

On a collection of thoracotreme crabs (Crustacea: Brachyura: Ocypodidae, Macrophthalmidae, Dotillidae) from two offshore islands of Papua, eastern Indonesia, with descriptions of two new species

Dewi Citra Murniati^{1,2,*}, Akira Asakura³, Dharma Arif Nugroho¹, Udhi Eko Hernawan⁴, I Wayan Eka Dharmawan⁴.

Abstract. In the present study, crab species of the families Ocypodidae Rafinesque, 1815, Macrophthalmidae Dana, 1851, and Dotillidae Stimpson, 1858, are reported from the islands of Liki and Bepondi, in Papua, eastern Indonesia, on the basis of specimens collected during the Nusa Manggala Expedition in 2018. *Ocypode ceratophthalmus* (Pallas, 1772), *O. cordimana* Latreille, 1818, *Gelasimus jocelynae* (Shih, Naruse and Ng, 2010), and *Paraleptuca crassipes* (White, 1847), all of which belong to the Ocypodidae, are recorded. In addition, two new species from Liki Island, *Macrophthalmus* (*Macrophthalmus*) *manggala* (Macrophthalmidae) and *Tmethypocoelis liki* (Dotillidae), are described. *Macrophthalmus* (*Macrophthalmus*) *manggala*, new species, belongs to the *Macrophthalmus* (*Macrophthalmus*) *convexus* species-group and can be distinguished from the other members of the same group by a G1 that has a truncated apex with a short chitinous process being twisted and directed laterally, a vulva that is rounded and slightly protruded with a median transverse groove, and the gastric mill wherein the anterior margin of the propyloric ossicle of the median tooth plate is narrow and acute and the lateral tooth plate bears 15–16 teeth. *Tmethypocoelis liki*, new species, differs from the other four congeners in the male cheliped, which has a subdistal tooth on the upper margin of the dactylus, and the G1, which has a bilobed tip with five short and one long apical setae.

Key words: Dotillidae, Macrophthalmidae, *Macrophthalmus*, Papua, *Tmethypocoelis*

INTRODUCTION

Species of Ocypodidae Rafinesque, 1815, Macrophthalmidae Dana, 1851, and Dotillidae Stimpson, 1858, are common in estuaries and mangroves, which are mainly distributed in tropical and subtropical areas worldwide (Barnes, 1970; Davie & Kosuge, 1995; Naderloo et al., 2010; Sakai & Türkay, 2013). These families are currently placed under the superfamily Ocypodoidea Rafinesque, 1815, together with Camptandriidae Stimpson, 1858, Heloeciidae H. Milne-Edwards, 1852, Mictyridae Dana, 1851, Ucididae Števíč, 2005, and Xenophthalmidae Stimpson, 1858 (Ng et al., 2008; De Grave et al., 2009; Davie et al., 2015). Recent

molecular studies on Brachyura suggest, however, that the superfamilies Grapsoidea MacLeay, 1838, and Ocypodoidea are not monophyletic and exhibit some degree of paraphyly (Schubart et al., 2006; Tsang et al., 2014; Chen et al., 2019).

In their habitats, crabs of the above-mentioned three families play important roles as deposit feeders, and even as prey for shore birds (Botto et al., 2000; Bezerra et al., 2006; Correa and Uidea, 2008; Allen, 2010). They occur generally in high density, especially in habitats with high organic content in their substrates (Murniati, 2015). Species from Macrophthalmidae and Ocypodidae are easily recognised by their medium to large carapace size. In Indonesia, so far there are known to be 25 and 21 species of Macrophthalmidae and Ocypodidae respectively (Rahayu and Nugroho, 2012; Sakai and Türkay, 2013; Murniati & Pratiwi, 2015; Shih et al., 2016), while only nine species of Dotillidae have been recorded in Indonesia thus far (Tesch, 1918; De Man, 1926; Serène & Moosa, 1981; Rahayu & Setyadi, 2009; Allen, 2010; Darmarini et al., 2019; Wada, 2019).

There have been many studies on the taxonomy of these three families in Indonesia. The early collections were obtained through three expeditions by Dutch naturalists: the Dutch East Indies Expedition (1888), the Siboga Expedition (1899–1900), and the Snellius Expedition (1929–1930) (Tesch, 1918; Barnes, 1971; Pieters & de Visser, 1993). The first expedition was initiated by Max Wilhelm Carl Weber

Accepted by: Jose Christopher E. Mendoza

¹Research Center for Biosystematics and Evolution, National Research and Innovation Agency (BRIN), Jl. Raya Jakarta Bogor Km 46, Cibinong, Bogor, Indonesia; Email: dewicitramurniati@gmail.com (* corresponding author)

²Department of Zoology, Division of Biological Science, Graduate School of Science, Kyoto University, Japan.

³Seto Marine Biological Laboratory, Field Science Education and Research Center, Kyoto University, Japan

⁴Research Center for Oceanography, National Research and Innovation Agency (BRIN), Pasir Putih 1, Ancol Timur, Jakarta 14430, Indonesia.

in 1888 to explore the fauna of Sumatra, Java, Sulawesi and Flores. Working on the collection from this expedition, De Man (1892) reported 135 species of decapod crustaceans from Indonesia, including three species of ocypodoid crabs, *Macrophthalmus transversus* (Latreille, 1817), *Ocypode kuhlii* De Haan, 1835, *O. cordimana* Latreille, 1818, and a new species *Dotilla wichmanni* De Man, 1892.

The Siboga Expedition, which was also led by Max W. C. Weber was conducted from 1899 to 1900. The brachyuran species collected during the expedition were studied by Tesch (1918), who reported 18 species of “Ocypodidae” from the Indonesian Archipelago. Now these species are classified into three families and nine genera, i.e., Ocypodidae sensu stricto (*Austruca* Bott, 1973; *Gelasimus* Latreille, 1817; *Tubuca* Bott, 1973; *Ocypode* Weber, 1795), Macrophthalmidae (*Chaenostoma* Stimpson, 1858; *Macrophthalmus* Desmarest, 1823), and Dotillidae (*Dotilla* Stimpson, 1858; *Ilyoplax* Stimpson, 1858; *Tmethypocoelis* Koelbel, 1897).

The Snellius Expedition led by P. M. van Riel was conducted from 1929 to 1930 to explore the waters of eastern Indonesia. Barnes (1971) studied the taxonomy of the species of *Macrophthalmus* collected through this expedition. Taxonomic studies on these families in some areas of the Indo-West Pacific were also conducted by Serène (1973) who reported *M. verreauxi* H. Milne-Edwards, 1848, now considered a junior synonym of *M. (Macrophthalmus) telescopicus* (Owen, 1839), from Sumatra and Ambon. Pretzmann (1974) described *Macrophthalmus (Mareotis) pacificus tijlajapensis*, now considered a full species, from Java.

Several taxonomic studies were recently conducted on representatives of Ocypodidae, Macrophthalmidae and Dotillidae from Indonesia. Kitaura & Wada (2006) described *Ilyoplax pacifica* Kitaura & Wada, 2006, from the Philippines and Sulawesi. Shih et al. (2010) described *Uca (Gelasimus) jocelynae* Shih, Naruse & Ng, 2010, now *Gelasimus jocelynae*, from the Western Pacific, where some of their specimens were from Indonesia. Naderloo et al. (2010) described *Uca (Austruca) cryptica* Naderloo, Türkay & Chen, 2010, now *Austruca cryptica*, from Flores. Rahayu & Nugroho (2012) described *Macrophthalmus (Mareotis) fuscus* Rahayu & Nugroho, 2012, from Papua. Naderloo (2013) described *Chaenostoma java* Naderloo, 2013 (Macrophthalmidae) from Java.

In the present study, we report the diversity of Ocypodidae, Macrophthalmidae and Dotillidae from two offshore islands of Papua, i.e., Liki Island and Bepondi Island, Indonesia, mainly on the basis of the specimens collected during the Nusa Manggala Expedition in 2018. The two islands face the Western Pacific Ocean where the currents flow into Indonesian waters through the Makassar Strait (Gordon, 2005). In total, six species are recorded from the two islands, including one new species of Dotillidae and one new species of Macrophthalmidae. The keys to the species of the *Macrophthalmus (Macrophthalmus) convexus* group

and genus *Tmethypocoelis* including the new species are presented.

MATERIAL AND METHODS

The present study is one of the results of the Nusa Manggala Expedition in 2018, organised by the Research Center for Oceanography, Indonesian Institute of Sciences (LIPI) (recently renamed the National Research and Innovation Agency [BRIN]) under the COREMAP-CTI Project. The expedition aimed to explore biodiversity in the outer islands of Papua and Moluccas, Indonesia (Fig. 1) (LIPI, 2019; Raharjo et al., 2021). The name “Nusa Manggala” is derived from the Sanskrit language (Nusa = island, and Manggala = fore part, front line, or front border). Therefore, Nusa Manggala refers to the “Outer Islands”, and the main objective of the Nusa Manggala Expedition is to preserve Indonesian sovereignty (<https://www.youtube.com/watch?v=2CMPgVyaHUo>). Liki Island and Bepondi Island in Papua Province were among the targeted islands. Five collection stations were set up in Liki Village, Sarmi District, Sarmi Municipality, Liki Island and one station in Masyai Village, District of West Supiori, Supiori Municipality, Bepondi Island. The crab specimens were collected by hand in the intertidal zone up to the estuaries. Samplings were done during the day or the night, coinciding with the expected periods of activity of the crabs.

Before collecting the crabs, we observed and recorded their behaviour during low tide in the daytime. By using a digital camera (Canon EOS 600D), the waving behaviour in five males of one *Tmethypocoelis* species (*T. liki*, new species) was recorded in situ. The movement of the male chela was then illustrated with Adobe Illustrator CC 2015 from the recorded videos. The collected specimens were preserved in 85% ethanol. Identification of all specimens was based on Crane (1975), George & Jones (1982), Davie (1990), Davie & Kosuge (1995), Komai et al. (1995), Barnes (2010), Shih et al. (2010), Naderloo et al. (2011), Rahayu & Nugroho (2012), and Sakai & Türkay (2013). Terminology of morphology follows Davie et al. (2015). The abbreviations P1–P5 are for the pereopods 1–5 respectively, G1 is for the male first gonopod, and ovig. is for an ovigerous female. The chresonyms are limited to the records of crabs from Indonesia.

The carapace width (cw, measured across the widest point) and the carapace length (cl, measured from the mid-front to the mid-posterior margin) are expressed as cw × cl in millimetres (mm). The carapace was photographed, and the size ratio (cw/cl) was determined using ImageJ software. For the large-sized samples, the morphological characteristics were captured using a digital camera (Canon EOS 600D) equipped with a macro lens. Meanwhile, for the small-sized samples, the characters were captured using a stereomicroscope (Olympus SZ) equipped with a digital camera (Olympus E-330). Morphological characteristics and illustrations of small-sized samples and small-sized body parts were also obtained using a stereomicroscope (Nikon SMZ

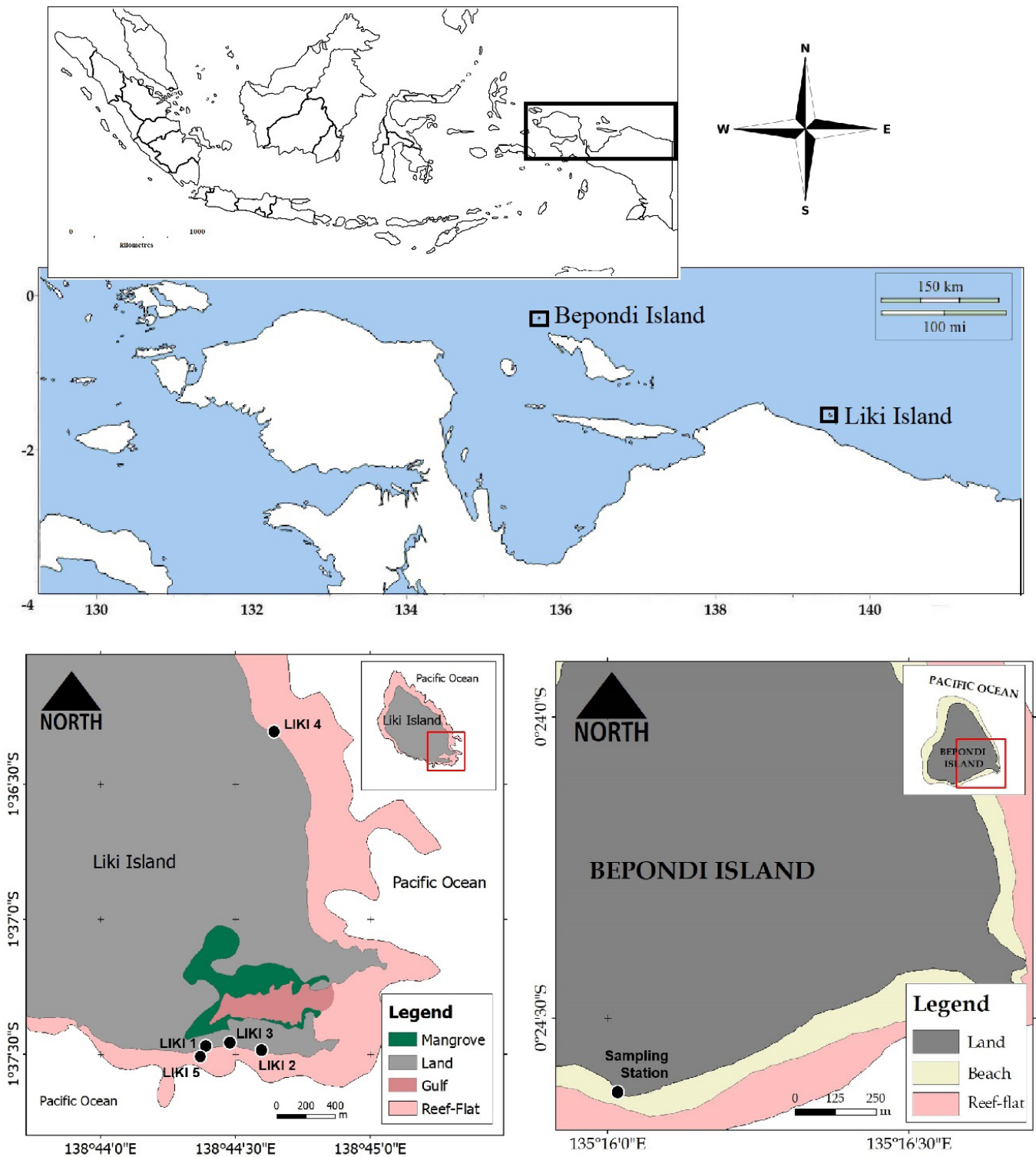


Fig. 1. Map of two outer Islands of West Papua, Indonesia. Liki sampling station, Liki 1, 01°37'26.31"S, 138°44'22.76"E; Liki 2, 01°37'27.46"S, 138°44'29.96"E; Liki 3, 01°37'25.29"S, 138°44'26.54"E; Liki 4, 01°36'18.05"S, 138°44'36.33"E; Liki 5, 01°37'27.35"S, 138°44'22.60"E. Bepondi sampling station. 00°24'37.30"S, 135°16'02.17"E (Source: d-maps.com; Research Center for Oceanography, LIPI).

800) equipped with a drawing tube. Camera lucida drawings were made by hand and enhanced using a Wacom drawing pad and Adobe Illustrator CC2015 software.

Using a scanning electron microscope (SEM), Jeol JSM 5310 LV, at an accelerating voltage of 5 kV, detailed photos of the teeth plate of the gastric mills, gonopods, and vulva were captured. The samples were prepared by fixing them in glutaraldehyde and cacodylate buffer, dehydrated in a

series concentration of ethanol gradually, i.e., 50%, 70%, 85%, 90% and absolute concentration, and vacuum-dried (TITEC VC-96N) for 10 minutes. Each prepared sample was then mounted on a specimen stub and coated with gold at 5–8 mA for 5 minutes using an ion coater (Dewi & Purwaningsih, 2020).

The materials examined are deposited in the following repositories: Museum Zoologicum Bogoriense (MZB),

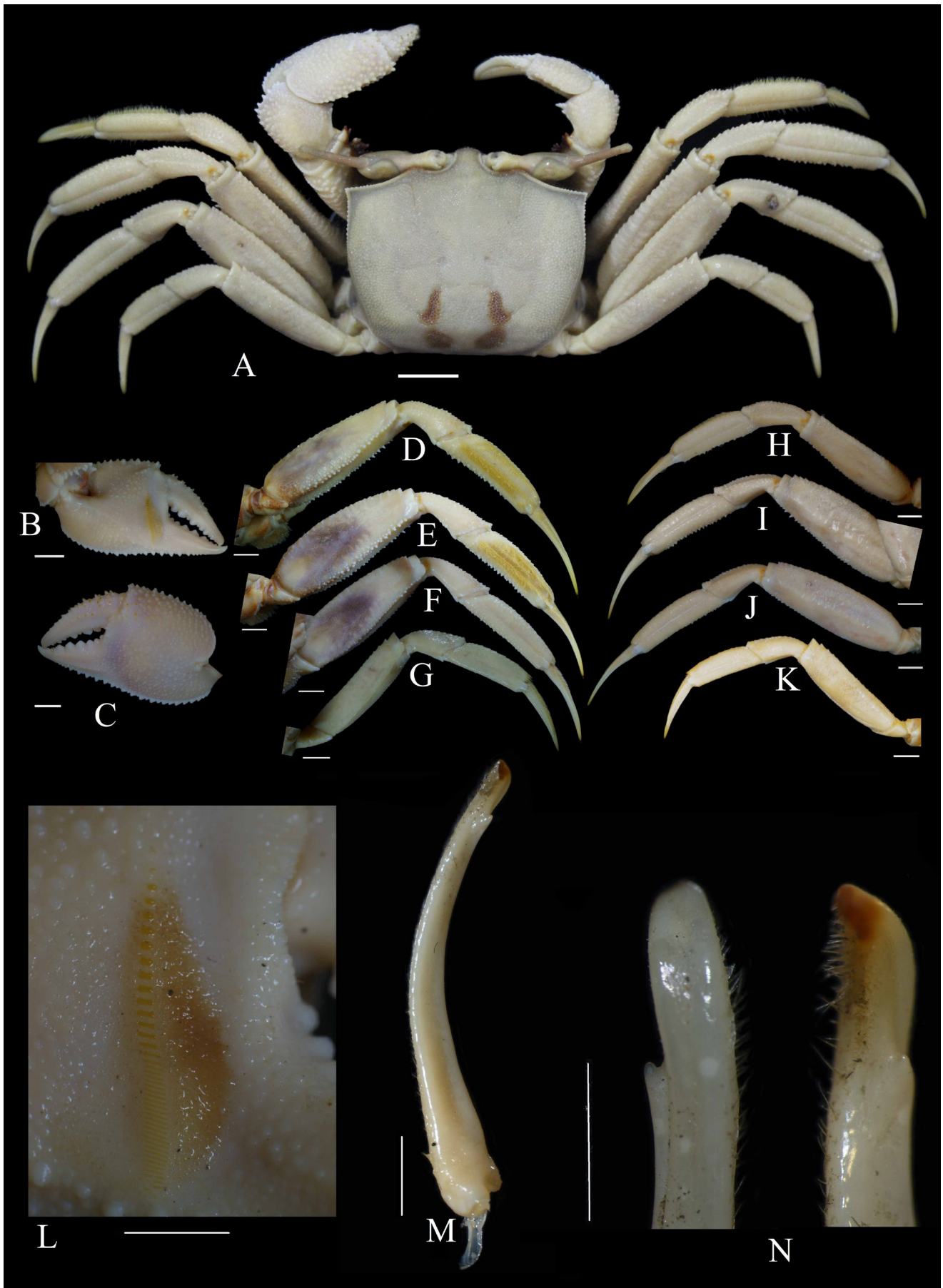


Fig. 2. *Ocypode ceratophthalmus* (Pallas, 1772). MZB.Cru.5017, male, 38.7 × 34.1 mm; Papua: Bepondi Island. A, dorsal habitus, preserved colouration. B–K, left appendages. Chela: B, inner surface; C, outer surface. P2–P5: D–G, anterior surface; H–K, posterior surface; L, stridulating ridge on inner surface of palm of chela. G1: M, whole morphology; N, apical portion. Scale bars: A, 10 mm; B–K, 5 mm; L–N, 3 mm.

Directorate of Scientific Collection Management-BRIN, Cibinong, Indonesia; Lee Kong Chian Natural History Museum, National University of Singapore, Singapore (ZRC); Osaka Museum of Natural History, Japan (OMNH); and the Naturalis Biodiversity Center, The Netherlands (RMNH).

TAXONOMIC ACCOUNT

Family Ocypodidae Rafinesque, 1815

Subfamily Ocypodinae Rafinesque, 1815

Ocypode ceratophthalmus (Pallas, 1772)

(Fig. 2)

Cancer ceratophthalmus Pallas, 1772: 83, pl. 5, figs. 7, 8 (unknown locality); Fabricius, 1781: 499.

Ocypode ceratophthalma – Sakai & Türkay, 2013: 685 (Sumatra; Nias Island; We Island; Padang; Bengkulu; Lampung; Java Sea; Jakarta Bay, Java; Lesser Sunda Islands; Lombok Island; Flores Island; Sumba Island; Dobo Island; Ambon Island; Kalimantan; Cendrawasih Bay, Papua), figs. 1D–I, 10A–E, 32A–C.

Ocypoda ceratophthalma – Tesch, 1918: 36 (Labuan Bajo, Flores; Solor Island, East Nusa Tenggara; Makassar, Sulawesi; Kaniungan Island, east of Kalimantan; Sulu Archipelago; Talaut Islands, Karakelang; west coast of Seram Island; Kei Island); Wada, 2019: e147 (Lukupang, Sulawesi).

Ocypode ceratophthalmus – Shih et al., 2015: 159 (Southeast Asia).

Material examined. 9 males (13.7 × 11.4 mm – 26.1 × 22.8 mm), 3 females (16.8 × 13.7 – 21.9 × 18.7 mm) (MZB.Cru.4913), Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'27.46"S 138°44'29.96"E, 22 November 2018, DC Murniati, SNI Raharjo, Melati; 10 males (14.1 × 12.0 mm – 38.7 × 34.1 mm) (MZB.Cru.5017), Masyai Village, West Supiori District, Supiori Municipality, Bepondi Island, Papua Province, 00°24'37.30"S, 135°16'02.17"E, 22 November 2018, DC Murniati & SNI Raharjo; 1 male (32.7 × 28.1 mm) (MZB.Cru.532), Lampung, Sumatra Island, 08 November 1975, F Sabar; 1 male (22.6 × 19.1 mm) (MZB.Cru.1918), Seribu Islands, near Jakarta, 21 May 1972, Sidabutar; 1 male (41.7 × 37.6 mm) (MZB.Cru.1634), Adonara Timur, East Nusa Tenggara, 02 June 1982, D Wowor; 1 male (31.7 × 28 mm) (MZB.Cru.2683), Teluk Terima, Gerokgak, Buleleng, Bali, 18 July 2009, Dian & DC Murniati; 1 male (40.2 × 35.7 mm) (MZB.Cru.1996), Mumes Beach, Waigeo Island, Raja Ampat, Papua, 12 June 2007, CM Sidabalok.

Remarks. The morphology of the present specimens agrees well with the description and figures by Sakai & Türkay (2013). The inner surface of the major palm has a stridulating ridge which consists of 30–49 elements (tubercles and striae) (Fig. 2B), and the G1 is three sided proximally and has a small thumb-shaped projection subdistally (Fig. 2M–N). There are variations in the number of stridulatory elements on the inner surface of the palm of the major cheliped (35–51) and minor chelipeds (0–10). These variations are related to size of the carapaces. Larger crabs have a larger number of stridulatory elements. On the inner surface of the palm of

the minor cheliped, only specimens with more than 40.0 mm cw have this element (Fadhillah et al., 2018).

This species inhabits high intertidal areas with sandy substrate and is typically nocturnal. They are widely distributed in the Indonesian Archipelago; i.e., Sumatra Island, Java Island, Sulawesi Island, the Lesser Sunda Islands, the Moluccas, the Aru Islands, and Papua (Rathbun, 1910; Tesch, 1918; Sakai & Türkay, 2013; Wada, 2019). The present study gives a new distribution record of the species in Indonesia.

Ocypode cordimana Latreille, 1818

(Fig. 3)

Ocypode cordimana Latreille, 1818: 198 (Indes Orientalis).

Ocypoda cordimana – Tesch, 1918: 35 (Kawassang Island, South Sulawesi; Labuan Bajo, west coast of Flores; Kawa Bay, west coast of Seram).

Ocypode cordimanus – Sakai & Türkay, 1977: 178, figs. 12A–F, 34A–C (Ambon, Moluccas); Sakai & Türkay, 2013: 696 (Bintan Island, Riau Islands; West Sumatra; Lampung, Sumatra; Bali; Ternate, North Moluccas; Ternate, North Moluccas; Aru Islands).

Material examined. 3 males (35.3 × 31.1 mm – 38.3 × 34.7 mm), 2 females (36.8 × 32.4 mm – 37.2 × 44.7 mm) (MZB.Cru.4914), Masyai Village, District of West Supiori, Supiori Municipality, Bepondi Island, Papua, 00°24'37.30"S 135°16'02.17"E, 22 Nov. 2018, DC Murniati, SNI Raharjo, D Nurdiansyah, A Kurnia; 2 males (20.3 × 17.5 mm – 26.1 × 22.2 mm) (MZB.Cru.74), Djoemiang Island, near Madura, 21 September 1919, Ouwens; 1 male (35.1 × 32.3 mm) (MZB.Cru.2201), Big Krakatau Island, Banten, 15 September 1979, H Wiradinata; 1 male (20.1 × 17 mm) (MZB.Cru.1375), Pelabuhan Ratu, West Java, 29 December 1969, F Sabar & Nurhasan; 1 male (21.6 × 17.8 mm) (MZB.Cru.2442), Raja Ampat, Papua, 1 May 2008, D Wowor, RK Hadiaty, A Mun'im.

Remarks. The present specimens morphologically fit the description by Sakai & Türkay (2013). The carapace size ratio (cw/cl) is greater on smaller specimens. *Ocypode cordimana* is easily distinguished from congeners in having no stridulating ridge on the inner surface of the palm of the major cheliped (Fig. 3D) and in the G1 having a curved apical portion (Fig. 3M–N). The thumb-shaped projection on the G1 of *O. cordimana* is larger than that of *O. ceratophthalmus*.

Ocypode cordimana is widely distributed in the Indo-West Pacific region, i.e., Hawaii, Central and Southern Pacific, Australia, China, Japan, the Gulf of Thailand, Indonesia, India, Red Sea, Madagascar, Eastern and Southern Africa (Sakai & Türkay, 2013). In Indonesia, it was recorded from the Riau Islands, Sumatra, the Lesser Sunda Islands, Moluccas, and Seram Island (Tesch, 1918; Sakai & Türkay, 1977; Sakai & Türkay, 2013). The present record extends the distribution of this species further eastward within the Indonesian Archipelago.

The habitat of this species tends to be more terrestrial than those of other species of the genus *Ocypode* (Tesch, 1918).



Fig. 3. *Ocypode cordimana* (Latreille, 1818). MZB.Cru.4914, male, 38.3 × 34.7 mm; Papua: Bepondi Island. A, dorsal habitus, preserved colouration. B–L, right appendages. Chela: B, inner surface; C, outer surface; D, inner surface of palm indicating no stridulating ridge. P2–P5: E–H, anterior surface; I–L, posterior surface. G1: M, whole morphology; N, apical portion. Scale bars: A, 10 mm; B–C, E–L, 5 mm; D, M, N, 3 mm.

In the present study, specimens were collected from the high intertidal zone with sandy substrates together with *O. ceratophthalmus*, which is in concordance with the report of Huang et al. (1998).

Subfamily Gelasiminae Miers, 1886

Gelasimus jocelynae (Shih, Naruse and Ng, 2010).

(Fig. 4)

Mesuca (Latuca) neocultrimana Bott, 1973: 317 (in part: Halmahera, Sulawesi). Not *Mesuca (Latuca) neocultrimana* Bott, 1973 (= *Gelasimus excisus* (Nobili, 1906)).

Uca (Thalassuca) vocans pacificensis Crane, 1975: 90 (in part: Ambon). Not *Uca (Thalassuca) vocans pacificensis* Crane, 1975 (= *Gelasimus excisus* (Nobili, 1906)).

Uca jocelynae Shih et al., 2010: 51, fig. 2, fig. 3, fig. 4 (Sulawesi)
Gelasimus jocelynae – Shih et al., 2016: 151, fig. 7D (Bunaken, North Sulawesi).

Material examined. 17 males (14.0 × 9.4 mm – 18.4 × 12.8 mm) (MZB.Cru.4912), Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'25.29"S, 138°44'26.54"E, 23 November 2018, DC Murniati; 2 males (14.3 × 9.6 mm – 18.2 × 11.8 mm) (MZB.Cru.3723), Kaimana, West Papua Province, 26 June 2001, DL Rahayu; 1 male (24.5 × 15.4 mm) (MZB.Cru.3911) Kamora Village, Mimika, Papua Province, DL Rahayu.

Comparative material examined. *Gelasimus vocans* (Linnaeus, 1758), 4 males (17.4 × 12.0 mm – 20.0 × 13.2 mm) (MZB.Cru.3728), Gilimanuk Bay, Malaya District, Jembrana Municipality, West Bali National Park, Bali Province, 14 July 2009, DC Murniati; (18.3 × 12.4 mm – 23.1 × 14.8 mm) (MZB.Cru.4179), Jebak River, Blonsong, Kidang Village, East Praya District, Central Lombok Municipality, 25 April 2015, DC Murniati, Mariana.

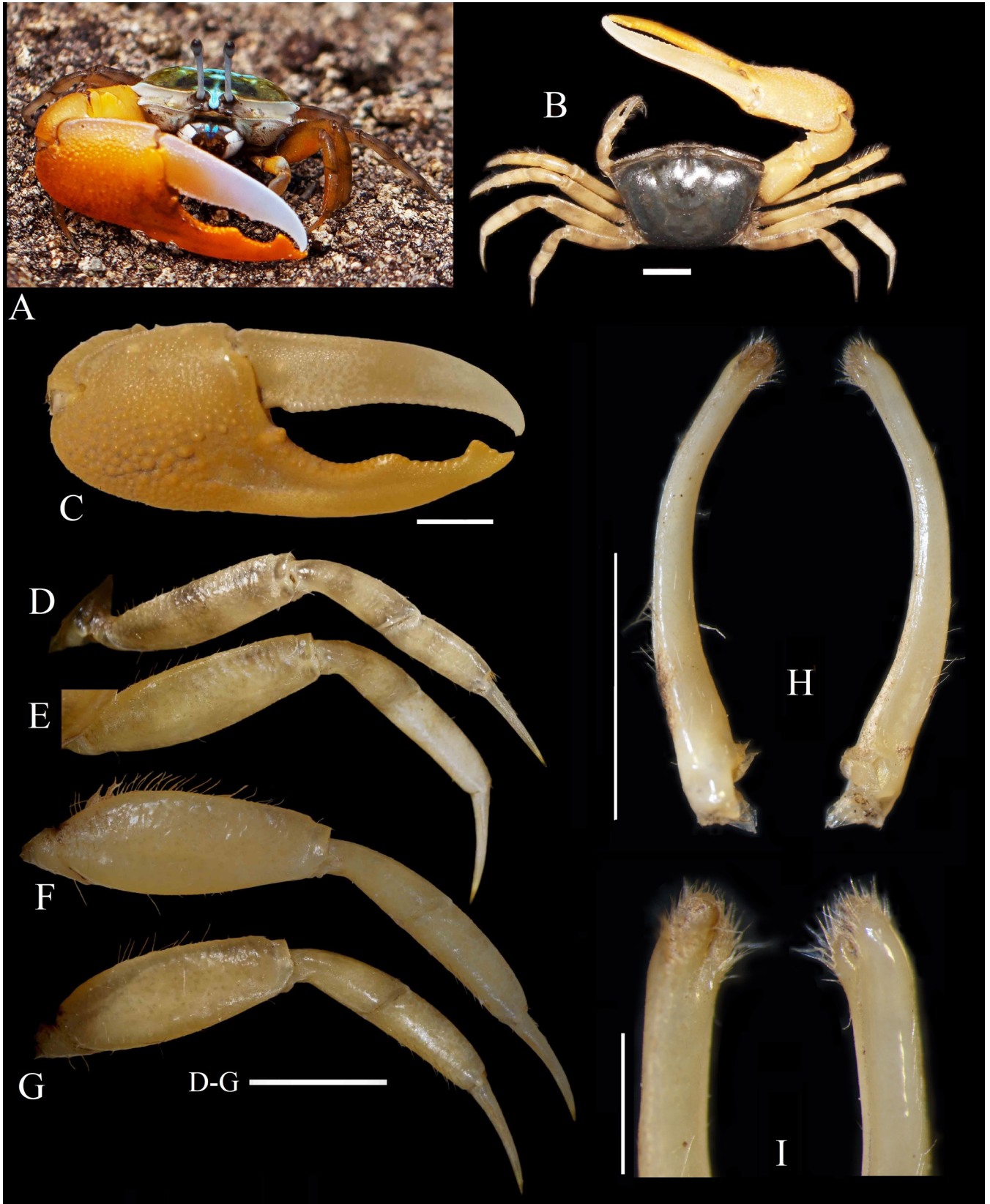


Fig. 4. *Gelasimus jocelynae* (Shih et al., 2010). MZB.Cru.4912, male, 18.4 × 12.9 mm; Papua: Liki Island. A, in-situ with live colouration (photograph by Sumaryanto Bronto); B, dorsal habitus, preserved colouration. C, outer surface of major chela. P2–P5: D–G. Right G1: H, dorsal and ventral view; I, apical portion. Scale bars: B–G, 5 mm; H, 3 mm; I, 1 mm.



Fig. 5. *Paraleptuca crassipes* (White, 1847). MZB.Cru.4918, male 13.7×9.0 mm; Papua: Liki Island. A, in situ with live colouration. MZB.Cru.4918, male, 14.0×9.2 mm; Papua: Liki Island. B, dorsal habitus, preserved colouration. C, outer surface of major chela. P2–P5: D–G. Right G1: H, dorsal and ventral view; I, apical portion. Scale bars: B–G, 5 mm; H, 3 mm; I, 1 mm.

Remarks. This species belongs to the *Gelasimus vocans* complex, and was described as new based on morphological and molecular data by Shih et al (2010). Close similarities are present between *G. vocans* and *G. jocelynae* in the live colouration of the body and morphology of the major chela of the male. In both species, the carapace is generally white to greyish-white and the cheliped is deep yellow to orange in the lower part of the palm and fixed finger (Fig. 4A); the major chela has two distinct teeth with a wide gap on the cutting margin of the fixed finger (Fig. 4C). Our careful examination has shown that the specimens agree well with the description by Shih et al. (2010) for *Uca jocelynae*.

Based on our observation of comparative materials, *Gelasimus jocelynae* differs from *G. vocans* in the shape of the major chela. In *G. jocelynae*, the proximal portion of the dactylus is slightly wider than that of the fixed finger, and the distal tooth of the fixed finger is small and positioned subdistally (Fig. 4C). Meanwhile, in *G. vocans*, the proximal portion of the dactylus is narrower than that of the fixed finger, and the distal tooth of the fixed finger is large and positioned distally.

We found some morphological variations in the male chela within the population of *G. jocelynae* from Liki Island. In some specimens, the width of the proximal portion of the dactylus and fixed finger are similar, while others have a slightly wider proximal portion of the fixed finger compared to the dactylus. Nonetheless, the morphology of the G1 of all our specimens (Fig. 4H–I) is well in agreement with the illustration given by Shih et al. (2010).

According to Shih et al. (2010), the geographical distribution of this species is confined to the Western Pacific islands including Papua New Guinea. The present record extends the distribution of this species further eastward in the Indonesian Archipelago. This species inhabits sandy-muddy substrates on the intertidal zone of the coast.

***Paraleptuca crassipes* (White, 1847)**

(Fig. 5)

Uca gaimardi – Tesch, 1918: 39, 40 (Flores)

Uca (Amphiuca) chlorophthalmus crassipes – Crane, 1975: 101 (Buru Island, Moluccas; Aru Island, Moluccas)

Uca crassipes – Shih et al., 2012: 85, fig. 1 (Kuta, Lombok Island).

Uca (Paraleptuca) crassipes – Murniati & Pratiwi, 2015: 62. (Bali Island; Moluccas; Papua)

Paraleptuca crassipes – Shih et al., 2016: 156, fig. 10d (Indo West Pacific).

Material examined. 5 males (12.4 × 8.0 mm – 14.0 × 9.1 mm), 10 females (11.7 × 7.9 mm – 13.7 × 9.1 mm) (MZB.Cru.4918), Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'25.29"S, 138°44'26.54"E, 26 November 2018, DC Murniati; 2 males (MZB.Cru.2678) (15.6 × 10.1 – 18.2 × 11.4 mm), Gilimanuk Bay, Malaya District, Jembrana Municipality, Bali Province, 08°10'227"S, 114°26'680"E, 14 July 2009, DC Murniati; 5 males (11.8 × 6.7 mm – 15.5 × 9.2 mm) (MZB.Cru.4174), Gili Lawang Island, near Lombok Island, West Nusa Tenggara Province,

08°18'8.5"S, 116°42'10.1"E, 25 April 2008, DC Murniati & Satriawan; 3 males (14.8 × 8.5 mm – 17.1 × 10.6 mm) (MZB.Cru.2464), Sagawin Strait, Raja Ampat, West Papua Province, 00°50'17.7"S, 130°53'16.0"E, 26 April 2008, D Wowor, RK Hadiaty, A Munim.

Remarks. *Paraleptuca crassipes* is easily recognised in the field by the red colouration on the dorsal surface of the carapace, chelipeds, and legs. The morphological characteristics of our samples fit the descriptions by Crane (1975), Shih et al. (2012) and Shih et al. (2016). The G1 of our samples from Liki Island (Fig. 5H–I) resembles that of Crane's (1975: fig. 13G) specimens from Hong Kong, in which the apical portion is distinctly long and the flange is distinctly short.

Shih et al. (2012) reported that *P. crassipes* is widely distributed in the western and central Pacific Ocean and the eastern margin of the Pacific region. The present record extends the distribution of this species further eastward within the Indonesian Archipelago. This species inhabits muddy substrates on the intertidal area.

Family Macrophthalmidae Dana, 1851

Subfamily Macrophthalminae Dana, 1851

***Macrophthalmus* Desmarest, 1823**

***Macrophthalmus (Macrophthalmus) manggala*, new species**

(Figs. 6–10, 13A–C)

Material examined. Holotype: male (23.1 × 10.9 mm) (MZB.Cru.5013), Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'25.29"S, 138°44'26.54"E, 21 November 2018, coll. DC Murniati.

Paratypes: 10 males (8.5 × 4.5 mm – 22.2 × 10.8 mm), 5 females (13.4 × 6.7 mm – 18.9 × 9.0 mm) (MZB.Cru.5014), Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'25.29"S, 138°44'26.54"E, 21 November 2018, coll. DC Murniati; 2 males (18.0 × 9.7 mm, 23.2 × 12.3 mm), 1 female (20.3 × 10.8 mm) (ZRC 2022.0913) Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'25.29"S, 138°44'26.54"E, 21 November 2018, coll. DC Murniati.

Comparative material examined. *Macrophthalmus (Macrophthalmus) convexus* Stimpson, 1858, 1 male (20.1 × 10.3 mm) (MZB.Cru.1386), Sosobok, Halmahera Island, 10 April 1987, S Harminto; 5 males (16.6 × 8.2 mm – 23.4 × 10.7 mm), 4 females (15.1 × 7.8 mm – 17.2 × 9.3 mm) (MZB.Cru.5060), Terima Bay, Sumber Klampok Village, Gerokgak District, Buleleng Municipality, Bali Province, 12 June 2020, H Kusumanegara, TEN Dian. *Macrophthalmus (Macrophthalmus) parvimanus* Guérin, 1834, 2 males (14.6 × 8.1 mm – 24.0 × 12.4 mm), 3 females (12.5 × 6.9 mm – 2.2 × 11.1 mm) (MZB.Cru.4718), Saparua Island, Moluccas, S03°34'25.9", E34°39'27.4", 22 September 2016,

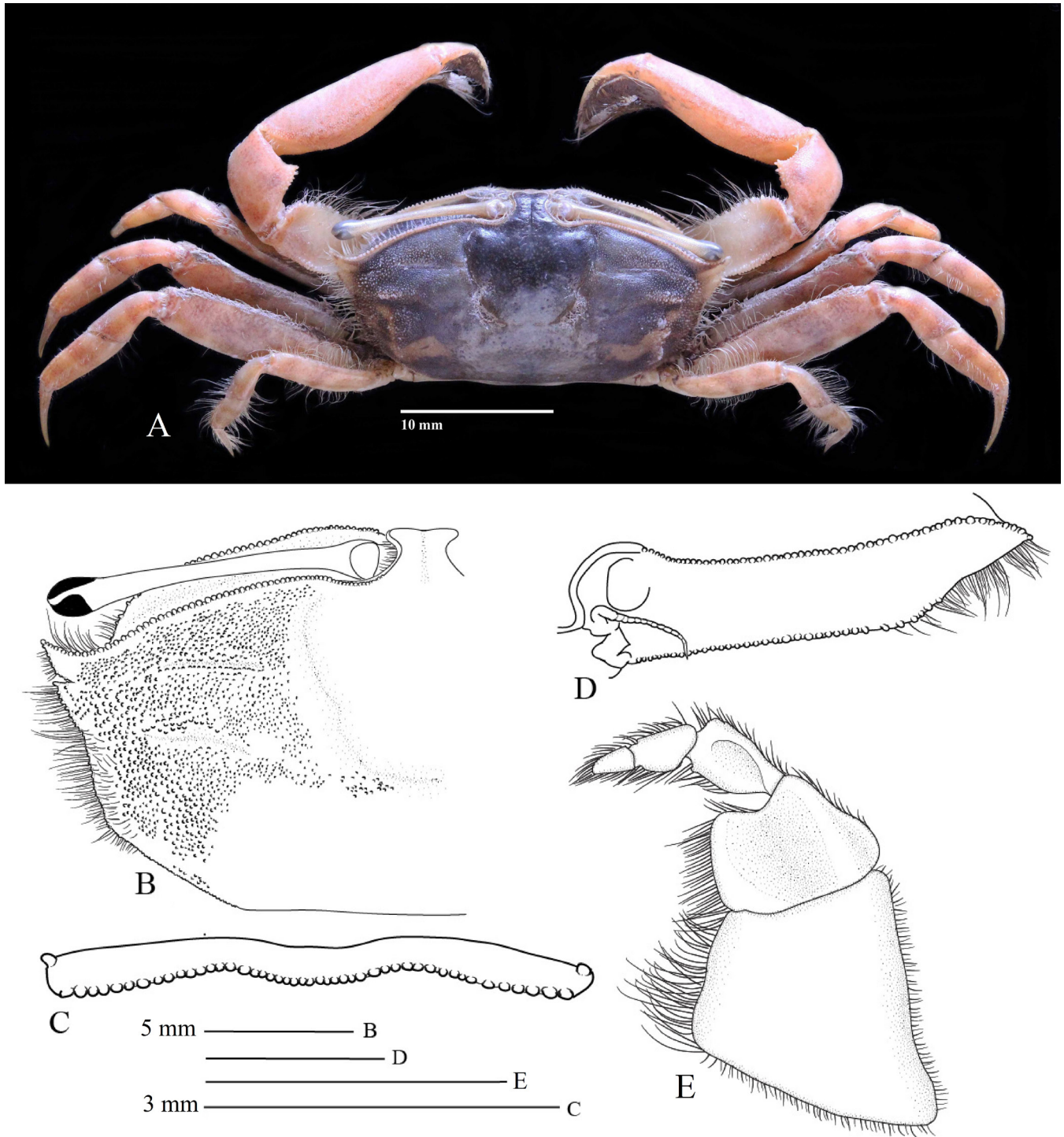


Fig. 6. *Macrophthalmus manggala*, new species. Holotype. MZB.Cru.5013, male, 23.1 × 10.9 mm; Papua, Liki Island. A, dorsal habitus, preserved colouration; B, dorsal surface of carapace; C, epistome; D, orbit area; E, 3rd maxilliped.

DA Nugroho; 1 male (13.5 × 8.0 mm) (MZB.Cru.3268), Eka's Bay, East Lombok Municipality, Lombok Island, West Nusa Tenggara Province, 10 April 2018, DL Rahayu.

Diagnosis. Carapace rectangular, broad, about 1.9 times as broad as long. Front narrow, less than 0.2 times external orbital angles width. Lateral margins with two anterolateral teeth including external orbital angle. Chelipeds long, subequal. Palm long; inner surface of palm with microscopic granules, distally covered by mat of setae. Fixed finger short,

deflexed; cutting margin with one low, subquadrate tooth submedially. Dactylus directed downward, cutting margin with one large, squarish tooth. Pleon moderately narrow, 1.2 times as long as wide. P4 longest. P5 shortest, margins with long setae. G1 stout, slightly curved subproximally; mesial surface slightly concave; apical portion truncated, deeply depressed medially, with long setae; chitinous process very short, C-shaped or crescent-shaped. Female vulva rounded; protruded, with transverse groove medially, concave portion facing median portion of sternum; outer margin circular.

Description. Carapace rectangular, broad, about 1.9 times as broad as long, greatest width across external orbital angles (Fig. 6A). Regions on dorsal surface clearly defined, furrow on gastric region distinct; hepatic region with two distinct transverse ridges, anterior ridge straight on deep furrow, posterior ridge curved on bulging area; epigastric and mesogastric regions smooth; mesobranchial region covered by granules, larger laterally; scattered short setae on hepatic and branchial regions. Front narrow, less than 0.2 times external orbital angles width, constricted at bases of eyestalks (Fig. 6A), with deep longitudinal groove medially (Fig. 6B); frontal margin slightly concave medially, with microscopic tubercles. Supra-orbital margin moderately curved, regularly granular, granules smallest near base of eyestalk (Fig. 6B, D). Infra-orbital margin strongly granular, with larger granules in middle portion and smaller near base of eyestalk and lateral portion, shape of each granule similar to those in supra-orbital margin (Fig. 6D). Lateral margins of carapace oblique, strongly divergent anteriorly, with two anterolateral teeth including external orbital angle, dense long setae along margin; external orbital angle pointed anterolaterally, triangular, with acute angle, one distinct granule on its tip and one row of lateral granules; second anterolateral tooth triangular, separated by V-shaped incision from external orbital angle, apex pointed outward; distinctly smaller than preceding tooth, with granules on lateral margin, last granule adjacent to lateral margin; lateral margin straight, with several tubercles; posterior margin straight (Fig. 6B).

Epistome with posterior margin bearing regular row of tubercles, posteromedian margin distinctly convex, posterolateral margin slightly convex, anterior margin curved and without tuberculation (Fig. 6C).

Eyestalks slender, long, 0.4 times as long as carapace width; cornea not reaching beyond external orbital angle (Fig. 6B).

Third maxillipeds leaving large gap in between them even when closed. Ischium nearly subtrapezoidal; mesial margin with long setae, setae longer posteriorly; lateral margin nearly straight; lateral and posterior margins with short setae; outer surface smooth. Merus quadrate, smaller than ischium, about 0.5 times as long as ischium laterally; outer surface with wide depression near mesial margin, narrow depression near lateral margin; mesial margin with long and short setae, setae shorter anteriorly; lateral margin slightly curved, arched anteriorly, anterior margin distinctly concave, lined with long setae; anterolateral margin with scattered short setae, posterolateral margin without setae. Carpus trihedral, mesial and lateral margins with dense short setae. Propodus longer than dactylus, margins with dense short setae. Dactylus tubular, margins with dense setae (Fig. 6E).

Male chelipeds (P1) long, subequal. Merus with cross-section triangular, upper surface bearing scattered short setae, without granules (Fig. 7A); lower surface granular mainly on lower half, granules larger distally, densest near lower margin (Fig. 7B); outer surface coarse, with granules laterally, sparse setae near upper margin, median portion glabrous (Fig. 7C); upper margin distinctly tubercular, tubercles larger

medially, no spine near articulation with carpus, with sparse long setae (Fig. 7D); lower margin evenly tubercular (Fig. 7E); outer margin with two rows of granules proximal half length, continuous with three row of granules and denser near distal portion, distal portion without granules except near distal margin (Fig. 7E). Carpus short, outer surface rectangular, with microscopic granules, without setae (Fig. 7A); inner surface with single curved row of granules (Fig. 7G); upper and lower margins distinctly tubercular (Fig. 7A, F), tuberculation on upper margin larger than that of lower margin (Fig. 7A). Palm long, 2.2 times as long as high, 2.6 times as long as fixed finger (Fig. 7J–K); inner surface with microscopic granules on upper and median portions, larger granules on lower portion, distal margin to inner surface of fingers covered by mat of setae, without spine near articulation with carpus (Fig. 7J); outer surface with microscopic granules covered almost entirely, longitudinal row of microscopic granules from proximal portion of palm to fixed finger along lower margin (Fig. 7K); upper margin slightly arched, tubercular; lower margin straight, tubercular, tuberculation smaller distally. Fixed finger short, deflexed; cutting margin with one large, subquadrate submedial tooth, followed distally by denticulate teeth; lower margin tubercular 1/2 length; outer surface with row of granules parallel to cutting margin, one row of setae present half-distally parallel to cutting margin; tips of fingers spoon-shaped (Fig. 7J–K). Dactylus directed downward, cutting margin with one large, squarish, subproximal tooth, distally followed by single row of denticulate teeth; upper margin granular 3/4 length, one short row of long setae present distally; outer surface with microscopic granules on proximal portion, one row of setae present half-distally parallel to cutting margin (Fig. 7K).

Ambulatory legs (P2–P5) medium sized. P2 shorter than P3. Merus 3.5 times as long as wide, with anterior surface nearly smooth, bearing dense setae near upper margin, densest setae proximally, setation extending to 3/4 length of anterior surface, microscopic granules near lower margin (Fig. 8A); posterior surface with sparse microscopic granules laterally (Fig. 8B); upper margin narrow, with one row of tubercles forming ridge structure, dense short setae extending whole length of margin (Fig. 9A); lower margin wide, slightly convex, with microscopic granules distributed irregularly, without setation (Fig. 9E). Carpus slightly shorter than propodus; anterior surface with irregular microscopic granules on median portion, lateral portion smooth (Fig. 8A); posterior surface with one row of microscopic granules near upper margin, irregular granules near lower margin, sparse setae on median portion (Fig. 8B); upper margin tubercular (Fig. 9A); lower margin nearly smooth (Fig. 9E). Propodus with anterior surface bearing one narrow groove, microscopic granules distributed near upper margin (Fig. 8A); posterior surface with one row of microscopic granules medially, with setae present along granulation, other granulation distributed between median granulation and upper margin (Fig. 8B); upper margin narrow, with one distinct row of tubercles (Fig. 9A); lower margin wide, nearly smooth, with sparse granules on distal portion (Fig. 9E). Dactylus slightly shorter than propodus, with one row of setae on upper margin, tuberculation rarely present on each margin and surface.

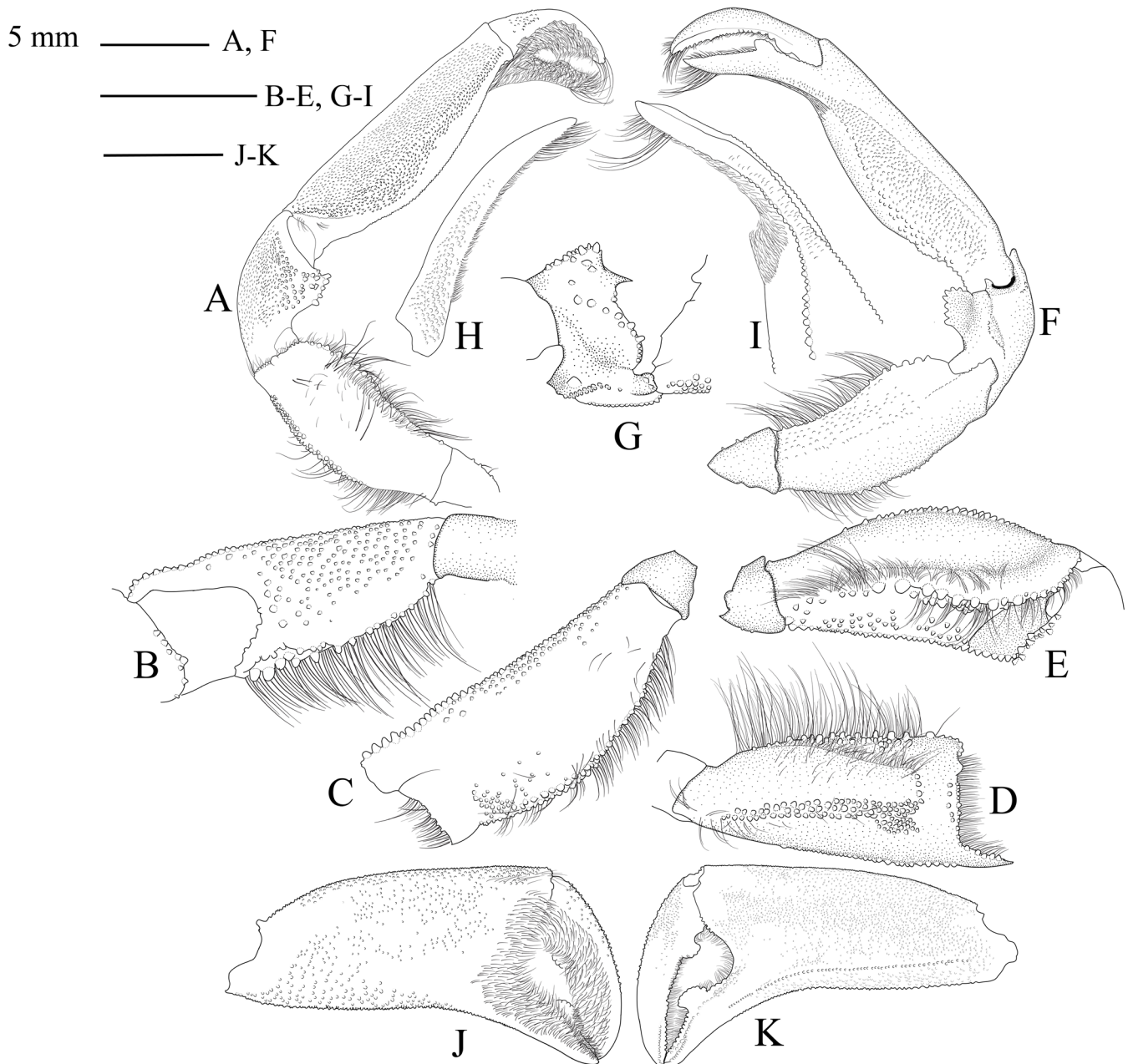


Fig. 7. *Macrophthalmus manggala*, new species. Holotype, MZB.Cru.5013, male, 23.1 × 10.9 mm; Papua: Liki Island. Left cheliped: A, upper view; B, lower surface of merus; C, outer surface of merus; D, outer margin of merus; E, upper margin of merus; F, lower view; G, inner surface of carpus; H, upper margin of dactylus; I, lower margin of fixed finger. Left chela: J, inner surface; K, outer surface.

P3 longer than P2. Merus 3.2 times as long as wide, anterior surface with microscopic granules near lower margin, row of dense short setae on upper portion continuing to upper margin, setation extending whole length, sparse granules on upper portion within row of setae, median portion glabrous; posterior surfaces with dense microscopic granules near upper and lower margins, more granular than that of anterior surface, median portion without granules (Fig. 8C–D); upper margin with one row of tubercles extending whole length, tuberculation nearly forming one ridge, dense short setae and sparse long setae in one row, setation extending whole length (Fig. 9B); lower margin wide, with dense microscopic granules distributed almost whole length (Fig. 9F). Carpus slightly shorter than propodus; anterior surface with microscopic granules distributed evenly except near lower margin (Fig. 8C); posterior surface with sparse microscopic

granules on median portion, one row of granules parallel to upper margin, sparse granules between row of granules and upper margin, single row of short setae on articulation with propodus (Fig. 8D); upper margin with sparse granules (Fig. 9B); lower margin wide, with microscopic granules distributed irregularly (Fig. 9F). Propodus with anterior surface bearing one narrow furrow, microscopic granules medially (Fig. 8C); posterior surface with microscopic granules, densest proximally, more granular than that of anterior surface and one row of spaced long setae medially (Fig. 8D); upper margin narrow, tubercular on whole length; lower margin wide, covered with microscopic tubercles (Fig. 9B, F). Dactylus with anterior and posterior surfaces smooth (Fig. 8C–D), upper margin smooth, lower margin with sparse tubercles and setae (Fig. 9B, F).

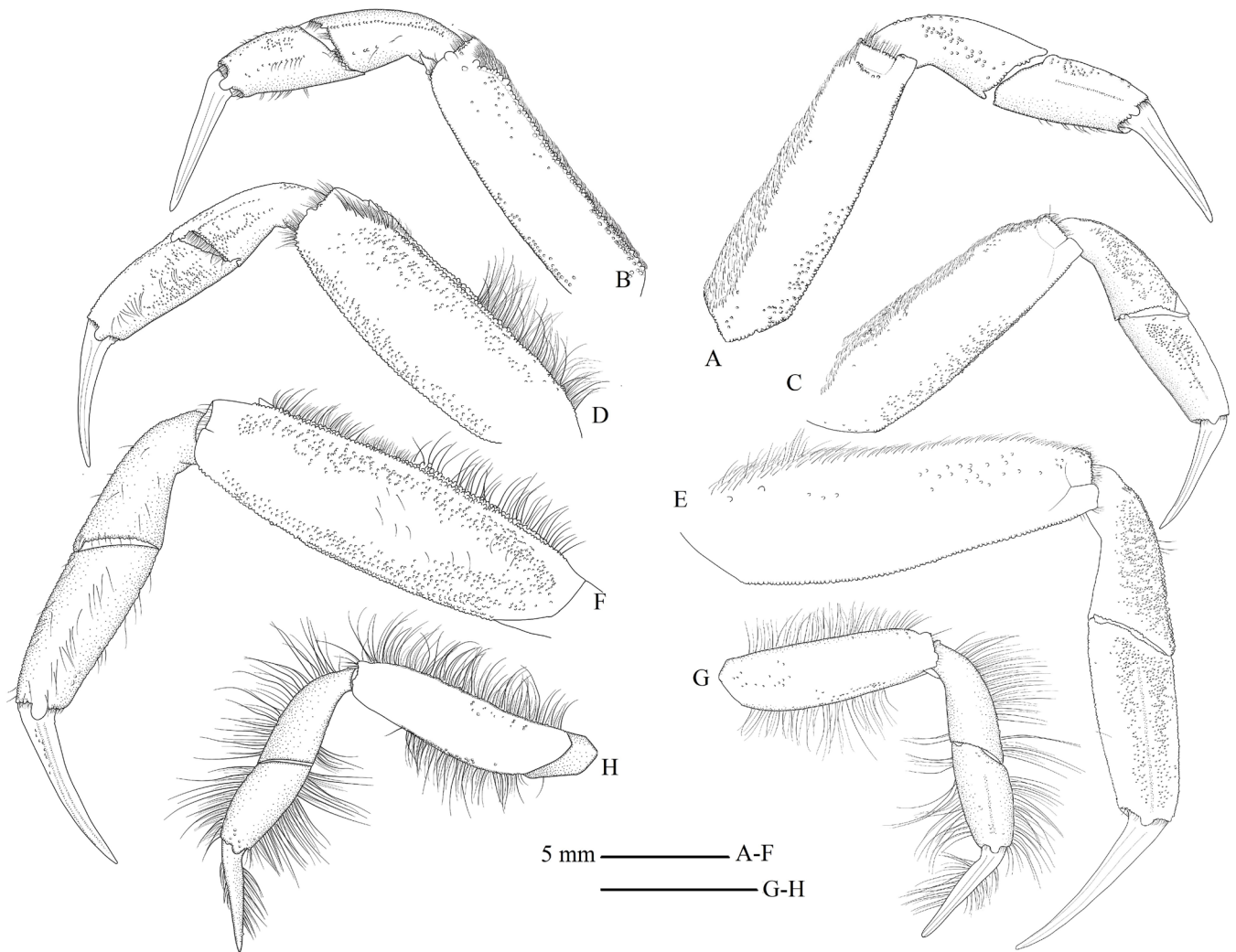


Fig. 8. *Macrophthalmus manggala*, new species. Holotype, MZB.Cru.5013, male, 23.1 × 10.9 mm; Papua: Liki Island. Left pereopods 2–5. Left side, anterior surfaces; right side, posterior surfaces. A–B, P2; C–D, P3; E–F, P4; G–H, P5.

P4 longest. Merus long, 3.4 times as long as wide; anterior surface nearly smooth, without setae medially, with setae proximo-laterally, sparse granules distributed unevenly on upper half portion (Fig. 8E); posterior surface with dense granules near upper and lower margins, granulation densest proximally, sparse short setae medially, median portion smooth (Fig. 8F); upper margin distinctly narrow, with one row of tubercles, one subdistal tooth, and dense setae around tuberculation (Fig. 9C); lower margin wide, with microscopic granules, granulation more spaced than that of merus of P3, without setae (Fig. 9G). Carpus shorter than propodus; anterior surface with microscopic granules median to upper portion, more granular than that of P3, smooth near lower margin (Fig. 8E); posterior surface smooth, with sparse long setae (Fig. 8F); upper margin narrow, with one row of tubercles (Fig. 9C); lower margin wide, sparsely tubercular (Fig. 9G). Propodus with anterior surface bearing one narrow furrow medially, covered by microscopic granules except on lower portion (Fig. 8E); posterior surface nearly smooth, covered with one row of spaced long setae (Fig. 8F); upper margin narrow, with microscopic tubercles distributed irregularly and sparse long setae; lower margin narrow, with one row of tubercles and sparse long setae (Fig. 9C, G). Dactylus with anterior surface smooth (Fig. 8E); posterior surface

with sparse granules (Fig. 8F); upper margin smooth (Fig. 9C); sparse tubercles and setae on lower margin (Fig. 9G).

P5 shortest. Merus 3.1 times as long as wide, with anterior and posterior surfaces nearly smooth, sparse microscopic granules distributed unevenly (Fig. 8G–H); upper margin narrow, with one row of microscopic tubercles and one row of long setae extending whole length of upper margin; lower margin wide, with one row of microscopic tubercles, one row of long setae extending 2/3 length of lower margin (Fig. 9D, H). Carpus almost as long as propodus; anterior and posterior surfaces smooth (Fig. 8G–H); upper margin narrow, with one row of microscopic tubercles and one row of long setae extending whole length (Fig. 9D); lower margin with long setae near distal portion, without tubercles (Fig. 9H). Propodus with anterior and posterior surfaces nearly smooth (Fig. 8G–H); upper and lower margins narrow, with one row of microscopic tubercles and one row of long setae extending whole length (Fig. 9D, H). Dactylus with anterior and posterior surfaces smooth (Fig. 8G–H); upper margin with one row of short setae medially; lower margin with one row of long setae extending whole length of lower margin (Fig. 9D, H).

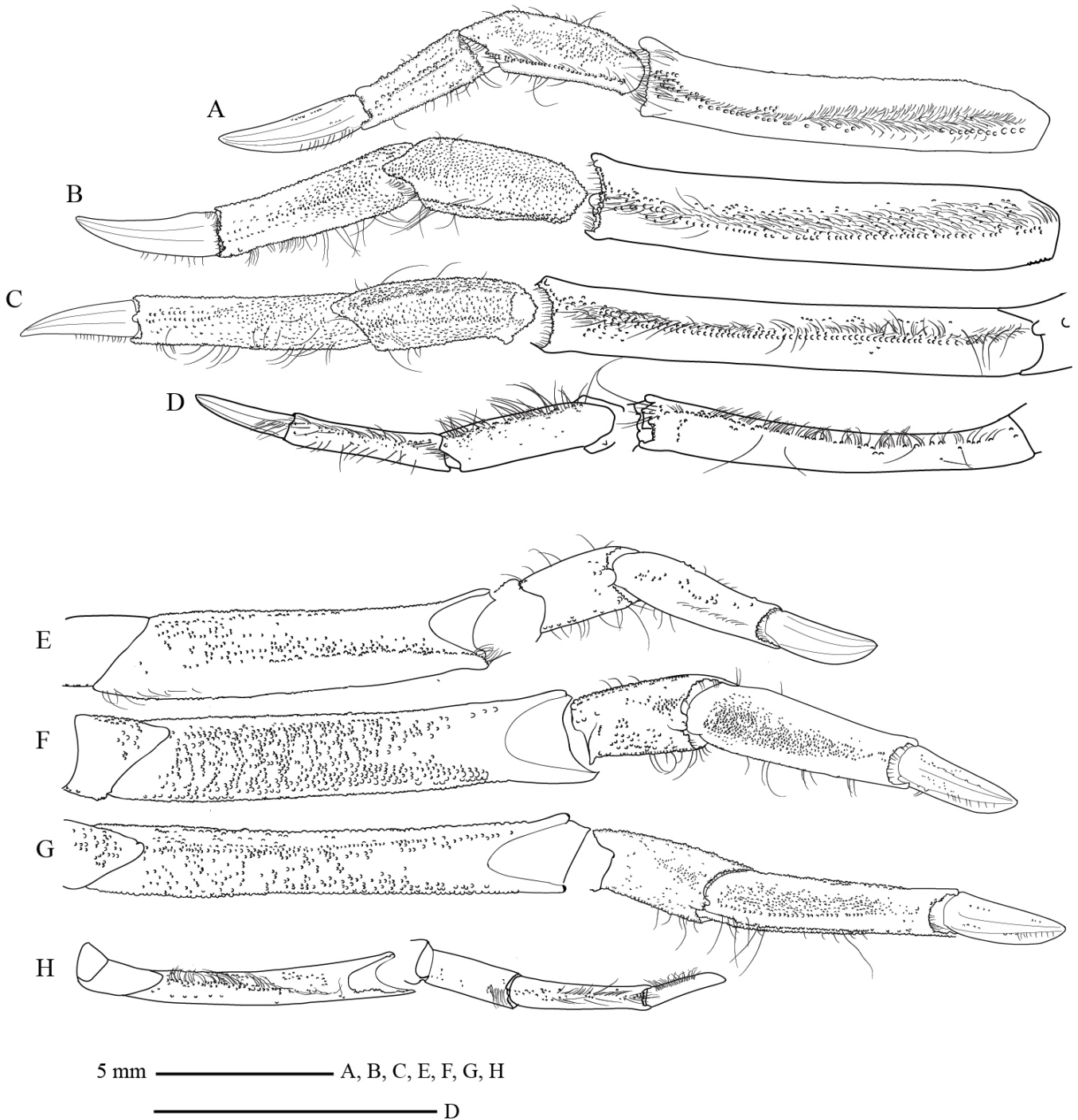


Fig. 9. *Macrophthalmus manggala*, new species, holotype, MZB.Cru.5013, male, 23.1 × 10.9 mm; Papua, Liki Island. Left pereopods 2–5: A–D, upper margin; E–H, lower margin; A, E, P2; B, F, P3; C, G, P4; D, H, P5.

Male pleon moderately narrow, 1.2 times as long as wide; first and third somites wider than other somites. First somite 13.7 times as wide as long, anterior margin concave, posterior margin convex. Second somite shortest among all somites, wider than fourth somite. Third and fourth somites trapezoidal in shape. Third somite as wide as first somite, 5.1 times as wide as long, anterior and posterior margins slightly straight. Fourth somite as long as third somite, narrower than third somite, 15.7 times as wide as long. Fifth somite 2.8 times as wide as long, longer and narrower than fourth somite, anterior and posterior margins slightly convex. Sixth somite

longest, 2.4 times as wide as long, posterolateral margins weakly constricted, anterior and posterior margins concave. Telson 1.7 times as wide as long, slightly shorter than sixth somite, apically rounded (Fig. 10A).

G1 moderately long, stout, slightly curved subproximally (Fig. 10B); mesial surface slightly concave; dense short setae at outer margin of stem; apical portion with long setae, truncated, deeply depressed medially; apical chitinous process very short, C-shaped or crescent shape, directed distolaterally (Fig. 10C–E).

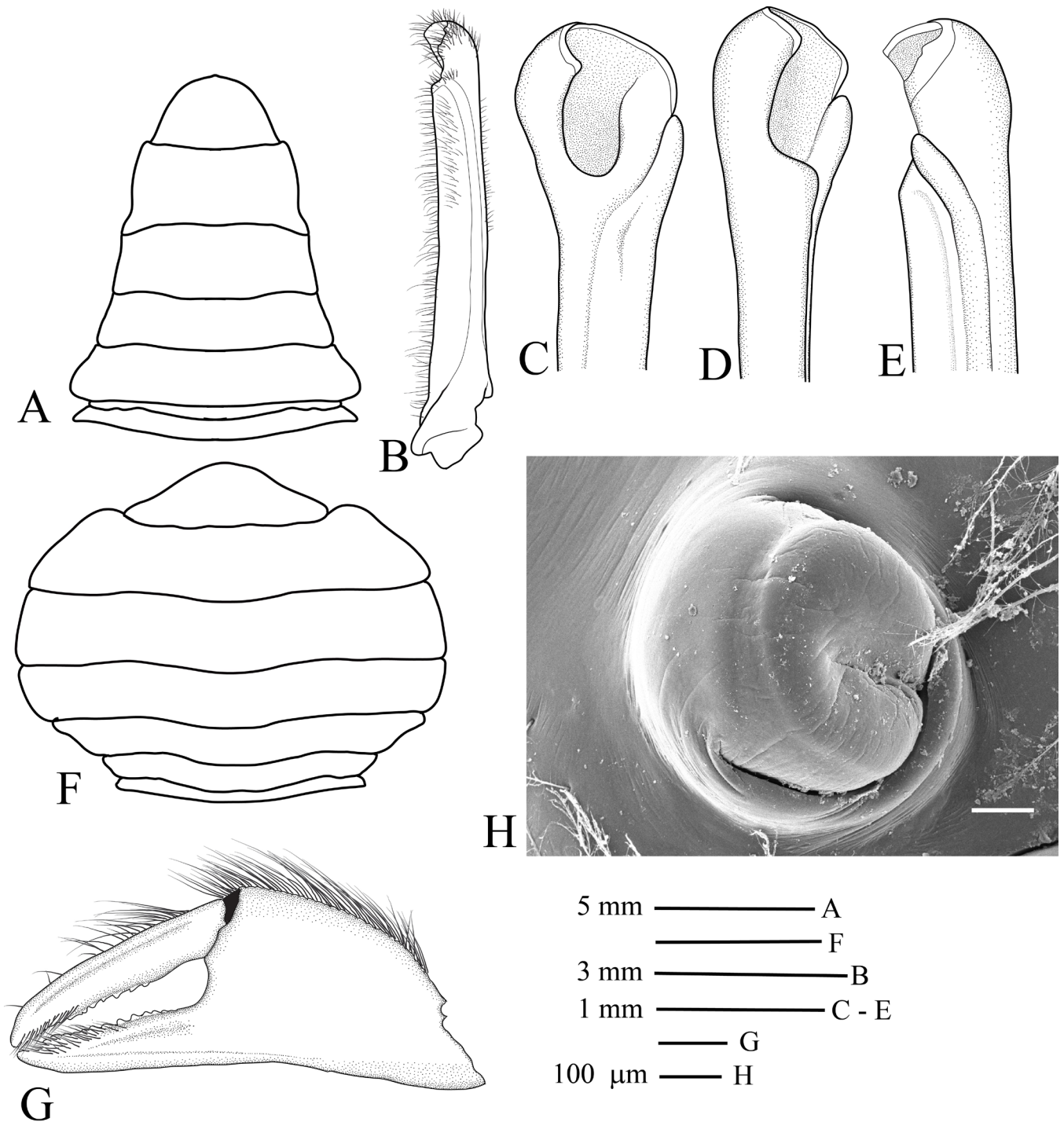


Fig. 10. *Macrophthalmus manggala*, new species. A, holotype, MZB.Cru.5013, male, 23.1 × 10.9 mm; Papua, Liki Island. B–E, paratype, male, 21.6 × 10.7 mm, MZB.Cru.5014. A, pleon. Left G1: B, dorsal surface of stem; apical portion: C, mesial view; D, ventral view; E, dorsal view. Paratype, MZB.Cru.5014, female, 13.4 mm × 6.7 mm; Papua, Liki Island. F, pleon; G, outer surface of left cheliped; H, left vulva.

Gastric mill with median tooth plate 2.5 times as long as wide, consisting of two pairs of teeth, gap between two posterior teeth narrow (Fig. 13A); posterior margin of propyloric ossicle with narrow and acute shape; upper portion of anterior trunk shaped triangularly. Lateral tooth plate with 15–16 comb shape teeth, anterior tooth short and slender (Fig. 13B).

Female chelipeds small, equal. Palm convex medially, concave in lower-half portion; outer surface granular on

upper half, smooth on lower half; upper and lower margins tubercular, upper margin with long setae (Fig. 10G); inner surface smooth, with row of long setae along upper margin. Fixed finger as long as dactylus; cutting margin serrated; outer surface with inferior ridge parallel to lower margin; inner surface smooth, with single row of long setae medially; distally spoon-shaped, margin chitinous (Fig. 10G). Dactylus as long as palm, convex; cutting margin serrated; upper margin tuberculate only on proximal portion; inner surface smooth, with single row of long setae along upper margin;

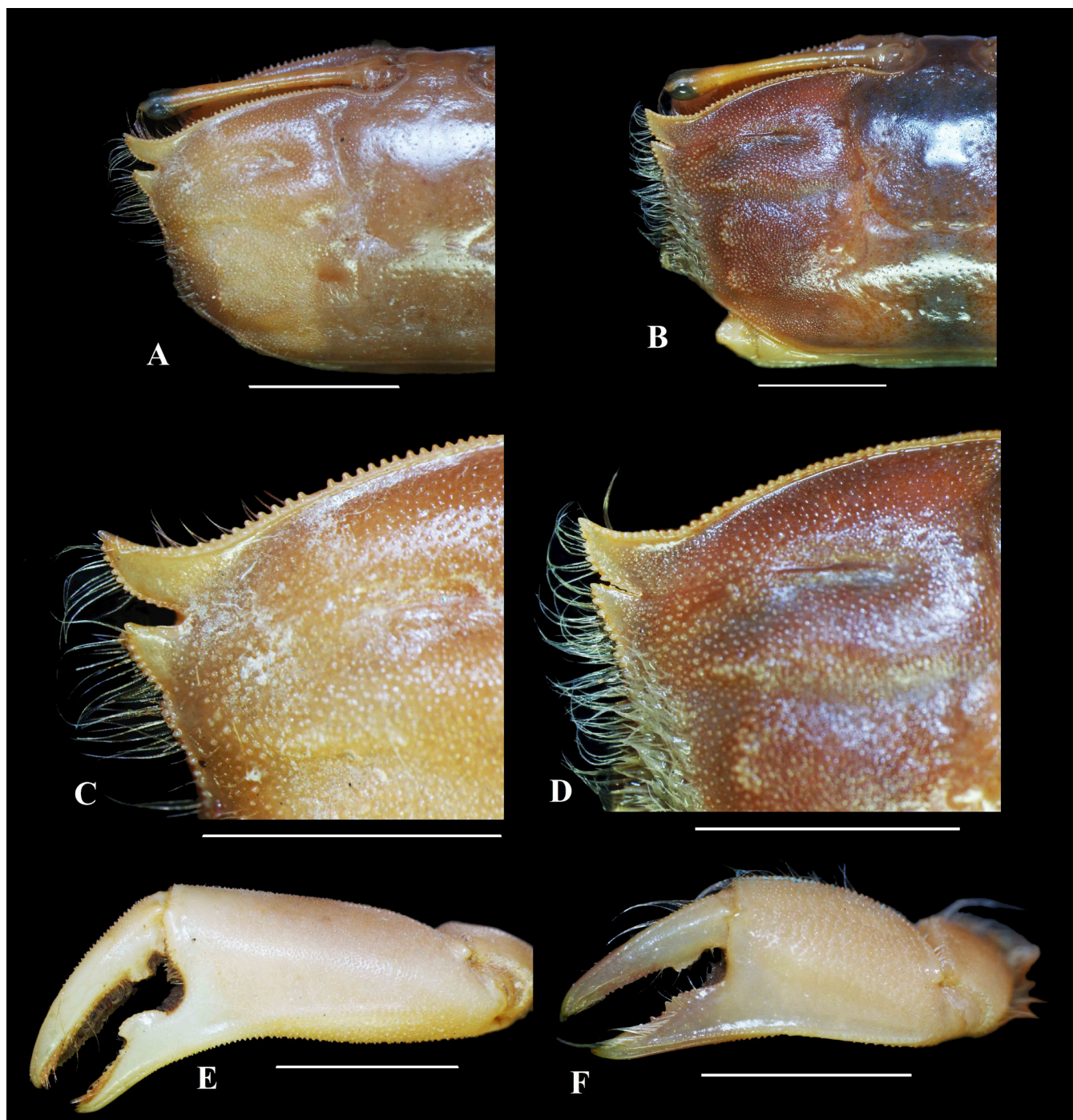


Fig. 11. Morphological comparison. A, C, E, *Macrophthalmus convexus*, MZB.Cru.1386, male, 20.1 × 10.3 mm; North Moluccas, Halmahera. B, D, F, *Macrophthalmus parvimanus*, MZB.Cru.4718, male, 24.0 × 12.4 mm; Moluccas, Saparua Island. A–B, carapace; C–D, external orbital angle; E–F, male left cheliped. Scale bars: 5 mm.

distally spoon-shaped, accessorised with margined chitinous process.

Female pleon broad, subcircular, 0.8 as long as wide. First somite much narrower and shorter than other somites, 21 times as wide as long. Second somite 10.4 times as wide as long, with short and shallow furrow parallel to mid-posterior margin. Third somite 9.7 times as wide as long, as long as fourth somite. Fourth somite 7.5 times as wide as long, longer than third somite, as wide as fifth somite. Fifth somite six times as wide as long, slightly longer than fourth somite; as long as sixth somite. Sixth somite 5.3 times as

wide as long, nearly as wide as third somite. Telson three times as wide as long; anterolateral margins slightly concave; posterolateral angles rounded, shallowly embedded in distal margin of sixth somite (Fig. 10F).

Vulva rounded; slightly protruded, with transverse groove medially, concave portion facing median portion of sternum; outer margin circular (Fig. 10H).

Etymology. The specific epithet is derived from the Nusa Manggala Expedition, and *manggala* is used here as a noun in apposition.

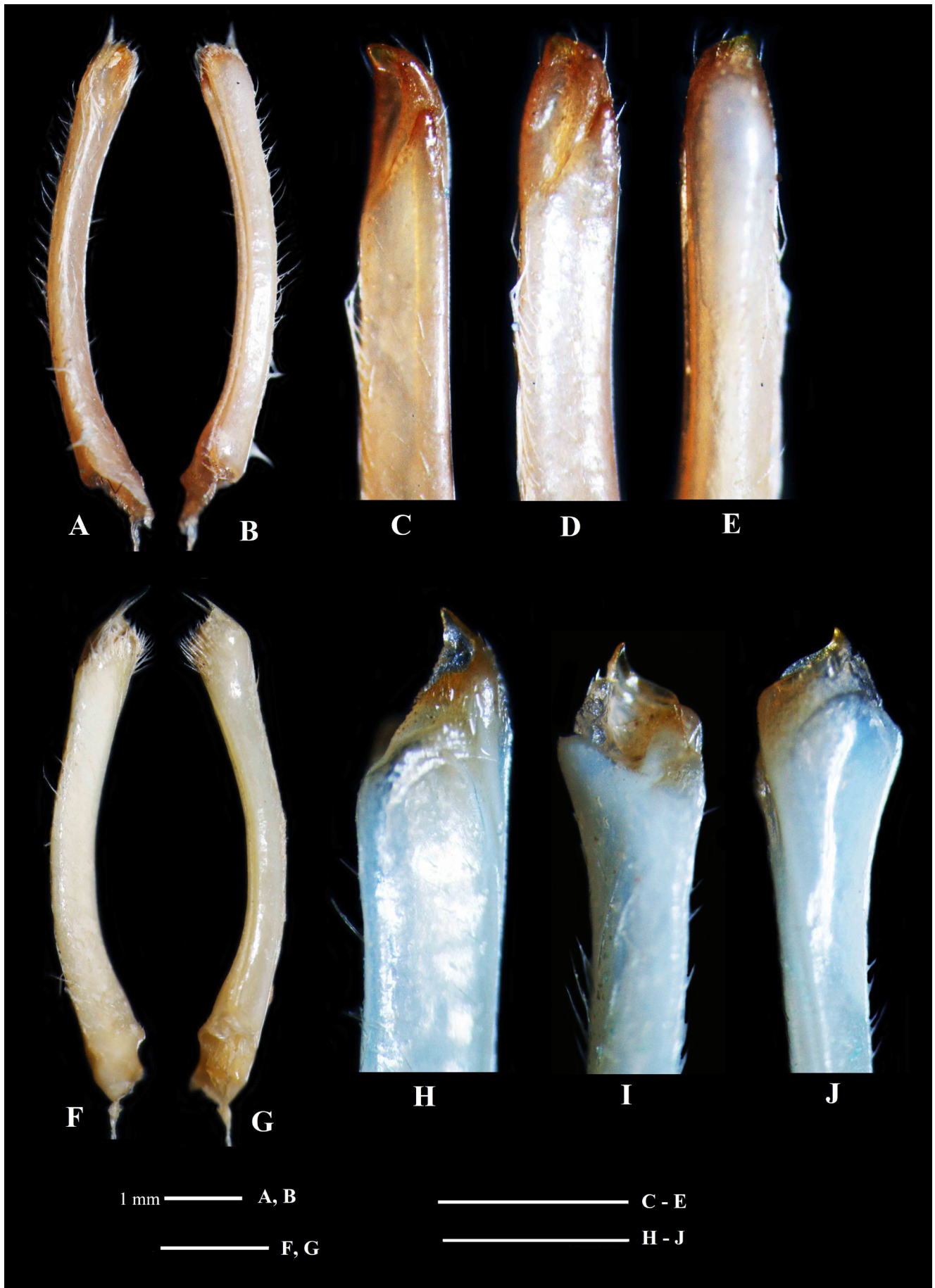


Fig. 12. Comparison of left G1. A-E, *Macrophthalmus convexus*, MZB.Cru.1386, male, 20.1 × 10.3 mm; North Moluccas, Halmahera. F-G, *Macrophthalmus parvimanus*, MZB.Cru.4718, male, 24.0 × 12.4 mm; Moluccas, Saparua Island. H-J, *Macrophthalmus parvimanus*, MZB.Cru.3268, male, 13.5 × 8.0 mm; Lombok Island.

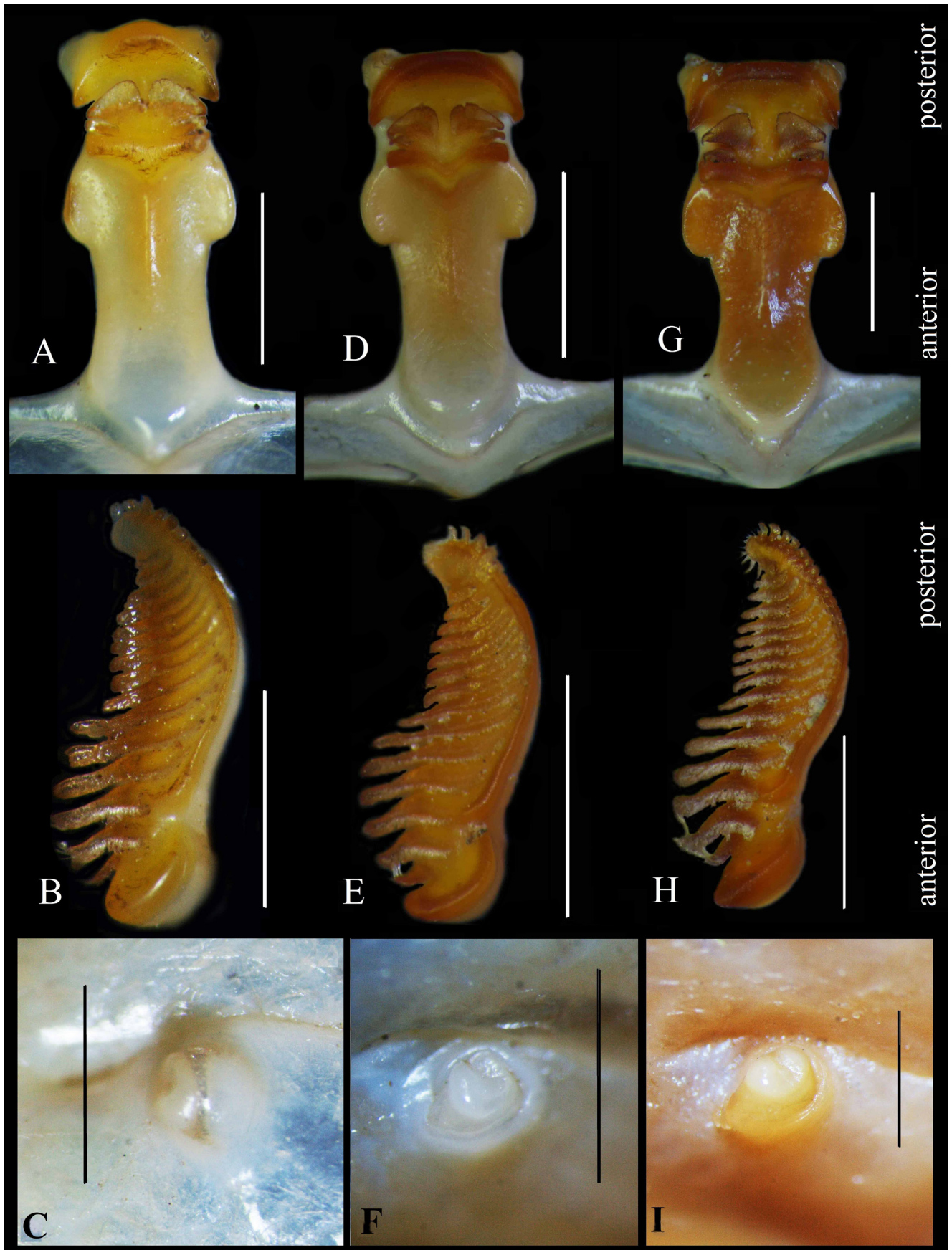


Fig. 13. Teeth plate of the gastric mill: A, D, G, median tooth plate; B, E, H, left lateral tooth plate. A–B, *Macrophthalmus manggala*, new species; paratype, MZB.Cru.5014, male, 21.6 × 10.7 mm; Papua, Liki Island. D–E, *Macrophthalmus convexus*, MZB.Cru.1386, male, 20.1 × 10.3 mm; North Moluccas, Halmahera. G–H, *Macrophthalmus parvimanus*, MZB.Cru.4718, male, 24.0 × 12.4 mm; Moluccas, Saparua Island. Vulva: C, *Macrophthalmus manggala*, new species; paratype, MZB.Cru.5014, female, 13.4 mm × 6.7 mm; Papua, Liki Island. F, *Macrophthalmus convexus*, MZB.Cru.5060, female, 17.2 × 9.3 mm; Bali. I, *Macrophthalmus parvimanus*, MZB.Cru.4718, female, 21.9 × 11.1 mm; Moluccas, Saparua Island. Scale bars: 1 mm.

Table 1. Morphological comparison among three species of the *Macrophthalmus convexus* group

Characters		<i>M. consobrinus</i>	<i>M. convexus</i>	<i>M. parvimanus</i>	<i>M. manggala</i> , new species
Male cheliped	Size	Small, feeble, similar to female cheliped	Elongate, robust, different from female cheliped	Small, feeble, slightly similar to female cheliped	Elongate, robust, different from female cheliped
	Fixed finger	Straight	Deflexed	Straight	Deflexed
		With differentiated tooth	With wide differentiated tooth	Without differentiated tooth	With narrow tooth
	Dactylus	Without differentiated tooth	With differentiated tooth	Without differentiated tooth	With differentiated tooth
G1	Terminal process	Slightly with process	Arched	Pointed	Truncated, C-shaped
Gastric mill					
Median tooth plate	Size ratio (length/width)	No information	2.1	2.3	2.5
	Posterior margin of propyloric ossicle	No information	Wide, nearly flat	Wide, flat	Narrow, acute shape Wide, flat
	Gap between posterior teeth	No information	Wide	Wide	Narrow
Lateral tooth plate	Number of teeth	No information	13–14	15–16	15–16
	Anterior tooth	No information	Short and stout	Short and stout	Short and slender
Data sources		Poupin (1997, fig. 7); Barnes (2010: in key)	MZB.Cru.1386; MZB.Cru.5060.	MZB.Cru.3268; MZB.Cru.4718; Barnes (2010: in key); Komai (1995: figs. 3, 7)	Present study

Remarks. *Macrophthalmus (Macrophthalmus) manggala*, new species, is most closely related morphologically to species of the *Macrophthalmus (Macrophthalmus) convexus* group sensu Barnes (2010). They share several diagnostic characters: the corneas are not positioned beyond the external orbital angle; the cornea is without a projection on its tip; the carapace is very broad (twice as broad as long); a small external orbital angle is followed with the second lateral tooth which has a larger and broader base; the shape of the second anterolateral tooth is flatter than that of the external orbital angle; the front is narrow, male chelipeds are elongate and the fixed finger is deflexed; the external orbital angle is large, flat, and forwardly curved; no spine is present on inner surface of the palm of the male cheliped.

The *M. (M.) convexus* group consists of *M. (M.) consobrinus* Nobili, 1906, *M. (M.) convexus* Stimpson, 1858 and *M. (M.) parvimanus* Guérin, 1832 (Poupin, 1997; Barnes, 2010). Among the three species, *M. (M.) manggala*, new species, most closely resembles *M. (M.) convexus* morphologically in having large male chelipeds with deflexed fixed fingers and a differentiated tooth on the cutting margin of the fixed finger on each cheliped. The new species, however, differs from

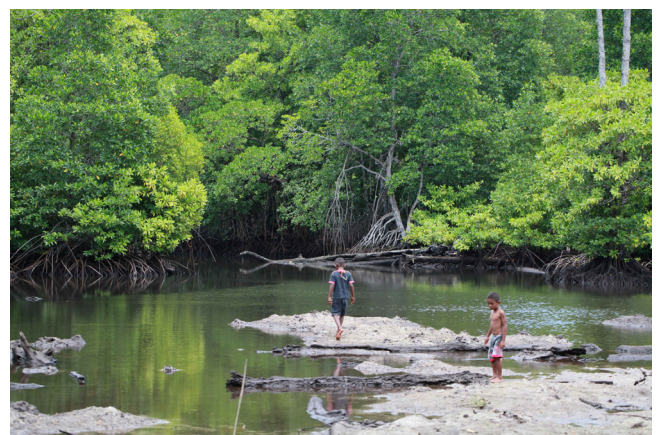


Fig. 14. Habitat of *Macrophthalmus manggala*, new species (Photograph by Sumaryanto Bronto).

M. (M.) convexus in the morphology of the male cheliped and G1 as listed in Table 1. The new species clearly has a narrow tooth on the fixed finger of the male cheliped (Fig. 7K), and a C-shaped process on its truncated apical portion of the G1 (Fig. 10C–E). In contrast, *M. (M.) convexus* has a wide tooth on the fixed finger of the male cheliped (Fig.

Table 2. Morphological comparison among *Tmethypocoelis koelbeli*, *T. odontodactylus* and *T. liki*, new species.

Characters		<i>T. koelbeli</i>	<i>T. odontodactylus</i>	<i>T. liki</i> , new species
Male chela	Dactylus upper margin	Straight, terminates in an overhanging 'shelf' at 3/4 length of margin	Granular, culminating with one strong tooth on subdistal portion	Granular, culminating with one strong tooth on subdistal portion
Male G1	Apical lobe	Bilobed, similar height	Unilobed	Bilobed, different height
	Apical setation	2 long setae, 5 short setae	10 setae with gradual size	1 long setae, 4 short setae
Data sources		Davie (1990)	Davie (1990)	Present study

11E), and an arched or pointed process on its apical portion of the G1 (Fig. 12A–E; Komai et al., 1995: fig. 3O–Q).

Distinct differences exist in the morphology of the gastric mill between the new species *M. (M.) manggala* and *M. (M.) convexus*. The median tooth plate of the gastric mill of *M. (M.) convexus* is shorter than that of the new species, which is 2.1 as long as wide, the posterior margin of the propyloric ossicle is wide and nearly flat, and the gap between the pair of posterior teeth is wider than that of the new species (Fig. 13D). The lateral tooth plate of the gastric mill of *M. (M.) convexus* has 13–14 teeth which are arranged in a comb shape (Fig. 13E). On the other hand, that of the new species has 15–16 teeth (Fig. 13B). The anterior tooth of the lateral tooth plate of *M. (M.) convexus* is short and stout (Fig. 13E); meanwhile, in the new species, the tooth is short and slender (Fig. 13B). Naderloo et al. (2010) used morphological characters of the median and lateral teeth plates of the gastric mills to distinguish closely related species.

The new species, *M. (M.) manggala*, is easily distinguished from the other two species of the *M. (M.) convexus* group, i.e., *M. (M.) parvimanus* and *M. (M.) consobrinus*. The latter two species have small and feeble chelipeds with straight fixed fingers in the males (Komai et al., 1995: fig. 7; Poupin, 1997: fig. 7; MNHN, 2008; Barnes 2010: in key), whereas the new species has a pair of long and robust chelipeds in the males (Komai et al., 1995: fig. 3) (see Table 1 for other minor differences between the new species and *M. (M.) parvimanus* and *M. (M.) consobrinus*).

Poupin (1997) examined the morphology of the G1 of the three species of the *M. (M.) convexus* group, i.e., *M. (M.) consobrinus*, *M. (M.) convexus* and *M. (M.) parvimanus*, from different regions of the Indo-West Pacific region. He found two types of G1 in these species: a G1 with a truncated apical portion (the typical form) and a G1 with an arched or pointed apical portion (Indo-Malaysian form). In *M. (M.) convexus* (type locality: Ryukyu Islands), specimens collected from the Western and Central Pacific have generally the typical form G1, and specimens collected from the Indo-Malaysian area have the Indo-Malaysian form G1. In *M. (M.) parvimanus* (type locality: Mauritius Island), specimens collected from the western Indian Ocean have the typical form G1, and specimens collected from the Indo-Malaysian area have the Indo-Malaysian form G1. Despite the geographical

difference in G1 morphology, Poupin (1997) concluded that all populations of *M. (M.) convexus* he examined belonged to a single species, and he likewise considered the populations of *M. (M.) parvimanus* to be all conspecific, as judged from other morphological characteristics. The Indo-Malaysian form is not given with a specific status because the specimens from Hong Kong and the Philippines, belonging to the fifth group, are morphologically different from those of the Indo-Malaysian. The specimen of *M. (M.) convexus* from Hong Kong has the similar G1 with *M. (M.) parvimanus* from Tanzania but distinctly different from *M. (M.) convexus* from Japan and Indonesia (Poupin, 1997: fig. 3A–E).

In the present study, we examined the G1 of *M. (M.) convexus* from Halmahera Island and *M. (M.) parvimanus* from Saparua Island, both in the Maluku Islands, Indonesia, for comparison with the G1 of the new species. The G1 of the specimens of *M. (M.) convexus* (Fig. 12A–E) and *M. (M.) parvimanus* (Fig. 12F–G) agree well with that of the Indo-Malaysian form of *M. (M.) convexus* (Poupin, 1997: fig. D') and *M. (M.) parvimanus* (Poupin, 1997: fig. 3B), respectively. Our specimens of *M. (M.) parvimanus* from Saparua and Lombok Islands (Fig. 12H–J) have the G1 with the pointed apex, similar to that from Thailand redescribed by Komai (1995: fig. 7N–P).

There is further minor variation in the G1 morphology within the Indo-Malaysian form of *M. (M.) convexus*; the apical portion is either arched (like a human nail) or pointed (Poupin, 1997: figs. 3D, D'). Specimens of *M. (M.) convexus* from Thailand that were illustrated by Komai et al. (1995: fig. 3O–Q) have the G1 with the pointed apex. Our samples of *M. (M.) convexus* from Halmahera Island, on the other hand, have the G1 with the arched apex (Fig. 12A–E). In contrast, the apical portion of the G1 of *M. (M.) manggala* is truncated, similar to that of *M. (M.) convexus* from Japan, which is the truncated (typical form) (Fig. 10C–E; Poupin, 1997: fig. 3C).

In females, the new species differs from *M. (M.) convexus* and *M. (M.) parvimanus* in morphology of the vulva; there is no transverse groove on the vulva of *M. (M.) convexus* and *M. (M.) parvimanus* (Komai et al., 1995, figs. 3G, 7G; Fig. 13F, I), but there is a median transverse groove on the vulva of *M. (M.) manggala* (Fig. 13C).

The new species is also morphologically related to species of the *M. (M.) brevis* group sensu Barnes (2010). However, the *M. (M.) convexus* group, now including the new species, distinctly differs from the *M. (M.) brevis* group in having a large, flat, forwardly curved external orbital angle, and no spine on inner surface of the palm in the male cheliped.

Habitat. This species inhabits muddy substrates. The habitat is submerged by sea water even at low tide (Fig. 14).

Behavior. This species lives in a narrow burrow in a habitat similar to that of *Gelasimus jocelynae* on the sampling site but prefers fine mud substrates instead of sandy mud. Unlike *G. jocelynae*, this species rarely uses its chelipeds for waving display behaviour, and they are mostly used for feeding and burrowing.

Key to the species of the *Macrophthalmus convexus* group (adapted from Barnes, 2010; Davie, 2012; Shih et al., 2015)

1. Chelae large and elongate, with clearly differentiated teeth on cutting margins of fingers2
- Chelae small and feeble (as in those in female *Macrophthalmus*), with poorly differentiated or no teeth on cutting margins of fingers3
2. Lateral margin of carapace with three anterolateral teeth (including external orbital angle); G1 with apical portion not truncated, armed with one short, arched chitinous process; posterior margin of propyloric ossicle of median tooth plate with wide and nearly flat shape, lateral tooth plate with 13–14 teeth, anterior tooth short and stout..... *M. (M.) convexus*
- Lateral margin of carapace with two anterolateral teeth (including external orbital angle); G1 with apical portion truncated, armed with C-shaped chitinous process; posterior margin of propyloric ossicle of median tooth plate with narrow and acute shape, lateral tooth plate with 15–16 teeth, anterior tooth short and slender..... *M. (M.) manggala*, new species
3. Fixed finger of male with long, low tooth along proximal half of cutting margin; apical portion of G1 not truncated, armed with one pointed chitinous process *M. (M.) parvimanus*
- Fixed finger of male with small, distinct quadrangular tooth on median of cutting margin; apical portion of G1 truncated, without chitinous process..... *M. (M.) consobrinus*

Family Dotillidae Stimpson, 1858

***Tmethypocoelis* Koelbel, 1897**

***Tmethypocoelis liki*, new species**

(Figs. 15–21)

Material examined. Holotype: male (6.2 × 3.5 mm) (MZB.Cru.5011), Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'25.29"S, 138°44'26.54"E, 21 Nov. 2018, DC Murniati.

Paratypes: 15 males (5.3 × 3.1 mm – 5.8 × 3.2 mm), 3 females (3.5 × 2.1 mm – 3.9 × 2.5 mm) (MZB.Cru.5012), Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'25.29"S, 138°44'26.54"E, 21 Nov. 2018, DC Murniati; 5 males (4.0 × 2.4 – 4.8 × 2.8

mm) (ZRC 2022.0914), Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'25.29"S, 138°44'26.54"E, 21 Nov. 2018, DC Murniati; 5 males (3.7 × 2.4 – 4.9 × 2.8 mm) (OMNH Ar-12646), Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'25.29"S, 138°44'26.54"E, 21 Nov. 2018, DC Murniati; 5 males (5.1 × 2.9 – 5.3 × 3.0 mm) (RMNH.CRUS.D.58042), Liki Village, Sarmi District, Sarmi Municipality, Liki Island, Papua Province, 01°37'25.29"S, 138°44'26.54"E, 21 Nov. 2018, DC Murniati.

Diagnosis. Carapace pentagonal, broad, 1.7 times as broad as long. Front gently narrowed anteriorly; lateral border of carapace distinctly curved, with single row of tubercles and stiff short setae. External orbital angle triangular, posteriorly followed by broad U-shaped sinus. Chelipeds stout, long, subequal. Palm bulky, inner surface coarsely granular on upper half, outer surface distinctly granular over distal-upper half. Fingers not gaping at base; fixed finger short, triangular. Dactylus with outer surface bearing one median ridge of granules; cutting margin with blunt and wide serration; upper margin with median row of granules culminating in one prominent tooth. Male pleon 1.8 times as long as wide. G1 long, slender, curved; apex forming two lobes; apical setae consisting one long and five short setae. Vulva D-shaped, mesial margin of operculum with triangular projection.

Description. Carapace pentagonal, broad; convex longitudinally, slightly convex transversely; 1.7 times as broad as long, greatest width across external orbital angles (Fig. 15B, 16A). Dorsal surface almost smooth, sparsely tubercular; regions defined by shallow grooves, epigastric lobe just visible (Fig. 16A). Cervical groove dividing gastric and cardiac regions, well-marked; cardiac regions with slight central depression. Branchial region sloping, with small, well-spaced, low tubercles, each bearing single seta. Sub-branchial region bulging, bearing regular setae, separated from branchial region by sinuous lateral border fringed with short setae. Front gently narrowed anteriorly, basal and distal widths 0.22 and 0.12 times as wide as external orbital width, respectively; distolateral angles rounded (Fig. 16A); anterior margin with small central blunt prominence. External orbital angle triangular, anterior and lateral margins slightly convex, with microscopic tubercles, one small ridge extending from mid-lateral margin, parallel to anterior margin, as long as anterior margin, posteriorly followed by broad U-shaped sinus (Fig. 16A, B). Second anterolateral tooth posterior to U-shaped sinus, concave posteriorly, distance between second anterolateral teeth less than between external orbital angles. Lateral margin of carapace distinctly curved, with single row of tubercles and stiff short setae (Fig. 16A). Anterolateral margin convex; posterolateral margin concave, adjoin with posterior margin without sharp angle. Posterior margin slightly concave, c.0.53 distance between external orbital angles; fine ridge parallel with posterior margin forming broad rim (Fig. 16A). Supra-orbital margin sinuous, diverging backward, microscopically tuberculate (Fig. 16C). Infraorbital margin with medial notch, below which, on pterygostome, oblique channel running inwardly; inner portion of infraorbital margin consisting

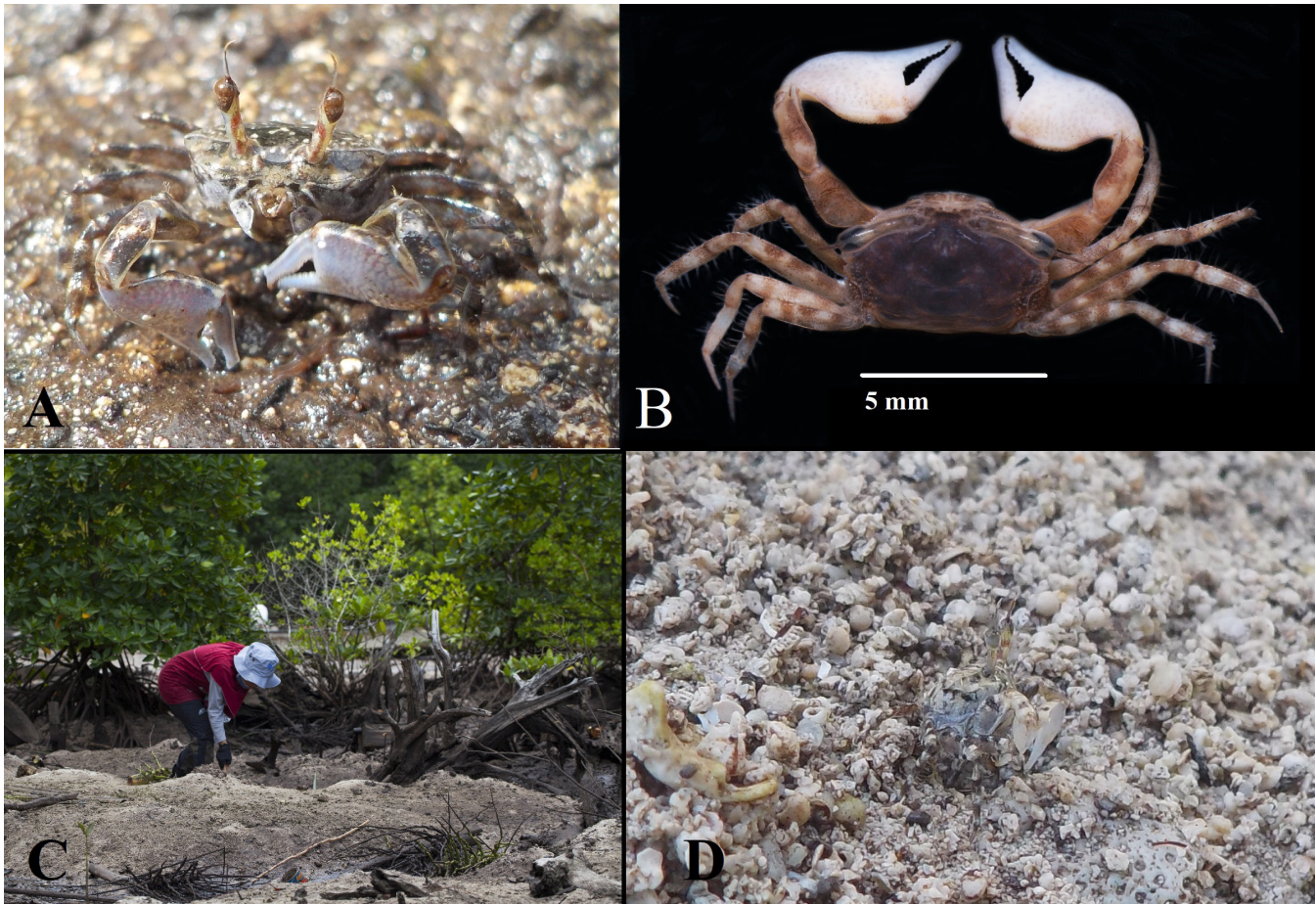


Fig. 15. *Tmethypocoelis liki*, new species. A, paratype, MZB.Cru.5012, male, 5.3×3.1 mm, in situ with life colouration. B, holotype, MZB.Cru.5011, male, 6.2×3.5 mm, dorsal habitus, preserved colouration; Papua, Liki Island. C–D, habitat of *Tmethypocoelis liki*, new species (photograph C by Sumaryanto Bronto).

of two granular ridges separated by shallow channel; outer portion of infraorbital border granular, concave, ending in broad notch below external orbital angle (Fig. 16C).

Epistome forming three lobes posteriorly, distinctly convex laterally and medially, margins without tuberculation (Fig. 16E).

Eyestalks long, widening distally, distal end of cornea reaching slightly beyond external orbital angles, distally with short projection, projection 0.3 times as long as cornea, tip with several short setae; cornea bulging; medial thickening gives twisted appearance (Figs. 15A, 16D).

Third maxillipeds distinctly vaulted, almost completely covering buccal cavern. Ischium subquadrate, antero-mesial angle narrowly triangular; mesial and lateral margins with dense short setae; outer surface smooth, with one oblique row of setae. Merus trapezoidal, subequal in size to ischium, about 1.1 times as long as ischium laterally; outer surface covered sparsely by regular short setae, without granules; mesial margin slightly convex, with long feathered setae; lateral margin convex, converged distally, covered with short setae; anterior margin slightly concave, without setae. Carpus trihedral, distal portion with dense long setae, lateral margin with sparse short setae, mesial margin with dense long setae. Propodus, shorter than dactylus, lateral margins with sparse

short setae. Dactylus slender, two times as long as propodus, margins serrated, with long stiff setae apically (Fig. 16F).

Male chelipeds (P1) stout, long, subequal (Fig. 15B). Merus with cross-section triangular (Fig. 17A–F); higher than external orbital angle when held against external orbital angle; outer margin with two irregular rows of sharp tubercles (Fig. 17A); lower margin with one row of tubercles (Fig. 17B); upper margin covered by scattered granules, granulation on distal portion continuous to outer surface, distal margin with one row of tubercles (Fig. 17C); oval tympani on outer and upper surfaces (Fig. 17E–F), tympanum on outer surface smaller than that of upper surface, microscopic granules present outside tympanum (Fig. 17F); lower surface smooth, without tympanum (Fig. 17D). Carpus shorter than merus; elongate, 2.15 times as long as wide; all margins tubercular (Fig. 17J–L); upper surface flattened, with triangular shape (Fig. 17G); lower surface smooth (Fig. 17H); outer surface peak with microscopic granules (17I). Palm bulky, 1.4–1.5 times as long as high (excluding fixed finger); inner surface coarsely granular on upper half, granulation extending to sharply cut upper margin (Fig. 17M); outer surface distinctly granular over distal-upper half, distinct groove extending below granular rows forming clear granular string near upper margin, half-lower part smooth (Fig. 17N); upper margin with granules (Fig. 17O); lower margin tubercular (Fig. 17P). Fingers without gaping proximally; curved

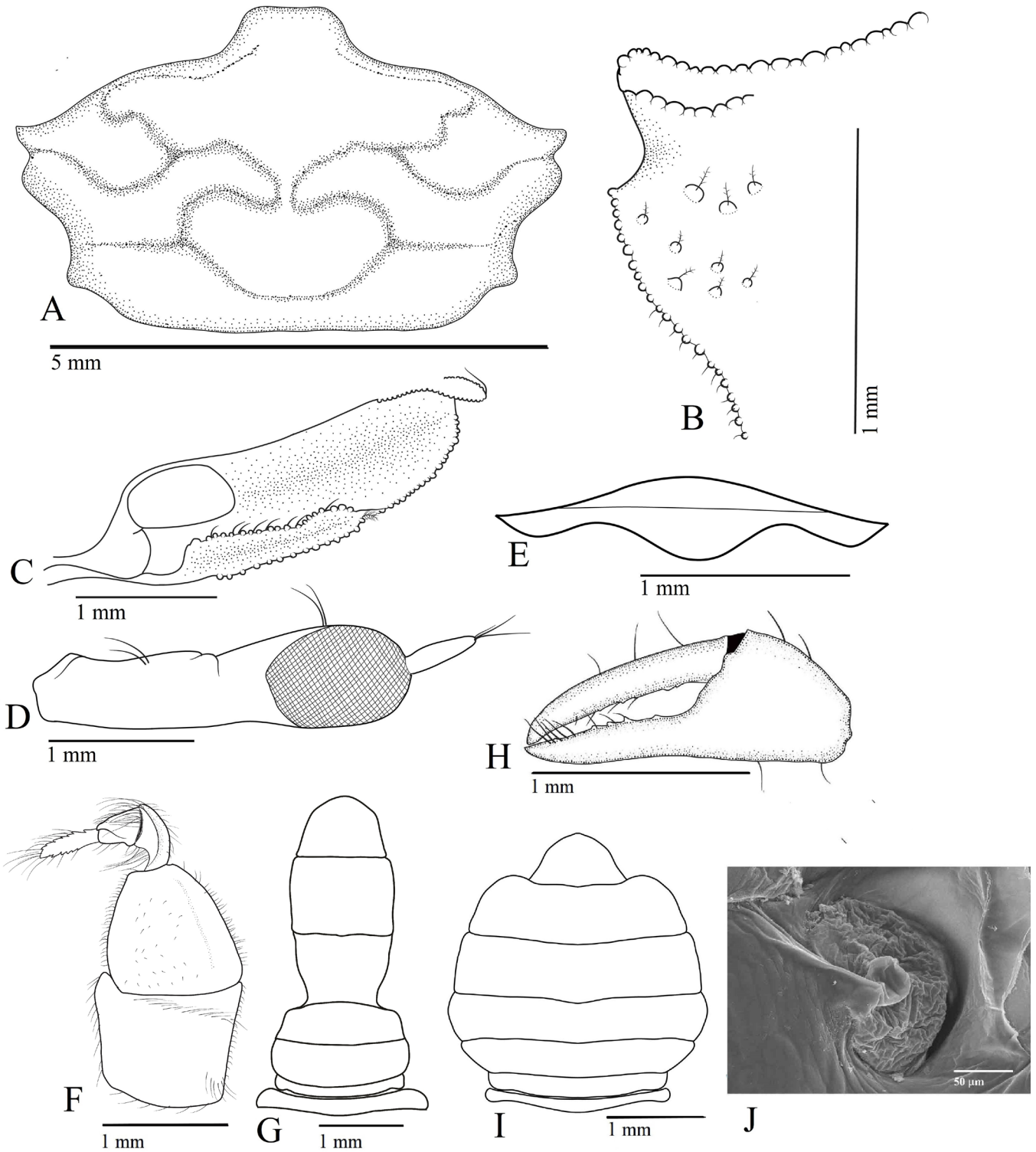


Fig. 16. *Tmethypocoelis liki*, new species. Holotype, MZB.Cru.5011, male, 6.2 × 3.5 mm; Papua, Liki Island. A, carapace; B, external orbital angle; C, orbit area; D, eystalk; E, epistome; F, outer surface of left third maxilliped; G, male pleon. Paratype, MZB.Cru.5012, female, 3.5 mm × 2.1 mm; Papua, Liki Island. H, outer surface of left chela; I, pleon; J, left vulva.

inwards, expanded distally to form spooned tip; cutting margins evenly serrated; inner margins at tip of both fingers with short row of stout setae (Fig. 17M, N). Fixed finger short, triangular shape, 0.34 times as long as palm; inner surface with granules near cutting margin; outer surface with granules near cutting margin; cutting margin slightly convex over entire length, but without one large differentiated tooth or lobe; lower margin granular only along middle to base (Fig. 17P). Dactylus with outer surface bearing one median

ridge of granules extended nearly whole length, scattered granules between ridge and cutting margin, flat depression with microscopic granules between granular ridge and upper margin, dense granulation on proximal portion near upper margin (Fig. 17N); inner surface granular near cutting margin and near upper margin, median portion smooth (Fig. 17M); cutting margin with blunt and wide serrates; upper margin with median row of granules culminating into one prominent tooth (Fig. 17M–O).

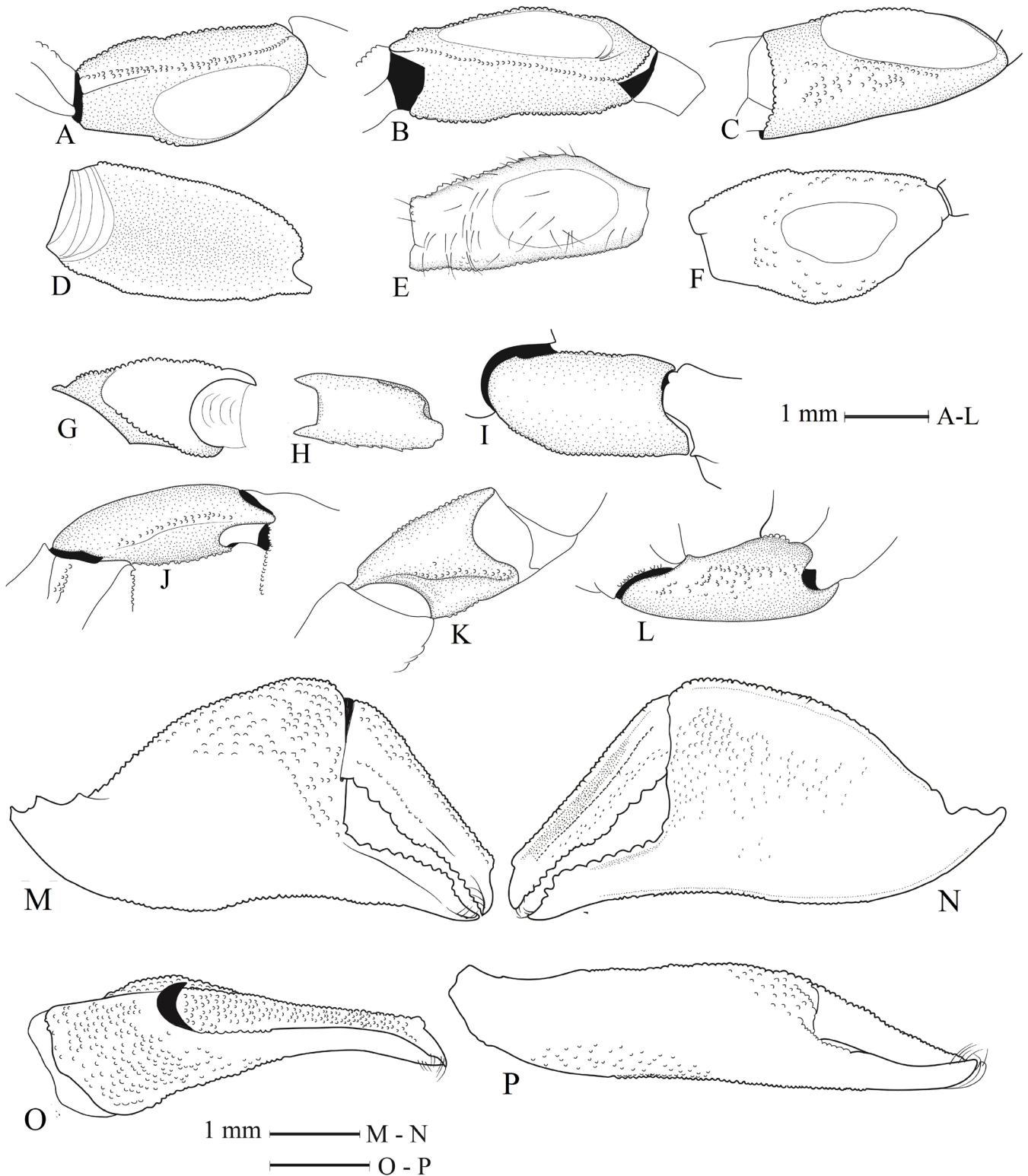


Fig. 17. *Tmethypocoelis liki*, new species. Holotype, MZB.Cru.5011, male, 6.2 × 3.5 mm; Papua, Liki Island. Merus of the left cheliped: A, outer margin; B, lower margin; C, upper margin; D, lower surface; E, upper surface; F, outer surface. Carpus of the left cheliped: G, upper surface; H, lower surface; I, outer surface; J, upper margin; K, lower margin; L, outer margin. Left palm: M, inner surface; N, outer surface; O, upper margin; P, lower margin.

Ambulatory legs (P2–P5) slender, elongate. P2 shorter than P3. Merus 2.9 times as long as wide; tympani on anterior and posterior surfaces; anterior surface without granules; posterior surface with scattered granules near upper margin; upper margin narrowed, convex in cross section, with spaced tubercles, tuberculation not forming ridge, sparse setae

distributed irregularly; surface of lower margin wider than that of upper margin, smooth, nearly without setae. Carpus shorter than propodus, surfaces smooth; upper margin with sparse tubercles proximally, sparse setae distributed irregularly; lower margin smooth. Propodus shorter than merus, with anterior surface smooth; posterior surface with

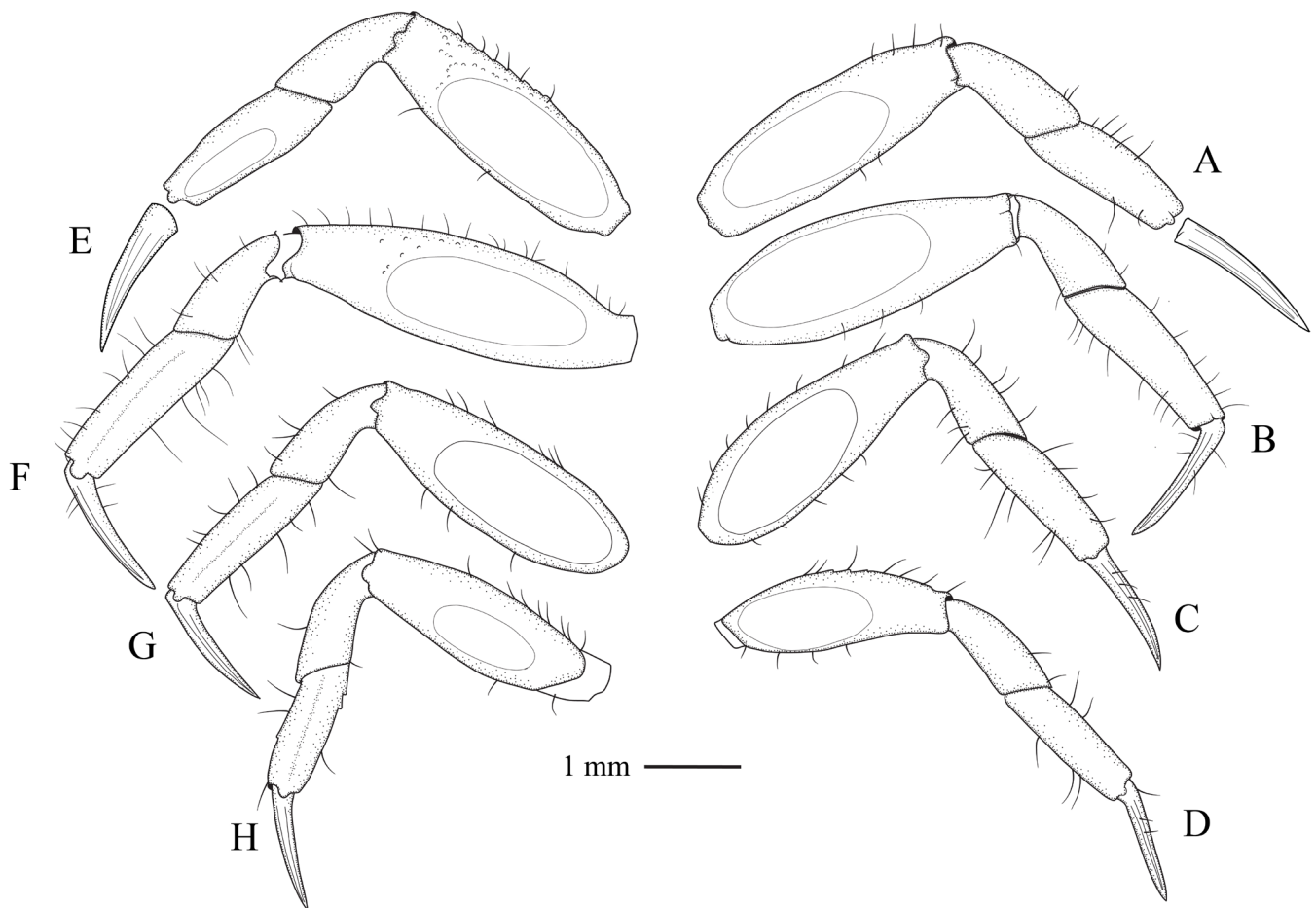


Fig. 18. *Tmethypocoelis liki*, new species. Holotype, MZB.Cru.5011, male, 6.2 × 3.5 mm; Papua, Liki Island. Left pereopods: A–D, anterior surfaces; E–H, posterior surfaces; A, E, P2; B, F, P3; C, G, P4; D, H, P5.

oval tympanum, tympanum smaller than that of merus; upper margin smooth, with sparse setae; lower margin smooth, without setation (Figs. 18A, E, 19A, E).

P3 longest. Merus 3.8 times as long as wide; oval tympani present on both surfaces; anterior surface without granules; posterior surface with sparse granules near tympanum; upper and lower margins convex, narrowed medially by two tympani on two surfaces; upper margin with scattered tubercles and setae; lower margin smooth. Carpus shorter than propodus; anterior and posterior surfaces smooth; surface of upper margin narrow, with sparse setae; surface of lower margin wide, smooth. Propodus shorter than merus; anterior surface smooth; posterior surface with one shallow groove, without granules; upper and lower margins with sparse setae (Figs. 18B, F, 19B, F).

P4 shorter than P2. Merus 3.6 times as long as wide; tympani present on anterior and posterior surfaces, without granules on both surfaces; upper and lower margins convex, narrowed medially by tympani on anterior and posterior surfaces; upper margin with one row of spaced microscopic tubercles, one row of spaced short setae parallel to tuberculation; surface of lower margin smooth, with sparse setae. Carpus shorter than propodus; anterior and posterior surfaces smooth; surface of upper margin narrow, lower margin wide, both margins with sparse setae, without tuberculation. Propodus

shorter than merus, anterior and posterior surfaces smooth; posterior surface with one shallow groove; upper and lower margins narrow, without tuberculation, with sparse setae (Figs. 18C, G, 19C, G).

P5 shortest. Merus 3.2 times as long as wide; tympani present on both surfaces, tympanum on anterior surface larger than that on posterior surface; upper and lower margins without tubercles, with sparse short setae. Carpus shorter than merus; upper and lower margins smooth; surface of upper margin narrow, with sparse short setae; lower margin wide, with sparse short setae. Propodus slightly as long as carpus; anterior and posterior surfaces smooth; surfaces of upper and lower margins narrowed, with sparse short setae. Dactylus with all surfaces and margins smooth (Figs. 18D, H, 19D, H).

Tympani on anterior surfaces of all meri larger than tympani on posterior surfaces, smaller from P2 to P5. Dactyli of P2–P5 proximally straight, slightly curved distally, pointed, slightly shorter than propodi; anterior and posterior surfaces with one ridge extending slightly whole length; surfaces without granules, with sparse setae.

Male pleon 1.8 times as long as wide. First somite trapezoid, 13 times as wide as long; anterior margin 0.86 times as long as posterior margin; 1.3 times wider than second somite. Second somite distinctly curved downward, 10 times as

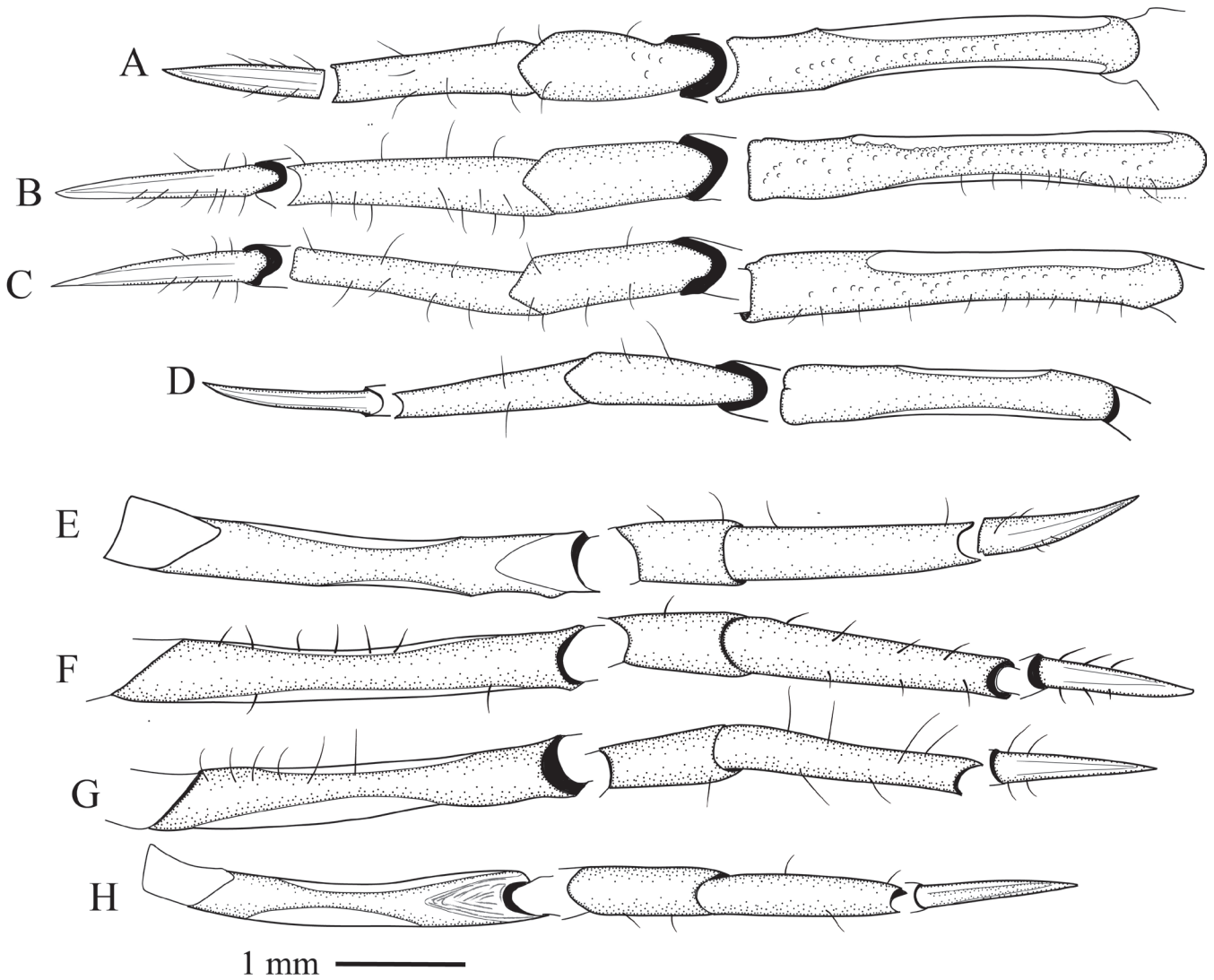


Fig. 19. *Tmethypocoelis liki*, new species. Holotype, MZB.Cru.5011, male, 6.2 × 3.5 mm; Papua, Liki Island. Left pereopods: A–D, upper margin; E–H, lower margin; A, E, P2; B, F, P3; C, G, P4; D, H, P5.

wide as long. Third somite 3.4 times as wide as long, anterior margin slightly concave, posterior edge convex. Fourth somite 2.8 times as wide as long; lateral margins concave, anterolateral angle rounded, posterolateral angle pointed; anterior margin convex; posterior margin nearly straight. Fifth somite 1.3 times as wide as long (at widest point), markedly constricted subproximally; proximal margin distinctly concave. Sixth somite 1.2 times as wide as long; anterior margin slightly concave, posterior margin slightly convex; lateral margins slightly wider subdistally; total length slightly as long as fifth somite, with slightly concave, parallel sides. Telson rounded; 1.3 times as wide as long; mid-posterior margin convex (Fig. 16G).

G1 long, very slender, curved; subproximal portion weakly bulging; apex forming two lobes; apical setae consisting one long setae and five short setae (Fig. 20A–E).

Female chelipeds equal, small. Palm with outer surface smooth; upper and lower margins with microscopic tubercles (Fig. 16H); inner surface smooth. Fingers longer than palm. Fixed finger straight; cutting margin serrated; lower margin

entire; tip with spoon shaped, with setae at tip; inner surface smooth. Dactylus with one furrow on outer surface; cutting margin slightly serrated; upper margin smooth and with setae; tip with spoon shaped and setae; inner surface smooth.

Female pleon rounded, nearly as long as wide (Fig. 16I). First somite distinctly curved, 13.6 times as wide as long; wider than second somite. Second somite 8.2 times as wide as long. Third somite 6.7 times as wide as long; anterior margin slightly concave; posterior margin nearly straight; lateral margins wider anteriorly. Fourth somite 6.4 times as wide as long; lateral margins concave; anterior margin convex; posterior margin nearly straight. Fifth somite 4.2 times as wide as long (at widest point), narrower and longer than fourth somite. Sixth somite 3.9 times as wide as long; narrower than fifth somite, anterior margin concave, posterior margin slightly convex; lateral margins wider posteriorly. Telson triangular; 1.7 times as wide as long; mid-posterior margin convex.

Vulva D-shaped, mesial margin of operculum with triangular projection (Fig. 16J).



Fig. 20. *Tmethypocoelis liki*, new species. Paratypes: A–C, MZB.Cru.5012, male, 5.0 × 3.0 mm; D–E, MZB.Cru.5012, male, 5.1 × 3.2 mm; Papua, Liki Island. Left G1: A, D, whole morphology; apical portion: B, E, lateral; C, mesial.

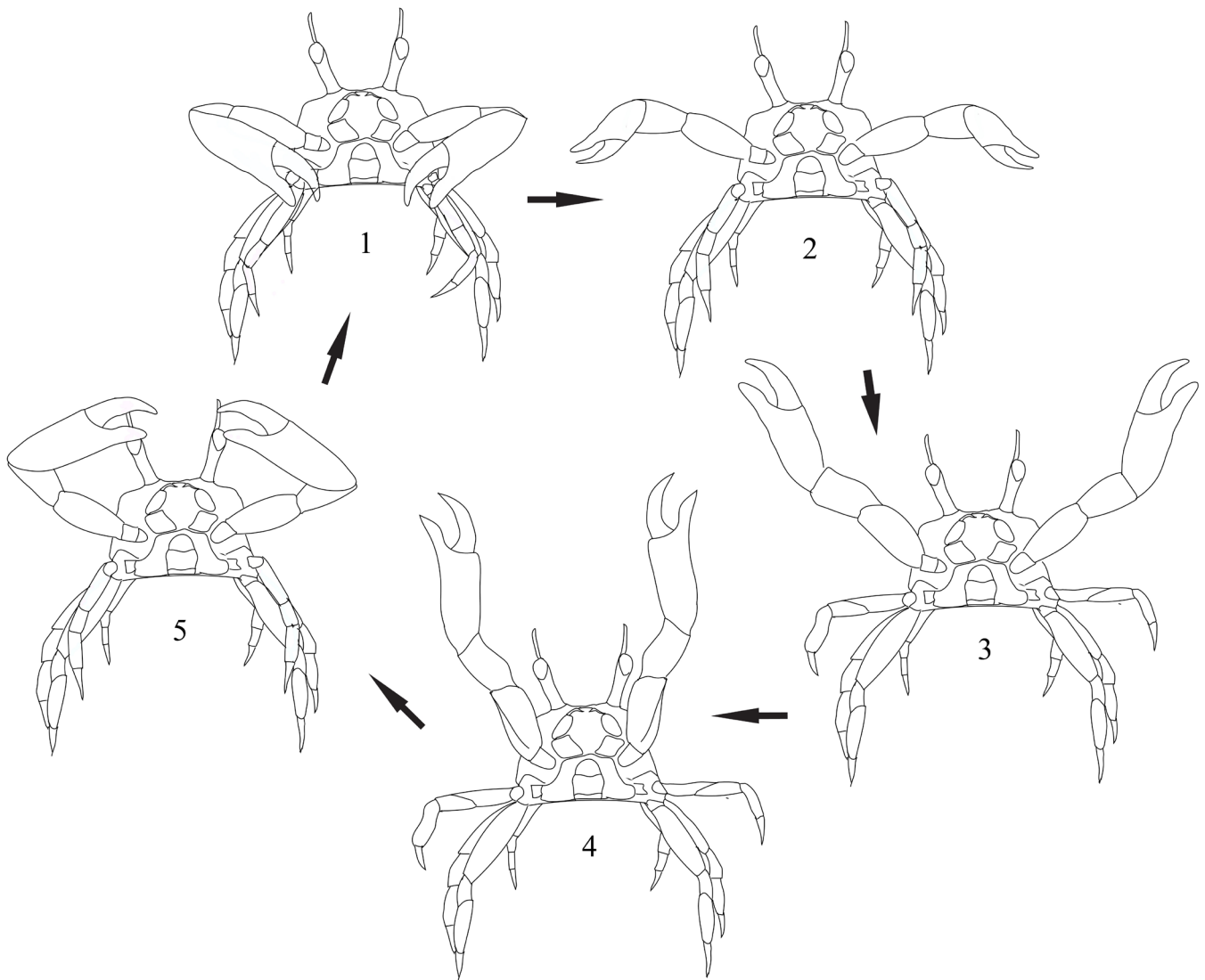


Fig. 21. Successive motion of waving display by male *Tmethypocoelis liki*, new species. Refer to text for details.

Etymology. The specific epithet of the new species is derived from the name of the type locality, Liki Island. The name is used as a noun in apposition.

Remarks. There were four species of *Tmethypocoelis* worldwide, all of which are distributed in the Indo-West Pacific, *T. ceratophora* (Koelbel, 1897) (type locality: Hong Kong), *T. choreutes* Davie & Kosuge, 1995 (type locality: Okinawa, Ryukyu Islands), *T. koelbeli* Davie, 1990 (type locality: Northern Territory, Australia), and *T. odontodactylus* Davie, 1990 (type locality: South of Madang, Papua New Guinea). The key characters to distinguish those species are on the male cheliped and G1. In *T. ceratophora*, the upper margin of the dactylus has a subdistal tooth formed by a crest without distinct median granules, while in *T. choreutes* the upper margin of the dactylus has a subdistal tooth formed by a crest with clear median granules (Davie & Kosuge, 1995: fig. 1A–F). In *T. odontodactylus*, the upper margin of the dactylus of the cheliped is granular, which culminates subdistally as a strong upturned tooth (Davie, 1995, fig. 3C). On the other hand, the upper margin of the same portion in *T. koelbeli* is straight, extending three quarters of the

length of the dactylus, which terminates in an overhanging ‘shelf’ (Davie, 1990). *Tmethypocoelis liki*, new species, has a small tooth formed by one big granule on the subdistal portion of the dactylus upper margin. This tooth is the last granule on a granular ridge which runs from the proximal to the subdistal portion of the dactylus upper margin (Fig. 17M–N). The morphology of the projected tooth varied within the samples. Some specimens had a low tooth, whereas the others had a high tooth. There is no correlation between the tooth size and carapace size.

Tmethypocoelis ceratophora has 7–8 apical setae on the G1 (Davie & Kosuge: 1995, fig. 2A–B; Shih et al., 2015: fig. 62A–D), while *T. choreutes* has 12 apical setae (Davie & Kosuge, 1995: fig. 2C–D). In *T. odontodactylus*, the apical portion of the G1 is unilobed with one row of regular setae, with a simple pattern of setation (Davie, 1990: fig. 3E–G). In *T. koelbeli*, the apical portion of the G1 is symmetrically bilobed, with five short and two long setae (Davie, 1990: fig. 2). In contrast, the apical portion of the G1 of *T. liki*, new species, is asymmetrically bilobed and armed with five short setae and one long seta (Fig. 20).

Habitat. This species inhabits mangrove areas with a sandy substrate, mixed with very small gravel. Around its habitat, there are some long and narrow trenches which are inundated by water remaining from the previous high tide (Fig. 15C, D).

Behavior. Male waving display of the new species is distinctly different from those of *T. ceratophora* and *T. choreutes* (Davie & Kosuge, 1995). The display of five males was recorded with a digital camera. The waving (Fig. 21) is started with both chelipeds positioned in front of the buccal cavern, the finger tips directed downward; they are then swung forward with the inner surface of the chela facing downward (1). The chela are then raised and directed outward, with fingertips also directed outward (2), then raised and directed centrally (3). The maximum height of the fingertips reaches beyond the projecting eyestalks. When reaching maximum height, the cheliped is in a nearly straight position with the fingertips pointing forward slightly (not pointing upward), meanwhile the P2 is raised (4). The chelipeds are then centrally gathered at a similar height to the maximum height, then refolded promptly (5) and returned to the initial position.

ACKNOWLEDGEMENTS

This paper is an output of the 2018 Nusa Manggala Expedition coordinated by the Research Center for Oceanography (RCO), Indonesian Institute of Sciences (LIPI) and funded by the FY 2018-2019 COREMAP-CTI Program. Special thanks to our precious team, the Second Leg of Nusa Manggala Expedition who helped us for collecting the specimens and Sumaryanto Bronto for photographing the specimens. We highly appreciate the kindness and sincerity of our colleagues, the crew of the research vessel K/R *Baruna Jaya VIII* (BJ VIII), for their generous help during the expedition. We also thank Peter Davie from Museums Queensland and Prof. Dwi Listyo Rahayu from RCO-BRIN for the discussions, Tohru Naruse from Ryukyu University for reviewing a pre-submission version of this manuscript, and our colleagues from Research Center for Biosystematics and Evolution-BRIN: Kartika Dewi and Reni Noor Fajareni for operating the SEM, and Nur Rohmatin Isnaningsih for searching for a reference. We also express our thanks to Museum Zoologicum Bogoriense (MZB), Directorate of Scientific Collection Management-BRIN, Cibinong, Indonesia. Some parts of the laboratory work were conducted during the doctoral program of the first author at the Division of Biological Science, Graduate School of Science, Kyoto University, Japan. The doctoral program was funded by the Indonesia Endowment Fund for Education (LPDP), from the Ministry of Finance of the Republic of Indonesia.

LITERATURE CITED

Allen CJ (2010) Ecology of the intertidal crab *Dotilla intermedia* from tsunami-impacted beaches in Thailand. Unpublished PhD Thesis. University of Southampton, Southampton, England, 194 pp.

- Barnes RSK (1970) The species of *Macrophthalmus* (Crustacea: Brachyura) in the collection of the British Museum (Natural History). Bulletin of the British Museum (Natural History) Zoology, 20(7): 206–250.
- Barnes RSK (1971) Biological results of the Snellius Expedition. XXIII. The genus *Macrophthalmus* (Crustacea, Brachyura). Zoologische Verhandlungen, 115: 4–40.
- Barnes RSK (2010) A review of the sentinel and allied crabs (Crustacea: Brachyura: Macrophthalmidae) with particular reference to the genus *Macrophthalmus*. Raffles Bulletin of Zoology, 58(1): 31–49.
- Bezerra LEA, Dias CB, Santana GX & Matthews-Cascon H (2006) Spatial distribution of fiddler crab (genus *Uca*) in a tropical mangrove of Northeast Brazil. Scientia Marina, 70(4): 759–766.
- Bott R (1973) Die verwandtschaftlichen Beziehungen der *Uca*-arten (Decapoda: Ocypodidae). Senckenbergiana Biologica, 54(4–6): 315–325.
- Botto F, Palomo G, Iribarne O & Martinez MM (2000) The effect of southern Atlantic burrowing crabs on habitat use and foraging activity of migratory shorebirds. Estuaries, 23(2): 208–215.
- Chen J, Xing Y, Yao W, Xu X, Zhang C, Zhang Z & Liu Q (2019) Phylomitogenomics reconfirm the phylogenetic position of the genus *Metaplex* inferred from the two grapsid crabs (Decapoda: Brachyura: Grapsoidea). PLoS ONE, 14(1): e0210763.
- Correa MODA & Uieda VS (2008) Composition of the aquatic invertebrate fauna associated to the mangrove vegetation of a coastal river, analyzed through a manipulative experiment. Pan-American Journal of Aquatic Sciences, 3(1): 23–31.
- Crane J (1975) Fiddler Crabs of the World, Ocypodidae: Genus *Uca*. Princeton University Press, New Jersey, xxiii +736 pp.
- Dana JD (1851) Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe reipublicae foederatae duce, lexit et descripsit. Proceedings of the Academy of Natural Sciences of Philadelphia, 5: 247–254.
- Darmarini AS, Soewardi K, Prartono T, Hakim AA, Nursiyamah S & Wardiatno Y (2019) New distribution record of the soldier crab, *Dotilla myctiroides* (Milne-Edwards) from Lubuk Damar coast, Aceh Province, Indonesia. AACL Bioflux, 12(1): 289–297.
- Davie PJF (1990) New and rare crabs of the subfamily Dotillinae (Crustacea: Ocypodidae) from northern Australia and Papua New Guinea. Memoirs of the Queensland Museum, 28(2): 463–473.
- Davie PJF & Kosuge T (1995) A new species of *Tmethypocoelis* (Crustacea: Brachyura: Ocypodidae) from Japan. Raffles Bulletin of Zoology, 43(1): 207–215.
- Davie PJF (2012) A review of *Macrophthalmus* sensu lato (Crustacea: Decapoda: Macrophthalmidae) from Australia, including two new species and new records. Memoirs of the Queensland Museum – Nature, 56(1): 149–219.
- Davie PJF, Guinot D & Ng PKL (2015) Anatomy and functional morphology of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FR & von Vaupel Klein JC (eds.) Treatise on Zoology — Anatomy, Taxonomy, Biology. The Crustacea. Volume 9, Part C-I. Brill, Netherlands, pp. 11–163.
- De Grave S, Pentcheff ND, Ahyong S, Chan T-Y, Crandall KA, Dworschak PC, Felder DL, Feldmann RM, Franssen CHJM, Goulding LYD, Lemaitre R, Low MEY, Martin JW, Ng PKL, Schweitzer CE, Tan SH, Tshudy D & Wetzer R (2009). A classification of living and fossil genera of decapod crustaceans. Raffles Bulletin of Zoology, Supplement 21: 1–109.
- De Haan W (1833–1850) Crustacea. In: Fauna Japonica sive Descriptio animalium, quae in itinere per Japoniam, jussu et auspiciis superiorum, qui summum in India Batava Imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus et adumbrationibus illustravit, P.F. von Siebold, ed. Amsterdam: Lugduni Batavorum, pp. 1–243.

- De Man JG (1892) Decapoden des indischen Archipels. In: M. Weber (ed.) Zoologische Ergebnisse einer Reise in Niederländisch Ost-Indien. Volume 2. Pp. 265–527, pls. 15–29.
- De Man JG (1926) *Ilyoplax delsmanni* n. sp., a new species of Ocypodidae. Zoologische Mededelingen, Leyden, 9(1): 16–27.
- Desmarest AG (1823) Malacostracés, Malacostraca. (Crust.). In: Cuvier F (ed.) Dictionnaire des Sciences Naturelles, dans lequel on trait Méthodiquement des Différens êtres de la Nature, considérés soit en eux-mêmes, d’après l’état actuel de nos connoissances, soit relativement à l’utilité qu’en peuvent retirer la Médecine, l’Agriculture, le Commerce et les Arts. Suivi d’une biographie des plus Célèbres Naturalistes. Ouvrage destiné aux médecins, aux agriculteurs, aux commerçans, aux artistes, aux manufacturiers, et à tous ceux qui ont intérêt à connoître les productions de la nature, leurs caractères généraux et spécifiques, leur lieu natal, leurs propriétés et leurs usages. Volume 28. F.G. Levrault et Le Normant, Strasbourg et Paris, pp. 138–425 [Malacostracés, pp. 211–285].
- Dewi K & Purwaningsih E (2020) Three new species of Cloacininae (Nematoda: Strongyloidea) parasitic in *Dorcopsis muelleri* (Schlegel, 1866) from Papua and Salawati island, Indonesia. Zootaxa, 4747(3): 535–546.
- Fabricius JC (1781) Species Insectorum exhibentes eorum differentias specificas, Synonyma auctorum, Loca natalia, Metamorphosis adiectis Observationibus, Descriptionibus. Volume 1. Hamburg & Kilonii. viii + 552 pp.
- Fadhillah NF, Prihatini W & Murniati DC (2018) Laporan praktik kerja magang di Bidang Zoologi (Museum Zoologicum Bogoriense) Pusat Penelitian Biologi, LIPI. Unpublished internship report. Program Studi Biologi, Fakultas Matematika dan Ilmu Pengetahuan Alam, Universitas Pakuan, Bogor, 27 pp. [In Indonesian]
- George RW & Jones DS (1982) A revision of the fiddler crabs of Australia (Ocypodidae: *Uca*). Records of the Western Australian Museum, Supplement 14: 1–99.
- Gordon AL (2005) Oceanography of the Indonesian seas and their throughflow. Oceanography, 18(4): 14–27.
- Guérin-Méneville FE (1829–1845) Iconographie du Règne Animal de G. Couvier, Représentation d’après nature de l’une des espèces les plus remarquables et souvent non encore figurées, de chaque genre d’animaux. Avec un texte descriptif mis au courant de la science. Ouvrage pouvant servir d’atlas à tous les traités de zoologie. Tome 2. Planches des animaux invertébrés. J. B. Baillièrre, Paris. 576 pp.
- Huang JF, Yang SL & Ng PKL (1998) Notes on the taxonomy and distribution of two closely related species of ghost crabs, *Ocypode sinensis* and *O. cordimanus* (Decapoda, Brachyura, Ocypodidae). Crustaceana, 71(8): 942–954.
- Kitaura J & Wada K (2006) New species of *Ilyoplax* (Brachyura: Ocypodidae: Dotillinae) from the Philippines and Indonesia: behavioral, molecular, and morphological evidence. The Raffles Bulletin of Zoology, 54(2): 373–379.
- Koelbel K (1897) Beschreibung der Krebse. In: Wissenschaftliche Ergebnisse der Reise des Grafen Béla Széchenyi in Ostasien. Volume 2. Pp. 709–718.
- Komai T, Goshima S & Murai M (1995) Crabs of the genus *Macrophthalmus* of Phuket, Thailand (Crustacea, Decapoda, Ocypodidae). Bulletin of Marine Science, 56(1): 103–149.
- Latreille PA (1817) Gelasime, *Gelasimus* (Buffon). Nouveau dictionnaire d’histoire naturelle, appliquée aux arts, à l’agriculture, à l’économie rurale et domestique, à la médecine, etc. Par une Societe de Naturalistes et d’Agriculteurs. Deterville, Paris. Edition 2, 12: 517–520.
- Latreille PA (1818) Ocypode, *Ocypode* Fab. Nouveau dictionnaire d’histoire naturelle, appliquée aux arts, à l’agriculture, à l’économie rurale et domestique, à la médecine, etc. Par une Société de Naturalistes et d’Agriculteurs. Deterville, Paris. Edition 2, 23: 194–199, pl. 15.
- Linnaeus C (1758) Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. Laurentii Salvii, Holmiae [= Stockholm], 823 pp.
- LIPI (2019) Ekspedisi Nusa Manggala: Kisah 8 Pulau Terluar. <https://www.youtube.com/watch?v=2CMPgVyaHUo> (Accessed 10 May 2021).
- MacLeay WS (1838) On the brachyurous decapod Crustacea brought from the Cape by Dr. Smith. In: Smith A (ed.) Illustrations of the Annulosa of South Africa; being a portion of the objects of natural history chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835. and 1836; fitted out by “The Cape of Good Hope Association for Exploring Central Africa”. Smith, Elder & Co., London, pp. 53–71, pls. 2–3.
- Miers EJ (1886) Report on the Brachyura collected by H.M.S. Challenger during the years 1873–1876. In: Murray J (ed.) Zoology. Report on the scientific results of the voyage of H.M.S. Challenger during the years 1873–76 under the command of Captain George S. Nares, R.N., F.R.S. and the late Captain Frank Tourle Thomson, R.N. Wyville Thomson, C. and J. Murray (series eds.) Volume 17. Neill and Company, Edinburgh, pp. 1–362, plates 1–29.
- Milne-Edwards H (1848) Note sur un crustacé nouveau du genre macrophthalme. Annales des Sciences Naturelles, Series 3, 9: 358.
- Milne-Edwards H (1852) Observations sur les affinités zoologiques et la classification naturelle des Crustacés. Annales des Sciences Naturelles, Series 3, 18: 109–166.
- MNHN (2008) Muséum national d’Histoire naturelle, Paris (France). Collection: Crustaceans (IU). Specimen MNHN-IU-2008-10586. <http://colddb.mnhn.fr/catalognumber/mnhn/iu/2008-10586> (Accessed 2 January 2020).
- Murniati DC & Pratiwi R (2015) Kepiting *Uca* di Hutan Mangrove Indonesia: Tinjauan Aspek Biologi dan Ekologi. LIPI Press, Jakarta, xii + 117 pp. [In Indonesian]
- Naderloo R, Türkay M & Chen H (2010) Taxonomic revision of the wide-front fiddler crabs of the *Uca lactea* group (Crustacea: Decapoda: Brachyura: Ocypodidae) in the Indo-West Pacific. Zootaxa, 2500(1): 1–38.
- Naderloo R, Türkay M & Apel M (2011) Bracyuran crabs of the family Macrophthalmidae Dana, 1851 (Decapoda: Brachyura: Macrophthalmidae) of the Persian Gulf. Zootaxa, 2911(1): 1–42.
- Naderloo R (2013) The sentinel crabs of the genus *Chaenostoma* (Stimpson, 1858) (Crustacea: Brachyura: Macrophthalmidae), with description of a new species and new records. Journal of Natural History, 47(45–46): 2835–2848.
- Ng PKL, Guinot D & Davie PJF (2008) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bulletin of Zoology, Supplement 17: 1–286.
- Nobili G (1906) Faune carcinologique de la Mer Rouge. Decapodes et Stomatopodes. Annales des Sciences Naturelles. Zoologie, 4: 1–347.
- Owen R (1839) Crustacea. In: The zoology of Captain Beechey’s voyage; compiled from the collections and notes made by Captain Beechey, the officers and naturalist of the expedition during a voyage to the Pacific and Behring Straits performed in His Majesty’s Ship ‘*Blossom*’, under the command of Capt. E. W. Beechey, R.N., F.R.S., &c. in the years 1825, 26, 27 and 28. London. Pp. 77–92.
- Pallas SP (1772) Spicelegia Zoologica. Quibus novae imprimis et obscurae Animalium Species. Iconibus, descriptionibus atque commentariis illustrantur. Berolini [=Berlin]. Fasculus nonus, 9: 83–84, pl. 5

- Pieters FFJMM & de Visser J (1993) The scientific career of the zoologist Max Wilhelm Carl Weber (1852–1937). *Bijdragen tot de Dierkunde*, 62(4): 193–214.
- Poupin J (1997) Les *Macrophthalmus* de Polynésie française (Decapoda, Brachyura, Ocypodidae). *Zoosystema*, 19(1): 159–176.
- Pretzmann VG (1974) Die unterfamilie Macrophthalminae Dana im Wiener Naturhistorischen Museum. *Annalen Naturhistorischen Museum Wiener*, 78: 437–444.
- Rafinesque CS (1815) *Analyse de la Nature ou Tableau de l'Univers et des Corps organisés*. Palerme, pp. 1–224.
- Raharjo SNI, Oktafiani I, Irewati I, Kadir HA & Suyadnya IW (eds.) (2021) *Tanah, Laut dan Rakyat: Catatan perjalanan Ekspedisi Nusa Manggala di pulau kecil terluar utara Papua*. Jakarta. Yayasan Pustaka Obor Indonesia. 431 pp. xi + 431 pp. [In Indonesian]
- Rahayu DL & Setyadi G (2009) Mangrove estuary crabs of the Mimika Region, Papua, Indonesia. PT. Freeport Indonesia, Timika, Papua, 153 pp.
- Rahayu DL & Nugroho DA (2012) The Indonesian species of *Macrophthalmus* Desmarest, 1823, with the description of a new species (Crustacea: Decapoda: Brachyura: Macrophthalmidae). *Zootaxa*, 3158(1): 20–36.
- Rathbun MJ (1910) Decapod crustaceans collected in Dutch East India and elsewhere by Mr. Thomas Barbour in 1906–1907. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 52(16): 305–317.
- Sakai K & Türkay M (1977) Die Gattung *Ocypode* in der Sammlung des Genfer Naturhistorischen Museums (Crustacea: Decapoda). *Revue suisse de Zoologie*, 84(1): 177–180.
- Sakai K & Türkay M (2013) Revision of the genus *Ocypode* with the description of a new genus, *Hoplocypode* (Crustacea: Decapoda: Brachyura). *Memoirs of the Queensland Museum*, 56(2): 665–794.
- Serène K (1973) Notes on Indo-West Pacific species of *Macrophthalmus* (Crustacea: Brachyura). *Zoologische Mededelingen*, 46(8): 99–116.
- Serène R & Moosa MK (1971) New and few known species of Brachyura from Ambon. *Marine Research in Indonesia*, 11: 3–18.
- Schubart CD, Cannicci S, Vannini S & Fratini S (2006) Molecular phylogeny of grapsoid crabs (Decapoda, Brachyura) and allies based on two mitochondrial genes and a proposal for refraining from current superfamily classification. *Journal of Zoological Systematics and Evolutionary Research*, 44(3): 193–199.
- Shih HT, Naruse T & Ng PKL (2010) *Uca jocelynae* sp. nov., a new species of fiddler crabs (Crustacea: Brachyura: Ocypodidae) from the Western Pacific. *Zootaxa*, 2337(1): 47–62.
- Shih HT, Ng PKL, Wong KJH & Chan BKK (2012) *Gelasimus splendidus* Stimpson, 1858 (Crustacea: Brachyura: Ocypodidae), a valid species of fiddler crab from the northern South China Sea and Taiwan Strait. *Zootaxa*, 3490(1): 30–47.
- Shih HT, Chan BKK, Teng SJ & Wong KJH (2015) Crustacean Fauna of Taiwan. Brachyuran Crabs. Volume 2: Ocypodoidea. National Chung Hsing University, Taichung, 320 pp.
- Shih HT, Ng PKL, Davie PJF, Schubart CD, Türkay M, Naderloo R, Jones D & Liu MY (2016) Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea: Brachyura), based on phylogenetic relationships, with a reorganization of subfamily rankings and a review of the taxonomic status of *Uca* Leach, 1814, sensu lato and its subgenera. *Raffles Bulletin of Zoology*, 64: 139–175.
- Števičić Z (2005) The reclassification of Brachyuran crabs (Crustacea: Decapoda: Brachyura). *Natura Croatica*, 14(1): 1–159.
- Stimpson W (1858) *Prodromus descriptionis animalium evertrebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars V. Crustacea Ocypodoidea*. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 10: 93–110.
- Tesch JJ (1918) The Decapoda Brachyura of the Siboga-Expedition. I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. *Siboga-Expedition Monograph*, 39c(82): 1–148, pls 1–6.
- Tsang LM, Schubart CD, Ah Yong ST, Lai JCY, Au EYC, Chan TY, Ng PKL & Chu KH (2014) Evolutionary history of true crabs (Crustacea: Decapoda: Brachyura) and the origin of freshwater crabs. *Molecular Biology and Evolution*, 31(5): 1173–1187.
- Wada K (2019) Brachyuran species recorded from mangrove swamp in Indonesia in 1984–2001. *Cancer*, 28: e144–e147. [in Japanese]
- Weber F (1795) *Nomenclator entomologicus secundum entomologiam systematicam ill. Fabricii, adjectis speciebus recens detectis et varietatibus*. Chilonii and Hamburgi. viii + 172 pp.
- White A (1847) *List of the specimens of Crustacea in the collection of the British Museum*. Printed by order of the trustees. Edward Newman, London. viii + 143 pp.