-E](https://doi.org/10.1016/0040-1951(90)90188-E)
- Terao A (1915) The second intermediate host of lung *Distoma*. Part 2. *Zoological Magazine*, Tokyo 27: 502–503. [In Japanese]
- Wang CH (1984) Primary studies on the crabs in Kenting National Park in Taiwan. *Annual of National Taiwan Museum* 27: 39–44. [In Chinese]
- Wang SW, Chiu YW, Huang HD, Lee KS, Wang WL, Liu SL, Yang SH (2021) Notes on freshwater coated grains of the Hengchun Peninsula. *Collection and Research* 33: 29–40.
- Waples RS (1991) Pacific salmon, *Oncorhynchus* spp., and the definition of “species” under the Endangered Species Act. *Marine Fisheries Review* 53(3): 11–22.
- Yeo DCJ, Ng PKL (2004) Recognition of two subfamilies in the Potamidae Ortmann, 1896 (Brachyura, Potamidae) with a note on the genus *Potamon* Savigny, 1816. *Crustaceana* 76(10): 1219–1235. <https://doi.org/10.1163/156854003773123456>
- Yu HP, Jeng MS, Chan TY, Ho PH, Shy JY (1996) Studies on the Land and Aquatic Decapod Crustacean Fauna of the Kenting National Park. Kenting National Park, Pingtung, Taiwan, [2+]79 pp. [In Chinese]