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Description of a new species of the genus *Metaplax* H. Milne Edwards, 1852 (Decapoda: Brachyura: Varunidae) from Vietnam

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Abstract

Metaplax H. Milne Edwards, 1852, is a genus in the family Varunidae H. Milne Edwards, 1853, distributed across the Indo-West Pacific, with 10 described species. Among them, Metaplax crenulata (Gerstaecker, 1856) was previously thought to be present in both the Indian Ocean and the western Pacific (Vietnam). However, our study, based on morphological and molecular evidence, indicates that specimens from the Indian Ocean and Vietnam represent distinct species. Since the type locality of M. crenulata is unknown, we conducted comparative analyses of the syntypes alongside specimens from the Indian Ocean and Vietnam. Morphological examinations revealed that the syntypes closely resemble the Indian Ocean specimens, whereas the Vietnamese specimens exhibit clear morphological differences, particularly in the male suborbital cristae and the proportions of the ambulatory legs. Furthermore, cytochrome c oxidase subunit I (COI) sequence analysis showed a 5.8% genetic divergence between the two groups, further confirming that they represent separate species. Based on these findings, we describe the species from Vietnam as new.

Key words: new species, *Metaplax crenulata*, *M. pristis*, morphology, cytochrome *c* oxidase subunit I (COI)

Introduction

Metaplax H. Milne Edwards, 1852 is a genus within the family Varunidae H. Milne Edwards, 1853, with 10 species recorded to date (Naderloo 2011; Shih et al. 2019; Sasaki 2023). Species of Metaplax are widely distributed, inhabiting mudflats and mangroves across the Indo-West Pacific (Davie & Nguyen 2003; Naderloo 2017; Shih et al. 2019). Within this genus, considerable variation in body size exists among species, with Metaplax crenulata (Gerstaecker, 1857) exhibiting the most pronounced morphological differences. Compared to other species, M. crenulata is notably larger, with the largest male carapace width (CW) reaching approximately 44 mm, whereas other species have a maximum CW of less than 30 mm (De Man 1888; Davie & Nguyen 2003; N.K. Ng 2006; Shih et al. 2019; this study). In addition to size, M. crenulata also displays significant morphological differences from other species (N.K. Ng 2006; Ng et al. 2008).

Gerstaecker (1856) originally examined specimens from the Berlin Museum and described them as a new monotypic genus, *Rhaconotus*, with *Rhaconotus crenulatus* as the type species, based on morphological differences. However, the locality of the specimens was unknown (Gerstaecker 1856: 143). Despite this, the genus name *Rhaconotus* was already in use for another taxon prior to Gerstaecker's publication [*Rhaconotus* Ruthe, 1854 (Braconidae), a kind of wasp], rendering it an invalid genus name (N.K. Ng 2006). Subsequently, De Man (1888) transferred this species to genus *Metaplax* based on the characters of carapace, maxillipeds, and chelipeds, providing a detailed description and designating *Rhaconotus* Gerstaecker, 1856 as a junior synonym of *Metaplax*. Since then, "*M. crenulata*" has been recorded across the Bay of Bengal, the Andaman Sea, and several regions of Southeast Asia,

including West Bengal, the Andaman and Nicobar Islands, the Mergui Archipelago, Thailand, Vietnam, Malaysia, and Singapore (Tan & Ng 1994; Ng & Davie 2002; Trivedi *et al.* 2018; Sasaki 2023).

However, based on morphological examination and molecular analysis of cytochrome *c* oxidase subunit I (COI), we confirm that *M. crenulata* specimens from the Indian Ocean (western Thailand, western Peninsular Malaysia, and Singapore) and the western Pacific (Vietnam) represent two distinct species. Accordingly, in this study we describe the species from Vietnam as new.

Materials and methods

The examined specimens of species of *Metaplax* are deposited in the Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); the Museum für Naturkunde Berlin (previously the Zoologisches Museum Berlin), Berlin, Germany (ZMB); and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (ZRC).

The abbreviations used in this study includes: coll. denote collected by; G1 denotes the male first gonopod; and P2 to P5 denote the first to fourth ambulatory legs, respectively. Measurements provided, in millimeters, are of carapace width (CW) by carapace length. The proportions of the ambulatory legs were measured to assess their potential for distinguishing between the two species: specifically, the width/length ratio of the merus and propodus of P4 and P5, as well as the carpus length/propodus length ratio of P4 and P5 in both sexes (see Maenosono & Naruse 2015: fig. 1B). If a leg appeared damaged or regenerated, for example, if it was noticeably slimmer or smaller, it was excluded from both measurement and analysis.

Comparative material used in this study includes: Metaplax dentipes (Heller, 1865): 2 males (20.9 × 15.9 mm, 20.8 × 15.8 mm) (ZRC 2025.2002), Canning, Kolkata, West Bengal, India, coll. Z. Jaafar, 21 December 2003; 5 males $(20.4 \times 15.5 \text{ mm}, 19.1 \times 14.9 \text{ mm}, 18.3 \times 14.0 \text{ mm}, 17.3 \times 13.3 \text{ mm}, 15.5 \times 11.8 \text{ mm}), 1 \text{ female } (14.0 \times 10.9 \text{ mm}, 15.5 \times 11.8 \text{ mm})$ mm) (NCHUZOOL 17348), Jharkali, Sundarban, West Bengal, 8 September 2022; 2 males (20.1 × 15.3 mm, 18.6 × 14.3 mm), 1 female (19.2 × 14.9 mm) (NCHUZOOL 17349), Jharkali, Sundarban, West Bengal, 8 September 2022. — M. distincta H. Milne Edwards, 1852: 1 male (16.2 × 11.2 mm) (ZRC 2001.2330), Ranong, Thailand, 18 November 2001; 1 female (22.5 × 15.7 mm), 2 juveniles (ZRC 1998.1205), Phuket, Thailand, coll. P.K.L. Ng, December 1998; 4 males (23.5 × 16.8 mm, 21.6 × 15.7 mm, 18.5 × 13.5 mm, 18.4 × 13.2 mm) (NCHUZOOL 17345), Mudasalodai, Vellar River estuary, India, 6 August 2022; 2 males (16.6 × 12.0 mm, 12.8 × 9.2 mm) (NCHUZOOL 17346), Mumbai, Maharashtra, India, 6 March 2023; 1 male (10.8 × 7.9 mm), 1 female (12.6 × 9.3 mm), (NCHUZOOL 17346), Mumbai, Maharashtra, India, 6 March 2023. — M. elegans De Man, 1888: 4 males (12.2 × 8.4 mm–10.0 × 7.1 mm), 6 females (12.1 × 8.1 mm–8.1 × 6.2 mm) (NCHUZOOL 15487), Yuliao River estuary, Changhua, Taiwan, coll. J.-W. Hsu et al., 16 January 2017; 1 male (16.8 × 10.7 mm), 2 females (14.5 × 10.0 mm, 14.0 × 9.4 mm) (NCHUZOOL 15495), Dongzhai Harbor, Hainan, China, 23 June 2004; 8 males (16.5 × 10.7 mm-5.8 × 4.4 mm), 9 females (13.7 × 9.9 mm-6.5 × 4.7 mm) (NCHUZOOL 15490), Rung Sac, Long Hoa, Can Gio, Ho Chi Minh City, Vietnam, 12 October 2017; 3 ovigerous females (11.6 × 8.5 mm, 11.2 × 8.2 mm, 10.6 × 7.9 mm) (NCHUZOOL 17354), Mersing, Johor, Malaysia, 19 July 2010; 7 males (12.6 × 8.0 mm–7.7 × 5.3 mm), 14 females (12.0 × 8.2 mm-8.9 × 6.3 mm) (NCHUZOOL 15492), Mersing, Johor, Malaysia, 19 July 2010; 3 males (12.5 × 8.6 mm-11.4 × 7.9 mm) (NCHUZOOL 17355), Mersing, Johor, Malaysia, 20 July 2010. — M. gocongensis Davie & Nguyen, 2003: 2 males (29.1 × 20.7 mm, 18.9 × 14.2 mm) (ZRC 2024.0078), Phu Thanh Dong Commune, Ho Chi Minh City, Vietnam, coll. V.X. Nguyen, 2 February 2002. — M. longipes Stimpson, 1858: 3 males (22.3 × 16.0 mm-11.3 × 8.4 mm), 1 female (21.6 × 15.8 mm) (NCHUZOOL 15444), Mamu, Zhoushan, Zhejiang, China, 26 July 2018; 1 male (18.3 × 13.7 mm) (NCHUZOOL 15451), Tung Chung, Hong Kong, coll. K.J.H. Wong, 21 March 2009. — M. sheni Gordon, 1931: 5 males (12.8 × 8.6 mm-8.6 × 5.9 mm) (NCHUZOOL 15465), Xiamen, Fujian, China, coll. H.-T. Shih *et al.*, 1 August 2018; 1 male (13.3 × 8.6 mm) (NCHUZOOL 17050), Kinmen, Taiwan, coll. J.-W. Hsu et al., 18 August 2020. — M. tredecim Tweedie, 1950: 2 males (16.2 × 12.0 mm, 15.6 × 11.6 mm), 1 female (15.7 × 11.4 mm) (ZRC 1964.7.14.4-18), Labuan, Malaysia, August 1938.

Genomic DNA was extracted from the muscle tissue of legs, gills, or eggs using the GeneMark Tissue and Cell Genomic DNA Purification Kit (Taichung, Taiwan). A portion of the COI gene was amplified via PCR using the primers LCO1490 (5'-GGTCAACAAATCATAAAGATATTGG-3'), HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer *et al.* 1994), LCOB (5'-CAAAYCATAAAGAYATYGG-

3'), and HCOex3 (5'-GCTCANACTACRAATCCT A-3') (Shih *et al.* 2022). The PCR conditions were as follows: denaturation at 94°C for 50 s, annealing at 45–47°C for 70 s, and extension at 72°C for 60 s (40 cycles), followed by a final extension at 72°C for 10 min. Sequences were obtained using an automated Applied Biosystems 3730 sequencer (Applied Biosystems, CA, USA) and were aligned using the MUSCLE algorithm in MEGA (ver. 12.0, Kumar *et al.* 2024) after verification with the complementary strand. Haplotype sequences were deposited in the GenBank database, with accession numbers provided in Table 1. Molecular analyses also incorporated additional haplotypes from GenBank, as published in Shih *et al.* (2019).

TABLE 1. The haplotypes of COI for the specimens of *Metaplax* H. Milne Edwards, 1852 used in this study.

Species	Locality	Catalogue no.	Specimens	Haplotype of COI	Access. no. COI
Metaplax tredecim Tweedie, 1950	Thailand: Chonburi	ZRC 2025.0181	1	Mtr1	PV640760
M. sheni Gordon, 1931	Taiwan: Kinmen	NCHUZOOL 17050	1	Msh1	PV640761
M. elegans De Man, 1888	China: Dongzhai Harbor, Hainan	NCHUZOOL 15457	1	Mel1	PV640762
	Malaysia: Mersing, Johor	NCHUZOOL 15492	1	Mel2	PV640763
	Malaysia: Mersing, Johor	NCHUZOOL 17355	2	Mel2	PV640764 PV640765
	Malaysia: Mersing, Johor	NCHUZOOL 17354	1	Mel3	PV640766
M. distincta H. Milne Edwards, 1852	Thailand: Ranong	ZRC 2001.2330	1	Mdc1	PV640767
	Thailand: Phuket	ZRC 1998.1205	1	Mdc2	PV640768
	India: Vellar River estuary	NCHUZOOL 17345	1	Mdc3	PV640769
	India: Mumbai	NCHUZOOL 17346	1	Mdc4	PV640770
	India: Mumbai	NCHUZOOL 17347	1	Mdc4	PV640771
M. dentipes (Heller, 1865)	India: Kolkata, West Bengal	ZRC 2025.0182	1	Mdp1	PV640772
	India: Jharkali, West Bengal	NCHUZOOL 17349	1	Mdp1	PV640773
	India: Jharkali, West Bengal	NCHUZOOL 17348	1	Mdp2	PV640774
	India: Jharkali, West Bengal	NCHUZOOL 17348	1	Mdp2	PV640775
M. crenulate (Gerstaecker, 1856)	Singapore: Pandan Mangroves	ZRC 2009.0828	1	Mcr1	PV640776
	Thailand: Phuket	NCHUZOOL 17350	1	Mcr2	PV640777
	Thailand: Phuket	NCHUZOOL 17351	1	Mcr3	PV640778
M. pristis sp. nov.	Vietnam: T.T. Can Thanh, Ho Chi Minh City	NCHUZOOL 17353	1	Mpr1	PV640779
	Vietnam: T.T. Can Thanh, Ho Chi Minh City	NCHUZOOL 17352	1	Mpr2	PV640780

For the COI analysis, the best-fitting model for sequence evolution was determined using ModelFinder in IQ-TREE (version 2.2.0; Minh *et al.* 2020), with model selection based on the Bayesian Information Criterion (BIC). The best-fitting model obtained was TIM2+F+I, which was subsequently applied in the maximum likelihood (ML) analysis and approximated as the GTR model with empirical base frequencies and a proportion of invariable sites (GTR+I+F) in the Bayesian inference (BI) analysis. BI was performed using MrBayes (version 3.1.2; Ronquist *et al.* 2012), running four chains for 10 million generations with trees sampled every 1,000 generations. Convergence of the chains was assessed by ensuring the mean standard deviation of split frequencies remained below the recommended threshold of 0.01 (Ronquist *et al.* 2020), and the first 1,200 trees were discarded as burn-in. ML analysis was conducted using IQ-TREE with the best-fitting model, and 30,000 ultrafast bootstrap replicates were generated. Base pair (bp) differences and pairwise estimates of Kimura (1980) two-parameter (K2P) distances for COI diversity among specimens were calculated using MEGA.

Taxonomy

Family Varunidae H. Milne Edwards, 1853

Genus Metaplax H. Milne Edwards, 1852

Metaplax crenulata (Gerstaecker, 1856) (Figures 1, 2)

Rhaconotus crenulatus Gerstaecker, 1856: 140, pl. 5, fig. 5 [type locality: unknown (see Remarks and Discussion)]. Metaplax crenulatus – De Man 1888: 156 [Mergui Archipelago]. – De Man, 1889: 439 [Bay of Bengal].

Metaplax crenulata – Alcock 1900: 436 [Sunderbunds and Mergui]. – Tesch 1918: 116 (key). – Balss 1922: 153 [Penang, Malaysia]. – Tweedie 1936: 69 [Selangor, Malaysia]. – Tan & Ng 1994: 82 [western Malaysia and Singapore]. – Ghosh 1995: 235 [West Bengal, India]. – Ghosh 1998: 336 [West Bengal, India]. – Ng & Davie 2002: 379 [Phuket and western Thailand]. – Chakraborty et al. 2005: 154 (list). – Ng et al. 2008: 226 (list). – Dev Roy & Nandi 2008: 199, tab. 1 [West Bengal, India]. – Dev Roy & Nandi 2012: 216, tab. 1 [Andaman Islands]. – Trivedi et al. 2018: 75, tab. 1 (list). – Pati et al. 2018: 45, tab. 15 (list). – von Rintelen & Wolff 2025: 12 unnumbered figs.

Metaplax crenulaa [sic] – Ghosh 1995: 231.

Metaplax cernulata [sic] - Naiyanetr 2007: 112 [Thailand (Ranong and Phuket) and Andaman Sea].

Type material examined. Lectotype (herein designated): 1 male $(33.0 \times 26.0 \text{ mm})$, (ZMB 604), no collection data. – Paralectotypes (herein designated): 2 females $(23.1 \times 19.6, 23.0 \times 19.0 \text{ mm})$ (ZMB 604), no collection data (photo only; from von Rintelen & Wolff 2025).

Other material examined. 1 male (18.8×15.1 mm) (NCHUZOOL 17350), Chalong Bay, Phuket, Thailand, 29 May 2012; 1 male (18.3×15.0 mm), 1 female (16.1×13.2 mm) (NCHUZOOL 17351), Chalong Bay, Phuket, Thailand, 29 May 2012; 1 female (18.7×15.3 mm) (ZRC 2002.0327), Tang Khen Bay, Phuket, Thailand, coll. J.C.Y. Lai, 3 September 2001; 1 female (27.4×22.4 mm) (ZRC 2019.0591), Selangor, Kuala Langat, Malaysia, coll. Z. Jaafar; 4 males (14.6×12.0 , 11.6×9.2 , 9.8×8.3 mm, 1 specimen broken), 2 females (21.3×17.2 , 14.1×11.0 mm) (ZRC), Semantar, Selangor, Malaysia, coll. J.C.E. Mendoza, 10 February 2009; 1 male (36.6×28.3 mm), 1 ovigerous female (24.3×19.6 mm) (ZRC 2013.1199), Nibong Tebal, Malaysia, coll. Z. Jaafar, 22 December 2001; 2 females (33.1×25.0 , 32.6×25.2 mm) (ZRC 1989.2081-2082), Mandai mangrove swamp, Singapore, coll. D.H. Murphy, 1985; 1 male (25.7×19.5 mm), 1 female (30.7×24.1 mm) (ZRC 2009.0828), Pandan mangrove, Singapore, coll. Z. Jaafar, 2 October 2008; 2 males (43.7×33.0 mm, 34.1×27.0 mm), 1 female (23.2×18.7 mm) (ZRC 1997.696), Tanjong Kling, Singapore, coll. I. Polunin, 12 July 1965.

Diagnosis. Carapace rectangular, convex; surface almost glabrous, region well-defined (Figs. 1A, F, G, 2A–D). Front narrow, medially slightly concave (Figs. 1A, 2A). Lateral margin nearly parallel, with 5 teeth (including orbital tooth), anterior 3 teeth pronounced, posterior 2 relatively indistinct (Figs. 1A, 2A). Suborbital crista sexually dimorphic; in male, composed of 22–27 isomorphic tubercles; in females, composed of 22–23 small isomorphic tubercles (Figs. 1B–D, 2E–G). Chelipeds distinctly larger in male (Figs. 1A, B, 2A, B); merus relatively long, slightly shorter than palm; dactylus with several blunt teeth on cutting edge (Figs. 1A, 2A). Ambulatory legs long, slender (Figs. 1A, B, E, F, 2A–D); meri with several distinct spines on anterior and posterior margins; anterior margins of carpi and propodi almost glabrous, with several distinct spines; in male, carpi relatively longer [propodus length/

carpus length < 1.9 (P4); < 1.6 (P5)], P5 merus and propodus relatively stouter (merus length/width < 3.8; propodus length/width < 4.8) (Appendix 1B, D–F). G1 slender, distal part tapering, distinctly curved toward ventrolateral side; tip chitinous, blunt, distal part distinctly curved toward ventrolateral side.

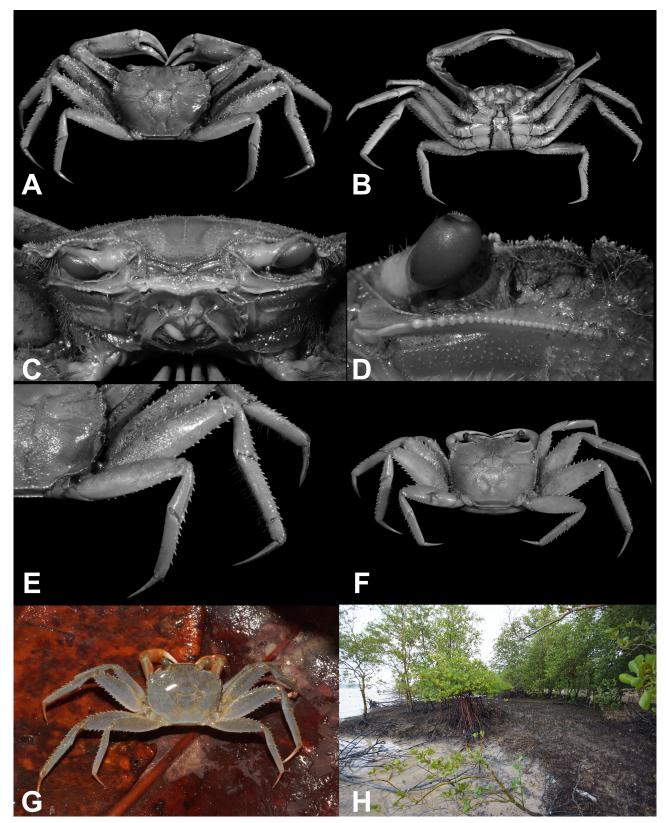


FIGURE 1. *Metaplax crenulata* (Gerstaecker, 1856). A–E, male ($36.6 \times 28.3 \text{ mm}$) (ZRC 2013.1199); F, female ($24.3 \times 19.6 \text{ mm}$) (ZRC 2013.1199); G, male ($18.8 \times 15.1 \text{ mm}$) (NCHUZOOL 17350). A, F, dorsal view; B, ventral view; C, frontal view; D, left suborbital crista; E, right third ambulatory leg (P4) and fourth ambulatory leg (P5); G, color in life; H, habitat in Chalong Bay, Phuket, Thailand.

Coloration. In dorsal view, the carapace is brown to gray, while the chelae are reddish-brown to light brown with a lighter color near the distal ends (Fig. 1G). The fingers are light brown to white, and the distal parts of the ambulatory legs are brown.

Size. Largest male CW 43.7 mm (ZRC 1997.696); largest female CW 33.1 mm (ZRC 1989.2081-2082) (N.K. Ng 2006; this study).

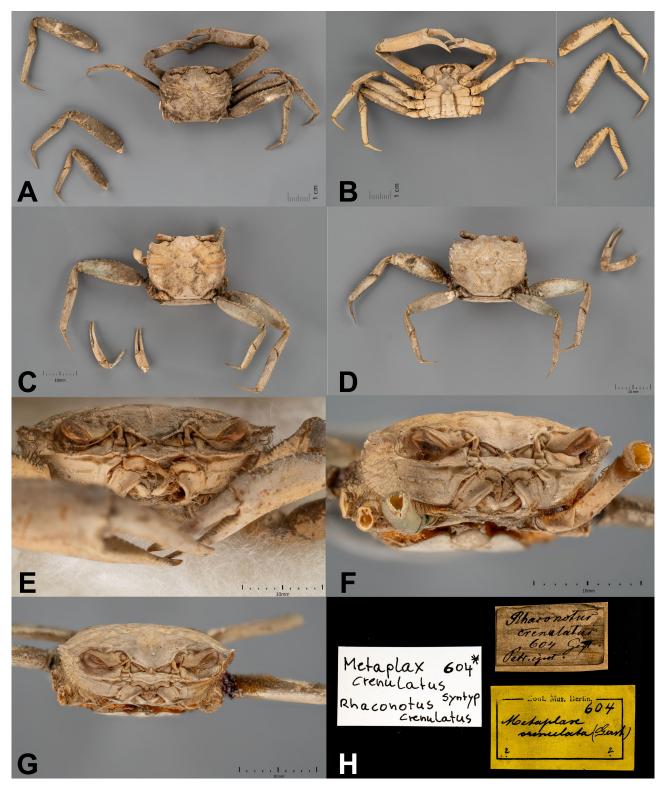


FIGURE 2. Syntypes of *Metaplax crenulata* (from von Rintelen & Wolff 2025). A, B, E, male, lectotype herein designated (33.0 × 26.0 mm) (ZMB 604); C, F, female, paralectotype herein designated (23.0 × 19.0 mm) (ZMB 604); D, G, female, paralectotype herein designated (23.1 × 19.6 mm) (ZMB 604); H, label of ZMB 604. A, C, D, dorsal view; B, ventral view; E, F, G, frontal view.

Habitat. At Chalong Bay, Phuket, Thailand, this species was found on muddy flats among mangroves (Fig. 1H).

Remarks. The type locality of this species is unknown (Gerstaecker 1856: 143), and two morphologically similar species, consistent with the original description and illustrations, have been found in both the Indian Ocean and the western Pacific. However, after comparing specimens from the Indian Ocean with those from the western Pacific (Vietnam), the results showed that the morphology (the proportions of the male ambulatory legs) of the specimens from the Indian Ocean more closely matches Gerstaecker's (1856) illustrations. Furthermore, we contacted the Berlin Museum to locate and photograph the syntype of *Metaplax crenulata*, and we were fortunate to obtain images of these specimen (ZMB 604), allowing us to examine its morphology (Fig. 2). In this male specimen, the suborbital cristae and the proportions of P4 and P5 are also similar to those of the Indian Ocean species (Appendix 1). Based on morphological evidence, our results indicate that the Indian Ocean species should be considered the true *Metaplax crenulata*, while the Vietnamese species represents a new species, *M. pristis* sp. nov. (see Discussion for details). For the purpose of nomenclatural stability, it is prudent to select a specimen from the syntype (ZMB 604) of *Rhaconotus crenulatus* (= *Metaplax crenulata*) to be the lectotype. Since the male can be morphologically distinguished from the similar species (*M. pristis* sp. nov.), we hereby designate the male specimen as the lectotype, with the remaining two female specimens as paralectotypes.

In addition, following the original publication of *Metaplax crenulata*, lots of records of this species have been reported, almost exclusively from the Indian Ocean region (as listed in the synonymy list above); by contrast, records from the western Pacific are limited to only two from Vietnam, including Wada (2019) and the present study (see Remarks of *M. pristis* sp. nov.).

Distribution. West Bengal, Andaman and Nicobar Islands, Mergui Archipelago, western Thailand, western Malaysia and Singapore (Tan & Ng 1994; Ng & Davie 2002; Trivedi *et al.* 2018; Sasaki 2023; others see the synonymy list above).

Metaplax pristis sp. nov.

(Figures 3–6)

Material examined. Holotype: 1 male (44.1 × 33.1 mm) (NCHUZOOL 17352), T. T. Can Thanh, Can Gio, Ho Chi Minh City, Vietnam, coll. H.-T. Shih & P.-Y. Hsu, 13 October 2017. – Paratype: 1 female (43.6 × 32.5 mm) (NCHUZOOL 17353), T. T. Can Thanh, Can Gio, Ho Chi Minh City, Vietnam, coll. H.-T. Shih & P.-Y. Hsu, 13 October 2017.

Diagnosis. Carapace rectangular, convex; surface almost glabrous, region well-defined (Figs. 3A, C, 4A, D, 5A). Front narrow, medially slightly concave (Fig. 5A). Lateral margin nearly parallel, with 5 teeth (including orbital tooth), anterior 3 teeth pronounced, posterior 2 relatively indistinct (Figs. 3A, C, 5A). Suborbital crista sexually dimorphic; in male, composed of 30–31 isomorphic tubercles; in females, composed of 22–24 small isomorphic tubercles (Figs. 4C, 5C). Chelipeds distinctly larger in male (Fig. 3A–D); in male, merus relatively long, slightly shorter than palm (Figs. 3A, 4A, 5D); dactylus with several blunt teeth on cutting edge (Fig. 5E). Ambulatory legs long, slender; meri with several distinct spines on anterior and posterior margins (Figs. 3A–D, 4F, G); anterior margins of carpi and propodi almost glabrous, with several distinct spines; in male, carpi relatively shorter (propodus length/carpus length > 1.9 (P4); > 1.6 (P5)), P5 merus and propodus relatively slender (merus length/width > 4.3; propodus length/width > 5.7) (Appendix 1B, D–F). G1 slender, distal part tapering, distinctly curved toward ventrolateral side; tip chitinous, blunt, distal part distinctly curved toward ventrolateral side (Fig. 6).

Description. Carapace rectangular, greatest width across third anterolateral teeth, approximately 1.3 (holotype male = 1.33; paratype female = 1.34) times broader than long (Figs. 3A, C, 4A, D, 5A); lateral margins convex, with 5 teeth (including exorbital tooth), anterior 3 teeth pronounced marked, posterior 2 relatively indistinct; first tooth (exorbital tooth) broad, blunt, pointed anteriorly, second tooth similar to first tooth in size, third and fourth teeth much smaller, fifth reduced to a tiny tooth or notch. Supraorbital margin lined with large rounded granules; outer margins of anterolateral teeth edged with small spines or acute granules; lateral margin edged with row of short setae. Carapace surface almost glabrous, smooth, scattered with several minute, smooth granules, with 3 oblique rows of granules short on posterolateral region. Front approximately 0.2 times maximum carapace width, deflexed,

slightly notched medially, broad shallow sulcus running posteriorly. Dorsal carapace regions well indicated, with gastric, cardiac and intestinal regions strongly demarcated. Suborbital crista sexually dimorphic (Figs. 3B, D, 5B, C); in male, composed of 30–31 isomorphic rounded tubercles; in females, composed of 22–24 small isomorphic rounded tubercles.

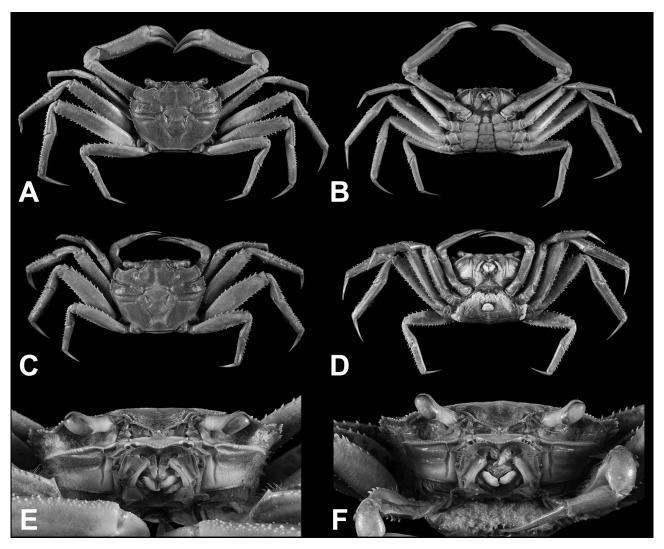


FIGURE 3. *Metaplax pristis* **sp. nov.** A, B, E, male, holotype (44.1 × 33.1 mm) (NCHUZOOL 17352); C, D, F, female, paratype (43.6 × 32.5 mm) (NCHUZOOL 17353). A, C, dorsal view; B, D, ventral view; E, F, frontal view.

Chelipeds equal, large and robust. Merus slender, markedly more elongated, margins armed with remarkable blunt spines or coarse granules (more blunt on ventral margin), denser on distal anterior margin; posterior surface without chitinous crest (Figs. 3A–D, 5D). Carpus with several distinct granules on inner margin, 3–4 granules more produced, almost blunt spines; outer surface almost smooth, without granules (Fig. 3A). Palm elongated; outer surface covered with tiny granules minutely, larger on part near upper and lower margins (Figs. 3A, 5E); granules becoming slightly more prominent along upper and lower margins and on fingers; inner surface with smaller granules on medial part and part near base of immovable finger, granules on medial part larger. Cutting margins bluntly serrated; male holotype with an obvious basal gape between the fingers. Fixed finger moderately deflexed, 0.7 times as palm in length.

Ambulatory legs elongated and slender, P3 and P4 longer than P2 and P5, P3 longest and approximately 1.6–1.9 times carapace width (Figs. 3A–D, 5F). Meri approximately 4.1 times longer than wide in P4 of holotype male (approximately 3.4 times in paratype female) (approximately 4.3 times longer than wide in P5 of holotype male; approximately 3.4 times in paratype female) (Fig. 5F); anterior and posterior margins slightly converging mesially and distally, margins with several curved spines, spines on anterior margin longer and more distinct than those on

posterior margin, spines longer in P3 and P4; dorsal surface almost glabrous, sparsely covered with small granules, with a line of larger granules on part near anterior margin. Carpi and propodi with several curved spines on anterior margins, posterior margins without spines; carpi almost glabrous, with a row of spines on dorsoanterior surfaces, and with a line of small granules on dorsal surface; carpi of P4 and P5 shorter in males, no distinct difference in females (Appendices 1B, E, 2B, E); propodi with sparse setae on posterior margins, anterior margins almost glabrous; P5 propodi slender in males, no distinct difference in females (Appendices 1F, 2F). Dactyli long, with rows of short setae on surfaces and margins.

Male abdomen with telson abruptly narrowed, longer than wide, gradually tapering, shorter than penultimate segment; sixth segment the longest, approximately 1.2 times wider than long (Figs. 3B, 4B). G1 slender, distal part tapering, distinctly curved toward ventrolateral side; tip chitinous, blunt, distal part distinctly curved toward ventrolateral side (Fig. 6).

Etymology. The species is named after *Pristis*, which is the genus of sawfish. This new species name is derived from the distinctive meri of its ambulatory legs, which have numerous curved spines along the meri margins, resembling the snout of a sawfish.

Coloration. In dorsal view, the carapace is dark brown to gray, while the chelae are brown with a lighter color near the distal ends (Fig. 4A, D, F, G). The fingers are light brown to white, and the distal parts of the ambulatory legs are brown. In ventral view, the body is predominantly white (Fig. 4B, C), with the upper part near the suborbital cristae appearing dark reddish-brown (Fig. 4C). The chelae are dark reddish-brown, while the pleon and ambulatory legs range from dark brown to gray.

Size. Largest male CW 44.1 mm (holotype); largest female CW 43.6 mm (paratype).

Habitat. This species inhabits the intertidal zone with a soft muddy substrate, located in front of mangroves (Fig. 4H).

Remarks. In Vietnam, apart from the collection records from this study, Wada (2019) also documented "*M. crenulata*" from Long Thanh, Can Gio (Wada 2019: e139, fig. 1A). Although the suborbital cristae and the precise proportions of the ambulatory legs cannot be confirmed from the photograph by Wada (2019: fig. 1A), based on the currently known geographic distribution and the proximity of Wada's collection site to the type locality of *M. pristis* **sp. nov.** (both at Can Gio, Ho Chi Minh City), the species recorded by Wada (2019) is more likely to be *M. pristis* **sp. nov.** However, the material will need to be examined to confirm the identity.

Metaplax pristis sp. nov. is most similar to M. crenulata in morphology but can be distinguished by the male suborbital cristae and male ambulatory legs (Appendices 1, 2). However, no morphological differences have been observed between the females of M. pristis sp. nov. and M. crenulata, and they can only be differentiated by the locality and molecular evidence (Fig. 7; Appendix 2). In male M. pristis sp. nov., the suborbital cristae consist with more granules (Fig. 5C) (versus suborbital cristae with less granules in M. crenulata; Fig. 1D); the carpi are relatively shorter (Fig. 5F) (versus the carpi are relatively longer in M. crenulata; Fig. 1E); and the merus and the propodus of P5 are relatively slender (Fig. 5F; Appendix 1D, F) (versus the merus and the propodus of P5 are stout in M. crenulata; Fig. 1E; Appendix 1D, F).

Among the 10 known species of *Metaplax*, this new species, *Metaplax pristis* **sp. nov.**, and *M. crenulata* is morphologically distinct from other species by their larger body size (versus smaller body size in other known species) and ambulatory legs with numerous spines (versus with less spines or without spines in other species). The margins of the ambulatory legs meri lack distinct spines in most *Metaplax* species, such as *M. elegans*, *M. gocongensis*, *M. indica*, *M. intermedia*, *M. longipes*, *M. sheni*, and *M. tredecim* (De Man 1888: pl. 11, fig. 7; Davie & Nguyen 2003: fig. 1A; Naderloo 2017: fig. 32.2; Shih *et al.* 2019: figs. 3A, 4A, 5A, 6A). In contrast, *M. dentipes*, *M. distincta*, *M. crenulata*, and *M. pristis* **sp. nov.** have distinct spines on the meri margins of the ambulatory legs (Figs. 1E, 5F; De Man 1888: pl. 10 fig. 7, pl. 11 fig. 1). Additionally, the anterior margins of the carpi bear several spines only in *M. crenulata* and *M. pristis* **sp. nov.**, whereas the other nine *Metaplax* species lack spines on the carpi margins.

Distribution. At present, only known from southern Vietnam.

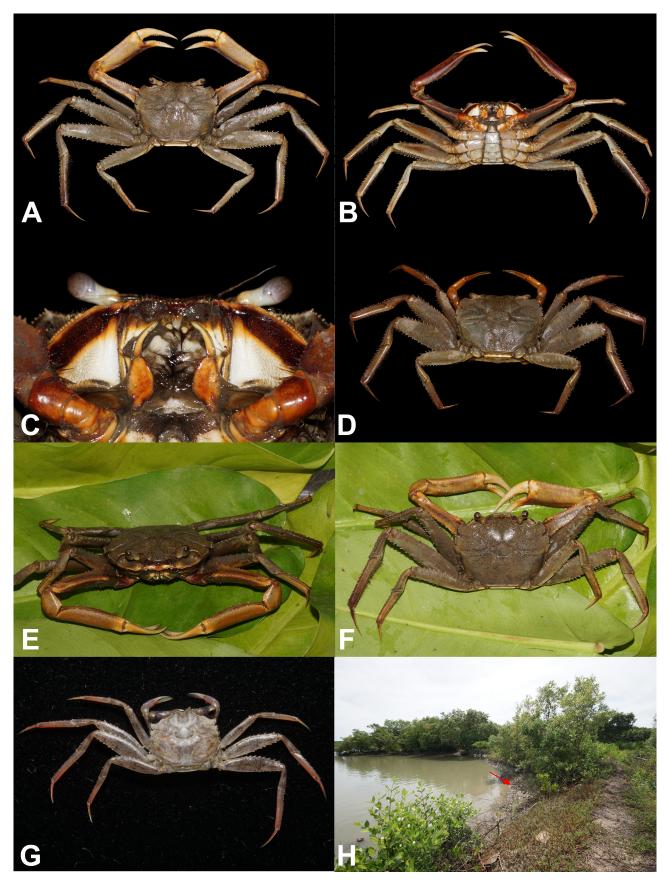


FIGURE 4. Color in life and habitat of *M. pristis* **sp. nov.** A–C, E, F, male, holotype (44.1×33.1 mm) (NCHUZOOL 17352); D, female, paratype (43.6×32.5 mm) (NCHUZOOL 17353); G, juvenile (specimen not examined); H, habitat in T. T. Can Thanh, Can Gio, Ho Chi Minh City, Vietnam (arrowed).

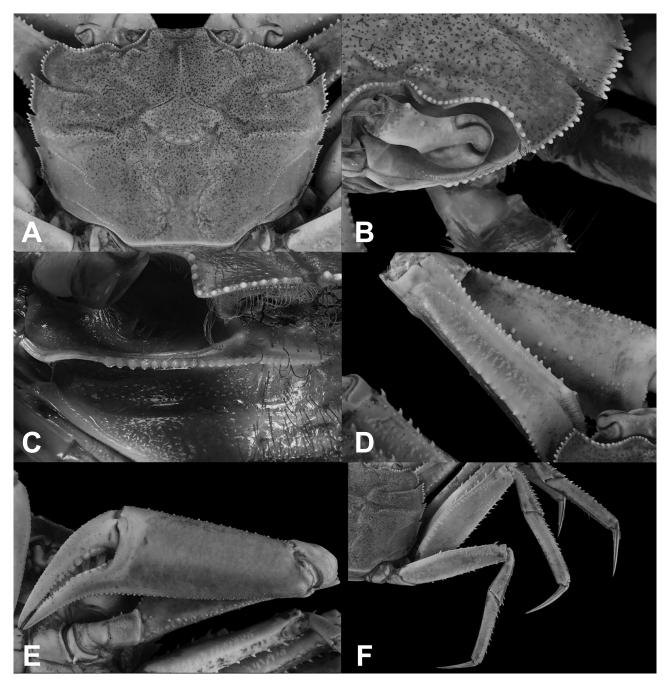


FIGURE 5. *Metaplax pristis* **sp. nov.**, male, holotype (44.1 × 33.1 mm) (NCHUZOOL 17352). A, carapace; B, left anterolateral teeth and supraorbital margin; C, left suborbital crista; D, left chelipedal merus; E, left chelipedal manus; F, right third ambulatory leg (P4) and fourth ambulatory leg (P5).

DNA analyses

The phylogenetic tree showed eight OTUs (operational taxonomic units) with high support, corresponding to one new species in this study and the other seven species previously described; *M. pristis* **sp. nov.** is most closely related to *M. crenulate* (Fig. 7). The pairwise nucleotide divergences of K2P distances and bp differences of haplotypes between the new species and the other species are shown in Table 2. The interspecific divergences are 5.76–21.47 % (36–116 bp) between *M. pristis* **sp. nov.** and the other species within *Metaplax* (Table 2).

TABLE 2. Matrix of percentage pairwise nucleotide divergence with Kimura 2-parameter (K2P) distances (upper) and mean numbers of differences (lower) based on the cytochrome c oxidase subunit I (COI) within and between *Metaplax pristis* **sp. nov.** and other seven species of *Metaplax* (see Table 1 and Fig. 7). Values of the range are shown in parentheses.

	M. crenulata (Gerstaecker, 1856)	M. dentipes (Heller, 1865)	M. tredecim Tweedie, 1950	M. longipes Stimpson, 1858	M. sheni Gordon, 1931	M. distincta H. Milne Edwards, 1852	M. elegans De Man, 1888
M. pristis	5.82	18.18	21.09	18.62	20.50	20.24	19.79
sp. nov.	(5.76–5.93)	(18.07-	(20.63 -	(18.25-	(20.30-	(20.01-	(19.36-
		18.28)	21.47)	18.66)	20.70)	20.94)	20.39)
	36.3	105.5	114.2	103.8	113.0	112.2	109.1
	(36–37)	(105-106)	(112–116)	(102-104)	(112-114)	(112-113)	(107-112)

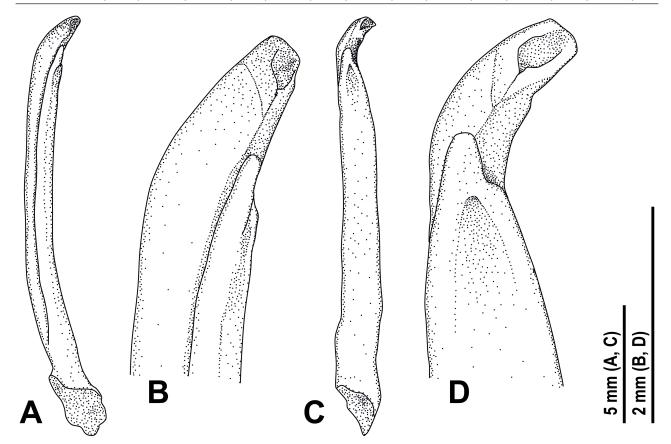


FIGURE 6. Right G1 of *Metaplax pristis* **sp. nov.**, male, holotype (44.1 × 33.1 mm) (NCHUZOOL 17352). A, B, dorsal view; C, D, lateral view.

Discussion

Morphological interspecific differences. This study examined specimens which previously identified as *M. crenulata*, from the Indian Ocean (Phuket, the western coast of the Malay Peninsula, and Singapore) and Vietnam. Due to the unclear type locality of *M. crenulata* (see Gerstaecker 1856: 143), it is challenging to determine whether the Indian Ocean or western Pacific species represents the true *M. crenulata*. However, we were fortunate to acquire photographs of the syntype of *M. crenulata* housed in the Zoologisches Museum Berlin (Fig. 2). Compared to the Vietnamese specimens, both the illustration by Gerstaecker (1856) and the syntype specimen (ZMB 604) align more closely with the morphology of other male specimens from the Indian Ocean (see below).

In terms of morphology, the male suborbital cristae of Indian Ocean specimens consist of fewer granules (22–27), while those of southern Vietnam specimens consist of more granules (30–31). For females, the number of granules

shows no obvious differences and overlaps in range (Indian Ocean: 21-23; southern Vietnam: 22-24). Although Gerstaecker (1856) neither described in detail nor illustrated the number of granules on the suborbital cristae, the specimen (ZMB 604) exhibits 24–25 granules in the male lectotype and 21–23 in female paralectotypes. In addition to the suborbital cristae, the proportions of male ambulatory legs are also different between the two species. The proportion of the ambulatory legs is considered an important taxonomic character for distinguishing closely related species in lots of crab taxa, such as Varunidae (Cyclograpsus H. Milne Edwards, 1853 in Li et al. 2019; Orcovita Ng & Tomascik, 1994 in Ng & Naruse 2024), Sesarmidae Dana, 1851 (Li et al. 2018) and Goneplacidae (Ng & Mitra 2019). In this study, two morphologically similar species within *Metaplax* can also be differentiated by the proportions of their male ambulatory legs. After comparing the lectotype (ZMB 604) and all examined specimens in this study, we found that both the lectotype and other male specimens from the Indian Ocean have relatively longer carpi on P4 and P5, and relatively stouter merus and propodus on P5. In contrast, southern Vietnam specimens exhibit relatively shorter carpi (P4 and P5) and relatively slender merus and propodus (only P5) (Appendix 1B, D-F). However, the proportions of P4 and P5 in females of the two species did not show obvious differences (Appendix 2). Based on these male morphological characters, the results show that the Indian Ocean specimens and the lectotype specimen represent the same species, should be true M. crenulata. Meanwhile, the specimens from Vietnam represent a distinct and undescribed species, here described as M. pristis sp. nov.

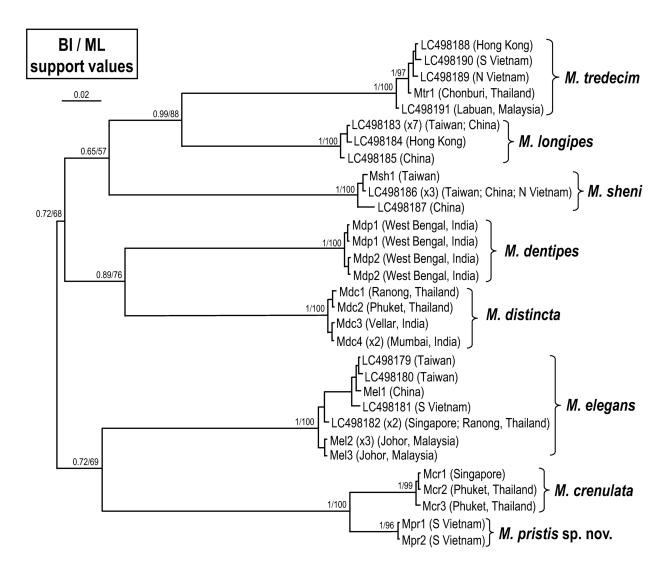


FIGURE 7. Bayesian inference (BI) tree of the of *Metaplax* H. Milne Edwards, 1852, based on the cytochrome c oxidase subunit I (COI) gene. The values at the node are the support values for BI and maximum likelihood (ML). Only values > 50% are shown.

Molecular analyses. In addition to their morphological similarity, the two species are also closely related in the molecular phylogeny. According to the constructed tree (Fig. 7), the two species form a group with high support, distinctly separated from other species within Metaplax. Regarding genetic distances, the minimum COI genetic divergence between Metaplax crenulata and M. pristis sp. nov. is 5.8% (36 bp) (Table 2). This divergence is lower than the genetic differences observed between some Metaplax species (15.87-19.45%; Shih et al. 2019) and certain taxa within the same family, such as Parahelice (between P. pilosa Sakai, Türkay & Yang, 2006 and P. sp. 2, 8.2%; Hsu & Shih 2024a), Parapyxidognathus (between P. tshiansue Hsu & Shih, 2024 and P. ongia Hsu & Shih, 2024, 10.17%; Hsu & Shih 2024b), and Ptychognathus (between P. amikee Hsu & Shih, 2024 and P. stimpsoni Hsu & Shih, 2020, 11.05%; Hsu & Shih 2024c). However, it is higher than the genetic divergences observed within some other genera in Varunidae, such as *Pseudohelice* (between *P. subquadrata* (Dana, 1851) and *P. annamalai* Prema, Hsu, Shih & Ravichandran, 2022, 1.54%; Prema et al. 2022) and Helice (between the H. latimera Parisi, 1918 complex and H. epicure NK Ng, Naruse & Shih, 2018, 2.97%; N.K. Ng 2018). Furthermore, this genetic distance (5.8%) is higher than the interspecific divergences reported for many intertidal crab taxa, including Parasesarma De Man, 1895 (Sesarmidae) (between P. bidens (De Haan, 1835) and P. chiahsiang Shih, Hsu & Li, 2023, 0.92%; Shih et al. 2023), Tuerkayana Guinot, NK Ng & Rodríguez Moreno, 2018 (Gecarcinidae MacLeay, 1838) (between T. celeste (Ng & Davie, 2012) and T. magnum (Ng & Shih, 2014), 0.92%; Ng & Shih 2023), and Minuca Bott, 1954 (Ocypodidae Rafinesque, 1815) (between M. aff. burgersi and M. panema (Coelho, 1972), 4.61%; Thurman et al. 2023).

Furthermore, the molecular phylogenetic tree constructed using COI (Fig. 7) indicates that the genus *Metaplax* can be preliminarily divided into four groups. Species within the same group exhibit similar morphologies and, in some cases, more similar distribution ranges. The first group includes three species distributed in the western Pacific: *M. tredecim*, *M. longipes*, and *M. sheni*. The second group consists of two species from the Indian Ocean, *M. dentipes* and *M. distincta*. The third group comprises *M. elegans*, while the fourth group includes two species with large body size, *M. crenulata* and *M. pristis* **sp. nov.** (Fig. 7). However, the phylogenetic tree presented in this study is based solely on a single mitochondrial gene (COI) and does not include all *Metaplax* species. The comprehensive phylogeny within *Metaplax* requires further studies involving additional species and gene fragments.

In summary, both morphological and molecular evidence support the existence of two distinct species within the "Metaplax crenulata" complex, one from the Indian Ocean (Phuket, the western coast of the Malay Peninsula, and Singapore) and the other from the western Pacific (Vietnam). The Indian Ocean species is identified as the true M. crenulata, while the species from Vietnam represents a new species, Metaplax pristis sp. nov.

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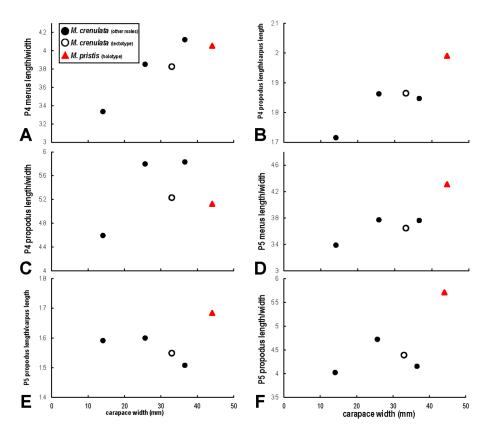
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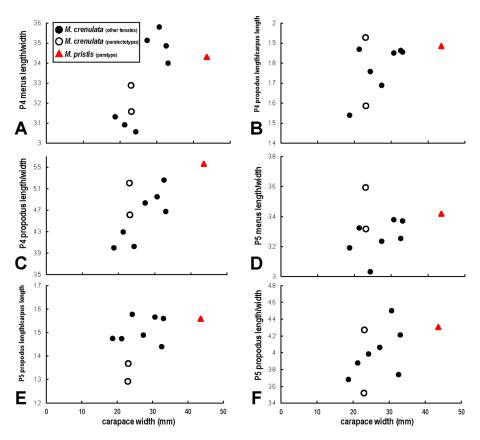
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Appendix



APPENDIX 1. Scatter plots of the measured ratios of male morphological characters. A, merus of P4 length to width; B, P4 propodus length to carpus length; C, propodus of P4 length to width; D, merus of P5 length to width; E, P5 propodus length to carpus length; F, propodus of P5 length to width. Horizontal and vertical axes indicate the CW and the ratios of measurements, respectively.



APPENDIX 2. Scatter plots of the measured ratios of female morphological characters. A, merus of P4 length to width; B, P4 propodus length to carpus length; C, propodus of P4 length to width; D, merus of P5 length to width; E, P5 propodus length to carpus length; F, propodus of P5 length to width. Horizontal and vertical axes indicate the CW and the ratios of measurements, respectively.