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On the identities of two closely related sentinel crabs, *Macrophthalmus* (*Euplax*) *leptophthalmus* (H. Milne Edwards, 1852) and *M.* (*E.*) *dagohoyi* Mendoza & Ng, 2007 (Crustacea: Decapoda: Brachyura: Macrophthalmidae)

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Abstract. The sentinel crabs, *Macrophthalmus* (*Euplax*) *leptophthalmus* (H. Milne Edwards, 1852) and *M.* (*E.*) *dagohoyi* Mendoza & Ng, 2007 are two closely related macrophthalmid species. Previous studies, which examined only the adult male syntype of *M. leptophthalmus* and the type series of *M. dagohoyi*, consisting of mostly sub-adults and juveniles, still left some room for doubt regarding reliable diagnostic morphological characters. In the present study, additional specimens of various size, including fully adult individuals, from eastern India, the Ryukyus in Japan, and Hainan Island in China were compared. The two species can now be distinguished by differences in the form of the eyestalks, carapace, and male first gonopod, and this is supported by the molecular evidence from the mitochondrial 16S rDNA and cytochrome c oxidase subunit I. Our findings confirm the identities of these species based on morphological, genetic, and biogeographic data. In addition, the status of the subgenera or genera *Euplax* H. Milne Edwards, 1852 and *Venitus* Barnes, 1967 are discussed.

Key words. taxonomy, 16S rDNA, cytochrome c oxidase subunit I (COI), *Macrophthalmus* (*Venitus*)

INTRODUCTION

The crabs of the family Macrophthalmidae Dana, 1851, known as sentinel crabs, are distributed across the Indo-West Pacific, inhabiting various habitats ranging from intertidal zones to shallow waters at depths reaching about 50 meters (Barnes, 1967, 2010; Hsu et al., 2023). Currently, this family contains 84 species belonging to three subfamilies (Ng et al., 2008; Sasaki, 2023). Some authors have suggested that certain subgenera could be elevated to the status of genera (Ng et al., 2008; McLay, 2010; Davie, 2012), with McLay et al. (2010), summarising from work done by Kitaura et al. (2002, 2010), proposing that *Euplax*, *Venitus*, and *Hemiplax* Heller, 1865 should be regarded as separate genera, leaving *Macrophthalmus* with three subgenera, *Macrophthalmus* sensu stricto, *Mareotis* Barnes, 1967, and *Paramareotis* Komai, Goshima & Murai, 1995. The available supporting data for this, however, remains poor, and in this study, we follow the classification scheme of Davie (2012), recognising only *Chaenostoma* and *Macrophthalmus* under Macrophthalminae, while treating others as subgenera for the time being.

The subgenera, *Euplax* H. Milne Edwards, 1852 and *Venitus* Barnes, 1967, are similar in their main characters (Mendoza & Ng, 2007). The subgenus *Euplax* contains two species, *M.* (*E.*) *leptophthalmus* (type locality: purportedly Chile, but see Remarks for this species) and *M.* (*E.*) *dagohoyi* (type locality: Bohol, central Philippines). The former was first described by H. Milne Edwards (1852), who established *Euplax* in the process. Subsequently, Rathbun (1918) formally recognised *E. leptophthalmus* as the type species of *Euplax*. Barnes (1966) synonymised *Euplax* under *Macrophthalmus* Desmarest, 1823, due to the lack of sufficient generic characters to distinguish *Euplax* from certain species of *Macrophthalmus*. Subsequently, Barnes (1967) transferred *M. leptophthalmus* to a new subgenus,

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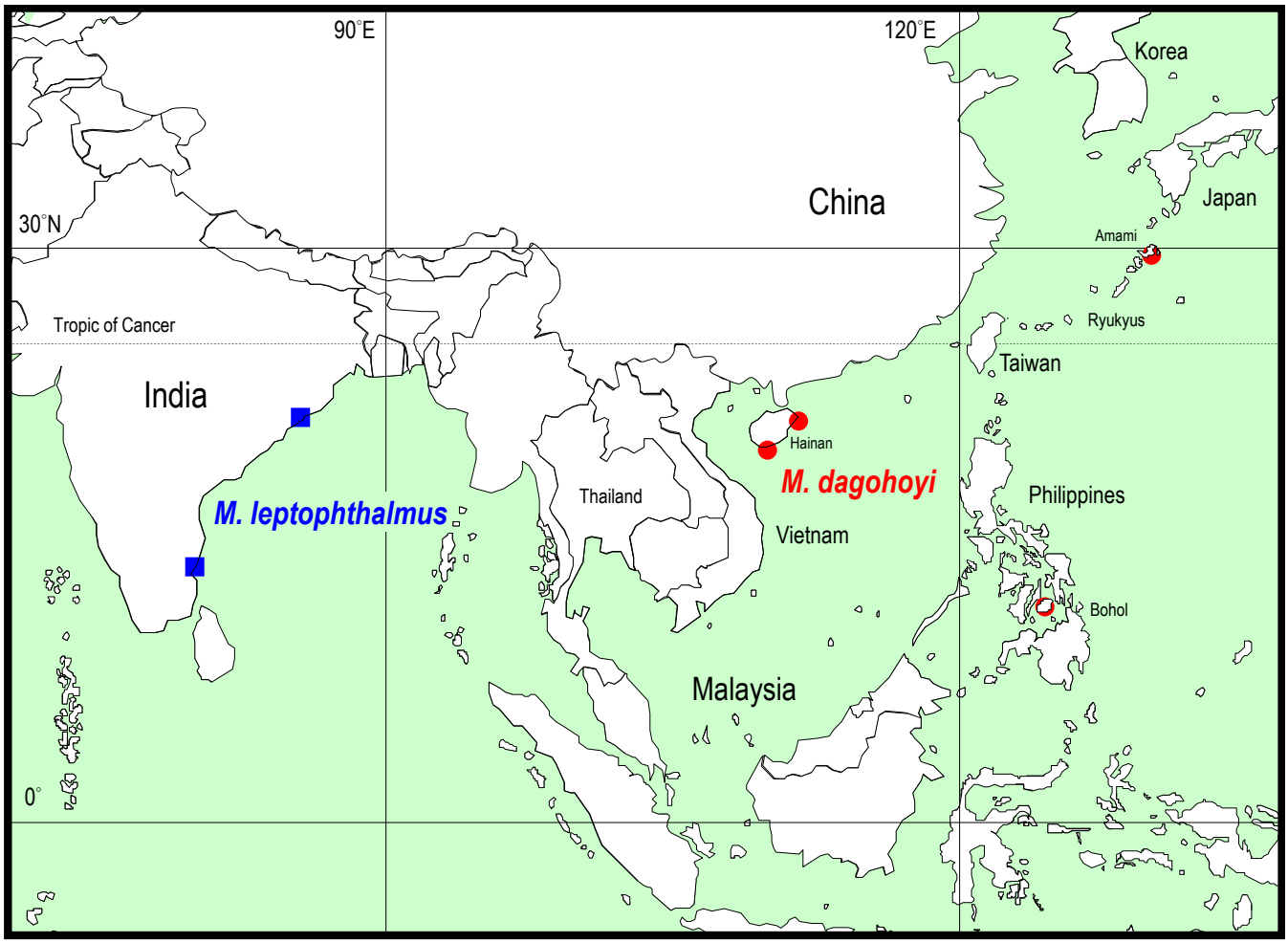

Fig. 1. Map showing the collection sites of *Macrophthalmus* (*Euplax*) *leptophthalmus* (blue squares) and *M.* (*E.*) *dagohoyi* (red circles) specimens used in this study.

Venitus Barnes, 1967, not recognising that *Euplax* H. Milne Edwards, 1852, should take priority over *Venitus* Barnes, 1967. Karasawa & Matsuoka (1992) also highlighted that if the two subgenera were synonymous, then *Euplax* has clear priority (see also Ng et al., 2008: 238). Mendoza & Ng (2007: 671, 673) re-examined the issue, concluding that *Euplax* and *Venitus* are distinct subgenera based on the discernible morphological differences in the carapace, front, anterolateral teeth, epistome, suborbital ridges, and telson. Mendoza & Ng (2007), however, relied only on photographs of the dry male syntype of *M. leptophthalmus* for their study. Their description was modified from Kemp (1915) and Barnes (1977) for *M. leptophthalmus* and the synonymised *M. gastrodes* Kemp, 1915. The male 'holotype' of *M.* (*E.*) *leptophthalmus* (MNHN-B3116) mentioned and figured in Mendoza & Ng (2007) is actually a syntype and not a holotype. The actual lot contains two specimens, one male and one female, as reported by Barnes (1966) (also see https://science.mnhn.fr/institution/mnhn/collection/iu/item/2000-3116). As such, we formally designate the male specimen (MNHN-B3116; = MNHN-IU-2000-3116) as the lectotype of *Euplax leptophthalmus* H. Milne Edwards, 1852. In addition, due to the lack of descriptions or illustrations in previous studies, the morphology of certain important characters in the true *M. leptophthalmus*, such as the first gonopod, have remained unknown, and are described in the present work. *Euplax leptophthalmus* was reported from Japan by Kishino et al. (2011), Koyama et al. (2022), and Nunobe et al. (2023), but the diagnostic characters used to distinguish the two species have not previously been reliable.

To clarify the identity of this material, we obtained additional specimens of *M. leptophthalmus* from India and "*E. leptophthalmus*" from the Ryukyus, Japan and Hainan, China, to compare. This has allowed for the study of characters across different specimen sizes. Molecular evidence from mitochondrial 16S rDNA and cytochrome c oxidase subunit I sequences was also generated and analysed. In this paper, we refine the morphological diagnoses to distinguish the two closely related species, with additional support from molecular data.

MATERIAL AND METHODS

Specimens examined or sequenced in this study (Fig. 1) were deposited in the Australian Museum, Sydney, Australia (AM); the reference collections of the Crustacean Research Laboratory, Centre of Advanced Study in Marine Biology, Annamalai University (CASAU); Zoological Collections of the Department of Life Science, National Chung Hsing University, Taichung, Taiwan (NCHUZOOL); National

Museum of Natural History, Manila, Philippines (NMCR); National Museum of Marine Biology and Aquarium, Pingtung, Taiwan (NMMB); and the Zoological Reference Collection of the Lee Kong Chian Natural History Museum, National University of Singapore (ZRC) (Table 1). The carapace measurements of the specimens are expressed as CW × CL (carapace width × carapace length) in millimetres, with values rounded to one decimal place. The abbreviation G1 is used for male first gonopods.

Genomic DNA was isolated from muscle tissue of the legs using the GeneMark Tissue and Cell Genomic DNA Purification Kit (Taichung, Taiwan). Approximately 550 base pairs (bp) of the 5′-end of the 16S rDNA gene were amplified via polymerase chain reaction (PCR) using the primers 16H10 and 16L29 (Schubart, 2009). A portion of the COI gene was also amplified using PCR with the primers LCO1490, HCO2198 (Folmer et al., 1994), COL14, COH6 (Schubart, 2009), LCOB, HCOex, HCOex2, HCOex3 (Shih et al., 2022b), and HCOex0 (Shih et al., 2023a). The PCR conditions for these primers were as follows: denaturation for 50 s at 94°C, annealing for 70 s at 45–47°C, and extension for 60 s at 72°C (40 cycles), followed by a final extension for 10 min at 72°C. Sequences were obtained using an automated Applied Biosystems 3730 sequencer (Applied Biosystems, CA, USA) and were aligned using the MUSCLE function of MEGA (vers. 11, Tamura et al., 2021) after verification with the complementary strand. Sequences of haplotypes were deposited in the GenBank database, with their accession numbers listed in Table 1.

According to a preliminary analysis (not shown), there are four closely related species, viz., *M. leptophthalmus*, *M. dagohoyi*, *M. latreillei* (Desmarest, 1817), and *M. barnesi* (Serène, 1971). Based on this, a phylogenetic tree combining 16S and COI sequences for the four species, with adequate outgroups, was constructed.

For the combined 16S and COI analysis, the best-fitting models for sequence evolution for individual datasets were determined using PartitionFinder (vers. 2.1.1, Lanfear et al., 2017), with model selection based on the Bayesian information criterion (BIC). The best models obtained were both GTR+G, which were subsequently applied in the Bayesian inference (BI) analysis. BI was performed using MrBayes (vers. 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 frequency values was below the recommended 0.01 (Ronquist et al., 2020), and the first 1,000 trees were discarded as the burnin. Maximum likelihood (ML) analysis was conducted using IQ-TREE (vers. 2.2.0, Minh et al., 2020) with the best models, and 30,000 ultrafast bootstrap replicates were generated (Hoang et al., 2017). A maximum parsimony (MP) consensus tree was constructed using MEGA with 2,000 bootstrap iterations via the Tree-Bisection-Reconnection (TBR) search method (100 random-addition sequence replications; search level = 2; max no. of trees to retain = 10,000). Bp differences and pairwise estimates of the Kimura (1980) two-parameter (K2P) distances for COI diversity between specimens were also calculated in MEGA.

RESULTS

SYSTEMATICS

Family Macrophthalmidae Dana, 1851

Genus *Macrophthalmus* Desmarest, 1823

Subgenus *Euplax* H. Milne Edwards, 1852

Macrophthalmus (*Euplax*) *leptophthalmus* (H. Milne Edwards, 1852)

(Figs. 2A–D, 3A–C, 4A–C, 5A–C)

Euplax leptophthalmus H. Milne Edwards, 1852: 160 [type locality: "Chili" (certainly incorrect, probably India; see Mendoza & Ng, 2007)]; Trivedi et al., 2018: tab. 1 (list) (India); Pati et al., 2018: 41, tab. 15 (list) (India); Sasaki, 2023: 15153 (list).

Euplax leptophthalma – Rathbun, 1910: 593 (list); Porter, 1913: 317; Porter, 1917: 159; Rathbun, 1918: 423; Garth, 1957: 107.

Euplax leptophthalma – Boschi, 2000: 81, appendix (list) (Perú-Chilean Province); Retamal & Moyano, 2010: 316, tab. 1 (list) (Chile).

Macrophthalmus gastrodes – Kemp, 1915: 228, fig. 9, pl. 12, fig. 5 (Orissa, India); Kemp, 1919: 394 (Orissa, India).

Macrophthalmus leptophthalmus – Barnes, 1966: 370, pl. 24, figs. 3, 4; Barnes, 2010: 36, 37 (key).

Macrophthalmus (*Venitus*) *leptophthalmus* – Barnes, 1977: 269, fig, 1 (Orissa, India); Ng et al., 2008: 238 (list).

Macrophthalmus (*Euplax*) *leptophthalmus* – Mendoza & Ng, 2007: 677, figs. 1–2; Ng et al., 2008: 237 (list); Barnes, 2010: 36 (key).

Macrophthalmus (*Venitus*) *gastrodes* – Ng et al., 2008: 238 (list).

Not *Macrophthalmus* (*Euplax*) *leptophthalmus*: Kishino et al., 2011: 14, figs. 1–3 (Amami Island, Ryukyus) (= *Macrophthalmus* (*Euplax*) *dagohoyi* Mendoza & Ng, 2007); Koyama et al., 2022: 64, fig. 1 (Kyushu, Japan) (= *Macrophthalmus* (*Euplax*) *dagohoyi* Mendoza & Ng, 2007); Nunobe et al., 2023: 35, fig. 1 (Shikoku, Japan) (= *Macrophthalmus* (*Euplax*) *dagohoyi* Mendoza & Ng, 2007).

Material examined. 6 males (24.4 × 19.5, 24.0 × 18.9, 23.7 × 18.9, 21.5 × 17.0, 19.3 × 16.0, 18.6 × 15.3 mm) (NCHUZOOL 17222), Vellar River, India, coll. M. Prema, September–December 2020; 2 males (23.4 × 18.8, 19.1 × 15.7 mm) (ZRC 2024.0599), Vellar River, India, coll. M. Prema, September–December 2020; 1 male (18.1 × 14.8 mm) (NCHUZOOL 17290), Vellar River, India, coll. M. Prema, September 2020; 1 male (24.3 × 19.5 mm) (NCHUZOOL 17291), Vellar River, India, September–December 2020; 1 female (18.9 × 15.8 mm) (NCHUZOOL 17292), Vellar River, India, coll. M. Prema, September–December 2020; 4 males (23.4 × 18.9, 21.8 × 17.3, 19.0 × 16.2, 18.7 × 15.7 mm) (NCHUZOOL 17296), Vellar River, India, coll. M. Prema, September–December 2020; 4 males (23.5 × 18.9, 21.6 × 17.6, 19.7 × 16.8, 18.8 × 15.4 mm) (ZRC 2024.0600), Vellar River, India, coll. M. Prema, September–December 2020; 4 males (19.5 × 16.5, 18.9 × 16.6, 18.4 × 16.2, 16.5 × 14.3 mm) (CASAU-1051), Vellar River, India, coll. M.

Table 1. Haplotypes of the 16S rDNA and cytochrome c oxidase subunit I (COI) for specimens of *Macrophthalmus* species used in this study.

Species	Locality	Catalog no. of NCHUZOOL (unless indicated)	Haplotype of 16S	Access. no. of 16S	Haplotype of COI	Access. no. COI
M. leptophthalmus	India: Odisha: Chilka	ZRC 2019.1852	Mle	PV471259	Mle_C1	PV469829
	India: Tamil Nadu: Vellar River estuary	17290	Mle	PV471260	Mle_C2	PV469830
	India: Tamil Nadu: Vellar River estuary	17222	Mle	PV471261	Mle_C3	PV469831
	India: Tamil Nadu: Vellar River estuary	17222	Mle	PV471262	Mle_C3	PV469832
	India: Tamil Nadu: Vellar River estuary	17291	Mle	PV471263	Mle_C4	PV469833
	India: Tamil Nadu: Vellar River estuary	17222	Mle	PV471264	Mle_C5	PV469834
M. dagohoyi	Japan: Ryukyus: Amami	ZRC 2024.0077	Md1	PV471265	-	
	Japan: Ryukyus: Amami	17340 (3 ind.)	Md2	PV471266, PV471267, PV471268	Md_C1	PV469835, PV469836, PV469837
	Philippines: Bohol	ZRC 2007.0001 (paratype)	Md1	PV471269	Md_C2	PV469838
	China: Hainan: Sanya	17295	Md1	PV471270	Md_C3	PV469839
	China: Hainan: Wenchang	17294	Md2	PV471271	Md_C1	PV469840
	China: Hainan: Wenchang	17294	Md2	PV471272	Md_C4	PV469841
	China: Hainan: Wenchang	17294	Md2	PV471273	Md_C5	PV469842
	China: Hainan: Wenchang	17294	Md2	PV471274	Md_C6	PV469843
M. latreillei	Taiwan: Pingtung: Donggang	NMMBCD987	Mla	LC097101	Mla_C1	LC097126
	Vietnam: Nha Trang	17358	Mla	PV471275	Mla_C1	PV469844
	SW Taiwan	17357	Mla	PV471276	Mla_C1	PV469845
	Hong Kong	17329	Mla	PV471277	Mla_C1	PV469846
	Australia: Northern Territory: Point Charles	AM P.73247	Mla	PV471278	Mla_C1	PV469847
	India: Tamil Nadu: Vellar River estuary	17330	Mla	PV471279	Mla_C2	PV469848
	India: Tamil Nadu: Vellar River estuary	17331 17332	Mla	PV471280, PV471281	Mla_C2	PV469849, PV469850
	India: Kerala	17333	Mla	PV471282	Mla_C3	PV469851
M. barnesi	Taiwan: Penghu	17176	Mb1	PV471283	Mb_C1	PV469852
	Taiwan: Penghu	17175	Mb2	PV471284	Mb_C2	PV469853
	Taiwan: Penghu	17174	Mb3	PV471285	Mb_C3	PV469854
	Taiwan: Penghu	17177	Mb4	PV471286	Mb_C4	PV469855
	Philippines: Luzon	ZRC 2015.0481	Mb3	PV471287	Mb_C5	PV469856
	Vietnam: Nhatrang	ZRC 1970.1.23.3	Mb3	PV471288	Mb_C6	PV469857
M. fusculatus	Indonesia: West Papua	ZRC 2011.1001 paratype		PV471289		PV469858
M. definitus	Taiwan: Kaohsiung	14762		PV471290		PV469859
M. banzai	Taiwan: Changhua	14807		PV471291		LC155131

Prema, 13 November 2023; 2 males (20.4 × 16.9, 22.4 × 16.5 mm) (CASAU-1052), Vellar River, India, coll. M. Prema, 10 November 2022; 2 males (19.4 × 16.4, 16.8 × 14.0 mm) (CASAU-1052), Vellar River, India, coll. M. Prema, 22 September 2022.

Diagnosis. Carapace (Fig. 2A–C) subquadrate, almost circular, 1.2–1.3 times wider than long; surface granular, with scattered, short setae. Supraorbital margin (Fig. 3A–C) slightly backward-sloping. Anterolateral margin (Fig. 3A–C) granulated, setose, with 3 relatively well-defined teeth (including exorbital tooth). First tooth (exorbital tooth) broadly to acutely triangular; second tooth broad, lobular or subrectangular, with rounded to acutely angular tip, directed upwards and outwards; U-shaped incision between first and second teeth narrow, pronounced, deep; third tooth distinct, small, bluntly triangular, directed upwards and outwards. Front moderate in width. Eyestalk (Fig. 3A–C) slightly curved, more-or-less uniform in width throughout its length, cornea less inflated. Male chelipeds subequal. Merus inner and outer margins with fringe of long setae. Inner surface of carpus with dense long setae; outer surface smooth. Palm short, inflated; upper margin and inner surface with thick mat of setae. Ambulatory legs (Fig. 2A–C) long, slender. Male pleon (Fig. 4A–C) tapering gradually toward telson, tip of telson rounded anteriorly. G1 (Fig. 5A–C) relatively stout; subdistal region gently tapered, short and gently curved.

Habitat. Subtidal muddy bottoms of the estuaries (Kemp, 1915). In the Vellar River estuary, Tamil Nadu, India (Fig. 6A, B), *M. leptophthalmus* and *M. latreillei* specimens were collected using fishing nets at depths of 4–10 m.

Size. Largest male CW 24.4 mm (NCHUZOOL 17222); largest female CW 18.9 mm (NCHUZOOL 17292).

Distribution. India (Kemp, 1915; Mendoza & Ng, 2007; this study). East coast of India; so far known from Chilka Lake in the north and Vellar River in the south (Fig. 1).

Remarks. The type locality of *M. leptophthalmus* was indicated as "Chili" in South America (H. Milne Edwards, 1852: 160). Others have suggested that the type locality is likely not Chile, but rather India (Mendoza & Ng, 2007: 677), particularly since *Macrophthalmus* and Macrophthalminae are not known from the eastern Pacific (Barnes, 1967, 2010), and a synonymised species, *M. gastrodes* Kemp, 1915, has its type locality in Chilka Lake in Orissa, India. From this, it can even be surmised that the "Chili" in the original label/s of the types of *M. leptophthalmus* may have been a mis-spelling of "Chilka" (P.J.F. Davie, pers. comm.). Subsequent studies focusing on the region around Chile, such as Boschi (2000) and Retamal & Moyano (2010), have not provided any specimen collection data for *M. leptophthalmus*, with the authors basing this record solely on H. Milne Edwards' original report (H. Milne Edwards, 1852). In contrast, apart from records in the western Pacific (which were actually *M. dagohoyi*, see later), *M. leptophthalmus* has only been reliably recorded in India (see the synonymy list above for details).

Macrophthalmus (*Euplax*) *dagohoyi* Mendoza & Ng, 2007

(Figs. 2E–H, 3D–F, 4D–F, 5D–F)

Macrophthalmus (*Euplax*) *dagohoyi* Mendoza & Ng, 2007: 677, figs. 3–5 [type locality: Bohol Island, Philippines]; Ng et al., 2008: 237 (list).

Macrophthalmus dagohoyi – Barnes, 2010: 36 (key).

Euplax leptophthalmus – Kishino et al., 2011: 14, figs. 1–3 (Amami Island, Ryukyus); Koyama, et al. 2022: 64, fig. 1 (Kyushu, Japan); Nunobe et al., 2023: 35, fig. 1 (Shikoku, Japan) (not *Euplax leptophthalmus* H. Milne Edwards, 1852).

Euplax dagohoyi – Sasaki, 2023: 15152 (list).

Material examined. Holotype: 1 male (14.9 × 13.4 mm) (NMCR 27008), subtidal mangrove mud, Abatan River Estuary, Bohol Island, Philippines, coll. Panglao 2004 Expedition, 28 June 2004. Paratypes: 1 male (13.5 × 12.1 mm) (NMCR 27009), 1 female (17.5 × 15.6 mm) (ZRC 2007.0004), subtidal mangrove mud, Abatan River Estuary, Bohol Island, Philippines, coll. Panglao 2004 Expedition, 28 June 2004. Others: 2 males (17.2 × 14.2, 15.0 × 12.5 mm), 1 female (14.0 × 11.8 mm) (NCHUZOOL 17340), Amami Island, Japan, coll. T. Yonezawa, 4 September 2024; 1 male (19.5 × 15.8 mm), 1 female (13.3 × 11.6 mm) (NCHUZOOL 17293), Yakugaki River, Amami Island, Japan, coll. T. Yonezawa, 6 October 2013; 1 male (16.2 × 13.7 mm), 1 female (13.3 × 11.6 mm) (ZRC 2024.0077), Yakugaki R., Amami Island, Japan, coll. T. Yonezawa, 6 October 2013; 5 males (24.4 × 20.3, 20.9 × 17.4, 20.6 × 16.9, 19.4 × 16.3, 17.6 × 14.7 mm), 2 females (21.2 × 17.2, 17.2 × 14.4 mm) (NCHUZOOL 17294), Wenchang, Hainan Island, China, coll. X. Zhang, 30 November 2023; 1 male (20.7 × 16.9 mm), 1 female (20.3 × 16.7 mm) (ZRC 2024.0598), Wenchang, Hainan Island, China, coll. X. Zhang, 30 November 2023; 1 male (18.9 × 16.1 mm) (NCHUZOOL 17295), Sanya, Hainan Island, China, coll. You-Qi Hao, 18 March 2023.

Diagnosis. Carapace (Fig. 2E–G) subquadrate, almost circular, 1.15–1.23 times wider than long; surface granular, with scattered, short setae. Supraorbital margin (Fig. 3D–F) distinctly backward-sloping. Anterolateral margin (Fig. 3D–F) granulated, setose, with 3 relatively weak teeth (including exorbital tooth). First tooth (exorbital tooth) broadly subtriangular, never acutely tipped; second tooth broad, lobular or subrectangular, with rounded tip, directed upwards and outwards; U-shaped incision between the first and second teeth wide, less pronounced, shallow; third tooth relatively indistinct, small, bluntly triangular, directed upwards and outwards. Front moderate in width. Eyestalk (Fig. 3D–F) relatively more curved, more tapering, cornea more inflated. Male chelipeds subequal. Merus inner and outer margins with fringe of long setae. Inner surface of carpus with dense long setae; outer surface smooth. Palm short, inflated; upper margin and inner surface with thick setae. Ambulatory legs (Fig. 2E–G) long, slender. Male pleon (Fig. 4D–F) tapering gradually toward telson, tip rounded anteriorly. G1 (Fig. 5D–F) relatively slender; subdistal part tapering, long and curved.

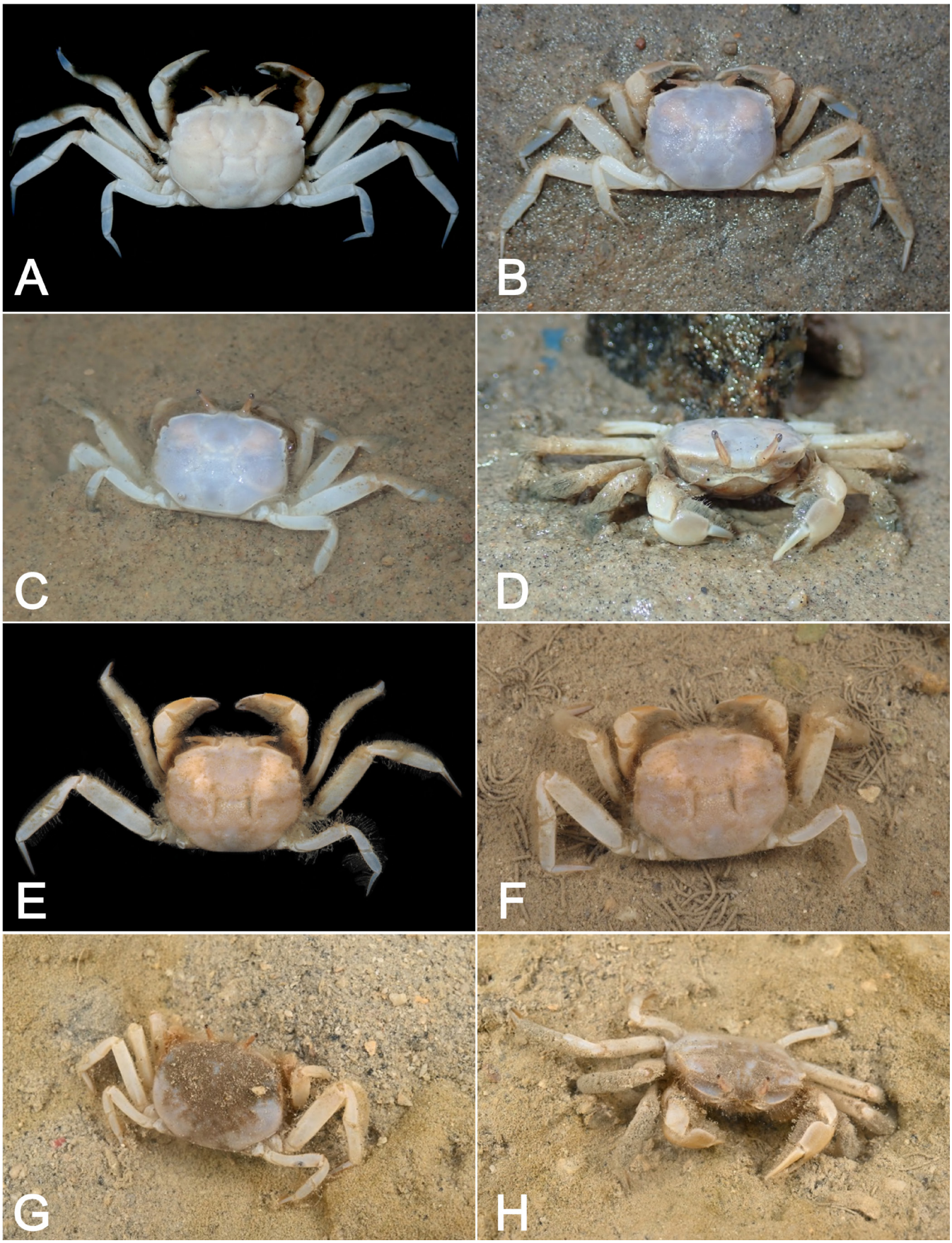

Fig. 2. Colour in life of the two species. A–D, *Macrophthalmus* (*Euplax*) *leptophthalmus*; E–H, *M.* (*E.*) *dagohoyi*. A, B, C, CW 21.8 mm, NCHUZOOL 17296, Vellar River, India; E, F, CW 18.9 mm, NCHUZOOL 17295, Hainan Island, China; G, CW 21.2 mm, NCHUZOOL 17294, Hainan Island, China. D, H, specimens not located.

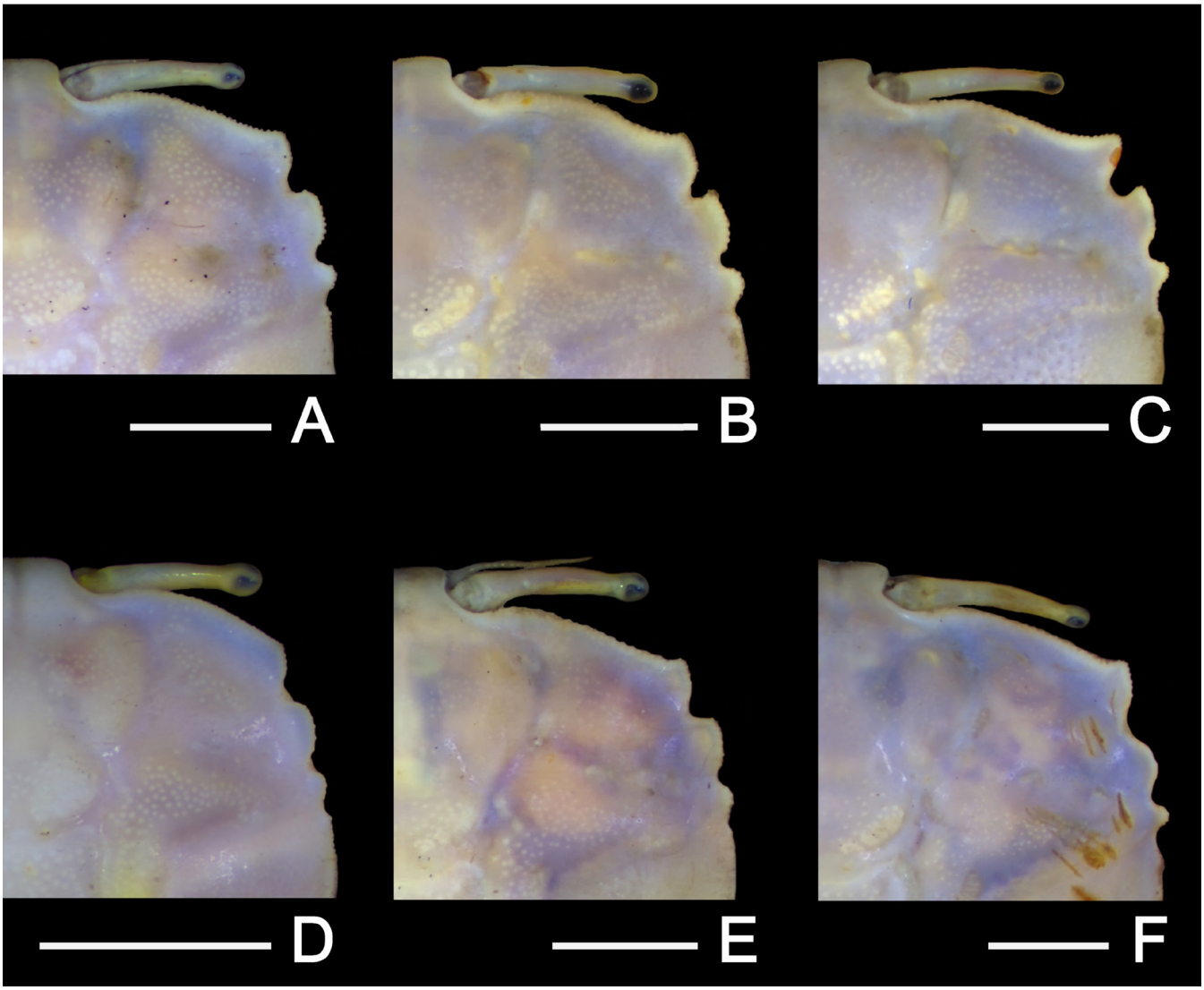

Fig. 3. Right carapace anterolateral margin and eyes of the two species. A–C, *Macrophthalmus* (*Euplax*) *leptophthalmus* (A, CW 18.6 mm, NCHUZOOL 17222; B, CW 21.5 mm, NCHUZOOL 17222; C, CW 24.4 mm, NCHUZOOL 17222); D–F, *M.* (*E.*) *dagohoyi* (D, CW 13.5 mm, NMCR 27009; E, CW 20.6 mm, NCHUZOOL 17294; F, CW 24.4 mm, NCHUZOOL 17294). Scale bars = 5 mm.

Habitat. Subtidal muddy bottoms of mangrove estuaries or creeks at water depths ranging from 20 cm to 10 m (Mendoza & Ng, 2007; Kishino et al., 2011; Koyama et al., 2022; this study). On Amami Island, the habitat is a muddy slope in a mangrove area with gentle flow and minimal freshwater influence. The area remains submerged even at low spring tides, with soft, deeply deposited mud and occasional plant debris, sometimes forming a reduced (anoxic) layer (Fig. 6C, D). In Hainan, specimens were captured using entangling nets from soft bottoms at a depth of about 10 m.

Size. Largest male CW 24.4 mm (NCHUZOOL 17294); largest female CW 21.2 mm (NCHUZOOL 17294).

Distribution. Japan (Shikoku, Kyushu, and Ryukyu Islands), China (Hainan Island) and the Philippines (Bohol Island) (Mendoza & Ng, 2007; Kishino et al., 2011; Koyama et al., 2022; Nunobe et al., 2023; this study) (Fig. 1).

Remarks. Since its original description (Mendoza & Ng, 2007), this species has not been recorded under this name, with only a few studies mentioning it in lists (e.g., Ng et al., 2008; Sasaki, 2023) or keys (Barnes, 2010). Based on the morphological and molecular results of our study, this species is now confirmed to also occur in Amami Island, Ryukyu Islands, Japan (Kishino et al., 2011, as "*Euplax leptophthalmus*") and Hainan, China (this study). By extension, the record of *Euplax leptophthalmus* from Miyazaki Prefecture in Kyushu, Japan, should also be treated as *M. dagohoyi*. Although *M. dagohoyi* and *M. leptophthalmus* are very similar in morphology, they can be distinguished by differences in the carapace and male G1 (see "Morphological differences and variation" in the Discussion).

Molecular analyses. The analysis has revealed a number of distinct haplotypes for each species for both 16S and COI genes (Table 1). The mean pairwise nucleotide divergences of K2P distances and bp differences for the COI haplotypes are shown in Table 2. K2P values (and bp differences) for *M. leptophthalmus* are 0.15–1.38% (1–9 bp), and for *M. dagohoyi* are 0–0.61% (0–4 bp). Conversely, interspecific

Table 2. Matrix of percentage pairwise nucleotide divergences with Kimura 2-parameter (K2P) distances and number of base pair differences based on cytochrome c oxidase subunit I (COI) within and between four closely related species of *Macrophthalmus*. In the right half, the lower-left values represent K2P distances, and the upper-right values represent base pair differences. Ranges are shown in parentheses.

	Intraspecific		**Interspecific**			
	Nucleotide divergence	**Mean nucleotide difference**	***M. leptophthalmus***	***M. dagohoyi***	***M. latreillei***	***M. barnesi***
M. leptophthalmus	0.31 (0–0.61)	2 (0–4)		10.3 (5–16)	81.33 (80–83)	99.92 (98–103)
M. dagohoyi	0.48 (0–1.38)	3.11 (0–9)	1.59 (0.76–2.48)		86.22 (83–88)	99.08 (97–102)
M. latreillei	0.12 (0–0.3)	0.78 (0–2)	13.77 (13.51–14.1)	14.73 (14.11–15.08)		103.81 (102–107)
M. barnesi	1.15 (0.77–1.54)	7.5 (5–10)	17.25 (16.86–17.88)	17.08 (16.66–17.69)	17.96 (17.59–18.6)	

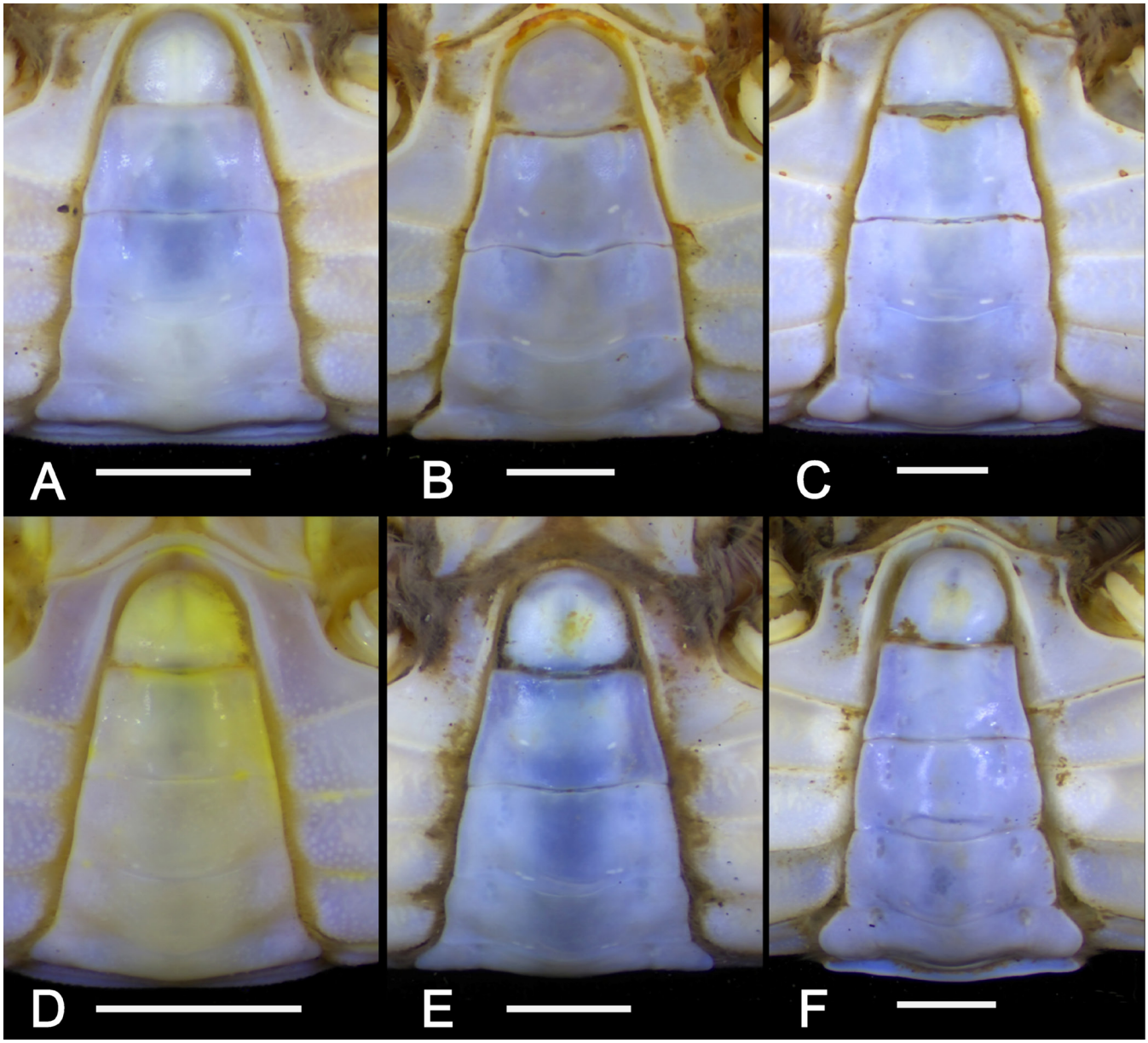

Fig. 4. Male pleon of the two species. A–C, *Macrophthalmus* (*Euplax*) *leptophthalmus* (A, CW 18.6 mm, NCHUZOOL 17222; B, CW 21.5 mm, NCHUZOOL 17222; C, CW 24.4 mm, NCHUZOOL 17222); D–F, *M.* (*E.*) *dagohoyi* (D, CW 13.5 mm, NMCR 27009; E, CW 20.6 mm, NCHUZOOL 17294; F, CW 24.4 mm, NCHUZOOL 17294). Scale bars = 4 mm.

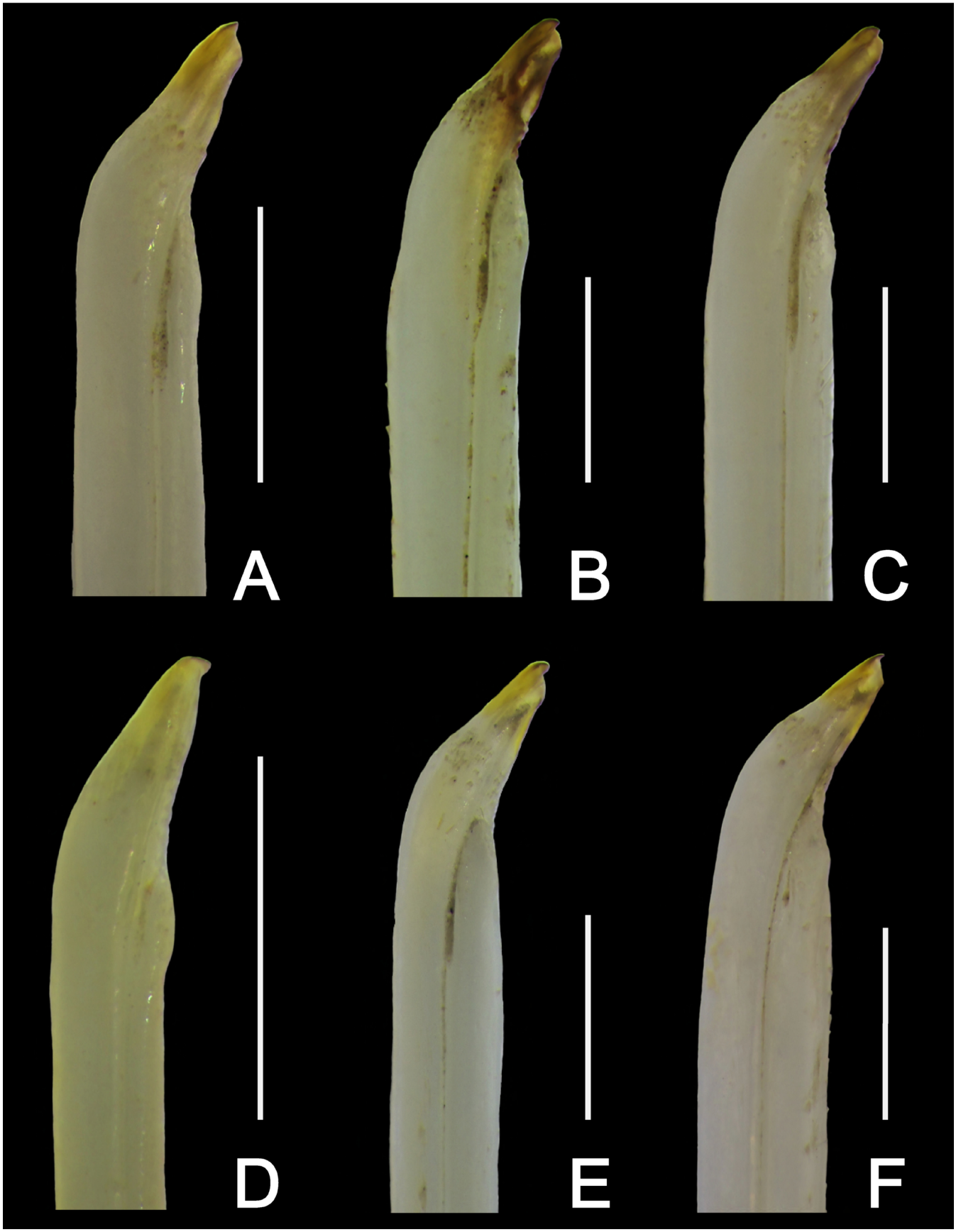

Fig. 5. First gonopod (G1) of two species (dorsal view). A–C, *Macrophthalmus* (*Euplax*) *leptophthalmus* (A, CW 18.6 mm, NCHUZOOL 17222; B, CW 21.5 mm, NCHUZOOL 17222; C, CW 24.4 mm, NCHUZOOL 17222); D–F, *M.* (*E.*) *dagohoyi* (D, CW 13.5 mm, paratype, NMCR 27009; E, CW 20.6 mm, NCHUZOOL 17294; F, CW 24.4 mm, NCHUZOOL 17294). A–E, right G1s; F, left G1 (horizontally flipped for comparison with the right G1s of other specimens). Scale bars = 1 mm.

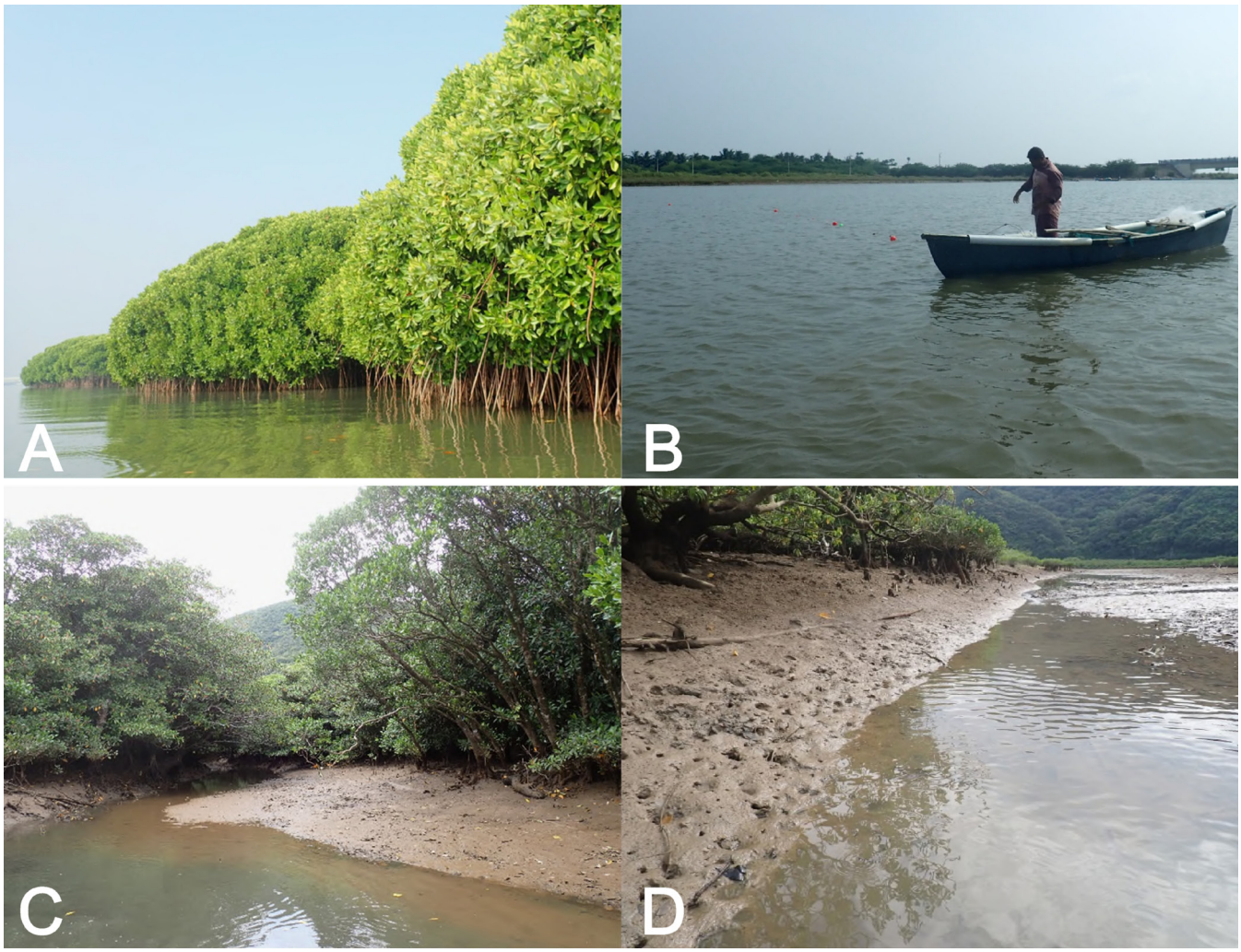

Fig. 6. Habitats of *Macrophthalmus* (*Euplax*) *leptophthalmus* in the Vellar River estuary, Tamil Nadu, India (A, B), and of *M.* (*E.*) *dagohoyi* in Amami Island, Japan (C, D). A, artificial mangroves near the estuary; B, collection with entangling fish nets on soft bottoms at 4–10 m depth; C, D, muddy slope beside mangroves with gentle flow and minimal freshwater influence.

differences between these two species range from 0.76% to 2.48% (5–16 bp). Both species differ from *M. latreillei* and *M. barnesi* by larger values of ≥ 13.51% (≥ 80 bp).

The phylogenetic analysis based on these sequences (Fig. 7) shows that *M. leptophthalmus* and *M. dagohoyi* are closely related, but the support values are not high. The two species and *M. latreillei* form a highly supported monophyletic group. However, the support values for a larger clade comprising this group of three species together with *M. barnesi* are weak.

DISCUSSION

Molecular analyses and subgeneric classification. Genetically, *M. leptophthalmus* and *M. dagohoyi* can be separated into two clades by mitochondrial 16S and COI markers, although the support values for the two clades are not high (Fig. 7). Similarly, the COI distances between them are also low, with a minimum interspecific distance of 0.76% (Table 2). However, each species possesses unique haplotypes (distinct genetic variations) for both 16S and COI genes, meaning that these genetic markers can effectively differentiate species based on their DNA sequences (Table 1). Consequently, we consider that the distinction of these two species is also supported by molecular evidence. Such a close genetic relationship between species has been reported in other crab taxa. For example, the minimum interspecific distance of COI is 0.15% between the fiddler crabs, *Paraleptuca crassipes* (White, 1847) and *P. boninensis* (Shih, Komai & Liu, 2013) (Shih et al., 2013); 0.92% between the gecarcinids, *Tuerkayana celeste* (Ng & Davie, 2012) and *T. magnum* Ng & Shih, 2014 (Ng & Shih, 2014, 2023); 0.92% between the sesarmids, *Parasesarma bidens* (De Haan, 1835) and *P. chiahsiang* Shih, Hsu & Li, 2023 (Shih et al., 2023b); and 1.08% between the gecarcinids, *Gecarcoidea natalis* (Pocock, 1889) and *G. lalandii* H. Milne Edwards, 1837 (Lai et al., 2017). Additional studies using other markers with higher resolution should be done in the future to confirm the differentiation between these two species. For example, the mitochondrial control region marker (Shih et al., 2022a) has been used to differentiate pseudocryptic species such as *Paraleptuca boninensis* and *Tuerkayana latens* Ng & Shih, 2023 (see Shih et al., 2013; Ng & Shih, 2023).

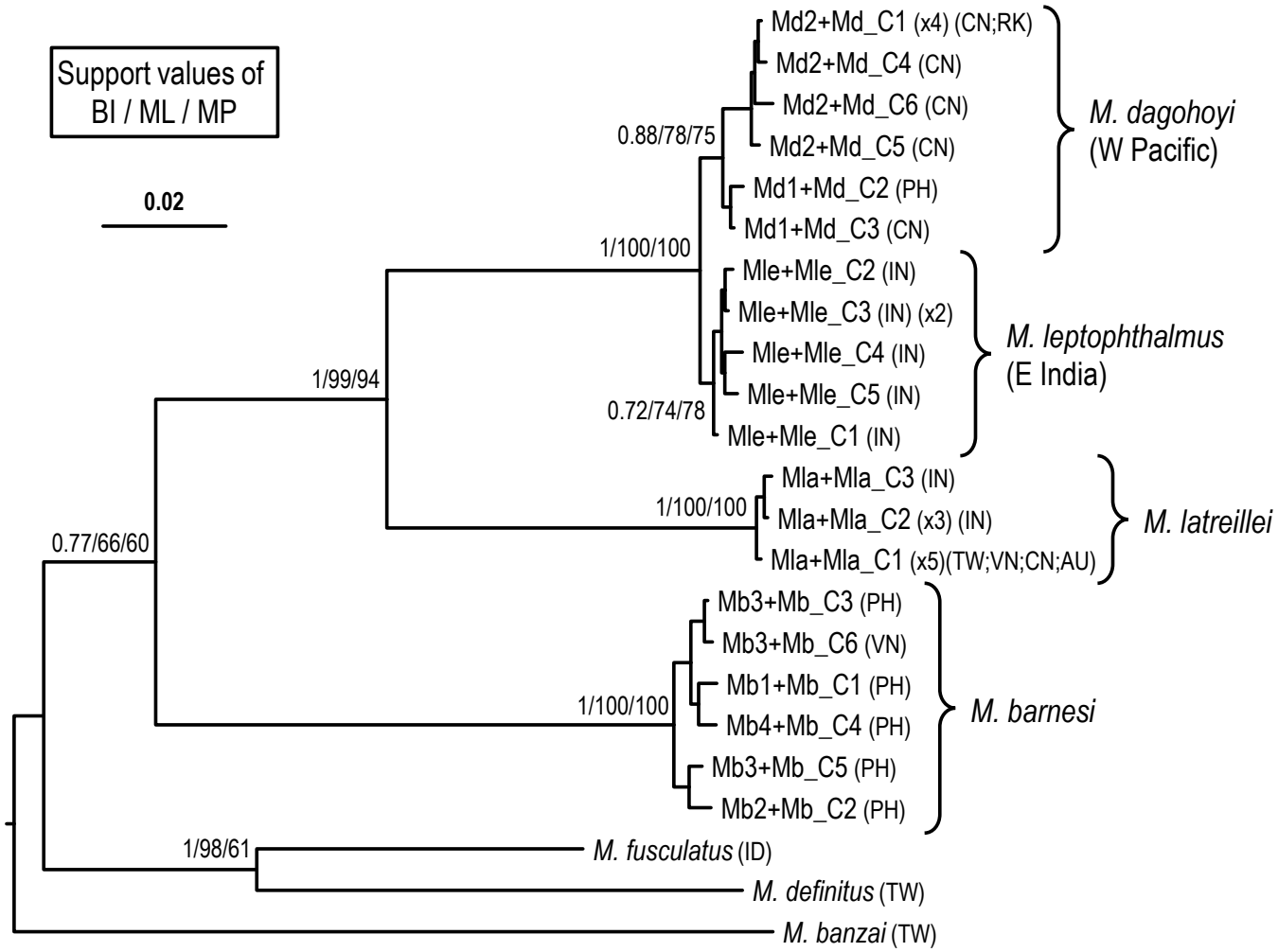

Fig. 7. Bayesian inference (BI) tree of *Macrophthalmus* (*Euplax*) *leptophthalmus* and *M.* (*E.*) *dagohoyi*, along with other related congeneric species, based on the combined 16S and COI markers. The values at the nodes represent the support values from the BI, maximum likelihood (ML), and maximum parsimony (MP) analyses. AU, Australia; CN, China; ID, Indonesia; IN, India; PH, Philippines; RK, Ryukyus, Japan; TW: Taiwan; VN: Vietnam. Only support values > 50% are shown. Refer to Table 1 for haplotype names.

The phylogenetic tree (Fig. 7) also raises issues regarding the subgeneric placement of these taxa. According to Barnes (2010), the subgenus *Euplax* includes *M. leptophthalmus* and *M. dagohoyi*, while *Venitus* comprises *M. barnesi*, *M. dentipes*, and *M. latreillei*. In the present study, however, *M. leptophthalmus* and *M. dagohoyi* form a small clade corresponding to *Euplax*, which, in turn, forms a larger clade with *M. latreillei*. On the other hand, *M. barnesi* is not sister to *M. latreilli* and support for any relationship is low. This suggests that *M. barnesi* may warrant its own subgenus. The use of of conserved nuclear markers, e.g., 28S and H3 (Shih et al., 2016, 2023b), will probably be needed to better resolve their subgeneric/generic status. In any case, further genetic studies across a wider range of taxa are needed to resolve the generic and subgeneric relationships across the whole of Macrophthalmidae.

Morphological differences and variation. Four reliable characters have been identified to differentiate *M. leptophthalmus* and *M. dagohoyi* at similar body sizes: (1) the eyestalk is relatively straighter and less tapering, with a less inflated cornea in *M. leptophthalmus* (Fig. 3A–C; Kemp, 1915: pl. 12, fig. 5) (vs. eyestalk more curved, more tapering, and with a more inflated cornea in *M. dagohoyi*; Fig. 3D–F; Mendoza & Ng, 2007: figs. 3A, 4A; Kishino et al., 2011: figs. 1A, 2A, C); (2) the supraorbital margin of the carapace in dorsal view is only slightly backward-sloping in *M. leptophthalmus* (Fig. 3A–C; Kemp, 1915: pl. 12, fig. 5) (vs. distinctly backward-sloping in *M. dagohoyi*; Fig. 3D–F; Mendoza & Ng, 2007: figs. 3A, 4A; Kishino et al., 2011: figs. 1A, 2A); (3) the first (exorbital) tooth of the anterolateral margin is usually more pronounced and acutely triangular, the U-shaped incision between the first and second anterolateral teeth is narrower, better defined, and deeper, and the third tooth is more distinct in *M. leptophthalmus* (Fig. 3A–C; Kemp, 1915: pl. 12, fig. 5) (vs. first (exorbital) tooth subtriangular, less acute and projecting, U-shaped incision much wider, poorly defined, and shallower due to the effacing of the mesial margin of the second tooth, and third tooth less distinct in *M. dagohoyi*, Fig. 3D–F; Mendoza & Ng, 2007: figs. 3A, 4A; Kishino et al., 2011: figs. 1A, 2A, B); and (4) the G1 is relatively stouter with the subdistal part relatively tapering, shorter and curved to a lesser degree in *M. leptophthalmus* (Fig. 5A–C) (vs. slender; with the

subdistal part less tapering, longer and more curved in *M. dagohoyi*; Fig. 5D–F; Mendoza & Ng, 2007: fig. 5D, F, G; Kishino, et al. 2011: fig. 2F, G).

Several characters commonly used to distinguish some macrophthalmid crabs, e.g., the form of the third maxillipeds, the setation on the chelae and ambulatory legs, the posterior margins and ratios of ambulatory legs, the margin of male somite 4 and the pleon, and the female vulvae (cf. Barnes, 2010; Teng et al., 2016; Maenosono & Naruse, 2018; Hsu et al., 2023) could not be used to separate *M. leptophthalmus* and *M. dagohoyi* as they are too variable.

Some studies (Mendoza & Ng, 2007; Kishino et al., 2011; Koyama et al., 2022) have indicated that the sternal rim bordering the telson and the penultimate pleonal somite can distinguish *M. leptophthalmus* (granular) from *M. dagohoyi* (smooth). However, the present results found this character to also be unreliable as both granular and smooth sternal rims were observed in both species (Fig. 4).

Our results show there is some morphological variation across different sizes within the same species. Smaller specimens of both *M. leptophthalmus* and *M. dagohoyi* typically have: (1) a more backward-sloping supraorbital margin of the carapace (Fig. 3A, D) (vs. less backward-sloping in larger specimens (Fig. 3C, F)); (2) blunter anterolateral teeth (especially the exorbital tooth) (Fig. 3A, D) (vs. more acute teeth in larger specimens (Fig. 3C, F)); (3) less pronounced incisions between anterolateral teeth (Fig. 3A, D) (vs. more pronounced incisions in larger specimens (Fig. 3C, F)); and (4) straighter subdistal part of G1 (Fig. 5A, D) (vs. more curved in larger specimens (Fig. 5C, F)).

Geographical distributions. Based on their distributions, *M. leptophthalmus* is currently found exclusively in the eastern Indian Ocean, while *M. dagohoyi* is distributed across East and Southeast Asia in the western Pacific (Fig. 1). The Sunda Shelf appears to act as a geographical barrier between these two species, with isolation due to fluctuations in sea levels during glacial periods as the primary driver (Randall, 1998; Voris, 2000; Ameri et al., 2023). Some closely related intertidal or terrestrial crabs are either largely confined to the western Pacific [e.g., *Gelasimus vocans* (Crane, 1975), *Austruca perplexa* (Crane, 1975; Shih & Poupin, 2020), *Gecarcoidea lalandii* (Lai et al., 2017), and *Sesarmops imperator* (Ng et al., 2020)] or to the eastern Indian Ocean [e.g., *Gelasimus hesperiae* (Crane, 1975; Shih et al., 2022b), *Austruca variegata* (Shih et al., 2019), *Gecarcoidea humei* (Lai et al., 2017), and *Sesarmops indicus* (Ng et al., 2020)], despite evidence of some range extension along the Strait of Malacca and Christmas Island in the case of *G. humei*.

Conversely, other taxa such as *Austruca annulipes* (H. Milne Edwards, 1837) (Crane, 1975; Shih et al., 2021, 2022b, c), *Tubuca paradussumieri* (Bott, 1973) (Crane, 1975; Shih et al., 2021, 2022c), the varunid *Parapyxidognathus deianira* (De Man, 1888) (Hsu & Shih, 2024), and the macrophthalmid *M. latreillei* (this study), exhibit continuous distribution across the potential boundaries (e.g., the Straits of Malacca and the Sunda Strait). The continuous distribution of such marine organisms may be due to dispersal from the West Pacific to the Indian Ocean via the Strait of Malacca and the Sunda Strait during interglacial or recent postglacial periods, as observed in the case of sea urchins (Lessios et al., 2003), barnacles (Tsang et al., 2008; Chan et al., 2022), portunid crabs (He et al., 2011), and seaweeds (Chan et al., 2014). An alternative dispersal route via the southern Indonesian islands during glaciations has also been proposed or implied for barnacles (Chan et al., 2022) and seaweeds (Liang et al., 2022). During glacial periods, however, particularly in the summer, existing ocean currents would not have permitted dispersal of planktonic larvae from the West Pacific to the Indian Ocean (Kuhnt et al., 2004; He et al., 2011). During these periods, the only currents flowing from the West Pacific to the Indian Ocean would have been through the Makassar Strait, between Borneo and Sulawesi, during winter (Kuhnt et al., 2004) which may have limited the dispersal potential of some species.

To provide a more complete understanding of the distributional ranges of *M. leptophthalmus* and *M. dagohoyi* (Fig. 1), greater sampling effort across various sites, especially in the intervening region between the eastern coast of India and archipelagic Southeast Asia, must be done. Moreover, due to the cryptic habits of these crabs, passive sampling methods, such as the use of entangling fish nets on soft bottoms at depths of 2–10 m (Fig. 6B), have proven effective for collection in Vellar and Hainan in our study. Similarly, tangle nets were successfully employed on Balicasag Island, Philippines, to sample rare crustaceans (Ng et al., 2009). It should also be noted that relatively large numbers of *M. dagohoyi* were collected in Bohol during the PANGLAO 2004 Expedition by using a scuba-assisted vacuum-suction method (Mendoza & Ng, 2007; Bouchet et al., 2009), although most of the specimens collected were juveniles and sub-adults. Better understanding of the habits of these crabs is expected to improve the chances of collecting a good series of specimens.

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