

Hermit crabs of Singapore (Crustacea: Decapoda: Anomura: Diogenidae, Paguridae), with description of two new species

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Abstract. The hermit crabs of Singapore are relatively well studied in the last few years and 42 species have been reported so far. This paper deals with 31 species of hermit crabs from the families Diogenidae and Paguridae, of which two are described as new: *Diogenes pisinnus*, new species (Diogenidae), and *Pagurus tenuilineatus*, new species (Paguridae). Seven species are also newly recorded, *Clibanarius ransoni* Forest, 1953, *Diogenes mixtus* Lanchester, 1902, *D. spinicarpus* Rahayu & Forest, 1995, *Pseudopaguristes monoporus* (Morgan, 1987), *P. hians* (Henderson, 1888), *Pagurus pitagsaleei* McLaughlin, 2002, and *P. hedleyi* (Lanchester, 1902). *Diogenes platyops* Rahayu & Forest, 1995, previously synonymised with *D. jubatus* (Nobili, 1903) is resuscitated based on the live colouration and several morphological characters. Among the specimens identified from the family Diogenidae, the genus *Diogenes* was the most species-rich with 17 species, while the genera *Clibanarius*, *Dardanus*, *Paguristes*, and *Pseudopaguristes* were represented only by four, three, one, and two species, respectively. As for the family Paguridae, four species of *Pagurus* and one species of *Spiropagurus*, were reported.

Key words. Crustacea, Diogenidae, Paguridae, new species, new record, Singapore

INTRODUCTION

The hermit crabs of Singapore have been relatively well studied in the last few decades (McLaughlin & Clark, 1997; Lemaitre & Ng, 1996; Rahayu, 1996, 2015; McLaughlin, 2002b, 2005; Rahayu et al., 2016), and so far, 42 species have been reported. A total of 31 species of the families Paguridae and Diogenidae were collected during the Comprehensive Marine Biodiversity Survey (CMBS) in Singapore in 2011–2014. Since the surveyed habitats were mostly sand and mud, the specimens collected were those typically living in that environment. In the family Diogenidae, the genera *Clibanarius* Dana, 1852 and *Dardanus* Paul'son, 1875, were each represented by four species, while *Paguristes* Dana, 1852 and *Pseudopaguristes* McLaughlin, 2002c, were represented by one and two species, respectively, with very few individuals. The genus *Diogenes* Dana, 1851 was the most collected with 17 species and about 800 specimens, comprising two species of the group 1 as defined by Forest (1952), three species of the *Troglopagurus* group as defined by McLaughlin (2005), as well as three species of the *pallidus* group and nine species of the *edwardsii* group as defined by Asakura & Tachikawa (2010). While the morphological characters are indispensable to distinguish

species, recognition of hermit crab species frequently relies on their colour and colour pattern in life (e.g., Poupin, 1997; Poupin & McLaughlin, 1998; Rahayu & Forest, 1999). The living colouration of *Diogenes platyops* Rahayu & Forest, 1995 which was considered a junior subjective synonym of *D. jubatus* (Nobili, 1903) by McLaughlin (2005), is recorded for the first time. The analysis of the colour information combined with morphological characters, using 36 specimens referable to these two taxa, showed that *D. platyops* needs to be revived as a distinct species. Specimens of *Diogenesinglei* McLaughlin & Clark, 1997, a species described from specimens collected in 1905, were gathered in a good number, and the species' living colour is described for the first time. Detailed examination of more than 70 specimens of *D. laevis* Rahayu, 1996 revealed morphological variation correlated to the size of individuals. Of the family Paguridae, four species of *Pagurus* Fabricius, 1798 and one species of *Spiropagurus* Stimpson, 1858 were collected during the CMBS project. Two new species are described in this paper, one species from the genus *Diogenes* and the other species from the genus *Pagurus*.

MATERIAL AND METHODS

Hermit crabs for this study came from the Comprehensive Marine Biodiversity Survey (CMBS) in Singapore in 2011–2014, including the Johor Strait workshop in 2012 and Singapore Strait workshop in 2013, and from the collection of Lee Kong Chian Natural History Museum, National University of Singapore. General morphology for species diagnosis and description follows that of Komai & Rahayu (2014) and Rahayu (2015). Animal size indicated

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by measurement of shield length (sl), measured from the midpoint of the rostral lobe to the midpoint of the posterior margin of the shield. Abbreviations used: P2, P3, P4, P5 = second, third, fourth, and fifth pereopods (ambulatory legs 1–4), respectively, st. = station, D = hand dredge, DR = rectangular dredge, DW = deep water, IT = intertidal, M = mangrove, MF = mudflat, SB = coral brushing, SD = scuba diving, SEA = seabed, SW = shallow water, TB = beam trawl. The synonymies for the species are restricted to the original description, record(s) from Singapore, illustrated work(s), primary synonym(s), clarifications of systematic problems, and incorrect identifications. Genera and species are presented in alphabetical order, except for the genus *Diogenes* which is presented according to the informal groupings by Forest (1952), McLaughlin (2005), and Asakura & Tachikawa (2010), i.e., group 1, *Troglopagurus* group, and *edwardsii* and *pallescens* groups, respectively. Complete descriptions are given for new species, and diagnoses are only for those that need clarification of species status. The holotypes and all other specimens studied are deposited in the Zoological Reference Collection (ZRC) of Lee Kong Chian Natural History Museum, National University of Singapore; paratypes are deposited in the Museum Zoologi Bogor (MZB), National Research and Innovation Agency (BRIN), Indonesia.

TAXONOMY ACCOUNT

Family Diogenidae Ortmann, 1892

Clibanarius Dana, 1852

Remarks. *Clibanarius* is characterised by an elongated shield with relatively long ocular peduncles, small ocular acicles, long with very short and sparse setae of the antennal flagella, equal or subequal chelipeds, and a short telson with the posterior lobes rounded and lined with spinules. The genus comprises 58 species (McLaughlin et al., 2010; Negri et al., 2014; Marin, 2016) distributed in tropical and subtropical areas of the world oceans, but most of the species live in the Indo-West Pacific. With two species newly recorded here, eight species are now found in Singapore water (Rahayu, 1996; present study).

Clibanarius infraspinatus Hilgendorf, 1869 (Fig. 1A, B)

Clibanarius infraspinatus Hilgendorf, 1869: 97 (type locality: Singapore); Fize & Serène, 1955: 77, fig. 10; Rahayu, 1996: 336; McLaughlin et al., 2007: 113, unnumbered fig.; Malay et al., 2018: 33, fig. 2G.

Material examined. 1 male, not collected, st. SW33, Changi, 1°22.432'N 104°00.350'S, 18 October 2012; 1 female, 9.0 mm (ZRC 2021.0101), Chek Jawa, 1 July 2009; 1 ovigerous female, not collected, st. SW156, St. John's Island, 1°13.348'N 103°50.834'E, 3 June 2013.

Colour in life. Shield cream, mottled with light and dark brown. Ocular peduncles whitish cream with dark brown longitudinal stripe on dorsal face, broader stripe proximally. Chelipeds greenish brown or dark brown with white spines and tubercles, dactyl and fixed finger light brown. P2 and P3 greenish brown or dark brown, each with light orange or tannish orange longitudinal stripe on dorsal and lateral faces extending from base of claw to proximal margin of merus (Fig. 1A, B).

Distribution. Widely distributed in the Indo-West Pacific, from the Red Sea, Indian Ocean, Indonesia, Singapore, North of Australia, Philippines, Vietnam, and Japan; intertidal.

Remarks. A common inhabitant of sandy mud substrates, sometimes also found in mangrove environment. *Clibanarius infraspinatus* is easily recognised by the longitudinal stripes on the ocular peduncles and P2 and P3, and the presence of a prominent spine on the ventral margin of the merus of the chelipeds.

Clibanarius longitarsus (De Haan, 1849) (Fig. 1C, D)

Pagurus longitarsus De Haan, 1849: 211, fig. 3 (type locality: Japan). *Pagurus asper* H. Milne Edwards, 1848: 62 (type locality: Indian Seas); Low & Rahayu, 2014: 393.

Clibanarius longitarsus – Fize & Serène, 1955: 83, fig. 11, pl. 3, figs. 1, 7, 10, 13; Dechancé, 1964: 31, fig. 4; Rahayu & Forest, 1992: 762, figs. 4b, 5b, 6b; Rahayu, 1996: 336; McLaughlin et al., 2007: 119, unnumbered fig.

Material examined. 1 female, 9.5 mm (ZRC 2021.0102), St John's Island, 18 May 2011; 1 male, 4.8 mm, 2 females, 8.9–9.4 mm (ZRC 2021.0103), st. SW95, mouth of Sungei Besar, 01°25.0258'N 103°67.607'E, mudflat with mangrove, 26 October 2012.

Colour in life. In general greenish brown or blackish brown with longitudinal bright blue stripe on the lateral faces of P2 and P3 (Fig. 1C, D). Haig & Ball (1988) and Rahayu (2003) gave descriptions of colouration and colour variation of this species.

Distribution. Widely distributed in the Indo-West Pacific; intertidal.

Remarks. *Clibanarius longitarsus* is commonly found in brackish waters, mudflat, and mangrove environments. In its habitat, this species is easily recognised by its bright blue longitudinal stripe on the pereopods.

Clibanarius ransonii Forest, 1953

Clibanarius ransonii Forest, 1953a: 446, figs. 2, 6. (type locality: Tahiti); Fize & Serène, 1955: 150, fig. 23; McLaughlin et al., 2007: 131, unnumbered fig.

Material examined. 1 male, 3.6 mm (ZRC 2021.0104), st. MF64, Pulau Pawai, 01°11.088'N 103°43.683'E, 1 July 2012.

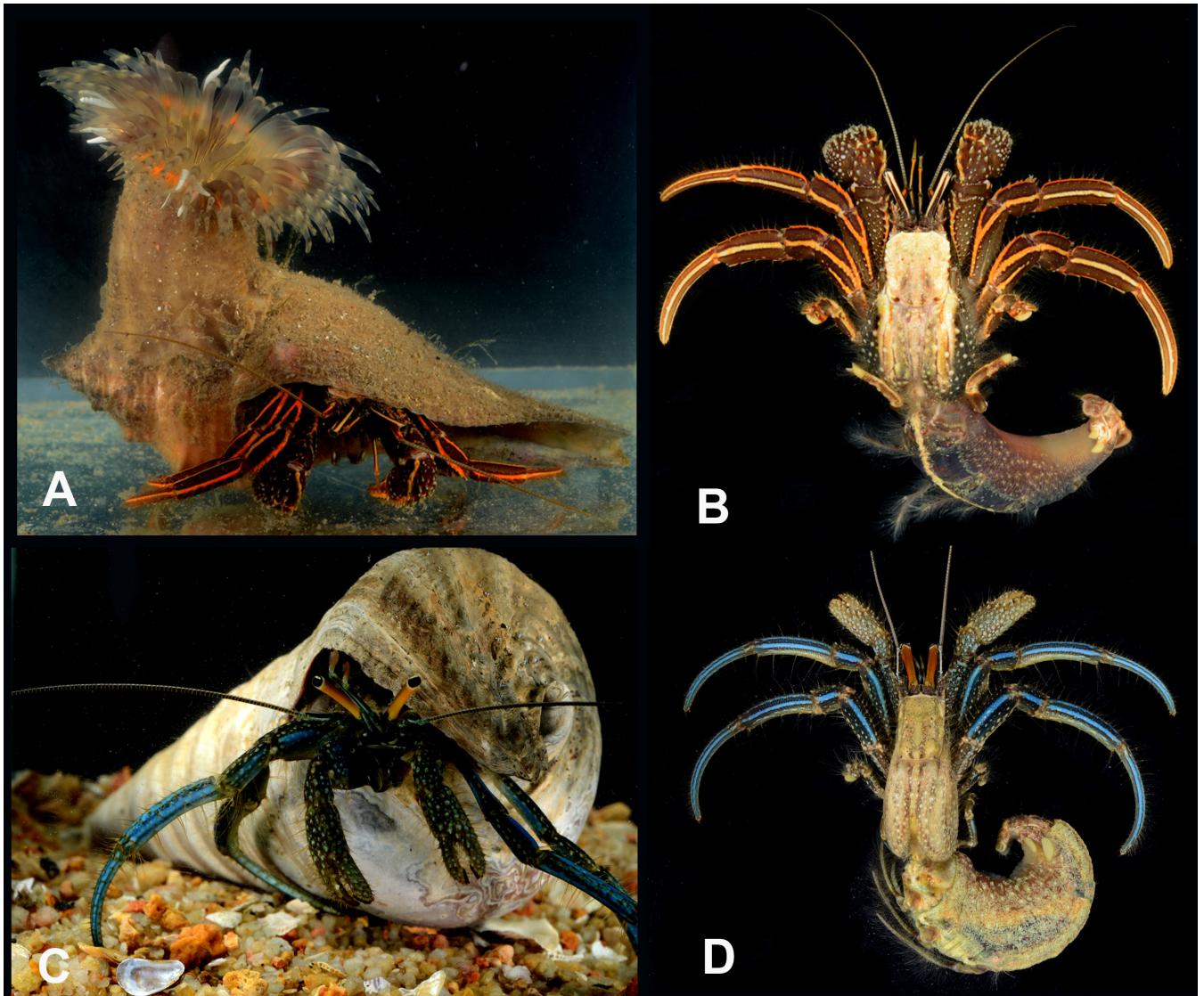


Fig. 1. A, B, *Clibanarius infraspinatus* Hilgendorf, 1869, male, not collected; C, D, *Clibanarius longitarsus* (De Haan, 1849), female, 9.4 mm (ZRC 2021.0103).

Colour in life. Shield mottled light green and brown. Ocular peduncles reddish orange, each with bluish white band at base of corneas, tinge of dark brown proximally. Chelipeds brownish black with yellowish spines and tubercles. P2 and P3 brown or brownish black, each with broad light orange or tannish orange stripe on lateral face extending from base of claw to proximal margin of merus.

Distribution. Indonesia, Vietnam, Tahiti, and now Singapore; intertidal, on sandy mud and gravel substrates.

Remarks. Rahayu (1996) included Singapore in the distributional range of this species by mistake as she examined only a specimen from Batam, Indonesia (Rahayu, 1996: 352, table 1). This is the first confirmed record of *C. ransoni* from Singapore, represented only by one specimen.

Clibanarius striolatus Dana, 1852

Clibanarius striolatus Dana, 1852: 463 (type locality: Fiji); Dana, 1855: pl. 29, fig. 3a–c; Fize & Serène, 1955: 97, fig. 13, pl. III, 4; Dehancé, 1964: 32, fig. 6; McLaughlin et al., 2007: 121, unnumbered fig.

Clibanarius A Fize & Serène, 1955: 109, fig. 15, pl. III, 6.

Material examined. 1 specimen (not preserved), Sungei Pandan, 30 March 2011.

Colour in life. Shield mottled green and brown on yellowish white background, ocular peduncles greenish white; chelipeds greenish white mottled brown, spines white; P2 and P3 greenish white with brown longitudinal stripes.

Distribution. Widely distributed in the Indo-West Pacific: Red Sea, Indian Ocean, West Pacific; intertidal, in sandy mud substrate.

Remarks. Although this species has a wide distribution in the Indo-Pacific, the present record is the first from Singapore.

***Dardanus* Paul'son, 1875**

Remarks. The genus *Dardanus* is characterised by the obsolete or very short rostrum, relatively stout ocular peduncles, frequently with large corneas and ocular acicles, usually unequal chelipeds with the left much larger than the right (but subequal in a few species), and asymmetrical telson. Forty-six valid species of *Dardanus* are presently recognised (McLaughlin et al., 2010; Rahayu, 2010; Malay et al., 2018), living in intertidal and subtidal areas in the world oceans but mostly found in the Indo-West Pacific. Four species were previously reported from Singapore (Rahayu, 1996), and one species [*D. lagopodes* (Forskål, 1775)] is here added to the fauna of Singapore.

***Dardanus hessii* (Miers, 1884)**

(Fig. 2A, B)

Pagurus hessii Miers, 1884: 264, pl. 28, fig. 4 (type locality: Arafura Sea); Alcock, 1905b: 93, pl. 8, fig. 4.

Pagurus similimanus Henderson, 1888: 59, pl. 6, fig. 6.

Pagurus hessi – Fize & Serène, 1955: 158, fig. 34, pl. 4.

Dardanus hessii – Forest & McLaughlin, 2000: 85, fig. 27; McLaughlin et al., 2007: 87, unnumbered fig.; Rahayu & Ong, 2015: 145, figs. 1–4.

Material examined. 1 male, 13.8 mm (ZRC 2021.0105), SEA8656, 01°15.925'N 103°53.779'E, 4 November 2014.

Colour in life. In general, body and appendages creamy white (Fig. 2A, B). Shield mottled grey and white; ocular peduncle broken white or greyish white with longitudinal red stripe on lateral and mesial face, corneas black; chelipeds with dactyl, fixed finger, and dorsomesial surface of palm red, rest of chelipeds mottled light brown, grey and white. P2 and P3 greyish white, light brown or creamy white with red streaks on lower lateral face of propodi.

Distribution. Red Sea to Torres Strait, Vietnam, and Taiwan, at depths of 15–55 m, possibly to 80 m, on sandy mud substrate.

Remarks. This is not a very common species but is easily recognised by the subequal, spinuous chelipeds, and obviously dilated corneas.

***Dardanus lagopodes* (Forskål, 1775)**

(Fig. 2C, D)

Cancer lagopodes Forskål, 1775: 93 (type locality: Red Sea).

Pagurus sanguinolentus – Forest, 1953b: 559, 560, figs. 12–14 (in part); Fize & Serène, 1955: 166–173, fig. 25, pl. 4 no. 4–5 (in part) (Not *Pagurus sanguinolentus* Quoy & Gaimard, 1824).

Pagurus affinis H. Milne Edwards, 1836: 274 (type locality: Sri Lanka).

Pagurus euopsis Dana, 1852: 452, 453 (type locality: Upolu, Samoa); Estampador, 1937: 503 (in part).

Dardanus lagopodes – Lewinsohn, 1969: 32, figs. 1, 2, pl. 2; Ball & Haig, 1972: 92, 93; Haig & Ball, 1988: 166; McLaughlin et al., 2007: 91–93, unnumbered fig.; Malay et al., 2018: 39, figs. 3H, 5A, B.

Material examined. 1 male, 14.9 mm (ZRC 2021.0106), Singapore Strait, 7 June 2013.

Colour in life. Shield mottled grey and dark brown, large reddish brown blotch anteriorly; ocular peduncles whitish yellow, narrow orange line just next to corneas; cheliped brownish grey, fingers with tinge of dark red or dark brown. P2, P3 whitish yellow, carpi and meri with large blotch of dark brown on dorsal surface. All setae reddish brown with yellowish white tip (Fig. 2C, D).

Distribution. Widely distributed in the Indo-West Pacific; intertidal to shallow subtidal on coral rubble bottom.

Remarks. Malay et al. (2018) revised the status of the two forms of colour (black/blue/brown form and red form) long identified with *D. lagopodes* (e.g., Fize & Serène, 1955; Ball & Haig, 1972; Haig & Ball, 1988; McLaughlin et al., 2007), and determined that the black/blue/brown form represents the true *D. lagopodes*.

***Dardanus megistos* (Herbst, 1804)**

(Fig. 2E)

Cancer megistos Herbst, 1804: 23, pl. 61, fig. 1 (type locality unknown).

Pagurus megistos; Fize & Serène, 1955: 160, fig. 24, pl. 4A, figs. 1–3.

Dardanus megistos; Rahayu, 1996: 339; McLaughlin et al., 2007: 94, unnumbered fig.; Malay et al., 2018: 51, fig. 4C.

Material examined. 1 specimen (not preserved), St. John's Island, 2013.

Colour in life. Shield, abdomen, and appendages orangish red or bright red with white spots. Ocular peduncles bright red, narrow white band at base of corneas; corneas brownish red; antennal and antennular peduncles orange, antennal flagella white.

Distribution. Widely distributed in the Indo-West Pacific; intertidal, sandy muddy substrate.

Remarks. The species is easily recognised by the orangish red colour with white spots on the shield and appendages. This is a common species in the Indo-West Pacific, but rarely collected in Singapore.

***Diogenes* Dana, 1851**

Remarks. This genus is characterised by the presence of spinous, simple, very tiny or vestigial intercalary rostriform process between the ocular acicles, and absent or reduced crista dentata on the third maxilliped ischium. Forest (1952) and Rahayu & Forest (1995) separated the genus *Diogenes* into two informal groups based on the presence or absence of the lateral process on the endopod of the maxilla, and on the marginally spinose or simple intercalary rostriform process. Species with simple intercalary rostriform process (group 2 of

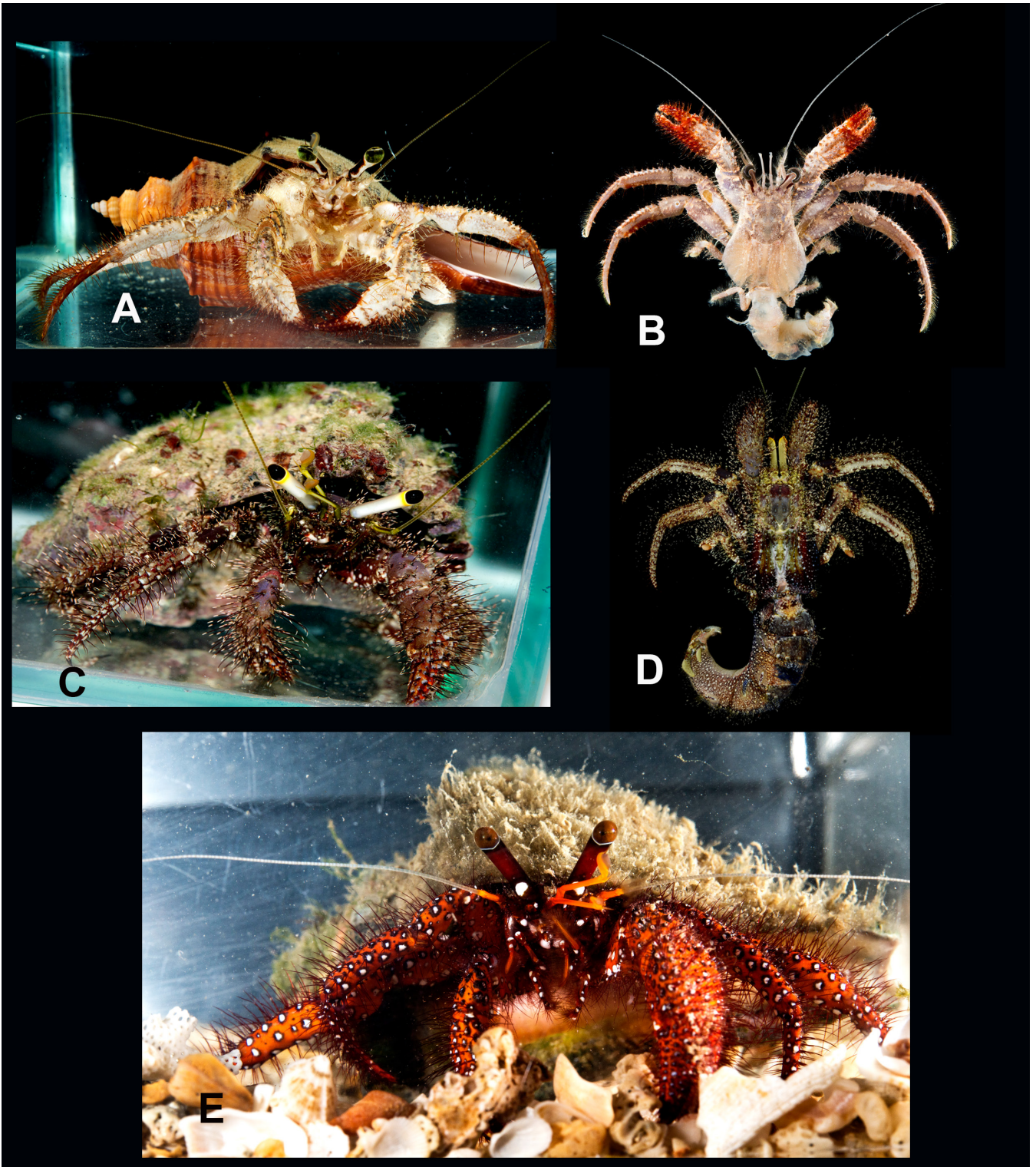


Fig. 2. A, B, *Dardanus hessii* (Miers, 1884), male, 13.8 mm (ZRC 2021.0105), B, photo from Rahayu & Ong, 2015; C, D, *Dardanus lagopodes* (Forskål, 1775), male, 14.9 mm (ZRC 2021.0106); E, *Dardanus megistos* (Herbst, 1804), not measured, St John's Island, 2013.

Forest (1952)) were further grouped into the *Troglopagurus* group as defined by McLaughlin (2005), and the *pallascens* and *edwardsii* groups as defined by Asakura & Tachikawa (2010). At present, the genus *Diogenes* comprises 76 species, living in intertidal and subtidal areas, among coral rubbles, sand or mud substrates, distributed in the East Atlantic and Indo-West Pacific (absent in the Atlantic and the Pacific

coast of American continent) (Almon et al., 2021; Rahayu, 2021; Rahayu & Pratiwi, 2022). Previously 17 species of *Diogenes* were reported from Singapore (Lemaitre & Ng, 1996; Rahayu, 1996, 2015; McLaughlin & Clark, 1997; McLaughlin, 2002b). In this paper one specific taxon is revived, and three more species are added to the fauna of Singapore, of which one is new to science.

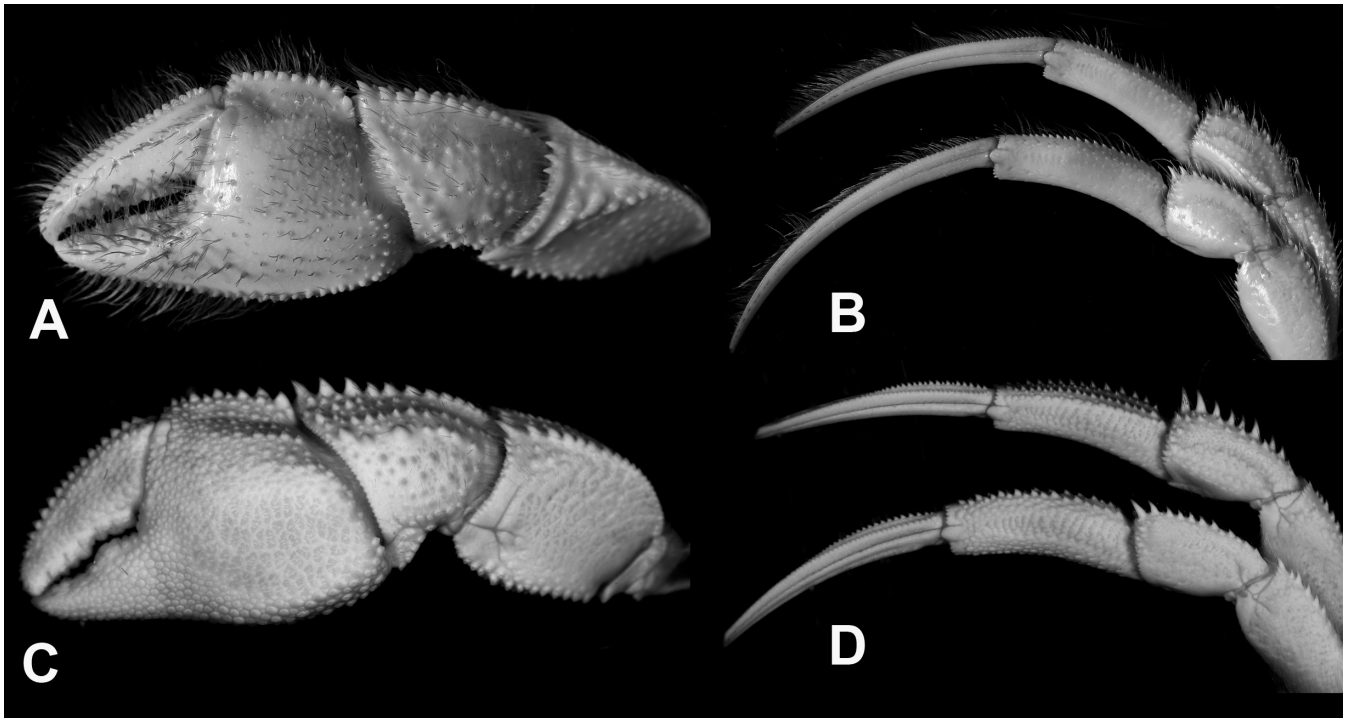


Fig. 3. A, B, *Diogenes mixtus* Lanchester, 1902, male, 8.0 mm (ZRC 2021.0111); C, D, *Diogenes planimanus* Henderson, 1893, male, 6.7 mm (ZRC 2021.0112). A, C, left cheliped, dorsal view; B, D, left P2 and P3, lateral view.

***Diogenes mixtus* Lanchester, 1902**
(Figs. 3A, B, 4A)

Diogenes mixtus Lanchester, 1902: 367, pl. 34, figs. 2, 2a, 2b (type locality: Pulau Bidan, Penang, Malaysia); Nobili, 1903: 16; McLaughlin & Clark, 1997: 45, figs. 7f, 8f, 9i, 13a; McLaughlin, 2002a: 424, figs. 5D, E, 6A.

Material examined. 2 males, 6.3–5.1 mm (ZRC 2021.0107), st. TB98, Eastern Bunkering A, 1°18.938'N 104°05.312'E, 30.2–33.6 m, 28 May 2013; 1 male, 5.8 mm (MZB Cru 5199), Coney Island, otter trawl, 10–15 m, 8 March 2012; 1 male, 2.0 mm (ZRC 2021.0108), st. DW28, Singapore Port Limit, Eastern Boarding Ground A, 1°13.181'N 103°52.900'E, 94.3–97.6 m, gravel, rock, 22 May 2013; 1 male, 3.1 mm (ZRC 1990.4088), Pulau Tekong, 27 March 1987; 1 male, 9.1 mm (ZRC 2021.0109), st. SW23, St John's Island, 1°13.120'N 103°51.417'E, intertidal, 21 May 2013; 1 ovigerous female, 5.7 mm (ZRC 2021.0110), DW17, Pulau Ubin, 1°25.110'N 103°55.722'E, 16 October 2012; 1 male, 8.0 mm (ZRC 2021.0111), DW40, opposite Changi Chalet Radar, 1°23.797'N 103°58.751'E, 21–15.6 mm, 19 October 2012.

Colour in life. In general, light cream or pinkish cream (Fig. 4A). Carapace mottled brown and cream; shield mottled cream, dark and light brown on middle of dorsal surface; antennal peduncle cream with streak of greenish brown on distal part of fifth peduncular segment; antennular peduncle cream, longitudinal brown stripe on dorsal surfaces of penultimate and ultimate segments; ocular peduncle cream with longitudinal dark brown stripes on dorsal and lateral surfaces. Chelipeds cream, streak of dark brown on dorsal surface of dactyl proximally, on middle of palm, and distal

part of carpus. P2 and P3 cream with streak of light brown on median part of propodi and carpi.

Distribution. Thailand, Malaysia, and Singapore; intertidal to depth of 97 m, on sandy, gravel-rock, and broken shell substrates.

Remarks. *Diogenes mixtus* belongs to the group 1 sensu Forest (1952), and is related to the six species, viz., *D. alias* McLaughlin & Clark, 1997, *D. custos* (Fabricius, 1798), *D. dubius* (Herbst, 1804), *D. miles* (Fabricius, 1787), *D. planimanus* Henderson, 1893, and *D. violaceus* Henderson, 1893 by the presence of bifurcate antennal acicle. Morphological characters that differentiate this species from the congeners include the deep bifurcate antennal acicles with the mesial and lateral forks reaching and well exceeding the distal margin of the fourth peduncular segment, the covering of sparse spines and stiff setae on the cheliped palms, with denser and longer tuft of stiff setae on the dactyl and fixed finger (Fig. 3A), and the long, slender dactyl of P2 and P3, and the presence of row(s) of small spines on the dorsal margin of the dactyls and propodi of P2 and P3 (Fig. 3B).

The living colour of the species is described and illustrated for the first time (Fig. 4A). The characteristic longitudinal stripes on the dorsal surface of the ocular peduncles, which are still preserved after preservation in ethanol, have already been mentioned by McLaughlin (2002a) for the specimens from Phuket. This species was reported from Singapore by Nobili (1903), but McLaughlin & Clark (1997) failed to re-examine Nobili's specimens, thus the occurrence in Singapore has been uncertain. This study confirms the presence of this species in Singapore waters.

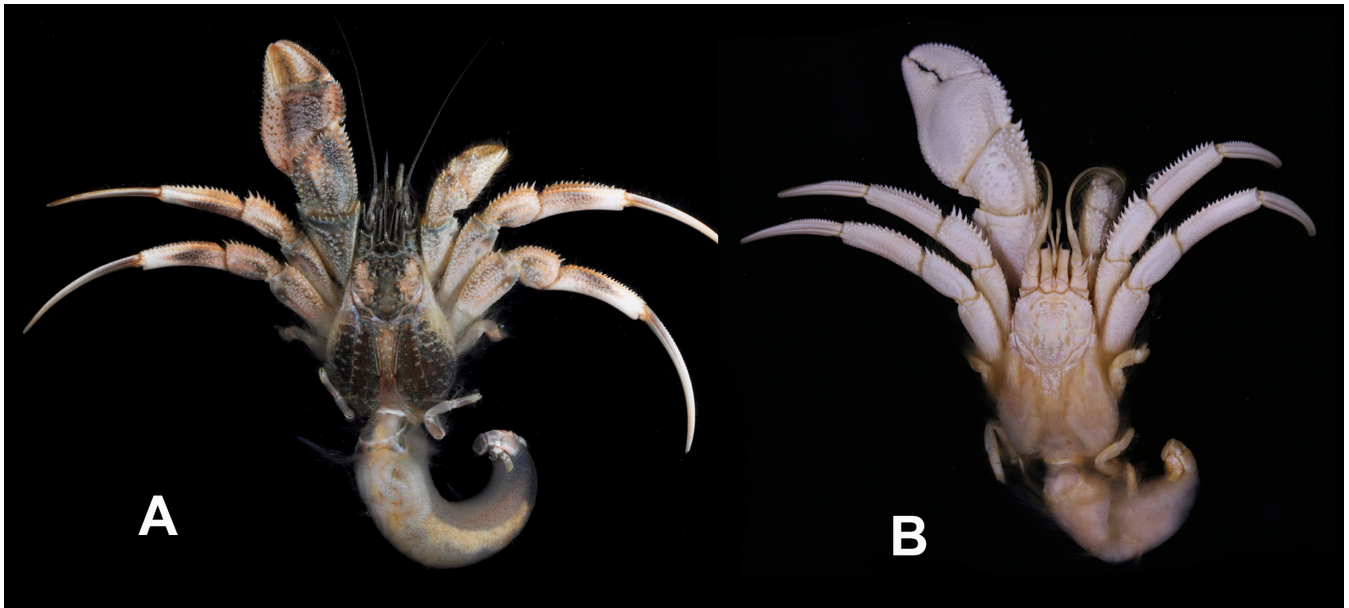


Fig. 4. A, *Diogenes mixtus* Lanchester, 1902, male, 8.0 mm (ZRC 2021.0111); B, *Diogenes planimanus* Henderson, 1893, male, 6.7 mm (ZRC 2021.0112).

***Diogenes planimanus* Henderson, 1893**
(Figs. 3C, D, 4B)

Diogenes planimanus Henderson, 1893: 416, pl. 39, figs. 5, 6 (type locality: Madras, India); Tirmizi & Siddiqui, 1982: 43, figs. 21, 22; Rahayu, 1996: 345, fig. 3; McLaughlin & Clark, 1997: 40, figs. 4a, 9c, e, 12a; McLaughlin, 2002a: 422, fig. 5A–C; Siddiqui, Kazmi & McLaughlin, 2004: 164, figs. 3, 4.

Material examined. 3 males, 4.0–6.7 mm, 1 female, 6.7 mm (ZRC 2021.0112), Red Cliff shoal area, Changi, 27 April 1982; 1 male, 8.44 mm (ZRC 2021.0113), Kranji Reservoir park, 1°26.27.9'N 103°44.16.26'E, 4 July 2009.

Distribution. Northern Arabian Sea, Bay of Bengal, Andaman Sea, Singapore, Malaysia, Gulf of Thailand, and northern Australia; intertidal to 7 m, inhabits sandy mud substrate.

Remarks. In having a shield that is denticulate over the entire length of its anterior margin, a weakly bifurcated antennal acicle, tuberculation of the chelipeds, the covering of tubercles on the lateral faces of the propodi, carpi, and meri, and the rows of spines on the dorsal surface of propodi and carpi of P2 and P3 (Fig. 3D), the present specimens agree well with the lectotype of *D. planimanus* redescribed by McLaughlin & Clark (1997) and specimens from Pakistan examined by Siddiqui et al. (2004). They differ from the lectotype in having only one spine on each side of the intercalary rostriform process (two or five spines on each side in the lectotype). Rahayu (1996), McLaughlin & Clark (1997), and Siddiqui et al. (2004) mentioned the presence of blunt or acute tubercles on the surface of the palm and fixed finger of the left cheliped. The tubercles on the outer surface of the palm and fixed finger of the left cheliped in the present specimens are more flattened, none of which are acute (Fig. 3C), however a prominent row of tubercles on

the outer surface of the carpus of the left cheliped is clearly indicated (Fig. 3C).

***Diogenes jubatus* (Nobili, 1903)**
(Figs. 5A–C, 6A, 7A, B)

Troglopagurus jubatus Nobili, 1903: 17 (type locality: Singapore). *Diogenes jubatus* Forest, 1952: 9; Lemaitre & Ng, 1996: 324, figs. 1–5; Rahayu, 1996: 344; McLaughlin, 2005: 601, 612, figs. 3, 4a–c.

Material examined. 1 male, 5.1 mm (ZRC 2021.0114), st. TB99, Eastern Bunkering A, 1°18.861'N 104°05.128'E, silt, 33.7–36.7 m, 28 May 2013; 1 male, 5.5 mm, 1 female, 5.5 mm (MZB Cru 5200), st. TB58, Around Tanah Merah, 1°16.808'N 103°58.246'E, mud, 38.7–39.9 m, 24 May 2013; 2 males, 1.1–3.1 mm (MZB Cru 5201), st. SW27, along seawall at south lagoon of St John's Island, 1°12.911'N 103°51.718'E, 0.5 m, 22 May 2013; 1 ovigerous female, 2.2 mm, 1 female, 2 mm (ZRC 2021.0115), st. SB55, Kusu Island, 1°13.9'N, 103°52'E, 4 m, 24 May 2013; 1 male, 1.5 mm, 1 female, 1.8 mm (ZRC 2021.0116), no locality; 1 female, 2.4 mm (ZRC 2021.0115), st. TB113, South of Sisters' Island, 1°12.001'N 103°50.261'E, rock, 29.3–30.5 m, 29 May 2013.

Diagnosis. Shield (Figs. 5A, 7A, B) as long as broad or very slightly broader than long, with few short tubercles and tufts of setae on dorsal surface; dorsal surfaces of branchiostegites unarmed or with few minute or miniscule spinules. Rostrum short, triangular, reaching level of lateral projections. Intercalary rostriform process vestigial or reaching proximal 0.20 of ocular acicles. Ocular peduncles 0.7–0.8 times as long as shield, dilated proximally, slightly tapering to cornea, with tufts of sparse setae on dorsal surface proximally; corneal diameter 0.2 times as long as ocular peduncle; ocular acicles each with 3–5 spines. Antennular

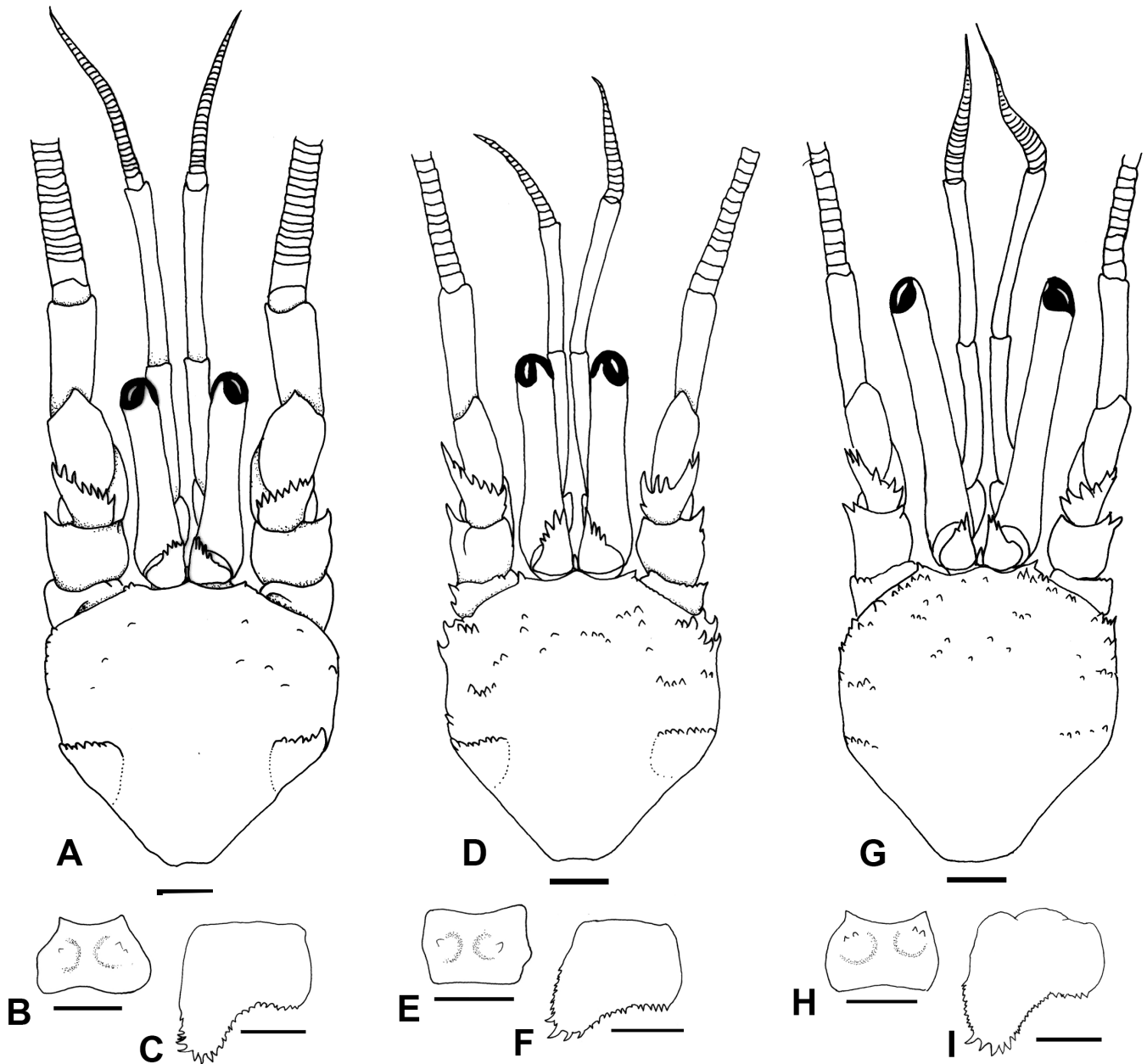


Fig. 5. A–C, *Diogenes jubatus* (Nobili, 1903), male, 5.1 mm (ZRC 2021.0114); D–F, *Diogenes platyops* Rahayu & Forest, 1995, male, 4.9 mm (ZRC 2021.0118); G–I, *Diogenes jousseaumei* (Bouvier, 1897), ovigerous female, 5.8 mm (ZRC 2021.0128). A, D, G, shield and cephalic appendages; B, E, H, anterior lobe of sternite of third pereopods; C, F, I, telson. Scale = 1 mm.

peduncle overreaching distal corneal margin by entire length of ultimate segment. Antennal peduncle stout, reaching mid-length of ultimate segment of antennular peduncle, reaching beyond distal corneal margin by 0.25 to entire length of fifth peduncular segment; antennal acicle relatively broad, short, not reaching half length of fourth segment, with 8–9 spines on oblique or truncate inner margin; flagellum with very long setae, primarily inserted ventrally. Left cheliped dactyl (Figs. 6A, 7A, B) with rows of strong spines on upper margin, and few granules, tubercles or spinules on outer surface; palm upper margin with tubercles or spines, lower margin with row of tubercles or spines continuing onto fixed finger, outer face with scattered small spines or tubercles; long plumose setae covering dactyl and palm entirely, concealing armature, those setae extending on inner face near upper and lower margin; carpus with numerous

tufts of setae, but not concealing armature, upper margin with row of acute or subacute spines, outer face with scattered spinules or spines, distal margin usually with row of spines. Right cheliped with chela completely masked by setae; dactyl usually with row of small spines or spinules on upper margin; palm and fixed finger unarmed; carpus with prominent spine on upper distal margin and one or two somewhat smaller spines on outer distal margin. P2 and P3 (Figs. 6A, 7A, B) with dactyls equal to 1.5 times as long as propodi, unarmed, except for small dorsodistal spine on each carpus and occasionally few tubercles or spinules on ventral margins of meri of P2; left P3 covered entirely with dense setae, while left P2, right P2 and P3 with less dense setae. Sternite of third pereopods (thoracic sternite 6) subquadrate (Fig. 5B), anterior lobe subsemicircular with median longitudinal depression, armed with spinules and/or



Fig. 6. A, *Diogenes jubatus* (Nobili, 1903), male, 5.1 mm (ZRC 2021.0114); B, *Diogenes platyops* Rahayu & Forest, 1995, male, 4.9 mm (ZRC 2021.0118). A, B, left cheliped, P2 and P3.

with central tubercle(s) on either side of median depression. Telson (Fig. 5C) with left posterior lobe strongly produced, right very short, terminal margins each with series of small to moderately large spines, strongest at outer angles and on left extending onto lateral margin.

Colour in life. Shield generally cream, mottled with brown and dark brown, setae white. Ocular peduncles dark brown or black with white streak proximally and distally, corneas black. Antennular peduncle penultimate segment cream with black streak proximally, ultimate segment and flagella cream. Antennal peduncle first to fourth segments and antennal acicle brown, fifth segments and flagella cream. Cheliped mottled with cream and dark brown; P2 and P3 generally cream, with brown band on each segment (Fig. 7A, B).

Distribution. Malaysia and Singapore; at 0.5–39.9 m depth, on substrates consisting of mixture of rock, gravel, mud, and sandy mud.

Remarks. See Remarks section of *Diogenes platyops* for the taxonomic clarification.

Lemaitre & Ng (1996) described the colour of the dark parts of this species as “black”, but in the newly collected specimens the dark parts are attributed as dark brown. The colour pattern is quite consistent between the present specimens and those described by Lemaitre & Ng (1996).

Diogenes platyops Rahayu & Forest, 1995

(Figs. 5D–F, 6B, 7C, D)

Diogenes platyops Rahayu & Forest, 1995: 399, fig. 4a–h (type locality: Pari Island, Jakarta Bay, Indonesia); Lemaitre & Ng, 1996: 330; Rahayu, 1996: 348.

Diogenes jubatus McLaughlin, 2005: 612 (part), fig. 3.

Material examined. 1 male, 4.9 mm (ZRC 2021.0118), st. SD133, South of Kusu Island, hand collecting, dive, 11 m,

31 May 2013; 1 female, 3.3 mm (ZRC 2021.0119), TB142, east Johor Strait, 1°17.838'N 104°04.157'E, beam trawl, mud, gravel, dead shell, 28.8 m, 31 May 2013; 1 female, 2.5 mm, 3 males, 2.2–3.3 mm (ZRC 2021.0120), st. DR174, near Kusu Island, 1°12.202'N 103°52.178'E, rectangular dredge, mud and gravel, 79.6–135 m, 4 June 2013; 1 female, 2.4 mm, st. TB185, Pulau Senang, 1°09.942'N 103°43.458'E, beam trawl, mud, 24.5 m, 5 June 2013; 2 males, 1.1–2.4 mm, 5 individuals in shell (ZRC 2021.0121), st. DR184, beside Raffles light house, 1°09.280'N 103°44.049'E, rectangular dredge, rock, sand, shell fragment, 31.6–35.4 m, 5 June 2014; 2 males, 0.9–1.6 mm, 1 female, 1.5 mm (MZB Cru 5217), st. DR128, beside Eastern Boarding Ground, 1°09.942'N 103°43.458'E, 30 May 2013; 1 male, 2.4 mm, 1 female, 1.5 mm (MZB Cru 5218), st. DR161, beside St John's Island, 1°12.843'N 103°51.449'E, 44.4–41.2 m, gravel, 13 June 2013; 1 female, 2.4 mm (ZRC 2021.0122), st. TB113, South Sister Island, 1°09.942'N 103°43.458'E, rock, 29.3–30.5 m, 29 May 2013; 1 female, 2.2 mm (ZRC 2021.0123), st. TB91, near St John's Island, 1°12.561'N 103°51.322'E, rock, 46.1–72 m, 27 May 2013; 1 male, 2.3 mm (ZRC 2021.0124), SEA8139, Singapore; 2 males, 2.8–4.0 mm, 1 ovigerous female, 3.5 mm (ZRC 2021.0125), SEA8128, 01°14.803'N 103°54.173'E, 41–45 m, 13 May 2013; 1 female, 3 mm (ZRC 2021.0126), 01°14.414'N 103°54.491'E, sand, rock, 61–68 m, 13 May 2013; 2 males (ZRC 2021.0127), st. TB91, Southern Fairway near St John's Island, 1°12.561'N 103°51.946'E, rectangular dredge, sandy, broken shell, laterite gravel, 48.3–49.7 m, 27 May 2013.

Diagnosis. Shield (Figs. 5D, 7C) 1.1–1.2 times as long as broad, with sparse tubercles and scattered long setae on dorsal surface; dorsal surface of branchiostegites with 4–5 small spines. Rostrum short, rounded, reaching level of lateral projections. Intercalary rostriform process vestigial, or reaching proximal 0.20 of ocular acicles. Ocular peduncles 0.7–0.8 times as long as shield, dilated proximally, very slightly inflated distally, with long, dense plumose setae on dorsal surface subproximally; corneal diameter 0.1–0.2 times

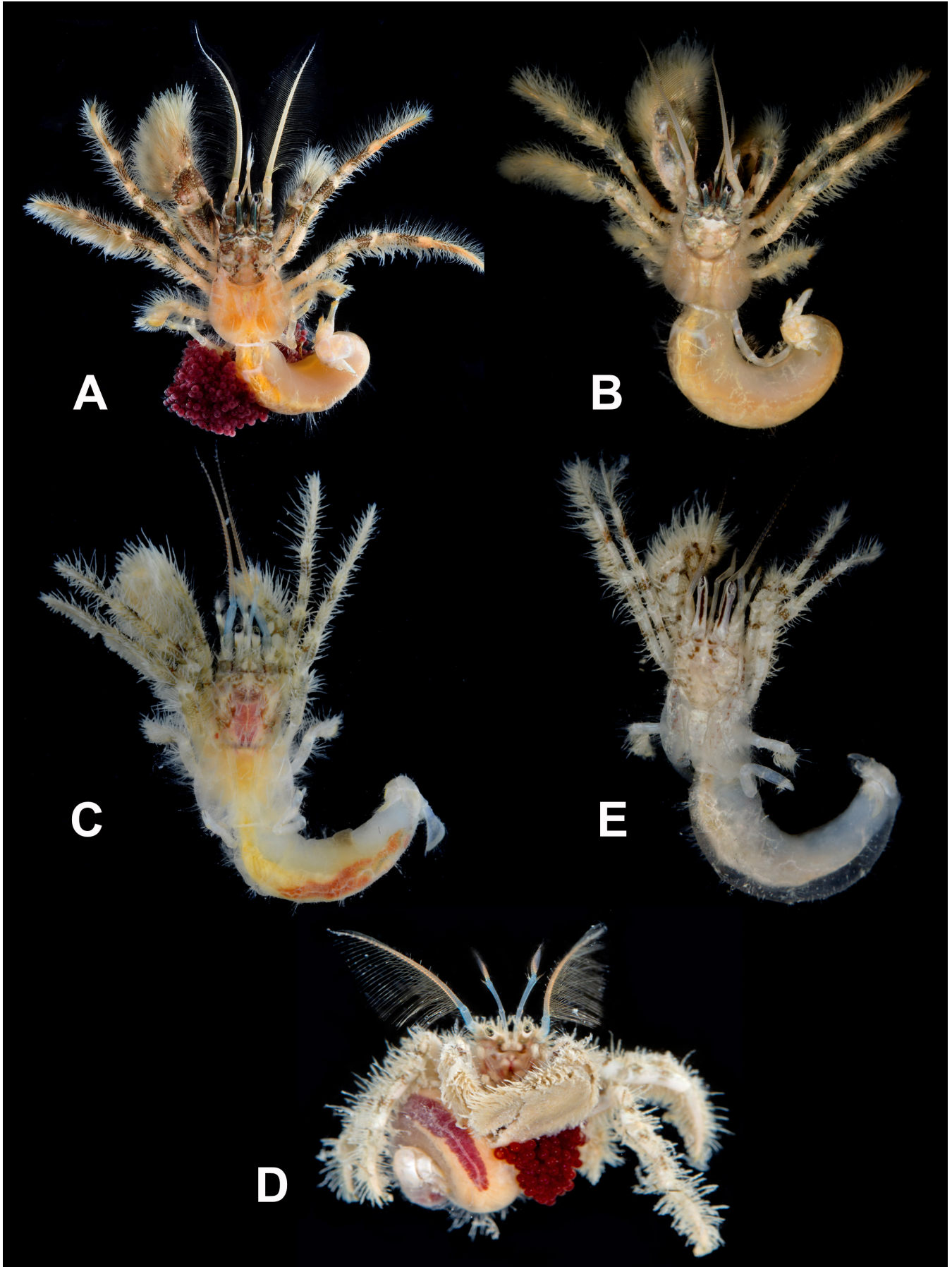


Fig. 7. A, B, *Diogenes jubatus* (Nobili, 1903); A, ovigerous female, not collected, Johor Strait, 21 October 2012; B, male, 5.1 mm (ZRC 2021.0114); C, D, *Diogenes platyops* Rahayu & Forest, 1995; C, male (not collected), st. TB29, Singapore Strait, 01°13.036'N 103°52.820'E, 22 May 2013; D, ovigerous female, 3.5 mm (ZRC 2021.0125); E, *Diogenes jousseaumei* (Bouvier, 1897), male, 2.2 mm (ZRC 2021.0129).

as long as ocular peduncles; ocular acicles elongate, each with 3–5 strong spines. Antennular peduncles overreaching distal corneal margin by two thirds or entire length of ultimate segment. Antennal peduncles slender, reaching mid-length of ultimate segment of antennular peduncle, reaching beyond distal corneal margin by half length of fifth peduncular segment; antennal acicles relatively narrow, short, slightly overreaching mid-length of fourth peduncular segment, with 5–6 strong mesial spines on oblique inner margin. Flagellum with very long and dense setae, primarily inserted ventrally. Left cheliped dactyl (Figs. 6B, 7D) broad, not recurved, slightly flattened, with row of calcareous-tip spines on upper margin, and few tubercles on outer surface; palm with row of strong spines on both upper and lower margins, continuing onto fixed finger, at ventroproximal angle row of spines parallel with carpal articulation curving distally along midline, terminating abruptly at about 0.2 proximal of palm; longitudinal furrow adjacent to upper margin, outer surface with scattered tubercles; long plumose setae on upper and lower margins of dactyl, palm, and fixed finger, outer surface pubescent, obscuring armature; carpus with numerous long setae but not obscuring armature, upper margin with row of strong spines, outer face with scattered tubercles. Right cheliped with chela entirely masked by long, plumose setae; dactyl with row of small spines on upper margin, palm with one dorsodistal spine followed by denticles; fixed finger with row of small spines on ventral margin; carpus with upper margin denticulate; longitudinal furrow adjacent to upper margin of palm and carpus. Left P3 more robust than P2, right P2, P3 (Fig. 7C, D) with dactyl about same length as propodi, unarmed except for minute dorsodistal spinule on each carpus, and occasionally two or three denticles on proximodorsal margin of carpus of left P2; dactyl and propodus of left P3 slightly compressed laterally, abundant long, plumose setae on dorsal and ventral margins, lateral surfaces pubescent (Fig. 6B); left P2, right P2, P3 with less dense setae on dorsal and ventral margin, lateral surface with few tufts of setae. Sternite of third pereopods (thoracic sternite 6) squarish (Fig. 5E), anterior lobe subsemicircular with median longitudinal depression, armed with spinules and/or with central protuberance on either side of depression. Telson (Fig. 5F) with left posterior lobe produced, right slightly shorter than left, median cleft barely indicated; terminal margin with series of small to moderately large spines, strongest at outer angle, on left extending onto lateral margin.

Colour in life. Shield cream or pinkish white mottled with brown and light pink, setae white. Ocular peduncle white with greenish brown blotch on half proximal. Antennular peduncle penultimate segment white, ultimate segment and proximal part of flagella blue, distal part of flagella orange. Antennal peduncle second segment brown, fourth, fifth segments and proximal part of flagella blue, rest of flagella light orange. Cheliped mottled with cream and dark brown; P2 and P3 cream with greenish brown blotch dorsoproximally on each segment (Fig. 7C, D).

Distribution. Indonesia and Singapore; at 24–135 m depth, on mud, sand, gravel substrates.

Remarks. McLaughlin (2005) demonstrated that the characters used to separate the species in the *Troglopagurus* group of *Diogenes* are mostly unreliable as they are variable depending or not, on the size and sex of individuals. These characters include the relative length of the ocular peduncles against the shield, the corneal diameter against the length of the ocular peduncles, the relative length of the antennular and antennal peduncles against the length of the ocular peduncles, the relative length of the dactyl against the propodus in the P2 and P3, the setation on the left P3 dactyl and propodus, and the armature on the ocular acicle. Based on the variability of these presumably diagnostic characters, she considered that *D. platyops* was a junior subjective synonym of *D. jubatus*. Furthermore, she gave three characters that are useful to distinguish species of the *Troglopagurus* group: the live colouration, the shape of the anterior lobe of the sternite of the third pereopods, and the asymmetry of the telson.

Examination of the specimens initially identified as *D. jubatus* in this study revealed two separable forms on the basis of the living colouration and the setation of the chelipeds and ambulatory legs. The first form is characterised by the following attributes: shield cream mottled with brown and dark brown; ocular peduncles dark brown or black with white band on proximal area and on area just proximal to cornea; ocular acicle white; penultimate segment of antennular peduncles, first to fourth segments of antennal peduncle, and antennal acicle dark brown with some white spot; penultimate segment of antennular peduncles, and fifth segment and flagellum of antenna cream; ground colour of chelipeds and pereopods cream to white with mottling of dark brown or light brown on proximal part of palms, most of carpi and meri of chelipeds, dactyls, median parts of propodi, carpi, and meri of P2 and P3 (Fig. 7A, B); left cheliped covered with long, sometimes plumose setae on margins and entire surface of fingers and palm, obscuring armature; dactyl and propodus of left P3 covered with dense, long plumose setae on dorsal, lateral, and ventral surfaces; carpus and merus having fewer setae (Figs. 6A, 7A, B). The second form is characterised by the following attributes: shield cream or pinkish white mottled with brown and light pink; ocular peduncle with distal half white, greenish brown blotch proximally; ocular acicle also white; antennular peduncles blue; antennal peduncles generally dark brown, third and fourth segments with blue tinge on brown; fifth segment blue, flagellum orange; antennal acicle white; ground colour of chelipeds and pereopods cream to white with mottling of greenish brown or light brown on proximal part of propodi, carpi, and meri (Fig. 7C, D); margins of fingers and palm of left cheliped, and margins of dactyl and propodus of left P3 bearing fringe of long dense plumose setae, outer surface with short pubescence, giving impression of flattened lateral surfaces of dactyls and propodus (Figs. 6B, 7D); carpus and merus covered with long, dense setae.

McLaughlin (2005) used the shape of the anterior lobe of the sternite of third pereopods to distinguish between *D. jubatus* and *D. jousseaumei*, while the asymmetry of the posterior lobes of the telson and the absence of row of spines on the

branchiostegites were used to distinguish between *D. jubatus* or *D. platyops* and *D. manaarensis*.

The specimens of the two forms studied here have distinctly asymmetrical posterior lobes of the telson and the subquadrate-shaped anterior lobe of the sternite of P3, although it is slightly more trapezoidal in the first form specimens (Fig. 5B, C, E, F), while branchiostegite is unarmed or with few minute spinules in *D. jubatus*, in contrast to *D. platyops* which has a row of four to five small spines. In addition to the differences mentioned above, other distinct morphological characters were also observed. The first form has the following features: shield as long as broad, or slightly broader than long; antennal peduncles stout, and left cheliped palm with outer surface armed with scattered small spines or tubercles. The second form has the following features: shield slightly longer than broad, antennal peduncles slender, and left cheliped with outer surface of palm armed with short row of spines medially not reaching articulation with dactyl, and with shallow longitudinal furrow between midline and upper margin. These two forms of colouration and setation, and morphological differences are not influenced by size and sex and could represent morphological markers for species discrimination.

Therefore, there is little doubt that the two forms recognised herewith represent two distinct species. The first form is referred to *Diogenes jubatus* because it closely agrees with the redescription of Lemaitre & Ng (1996), particularly in the living colouration and the setation of the chelipeds and pereopods. Although no information on the living colouration was available for *D. platyops*, the second form is considered to represent *D. platyops*, resurrected from the synonymy of *D. jubatus*, because the setation of the chelipeds and ambulatory legs agrees well with that of the type specimens of the taxon.

Bathymetry range is overlapped between these two species, 24–135 m for *D. platyops* and 0.4–39.9 m for *D. jubatus*, but they do not live sympatrically.

Diogenes jousseaumei (Bouvier, 1897)

(Figs. 5G–I, 7E)

Troglopagurus jousseaumei Bouvier, 1897: 231, fig. 6 (type locality: Red Sea); Nobili, 1906a: 79, 81 (key); 1906b: 120.

Diogenes senex – Lankester, 1902: 366 (Not *Diogenes senex* Heller, 1865).

Diogenes jousseaumei – Forest, 1952: 8, fig. 15; Morgan, 1987b: 179; Morgan & Forest, 1991: 677, fig. 11; McLaughlin, 2005: 609, figs. 1d–f, 2.

Diogenes setocristatus Morgan & Forest, 1991: 665, figs. 7, 8 (type locality: Southwest Peel Island, Southwest Queensland, Australia).

Diogenes stenops Morgan & Forest, 1991: 671, figs. 9, 10 (type locality: Cape Bowling Green, Queensland, Australia); Rahayu, 1996: 349; McLaughlin & Clark, 1997: 43, figs. 7a, 9g, 13b; Rahayu & Hurtle, 2002: 617.

Not *Troglopagurus jousseaumei* – Alcock, 1905b: 75, pl. 5, fig. 6 (in part). = *Diogenes manaarensis* (Henderson, 1893), and *D. persicus* (Nobili, 1905) (misspelling of *jousseaumei*).

Not *Troglopagurus jousseaumei* – Thompson, 1943: 416. = *Diogenes persicus* (Nobili, 1905).

Material examined. 1 ovigerous female, 5.8 mm (ZRC 2021.0128), st. 4815TB1, Along Sentosa, beside Rasa Sentosa, 1°15.232'N 103°48.475'E–1°14.910'N 103°48.825'E, 20.1–17.7 m, sand, 11 January 2013; 1 male, 3.3 mm (MZB Cru 5204), st. TB 98, Eastern Bunkering A, 1°18.938'N 104°05.312'E, 33.6–30.2 m, broken shell, silt, 28 May 2013; 1 male, 2.2 mm (ZRC 2021.0129), st. 5416TB2, Outside Tanjung Rhu, 01°23.500'N 103°59.500'E, 22.7–23.7 m, 14 January 2013.

Colour. Shield cream mottled with greenish brown; ocular peduncles creamy white with dark brown longitudinal stripe dorsally, cornea silvery black; chelipeds cream with brown streak on palm, carpus, and merus with brown band medially. P2 and P3 creamy white, with brown band proximally on dactyls, medially and proximally on propodi, medially on carpi and meri (Fig. 7E).

Distribution. From the Red Sea to Thailand, Singapore, Malaysia, Indonesia, and Australia (Northern Territory, Queensland, and Western Australia); subtidal, 10–150 m, on sandy, mud substrate.

Remarks. The colour in life of the specimens in this study agrees well with Haig & Ball (1988) for the specimens from Arafura. Rahayu & Hurtle (2002) gave the description of the colour in life of this species as *D. stenops*. Among the species of *Diogenes* in the *Troglopagurus* group, *D. jousseaumei* is recognisable by the long and slender ocular peduncle, which is as long as or slightly longer than the shield, and the presence of a longitudinal stripe on the dorsal surface, which persists in preserved specimens (Figs. 5G, 7E). This species was already recorded from Singapore waters as *D. stenops* by Rahayu (1996).

Diogenes avarus Heller, 1865

(Fig. 8A)

Diogenes avarus Heller, 1865: 83, pl. 7, fig. 2 (type locality: Nicobar Island); Alcock, 1905b: 68, pl. 6, figs. 6–6a; Forest, 1956a: 524, figs. 1–4; Rahayu & Forest, 1995: 398, fig. 2b, g, h; Rahayu, 1996: 340; McLaughlin & Clark, 1997: 39, figs. 3b, 8b, 9b–d; McLaughlin & Dworschak, 2001: 143, figs. 9–12; McLaughlin, 2002a: 416, fig. 3A–C; Siddiqui, Kazmi & McLaughlin, 2004: 191, fig. 16.

Diogenes rectimanus – Lankester, 1902: 366 (in part) (not *Diogenes rectimanus* Miers, 1884).

Diogenes pugilator – Bouvier, 1892: 55; Nobili, 1903: 16; 1906a: 76 (not *Diogenes pugilator* Roux, 1829).

Material examined. 4 males, 1.0–2.0 mm, 5 ovigerous females, 2.0–2.5 mm (ZRC 2021.0175), st. SW53, Seringat Kias, artificial lagoon, 1°13.630'N 103°51.218'E, hand collecting, sandy beach, seagrass, 24 May 2013; 1 male, 2.2 mm (ZRC 2021.0176), Sungai Loyang, River mouth of Pasir Ris Park, 25 May 2012; 3 males, 2.2–3.6 mm (ZRC 2021.0177), Seletar, Yishun avenue, 8 January 2012; 7 males, 1.1–2.7 mm, 6 ovigerous females, 1.45–2.4 mm (MZB Cru 5212), st. MF63, Pulau Senang, 1°10.469'N 103°44.183'E, 30 June 2012; 15 males, 1.6–3.4 mm, 5 ovigerous females, 2.2–2.9 mm (MZB Cru 5213), st. MF29, Seletar, North shore

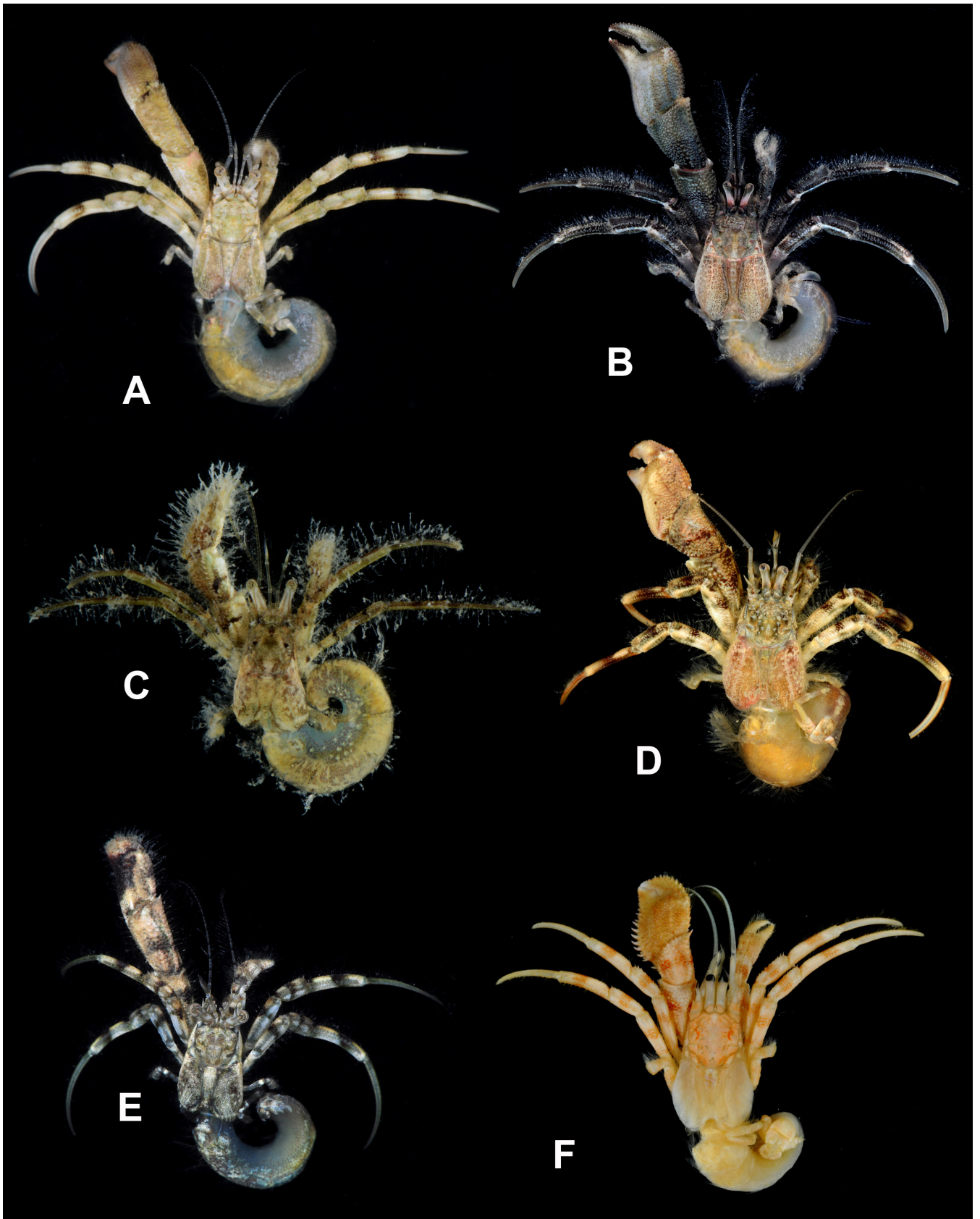


Fig. 8. A, *Diogenes avarus* Heller, 1852, not collected, IT86, Cyrene Reef, 1°15.374'N 103°44.816'E, 27 May 2013; B, *Diogenes fasciatus* Rahayu & Forest, 1995, male, 5.3 mm (ZRC 2021.0132); C, *Diogenes klaasi* Rahayu & Forest, 1995, male, not collected, Singapore Strait; D, *Diogenes laevicarpus* Rahayu, 1996, male, 5.1 mm (ZRC 2021.0139); E, *Diogenes moosai* Rahayu & Forest, 1995, male, 1.8 mm (ZRC 2021.0160); F, *Diogenes rectimanus* Miers, 1884, male, not collected, DW58, East of Pulau Tekong, 01°25.064'N 104°04.992'E, 10.9–11.3 m, 22 October 2012.

of Yishun Avenue 1, 13 August 2011; 8 males, 2.2–3.5 mm, 3 females, 2.7–3.5 mm, 5 ovigerous females, 2.0–4.0 mm (ZRC 2021.0178), st. IT87, Pulau Semakau, 01°12.480'N 103°45.333'E, intertidal, 27 May 2013; 1 male, 2.9 mm, 2 ovigerous females, 2.2–2.5 mm, st. M24, Pulau Ketam, mudflat, 8 March 2012; 3 males, 1.8–2.7 mm, 1 ovigerous female, 2.00 mm (ZRC 2021.0179), st. MF54, St John's Island, 01°13.298'N 103°50.903'E, mudflat, 13 April 2012; 2 males, 1.1–1.6 mm, 1 ovigerous female, 1.6 mm (MZB Cru 5211), st. SW101, Pasir Ris, Sungei Tampines River mouth, 01°22.910'N 103°57.232'E, 27 October 2012; 2 males, 1.5 mm, st. DW39, off Pulau Ubin, 01°23.608'N 103°58.355'E, 22–24 m, 19 October 2012; 2 ovigerous females, 2.2–2.4 mm (ZRC 2021.0180), st. SW117, 01°23.619'N 103°59.441'E, 5–9.9 m, 29 October 2012; 16 males, 0.8–1.7 mm, 1 female, 1.3 mm, 8 ovigerous females, 1.0–2.5 mm (ZRC 2021.0181), st. DW40, 01°23.797'N 103°58.751'E, Changi, 15–26 m, 19 October 2012; 1 male, 3.4 mm (ZRC 2021.0182), st. D22, Pulau Ubin, 8 March 2012; 2 males, 3.3–2.5 mm, st. IT124, Terumbu Pampang Laut, 1°13.912'N 103°43.402'E, 30 May 2013; 3 ovigerous females, 2.00 mm (ZRC 2021.0183), Chek Jawa, Pulau Ubin, 21 September 2001; 6 males, 2.2–3.8 mm (ZRC 2021.0184), st. MF24, Tuas, 6 July 2011; 8 males, 1.4–2.5 mm, 3 ovigerous females, 1.8 mm (ZRC 2021.0185), st. SW75, St John's Island, 25 May 2013; 3 males, 2.4–3.1 mm, 4 ovigerous females, 2.0–2.5 (ZRC 2021.0186), Kranji Reservoir Park, 01°26.90'N 103°16.26'E, 5 July 2009; 1 male (sl 2.4 mm), st. MF26, off Pulau Pergam, 19 July 2011; 1 male, 2.5 mm (ZRC 2021.0187), st. SW10, Pulau Ubin, Sungei Besar, 01°25.151'N 103°57.196'E, 16 October 2012; 1 male, 2.2 mm (ZRC 2021.0188), Sungei Jurong, along Jalan Papan, 19 August 2011; 14 males, 1.6–3.1 mm, 10 ovigerous females, 1.8–2.2 mm (ZRC 2021.0189), Changi, 18 January 1995; 6 males, 1.4–2.9 mm, 1 female, 2.4 mm (ZRC 2021.0190), st. MF40, Pulau Semakau, 10 November 2011; 1 male, 2.9 mm, st. MF9, Pulau Ubin, 13 May 2011; 20 males, 2.0–3.3 mm, 1 female, 2.2 mm (ZRC 2021.0191), st. MF52, Changi creek, 12 April 2012; 1 male, 2.7 mm (ZRC 2021.0192), st. IT120, Pulau Hantu, 30 May 2011; 1 male, 2.2 mm, st. MF59, Sungei Loyang, 25 May 2012; 1 male, 3.3 mm (ZRC 2021.0193), st. MF48, Sarimbun Beach, 01°26.279'N 103°41.915'S, 14 February 2012; 2 males, 2.4 mm (MZB Cru 5214), Sentosa beach, 16 July 2010; 1 male, 2 mm, 1 ovigerous female, 1.6 mm (ZRC 2021.0194), st. IT101, St John's Island, 29 May 2013; 7 males, 1.8–2.2 mm, 6 ovigerous females, 1.5–1.8 mm (MZB Cru 5210), MF38, Pulau Ubin, 26 September 2011; 7 males, 1.8–3.3 mm, 1 ovigerous female, 2.4 mm (ZRC 2021.0195), Pulau Semakau, 11 September 2010; 1 male, 1.3 mm, st. DW120, Johor Strait, 20.6–21.4 m, 29 October 2012; 7 males, 1.8–3.1 mm, 1 ovigerous female, 2.2 mm (ZRC 2021.0196), Pulau Semakau, 31 July 2010 and 11 September 2010.

Colour. Shield mottled light and dark yellowish brown; ocular peduncles white with greenish brown speckled medially, yellowish brown band proximally and distally adjacent to corneas, cornea dark brown; chelipeds light brownish yellow, white on dactyl, fixed finger, and lateroventral surface of palm; P2 and P3 light brown, dactyls white, propodus with

transverse brown band medially, carpi and meri mottled with light and dark brown (Fig. 8A).

Distribution. From Red Sea, East Africa across Indian Ocean to Malaysia, Thailand, Singapore, Indonesia, and Australia; intertidal, inhabit sandy, mud substrate.

Remarks. Thanks to the redescription by McLaughlin & Dworschak (2001), the diagnostic characters of *D. avarus* are clarified. Those include: relatively short ocular peduncle, about 0.6 times as long as shield with the corneal diameter 0.4 times as long as the ocular peduncle; the presence of proximo-medially weak crest of spines or tubercles (not continuing to the articulation with the dactyl) on the outer surface of the palm of the left cheliped; the presence of row(s) of spines on the dorsal margin of the propodus and carpus of P2; similar row of spines usually, but not always, on the dorsal margin of the propodus and carpus of P3; and a noticeable hiatus between fingers of the right cheliped.

Most of the specimens examined in this study have dorsally unarmed propodi of P2 and P3; the carpi of P2 and P3 bear a row of spines on each dorsal margin, although the spines are smaller and fewer on the P3. The ocular peduncles also vary from stout (0.7 times as long as the shield with the corneal diameter 0.2 times as long as the ocular peduncle) to slender (0.9 times as long as the shield with the corneal diameter 0.3 times as long as the ocular peduncle). Nevertheless, the specimens from Singapore agree well with *D. avarus* in other diagnostic characters cited above (McLaughlin & Dworschak, 2001).

Diogenes fasciatus Rahayu & Forest, 1995 (Fig. 8B)

Diogenes fasciatus Rahayu & Forest, 1995: 388, fig. 1 (type locality: Muara Karang, Jakarta Bay, Indonesia); Rahayu, 1996: 340; Siddiqui, Kazmi & McLaughlin, 2004: 185, fig. 13.

Material examined. 96 males, 0.7–2.9 mm, 5 females, 1.8–2.5 mm, 20 ovigerous females, 1.8–2.5 mm (ZRC 2021.0130), Changi, 18 January 1995; 20 males, 2.4–4.2 mm, 12 females, 1.6–2.4 mm, 20 ovigerous females, 1.6–2.9 mm (ZRC 2021.0131), Changi, 16 February 1995; 8 males, 2.3–5.3 mm (ZRC 2021.0132), DW58, East of Pulau Tekong, 01°25.064'N 104°04.992'E, 10.9–11.3 m, 22 October 2012; 15 males, 1.6–2.2 mm, 4 females, 1.6–2.0 mm, 5 ovigerous females, 1.8–2.0 mm (ZRC 2021.0133), Chek Jawa, 21 September 2001; 1 male, 1.0 mm (ZRC 2021.0134), Pulau Hantu, 7–10 m, 16 December 2012; 1 male, 3.9 mm (ZRC 2021.0135), st. M24, Pulau Ketam, 8 March 2012; 1 ovigerous female, 4.5 mm (ZRC 2021.0136), st. M13, Pulau Ubin, 7 March 2012; 7 males, 4.5–6.0 mm (ZRC 2021.0137), Changi, beach seine, 16 July 1993; 3 males, 3.1–4.2 mm, 3 females, 2.5–3.5 mm, Perak, Malaysia.

Colour in life. Shield mottled with dark grey and light brown. Ocular peduncle white with greyish brown blotch on dorsomesial face distally, light brown patch proximally.

Antennular peduncle generally greyish brown, with dark brown band on distal margin of ultimate and penultimate segments, flagella white; first to fourth segments and antennal acicle of antennal peduncle greyish brown, fifth segment and flagella white. Chelipeds palm whitish grey; dactyl and fixed finger with tint of light brown, carpi and meri dark brown or dark grey. P2 and P3 dark brown or dark grey, lighter grey dorsally and ventrally on propodi and carpi, with white spot on articulation dactyl, propodus and carpus (Fig. 8B).

The general colouration in life varies from yellowish light brown to dark brown or dark grey, but the pattern is the same.

Distribution. Pakistan, Singapore, Malaysia, and Indonesia; 0–7 m, inhabit sandy, muddy substrate.

Remarks. Among the species in the *edwardsii* group, this species is readily recognised by an ensemble of characters as follows: antennal peduncles stout, flagellum with abundant setae; left cheliped dactyl broad, flattened, covered with small tubercles; fixed finger outer surface tuberculate and devoid of longitudinal ridge; and palm with row of strong spines on upper and lower margins, at proximoventral angle row of strong spines parallel to carpal articulation, reaching to distal quarter, then continued as longitudinal row/rows of small spines on outer surface. The differences between *D. fasciatus*, *D. avarus* Heller, 1865, and *D. investigatoris* Alcock, 1905b were already discussed by Rahayu & Forest (1995), and the significance of those characters has been confirmed. The flattened dactyl of the left cheliped and the presence of a row or rows of spines on the propodi of P2 and P3 placed *D. fasciatus* close to *D. lophochir* Morgan, 1989. But these two species differ in the presence of pronounced ridge on the fixed finger of the left cheliped in *D. lophochir* (absence in *D. fasciatus*), the tuberculate crest on the outer face of the palm of the left cheliped is positioned in the midline in *D. lophochir* while in *D. fasciatus* this crest is located adjacent to upper margin.

Rahayu & Forest (1995) did not mention the presence of row of spines on the dorsal margin of the propodi of P2 and P3 but indicated that the spines on the carpi are present only in the large individual. Siddiqui et al. (2004) stated that these spines are present or absent in their material and that the specimens from Pakistan have one or two rows of spines on carpi, while Asakura (2020) stated that, in the material from Singapore and Thailand, the dorsal margins of propodi of ambulatory legs have a row of spines, and also figured the spines on the dorsal margin of carpi (Asakura, 2020: fig. 11A, C, E). In some specimens in this study, the propodi and carpi of P2 and P3 have one or two rows of spines on the dorsal margin. Additionally, a tiny spine on the dorsodistal margin of the fourth segment of the antennal peduncles was also detected in some individuals. The spines on the mesial margin of the antennal acicle varies from very prominent to moderately large, and one additional spine is sometimes present at the midlength of the lateral margin. The same character was also observed by Asakura (2020)

in his specimens. Further study is necessary to confirm that these characters mentioned above are merely attributed to intraspecific variations or interspecific differences.

***Diogenes inglei* McLaughlin & Clark, 1997**
(Fig. 9A, B)

Diogenes inglei McLaughlin & Clark, 1997: 34, figs. 1, 2 (type locality: Blakang Mati, Singapore).

Material examined. 1 male, 1.1 mm (ZRC 2021.0197), st. DR87, Outside Tanjong Rhu, 1°16.899'N 103°53.825'E, sand, mud, 19.5–20.7 m, 4 November 2012; 1 female, 1.6 mm (ZRC 2021.0198), st. TB5, beside Sebarok, 1°10.5'N 103°46.512'E, rocky bottom, 63.8–64.1 m, 20 May 2014; 1 ovigerous female, 2.4 mm (ZRC 2021.0199), st. DR208, East of Semakau, South of Sebarok, 1°11.149'N 103°47.702'E, rock, barrel sponge, 17.4–24.7 m, 24 September 2013; 1 female, 1.8 mm (ZRC 2021.0200), no locality; 1 male, 1.1 mm (ZRC 2021.0201), 2 ovigerous females, 1.3–1.8 mm (ZRC 2021.0201), st. TB113, South of Sisters' Island, 1°12.001'N 103°50.261'E, rocky bottom, 29.3–30.5 m, 29 May 2013; 1 female, 1.6 mm (ZRC 2021.0202), st. DR174, near Kusu Island, 1°12.202'N 103°52.178'E, red clay, dead shell, 79.6–135 m, 4 June 2013.

Colour in life. Shield mottled with cream and light brown, with two brown spots proximally; ocular peduncle cream with red longitudinal stripes on dorsal and mesial faces; chelipeds mottled with cream and light brown, dactyl and fixed finger greenish brown; P2 and P3 cream, almost transparent, with greenish brown broad band, proximally on dactyls and carpi, subdistally and proximally on propodi, and medially and proximally on meri (Fig. 9A, B).

Distribution. At present known only from Singapore; 17–135 m, on rocky substrate.

Remarks. This is the first record of the species after its description and also the first discovery of male specimens. The species is very characteristic in having tapering corneas, short antennal acicles, and subequal posterior lobes of the telson. McLaughlin & Clark (1997) described this species on the basis of four female specimens collected in Singapore in 1899. The female specimens examined in this study agree with the female type series. The male specimens differ from female specimens in its unarmed pleomere 6 (armed with a spine in female specimens, including the type specimens). The male pleopods are uniramous, typical of *Diogenes*. One specimen was found occupying the hole of a polychaete attached to a large rock (Fig. 9A).

***Diogenes klaasi* Rahayu & Forest, 1995**
(Fig. 8C)

Diogenes klaasi Rahayu & Forest, 1995: 395, fig. 3 (type locality: Balikpapan, Kalimantan, Indonesia); McLaughlin, 2002a: 419, fig. 3D–F; Siddiqui et al., 2004: 187, fig. 14; Rahayu, 2015: 183, figs. 1, 7A.

Material examined. 2 males, 1.5–2.2 mm, 1 female, 1.8 mm, 2 ovigerous females, 2.2 mm (ZRC 2021.0151), SW53, Seringat Kias, artificial lagoon, 1°13.630'N 103°51.218'E, hand collecting, sandy beach, seagrass, 24 May 2013; 1 male, 2.5 mm (ZRC 2021.0152), MF63, Pulau Senang, 01°10.469'N 103°44.183'E, mudflat, 30 June 2012; 2 males, 1.8–2 mm (MZB Cru 5203), st. SW155, north lagoon St John's Island, 1°13.116'N 103°51.079'S, 3 June 2013; 1 male, 2.4 mm (ZRC 1994.4412), Kallang basin, 15 December 1994.

Distribution. Persian Gulf, Pakistan, western Thailand, Singapore, Indonesia; intertidal, on rocky or sandy-muddy beach.

Remarks. Rahayu (2015) gave a short diagnosis and a description of the living colouration of this species. *Diogenes klaasi* is readily recognised by the presence of strong spines on the ventrolateral margin of the merus of the left cheliped which extends to the ventral surface and ventromesial margin. In life, the presence of fine brown oblique stripes on the ocular peduncle, which extends from the proximolateral and proximomesial angle towards the base of the cornea, and with slightly broader longitudinal stripe medially, and also the two black or dark brown spots on the shield, are characteristic to the species.

***Diogenes laevis* Rahayu, 1996**

(Fig. 8D)

Diogenes laevis Rahayu, 1996: 341, fig. 1 (type locality: Singapore); McLaughlin et al., 2010: 21 (list).

Material examined. 1 female, 4.2 mm (ZRC 2021.0138), st. M18, End of Jalan Durian, 7 March 2012; 1 male, 5.1 mm (ZRC 2021.0139), st. DW17, Pulau Ubin, 12 October 2012; 1 male, 2.2 mm (ZRC 2021.0140), st. MF58, Pasir Ris 01°22.955'N 103°57.130'E, 11 May 2012; 2 females, 2.0 mm, 2.7 mm, 2 ovigerous females, 3.6 mm, 2.5 mm (ZRC 2021.0141), st. DW36, Pulau Serangoon, 1°24.545'N 103°55.992'E, 16–18.6 m, 19 October 2012; 2 males, 3.2 mm, 3.5 mm (ZRC 2021.0142), Changi, 16 February 1995; 1 female, 3.1 mm (ZRC 1994.4412), Kallang basin, 15 December 1994; 4 males, 2.4–3.3 mm, 2 ovigerous females, 2.5 mm, 2.7 mm (ZRC 2021.0144), Singapore Strait, June 2013; 2 males, 2.00 mm, 2.7 mm, 1 female, 2 mm, 1 ovigerous female, 3.1 mm (ZRC 2021.0145), st. D07, Pulau Ubin, 6 March 2012; 1 male, 6.2 mm (ZRC 2021.0146), st. MF48, Sarimbun Beach, 01°26.279'N 103°41.915'S, 14 February 2012; 23 males, 1.8–6.0 mm, 8 females, 1.8–3.3 mm, 12 ovigerous females, 2.4–4.4 mm (ZRC 2021.0148), Chek Jawa, 1 July 2009; 3 males, 3.1–4.2 mm (ZRC 2021.0149), st. DW58, East Pulau Tekong, 01°25.064'N 104°04.992'E, 10.9–11.3 m, 22 October 2012; 1 male, 4.7 mm, 5 females, 1.6–3.8 mm (ZRC 2021.0150), Red Cliff shoal area, Changi, 16 November 2008; 1 male, 5.3 mm (ZRC 2021.0147), st. DW40, Opposite Changi Chalet Radar, 01°23.797'N 103°58.751'E, 19 October 2012; 1 female, 1.8 mm, 1 ovigerous female, 2.5 mm (ZRC 2021.0143).

Colour in life. Shield light brown, mottled with dark brown and bluish white; ocular peduncles generally tan with tinge of light brown distally, dark brown proximally; antennular peduncles transparent with dark brown spot proximally on dorsal surface of ultimate and penultimate segments; antennal peduncles light brown or tan with dark brown streak on second segment. Chelipeds mottled with tan and white, dark brown blotch on carpus and merus. P2 and P3 generally light brown, dactyls reddish brown, propodi with dark brown transverse band medially, longitudinal dark brown stripe ventromesially; carpi and meri with two large greenish brown longitudinal stripes on lateral face, dorsal face with large brown marking (Fig. 8D).

Distribution. Singapore, intertidal, on sandy muddy substrate.

Remarks. The specific characteristics of this species include: shield as long as broad, antennular peduncles slightly overreach antennal peduncles; outer surface of the left cheliped dactyl with broad longitudinal sulcus flanked by row(s) of tubercles; outer surface of left cheliped palm with spinous or drop-like tubercles crest extending from proximoventral angle, parallel with carpal articulation then curving distally along midline, reaching only to proximal 0.2, crest terminating abruptly, replaced by rows of small flattened tubercles, continued to almost reaching articulation with dactyl; longitudinal row of small spines or tubercles on outer surface of left cheliped palm between median row of tubercles and upper margin of palm; lower margin of left cheliped palm with row of tubercles; convex fixed finger of left chela covered by spines/tubercles that form broad longitudinal ridge.

Diogenes laevis was described from two specimens with 2 mm shield length. Examination of 76 specimens in this study showed morphological variation on the armature of the ambulatory legs that related to the size of the animal. In the small specimens (sl ≤ 2.5 mm), the dorsal margin of each carpus of P2 is armed with a row of spinules and sometimes spinules are also detected on the propodus, while in P3 the propodi are usually unarmed and the carpi each bear a dorsodistal spine. In the larger specimens (sl > 2.5 mm), the dorsal margins of propodi and carpi of P2 and P3 bear a row or rows of spines, although the spines are smaller on P3.

The differences of this species with *D. lophochir* and *D. costatus* discussed by Rahayu (1996) were only on the proportion of the antennal and antennular peduncles against the ocular peduncles, and the presence of row of spines on the dorsal margins of the propodus and carpus of the ambulatory legs. As mentioned earlier, the presence of row of tubercles on the dorsal margin of the propodus and carpus of the ambulatory legs in this species is variable, therefore this character cannot be used to distinguish these three species. Although McLaughlin (2002b, 2005) showed that the proportion of antennal and antennular peduncles against ocular peduncles is variable and unreliable to separate the species in the genus *Diogenes*, this proportion is constant

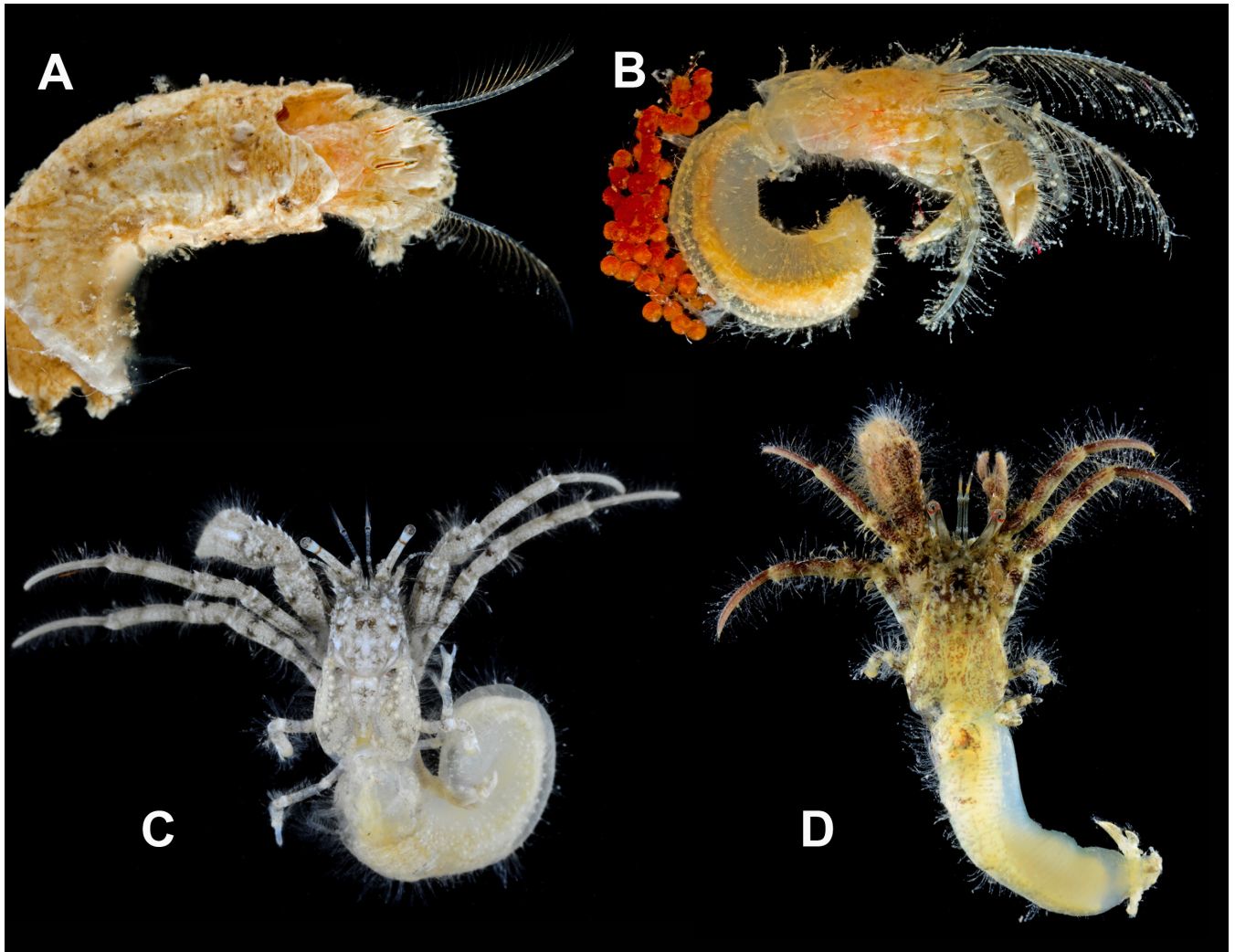


Fig. 9. A, B, *Diogenes inglei* McLaughlin & Clark, 1997, ovigerous female, 1.8 mm (ZRC 2021.0201); C, *Diogenes pallescens* Whitelegge, 1897, male, not collected, st. SD40, West P. Semakau, 1°12.389'N 103°45.24'E, 23 May 2013; D, *Diogenes tumidus* Rahayu & Forest, 1995, male, not collected, SW53, Seringat Kias, artificial lagoon, 1°13.630'N 103°51.218'E, 24 May 2013.

in all sizes of *D. laevis*. Other left cheliped characters of *D. costatus* and *D. lophochir* that separate them from *D. laevis* are as follows: dactyl without longitudinal sulcus; outer surface of palm without row of spines between medial crest and upper margin; fixed finger deflexed, without longitudinal ridge in *D. costatus*, with pronounced, narrow longitudinal ridge in *D. lophochir*.

***Diogenes moosai* Rahayu & Forest, 1995**
(Fig. 8E)

Diogenes moosai Rahayu & Forest, 1995: 392, fig. 2a, c–f, i (type locality: Muara Karang, Jakarta Bay, Indonesia); Rahayu, 2015: 183, figs. 2, 7B.

Material examined. 3 ovigerous females, 2.0–2.2 mm (ZRC 2021.0153), st. M24, Pulau Ketam, mud flat, 8 March 2012; 7 males, 2.5–3.5 mm, 1 ovigerous female, 2.3 mm (MZB Cru 5205), st. DW36, Pulau Serangoon, 1°24.545'N 103°55.992'E, 16–18.6 m, 19 October 2012; 1 male, 2.9 mm (ZRC 2021.0154), st. DW61, off Pulau Serangoon, 01°24.962'N 103°55.341'E, 7–11 m, 23 October 2012; 1 female, 2.0 mm (ZRC 2021.0155), st. DR11-191,

01°24.046'N 103°39.574'E, 7.2–11.2 m, 27 June 2012; 1 male, 3.1 mm (ZRC 2021.0156), st. SW110, Singapore Port Limit, 1°12'988 N 103°52'891 E, mangrove, 29 May 2013; 1 male, 2.4 mm (ZRC 2021.0157), st. MF12, Kranji natural trail, 01°26.590'N 103°44.240'E, mud flat, 21 May 2011; 1 male, 3.8 mm (ZRC 2021.0158), Singapore, 20 March 2014; 1 male, 1.1 mm (ZRC 2021.0159), JS1275, st. DW40, 01°23.797'N 103°58.751'E, 15.6–21 m, 19 October 2012; 2 males, 1.6–1.8 mm (ZRC 2021.0160), st. SW13, Chek Jawa, Pulau Ubin, mud flat, 16 October 2012.

Distribution. Singapore, Indonesia; intertidal and subtidal to 21 m, on mud flat, and sandy, gravel substrates.

Remarks. Rahayu (2015) gave a short diagnosis and a description of the colouration in life on the basis of the material from Johor Strait. The specimens examined in this study are smaller than those examined by Rahayu (2015), however because of the following specific characters, the identification is justified: the possession of a long antennal acicle that is overreaching the base of the fourth antennal peduncular segment; the relatively small corneas; the convex outer surface of the palm of the left cheliped that is covered

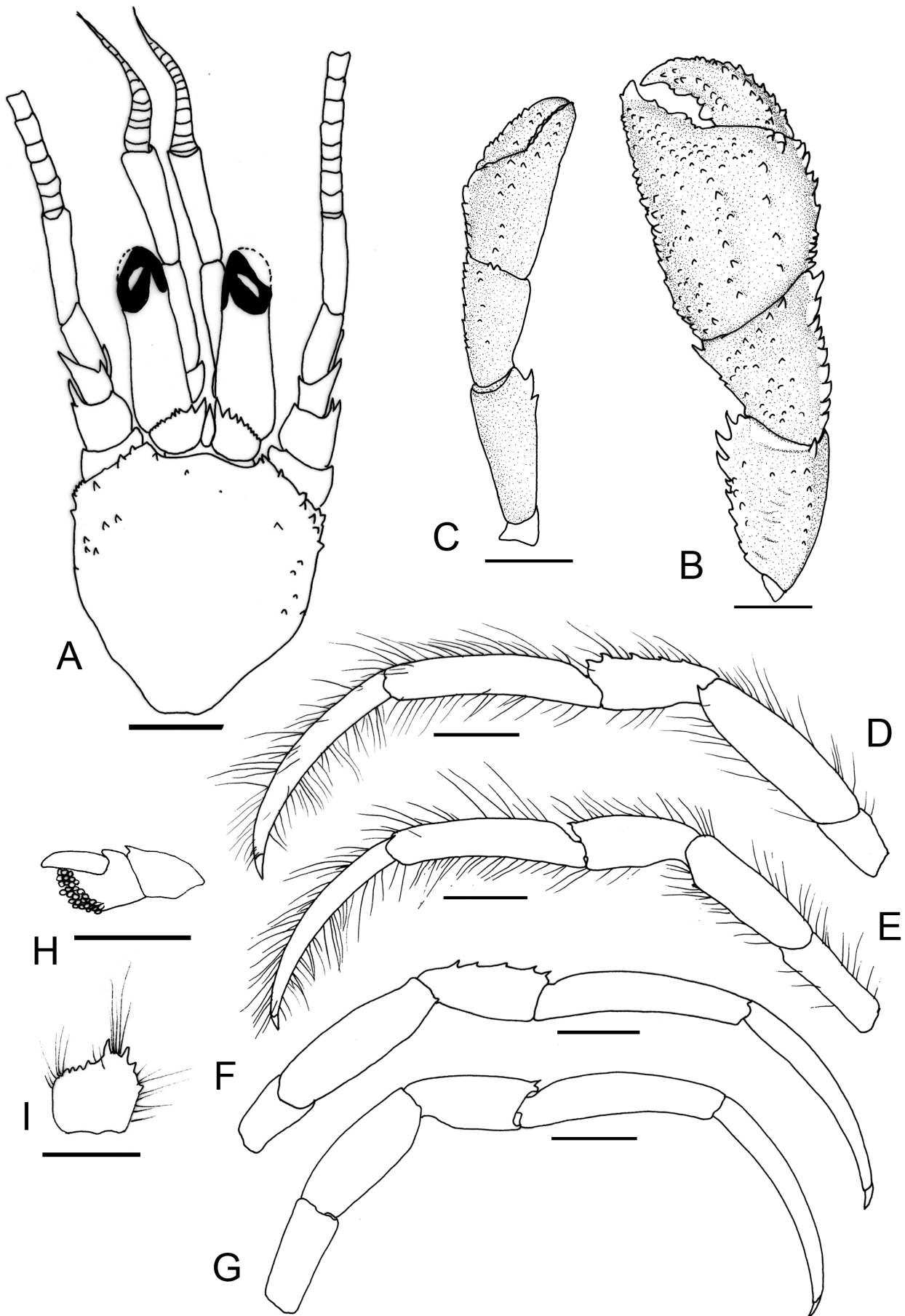


Fig. 10. *Diogenes pisinnus*, new species. Holotype, male, 1.3 mm (ZRC 2021.0203). A, shield and cephalic appendages; B, chela, carpus and merus of left cheliped, dorsolateral view; C, chela and carpus of right cheliped, dorsolateral view; D, left second pereopod, lateral view; E, left third pereopod, lateral view; F, right second pereopod, lateral view; G, right third pereopod, lateral view; H, left fourth pereopod, lateral view; I, telson. Scale = 0.5 mm.

with spinulose tubercles and with a strong median ridge; and the presence of a longitudinal brown stripe on the dorsal surface of the ocular peduncle.

***Diogenes pisinnus*, new species**
(Fig. 10)

Material examined. Holotype, male, 1.3 mm (ZRC 2021.0203), st. DR02, off Seringat Kias, Lazarus Island, coll. CMBS, 11 m, 23 April 2012.

Description. Shield (Fig. 10A) slightly longer than broad; rostrum broadly rounded; anterior margin between rostrum and lateral projections somewhat concave; lateral projections triangular, exceeding tip of rostral lobe, each with small marginal spine; anterolateral angle rounded; lateral margins glabrous; posterior margin slightly concave; dorsal surface with few small spines and tufts of sparse setae. Dorsal margins of branchiostegites each with row of 6 small spines.

Ocular peduncle (Fig. 10A) moderately stout, cylindrical, about 0.8 length of shield, slightly inflated proximally, with tufts of very sparse setae dorsally; cornea not dilated, its diameter about 0.3 of peduncular length. Ocular acicles broad, subrectangular, basally separated by approximately 0.2 width of 1 acicle, with row of spinules on terminal margin, mesialmost spine largest. Intercalary rostriform process stout, simple at tip, not reaching tip of mesial spine of ocular acicle, with few long setae; no ventral spine.

Antennular peduncle (Fig. 10A), when fully extended, overreaching distal corneal margin by whole length of ultimate segment. Ultimate and penultimate segments unarmed, but with few short setae. Basal segment with few long setae.

Antennal peduncle (Fig. 10A) overreaching distal corneal margin by 0.7 length of fifth segment; fifth segment with row of long setae laterally; fourth segment with triangular dorsodistal margin, unarmed; third segment short, stout, unarmed; second segment with dorsolateral distal angle produced into small but prominent spine, dorsomesial distal angle with or without small spine, mesial and lateral margins with few setae; first segment unarmed. Antennal acicle short, subtriangular, reaching midlength of fourth segment, with strong terminal spine; mesial margin with 1 large spine and few setae. Antennal flagellum long, overreaching tip of left cheliped; each article with three or four long plumose setae.

Third maxilliped with coxa and basis unarmed; crista dentata on ischium obsolete; merus subequal in length to carpus, both segments with long setae on mesial margin, lateral margin with fewer setae; propodus slightly shorter than carpus; dactyl shorter than propodus, both with dense setae ventrally.

Left cheliped (Fig. 10B) much larger than right, narrow hiatus between dactyl and fixed finger. Dactyl slightly longer than palm, arched; cutting edge with row of blunt calcareous teeth increasing in size proximally and few tufts of short setae, terminating in small calcareous claw overlapped by

claw of fixed finger; outer surface with sparse short setae, smooth medially, longitudinal row of tubercles near upper margin, not reaching distal end of dactyl, and irregular row of tubercles near cutting edge; upper margin with row of small spines decreasing in size distally and long plumose setae; inner surface slightly convex, with longitudinal row of tufts of short setae. Palm upper margin with row of moderately small spines; convex outer surface with irregular longitudinal row of small spines on midline not reaching articulation with dactyl; additional row of large but widely spaced spines between midline and upper margin; lower outer surface of palm with sparse spines forming irregular longitudinal rows; lower margin delimited by row of subacute spines or tubercles; inner surface almost smooth and glabrous except for few setae. Fixed finger outer surface with sparse small blunt tubercles; lower margin delimited by row of moderately small spines, interspersed with long plumose setae; cutting edge with row of calcareous teeth, large tooth subdistally; terminating in large calcareous claw; inner surface with scattered small tubercles near cutting edge and few scattered tufts of short setae. Carpus slightly longer than palm; upper margin with row of prominent spines and sparse long setae; outer surface convex bearing scattered small tubercles; lower margin with large spine distally and few small spines medially; inner surface with few tubercles and sparse setae. Merus subtriangular in dorsal view; dorsodistal margin with strong spine; dorsal surface with rows of moderately small spines and tufts of long plumose setae; lateral face tuberculate, ventrolateral margin with row of large spines, distal spines strongest and accompanied by long setae; mesial face flattened, smooth, ventromesial margin with row of moderately large spines, distal spines strongest and accompanied by plumose setae; ventral surface tuberculate. Ischium unarmed, with sparse short setae on ventromesial margin.

Right cheliped (Fig. 10C) reaching proximal third of palm of left cheliped; no hiatus between dactyl and fixed finger. Dactyl slightly longer than palm; upper margin with row of evenly spaced small spines and numerous long setae; outer surface smooth but with moderately dense long setae; cutting edge with row of low, blunt calcareous teeth, terminating in moderately large calcareous claw overlapped by fixed finger. Palm with row of moderately small spines and tufts of long setae on upper margin; outer surface smooth but with long setae; fixed finger with sparse tubercles partially obscured by long setae on outer surface; lower margin smooth but with sparse long setae; cutting edge with row of small calcareous teeth, terminating in moderately large calcareous claw. Carpus with row of small spines on upper margin; outer face almost smooth, small dorsodistal spine and two small spines on distolateral margin. Merus with numerous long, simple or plumose setae; ventromesial (not illustrated) and ventrolateral margins each with 2 large spines distally and long, simple and plumose setae. Ischium unarmed, but with few long setae.

P2 and P3 (Fig. 10D–G) slender. P2 (Fig. 10D, F) with dactyls 1.2 times as long as propodi, somewhat curved ventrally, but not twisted in dorsal view, terminating in moderately

small corneous claws; dorsal and ventral margins each with moderately dense mixture of short and long, plumose, and simple setae; mesial surfaces each with row of plumose setae near dorsal margin. Propodi 1.5 times as long as carpi, unarmed, each with moderately dense long setae on dorsal and ventral margins; mesial faces each with few setae. Carpi 0.7 times as long as meri; dorsal margins each with row of small spines and sparse, long setae; ventral margins unarmed. Meri each with sparse setae on each dorsal and ventral margin, otherwise unarmed. Ischia unarmed, each with sparse setae. P3 (Fig. 10E, G) with dactyls and propodi same as in P2; carpi 0.9 times as long as meri, each with prominent dorsodistal spine, and sparse setae, lateral faces and ventral margins unarmed; meri and ischia also unarmed but with few setae. P4 semichelate (Fig. 10H); propodal rasp consisting of three rows of calcareous scales, carpi each with dorsodistal spine.

Telson (Fig. 10I) without median cleft; left posterior lobe longer than right, left terminal margin with row of strong spines extending onto lateral margin, becoming smaller; right terminal margin also with row of small spines, but not extended onto lateral margin; long setae at outer angles continued onto lateral margins.

Colour. Unknown.

Etymology. The name is derived from Latin *pisinnus*, meaning small, alluding to the small antennal acicle which has only two spines.

Distribution. At the moment found only in Singapore Strait, at 11 m depth, on shell fragment substrate.

Remarks. One of the characteristics of the new species is the short antennal acicle, which barely reaches to the midlength of the fourth segment of the antennal peduncle. This feature is shared with only six congeneric species among the 31 known species of the *D. edwardsii* group: *D. dorotheae* Morgan & Forest, 1991, *D. guttatus* Henderson, 1888, *D. holthuisi* Asakura & Tachikawa, 2010, *D. tirmiziae* Siddiqui & McLaughlin, 2003, *D. takedai* Rahayu, 2012, and *D. heteropsammicola* Igawa & Kato, 2017. The antennal acicle of this new species is widely bifid, and in this regard, the new species resembles *D. holthuisi* and *D. heteropsammicola*. *Diogenes pisinnus*, new species, however, is readily distinguished from the latter two species by the subrectangular ocular acicle (subtriangular in *D. holthuisi* and *D. heteropsammicola*), the presence of row of spines on dorsal margin of the carpus of P2 (only a distal spine in *D. holthuisi* and *D. heteropsammicola*), the presence of a strong dorsodistal spine on P4 carpus (no spine in *D. holthuisi* and *D. heteropsammicola*), and the asymmetrical lobe of the telson with row of small spines on the right lobe, larger spines on the left lobe (asymmetrical with one to five spines of various size on each lobe in *D. holthuisi*, symmetrical with strong spines on each lobe in *D. heteropsammicola*) which separate these three species.

In the unique holotype, the ocular peduncle apparently tapers distally, though it is not yet ascertained if the condition is real or an artefact caused by preservation. Nevertheless, comparison with *D. takedai*, which normally has a tapering ocular peduncle, would be interesting. The two species differ in the armature of the chelipeds and the telson. In *D. pisinnus*, the chelipeds are only sparsely spinose (covered by small, drop-like tubercles in *D. takedai*), and the telson with row of small spines on the right lobe, larger spines on the left lobe, and small spines continuing onto lateral margins (row of small spines on both lobes, interspersed by large spines and continued onto lateral margin of left lobe in *D. takedai*).

Diogenes dorotheae is readily distinguished from the new species by having the antennal acicles armed with three strong spines, and the subtriangular telson with strong spines on the terminal margin of each lobe, while *D. guttatus* and *D. tirmiziae* are very different from the new species in having mushroom-shaped tubercles on the palm of the left cheliped, as well as the propodi and carpi of P2 and P3 with row of spines on the dorsal margin in *D. tirmiziae* and the row of spines only on the carpi of P2 in *D. guttatus*.

Diogenes rectimanus Miers, 1884

(Fig. 8F)

Diogenes rectimanus Miers, 1884: 262, pl. 27, fig. c (type locality: Prince of Wales Channel, Torres Strait); McLaughlin & Clark, 1997: 37, fig. 10b; McLaughlin, 2002a: 414, fig. 2A–C; Asakura, 2020: 6, figs. 18–21.

? *Diogenes rectimanus* – Henderson, 1893: 419; Alcock, 1905b: 71, pl. 6, fig. 8, 8a, pl. 7, fig. 2, 2a.

Not *Diogenes rectimanus* – Lanchester, 1902: 366.

Material examined. 1 male (ZRC 1991.9678), Pulau Semakau; 1 female, 1.5 mm (ZRC 2021.0161), Between Pulau Hantu, Semakau and Senang, 1°13.437'N 103°44.521'E–1°13.526'N 103°44.634'E, Rectangular dredge, sand, 10.3–6.4 m, 13 March 2013; 3 males, 1.5–2.2 mm (ZRC 2021.0162), st. D05, Henderson Shoal, dredge, sand and mud, 7 m, 6 March 2012; 6 males, 0.9–3.6 mm, 2 females, 2.4 mm, 2.7 mm, 1 ovigerous female, 1.1 mm (ZRC 2021.0163), st. D06, between Pulau Ubin and Pulau Tekong, sand and mud, dredge, 16 m, 6 March 2012; 1 male, 2.4 mm (ZRC 2021.0164), st. D07, 1°25.189'N 103°58.630'E, 6 March 2012; 1 male, 2.2 mm (MZB Cru 5206), st. TB106, 01°15.588'N 103°51.527'E, dredge, 17.2–18 m, 21 March 2013; 3 males, 2.9–4.0 mm, 1 female, 3.5 mm, Bedok Sea, 27 April 1982; 2 males, 4.2–4.5 mm, 1 female, 3.9 mm, 1 ovigerous female, 4.2 mm (ZRC 2021.0165), Chek Jawa, 1 July 2009; 1 male, 1.5 mm (ZRC 2021.0166), st. DR327, between Changi beach and Tekong, 01°23.420'N 104°00.459'E, sandy, muddy, 24.4–26.7 m, 19 March 2014.

Distribution. Gulf of Aden, India, Sri Lanka, Thailand, Singapore, Malaysia, Arafura Sea, and Torres Strait; 6–27 m, on sandy muddy substrates.

Remarks. Most of the specimens examined in this study have the ocular peduncles being about 0.7 times as long as shield and having a small, not dilated cornea (about 0.3

times as long as ocular peduncles), the propodi of P2 and P3 devoid of dorsal spines and the carpi with a row of spines on the dorsal surface of P2 only, whereas on P3 only bearing a dorsodistal spine. According to the redescription of the holotype by McLaughlin & Clark (1997), the ocular peduncle is 0.8 times as long as the shield; the P2 and P3 propodi and carpi are all armed with a row of small spines. However, the present specimens agree with the holotype in every diagnostic aspect, such as the presence of a row of strong, outwardly directed spines on the ventral margin of the palm of the left cheliped, sometimes extending onto proximal margin parallel to the carpal articulation, the presence of a longitudinal row of strong curved spines on the upper margin of the palm, and the presence of a strong spine on the lower distal angle of the left cheliped carpus, and the presence of long spines interspersed with smaller spines on the lobes of telson.

One small specimen found in a scaphopod shell has a straight abdomen with almost symmetrical telson. This variation could be in response to the habitat structure, also seen in other hermit crab species using straight shaped carcinoecia (Lemaitre et al., 2018). The specimens of this study were collected from sandy, sandy-mud substrates.

Diogenes singaporensis Rahayu, 2015

Diogenes singaporensis Rahayu, 2015: 186, figs. 3–6 (type locality: Singapore).

Material examined. 1 male, 1.3 mm (ZRC 2021.0168), Changi, coll. C.M. Yang, 18 January 1995; 1 ovigerous female, 1.6 mm (ZRC 2021.0169), Changi, coll. H. K. Lua, 16 February 1995; 7 males, 1.6–2.2 mm, 5 females, 1.3–1.6 mm, 1 ovigerous female, 1.8 mm (ZRC 2021.0170), Chek Jawa, Pulau Ubin, 21 September 2001; 11 males, 2.5–3.1 mm (MZB Cru 5208), Red cliff, shoal area Changi, 16 November 2008; 15 males, 1.8–3.1 mm, 1 female, 2.4 mm, 1 ovigerous female, 1.8 mm (MZB Cru 5209), Chek Jawa, 1 July 2009; 17 males (sl 1.3–2.5 mm), 8 ovigerous females, 1.45–1.8 mm (ZRC 2021.0171), st. S16, Chek Jawa, seagrass bed, sandflat, 7 March 2012; 1 male, 1.8 mm (ZRC 2021.0172), st. M18, Kampung Sungai Durian, nipah mangrove, 7 March 2012; 3 males, 1.3–1.6 mm (ZRC 2021.0173) st. SW53, Seringat Kias, 1°13.630'N 103°51.218'E, artificial lagoon, hand collecting, sandy beach, seagrass, 24 May 2013; 7 males, 1.1–3.1 mm, 4 females, 1.1–2.7 mm, 1 ovigerous female, 1.3 mm (ZRC 2021.0174), st. IT86, Cyrene Reef, 1°15.374'N 103°44.816'E, intertidal, 27 May 2013.

Distribution. So far known only from Singapore; intertidal, on sandy substrate and seagrass bed.

Diogenes pallescens Whitelegge, 1897 (Fig. 9C)

Diogenes pallescens Whitelegge, 1897: 141, pl. 6, figs. 2, 2a–c (type locality: Funafuti, Ellise Islands); Ball & Haig, 1972: 89, fig. 2; Morgan, 1987b: 176; Rahayu, 1996: 435; McLaughlin, 2002a: 91, figs. 1–3; Rahayu & Osawa, 2012: 183, fig. 2.

Diogenes gardineri Alcock, 1905a: 830, pl. 68, fig. 1 (type locality: Maldives); 1905b: 73, pl. 7, fig. 3; Forest, 1956a: 530, fig. 16. *Diogenes senex* – Bouvier, 1892: 55; Nobili, 1906a: 78; 1906b: 118; Balss, 1927: 224 (not *Diogenes senex* Heller, 1865). *Diogenes serenei* Forest, 1956a: 530, figs. 12–15 (type locality: Vietnam); McLaughlin, 2002a: 420, fig. 4A–C; 2002b: 88, figs. 2C, 3C, 4C, 5C.

Material examined. 4 males, 1.6–3.8 mm, 2 females, 2.0–2.7 mm (ZRC 2021.0204), Pulau Jong, 7 m, 21 December 2012; 1 male, 1.6 mm, 1 female, 2.0 mm (ZRC 2021.0205), Pulau Semakau, 21 December 2012; 1 male, 2.0 mm (ZRC 2021.0206), Pulau Hantu, 23 March 2013; 17 males, 2.5–3.6 mm, 3 females, 1.8–3.6 mm, 2 ovigerous females, 4.4–4.7 mm (MZB Cru 5216), st. SD40, West P. Semakau, 1°12.389'N 103°45.24'E, dive, 7.5 m, 23 May 2013; 4 males, 1.8–3.1 mm, 1 ovigerous female, 3.5 mm (ZRC 2021.0207), st. SD45, Channel between Lazarus and St John's Island, dive, 16.2 m, 23 May 2013; 4 males, 1.6–2.2 mm (ZRC 2021.0208), st. IT65, Terumbu Semakau, 1°12.649'N 103°46.199'E, hand collecting, 0–0.5 m, 24 May 2013; 1 ovigerous female, 2.5 mm (ZRC 2021.0209), st. IT80, Terumbu Bemban, intertidal, 28 May 2013; 1 male, 2.7 mm (ZRC 2021.0210), st. IT87, Pulau Semakau, intertidal, 27 May 2013; 1 male, 2.2 mm, 1 female, 2.4 mm (ZRC 2021.0211), st. IT124, Terumbu Pempang Laut, 01°13.912'N 103°43.402'E, submerged reef, 30 May 2013; 1 male, 2.5 mm (ZRC 2021.0212), st. IT140, Tekukor, 1°13.899'N 103°50.265'E, intertidal, 31 May 2013; 2 males, 2.2–3.1 mm, 1 female, 1.6 mm, 7 ovigerous females, 2.4–3.6 mm (ZRC 2021.0167), st. SD143, east of Pulau Hantu, 10 m, 31 May 2013; 1 male, 3.6 mm, 3 ovigerous females, 1.3–1.8 mm (ZRC 2021.0213), st. SD150, Kusu Island, dive, 10.7 m, 1 June 2013; 1 male, 1.5 mm, 1 female, 2.2 mm (ZRC 2021.0214), st. SB152, P. Kusu, 01°13.274'N 103°51.659'E, dive, 3 June 2013; 1 male, 3.3 mm, 1 female, 2 mm (ZRC 2021.0215), st. SW155, St John's Island, 01°13.116'N 103°51.079'E, 3 June 2013; 1 male, 3.6 mm, 1 ovigerous female, 1.6 mm, 1 ovigerous female, 3.1 mm (ZRC 2021.0216), st. SD167, P. Jong, dive, 15.4 m, 4 June 2013; 1 ovigerous female, 2.2 mm (ZRC 2021.0217), SD179, Terumbu Raya, 01°12.750'N 103°44.983'E, coral reef, dive, 5 June 2013; 1 male, 1.6 mm, Pulau Hantu, dive, 7–10 m, 16 December 2012; 1 female, 2.0 mm (ZRC 2021.0218), MF64, Pulau Pawai, 01°11.088'N 103°43.683'E, 1 July 2012.

Colour in life. Shield mottled with light and dark brown, and white; ocular peduncles with brown ring subdistally, reticulated pattern of light brown on dorsal surface. Chelipeds and ambulatory legs cream mottled with dark and light brown; submedian black spot on dorsal margins of propodi, carpi, and meri of ambulatory legs (Fig. 9C).

Distribution. Widely distributed in the Indo-West Pacific; 0–10 m, occurring in intertidal to subtidal muddy-sand and gravel substrates.

Remarks. Among the species of the *Diogenes pallescens* group, *D. pallescens* is easily recognised by the long, slender ocular peduncles with a distinct brown subdistal ring and irregular reticulated pattern of brown, the convex outer surface of the palm of the left cheliped with row of strong

spines on the midline, and the presence of a row of spines on the ventral margin of the P2 merus.

***Diogenes spinicarpus* Rahayu & Forest, 1995**

Diogenes spinicarpus Rahayu & Forest, 1995: 406, figs. 6a–f, 7a–h (type locality: Tanjung Tiram, Ambon, Indonesia).

Material examined. 1 male, 1.6 mm (MZB Cru 5219), Pulau Hantu, dive, 7–10 m, 16 December 2012; 1 male, 1.3 mm (ZRC 2021.0219), st. SD143, east of Pulau Hantu, dive, 12 m, 13 May 2013; 1 male, 2.2 mm (ZRC 2021.0220), Pulau Semakau, near mangrove, 10 November 2011.

Distribution. Indonesia, Singapore; 0–10 m, in sandy substrate.

Remarks. Among the species of the *Diogenes pallescens* group, *D. spinicarpus* is recognisable by the short fourth segment of the antennal peduncles armed with a strong spine on the dorsodistal margin, the slender antennal acicles bearing two or three spines mesially, and the proximally inflated ocular peduncle with a similar dilated cornea. The specimens examined in this study agree well with the original description by Rahayu & Forest (1995) except for the right cheliped that has a prominent hiatus between dactyl and fixed finger. This species is recorded for the first time in Singapore waters.

***Diogenes tumidus* Rahayu & Forest, 1995**
(Fig. 9D)

Diogenes tumidus Rahayu & Forest, 1995: 402, fig. 5 (type locality: Sorong, Papua, Indonesia); Rahayu, 1996: 349; McLaughlin, 2002a: 420, fig. 4D–F; McLaughlin et al., 2007: 142, unnumbered figures.

Material examined. 14 males, 2.0–2.9 mm (ZRC 2021.0221), st. IT140, Tekukor, 1°13.899'N 103°50.265'E, hand collecting, intertidal, 31 May 2013; 2 males, 1.3–1.8 mm, 2 ovigerous females, 1.8 mm (ZRC 2021.0222), st. SW50, St John's Island, 1°13.21'N 103°50.46'E, rubble beach, 23 May 2013; 1 male, 2.5 mm (ZRC 2021.0223), Chek Jawa, 1 July 2009; 1 male, 2.5 mm, st. SW117, St John's Island north lagoon, 1°13.116'N 103°51.079'E, 30 May 2013; 8 males, 2.4–3.5 mm (MZB Cru 5220), Pulau Semakau, 11 September and 9 October 2010.

Colouration in life. Shield mottled with light brown and cream with dark brown spot medially; ocular peduncle creamy white with dark brown streak proximal to corneas to proximal part, corneas dark grey with reddish brown streak at base. Chelipeds generally light brown with dark brown streak on dorsolateral surface of palm and carpus, spines white. P2 and P3 light brown or cream with dark brown streak on dorsolateral margin of dactyls, propodi and carpi (Fig. 9D).

Distribution. Thailand, Singapore, Indonesia; intertidal to shallow subtidal; occurring in sandy and rubble beaches.

***Paguristes* Dana, 1852**

Remarks. The genus *Paguristes* has been well studied in the last twenty years (Forest & McLaughlin, 2000; Komai, 2001, 2009, 2010; McLaughlin, 2004, 2007a; McLaughlin & Rahayu, 2005; Rahayu, 2006, 2007, 2021; Rahayu & McLaughlin, 2006; Rahayu & Forest, 2009; Ayon-Parente & Hendrickx, 2013; Komai et al., 2015a), and currently 120 species are recognised living in subtidal to the deep sea, distributed in the world oceans (McLaughlin et al., 2010; Komai et al., 2015a; Rahayu, 2021). This genus is characterised by the presence of 13 pairs of gills, the first and second pleopods modified as gonopods in males, and the presence of paired first pleopods and a brood pouch in females. In Singapore only one species has been recorded (Rahayu, 1996).

***Paguristes longirostris* Dana, 1852**
(Fig. 11A)

Paguristes longirostris Dana, 1852: 436 (type locality: East Indies); Nobili, 1903: 21; Alcock, 1905b: 36, pl. 1, fig. 5; Rahayu, 1996: 350; McLaughlin, 2002a: 392.

Material examined. 1 male, 6.4 mm, 2 ovigerous females, 5.8 mm, 6.4 mm, st. TB58, Around Tanah Merah, 1°16.808'N 103°58.246'E, mud, 38.7–39.9 m, 24 May 2013; 1 male, 2.5 mm (ZRC 1991.9679), Pulau Semakau; 1 male, 9.5 mm (ZRC 2021.0225), st. DW58, Pulau Semakau, 10 August 2010.

Colour in life. Colour in general cream or cream with tinge of brown. Shield mottled yellowish tan or light brown; ocular peduncle light brown or dark orange, distal part bright orange, corneas yellow with black blotch medially; ocular acicle light brown or dark orange; ultimate segment and flagella of antennular peduncle light blue; antennal peduncle brown, flagellum blue; chelipeds cream, meri each with large blue spot on each lateral and mesial surfaces; P2 and P3 cream, dactyls with dark brown stripes distally and proximally, lateral surfaces of propodi each with longitudinal brown stripe medially, two stripes on carpi and meri (Fig. 11A).

Distribution. East coast of India, Andaman Sea off Phuket, Thailand, and Singapore; at depths of 30–40 m, in sandy mud substrate.

Remarks. The scale-like, imbricated tubercles on the chelipeds, and a large, rounded blue spot on lateral and mesial surfaces of the merus of the chelipeds immediately separate this species from other species in *Paguristes*.

***Pseudopaguristes* McLaughlin, 2002**

Remarks. Currently 14 species of *Pseudopaguristes* are recognised, occurring in intertidal to upper bathyal depths; restricted to the Indo-West Pacific (McLaughlin et al., 2010). Two species are now known from Singapore, of which one species, *P. hians* (Henderson, 1888), is newly recorded.

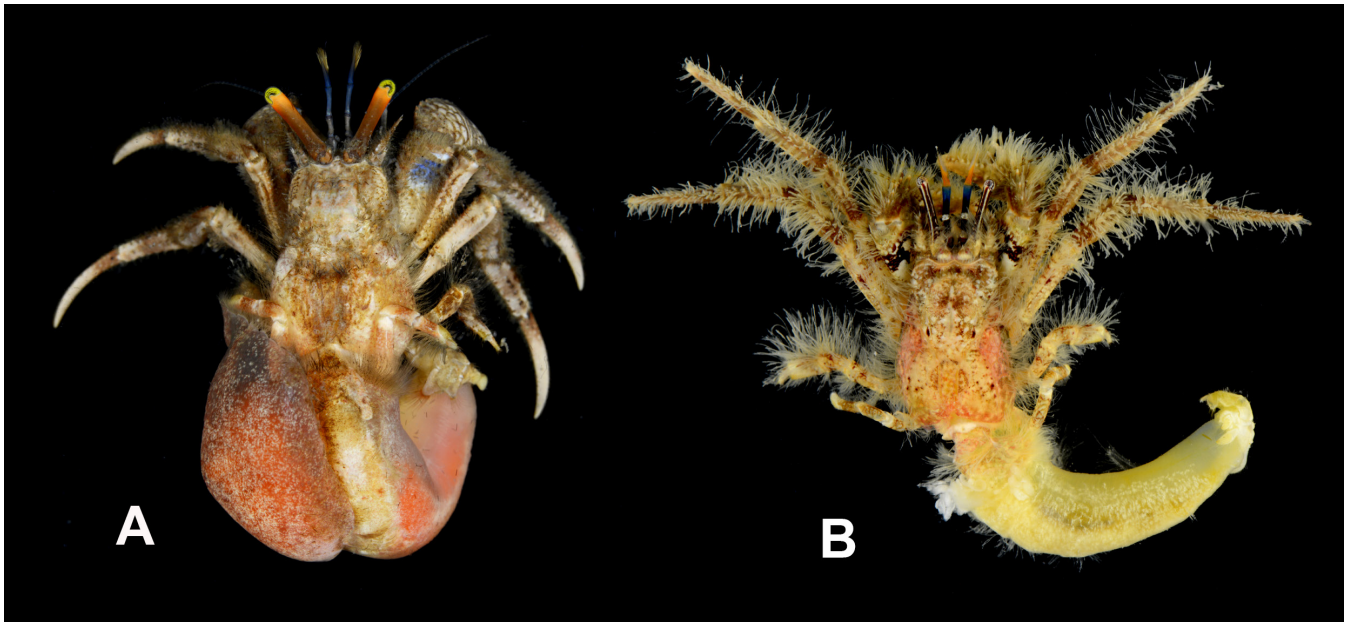


Fig. 11. A, *Paguristes longirostris* Dana, 1852, ovigerous female, 6.4 mm (ZRC 2021.0224); B, *Pseudopaguristes monoporus* (Morgan, 1987), male, 3.8 mm (ZRC 2021.0235).

Pseudopaguristes hians (Henderson, 1888)

Paguristes hians Henderson, 1888: 79, pl. 8, fig. 4 (type locality: off Manila, Philippines); Alcock, 1905b: 40, pl. 3, fig. 2; McLaughlin & Clark, 1997: 46, fig. 14; McLaughlin, 2002a: 393. *Diogenes desipiens* Lanchester, 1902: 366, pl. 34, fig. 1, 1a (type locality: Pulau Bidan, Penang, Malaysia).
Not *Paguristes hians* Grant & McCulloch, 1906: 33. [= *Pseudopaguristes monoporus* (Morgan, 1987)]
Pseudopaguristes hians; Rahayu, 2005: 32, fig. 12.

Material examined. 1 male, 3.3 mm (ZRC 2021.0226), Pulau Jong, dive, 21 December 2012; 2 males, 2.9–3.6 mm (ZRC 2021.0227), Pulau Jong, dive, 6 m, 15 September 2012; 1 male, 3.3 mm, 1 ovigerous female, 2.9 mm (ZRC 2021.0228), Pulau Jong, 1 October 2012.

Colour. McLaughlin (2002a) recorded the colouration in preservative of the specimen from Phuket, Thailand.

Distribution. Red Sea, Oman, Maldives, Arabian Sea, Indonesia, Singapore, Malaysia, and the Philippines, subtidal, 6–51 m depth, on reef and rubbles.

Remarks. This species has been rather rarely collected, easily recognisable by the short and broad antennal acicles that never reach the distal end of the fifth peduncular segment, the greatly reduced male first pleopods, and the absence of the male second pleopods. The specimens examined agree well with the redescription of the species by McLaughlin & Clark (1997) and Rahayu (2005).

Pseudopaguristes monoporus (Morgan, 1987) (Fig. 11B)

Paguristes monoporus Morgan, 1987a: 379, figs. 1–3 (type locality: Port Essington, Australia); Haig & Ball, 1988: 173; Jones & Morgan, 2002: 122, 1 unnumbered fig.

Paguristes hians: Grant & McCulloch, 1906: 33 (in part); McCulloch, 1913: 346. (Not *Paguristes hians* Henderson, 1888).
Pseudopaguristes monoporus: Rahayu, 2005: 27; McLaughlin, 2007a: 264, fig. 27.

Material examined. 1 male, 3.6 mm (ZRC 2021.0229), st. SB56, South Pulau Jong, 1°12.55'N 103°47.2'E, 17 m, 24 May 2013; 1 male, 2.4 mm, 1 female, 2.0 mm (ZRC 2021.0230), st. SB67, Pulau Hantu, western patch reef, 1°13.6'N 103°44.8'E, 15.7 m, 25 May 2013; 1 male, 4.0 mm (ZRC 2021.0231), st. SW89, small Sister's Island, 1°12.9'N 103°49.88'E, 14.7 m, 27 May 2013; 3 males, 2.5–3.8 mm, 5 females, 2.5–4.0 mm, 1 ovigerous female, 2.5 mm (ZRC 2021.0232), st. IT93, Pulau Jong, 1°12.901'N 103°47.194'E, 28 May 2013; 1 male, 2.5 mm, 1 female, 2.7 mm (ZRC 2021.0233), st. IT108, Raffles Lighthouse, 29 May 2013; 1 specimen in shell, st. DR112, South of Sister's Island, 1°12.024'N 103°50.170'E, broken shell and coral rubble, 33.6–34.4 m, 29 May 2013; 1 male, 3.1 mm, 1 female, 3.6 mm, 2 ovigerous females, 2.5–2.9 mm (ZRC 2021.0234), st. SD150, Kusu Island, 01°13.274'N 103°51.659'E, 10.7 m, 1 June 2013; 1 male, 3.8 mm (ZRC 2021.0235), st. SD167, Pulau Jong, 01°12.902'N 103°47.142'E, 15.4 m, 4 June 2013; 1 male, 4.0 mm (ZRC 2021.0230), P. Jong, dive, 6 m, 15 September 2013.

Colouration in life. Shield mottled with light brown and cream, with two dark brown spots posteriorly; ocular peduncles generally cream with red longitudinal stripes on dorsal, mesial, and lateral surfaces; basal and penultimate segments of antennular peduncle brownish blue, ultimate segment blue, flagellum orange. Chelipeds generally yellowish tan, dactyl and palm mottled with dark and light brown, spines white, carpus and merus with large dark brown streak distally. P2 and P3 also generally yellowish tan, lateral face of dactyl, propodi and carpi with brown irregular, longitudinal stripe on midline and on dorsal surface, and with dark brown streak proximally (Fig. 11B).

Distribution. Australia, Indonesia, Singapore; intertidal to 20 m deep, on sand, gravel, coral rubble substrates.

Remarks. This is a very common species in local waters and easily recognisable by the dark red stripes on the ocular peduncles, and the dense, plumose setae on the proximal part of cephalic appendages.

Family Paguridae Latreille, 1802

Pagurus Fabricius, 1775

Remarks. *Pagurus* is the richest genus in the family Paguridae with 175 valid species (McLaughlin et al., 2010; Osawa, 2012; Komai & Rahayu, 2014; Komai et al., 2015b; Lima & Lemaitre, 2016; Lemaitre et al., 2017; Landschoff et al., 2018; Lima et al., 2019). In Singapore waters, this genus has been represented only by two species, *P. kulkarnii* Sankoli, 1962 and *P. pergranulatus* (Henderson, 1896) (Rahayu, 1996). In this study three more species were added to the pagurid fauna of Singapore, one of which is a new species.

Pagurus hedleyi (Grant & McCulloch, 1906) (Fig. 14A)

Eupagurus kirkii Miers, 1884: 267, pl. 28, fig. C (name preoccupied by *Eupagurus kirkii* Filhol, 1883; type locality: Arafura Sea).
Eupagurus hedleyi Grant & McCulloch, 1906: 37 (type locality: Arafura Sea; replacement name for *Eupagurus kirkii* Miers, 1884).

Pagurus hedleyi; Haig & Ball, 1988: 185, fig. 13.

Pagurus kulkarnii: Morgan, 1987b: 182; Morgan, 1990: 27 (not *Pagurus kulkarnii* Sankoli, 1962).

Material examined. 1 male, 3.8 mm (ZRC 2021.0241), SEA3607, Outside Punggol jetty, 1°25.360'N 103°54.201'E, 11.3 m, sandy mud, 16 January 2014; 1 female, 4.0 mm (ZRC 2021.0242), SEA7151, 1°21.908'N 103°38.628'E, 11 m, gravel, mud, 9 April 2014; 1 male, 3.6 mm (ZRC 2021.0243), SEA5992, Between Tekong East and Pengarang, 01°23.914'N 104°05.353'E, 10.6–10.7 m, sandy, broken shell, 25 March 2014; 1 male, 2.7 mm, 1 ovigerous female, 2.9 mm (ZRC 2021.0244), SEA4280, 1°19.911'N 103°37.657'E, 7.5–7.7 m, sandy mud, fine shell, 11 February 2014; 3 males, 3.1–3.5 mm, 3 ovigerous females, 2.7–3.8 mm (ZRC 2021.0245), st. Beting Bornok, coll. H. Wong, 28 October 2015; 1 male, 3.1 mm, 1 female, 3.6 mm (ZRC 2021.0246), st. SD150, Kusu Island, 10.7 m, 1 June 2013; 1 male, 3.8 mm, st. IT80, Terumbu Bemban, rocky reef, 26 May 2013; 2 males, 4.2–4.4 mm (ZRC 2021.0247), st. IT86, Cyrene Reef, 1°15.374'N 103°44.816'E, 23 May 2013; 2 males, 1.6–2.7 mm (ZRC 2021.0248), Lazarus Island, 20 May 2011; 1 male, 1.6 mm (ZRC 2021.0249), st. DR91, 01°12.561'N 103°51.322'E, 46–72 m, 27 May 2013; 1 male, 3.3 mm (ZRC 2021.0250), st. SD84, southwest Tekukor, 01°13.800'N 103°50.250'E, 8 m, 27 May 2013.

Colour in life. Shield mottled with cream and light brown. Ocular peduncles white proximally, narrower white band distally just proximal to corneas, broad blue band medially

flanked by similar broad, orange band subproximally and subdistally; corneas grey. Antennular peduncle penultimate segment transparent blue proximally, orange distally; ultimate segment blue; flagella bright orange. Antennal peduncle and antennal acicle generally white with dark brown or black stripes. Chelipeds palm and dactyl cream with short, black or light brown stripes or blotches, spines white; carpus and merus bluish white with large black stripes and blotches. P2 and P3 generally pinkish white; dactyls with short black or dark brown stripes proximally, light brown blotch distally, propodi, carpi, and meri each with short black or dark brown stripes and faint shade of bluish band medially (Fig. 14A).

Distribution. Arafura Sea, Torres Strait, coast of Queensland, Singapore; 5–72 m, on sandy mud, gravel and fine shell fragment substrates.

Remarks. Haig & Ball (1988) illustrated the holotype and a specimen from Arafura Sea, and the specimens in this study agree well with their morphological discussion. Among the species of *Pagurus* having a wing-like projection or lobe on the mesial face of the carpus and merus of the right cheliped, *P. hedleyi* is most similar to *P. kulkarnii* in having broad longitudinal stripes on the pereopods. When alive, these two species are easily distinguished from each other by their colouration as follows: in *P. kulkarnii* the shield has a large dark brown blotch on the dorsal surface, and the ocular peduncle is white with a large brown blotch proximally and narrow brown band just proximal to the cornea (Fig. 14B); in *P. hedleyi*, the dorsal surface of the shield is mottled with white and light brown, the ocular peduncle is white proximally and distally, with a broad blue ring medially flanked by similar broad, orange bands subproximally and subdistally (Fig. 14A). Both species have dark brown or black broad stripes on the P2 and P3 that do not reach the distal and proximal ends of each segment, but these stripes are shorter in *P. hedleyi* and broader in *P. kulkarnii*. With regard to morphological characters, as stated by McLaughlin (2002a), the presence of one or two irregular rows of strong spines on the dorsal surface and dorsomesial margin of the dactyl of the right cheliped in *P. hedleyi*, in contrast to scattered low tubercles in *P. kulkarnii*, separates these two species.

Pagurus kulkarnii Sankoli, 1962 (Fig. 14B)

Pagurus kulkarnii Sankoli, 1962: 136, figs. 1, 2 (type locality: Bombay, India); Komai & Rahayu, 2014: 623, fig. 1B (complete synonymies).

Not *Pagurus kulkarnii* Morgan, 1987b: 182; Morgan, 1990: 27 (= *Pagurus hedleyi* Grant & McCulloch, 1906).

Material examined. 1 male, 3.6 mm (ZRC 2021.0251), East Coast beach, 25 June 2013; 1 male, 4.2 mm (MZB Cru 5224), st. D07, Pulau Ubin, 6 March 2012; 1 ovigerous female, 3.3 mm (MZB Cru 5225), Chek Jawa, 1 July 2009; 1 male, 3.8 mm (ZRC 2021.0252), st. SW31, Pulau Sekudu, 18 October 2012; 1 ovigerous female, 4.2 mm (ZRC 2021.0253), st. SW23, Chek Jawa, seagrass, 17 October 2012.

Colour in life. Shield mottled with greenish brown and pinkish white, bluish black large streaks on dorsal surface, smaller patches of dark blue on anterior and posterior parts. Ocular peduncle generally pinkish white, broad brown band proximally, narrower brown band proximal to cornea. Antennular peduncle generally brown but darker distally, articulation between ultimate and penultimate segments white, flagella light brown tinge and orange. Antennal peduncle and antennal acicle white with dark brown spots, flagellum alternately white and brown. Palm and dactyl of both chelipeds with broad dark brown stripe, light brown patch on distal area of dactyl and fixed finger, spines white, carpus and merus pinkish white with large black stripes and blotches. P2 and P3 generally pinkish white, with broad black stripes, not reaching distal and proximal ends of each segment (Fig. 14B).

Distribution. Iran, Pakistan, India, Thailand, Singapore, Philippines, Taiwan; intertidal, on sandy mud substrate on seagrass bed.

Remarks. The specimens examined in this study agree well with the original description of *P. kulkarnii* by Sankoli (1962). The living colouration is brighter (the ambulatory legs are pinkish white with broad black stripes sometimes tinged with orange) compared to the specimens reported by McLaughlin et al. (2007) from Taiwan and Komai & Rahayu (2014) from the Philippines in which the colour of the ambulatory legs was darker pink with brown stripes.

***Pagurus pitagsaleei* McLaughlin, 2002**
(Fig. 14C, D)

Pagurus pitagsaleei McLaughlin, 2002a: 444 (type locality: Cape Panwa, Phuket, Thailand).

Pagurus cf. *boreoaustraliensis* Rahayu & Komai, 2000: 30, figs. 4–8. (Not *Pagurus boreoaustraliensis* Morgan, 1990).

Material examined. 1 male, 4.0 mm (ZRC 2021.0237), st. SD45, Channel between Lazarus and St John's Island, 16.2 m, 23 May 2013; 1 male, 4.0 mm (ZRC 2021.0238), st. IT93 Pulau Jong, 1°12.901'N 103°47.194'E, 28 May 2013; 1 male, 4.9 mm (ZRC 2021.0239), st. IT95, Raffles Lighthouse, 01°09.600'N 103°44.456'E, intertidal reef, 28 May 2013; 1 ovigerous female, 3.1 mm (ZRC 2021.0240), st. IT108, Raffles Lighthouse, 01°09.600'N 103°44.456'E, intertidal reef, 29 May 2013; 1 male, 3.3 mm (MZB Cru 5221), st. SD133, South of Kusu Island, 11 m, 31 May 2013; 1 male, 4.5 mm (MZB Cru 5222), Pulau Jong, dive, coll. 7 July 2012; 1 ovigerous female, 3.4 mm (MZB Cru 5223), st. SW155, north lagoon of St John's Island, 1°13.116'N 103°51.079'E, intertidal, 3 June 2013.

Colour in life. Shield mottled with white and greenish blue, two bluish black blotches on each dorsal and anterior part of shield. Ocular peduncle bluish white, three short black incomplete stripes, with a shade of blue, proximally, two short black stripes distally, corneas grey. Antennular peduncle penultimate segment transparent blue with brown blotch, orange at articulation to ultimate segment; ultimate

segment transparent blue, bright orange distally; flagellum bright orange. Antennal peduncle and antennal acicle white with dark blue spots. Chelipeds with palms and dactyls white with black and light brown blotches dorsally, lateral faces with broad black interrupted stripes, spines white, carpus and merus bluish white with large black stripes and blotches. P2 and P3 generally white, lateral face of each segment with different pattern of short black stripes, not reaching extremity of each segment (dactyl with one complete stripe and one interrupted stripe, propodi with two stripes with dorsolateral stripe interrupted, carpus with three stripes, merus with three stripes with dosolateral stripe interrupted), propodi, carpi, and meri each with faint shade of bluish band medially (Fig. 14C, D).

Distribution. Northern and Western Australia, and now Singapore; 0–11 m, collected from intertidal reef, coral, and under stone on sandy muddy area.

Remarks. Morphological characters and colour pattern of the specimens examined in this study agree well with the description of *Pagurus pitagsaleei* by McLaughlin (2002a). *Pagurus pitagsaleei* is very similar to *P. boriaustraliensis*, and in fact, it had initially been provisionally identified with *P. boriaustraliensis* by Rahayu & Komai (2000). The differences of these two species have been discussed at length by Rahayu & Komai (2000) and McLaughlin (2002a).

***Pagurus tenuilineatus*, new species**
(Figs. 12, 13, 14D)

Material examined. Holotype, male 4.2 mm (ZRC 2021.0254), st. IT81, Sister Island, 01°12.789'N 103°50.187'E, rocky reef, intertidal, 26 May 2013. Paratypes, 1 male, 4.2 mm (ZRC 2021.0255), st. IT65, Terumbu Semakau, 01°12.649'N 103°46.199'E, sandy, rocky submerged reef, 24 May 2013; 3 males, 2.8 mm, 3.2 mm, 4.2 mm, 2 ovigerous females, 3.5 mm, 4.2 mm (ZRC 2021.0256), st. IT93, Pulau Jong, 1°12.901'N 103°47.194'E, intertidal, 28 May 2013; 2 ovigerous females, 2.2 mm, 2.5 mm, 1 female, 2.2 mm, 4 males, 1.8–2.7 mm (MZB Cru 5226), st. SD177, Kusu Island, 01°13.314'N 103°51.640'E, dive, 16.4 m, 4 June 2013; 10 males, 2.4–3.3 mm (ZRC 2021.0257), st. SD150, Kusu Island, 01°13.274'N 103°51.659'E, dive, 10.7 m, 1 June 2013.

Other material. 3 males, 2 females, 16 specimens in shell (MZB Cru 5227), st. TB91, 01°12.561'N 103°51.322'E, 46.1–72 m, 27 May 2013; 1 female (sl 1.6 mm), no locality, SS2689; 1 male, 1.3 mm (ZRC 2021.0258), st. DR128, 01°12.889'N 103°52.460'E, 75.3–85.7 m, rocky bottom, 30 May 2013; 3 males, 1.3–1.8 mm (ZRC 2021.0259), st. DR161; 2 males, 1.8 mm, 2.2 mm, 2 females, 2.5 mm, 2.9 mm (ZRC 2021.0260), st. SD145, Pulau Hantu, 01°13.514'N 103°44.784'E, dive, 11.7 m, 1 June 2013; 2 males, 2.4 mm, 3.3 mm (ZRC 2021.0261), st. SD150, Kusu Island, 01°13.274'N 103°51.659'E, dive, 10.7 m, 1 June 2013; 1 male, 2.0 mm (MZB Cru 5228), st. DW58, east of Pulau Tekong, 01°25.064'N 104°04.992'E, 10.9–11.3 m, 22 October 2012.

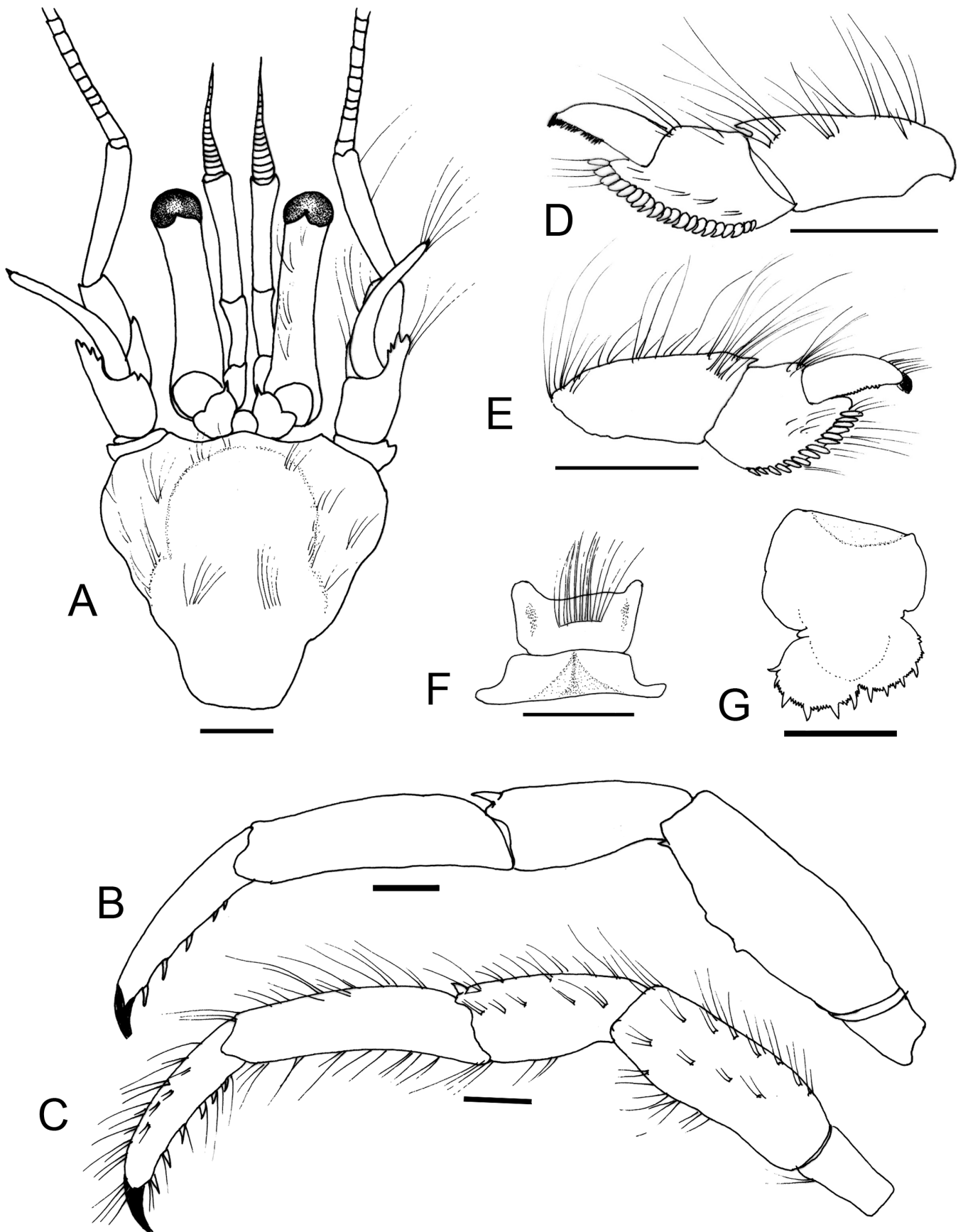


Fig. 12. *Pagurus tenuilineatus*, new species. Holotype, male, 4.4 mm (ZRC 2021.0254). A, shield and cephalic appendages; B, left P2; C, left P3; D, left P4; E, right P4; F, anterior lobe of sternite of third pereopods; G, telson. B–E, lateral view. Scale = 1 mm.

Description. Shield (Fig. 12A) approximately as long as broad; anterior margins between rostrum and lateral projections gently concave; anterolateral margins sloping; posterior margin truncate; dorsal surface slightly convex transversely, with longitudinal row of tufts of moderately long setae on either side of midline; paragastric grooves faint. Rostrum obtusely triangular, exceeding as far as lateral projections. Lateral projections broadly triangular, with small marginal spine. Posterior carapace (not figured), measured along midline, distinctly shorter than shield; carapace lateral lobe moderately narrow, not calcified; cardiac sulci parallel, barely reaching to midlength of posterior carapace.

Ocular peduncle (including cornea) (Fig. 12A) relatively long, about 0.9 times as long as shield; slightly inflated basally; cornea slightly dilated, diameter about 0.2 times peduncular length; dorsal surface with longitudinal row of tufts of moderately short setae. Ocular acicles narrowly subtriangular, separated basally by width of less than one acicle, with minute marginal spine distally. Interocular lobe partially overhung by rostrum, medially concave.

Antennular peduncle (Fig. 12A), when fully extended, slightly overreaching distal corneal margin. Ultimate segment about 1.5 times as long as penultimate segment, slightly widened distally in lateral view. Basal segment with distolateral margin produced in sharply pointed lobe; statocyst lobe weakly inflated, with small spine medially; ventromesial distal angle not produced.

Antennal peduncle (Fig. 12A) overreaching distal corneal margins by 0.3 length of fifth segment. Fifth segment with few setae laterally. Fourth and third segments unarmed, with several tufts of long stiff setae mesially. Second segment with dorsolateral distal angle not reaching midlength of fourth segment, with 3 to 5 spinules distomesially; dorsomesial distal angle with small spine; mesial and lateral faces with short to long stiff setae. First segment with subterminal spinule on lateral face. Antennal acicle not reaching base of cornea, gently arcuate, terminating in small spine obscured by long stiff setae; dorsomesial margin with several tufts of long stiff setae. Antennal flagellum about 4 times as long as shield; each article with 1 or 2 minute setae on distal margin.

Mouthparts not dissected. Third maxilliped moderately slender; dactyl slightly shorter than propodus; carpus, merus unarmed; ischium with crista dentata consisting of narrowly spaced, moderately large, subacute corneous teeth, and with 1 moderately strong accessory tooth; basis-ischium fusion incomplete; basis with 2 or 3 denticles on mesial margin; exopod reaching distal margin of merus.

Chelipeds unequal. Right cheliped larger but not necessarily longer than left (Fig. 13A, B, D, E); chela about 2 times as long as greatest width at base of dactyl, generally suboval in outline in dorsal view. Dactyl subequal in length to palm and slightly overlapped by fixed finger; dorsal surface with sparse, short setae and prominent median row of broad-based, closely set spines; dorsomesial margin with double row of closely set, moderately large spines, decreasing in size distally;

space between dorsal midline and dorsomesial margin smooth; ventral surface with scattered tufts of moderately short stiff setae; cutting edge with row of broad calcareous teeth and adjacent row of tufts of stiff setae, terminating in large calcareous claw. Palm slightly shorter than carpus; dorsomesial margin delimited by single row of moderately large, stout spines (Fig. 13A, D); dorsal surface convex, with numerous, small, scattered tubercles and tuft of short setae; dorsolateral margin delimited by small spines extending onto fixed finger, decreasing in size distally; fixed finger dorsal surface slightly depressed and with scattered tubercles, cutting edge with row of moderately large calcareous teeth, terminating in large calcareous claw; mesial face with scattered, very low, minute to small protuberances and sparse very short setae; lateral surface with scattered tufts of short stiff setae; ventral surface gently convex, with scattered tufts of short and long setae. Carpus slightly shorter than merus; dorsodistal margin with row of small spines, dorsomesial margin delimited by row of large spines accompanied by tufts of long stiff setae, dorsal surface with tufts of short to long stiff setae; dorsolateral margin delimited by row of small tubercles obscured by long setae; lateral face nearly glabrous except for some tufts of setae; mesial face (Fig. 13B, E) with few sparse long setae, ventromesial margin produced into flattened, wing-like crest in both sexes (Fig. 13A, D), edge of crest unarmed or with small tubercles in female (Fig. 13D); ventral surface with few tufts of setae. Merus with 1 prominent spine on dorsodistal margin; dorsal surface glabrous; lateral surface nearly glabrous except for few tufts of short setae, ventromesial margin produced in flattened, wing-like crest in males, edge of crest with tiny tubercles distally, strong spine proximally (Fig. 13B), in females no wing-like crest developed, but with row of spines and one prominent spine proximally (Fig. 13E); ventral surface with some low, blister-like protuberances and tufts of moderately long setae. Ischium with tufts of short setae on all surfaces.

Left cheliped (Fig. 13C, F) slenderer than right, moderately compressed laterally. Chela elongate subovate in dorsal view, 3.2 times longer than greatest width at base of dactyl. Dactyl about 2.7 times as long as palm, nearly straight with ventrally curved tip; dorsomesial margin with double row of strong spines on proximal 0.7, distal 0.3 smooth; dorsomesial margin and surfaces with tufts of long setae; cutting edge with row of minute, subacute calcareous denticles in proximal 0.4 and row of minute, closely set corneous teeth in distal 0.6, terminating in small corneous claw. Palm about half length of carpus; dorsomesial margin with row of spines, dorsal surface with double row of spines adjacent to dorsomesial margin, extending onto articulation with dactyl, remaining surface with scattered small tubercles; dorsolateral margin with row of spines extending onto tip of fixed finger; fixed finger dorsal surface with longitudinal row of moderately large spines extending along cutting edge, remaining dorsal surface with scattered tubercles; cutting edge bearing row of minute calcareous denticles terminating in moderately large corneous claw; moderately broad hiatus between dactyl and fixed finger. All surfaces with tufts of long setae. Carpus subequal in length to merus; dorsodistal margin with several

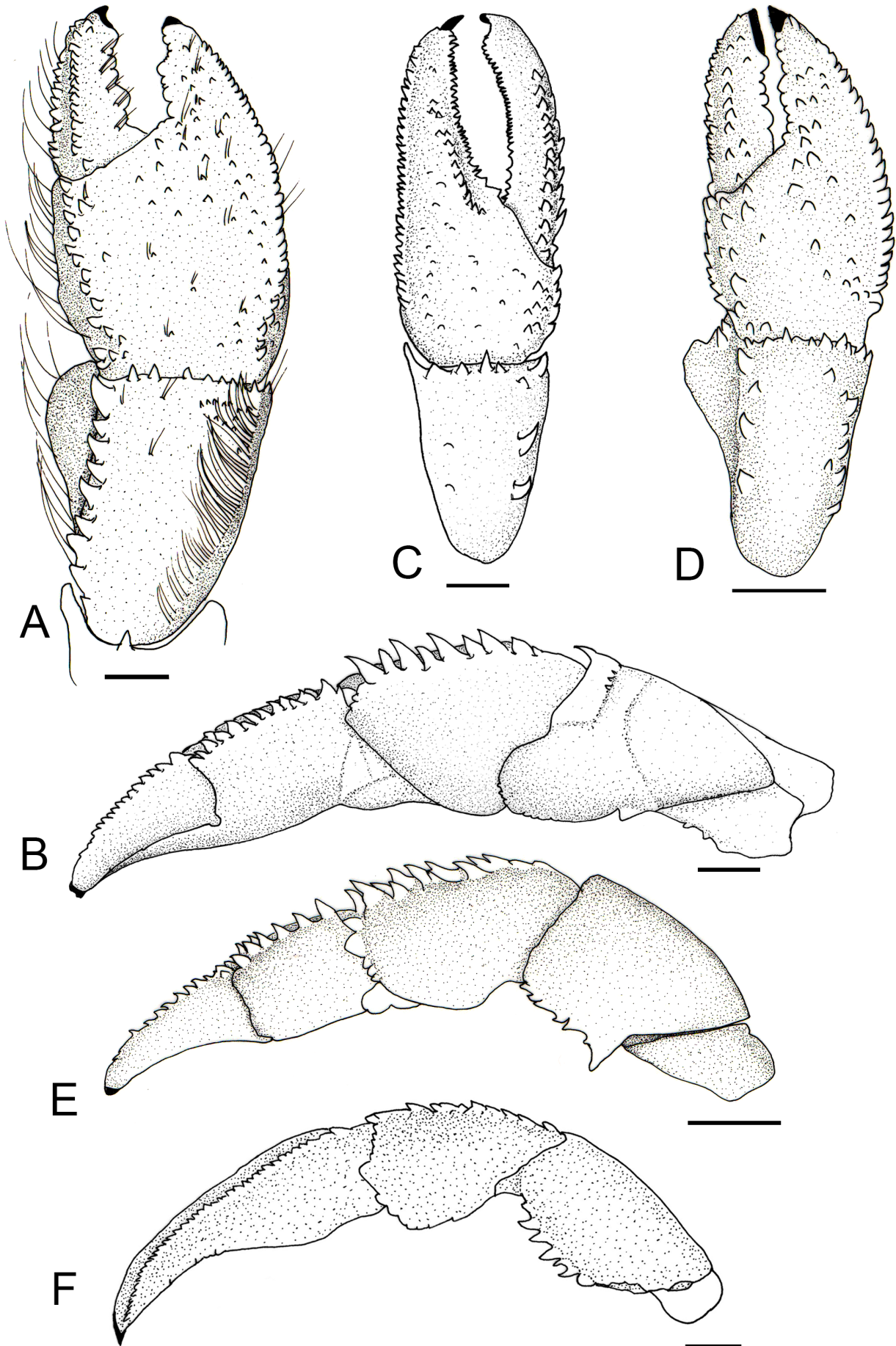


Fig. 13. A–C, *Pagurus tenuilineatus*, new species. Holotype, male, 4.4 mm (ZRC 2021.0254); D–F, paratype, ovigerous female, 4.2 mm (ZRC 2021.0256). A, D, chela and carpus of right cheliped, dorsolateral view; B, E, chela, carpus and merus of right cheliped, mesial view; C, chela and carpus of left cheliped, dorsolateral view; F, chela, carpus and merus of left cheliped, mesial view. Scale = 1 mm.

strong spines; dorsomesial margin with row of moderately large spines; dorsal surface with few tubercles and sparse setae; dorsolateral margin with row of small spines and tufts of short setae; mesial and lateral surface with tufts of short and long setae; ventrolateral margin with row of small spines. Merus with prominent spine on dorsodistal margin; dorsal surface with sparse short stiff setae; lateral and mesial surfaces nearly glabrous except for row of tufts of stiff setae adjacent to dorsal margin and few similar tufts near ventral margin; ventrolateral margin with row of slender, sharp spines and long stiff setae; ventromesial margin with row spines, 2 larger spines proximally. Female left cheliped same as male.

P2 and P3 (Fig. 12B, C) stout, right P2 slightly overreaching tip of extended right cheliped. Dactyls 0.9–1.0 times as long as propodi, 4.3–4.6 times longer than broad, in dorsal view nearly straight, in lateral view slightly curving ventrally; dorsal and ventral margins each with row of tufts of short to moderately long setae, ventral margins each with row of 5–6 moderately large corneous spines increasing in size distally. Propodi slightly narrowing distally; dorsal surfaces unarmed but with row of long stiff setae; lateral and mesial surfaces with few tufts of long stiff setae; ventral surfaces with few tufts of long stiff setae. Carpi each with small dorsodistal spine; with row of tufts of long stiff setae on dorsal margin; lateral surface convex, with row of tufts of long stiff setae along midline. Meri each with row of tufts of long stiff setae on dorsal surface; lateral surface almost smooth, with few tufts of long stiff setae distally; ventral surface unarmed but with row of tufts of short to long stiff setae, ventrodistal lateral margin unarmed. Ischia unarmed but with tufts of setae on dorsal and ventral margins.

P4 semichelate, left (Fig. 12D) slightly larger than right (Fig. 12E). Dactyls slightly curved ventrally, terminating in small corneous claw; each with row of minute, closely spaced corneous teeth on ventral margin; no preungual process. Propodal rasp consisting of 1 row of corneous scales. All segments with dorsal and/or ventral tufts of long stiff setae.

Anterior lobe of sternite of third pereopod (Fig. 12F) subrectangular, ventral surface with tufts of setae medially. Male with 3 unequally uniramous pleopods. Female second to fifth pleopods greatly unequally biramous with much elongate exopods; length third > second > fourth > fifth.

Telson (Fig. 12G) with distinct lateral indentations; posterior lobes strongly produced, rounded, unequal, median cleft shallow; each terminal margin with row of numerous slender spines interspersed by spinules, not extending onto lateral margin.

Colour in life. Shield mottled with light brown and white, with dark brown patches on anterolateral and dorsodistal surface. Ocular peduncle whitish proximally; narrow brown ring at base of cornea and broad brown patch proximally; cornea dark brown. Antennular peduncle generally blue, distal part of penultimate segment and flagella orange. Antennal peduncle generally white; second and fourth segments each with three dark brown longitudinal stripes on dorsal surface,

fifth segment with dark brown stripe on lateral and mesial margin; flagellum with brown stripe along lateral and mesial margin of each article, white on articulation of each segment. Right cheliped mottled with light brown and white in general, with large dark brown patches and stripes; mesial surfaces of carpus and merus with irregular patterns of dark brown on white background. Left cheliped with thin brown lines on white background on chela, carpus, and merus. Ambulatory legs with thin dark brown stripes on propodi, carpi, meri, and ischia; dactyls each with one dark brown median stripe and two broad light brown bands (one subdistal and one proximal); propodi, carpi, and meri each with three dark brown stripes on lateral surface, with broad light brown band medially. Dark brown stripes on chelipeds and ambulatory legs usually reaching ends of segments (Fig. 14E).

Distribution. At present known only from Singapore; 0–85 m, on reef, sandy and rocky bottom.

Etymology. The name is derived from Latin *tenuis*, meaning slender, and *linea*, meaning stripes, alluding to the narrow stripes on the chelipeds and pereopods, used as a noun in apposition.

Remarks. The characters of this new species correspond with the *Pagurus anachoretus* group as defined by Forest & Ngoc-Ho (1992) and McLaughlin & Forest (1999). Among the species in this group, *P. tenuilineatus*, new species, belongs to the group which have wing-like projection on mesial face of the carpus and merus of the right cheliped, i.e., *P. boriaustraliensis*, *P. gordonae* (Forest, 1956b), *P. hedleyi*, *P. kulkarnii*, *P. liochele* (Barnard, 1947), *P. pitagsaleei*, and *P. sticticus* McLaughlin, 2007b. The presence of a row of moderately large spines on the dorsal surface of the fixed finger of the left cheliped, extending along cutting edge but not reaching the distal part of the finger, separates this new species from its congeners. Furthermore, differences between congeners are also observed on the proportion of the dactyl and palm of the left cheliped. In *P. tenuilineatus*, new species, the dactyl of the left cheliped (2.7 times as long as palm) is much longer than that of *P. boriaustraliensis* and *P. pitagsaleei* (1.5 times as long as palm), *P. gordonae* (almost as long as palm), *P. liochele* (1.3–2 times as long as palm), *P. kulkarnii* (2.5 times as long as palm), and *P. sticticus* (1.8 times as long as palm), whereas in *P. hedleyi* the left cheliped has a much longer dactyl (3.3 times as long as palm).

Although living colouration of the species in the *anachoretus* group is quite specific, with colour pattern usually consisting of patches and longitudinal stripes of pigment that cover part or all of the segment of the chelipeds and ambulatory legs (McLaughlin & Forest, 1999), the position and colour pigmentation of the stripes and patches are different from one species to another. The colouration for *P. hedleyi*, *P. kulkarnii*, *P. pitagsaleei*, and *P. tenuilineatus* has been described above and differences can be seen in Fig. 14. Forest (1956b) described the colour of *P. gordonae* as follows: shield, ocular and antennal peduncles are greenish grey with brown longitudinal patches, antennular peduncle

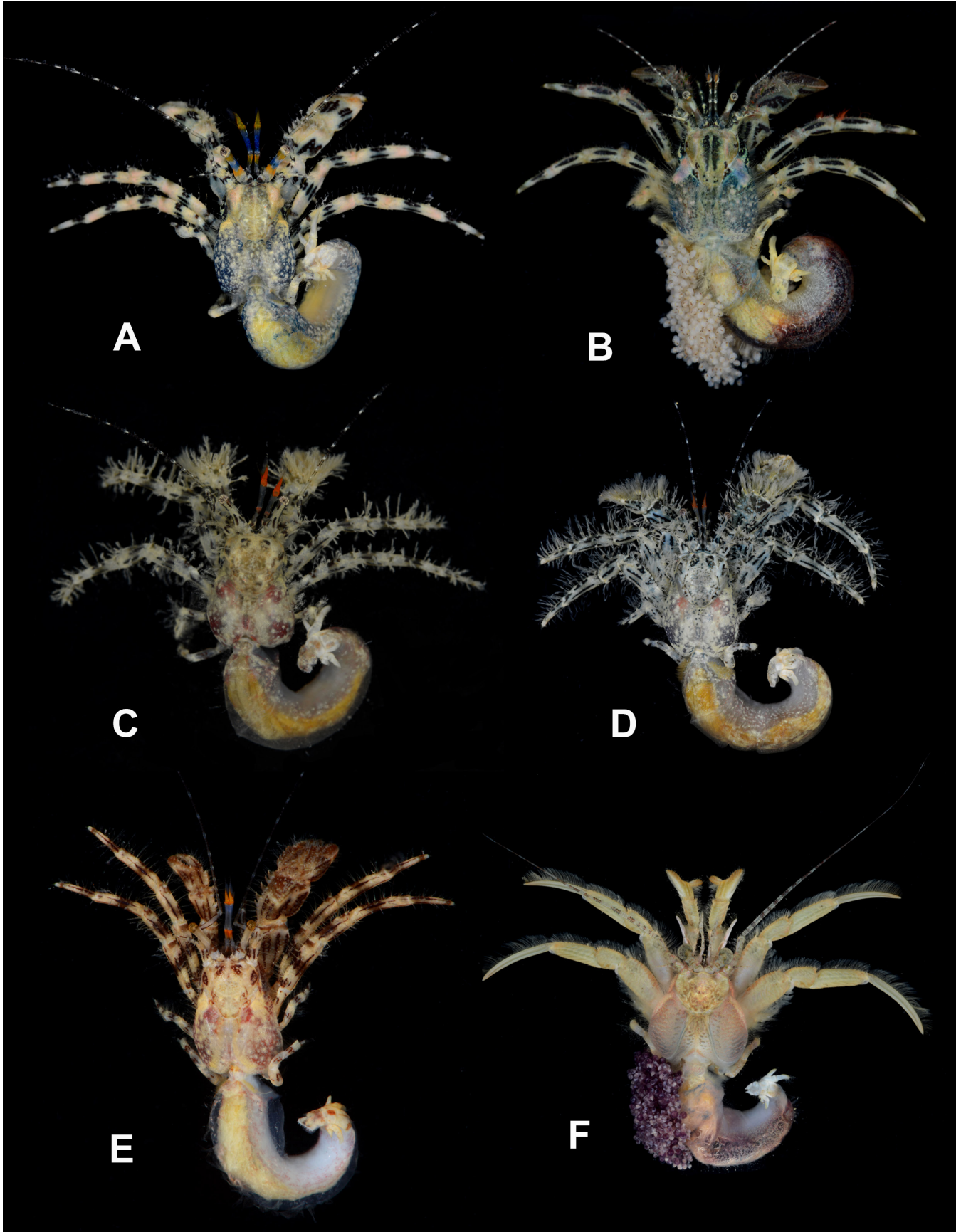


Fig. 14. A, *Pagurus hedleyi* (Grant & McCulloch, 1906), male, not measured and sexed, st. SD25, St John's Island, 01°12.882'N 103°50.952'E, 22 May 2013; B, *Pagurus kulkarnii* Sankoli, 1962, ovigerous female, 4.2 mm (ZRC 2021.0253); C, D, *Pagurus pitagsaleei* McLaughlin, 2002a, C, male, not collected, st. SD25, St John's Island, 01°12.882'N 103°50.952'E, 22 May 2013; D, male, 4.9 mm (ZRC 2021.0239); E, *Pagurus tenuilineatus*, new species, paratype, male, 4.2 mm (ZRC 2021.0255); F, *Spiropagurus spiriger* (De Haan, 1849), ovigerous female, not collected, Johor Strait.

with large brown band on penultimate segment, ultimate segment brown on distal half; antennal flagella alternately brown and white; chelipeds greenish brown, carpi and meri with irregular longitudinal stripes; ambulatory legs with irregular brown stripes on half proximal of each segment, half distal orange without any stripes. McLaughlin & Forest (1999: 322) cited the colour of *P. liochele* after Barnard (1950) as follows: ocular peduncle sienna at base, distal half cobalt, with narrow dark sienna ring immediately adjacent to black cornea, meral segment of left and right chelipeds with cobalt band border with sienna, and distal margin dark sienna; granules on dorsal surface of palm white on pale sienna ground, sienna longitudinal stripes on dactyl and fixed finger; proximal halves of meral segment of second and third pereopods sienna, distal halves pale, longitudinal sienna stripes on carpi and dactyls and dorsally on proximal halves of propodi, distal halves of propodi yellowish, passing into cobalt apically. *Pagurus boriaustraliensis* shield is cream or pale brown with dark brown mottling, ocular peduncle cream with black or reddish black short longitudinal stripes distally and proximally, chelipeds cream brownish with dark brown line, ambulatory legs with longitudinal brown stripes, and with brown band around midline (Morgan, 1990). The colouration in life of *P. sticticus* is not known, but in preservative the ambulatory legs have orange spots and patches on each segment (McLaughlin, 2007b).

Spiropagurus Stimpson, 1858

Remarks. The species in the genus *Spiropagurus* is easily recognised by the presence of squamiform ridges or tubercles bearing marginal setae on the chelipeds and ambulatory legs, the presence of long, usually coiled, terminally blunt sexual tube on the coxa of left P5 of male, and the characteristic posterior lobes of the telson being acutely triangular. Seven species are recognised (Han et al., 2016), but only one species, *Spiropagurus spiriger* (De Haan, 1849), has been recorded from Singapore.

Spiropagurus spiriger (De Haan, 1849) (Fig. 14F)

Pagurus spiriger De Haan, 1849: 206, pl. 49, fig. 2 (type locality: Japan).

Spiropagurus spiriger; Alcock, 1905b: 118, pl. 13, fig. 1; Miyake, 1978: 137, fig. 54; Miyake, 1982: 122, pl. 41, fig. 5; Lewinsohn, 1982: 216, fig. 2; Baba, 1986: 211, fig. 155; Rahayu, 1996: 351; McLaughlin, 2002a: 448, fig. 9A; McLaughlin, Rahayu, Komai & Chan, 2007: 213, unnumbered figures.

Material examined. 1 female, 3.8 mm (ZRC 2021.0262), st. TB96, near Eastern Bunkering A, 1°18.140'N 104°04.221'E, beam trawl, 22.4–25.1 m, clay, 28 May 2013; 1 male, 2.5 mm (ZRC 2021.0263), st. TB97, 1°18.425'N 104°04.607'E, beam trawl, clay, 22.4–22.7 m, 28 May 2013; 1 male, 3.8 mm (ZRC 2021.0264), DR09, Pasir Panjang, 01°16.229'N 103°45.358'E, 24 m, 12 June 2012.

Colour. In general brownish cream with darker brown speckled on shield and ocular peduncles, setae yellowish white (Fig. 14F).

Distribution. Bay of Bengal, Andaman Sea, Gulf of Thailand, East Indian Archipelago, Singapore, Malaysia, East China Sea, Japan, Taiwan, Northern Australia; 22–25 m, on sandy, muddy substrates.

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LITERATURE CITED

- Alcock A (1905a) Marine crustaceans XIV. Paguridae. In: Gardiner JS (ed.) The Fauna and Geography of the Maldives and Laccadive Archipelagoes. Being an Account of the Work Carried on and the Collections Made by an Expedition during the years 1899 and 1900. Volume 2. University Press, Cambridge, pp. 827–835.
- Alcock A (1905b) Catalogue of the Indian decapod Crustacea in the collections of the Indian Museum. Part 2. Anomura. Fasc. 1. Pagurides. Indian Museum, Calcutta, xi + 197 pp.
- Almon B, Cuesta JA, Schubart CD, Armenia L & Raso JEG (2021) Redescription of the hermit crab *Diogenes pugilator* (Decapoda: Anomura) reveals the existence of a species complex in the Atlanto-Mediterranean transition zone, resulting in the resurrection of *D. curvimanus* and the description of a new species. Zoological Journal of the Linnean Society, XX: 1–31.
- Asakura A (2020) Hermit crabs of the genus *Diogenes* Dana, 1851 (Crustacea: Decapoda: Diogenidae) collected during the Albatross Philippine Expedition, 1907–1910, including descriptions of three new species. Publications of the Seto Marine Biological Laboratory, 45: 1–4.
- Asakura A & Tachikawa H (2010) *Diogenes holthuisi*, a new species of hermit crab (Decapoda: Anomura: Diogenidae) from shallow water of the Ogasawara (Bonin) Islands, Japan. In: Fransen C, De Grave S & Ng PKL (eds.) Studies on Malacostraca: Lipke Bijdeley Holthuis Memorial Volume. Crustaceana Monographs, 14: 133–144.
- Ayon-Parente M & Hendrickx ME (2013) Redescription and taxonomic status of *Paguristes weddellii* (H. Milne Edwards)

- (Crustacea: Anomura: Paguroidea: Diogenidae) from the eastern Pacific. *Zootaxa*, 3616(6): 587–596.
- Baba K (1986) *Macrura Reptantia*. Anomura, Brachyura. In: Baba K, Hayashi M & Toriyama K (eds.) *Decapod crustacean from continental shelf and slope around Japan*. The intensive research of unexploited fishery resources on continental slopes. Japan Fisheries Resource Conservation Association, Tokyo, pp. 148–231, 279–316.
- Ball EE & Haig J (1972) Hermit crabs from eastern New Guinea. *Pacific Science*, 26: 87–107.
- Balss H (1927) Bericht über die Crustacea Decapoda (Natantia und Anomura). Zoological results of the Cambridge expedition to the Suez Canal, 1924. *Transactions of the Zoological Society of London*, 22(2): 221–227.
- Barnard KH (1947) Description of new species of South African decapod crustacea, with notes on synonymy and new records. *Annals and Magazine of Natural History*, Series 11, 13: 361–392.
- Barnard KH (1950) Descriptive catalogue of South African Decapod Crustacean (crabs and shrimps). *Annals of the South African Museum*, 38: 1–837.
- Bouvier EL (1892) Étude sur les Paguriens recueillis par M. le Dr. Jousseaume sur les côtes de la Mer Rouge. *Bulletin de la Société Philomathique de Paris*, Series 8, 4(2): 50–55.
- Bouvier EL (1897) Sur deux Paguriens nouveaux trouvés par M. Coutière dans le récif madréporiques à Djibouti. *Bulletin du Muséum d'Histoire Naturelle*, Paris, 3: 228–233.
- Dana JD (1851) *Conspectus Crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe Reipublicae Foederatae duce, lexit et descripsit*. *Proceeding of the Academy of Natural Sciences*, Philadelphia, 5: 267–272.
- Dana JD (1852) United States Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N., Volume 13. Crustacea. Part 1. C. Sherman, Philadelphia (Reprinted Antiquariaat Junk, Lochem, Netherlands, 1972).
- Dana JD (1855) United States Exploring Expedition, during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N., Volume 13. Atlas. Crustacea. C. Sherman, Philadelphia (Reprinted Antiquariaat Junk, Lochem, Netherlands, 1972), 27 pp., 96 pls.
- Dechanché M (1964) Sur une collection des Crustacés Pagurids de Madagascar et des Comores. *Cahiers O.R.S.T.O.M. (Série Océanographie)*, 2: 27–45.
- Estampador EP (1937) A checklist of Philippine crustacean decapods. *Philippine Journal of Science*, 62(4): 465–559.
- Fabricius JC (1787) *Mantissa insectorum sistens eorum species nuper detectas adjectis characteribus genericis, differentiis specificis, emendationibus, observationibus*. Volume 1. Hafniae, xx + 348 pp.
- Fabricius JC (1798) *Supplementum Entomologiae systematicae*. Hafniae, 572 pp.
- Filhol H (1883) Note sur quelques espèces nouvelles d'*Eupagurus* recueillies en Nouvelle-Zélande. *Bulletin de la Société Philomathique de Paris*, Series 7, 8: 66–68.
- Fize A & Serène R (1955) Les Pagures du Vietnam. *Institut Océanographique Nhatrang*, Note 45: ix + 1–228.
- Forest J (1952) Remarques sur les genres *Diogenes* Dana et *Troglopagurus* Henderson à propos de la description d'un Paguridae nouveau de la côte occidentale d'Afrique, *Diogenes mercatoris* sp. nov. *Bulletin Institut royal des Sciences naturelles de Belgique*, 26(11): 1–15.
- Forest J (1953a) Crustacés Décapodes Marcheurs des îles de Tahiti et des Tuamotu. –I. Paguridea. *Bulletin du Muséum national d'Histoire naturelle*, Series 2, 25: 441–450.
- Forest J (1953b) Crustacés Décapodes Marcheurs des îles de Tahiti et des Tuamotu. –II. Paguridea (suite). *Bulletin du Muséum national d'Histoire naturelle*, Series 2, 25: 555–561.
- Forest J (1956a) Les Pagures du Viet-Nam. I. Le genre *Diogenes* Dana. *Bulletin du Muséum national d'Histoire naturelle*, Series 2, 28: 524–532.
- Forest J (1956b) Sur une collection de Paguridae de la Côte de l'Or. *Proceedings of the Zoological Society of London*, 126: 335–367.
- Forest J & Ngoc-Ho N (1992) Description de *Pagurus dartavellei* (Forest, 1958) (Crustacea, Decapoda, Paguridae). *Bulletin du Muséum national d'Histoire naturelle*, Series 4, 14(A): 217–227.
- Forest J & McLaughlin PA (2000) Superfamily Coenobitoidea. In: Forest J, de Saint Laurent M, McLaughlin PA & Lemaître R (eds.) *The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae*. NIWA Biodiversity Memoir, 114: 31–103.
- Forskål P (1775) *Descriptiones Animalium, Avium, Amphibiorum, Piscium, Insectorum, vermium; quae in itinere orientali observavit*. Post mortem auctoris edidit Carsten Niebuhr. Hauniae, 19 + 164 pp.
- Grant FE & McCulloch AR (1906) On a collection of Crustacea from the Port Curtis district, Queensland. *Proceedings of the Linnean Society of New South Wales*, 1906: 1–53.
- Han Y-Y, An J-M & Sha Z-L (2016) A review of the genus *Spiropagurus* Stimpson, 1858 (Crustacea: Anomura: Paguridae) from the China Sea. *Zootaxa*, 4175(1): 75–89.
- Haan De W (1833–1850) Crustacea. In: Siebold PF von (ed.) *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*. Lugduni-Batavorum, Leiden, 243 pp.
- Haig J & Ball EE (1988) Hermit crabs from northern Australian and eastern Indonesian waters (Crustacea Decapoda: Anomura: Paguroidea) collected during the 1975 Alpha Helix Expedition. *Records of the Australian Museum*, 40: 151–196.
- Heller C (1865) Crustaceen. In: *Reise der Österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodors B. von Wüllerstorff-Urbair*. Zoologischer Theil, Bd. 2, Abt. 3. Kaiserlich-königlichen Hof- und Staatsdruckerei, Wien, 280 pp., 25 pls.
- Henderson JR (1888) Report on the Anomura collected by H. M. S. Challenger during the years 1873–76. *Scientific Results of the Exploratory Voyage of HMS Challenger*. Zoology, Volume 27. Published by Order of Her Majesty's Government, Edinburgh, 221 pp.
- Henderson JR (1893) A Contribution to Indian Carcinology. *Transactions of the Linnean Society of London*, Zoology, Vol. 5, Part 10. Printed for the Linnean Society by Taylor and Francis, London, pp. 325–458.
- Henderson JR (1896) Natural history notes from H.M. "Investigator" Commander C. F. Oldham, R. N., commanding — Series II, No. 24. Reports on the Paguridae collected during the season 1893–1894. *Journal of the Asiatic Society of Bengal*, 65: 516–536.
- Herbst JFW (1799–1804) *Versuch einer Naturgeschichte der Krabben und Krebse*. Bd. 3. Bei Gottlieb August Lange, Berlin, part 1: pp. 1–46, part 2: pp. 1–46; part 3: pp. 1–54; part 4: pp. 1–49.
- Hilgendorf F (1869) Crustaceen. In: van der Decken CC (ed.) *Reisen in Ost-Afrika in dem Jahren 1859–1865*. Volume 3. C.F. Winter'sche Verlagshandlung, Leipzig und Heidelberg, pp. 69–116.
- Igawa M & Kato M (2017) A new species of hermit crab, *Diogenes heteropsammicola* (Crustacea, Decapoda, Anomura, Diogenidae), replaces a mutualistic sipunculan in a walking coral symbiosis. *PLoS ONE*, 12(9): e0184311.
- Jones DS & Morgan GJ (2002) *A field guide to crustaceans of Australian waters*. Second Edition. Reed New Holland Publishers, Frenchs Forest, New South Wales, 223 pp.

- Komai T (2001) A review of the north-western Pacific species of the genus *Paguristes* (Decapoda: Anomura: Diogenidae). I. Five species initially reported by Ortmann (1892) from Japan. *Journal of Natural History*, 35: 357–428.
- Komai T (2009) A review of the northwestern Pacific species of the genus *Paguristes* (Decapoda: Anomura: Diogenidae). II. Species transferred to the genus *Stratiotes*, with descriptions of two new species. *Natural History Research*, 10(2): 59–92.
- Komai T (2010) A review of the northwestern Pacific species of the genus *Paguristes* (Decapoda: Anomura: Diogenidae). III. Clarification of the identity of a species heretofore referred to *Paguristes balanophilus* Alcock and descriptions of two new species from Japan. *Natural History Research*, 11(1): 9–33.
- Komai T & Rahayu DL (2014) New records and new species of the hermit crab genus *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae) from the Philippines. *Raffles Bulletin of Zoology*, 62: 620–646.
- Komai T, Reshmi R & Kumar AB (2015a) A new species of the hermit crab genus *Paguristes* Dana, 1851 (Crustacea: Decapoda: Anomura: Diogenidae) from southwestern India. *Zootaxa*, 3937(3): 517–532.
- Komai T, Saito Y & Morin E (2015b) A new species of the hermit crab genus *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae) from shallow coastal waters in Japan, with a checklist of the East Asian species of the genus. *Zootaxa*, 3918(2): 224–238.
- Landschoff J, Komai T, du Plessis A, Gouws G & Griffith CL (2018) MicroCT imaging applied to description of a new species of *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae), with selection of three-dimensional type data. *PLoS ONE*, 13(9): 1–26.
- Lanchester WF (1902) On the Crustacea collected during the “Skeat Expedition” to the Malay Peninsula. *Proceedings of the Zoological Society of London*, 1902: 363–381.
- Latreille PA (1802) *Histoire naturelle, générale et particulière, des Crustacés et des Insectes*, Vol. 3. Paris, 467 pp.
- Lemaitre L & Ng PKL (1996) Rediscovery and redescription of the rare hermit crab, *Diogenes jubatus* (Nobili, 1903) (Crustacea: Decapoda: Anomura: Diogenidae), from Singapore. *Raffles Bulletin of Zoology*, 44: 323–333.
- Lemaitre R, Felder D L & Poupin J (2017) Discovery of a new micro-pagurid fauna (Crustacea: Decapoda: Paguridae) in the Lesser Antilles, Caribbean Sea. *Zoosystema*, 39(2): 151–195.
- Lemaitre R, Rahayu DL & Komai T (2018) A revision of “blanket hermit crab” of the genus *Paguropis* Henderson, 1888 with the description of a new genus and five new species (Crustacea, Anomura, Diogenidae). *ZooKeys*, 752: 17–97.
- Lewinsohn C (1969) Die Anomuren des Roten Meeres (Crustacea Decapoda: Paguridea, Galatheidea, Hippidea). *Zoologische Verhandlungen*, 104: 1–213.
- Lewinsohn C (1982) Eine neue art der Gattung *Spiropagurus* Stimpson (Decapoda: Anomura) aus dem Roten Meer. *Crustaceana*, 42(1): 212–218.
- Lima DJM & Lemaitre R (2016) A new species of hermit crab of the genus *Pagurus* Fabricius, 1775 (Crustacea: Anomura: Paguridae) from the southern Caribbean off Venezuela. *Zootaxa*, 4161(3): 445–450. <http://doi.org/10.11646/zootaxa.4161.3.12>
- Lima D, Tavaréz M & De Mendoça JB Jr (2019) Paguroids (Decapoda: Anomura: Diogenidae and Paguridae) of the remote oceanic Archipelago Trindade and Martin Vaz, off southeast Brazil, with new records, description of three new species and zoogeographical notes. *Zootaxa*, 4694(1): 1–63.
- Low MEY & Rahayu DL (2014) *Pagurus asper* H. Milne Edwards, 1848, a subjective synonym of *Clibanarius longitarsus* (De Haan, 1849) and reversal of precedence (Crustacea: Decapoda: Anomura: Diogenidae). *Zootaxa*, 3811(3): 393–397.
- Malay MC, Rahayu DL & Chan T-Y (2018) Hermit crabs of the genera *Calcinus* Dana, *Clibanarius* Dana, and *Dardanus* Paul'son from the PANGLAO 2004 Expedition, with description of a new species and a checklist of the hermit crabs of the Philippines (Crustacea: Anomura: Paguroidea). *Raffles Bulletin of Zoology*, 66: 23–65.
- Marin I (2016) Notes on holotypes of hermit crabs (Decapoda: Anomura: Paguroidea) deposited in the collection of Zoological Museum of RAS (Saint-Petersburg, Russia) with remarks on hermit crab diversity along the Russian coast of the Sea of Japan. *Zootaxa*, 4105(2): 171–180.
- McCulloch AR (1913) *Studies in Australian Crustacea*. Records of the Australian Museum, 9(3): 321–354.
- McLaughlin PA (2002a) A review of the hermit crab (Decapoda: Anomura: Paguroidea) fauna of southern Thailand, with particular emphasis on the Andaman Sea, and descriptions of three new species. In: Bruce N, Berggren M & Bussawarit S (eds.) *Proceedings of the International Workshop on the Crustacea in the Andaman Sea*, Phuket Marine Biological Center 29 November – 20 December, 1998. Phuket Marine Biological Center Special Publication, 23(2): 385–460.
- McLaughlin PA (2002b) *Diogenes pallescens* Whitelegge, *D. gardineri* Alcock, *D. serenei* Forest (Decapoda; Anomura; Diogenidae): morphological variant or distinct species? *Raffles Bulletin of Zoology*, 50: 81–94.
- McLaughlin PA (2002c) *Pseudopaguristes*, a new and aberrant genus of hermit crabs (Anomura: Paguroidea: Diogenidae). *Micronesica*, 34(2): 185–199.
- McLaughlin PA (2004) *Paguristes puniceus* Henderson, 1896 (Decapoda: Anomura: Paguroidea: Diogenidae): a study in intraspecific variability. *Zootaxa*, 742: 1–28.
- McLaughlin PA (2005) The “*Troglopagurus* group” of *Diogenes* (Decapoda: Anomura: Paguroidea: Diogenidae) revisited. *Journal of Crustacean Biology*, 25(4): 598–619.
- McLaughlin PA (2007a) Australian hermit crabs of the genera *Paguristes* Dana, *Stratiotes* Thomson, and *Pseudopaguristes* McLaughlin (Crustacea: Anomura: Paguroidea: Diogenidae). *Records of the Western Australian Museum, Supplement No. 73*: 185–271.
- McLaughlin PA (2007b) Hermit crabs (Crustacea: Anomura: Paguroidea) of the Dampier Archipelago, Western Australia. *Records of the Western Australian Museum, Supplement No. 73*: 273–288.
- McLaughlin PA & Clark P (1997) A review of the *Diogenes* (Crustacea, Paguroidea) hermit crabs collected by Bedford and Lanchester from Singapore, and from the ‘Skeat’ Expedition to the Malay Peninsula, with a description of a new species and notes on *Diogenes intermedius* De Man, 1892. *Bulletin of the Natural History Museum, London (Zoology)*, 63: 33–49.
- McLaughlin PA & Dworschak PC (2001) Reappraisal of hermit crab species (Decapoda: Anomura: Paguridea) reported by Camill Heller in 1861, 1862 and 1865. *Annalen des Naturhistorische Museum in Wien*, 103B: 135–176.
- McLaughlin PA & Forest J (1999) Hermit crabs of the genus *Pagurus* Fabricius (Crustacea, Decapoda, Paguridae) from South-eastern South Africa. *Annals of the South African Museum*, 105(7): 297–344.
- McLaughlin PA, Komai T, Lemaitre R & Rahayu DL (2010) Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) Part I – Lithodoidea, Lomisoidea and Paguroidea. In: Low MEY & Tan SH (eds.) *Checklists of Anomuran Decapod Crustaceans of the world (Exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) and Marine Lobsters of the World*. *Raffles Bulletin of Zoology, Supplement 23*: 5–107.

- McLaughlin PA & Rahayu DL (2005) Two new species of *Paguristes* sensu stricto (Decapoda: Anomura: Paguroidea: Diogenidae) and a review of *Paguristes pusillus* Henderson. *Zootaxa*, 1083: 37–62.
- McLaughlin PA, Rahayu DL, Komai T & Chan T-Y (2007) A Catalog of the Hermit Crabs (Paguroidea) of Taiwan. National Taiwan Ocean University, 364 pp.
- Miers EJ (1884) Crustacea. In: Report on the zoological collections made in the Indo-Pacific Ocean during the voyage of H.M.S. "Alert" 1881-2. British Museum, London, pp. 178–322, 513–575.
- Milne Edwards H (1836) Observations zoologiques sur les Pagures et description d'un nouveau genre de la tribu des Paguriens. *Annales des Sciences Naturelle Zoologie*, Paris, Series 2, 6: 257–288.
- Milne Edwards H (1848) Note sur quelques nouvelles espèces du genre Pagure. *Annales des Sciences Naturelles Zoologie*, Paris, Series 3, 10: 59–64.
- Miyake S (1978) The crustacean Anomura of Sagami Bay. Biological Laboratory, Imperial Household, Tokyo, 200 pp. [English], 161 pp. [Japanese].
- Miyake S (1982) Japanese Crustacean Decapods and Stomatopods in colour, vol. 1. Macrura, Anomura, Stomatopoda. First printing, Hoikusha, Osaka, vii + 261 pp., 56 pls. [in Japanese]
- Morgan GJ (1987a) A new and aberrant species of *Paguristes* (Anomura: Diogenidae) from northern Australia. *Records of the Western Australian Museum*, 13(3): 379–386.
- Morgan GJ (1987b) Hermit crabs (Decapoda, Anomura: Coenobitidae, Diogenidae, Paguridae) of Darwin and Port Essington, Northern Australia. The Beagle: Records of the Museums and Art Galleries of the Northern Territory, 4: 165–186.
- Morgan GJ (1989) The hermit crabs (Decapoda: Anomura: Diogenidae, Paguridae) of southwestern Australia, with description of two new species. *Records of the Western Australian Museum*, 14(3): 391–417.
- Morgan GJ (1990) A collection of Thalassinidea, Anomura and Brachyura (Crustacea: Decapoda) from the Kimberley region of northwestern Australia. *Zoologische Verhandlungen*, 265: 1–90.
- Morgan GJ & Forest J (1991) Seven new species of hermit crabs from Northern and Western Australia (Decapoda, Anomura, Diogenidae). *Bulletin du Muséum national d'Histoire naturelle*, Paris, Series 4, 12(A): 649–689.
- Negri M, Lemaitre R & Mantelatto FL (2014) Molecular and morphological resurrection of *Clibanarius symmetricus* (Randall, 1840) a cryptic species hiding under the name for the "thinstripe" hermit crab *C. vittatus* (Bosc, 1802) (Decapoda: Anomura: Diogenidae). *Journal of Crustacean Biology*, 36(4): 848–861.
- Nobili G (1903) Crostacei di Singapore. *Bollettino del Museo di Zoologia ed Anatomia comparata della R. Università di Torino*, 18(455): 1–39.
- Nobili G (1905) Décapodes nouveaux des côtes d'Arabie et du Golfe Persique (Diagnoses préliminaires). *Bulletin du Muséum d'Histoire Naturelle*, 11(3): 158–164.
- Nobili G (1906a) Décapodes et Stomatopodes. Mission J. Bonnier et Ch. Perez (Golfe Persique, 1901). *Bulletin Scientifique de la France et de la Belgique*, 40: 13–159.
- Nobili G (1906b) Faune carcinologique de la Mer Rouge, Décapodes et Stomatopodes. *Annales des Science naturelle, Zoologie*, Paris, 9(4): 1–347.
- Osawa M (2012) A new species of the genus *Pagurus* Fabricius, 1775 (Crustacea: Decapoda: Anomura: Paguridae) from the Ryukyu Islands, southwestern Japan. In: Naruse T, Chan T-Y, Tan HH, Ah Yong ST & Reimer JD (eds.) Scientific Results of the Marine Biodiversity Expedition — KUMEJIMA 2009. *Zootaxa*, 3367: 155–164.
- Paul'son O (1875) *Izledovaniya rakoobraznykh krasnago morya s zametkami otnositel'no rakoobraznykh drugikh morei. Chast' 1. Podophthalmata i Edriophthalmata (Cumacea)*. S.V. Kul'zhenko, Kiev, xiv + 144 pp. [Studies on Crustacea of the Red Sea with notes regarding other seas. Podophthalmata and Edriophthalmata (Cumacea).] Translation, Israel Program for Scientific Translations, 1961, National Science Foundation and Smithsonian Institution.
- Poupin J (1997) Les pagures du genre *Calcinus* en Polynésie française avec la description de trois nouvelles espèces (Decapoda, Anomura, Diogenidae). *Zoosystema*, 19: 683–719.
- Poupin J & McLaughlin PA (1998) Additional *Calcinus* (Decapoda, Anomura, Diogenidae) from French Polynesia with three new species and a key to Indo-West Pacific species. *Crustacean Research*, 27: 9–27.
- Quoy JRC & Gaimard JP (1824–1826) *Zoologie*. In: de Freycinet LM (ed.) Voyage autour du monde, entrepris par ordre du roi, sous le ministère et conformément aux instructions de S. Exc. M. le Vicomte du Bouchage, secrétaire d'état du département de la marine, exécuté sur les Corvettes de SM l'Uranie et la Physicienne, pendant les années 1817, 1818, 1819 et 1820. Volume 3. Pillet Aîné, Paris, 712 pp.
- Rahayu DL (1996) Notes on littoral hermit crabs (excluding Coenobitidae) (Crustacea: Decapoda: Anomura) mainly from Singapore and Peninsular Malaysia. *Raffles Bulletin of Zoology*, 44(2): 335–355.
- Rahayu DL (2003) Hermit crab species of the genus *Clibanarius* (Crustacea: Decapoda: Diogenidae) from mangrove habitats in Papua, Indonesia, with description of a new species. *Memoires of Museum Victoria*, 60(1): 99–104.
- Rahayu DL (2005) Additions to the Indonesian fauna of the hermit crab genus *Pseudopaguristes* McLaughlin and a further division of the genus *Paguristes* Dana (Crustacea: Decapoda: Paguroidea: Diogenidae). *Zootaxa*, 831: 1–42.
- Rahayu DL (2006) The genus *Paguristes* (Crustacea, Decapoda, Diogenidae) from Indonesia. In: Richer de Forges B & Justine J-L (eds.) Tropical Deep-Sea Benthos. Vol. 24. *Mémoires du Muséum national d'Histoire naturelle*, 193: 349–374.
- Rahayu DL (2007) The hermit crabs *Paguristes* Dana, 1851 s.l. (Crustacea, Decapoda, Anomura, Diogenidae) from the western Indian Ocean. *Zoosystema*, 29: 515–534.
- Rahayu DL (2010) A new species of *Dardanus* Paul'son from the Southwestern Pacific (Decapoda, Anomura, Diogenidae). In: Fransen CHJM, De Grave S & Ng PKL (eds.) Studies on Malacostraca: Lipke Bijdeley Holthuis Memorial Volume. *Crustaceana Monographs*, 14: 627–635.
- Rahayu DL (2012) A new species of the hermit crab genus *Diogenes* Dana, 1851 (Decapoda Anomura Diogenidae) from Lombok, Indonesia. In: Komatsu H, Okuno J & Fukuoka K (eds.) Studies on Eumalacostraca: a homage to Matsasune Takeda. *Crustaceana Monographs*, 17: 263–274.
- Rahayu DL (2015) New record and new species of the hermit crab genus *Diogenes* Dana, 1851 (Decapoda: Anomura: Diogenidae) from Singapore. *Raffles Bulletin of Zoology*, Supplement 31: 182–192.
- Rahayu DL (2021) Hermit crabs of the family Diogenidae (Crustacea: Decapoda: Anomura) collected during the South Java Deep-Sea 2018 biodiversity cruise in Indonesia, with description of two new species. *Raffles Bulletin of Zoology*, Supplement 36: 162–180.
- Rahayu DL & Forest J (1992) Le genre *Clibanarius* (Crustacea, Decapoda, Diogenidae) en Indonésie, avec la description de six espèces nouvelles. *Bulletin du Muséum national d'Histoire naturelle*, Paris, Series 4, 14(A): 745–779.
- Rahayu DL & Forest J (1995) Le genre *Diogenes* (Crustacea, Decapoda, Diogenidae) en Indonésie, avec la description de

- six espèces nouvelles. Bulletin Muséum National d'Histoire Naturelle, Paris, 16(2–4): 383–415.
- Rahayu DL & Forest J (1999) Sur le statut de *Calcinus gaimardii* (H. Milne Edwards, 1848) (Decapoda, Anomura, Diogenidae) et description de deux espèces nouvelles apparentées. Zoosystema, 21(3): 461–472.
- Rahayu DL & Forest J (2009) Le genre *Paguristes* Dana aux Philippines avec la description de deux nouvelles espèces (Decapoda, Anomura, Diogenidae). Crustaceana, 82(10): 1307–1338.
- Rahayu DL & Hurtle KG (2002) The genus *Diogenes* (Decapoda, Anomura, Diogenidae) from Irian Jaya, Indonesia with description of a new species. Crustaceana, 75(3–4): 609–619.
- Rahayu DL & Komai T (2000) Shallow-water hermit crabs (Crustacea: Decapoda: Anomura: Diogenidae and Paguridae) of Phuket, Thailand. Phuket Marine Biology Center Research Bulletin, 63: 21–44.
- Rahayu DL & McLaughlin PA (2006) Clarifications of the identities of *Paguristes balanophilus* Alcock, 1905 and *P. calvus* Alcock, 1905 (Crustacea, Decapoda, Anomura, Paguroidea, Diogenidae), and the description of another broadly distributed new species. Zoosystema, 28(4): 865–886.
- Rahayu DL, Ng PKL & Shih S-T (2016) A new species of land hermit crab in the genus *Coenobita* Latreille, 1829 from Singapore, Malaysia and Indonesia, previously confused with *C. cavipes* Stimpson, 1858 (Crustacea: Decapoda: Anomura: Coenobitidae). Raffles Bulletin of Zoology, Supplement 34: 470–488.
- Rahayu DL & Ong R (2015) Rediscovery of the hermit crab, *Dardanus hessii*, in Singapore. Singapore Biodiversity Records, 2015: 145–147.
- Rahayu DL & Osawa M (2012) Hermit crabs (Crustacea: Decapoda: Diogenidae) from the KUMEJIMA 2009 Expedition, Japan. In: Naruse T, Chan T-Y, Tan HH, Ahyong ST & Reimer JD (eds.) Scientific Results of the Marine Biodiversity Expedition — KUMEJIMA 2009. Zootaxa, 3367: 176–190.
- Rahayu DL & Pratiwi R (2022) *Diogenes matabiru*, a new species of hermit crab from Lombok Island, Indonesia (Crustacea, Decapoda, Anomura, Diogenidae). Zootaxa, 5093(4): 493–500.
- Roux P (1829) Crustacés de la Méditerranée et de son littorale. Paris, 126 pp., pls. 1–45.
- Sankoli KN (1962) On a new species of hermit crab *Pagurus kulkarnii* sp. nov. (Anomura: Paguridae). Journal of Zoological Society of India, 13: 136–142.
- Siddiqui FA & McLaughlin PA (2003) A new species of the hermit crab genus *Diogenes* (Decapoda: Anomura: Paguroidea: Diogenidae) from Pakistan, with a comparative diagnosis of *D. guttatus* Henderson, 1888. Proceedings of the Biological Society of Washington, 116(4): 956–966.
- Siddiqui FA, Kazmi OB & McLaughlin PA (2004) Review of the Pakistani species of *Diogenes* Dana, 1951 (Decapoda Anomura Paguroidea Diogenidae). Tropical Zoology, 17: 155–200.
- Thompson EF (1943) Paguridae and Coenobitidae. In: The John Murray Expedition 1933–34, Scientific Reports, 7(5): 411–426.
- Tirmizi NM & Siddiqui FA (1982) The marine fauna of Pakistan. 1. Hermit crabs (Crustacea, Anomura). pp. 1–103.
- Whitelegge T (1897) The Crustacea of Funafuti. VI. The Crustacea. Australian Museum Memoirs, 3: 7–151.