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ORIGINAL ARTICLE

Description of a new species of brackish-water crab of the genus *Ptychognathus* Stimpson, 1858 (Crustacea: Brachyura: Varunidae) from southern Taiwan

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ZOOBANK: http://zoobank.org/urn:lsid:zoobank.org:pub:8C0525FC-D198-462C-9678-36A9D13A61C2

ABSTRACT

The brackish-water crabs of the genus *Ptychognathus* Stimpson, 1858, the most diverse genus in the family Varunidae, inhabit the estuaries or seashores influenced by freshwater. *Ptychognathus sakaii*, a new species from Kenting, southern Taiwan, is described in this study, with a comprehensive key to the ten species of this genus from Taiwan. This new species is similar to its congeners, but can be distinguished mainly by the features of the carapace, ambulatory legs, and male first gonopods.

KEYWORDS

Decapoda, morphology, *Ptychognathus sakaii*, species diversity, taxonomy

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INTRODUCTION

The brackish-water crabs of the genus, *Ptychognathus* Stimpson, 1858, composed of 27 species currently, is the largest genus in the family Varunidae (Ng *et al.*, 2008; N.K. Ng, 2010; Sasaki, 2019; Hsu and Shih, 2020). *Ptychognathus* species inhabit mainly brackish-water environments from lower reaches of rivers, estuaries to seashores in the Indo-West Pacific,

from Madagascar to Easter Island, and main islands of Japan to New Caledonia (A. Milne-Edwards, 1873; De Man, 1895; Rathbun, 1907; Sakai, 1976; Yamamoto *et al.*, 2007). Despite their wide distributional range, most species of *Ptychognathus* are distributed in the Western Pacific region, with higher species diversity in Japan (including Ryukyus), Taiwan, the Philippines, and Indonesia (Ortmann, 1894; Rathbun, 1914; Cai and Ng, 2001; Osawa and N.K. Ng, 2006; Hsu and Shih, 2020). This genus has a clear diagnostic morphological character, *i.e.*, the third maxilliped's exopod is distinctly broader than that of ischium (Stimpson, 1858). However, because the members of the genus have highly varied size and characters of the carapace, chelipeds, and ambulatory legs (N.K. Ng, 2010), together with the presence of sympatric varunids, especially young individuals, it is often the case that *Ptychognathus* species were sometimes misidentified (N.K. Ng, 2010; Hsu and Shih, 2020). In addition, due to the similar morphologies and small size, some species in this genus are difficult to distinguish (Hsu and Shih, 2020). It is now a common approach to use molecular evidence to help identify species with similar morphologies (*cf.* Chu *et al.*, 2015), which is also the case in the family Varunidae (*e.g.*, Naser *et al.*, 2012; Markert *et al.*, 2014; N.K. Ng *et al.*, 2018; Shih *et al.*, 2019a; 2020).

The taxonomy of *Ptychognathus* from Taiwan has been revised in Hsu and Shih (2020). Ten species are well separated based on mitochondrial cytochrome c oxidase subunit I (COI), with intraspecific distances < 1.54 % and interspecific distances > 12.2 %, together with morphological characters, *viz.*, *Ptychognathus altimanus* (Rathbun, 1914), *Ptychognathus* aff. *barbatus*, *Ptychognathus hachijoensis* Sakai, 1955, *Ptychognathus ishii* Sakai, 1939, *Ptychognathus insolitus* Osawa and N.K. Ng, 2006, *Ptychognathus makii* Hsu and Shih, 2020, *Ptychognathus pilosus* De Man, 1892, *Ptychognathus stimpsoni* Hsu and Shih, 2020, *Ptychognathus takahasii* Sakai, 1939, and *Ptychognathus* sp. In this study, the species treated as "*Ptychognathus* sp." in Hsu and Shih (2020) is confirmed as new and described herein. A comprehensive key to the species from Taiwan is also provided.

Material and Methods

Specimens of the genus *Ptychognathus* collected from Taiwan were examined and deposited in the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL). Morphological characters were illustrated with the aid of a drawing tube attached to a stereomicroscope. The morphological characters and terminology used follow those of Davie *et al.* (2015). The abbreviations G1 and G2 are used for the male first and second gonopods respectively; and P2–P5 are used for the first to fourth ambulatory legs. Measurements of the maximum carapace width (CW) and carapace length (CL) are in millimeters (mm).

Comparative material

Ptychognathus hachijoensis: 2 males (7.5–7.6 × 6.3–6.4 mm), NCHUZOOL 15807, Sizihwan, Gushan, Kaohsiung, Taiwan, coll. P.-Y. Hsu *et al.*, 23 Jan. 2017; 2 males (9.9–12.1 × 8.0–9.7 mm), 1 female (11.7 mm × 9.8 mm), NCHUZOOL 15808, Sizihwan, Gushan, Kaohsiung, Taiwan, coll. P.-Y. Hsu *et al.*, 23 Jan. 2017; 4 males (7.0–9.8 × 5.9–7.7), 6 females (6.3–8.0 × 5.4–6.7 mm), NCHUZOOL 15809, Yanliao, Shoufeng, Hualien, Taiwan, coll. J.-W. Hsu, 29 Jun. 2016; 5 males (7.1–9.3 × 6.0–7.9 mm), 4 females (8.2–9.6 × 7.1–7.9 mm), NCHUZOOL 15810, Yanliao, Shoufeng, Hualien, Taiwan, coll. J.-W. Hsu, 29 Jun. 2016.

Ptychognathus insolitus: 1 male (6.8 × 4.9 mm), NCHUZOOL 16040, Yanliao, Shoufeng, Hualien, Taiwan, coll. J.-W. Hsu *et al.*, 14 Aug. 2016; 1 male (9.1 × 6.3 mm), 2 females (6.0–7.9 × 4.6–5.8 mm), NCHUZOOL 16041, Dulanwan, Donghe, Taitung, Taiwan, coll. P.-Y. Hsu, 29 Jun. 2016; 1 male (5.2 × 4.0 mm), NCHUZOOL 16042, Houwan, Hengchun, Pingtung, Taiwan, coll. J.-W. Hsu *et al.*, 17 Aug. 2016; 2 males (6.1–8.3 × 4.6–6.4 mm), NCHUZOOL 16044, Houwan, Hengchun, Pingtung, Taiwan, 3 Dec. 2016; 1 male (10.1 × 7.5 mm), NCHUZOOL 16045, Houwan, Hengchun, Pingtung, Taiwan, 22 Jun. 2014; 9 males (9.0–11.4 × 6.7–8.3 mm), 1 female (9.5 × 7.0 mm), NCHUZOOL 16046, Houwan, Hengchun, Pingtung, Taiwan, coll. J.-J. Li, 7 Apr. 2018; 1 male (7.5 × 4.9 mm), NCHUZOOL 16047, Tanzih Fishing

Port, Hengchun, Pingtung, Taiwan, coll. P.-Y. Hsu *et al.*, 7 May 2019.

Ptychognathus stimpsoni: male, holotype, (7.9 × 6.6 mm), NCHUZOOL 16501, Wanlitong, Hengchun, Pingtung, Taiwan, coll. J.-W. Hsu, 15 Aug. 2016; 16 males (7.3–10.9 × 6.0–8.8 mm), 4 females (7.5–8.8 × 6.3–7.2 mm), paratypes, NCHUZOOL 16502, Camiguin, the Philippines, 31 Aug. 2003.

Ptychognathus takahasii: 1 male (7.6 × 6.6 mm), NCHUZOOL 16056, Yanliao, Shoufeng, Hualien, Taiwan, coll. J.-W. Hsu, 29 Jun. 2016; 1 male (7.9 × 6.7 mm), 1 female (8.7 × 7.4 mm), 4 ovigerous females (8.7–9.5 × 7.6–8.3 mm), NCHUZOOL 16057, Gihui, Chenggong, Taitung, Taiwan, coll. J.-W. Hsu, 28 Apr. 2017; 4 males (8.6–10.1 × 7.8–8.9 mm), 2 females (7.0–9.7 × 6.3–8.5 mm), 2 ovigerous females (8.0–8.9 × 6.9–7.7 mm), NCHUZOOL 16058, Gihui, Chenggong, Taitung, Taiwan, coll. J.-W. Hsu, 28 Apr. 2017; 13 males (4.1–8.3 × 3.6–7.2 mm), 8 females (4.6–7.2 × 4.1–6.3 mm), 10 ovigerous females (4.3–8.3 × 3.8–7.5 mm), NCHUZOOL 16059, Houwan, Hengchun, Pingtung, Taiwan, coll. P.- Y. Hsu *et al.*, 11 Jul. 2017; 19 males (4.0–7.0 × 3.7–6.3 mm), 4 females (4.3–6.0 × 3.7–5.2 mm), 3 ovigerous females (6.5–7.2 × 5.7–6.2 mm), NCHUZOOL 16060, Houwan, Hengchun, Pingtung, Taiwan, coll. P.-Y. Hsu *et al.*, 11 Jul. 2017; 1 male (8.4 mm × 7.2 mm), 1 female (7.5 mm × 6.3 mm), NCHUZOOL 16061, Lanyu Island, Taitung, Taiwan, coll. P.-H. Ho, 19 Apr. 2002.

Systematics

Family Varunidae H. Milne Edwards, 1853

Subfamily Varuninae H. Milne Edwards, 1853

Genus *Ptychognathus* Stimpson, 1858

Ptychognathus sakaii sp. nov.

(Figs. 1–2)

Zoobank: urn:lsid:zoobank.org:act:BB270821-F221-4BB5-AA00-7012BFF47C68

Ptychognathus sp. — Hsu and Shih, 2020: 59, tab. 1.

Material examined. Holotype: male (6.7 × 5.5 mm), NCHUZOOL 17047, Dingtanzih, Hengchun, Pingtung, Taiwan, coll. J.-J. Li, 3 Apr. 2019. Paratypes: 3 males (5.7 × 5.0 mm; 6.0 × 5.2 mm; 6.7 × 5.5 mm), 1 ovigerous female (5.9 × 5.2 mm), NCHUZOOL 16503, same data as holotype.

Diagnosis. Carapace subquadrate, slightly broader than long, flat; dorsal surface smooth, glabrous, with noticeable groove between epigastric regions. Front broad, frontal margin lined with small, rounded granules, concave medially in dorsal view, slightly divided into indistinct two lobes. Anterolateral margin with 1 or 2 teeth behind external orbital tooth. Third maxillipeds broad, exopod almost equal to ischium. Chelipeds symmetrical in both sexes; proximal half of fingers of male with long dense soft setae, with single small pulvinus at base of fingers; both long dense soft setae and pulvinus absent in female. Ambulatory legs slender, distoanterior part of carpus distinctly compressed. Male pleon narrow. Distal margin of telson not concave, without tuft of setae. Male G1 slender, almost straight; G2 shorter than 1/4 length of G1.

Description. Carapace (Figs. 1, 2A) subquadrate, slightly broader than long, 1.14–1.21 times (n = 5) as broad as long, flat; dorsal surface smooth, glabrous (except for metabranchial region), regions weakly defined, with noticeable groove between epigastric regions, metabranchial region weakly sloping outwards. Front broad, weakly sloping forward, part near orbital regions slightly convex; frontal margin lined with small, rounded granules, concave medially in dorsal view, divided into distinct two lobes; frontal region indistinct, only separated into obscure lobes by shallow grooves.

Supraorbital margins lined with small granules. Anterolateral margin not granulated, with 1 or 2 teeth behind external orbital tooth; external orbital tooth largest and most distinct, blunt, slightly sloping forward, first tooth indistinct, second tooth indistinct or absent. Posterolateral margins slightly convergent posteriorly; posterolateral regions regularly furnished with short, soft setae. Infraorbital ridge consisting of 16–21 small, rounded granules in both sexes. Surface of pterygostome with sparse soft setae. Epistome broad, median part triangular, margin with tiny granules.

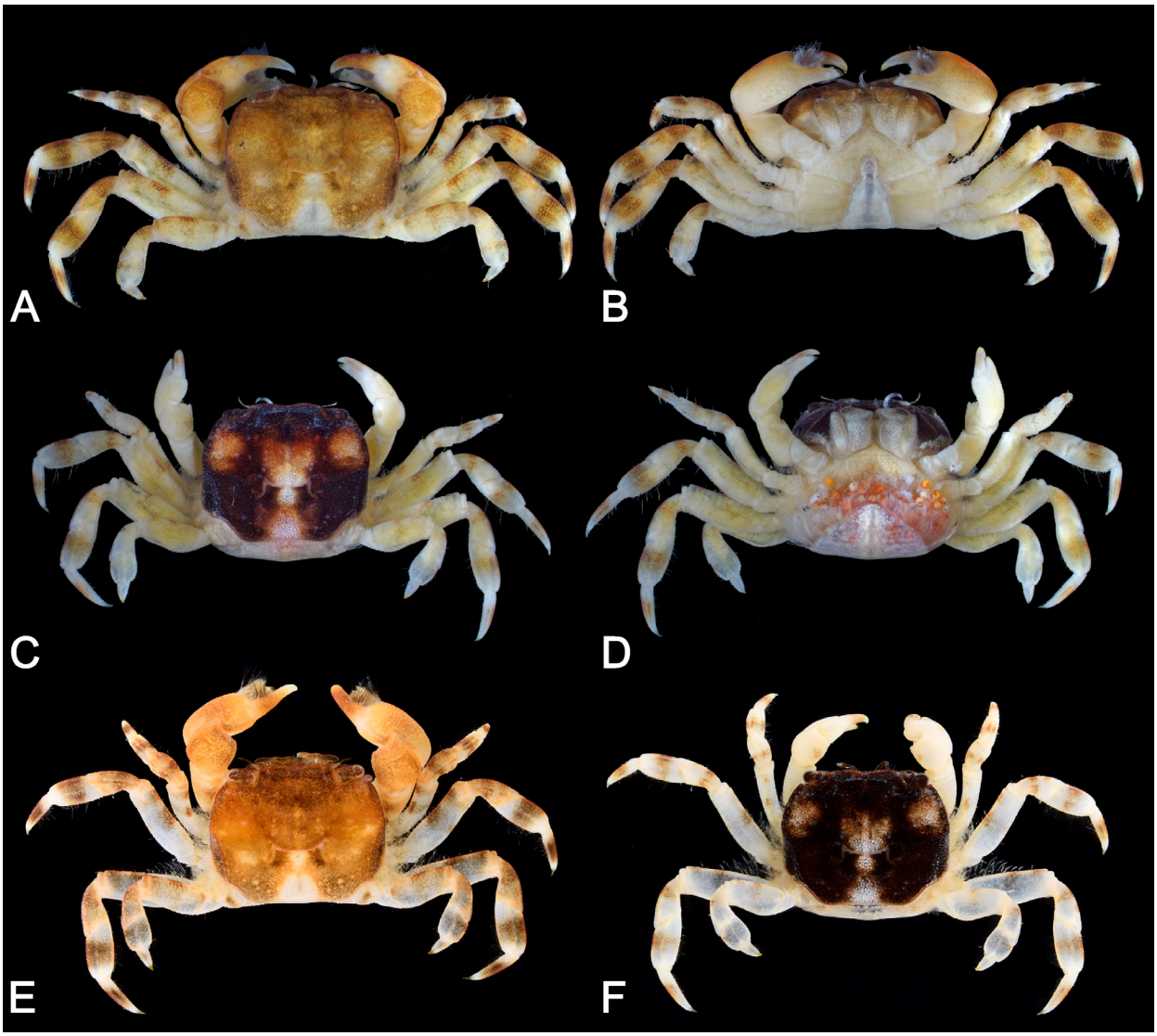

Figure 1. *Ptychognathus sakaii* sp. nov. **A, B, E,** holotype male (CW 6.7 mm; NCHUZOOL 17047). **C, D, F,** paratype female (CW 5.9 mm; NCHUZOOL 16503). **E, F,** color in life.

Third maxillipeds (Fig. 2B) broad, external surface glabrous, exopod almost equal to ischium; mesial part of merus with oblique shallow groove, anterolateral angle broadly rounded, slightly sloping laterally; ischium without distinct vertical shallow groove on external surface.

Chelipeds (Fig. 2D–F) symmetrical both in male and female, stronger in male. Merus without spines, dorsal margins with long soft setae, ventral margins glabrous. Surface of carpus glabrous, with several tiny granules, inner surface without obvious short setae, inner distal angle very blunt in male (Fig. 2C); inner distal angle obtuse triangular and with 2–3 tiny blunt teeth and a larger blunt spine in female. Outer surface of palm in male (Fig. 2D) smooth, without distinct granules; inner surface glabrous, slightly convex medially. Movable finger approximately as long as palm, cutting edges with 3–5 small blunt teeth subdistally; immovable finger slightly shorter than movable finger, cutting edges with 2–3 smaller teeth and 1 large blunt tooth; proximal half of fingers with long dense soft setae, with single small pulvinus at base of fingers in male, both long dense soft setae and pulvinus absent in female. Female (Fig. 2F) with outer surface of palm glabrous and granulated, inner surface glabrous, slightly convex medially; immovable finger with ridge consisting of small granules toward palm, fingers with sparse short setae at tips; movable finger slightly longer than palm.

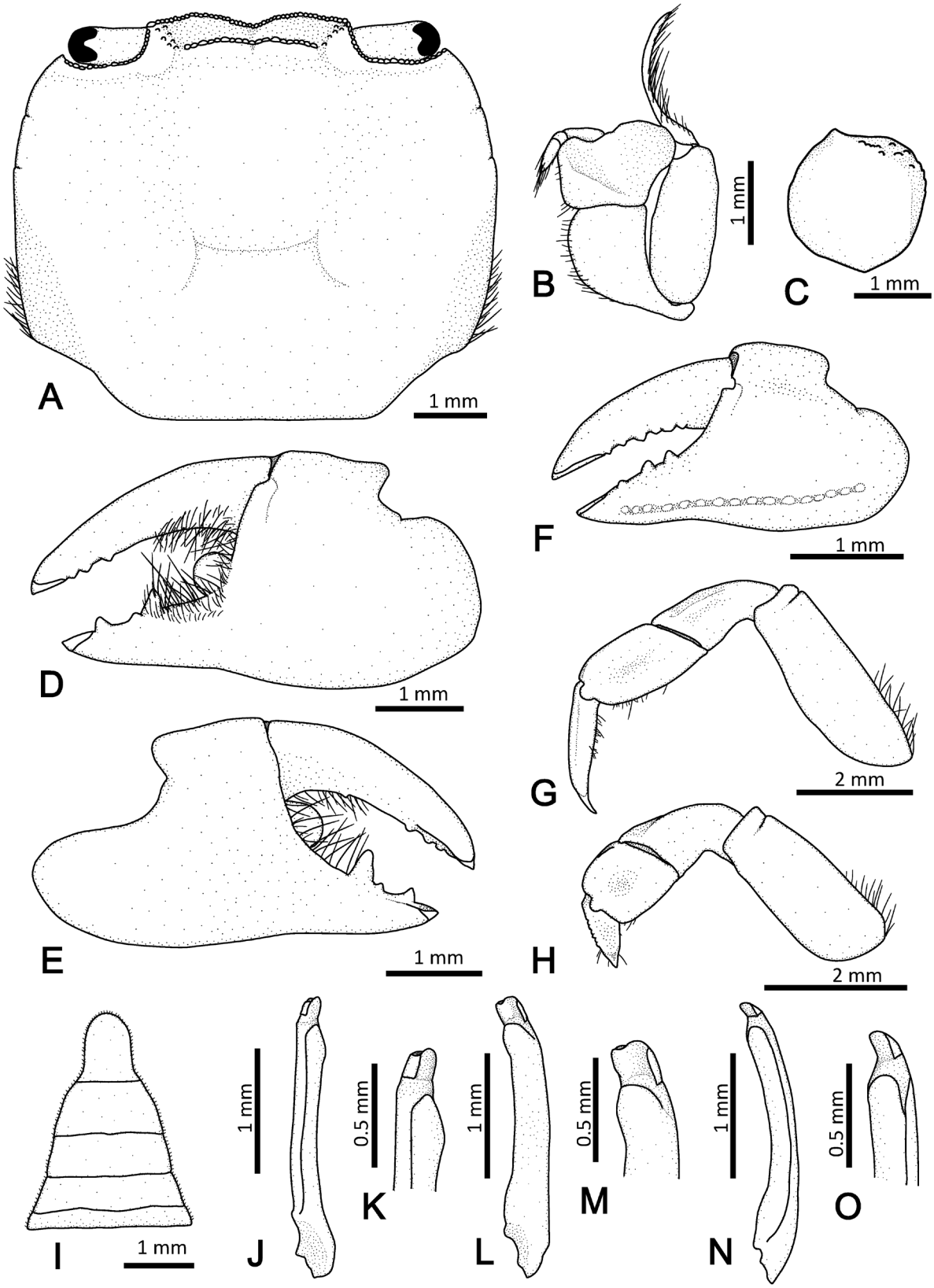

Figure 2. *Ptychognathus sakaii* sp. nov. **A–E, G–O**: holotype male (CW 6.7 mm, CL 5.5 mm; NCHUZOOL 17047); **F**, paratype female (CW 5.9 mm, CL 5.2 mm; NCHUZOOL 16503). **A**, carapace; **B**, left third maxilliped; **C**, left carpus of cheliped (dorsal view); **D**, outer view of male left cheliped; **E**, inner view of male left cheliped; pleon; **F**, outer view of female left cheliped; **G**, left third ambulatory leg; **H**, left forth ambulatory leg; **I**, male pleon; **J–O**, right G1; **J, K**, dorsal view; **L, M**, lateral view; **N, O**, ventral view.

Ambulatory legs (Figs. 1, 2G, H) slender, P3 and P4 longest. Meri without spines, with long soft setae on proximal half of anterior margin, proximal part of posterior margins with sparse short setae. Carpi in P2–P5 without setae on anterior and posterior margins, anterior margins of distal part distinctly compressed. Propodus as long as dactylus in P2–P4 (Figs. 1, 2G), propodus about 1.2 times length of dactylus in P5 (Fig. 2H), anterior margins of propodus and dactylus without setae, posterior margins of propodus sparsely setose, ventral surfaces of carpus and propodus almost glabrous. P4 (Fig. 2G) relatively long, anterior margins of propodus glabrous, posterior margins with sparse short setae. P5 (Fig. 2H) relatively short, anterior margins of propodus glabrous, posterior margins of distal part of propodus with tuft of short setae.

Male pleon (Fig. 2I) narrow, surface smooth, without any granules, lateral margins lined with short setae; telson tongue-shaped, slightly longer than sixth segment, distal margin of telson not concave, without tuft of setae.

Male G1 (Fig. 2J–O) slender, almost straight, distally curved outwards, tip chtinous, with two short semicircle-shaped lobes in lateral view (Fig. 2L, M), opened laterally and mesially, respectively; G2 shorter than 1/4 length of G1.

Coloration. Carapace and chelipeds varied from orange, yellowish-brown, deep wine to dark purple, with light brown or white spots on carapace; ventral surface of carapace and cheliped palm lighter than dorsal surface, usually light brown to white. Ambulatory legs white to light brown, with light brown spots or bands. Setae on cheliped palm light brown; setae on ambulatory legs dark brown to black.

Habitat. This species inhabits the intertidal area, with sediment composed of coral sand and pebbles. Individuals always hide under pebbles and were sometimes sympatric with *Ptychognathus* aff. *barbatus*, *P. hachijoensis*, and *Pseudograpsus albus* Stimpson, 1858 in Dingtanzih, Kenting, southern Taiwan.

Etymology. This species is named for the Japanese carcinologist Tune Sakai, who studied the crab fauna from Taiwan (*e.g.*, Sakai, 1939) and described two new species of *Ptychognathus* from Taiwan (*P. ishii* from Lanyu Island; *P. takahasii* from Danshuei).

Size. Largest male 6.7 × 5.5 mm (holotype, NCHUZOOL 17047); largest female (ovigerous) 5.9 × 5.2 mm (NCHUZOOL 16503).

Distribution. Only known from Kenting, southern Taiwan.

Remarks. This new species is similar to *P. hachijoensis*, *P. insolitus*, *Ptychognathus pusillus* Heller, 1865, *P. stimpsoni*, and *P. takahasii* in the characters of anterolateral margin of carapace (with indistinct teeth behind external orbital tooth), but can be distinguished by the features of carapace, ambulatory legs and male G1s.

Ptychognathus sakaii can be separated from *P. hachijoensis* by 1) posterior margins of the dactylus and propodus of ambulatory legs only sparsely setose (*vs.* with obvious dense setae on posterior margins of dactylus and propodus); 2) anterior margins of distal part of carpus distinctly compressed (*vs.* anterior margins of carpus are not distinctly compressed) (Figs. 2G, H, 3A; Sakai, 1976: text-fig. 349c; Fukui, 1989: figs. 15, 16; Osawa and Ng, 2006: fig. 2F); 3) part near tip of G1 straighter, only slightly curved outwards (*vs.* part near tip of G1 distinctly curved).

Ptychognathus sakaii can be separated from *P. insolitus* by 1) carapace subquadrate, with 1 or 2 teeth behind external orbital tooth on anterolateral margin (*vs.* carapace relatively broader, with only 1 indistinct tooth behind external orbital tooth on anterolateral margin, sometimes this tooth absent) (Figs. 2A, 3B; Osawa and Ng, 2006: figs. 1, 2A; Li, 2015: fig. 1E); 2) ambulatory legs comparatively broad and short, with short setae only on posterior margins of dactylus and propodus (*vs.* ambulatory legs comparatively slender, with long setae on anterior and posterior margins of dactylus and propodus) (Figs. 2G, H, 3B; Osawa and Ng, 2006: figs. 1, 4A–D); 3) G1s slender, almost straight, chitinous structures on tip comparatively slender (*vs.* G1s stout and slightly curved, chitinous structures stout) (Fig. 2J–O; Osawa and Ng, 2006: fig. 3E–G; Li, 2015: fig. 4B).

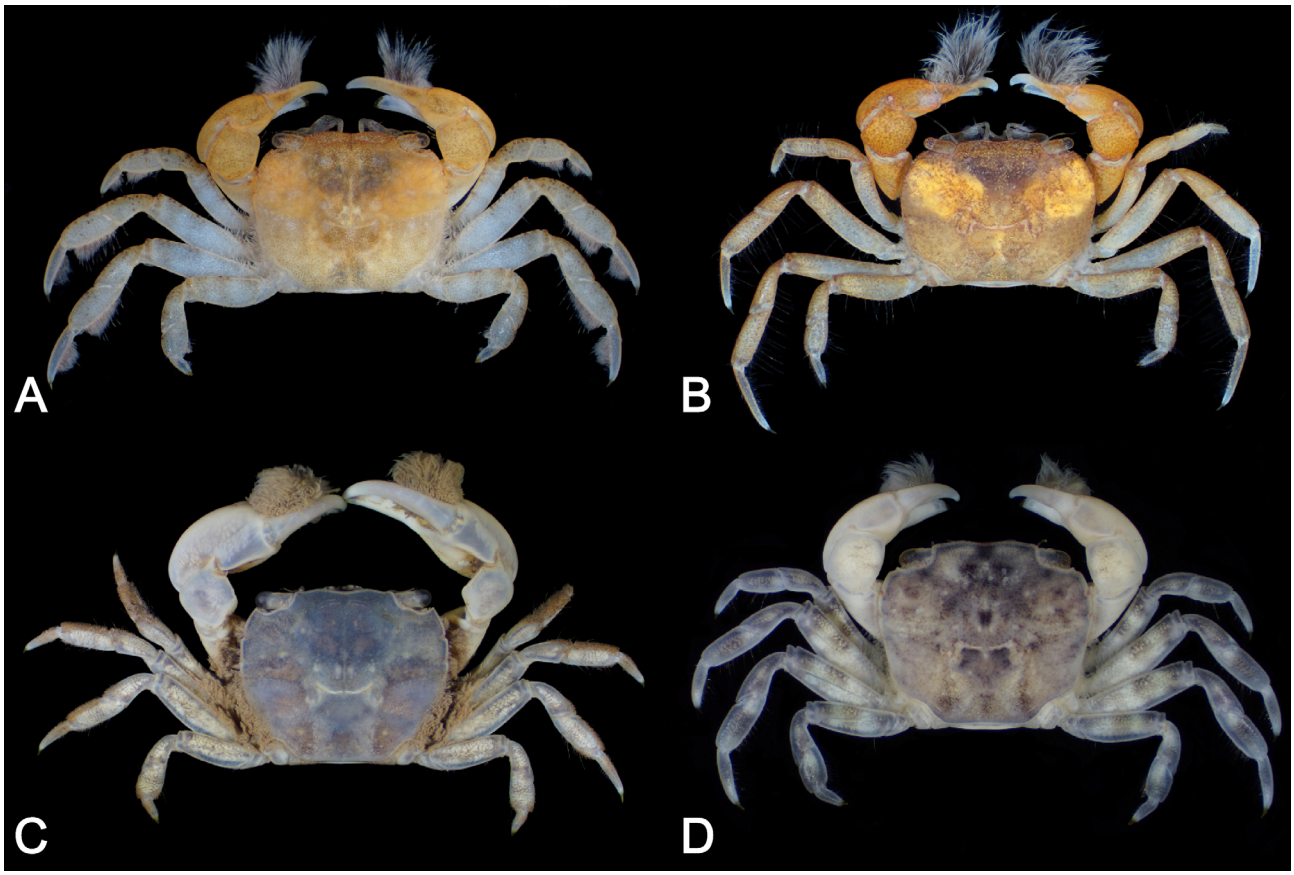

Figure 3. A, *Ptychognathus hachijoensis* (male, CW 7.0 mm; NCHUZOOL 15809); **B,** *Ptychognathus insolitus* (male, CW 7.5 mm; NCHUZOOL 16047); **C,** *Ptychognathus stimpsoni* (paratype male, CW 10.9 mm; NCHUZOOL 16502); **D,** *Ptychognathus takahasii* (male, CW 9.3 mm; NCHUZOOL 16507).

Ptychognathus sakaii can be separated from *P. pusillus* by 1) frontal region indistinct and separated into two obscure lobes by shallow grooves, lobes broader (*vs.* frontal region distinct and separated into two obvious lobes, lobes are narrower) (Fig. 2A; De Man, 1905: 539, pl. 17(1–2)); 2) anterior margins of distal part of carpus of ambulatory legs distinctly compressed (*vs.* anterior margins not obviously compressed) (Fig. 2G, H; De Man, 1905: 539, pl. 17(1)).

Ptychognathus sakaii can be separated from *P. stimpsoni* by 1) frontal margin concave, divided into two obvious lobes (*vs.* frontal margin only slightly concave, weakly divided into two indistinct lobes) (Figs. 2A, 3C; Hsu and Shih, 2020: figs. 2C, E, 4A); 2) anterior margins of distal part of carpus of ambulatory legs distinctly compressed, anterior margins of carpus and propodus almost glabrous (*vs.* anterior margins of distal part of carpus not compressed, anterior margins of carpus and propodus covered with dense short setae) (Figs. 2G, H, 3C; Hsu and Shih, 2020: figs. 2C, E, 4G, H).

Ptychognathus sakaii can be separated from *P. takahasii* by 1) frontal region of carapace divided into two obvious lobes, with 1 or 2 teeth behind external orbital tooth on each anterolateral margin, posterolateral margins only slightly convergent posteriorly (*vs.* frontal region weakly divided two lobes, with 3 teeth behind small external orbital tooth on each anterolateral margin, posterolateral margins apparently convergent posteriorly) (Figs. 2A, 3D; Sakai, 1939: text-fig. 115); 2) anterior margins of carpus of ambulatory legs distinctly compressed (*vs.* anterior margins of carpus of ambulatory legs not significantly compressed) (Figs. 2G, H, 3D; Sakai, 1939: text-fig. 115); 3) G1s slender in *P. sakaii* (*vs.* stout in *P. takahasii*).

Key to the species of *Ptychognathus* found in Taiwan

1. Carapace quadrate (width = length), anterolateral margin with an orbital tooth and two distinct teeth. 2

– Carapace subquadrate (width > length), anterolateral margin with an orbital tooth and one or two distinct teeth. 4

– Carapace subquadrate (width > length), anterolateral margin only with an orbital tooth, or with additional one to three indistinct teeth. 6

2. Outer surface of male cheliped manus with obvious long setae (on base of fingers and tip of immovable finger). ..... *P. pilosus* De Man, 1892

– Outer surface of male cheliped manus without obvious long setae. 3

3. Supraorbital margins strongly sinuous, posterolateral margins of carapace almost parallel, not divergent posteriorly. ..... *P. altimanus* (Rathbun, 1914)

– Supraorbital margins gently sinuous, posterolateral margins of carapace distinctly divergent posteriorly. ..... *P. makii* Hsu and Shih, 2020

4. Dorsal surface of carapace with short dense setae (especially part near margins). .... *P. ishii* Sakai, 1939

– Dorsal surface of carapace without dense setae. 5

5. With a row of small granules behind frontal margin; male telson without tuft of setae. .... *P. stimpsoni* Hsu and Shih, 2020

– Without row of granules behind frontal margin; male telson with a tuft of setae. .... *P.* aff. *barbatus*

6. Anterolateral margin of carapace with a very small orbital tooth and three indistinct teeth, orbital tooth significantly smaller than following teeth. .... *P. takahasii* Sakai, 1939

– Anterolateral margin of carapace only with an orbital tooth, or with an orbital tooth and one or two indistinct teeth. 7

7. Carapace broader (approximately 1.3–1.4 times as broad as long); ambulatory legs slender. .... *P. insolitus* Osawa and N. K. Ng, 2006

– Carapace narrower (approximately 1.2 times as broad as long); ambulatory legs short and stout. 8

8. Posterior margins of dactyli and propodi of ambulatory legs with obvious dense tufts of setae. ..... *P. hachijoensis* Sakai, 1955

9. Posterior margins of dactyli and propodi of ambulatory legs only sparsely setose. .... *P. sakaii* sp. nov.

Discussion

This new species of *Ptychognathus* has been mentioned in Hsu and Shih (2020) and supported genetically by the mitochondrial cytochrome c oxidase subunit I (COI) with the lowest interspecific divergence ≥ 12.29 % from other species from Taiwan. The DNA barcode gene COI is useful to help identify similar species in brachyuran crabs successfully (Chu *et al.*, 2015) and also commonly used in recent studies, including Ocypodidae (Shih *et al.*, 2019c; Shih and Poupin, 2020; Thurman *et al.*, 2021); Portunidae (Windsor *et al.*, 2019; Huang and Shih, 2021); Potamidae (Huang *et al.*, 2020; 2021; Shy *et al.*, 2021); Sesarmidae (Li *et al.*, 2019b; 2020; Shih *et al.*, 2019b; Kim *et al.*, 2020; Ng *et al.*, 2020); and Varunidae (N.K. Ng *et al.*, 2018; Shih *et al.*, 2019a; Shih *et al.*, 2020).

Although the genus *Ptychognathus* is widely distributed, most species are centered in western Pacific and eastern Indian Ocean, except a few species distributed in central Pacific (*e.g.*, *Ptychognathus easteranus* Rathbun, 1907 from French Polynesia and Easter Island; Rathbun, 1907; Marquet, 1991) and western Indian Ocean (*e.g.*, *Ptychognathus johannae* Rathbun, 1914 from Comoro islands; *Ptychognathus polleni* De Man, 1895 from Madagascar; Rathbun, 1914; De Man, 1895). The species diversity of this genus is higher (with 21 species) in the oceanic islands in East Asia and Southeast Asia, including Japan (including Ryukyus), Taiwan, the Philippines, Indonesia, and New Guinea. Among these species, 19

species could be found exclusively from this region (Ortmann, 1894; Rathbun, 1914; Sakai, 1976; Cai and Ng, 2001; Marquet *et al.*, 2002; Nakasone and Irei, 2003; Komai *et al.*, 2004; 2021; Osawa and N.K. Ng, 2006; N.K. Ng, 2010; Hsu and Shih, 2020; this study). In these regions, the species diversity is highest in the Ryukyu Islands, with ten described and four undescribed species (Nakasone and Irei, 2003; Osawa and N.K. Ng, 2006); the second highest is in Indonesia, with 11 species (De Man, 1892; 1895; 1905; Ortmann, 1894; Tesch, 1918; Sakai, 1976; Cai and Ng, 2001; Naruse *et al.*, 2005); whereas Taiwan and the Philippines have ten (Hsu and Shih, 2020; this study) and six species (Milne-Edwards, 1868; Rathbun, 1914; N.K. Ng, 2010; Hsu and Shih, 2020), respectively.

Among the ten species of *Ptychognathus* from Taiwan, there are two species widely distributed from Japan to Indonesia (*P.* aff. *barbatus* and *P. altimanus*; Sakai, 1976; Dai and Yang, 1991; Naruse *et al.*, 2005; Ng *et al.*, 2017); four temperate species (*P. hachijoensis, P. insolitus, P. ishii,* and *P. takahasii*; Sakai, 1976; Li, 2015); two tropical species (*P. stimpsoni* and *P. pilosus*; Li *et al.*, 2019a; Hsu and Shih, 2020); and two species with narrow distributional range (only in Taiwan currently) (*P. makii* and *P. sakaii* sp. nov.; Hsu and Shih, 2020; this study). The high diversity of this genus in Taiwan is suggested to be caused by the geographic position between the tropical and subtropical zones; complicated ocean currents around Taiwan, including the Kuroshio Current and China Coastal Current (Shih, 2012); as well as the diverse habitats and environment in Taiwan main island and the adjacent oceanic islands, *e.g.*, sandy mud habitat preferred by *P. altimanus* and *P. makii* (*cf.* Naruse *et al.*, 2005; Hsu and Shih, 2020) and coarse sand by *P. stimpsoni* (*cf.* Hsu and Shih, 2020).

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