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# 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)

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**Abstract.** A new species of land hermit crab in the genus *Coenobita* Latreille, 1829 (Anomura: Coenobitidae), *C. lila*, is described from Singapore and adjacent countries. The new species has previously been confused with *C. cavipes* Stimpson, 1858, but they can be distinguished by the former possessing dense tubercles on the outer face of the palm of the left cheliped and the presence of a large sternal protuberance between the male fifth pereopods. Recognition of the new species is further supported by molecular data. In this study, the presence of *C. cavipes* in Taiwan is confirmed, and the status of *C. baltzeri* Neumann, 1878, is discussed.

**Key words.** Land hermit crab, taxonomy, *Coenobita lila*, new species, *C. cavipes*, *C. baltzeri*, molecular data

## INTRODUCTION

The common land hermit crab *Coenobita cavipes* Stimpson, 1858, was described from Loo Cho (= Ryukyu Islands, Japan) (Nakasone, 1988: 172) by Stimpson (1858) and is regarded as widely distributed in the Indo-West Pacific region. As discussed by Fize & Serène (1955) and Nakasone (1988), this species had previously been confused with *C. violascens* Heller, 1862, probably because both species have purple or violet chelae, and lack laminar teeth on the upper part of the outer surface of their left palm (i.e., a stridulatory ridge). Fize & Serène (1955) synonymized the two species, but Nakasone (1988), who examined many specimens from the Ryukyus, regarded *C. cavipes* as a distinct species. He distinguished the two species by the shape of the lower margin of the palm of the left cheliped (concave or straight in *C. violascens*, convex or triangular in *C. cavipes*), the form of the inner margin and surface of the propodus of the left third pereopod (projecting and noticeably concave in *C. violascens*, projecting but straight or only very slightly concave in *C. cavipes*), the colour of the chela and body (violet in *C. violascens*, brown in *C. cavipes*), and the relative size of the sternal protuberance between the coxae of the male fifth pereopods (small in *C. violascens*, moderately large in *C. cavipes*). McLaughlin et al. (2010) followed Nakasone (1988) in recognising the species as distinct and treated *C. baltzeri* Neumann, 1878 (described from Java), as a junior subjective synonym of *C. cavipes*.

Recently, the authors examined a large series of museum and fresh specimens identified as "*C. cavipes*" from Singapore and adjacent areas, as well as from various localities in the Indo-West Pacific, as part of a reappraisal of Indo-West Pacific species of *Coenobita*. The material from Singapore and adjacent areas consistently differed from that of this species from other parts of Asia, notably from the Ryukyu Islands in Japan, the type locality of *C. cavipes*. The type of *C. baltzeri* Neumann, 1878, was also examined. *Coenobita baltzeri* is not related to *C. cavipes* and is probably a junior synonym of *C. violascens* instead (see later). What has been called "*C. cavipes*" from Singapore and adjacent areas is here recognised as a new species, *C. lila*. The morphological differences between the new species and *C. cavipes* s. str. are also supported by molecular data (viz. the mitochondrial cytochrome oxidase subunit I or COI).

The present paper describes the new species and compares it with *C. cavipes* s. str. Taxonomic notes are also provided for *C. cavipes* s. str. and the identity of *C. baltzeri*. The presence of *C. cavipes* s. str. in Taiwan is also confirmed.

## MATERIAL AND METHODS

The recent material used in this study originated from the Comprehensive Marine Biodiversity Survey (CMBS), a national programme to inventorise Singapore's marine fauna. They were obtained during the CMBS Singapore

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Table 1. The haplotypes of cytochrome c oxidase subunit I (COI) of specimens of *Coenobita* species used in this study. Abbreviations of museums or universities see methods.

| Species | Locality | Catalogue no. | Haplotype | Access. no. of COI |
|---|---|---|---|---|
| *C. lila* n. sp. | Singapore: Labrador Beach | ZRC 1992.8465–8468 | COs1 | AB998647 |
| | Singapore: Big Sister Island | NCHUZOOL 13634 | COs1 | AB998647 |
| | Singapore: St John's Island | NCHUZOOL 13624 | COs1 | AB998647 |
| | Singapore: St John's Island | NCHUZOOL 13635 | COs2 | AB998648 |
| | Singapore: Pulau Jong | NCHUZOOL 13636 | COs3 | AB998649 |
| | Singapore: St John's Island | NCHUZOOL 13635 | COs4 | AB998650 |
| | Singapore: St John's Island | NCHUZOOL 13624 | COs5 | AB998651 |
| | Indonesia: Batam | ZRC | COs6 | AB998652 |
| *C. cavipes* | Taiwan: Lyudao, Taitung | NCHUZOOL 13625 | COc1 | AB998653 |
| | Taiwan: Lyudao, Taitung | NCHUZOOL 13626 | COc2 | AB998654 |
| | Taiwan: Houwan, Kenting, Pingtung | NCHUZOOL 13627 | COc3 | AB998655 |
| | Taiwan: Yuanjhonggang, Kaohsiung | NCHUZOOL 13628 | COc4 | AB998656 |
| | Philippines: Kawasan Falls, Cebu | UF 11345 | COc5 | AB998657 |
| *C. violascens* | Taiwan: Yuanjhonggang, Kaohsiung | NCHUZOOL 13629, 13630 | COv1, 2 | AB998658, AB998659 |
| | Taiwan: Dongsha I., Kaohsiung | NCHUZOOL 13631, 13632, 13633 | COv3, 4, 5 | AB998660, AB998661, AB998662 |
| | Philippines: Kawasan Falls, Cebu | ZRC | COv6 | AB998663 |
| | Philippines: Kawasan Falls, Cebu | UF 11347 | COv7 | AB998664 |

Strait International Workshop in 2013. Specimens examined are deposited in the Zoological Reference Collection (ZRC) of the Lee Kong Chian Natural History Museum (ex Raffles Museum of Biodiversity Research), National University of Singapore; the Zoological Collections of the Department of Life Science, National Chung Hsing University (NCHUZOOL), Taichung, Taiwan; Museum Zoologi Bogor (MZB), Indonesian Institute of Sciences, Cibinong, Indonesia; Ryukyus University Museum, Fujukan (RUMF), Okinawa, Japan; Florida Museum of Natural History, University of Florida, Florida, USA (UF); Muséum national d'Histoire naturelle, Paris, France (MNHN); and Senckenberg Museum Forschunginstitut, Frankfurt am Main, Germany (SMF). Descriptive terminology follows that of McLaughlin et al. (2007), except for the coxae of P5; and for sexual tube which follows Tudge & Lemaitre (2006). Shield length (sl), in millimetres, is measured from the tip of the rostrum to the posterior margin of the shield. The abbreviations P2, P3, P4 and P5 refer to the second, third, fourth, and fifth pereopods, respectively.

Sequences of COI from the specimens of *C. cavipes*, *C.violascens* and *C. lila* n. sp. (Table 1) were obtained following the method described in Shih et al. (2013) and subsequently analysed. Pairwise estimates of Kimura 2-parameter (K2P) distance (Kimura, 1980) for genetic diversities between sequences were also calculated by MEGA (vers. 5, Tamura et al., 2011). Sequences of the different haplotypes were deposited in the DNA Data Bank of Japan (DDBJ) (accession numbers in Table 1).

**Comparative material.** ***Coenobita baltzeri*** **Newmann, 1878** – holotype male (sl 20.5 mm) (SMF 19223); 1 female (sl 10.1 mm) (SMF 9697), "Ost Indien". ***Coenobita violascens*** **Heller, 1862 – Taiwan**: 1 female (sl 13.4 mm) (NCHUZOOL 13629), Yuanjhonggang, Kaohsiung, coll. J-H Lee, 6 June 2012; 1 male (sl 7.2 mm) (NCHUZOOL 13630), Yuanjhonggang, Kaohsiung, coll. J-H Lee, 4 August 2012; 1 male (sl 20.2 mm) (NCHUZOOL 13631), Dongsha I., Kaohsiung, 17 November 2011; 1 male (sl 8.2 mm) (NCHUZOOL 13632), Dongsha I., Kaohsiung, 22 March 2012; 1 male (sl 22.2 mm) (NCHUZOOL 13633), Dongsha I., Kaohsiung, 2013. **Philippines**: 3 males (sl 8.2–15.1 mm) (ZRC), M56, Momo Beach, Panglao Island, 9°36.1'N, 123°45.2'E, upper intertidal rocky cliff at night, PANGLAO 2004, 2 July 2004; 1 male (sl 12.7 mm) (ZRC), station M9, Panglao Island, inside lagoon near Doljo Point, 9°35.1'N, 123°43.6'E, muddy sand flat with seagrass, fringe mangroves, PANGLAO 2004, 4 June 2004; 1 female (sl 13.2 mm) (ZRC), Panglao, 3 March 2004; 1 male (sl 7.2 mm) (ZRC), Kawasan Falls, Cebu, coll. PKL Ng et al., 30 July 2003; 1 female (sl 7.8 mm) (UF 11347), Kawasan Falls, Cebu, coll. H-C Liu, 25 April 2005. **Thailand**: 1 male (sl 15.3 mm) (ZRC 1992.8430), Phuket, May 1981; 1 male (sl 17.8 mm), 1 female (sl 19.2 mm) (ZRC), Phuket, coll. JCY Lai, 22 February 2006; 2 males (sl 7.3–7.7 mm), 3 females (sl 7.7–10.9 mm) (ZRC) Chalung, Palai, Phuket, 28 May 2012; 1 male (sl 10.7 mm), 2 females (sl 7.3–11.0 mm) (ZRC), Phangnga Province, 24 May 2012. **Madagascar:** 2 males (sl 8.7–17.4 mm) (ZRC THH04-12), southern Madagascar, coll. HH Tan, 29 January–2 February 2004. **Mayotte:** 2 females (sl 11.5–12.4 mm) (MNHN-IU-2009-1575), Plage de Trévani, coll. J Dumas, J Poupin & R Cléva, 1 November 2009.

## TAXONOMY

### Family Coenobitidae Dana, 1851

### Genus *Coenobita* Latreille, 1829

### *Coenobita lila* n. sp.

(Figs. 1–3, 4A–C, 5A–C, 6A–C, 10, 11A–C)

*Coenobita cavipes* – Lim et al., 1994: 29, 1 un-numbered fig.; Ng & Sivasothi, 1999: 85, 1 un-numbered fig.; Ng et al., 2007: 69. (not *Coenobita cavipes* Stimpson, 1858).

*Coenobita rugosus* – Ng et al., 2007: 70, 71, 3 un-numbered figs. (not *Coenobita rugosus* H. Milne Edwards, 1837).

*Coenobita purpureus* – Ng et al., 2008: 107, 2 un-numbered figs. (not *Coenobita purpureus* Stimpson, 1858).

**Material examined.** Holotype: male (sl 16.7 mm) (ZRC 2016.0037), station SW78, St John's Island, Singapore, 1°12.907'N, 103°51.069'E, grass patch, south of lagoon, coll. CMBS, 25 May 2013 (SS2693). Paratypes: **Singapore**: 2 males (sl 17.5–19.2 mm), 2 females (sl 11.8–14.2 mm), 1 ovigerous female (sl 10.8 mm) (ZRC 2016.0038), same data as holotype; 1 male (sl 18.9 mm), 3 females (sl 9.6–11.5 mm), 3 ovigerous females (sl 9.4–10.6 mm) (ZRC 2016.0039), station SW7, St John's Island, 1°12.928'N, 103°51.099'E, pontoon south lagoon, 20 May 2013; 1 female (sl 6.6 mm) (ZRC 2016.0040), station SW22, St John's Island, coll. CMBS, 21 May 2013; 3 males (sl 4.6–13.7 mm), 5 females (sl 8.5–10.2 mm) (ZRC 2016.0041), station IT93, Pulau Jong, 1°12.901'N, 103°47.194'E, coll. CMBS, 28 May 2013; 4 males (sl 8.7–13.0 mm), 3 females (sl 10.0–13.9 mm), 2 ovigerous females (sl 10.5–11.0 mm) (ZRC 2016.0042), station SW87, Pulau Semakau, coll. CMBS, 27 May 2013; 1 male (sl 18.6 mm) (ZRC 2016.0043) St John's Islands, coll. 28 April 1997; 1 ovigerous female (sl 7.2 mm) (ZRC 1992.8465-8468), Labrador Beach, coll. PKL Ng, 26 November, 1991; 1 male (sl 15.3 mm) (NCHUZOOL 13634), station IT102, Big Sister Island, 29 May 2013; 4 males (sl 10.0– 16.0 mm), 4 females (sl 8.0–11.1 mm), 4 ovigerous females (sl 8.5–12.7 mm) (NCHUZOOL 13635), station SW78, St. John Island, coll. CMBS, 25 May 2013; 1 male (sl 10.9 mm), 1 female (sl 5.4 mm) (NCHUZOOL 13624), St John's Island, coll. H-T Shih et al., 10 February 2014; 3 males (sl 4.0–13.9 mm), 7 females (sl 4.7–10.4 mm), 1 ovigerous female (sl 10.4 mm) (NCHUZOOL 13636), station IT93, Pulau Jong Island, coll. CMBS, 28 May 2013. Others: **Indonesia**: 6 males (sl 8.4–16.9 mm), 4 females (sl 8.8–13.9 mm), 2 ovigerous females (sl 9.0–10.6 mm) (ZRC 2016.0044), Sekupang, Batam, coll. PKL Ng, 1 October 1989. **Malaysia**: 3 males (sl 12.6–13.6 mm) (ZRC 2016.0045), Pulau Rumbia, Perak, 9–12 June 1994; 1 male (sl 7.3 mm) (ZRC 2016.0046), south of Golf Resort, Desaru, 11 May 1999.

**Description.** Shield (Fig. 1A) transversely convex, about 1.6 times as long as broad; anterior margin between rostrum and lateral projections slightly concave; lateral projection produced, terminating in blunt spine; posterior margin slightly rounded. Rostrum broadly rounded, obsolete. Lateral surface slightly punctate; dorsal surface scattered with small and large tubercles.

Ocular peduncles strongly compressed laterally, mesial surface shallowly concave distally, reaching half length of ultimate segment of antennal peduncles; cornea small, occupying only one-third of distal part of ocular peduncles laterally; dorsal surface with scattered small tubercles and short setae. Ocular acicles triangular, crossing at tip, terminating acutely.

Antennular peduncles (Fig. 1B) long. Basal segment 0.7 times as long as penultimate segment. Ultimate segment almost as long as or slightly longer than penultimate segment. Upper rami of flagella stick-like, terminating in rounded tip, with very short setae on lateral and mesial margins.

Antennal peduncles (Fig. 1A, C) exceeding ocular peduncles by half length of fifth segment, reaching half length of penultimate segment of antennular peduncles. First segment 1.2 times as long as broad. Second segment stout, covered with small tubercles. Third to fifth segments unarmed, with scattered, very short setae. Antennal acicle fused to second segment of peduncle. Flagella long, overreaching tip of right cheliped.

Chelipeds unequal, dissimilar; left distinctly larger than right (Figs. 2A, 4A–C). Dactylus of left cheliped approximately as long as palm; outer surface with numerous tubercles, with tufts of short setae, upper margin and inner surface with rows of corneous-tipped tubercles and tufts of short, stiff setae; cutting edge with one large tooth proximally followed by several smaller teeth, terminating in small corneous claw. Palm without stridulatory apparatus on upper outer surface, upper margin with brush of long, coarse setae on proximal half and row of large, corneous-tipped tubercles; upper half of outer face with rows of large tubercles, some corneous-tipped; rows of smaller corneous-tipped tubercles medially, fewer smaller tubercles on lower half; lower margin with corneous-tipped tubercles bearing tufts of short setae; lower proximal part angled, forming slightly oblique lobe-like projection, continued to slightly upright lower margin of fixed finger; inner surface with scattered corneous-tipped tubercles and short setae, brush of setae proximally near upper margin. Fixed finger with scattered, large tubercles on outer surface, each tubercle with two or three short setae; lower margin with row of large tubercles, some corneous-tipped; cutting edge with row of large teeth terminating in small corneous claw; inner surface with scattered corneous-tipped tubercles and short setae. Carpus with corneous-tipped tubercles on outer surfaces, slightly larger tubercles near upper margin; each tubercle with tufts of setae; inner face smooth but with long, dense setae on distal margin. Merus with transverse rows of flattened, corneous-tipped tubercles on outer surface, these tubercles with very short setae; lower outer and inner margins each with tubercles and tufts of short setae, inner surface smooth.

Palm of right cheliped (Fig. 2B) with thick brush of long coarse setae on upper margin; outer surface of palm and

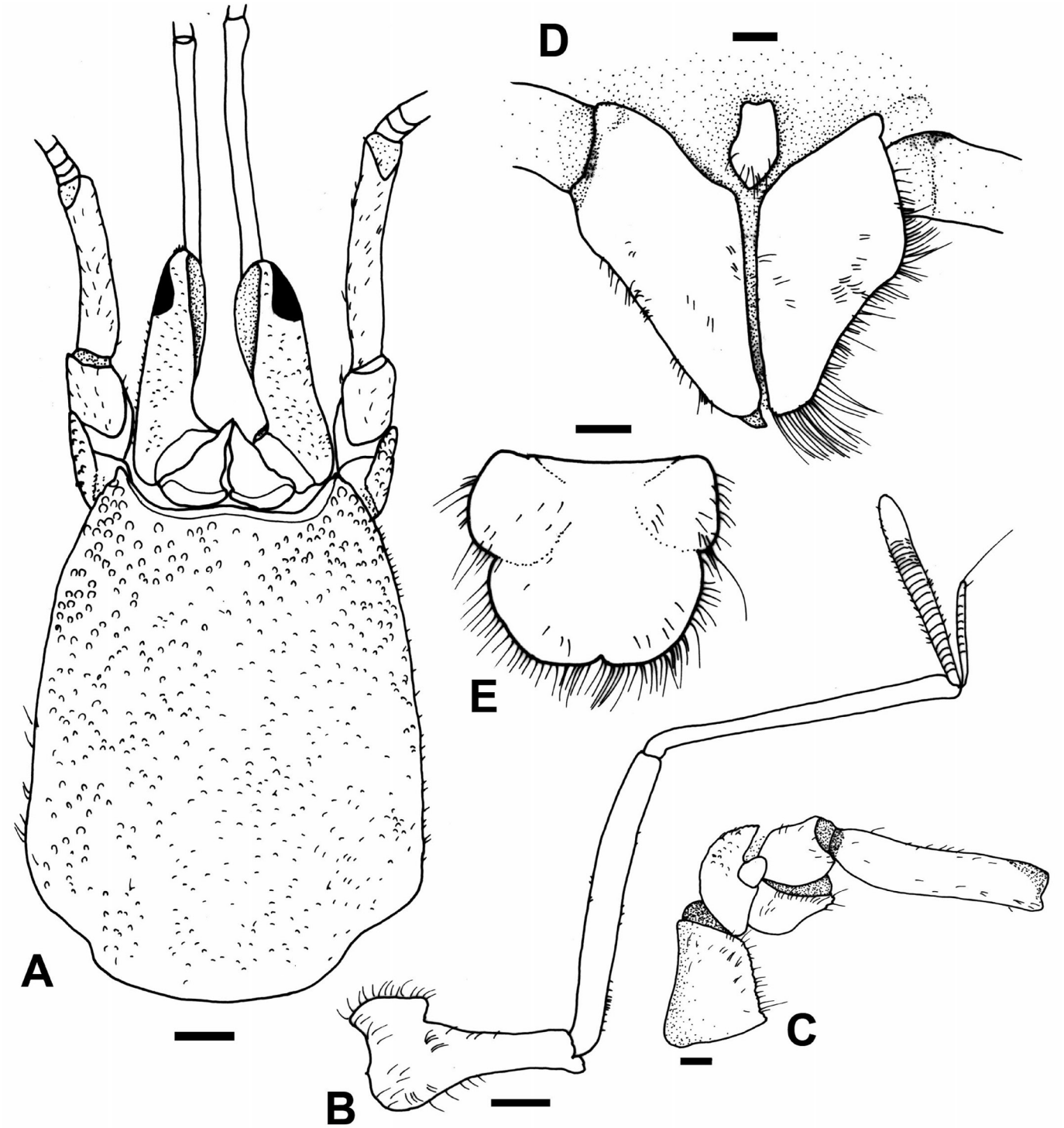


Fig. 1. *Coenobita lila* n. sp., holotype male (sl 16.7 mm) (ZRC 2016.0037). A, shield and cephalic appendages; B, right antennular peduncle, lateral view; C, right antennal peduncles, lateral view; D, sternite and coxae of male P5; E, telson. Setae partially omitted. Scale bars = 2.0 mm [A, B]; 1.0 mm [C–E].

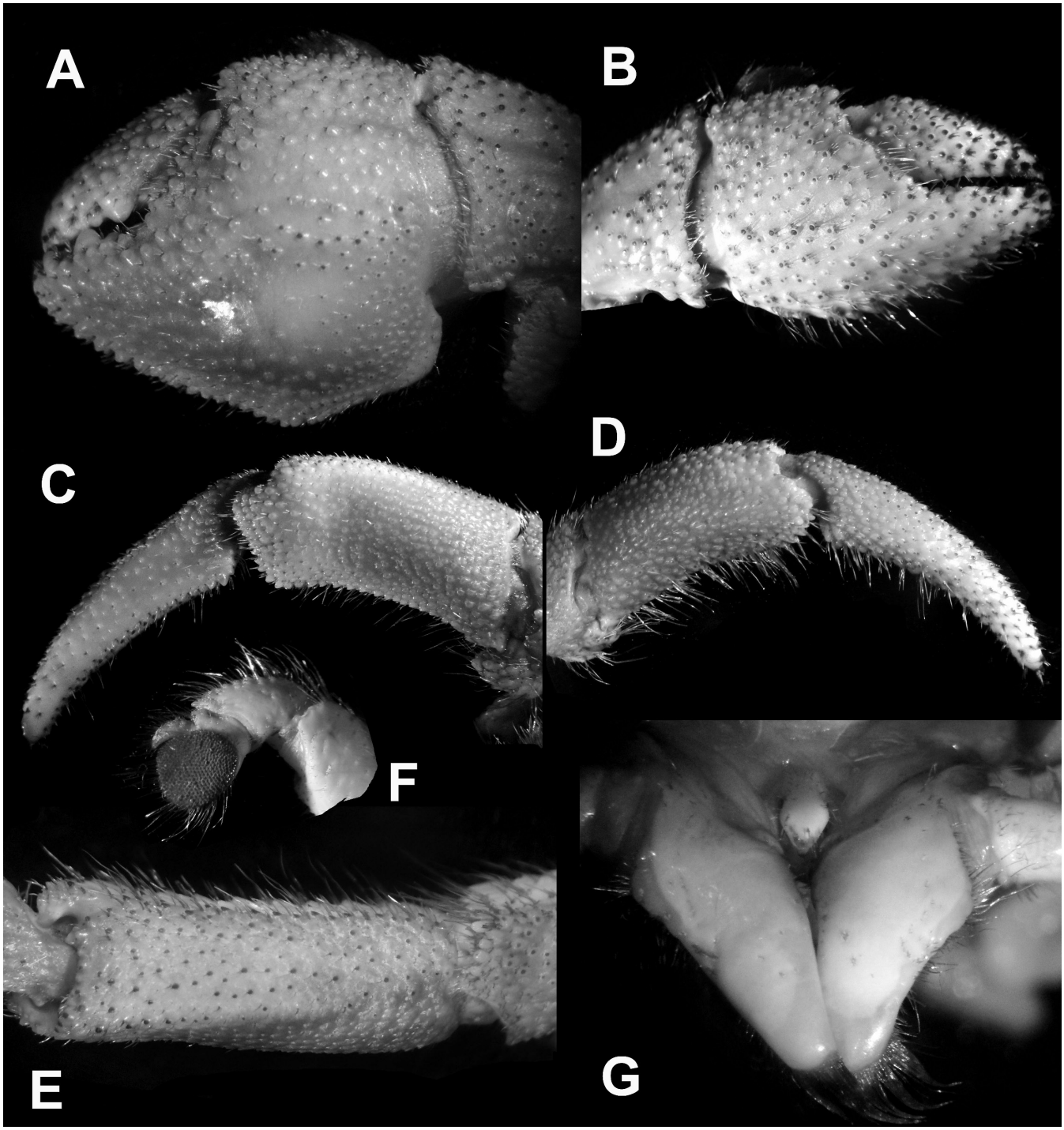


Fig. 2. *Coenobita lila* n. sp., holotype male (sl 16.7 mm) (ZRC). A, left cheliped, outer view; B, right cheliped, outer view; C, dactylus and propodus of left P3, lateral view; D, dactylus and propodus of right P3, lateral view; E, dorsal surface of propodus of left P3; F, left P4 lateral view; G, sternite and coxae of male P5.

dactylus with rows of corneous-tipped tubercles, each with two or three long setae. Inner surfaces of palm and dactylus with scattered corneous-tipped tubercles, each with tufts of setae; proximal area of palm with long, coarse setae near upper margin. Carpus and merus similarly armed as left cheliped.

P2 and P3 dissimilar, P2 slightly shorter, more slender than P3. Dactylus of left P2 with lateral and dorsal surfaces flattened, with rows of corneous-tipped, sometimes flattened, tubercles; mesial face with rows of numerous corneous-tipped tubercles each bearing tufts of short setae; ventral surface (Fig. 3A) with longitudinal ridge consisting of row of tiny corneous teeth, ventrolateral margin with row of corneous-tipped tubercles and tufts of short setae. Propodus with small corneous-tipped tubercles, with two or three setae on lateral surface; dorsal surface broad, with row of corneous-tipped tubercles on dorsomesial margin; mesial surface concave, smooth except for few small tubercles and setae, delimited ventrally by longitudinal row of corneous teeth; ventrolateral surface with row of corneous-tipped tubercles and relatively long setae. Carpus with rows of small tubercles on dorsolateral margin, each bearing two or three short setae; lateral surface with numerous corneous-tipped tubercles, each with tufts of setae; ventrolateral margin with larger corneous-tipped tubercles each with tufts of setae; mesial face slightly concave with scattered tufts of short setae; ventromesial face with sparse tufts of short setae. Merus compressed laterally and mesially, lateral and mesial faces smooth, except for several tubercles distolaterally. Right P2 slightly longer, more slender than left, dactylus (Fig. 3C) covered entirely with corneous-tipped tubercles, dorsal margin not delimited. Propodus covered with corneous-tipped tubercles on dorsal and lateral faces; dorsal margin with row of corneous-tipped tubercles and tufts of short setae; mesial face slightly concave with few tufts of short setae; ventral margin with row corneous-tipped tubercles and tufts of long setae. Carpus and merus as in left P2.

Left P3 with dactylus (Figs. 2C, 5A–C), 1.2–1.4 times longer than propodus, lateral face slightly convex distally, flat proximally, with small, corneous-tipped tubercles distally, punctate proximally, with tufts of short setae, delimited by row of corneous-tipped spines dorsally; dorsal surface broad, having longitudinal rows of corneous-tipped tubercles, decreasing in size proximally; mesial surface with rows of corneous-tipped spines each bearing tufts of setae; ventral margin with row of small corneous spines laterally; ventral surface (Fig. 3B) with longitudinal ridge consisting of row of tiny corneous teeth. Propodus slightly flattened distally on lateral surface, slightly convex proximally, covered with tubercles, some corneous-tipped, each tubercle with tufts of short setae; dorsolateral margin delimited in distal four-fifths by row of corneous-tipped tubercles; dorsal surface (Figs. 2E, 6A–C) flattened, broadened distally, slightly narrowing proximally, with rows of small tubercles, some with corneous tip; dorsomesial margin delimited by row of corneous-tipped tubercles and short setae; mesial surface with numerous corneous-tipped tubercles each with tufts of setae; ventral surface slightly concave with irregular rows of corneous-tipped tubercles, each with tufts of long setae; ventrolateral margin with longitudinal row of small corneous teeth with tufts of sparse setae. Carpus with rows of small tubercles each with two or three short setae on dorsolateral margin, lateral face with numerous corneous-tipped tubercles each with tufts of setae; ventrolateral margin with moderately large spines each with tufts of setae; mesial face almost smooth except for few tufts of short setae. Merus compressed laterally and mesially, transverse row of flattened tubercles on lateral surface; mesial face almost smooth, ventral margin with moderately large spines and tufts of long setae. Right P3 longer, more slender than left, with longer and denser setae on ventral margin. Dactylus and propodus (Fig. 2D) covered entirely with tubercles, corneous-tipped tubercles mainly on dorso- and ventrolateral surface (Fig. 3D); dorsal margin not delimited; mesial face of dactylus with rows of corneous-tipped tubercles and tufts of setae, mesial face of propodus with sparse small tubercles and short setae. Carpus and merus as in left P3.

P4 semi-chelate (Fig. 2F). Dactylus with row of small corneous teeth ventrally, long, coarse setae dorsally; propodal rasp well developed, occupying large, semicircular area, consisting of numerous corneous scales. P5 chelate.

In male, coxae of P5 thick, forming moderately long, calcified sexual tube, subtriangular, left tube slightly broader than right. Gonopore positioned on small, triangular posterior projection or papillae, obscured by coarse, dense setae; moderately large, subpentagonal sternal protuberance between both coxae (Figs. 1D, 2G).

Telson (Fig. 1E) with distinct lateral indentation, separating anterior and posterior lobes. Anterior lobe shorter than posterior lobe. Posterior lobes almost symmetrical, separated by narrow median cleft; margins with row of setae.

**Color in life.** Usually purple, violet, or pale violet in adults (Figs. 10A, C, F, 11A). Surface of shield with patch of dark purple or light brown anteriorly, transverse dark brown line distally; light purple medially and posteriorly. Ocular peduncles light purple with whitish purple tubercles dorsally, light brown mesially; cornea dark brown. Antennal and antennular peduncles brown. Chelipeds purple with corneous-tipped tubercles dark brown; setae on upper margin and inner surface of palm brown. P2 and P3 purple with corneous-tipped tubercles dark brown, carpus and merus with longitudinal streak of light brown. In some females, shield light purple or greenish brown tinge with patches of brown and dark brown; palm of left cheliped with large patch of brown on lower outer surface. Small females light purple, greenish white or yellowish green (Figs. 10D, E, 11C), with patches of dark brown on shield, ocular acicles and palm of left cheliped.

**Variation.** The species shows considerable variation in morphology and live colouration. The shape of the lobe-like projection on the lower margin of the left cheliped differs in specimens and this is not related to size or sex. In the male holotype (sl 16.7 mm) (ZRC) and one female paratype

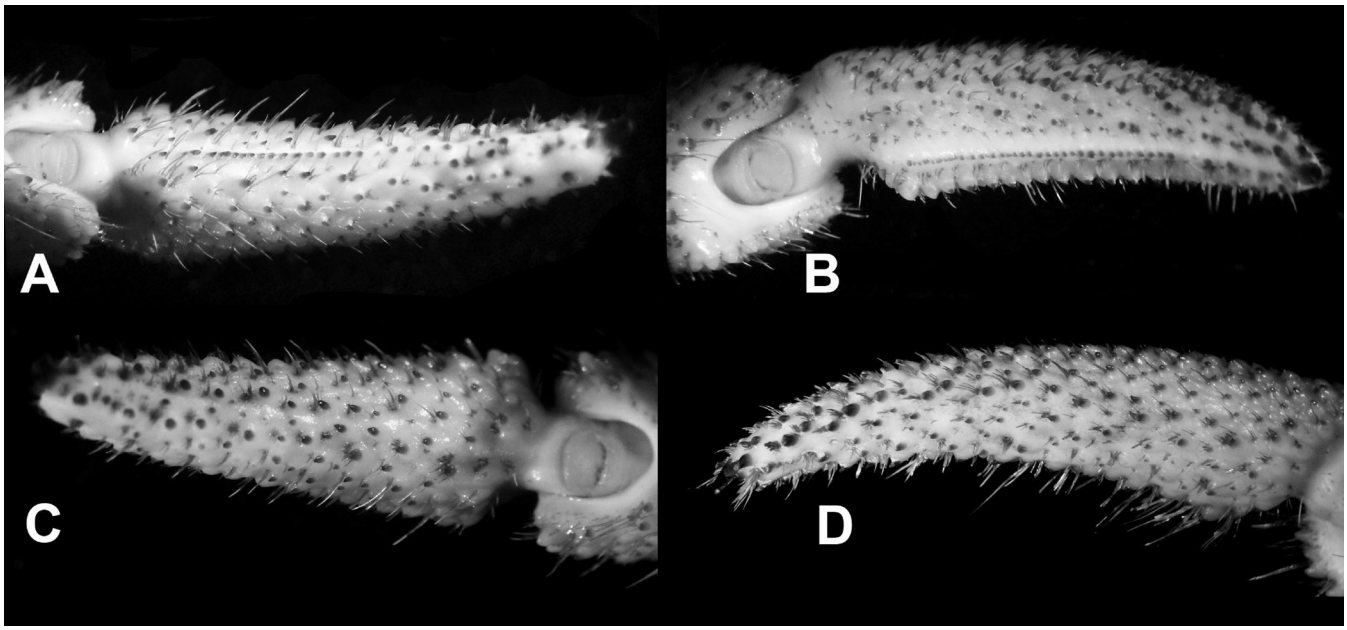


Fig. 3. *Coenobita lila* n. sp., holotype male (sl 16.7 mm) (ZRC 2016.0037). A, dactylus of left P2, ventral view; B, dactylus of left P3, mesioventral view; C, dactylus of right P2, ventral view; D, dactylus of right P3, ventral view.

(sl 10.1 mm) (ZRC), the lobe-like projection on the lower margin of palm of the left cheliped is broad, the oblique proximal lower margin forms triangular angle continued in a straight line to slightly upright lower margin of fixed finger (Figs. 2A, 4B); in other female paratypes the lobe-like projection is broad, rounded, continued in straight line to slightly upright lower margin of fixed finger (Fig. 4A, C). The dorsal surface of the propodus of the left P3 of male holotype is broad, delimited by row of weak tubercles (Fig. 2E), while in females paratypes, the dorsal surface of the left P3 is broad, only slightly delimited (Fig. 6C) or not at all (Fig. 6A, B). The coloration varied from dark to light purple, dark to light brown, or greenish white and yellowish green or brown.

**Etymology.** The name is derived from the Latin "*lila*" for lilac or light purple, alluding to the live colour of adult individuals. The name is used as noun in apposition.

**Habitat.** Upper intertidal to 100 m inland from the beach, sometimes crowding in the supralittoral grass beds or under stones during the day. It is typically found in reef habitats, but may also occur at the edge of mangroves and other estuarine habitats. It is the only species of *Coenobita* found in Singapore thus far.

**Distribution.** Singapore; Malaysia; and Indonesia.

**Remarks.** See discussion for next species.

### *Coenobita cavipes* Stimpson, 1858
(Figs. 4D–F, 5D–F, 6D–F, 7–9, 11D–F)

*Coenobita cavipes* Stimpson, 1858: 245; 1907: 200; Takahashi, 1934: 513 (in part?); Fize & Serène, 1955: 30 (in part), not fig. 5 (= *C. violascens*); Haig & Ball, 1988: 156; Nakasone, 1988: 171, fig. 172; Yu & Foo, 1991: 59, 1 unnumbered fig. (in part?); Chen & Luo, 2014: 167: 3 unnumbered figs.

*Coenobita violascens* – McLaughlin et al., 2007: 17–18, 2 unnumbered figs. (in part); Lin et al., 2011: 30–31, 2 unnumbered figs.

**Material examined**. **Japan:** 1 male (sl 14.5 mm) (RUMF-ZC-2407), off Ginowan Fishing Port, Okinawa Island, Ryukyus, coll. S Shokita, 27 August 1998; 1 female (sl 12.6 mm) (RUMF-ZC-2256), Nakanoshima Beach, Shimoji Island, Miyako Islands, Ryukyus, coll. Y. Fujita, 22 September 2012; 1 male (sl 16.1 mm) (RUMF-ZC-2255), Nakanoshima Beach, Shimoji Island, Miyako Islands, Ryukyus, coll. Y Fujita, 22 September 2012; 1 ovigerous female (sl 17.3 mm) (RUMF-ZC-2128), Kannonzaki, Ishigaki, Ryukyus, coll. Y Fujita, 11 August 2008. **Taiwan:** 1 female (sl 8.3 mm), 4 ovigerous females (sl 6.4–8.2 mm) (RUMF-ZC-656), Lanyu, Taitung, coll. S Shokita, 12 August 1979; 1 male (sl 4.0 mm) (NCHUZOOL 13625), Lyudao, Taitung, 21 April 2012; 1 male (sl 16.7 mm) (NCHUZOOL 13626), Lyudao, Taitung, 13 May 1998; 1 male (sl 15.5 mm) (NCHUZOOL 13627), Houwan, Kenting, Pingtung, 1 April 2012; 4 females (sl 13.5–17.4 mm) (NCHUZOOL 13637), Houwan, Kenting, Pingtung, 7 May 2012; 1 male (sl 14.4 mm) (NCHUZOOL 13628), Yuanjhonggang, Kaohsiung, coll. J-H Lee, 4 August 2012. **Philippines:** 2 females (sl 5.9–9.2 mm) (ZRC 2008.0501), Kawasan Falls, Matutinao, Cebu, coll. PKL Ng et al., 2 December 2001; 1 male (sl 13.5 mm) (UF 11345), Kawasan Falls, Cebu, Philippines, coll. H-C Liu, 25 April 2005. **Indonesia:** 10 males (sl 5.1–10.5 mm), 5 females (sl 7.4–11.5 mm) (MZB), Pantai Walengkabola, Pulau Muna, 05°11.05'5''S, 122°35'10.4''E, coll. D Wowor, 12 September 2007;1 male (sl 11.8 mm) (ZRC), Manado, North Sulawesi, coll. NK Ng, 25 September 2003. **Malaysia:** 1 male (sl 18.9 mm) (ZRC), Bako National Park, Ulu Assam, Sarawak, coll. PKL Ng, 29 June 1996.

**Description.** Shield (Fig. 7A) transversely convex, about 1.7 times as long as broad; anterior margin between rostrum

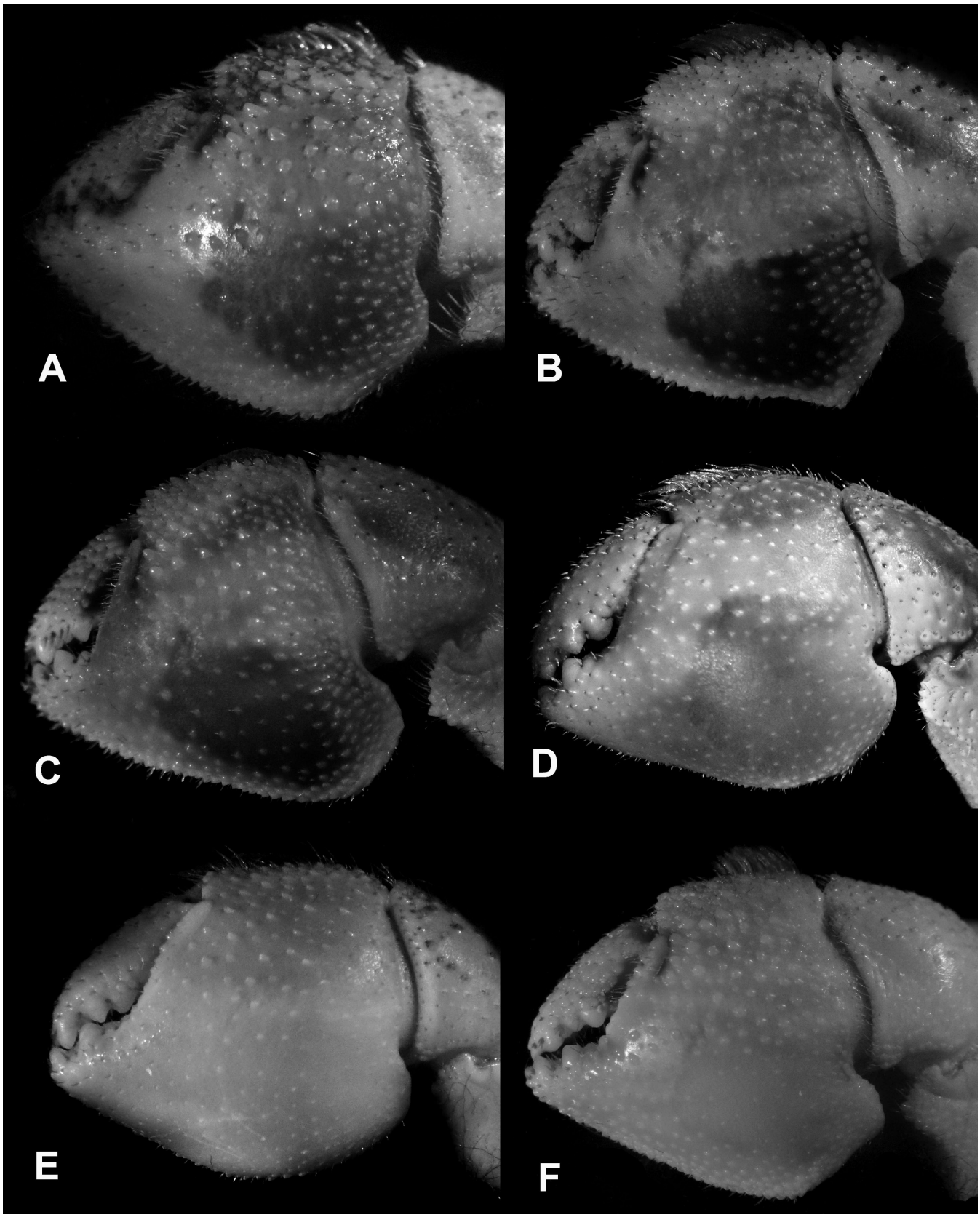


Fig. 4. Left cheliped, outer view. A–C, *Coenobita lila* n. sp.: A, paratype female (sl 10.1 mm) (ZRC); B, paratype female (sl 10.1 mm) (ZRC); C, paratype female (sl 6.6 mm) (ZRC). D–F, *C. cavipes* Stimpson, 1858: D, female (sl 12.6 mm) (RUMF-ZC-2256); E, female (sl 8.2 mm) (RUMF-ZC-656); F, female (sl 11.7 mm) (ZRC).


Fig. 5. Left P3, outer view. A–C, *Coenobita lila* n. sp.: A, paratype female (sl 10.1 mm) (ZRC); B, paratype female (sl 6.6 mm) (ZRC); C, paratype female (sl 10.1 mm) (ZRC). D–F, *C. cavipes* Stimpson, 1858: D, female (sl 12.6 mm) (RUMF-ZC-2256); E, female (sl 8.2 mm) (RUMF-ZC-656); F, female (sl 11.7 mm) (ZRC).

and lateral projections slightly concave; lateral projection produced, terminating in pointed spine; posterior margin straight. Rostrum broadly rounded, obsolete. Lateral surface smooth, with numerous tufts of long setae; dorsal surface punctate, small tubercles on dorsolateral surface, with tufts of short setae.

Ocular peduncles compressed laterally, mesial surface shallowly concave proximally, reaching one- fifth proximal of ultimate segment of antennal peduncles; cornea small, occupying half of distal part of ocular peduncles laterally; dorsal surface with scattered small tubercles and short, long setae on distal third quarter. Ocular acicles triangular, terminating acutely.

Antennular peduncles (Fig. 7B) long. Basal segment 0.9 times as long as penultimate segment. Ultimate segment 1.1 times as long as penultimate segment. Upper rami of flagella stick-like terminating in rounded tip, with very short setae on lateral and mesial margins.

Antennal peduncles (Fig. 7C) exceeding ocular peduncles by one-third length of fifth segment, reaching third proximal of penultimate segment of antennular peduncles. First segment 1.6 times as long as broad. Second segment slender, covered by small tubercles. Third to fifth segments unarmed, with scattered, very short setae. Antennal acicle fused to second segment of peduncle. Flagella long, far exceeding tip of left cheliped.

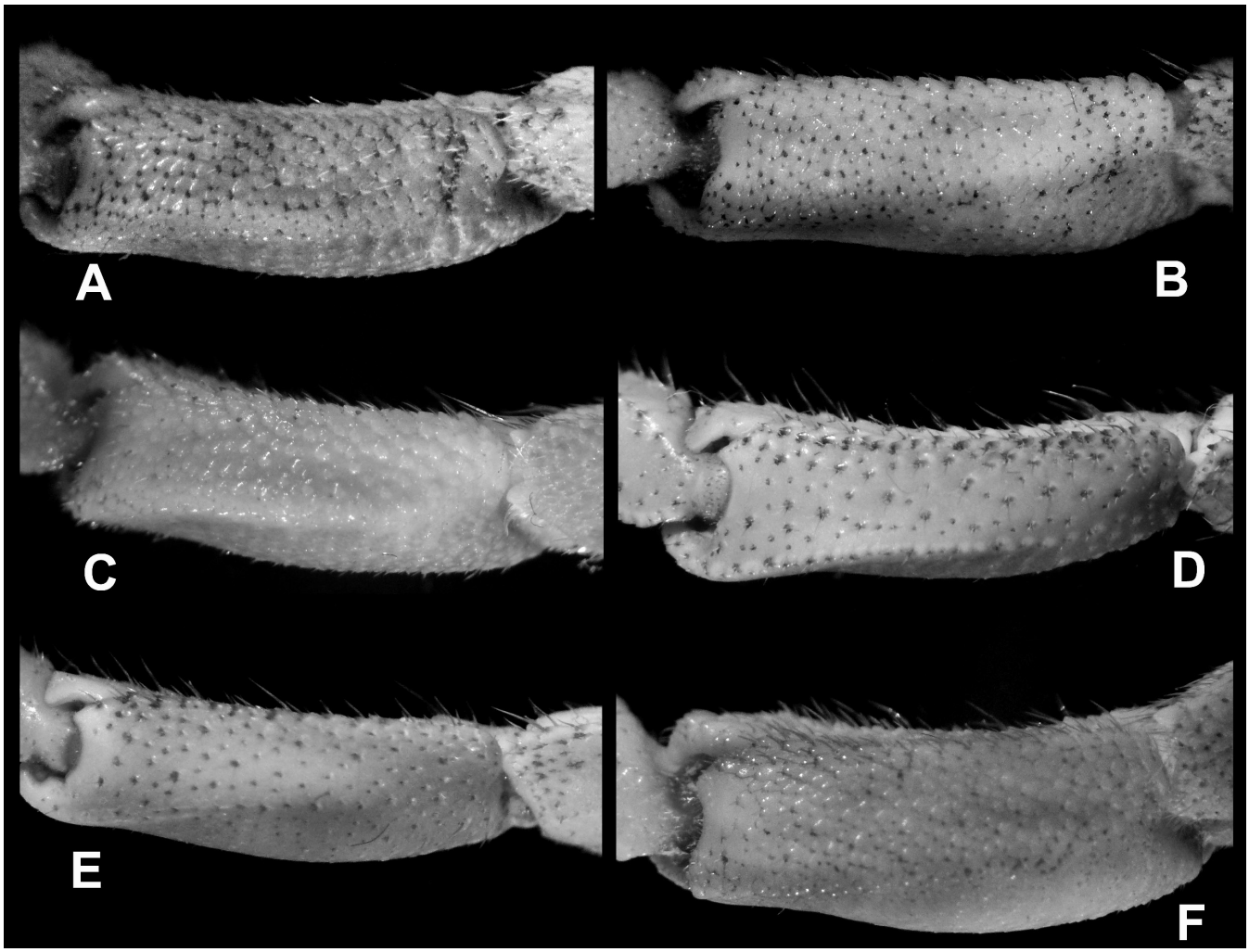


Fig. 6. Dorsal surface of propodus of left P3. A–C, *Coenobita lila* n. sp.: A, paratype female (sl 10.1 mm) (ZRC); B, paratype female (sl 10.1 mm) (ZRC); C, paratype female (sl 6.6 mm) (ZRC). D–F, *C. cavipes* Stimpson, 1858: D, female (sl 12.6 mm) (RUMF-ZC-2256); E, female (sl 8.2 mm) (RUMF-ZC-656); F, female (sl 11.7 mm) (ZRC).

Chelipeds unequal, dissimilar, left larger than right (Figs. 4D–F, 8A). Dactylus of left cheliped with numerous corneous-tipped tubercles bearing short setae on outer surface, upper margin with row of corneous-tipped spines and long, stiff setae; inner surface with rows of corneous-tipped tubercles bearing short setae; cutting edge with 4 large teeth terminating in small corneous claw. No stridulatory apparatus on upper outer surface of palm. Upper margin of palm with row of corneous spines and brush of long, coarse setae, outer surface with few rows corneous-tipped tubercles; tubercles slightly larger, closely-spaced near dorsal margin of palm, smaller and widely-spaced medially, becoming more sparse on outer lower margin. Lower margin of palm slightly sinuous, with corneous-tipped tubercles bearing tufts of short setae; lower proximal angled rounded or three-cornered. Inner surface of palm with numerous corneous-tipped tubercles bearing short setae; brush of setae proximally near upper margin. Outer surface of fixed finger with few tubercles, some corneous-tipped; lower margin straight with row of large tubercles, some corneous-tipped, each with tufts of short setae; inner surface with rows of corneous-tipped tubercles, more densely on lower inner half. Carpus with corneous-tipped tubercles arranged more or less in longitudinal rows on outer surface, slightly larger tubercles near upper margin, narrow, smooth area medially, less dense tubercles near lower margin; inner face with few small tubercles bearing short tufts of setae. Merus with transverse rows of flattened tubercles bearing very short setae on outer face; lower inner margin with tubercles, tufts of long setae; inner and lower surfaces smooth but with few transverse tufts of very short setae.

Right cheliped (Fig. 8B) with row of corneous spines and thick brush of long coarse setae on upper margin of palm; outer surface of dactylus and palm with rows of corneous-tipped tubercles, each with two or three long setae, lower margin of palm and fixed finger with row of long, stiff setae; cutting edge of dactylus and fixed finger with row of small teeth terminating in large corneous claw. Inner surface of palm and dactylus with scattered corneous-tipped tubercles, each with tufts of setae; proximal area of palm with long, coarse setae near upper margin. Carpus and merus similarly armed as left cheliped.

P2 and P3 dissimilar, P2 slightly more slender than P3. Dactylus of left P2 with rows of corneous-tipped tubercles on lateral surface; dorsal surface flattened, not delimited, with rows of corneous-tipped tubercles; mesial face with rows of numerous corneous-tipped tubercles, each with tufts

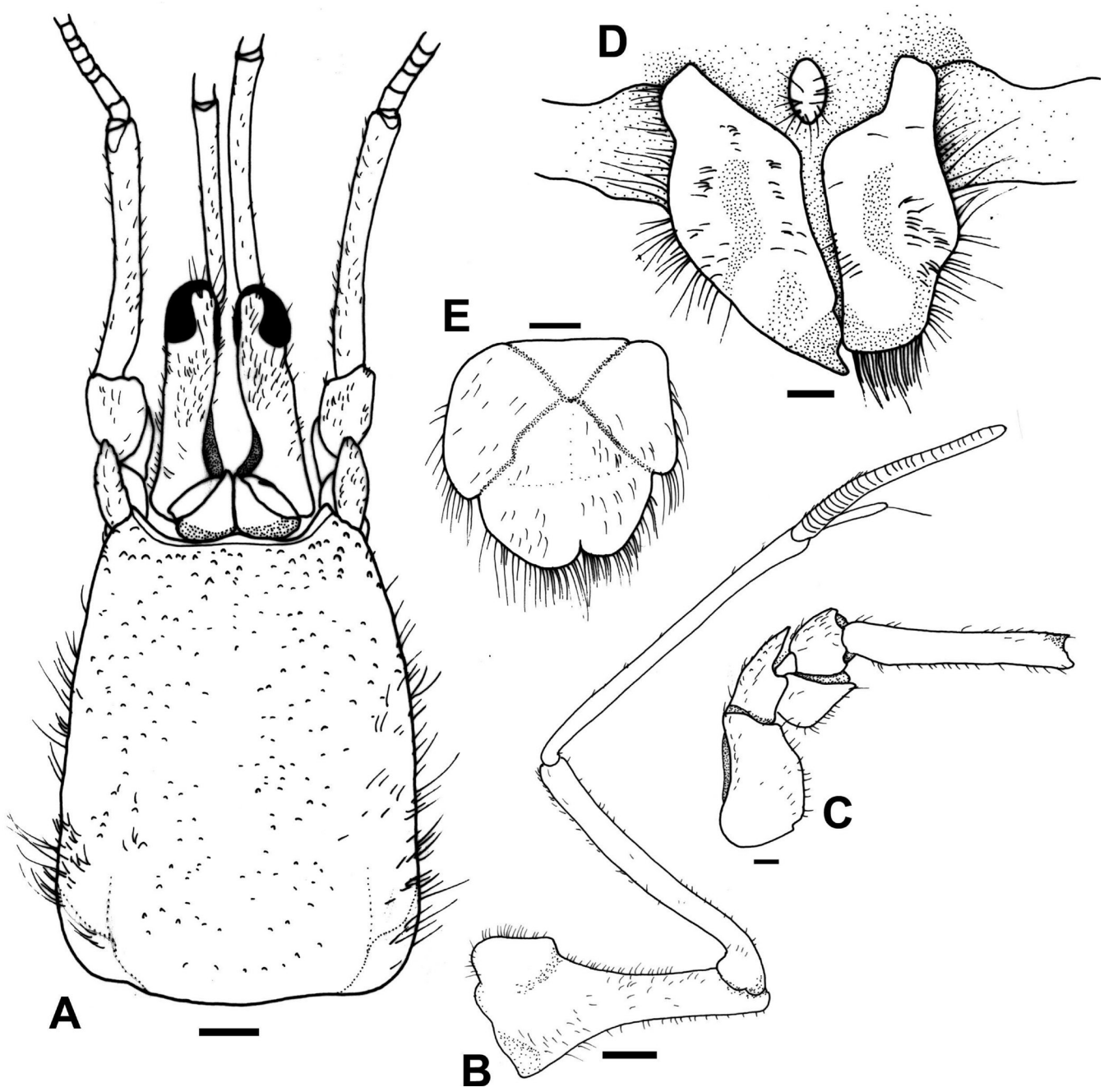


Fig. 7. *Coenobita cavipes* Stimpson, 1858, male (sl 16.1 mm) (RUMF-ZC-2255). A, shield and cephalic appendages; B, right antennular peduncle, lateral view; C, right antennal peduncles, lateral view; D, sternite and coxae of male P5; E, telson. Setae partially omitted. Scale bars = 2.0 mm [A, B]; 1.0 mm [C–E].

of short setae; ventral surface (Fig. 9A) with longitudinal ridge consisting of row of tiny corneous teeth, ventrolateral margin with row of corneous-tipped tubercles bearing tufts of short setae. Propodus with broad dorsal surface, medially smooth, rows of corneous-tipped tubercles on dorsomesial margin, dorsolateral surface delimited by longitudinal row of small corneous-tipped tubercles bearing two or three setae, lateral face with numerous small tubercles bearing tufts of long setae; ventrolateral surface with row of corneous-tipped tubercles, rather long setae, mesial surface concave, smooth except for low longitudinal ridge and few small tubercles and setae ventrally. Carpus with row of small tubercles each bearing two or three short setae on dorsolateral margin, lateral surface with shallow longitudinal sulcus medially, row of corneous-tipped tubercles each bearing tufts of setae adjacent to dorsal margin, few tubercles near distal margin; mesial surface compressed or slightly concave, with few tufts of short setae. Merus compressed mesially, with tufts of long setae on dorsal and ventral margin, transverse row of flattened tubercles on lateral surface; mesial face almost smooth, ventral margin with row of moderately large spines. Right P2 slightly more slender than left. Dactylus covered entirely with corneous-tipped tubercles bearing tufts of short setae, longer setae on ventral margin, dorsal margin not delimited, ventral surface (Fig. 9C) with longitudinal ridge consisting of tiny corneous teeth. Propodus with row of corneous-tipped tubercles bearing tufts of stiff setae on dorsal and ventral margins, dorsal surface with rows of small corneous-tipped tubercles adjacent to dorsal margin, remaining area smooth, lateral face with sparse short, stiff setae, mesial face slightly

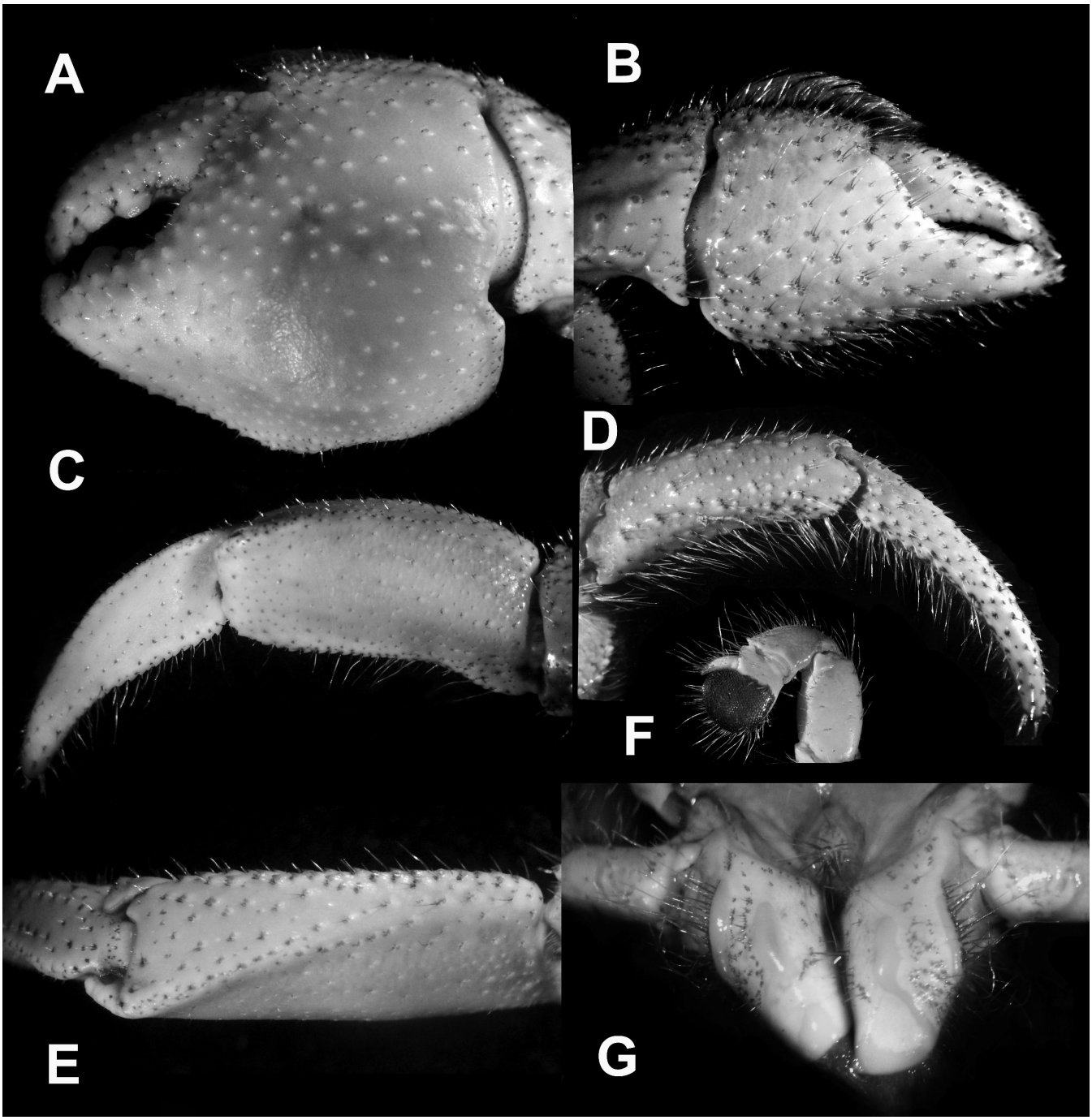


Fig. 8. *Coenobita cavipes* Stimpson, 1858, male (sl 16.1 mm) (RUMF-ZC-2255). A, left cheliped, outer view; B, right cheliped, outer view; C, dactylus and propodus of left P3, lateral view; D, dactylus and propodus of right P3, lateral view; E, dorsal surface of propodus of left P3; F, left P4, lateral view; G, sternite and coxae of male P5.

concave, smooth except for few tufts of long setae. Carpus with row of corneous-tipped tubercles on dorsal margin, dorsal surface with sparse corneous-tipped tubercles near dorsal margin, mesial face slightly concave, smooth. Merus compressed laterally and mesially, lateral and mesial faces smooth except for few tufts of short setae, ventral margin with row of small spines.

Left P3 (Figs. 5D–F, 8C) with dactylus 1.2–1.3 times as long as propodus, lateral face slightly convex distally, flattened or slightly concave proximally, with scattered short tufts of setae, delimited dorsally by row of small corneous-tipped spines bearing short setae, dorsal surface with longitudinal rows of corneous-tipped tubercles each with tufts of setae, decreasing in size proximally; mesial face with rows of corneous-tipped spines each with tufts of setae; ventrolateral margin with row of corneous small spines with long setae; ventral surface (Fig. 9B) slightly concave, median longitudinal ridge consisting of row of tiny corneous teeth. Propodus slightly flattened distally on lateral face, becoming convex proximally, with small flattened tubercles each with tufts of short setae, dorsolateral margin delimited by row of corneous-tipped tubercles; dorsal surface (Figs. 6D–F, 8E) flattened distally, broad, tapering to narrow surface proximally, with rows of small tubercles, some corneous-tipped; dorsomesial margin delimited by row of corneous-tipped tubercles and

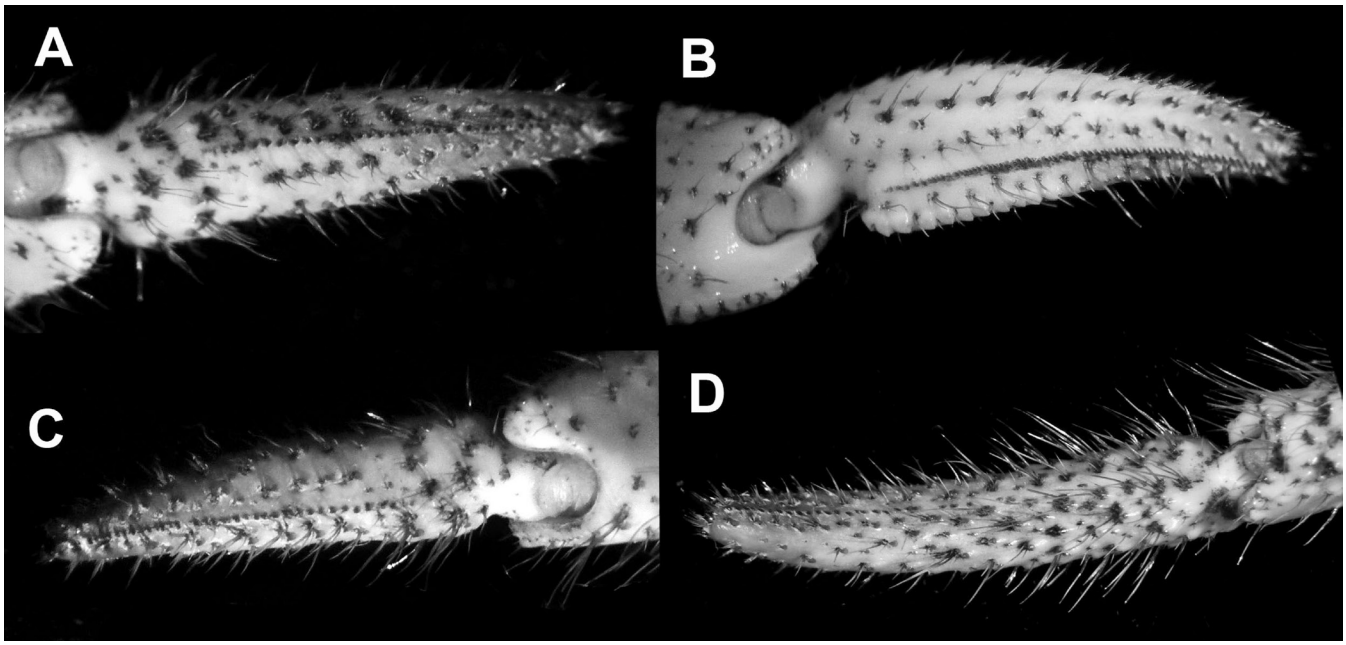


Fig. 9. *Coenobita cavipes* Stimpson, 1858, male (sl 16.1 mm) (RUMF-ZC-2255). A, dactylus of left P2, ventral view; B, dactylus of left P3, mesioventral view; C, dactylus of right P2, ventral view; D, dactylus of right P3, ventral view.

short setae; mesial face slightly concave, with scattered corneous-tipped tubercles, each bearing tufts of setae; ventral surface slightly concave with median longitudinal row of corneous-tipped tubercles and scattered tufts of long setae; ventrolateral margin with row of small spines and tufts of setae. Carpus with row of small tubercles each with two or three short setae on dorsolateral margin, lateral face smooth with shallow longitudinal sulcus medially, row of corneous-tipped tubercles each with tufts of setae adjacent to dorsal margin, few tubercles near distal margin; mesial face compressed, with few small corneous-tipped tubercles, each with tufts of short setae. Merus compressed laterally and mesially, transverse row of flattened tubercles on lateral surface; mesial face almost smooth, tufts of long setae on dorsal and ventral margins.

Right P3 more slender than left. Dactylus and propodus (Fig. 8D) with rows of tubercles, corneous-tipped tubercles especially on dorso- and ventrolateral surface; distal half of ventral surface (Fig. 9D) with row median longitudinal ridge consisting of row of tiny corneous teeth; dorsal margin not delimited; mesial face of dactylus with rows of corneous-tipped tubercles and tufts of setae, mesial face of propodus with sparse small tubercles, short setae. Carpus and merus as in left P3.

P4 semi-chelate (Fig. 8F), dactylus with row of small corneous teeth ventrally, long, coarse setae dorsally; propodal rasp well developed, occupying large, circular area, consisting of numerous corneous scales. P5 chelate.

In male, coxae of P5 thick, forming short subquadrate, calcified sexual tube, left tube slightly broader than right. Gonopore positioned on moderately broad with pointed tip posterior projection or papillae, obscured by coarse, dense setae; cylindrical, moderately large, sternal protuberance between both coxae (Figs. 7D, 8G).

Telson (Fig. 7E) with distinct lateral indentation, separating anterior and posterior lobes. Anterior lobe as long as posterior. Posterior lobes slightly asymmetrical separated by narrow median cleft; margins rounded, with row of setae.

**Colour in life.** In general brown or greenish brown (Fig. 11D–F). Shield dark brown with streak of white medially. Ocular peduncles dark brown, corneas black. Antennal peduncle dark brown, fifth segment orange. Antennular peduncles dark brown, penultimate segment dark orange. Chelipeds light brown, or greenish brown, tip of dactylus and fixed finger white, outer face of palm with rounded, large area dark brown. Carpus with dark brown longitudinal streak. P2 and P3 greenish brown or light brown tinge with dark brown.

This coloration slightly differs from that given by Haig & Ball (1988) for material from Indonesia: shield and posterior carapace with elaborate pattern of dark brown spots and streaks on almost white background. Ocular peduncles almost white or pale brown ventrally, darker laterally; cornea brown. Antennular peduncles brown, with flagellum brown to nearly orange. Antennae uniformly brown. Chelipeds dark brown, with broad white area at proximal end of merus and some white at end of carpus; most of palm and dactylus white. Ground colour of pereopod 2 dark brown; oblique, broad white stripe at proximal end of merus; longitudinal white stripe on carpus; white area at both ends of propodus. P3 with patches and bands of white on dark brown background.

**Distribution.** Ryukyu Islands, Japan; Taiwan; Philippines; Malaysia; and Indonesia.

**Remarks.** As in *C. lila* n. sp., the shape of the left cheliped of *C. cavipes* varies. The lobe-like projection on the lower margin of palm varies from rounded to three cornered (Figs. 4D–F, 8A). The longitudinal ridge consisting of corneous-

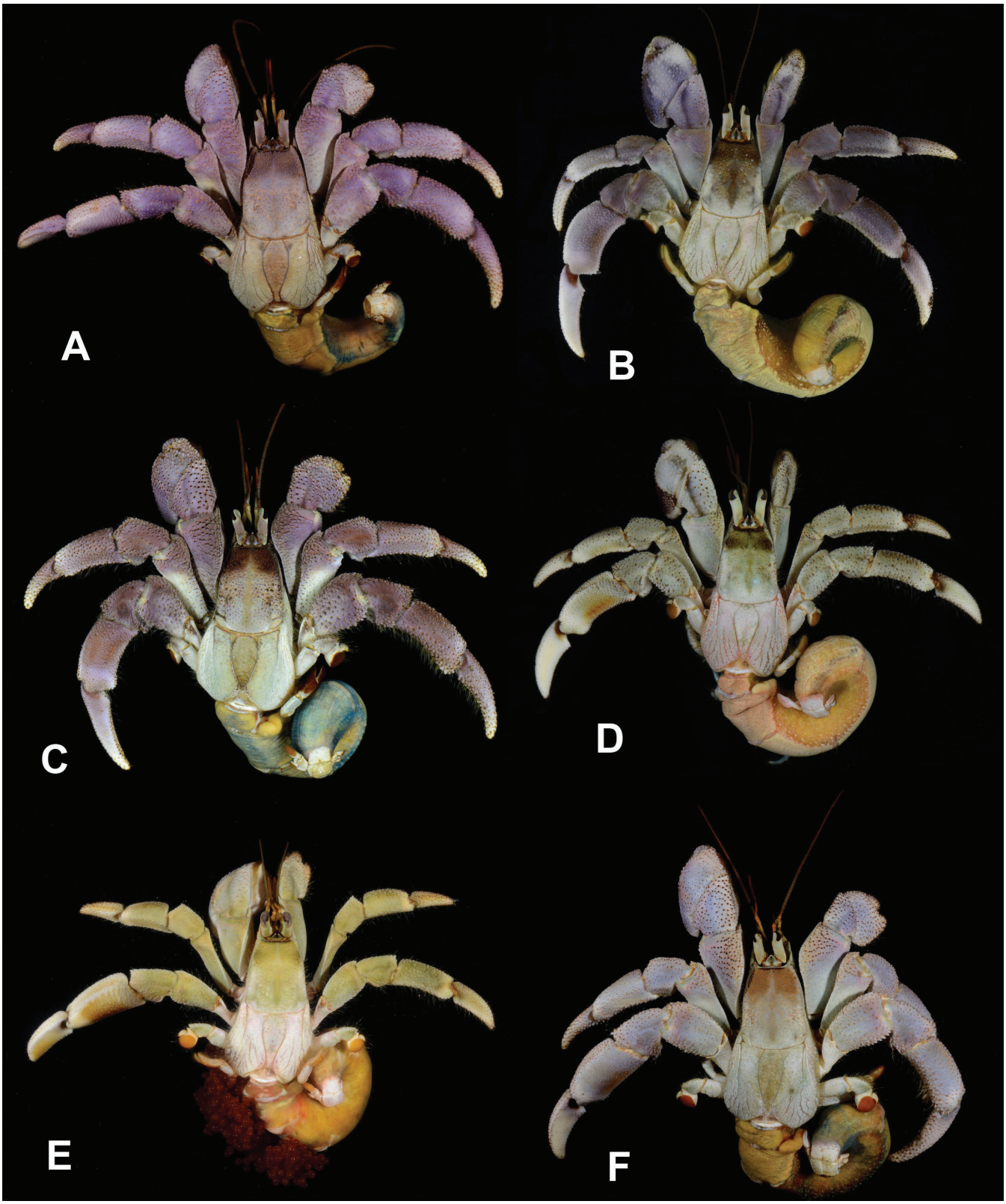


Fig. 10. *Coenobita lila* n. sp. A, holotype male (sl 16.7 mm) (ZRC); B, paratype female (sl 6.6 mm) (ZRC); C, paratype male (18.7 mm) (ZRC); D, paratype female (sl 10.1 mm) (ZRC); E, paratype female (sl 10.8 mm) (ZRC); F, paratype male (sl 17.5 mm) (ZRC).

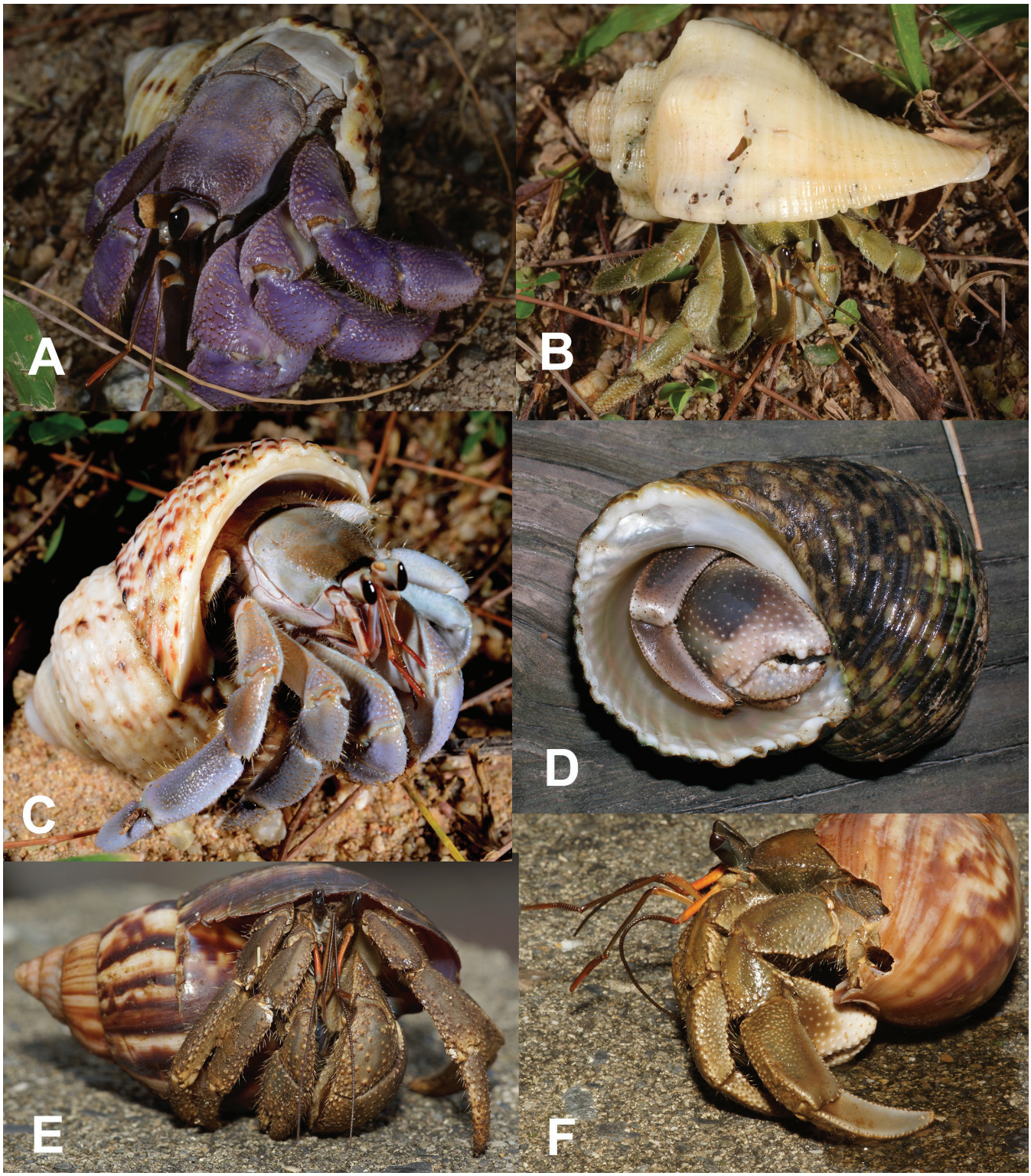


Fig. 11. A–C, *Coenobita lila* n. sp. A, holotype male (sl 16.7 mm) (ZRC); B, paratype ovigerous female (sl 10.8 mm) (ZRC); C, female (sl 11.8 mm) (ZRC); D–F, *C. cavipes* Stimpson, 1858, Houwan, Kenting, Pingtung, Taiwan (NCHUZOOL 13637). D, female (sl 13.8 mm); E, female (sl 13.5 mm); F, female (sl 14.9 mm).

Table 2. Matrix of percentage pairwise nucleotide divergences of K2P distance based on 658 bp of cytochrome c oxidase subunit I (COI) within and between species of *Coenobita*. Mean is indicated with values of range shown in parentheses.

| | Intraspecific | Interspecific | | |
|---|---|---|---|---|
| | | ***C. lila* n. sp.** | ***C. cavipes*** | ***C. violascens*** |
| *C. lila* n. sp. | 1 (0–2.01) | — | | |
| *C. cavipes* | 0.8 (0.46–1.08) | 16.68 (16.17–17.79) | — | |
| *C. violascens* | 0.63 (015–1.23) | 15.58 (14.62–16.41) | 13.98 (13.37–14.5) | — |

tipped teeth on the ventral surface of the dactylus of the left P3 and the dorsal surface of the propodus of the left P3 varies with the size of individual. In most small females (sl 5–7 mm), the ridge on the ventral margin of the dactylus of left P3 continues to the ventral face of the propodus as a faint row of longitudinal teeth without corneous tips, and the dorsal surface of the propodus is narrow, with rows of prominent corneous-tipped tubercles. In small males (sl 5–12 mm) and larger males and females (larger than 12 mm), the longitudinal ridge on the ventral surface of the left P3 continues to the ventral face of the propodus; and the dorsal surface of propodus is distally broad, becoming slightly narrow proximally. In one male (sl 16.1 mm), the broad dorsodistal surface tapers to a significantly narrow surface proximally (Fig. 8E).

McLaughlin et al. (2007) treated the records of *C. cavipes* from Taiwan as a misidentification of *C. violascens*. After that report, most workers have identified species without stridulatory apparatus on upper outer surface of left palm as *C. violascens*. In this study, using both morphological and molecular characters, we confirm that both *C. cavipes* s. str. and *C. violascens* occur in Taiwan (Tables 1, 2). In one locality (Yuanjhonggang, Kaohsiung), both *C. cavipes* and *C. violascens* were found together.

As discussed earlier, records of "*Coenobita cavipes*" from Singapore (e.g., Lim et al., 1994: 12) are all *C. lila* n. sp. The record of "*C. cavipes*" by Bouchard et al. (2013: 12, fig. 9A, B) from Mayotte is actually *C. violascens* (see comparative material examined). We examined the holotype of *C. baltzeri* Neumann, 1878, described from Java, which McLaughlin et al. (2010) had synonymised under *C. cavipes*. It proves not to be the case. *Coenobita baltzeri* is probably synonymous with *C. violascens* Heller, 1865, agreeing with the figures and descriptions by Heller (1865: pl. 7, fig. 1) and Nakasone (1988: 172, fig. 7), as well as specimens examined. Specimens we have examined from Madagascar and Mayotte also correspond to *C. violascens* (unpublished morphological and molecular data). It is beyond the scope of this study to discuss the taxonomy of *C. violascens* and *C. baltzeri* at length.

## DNA ANALYSES

A 658 basepair (bp) segment of COI of eight specimens of *C. lila*, five specimens of *C. cavipes* and seven specimens of *C. violascens* was amplified, resulting in 6, 5 and 7 different haplotypes, respectively (Table 1). The nucleotide divergences with the K2P distance within and between species are shown in Table 2. With regards to *C. lila*, the nucleotide divergence within species is $\leq$ 2.01%, and is $\geq$ 16.17% or $\geq$ 14.62%, between *C. lila* and *C. cavipes* or *C. violascens*, respectively (Table 2). The nucleotide divergence between *C. cavipes* and *C. violascens* is $\geq$ 13.37%

## DISCUSSION

*Coenobita* species with purple, violet or blue-purplish coloration and without a row of stridulatory granules on the upper outer surface of palm of the left cheliped have often been identified as either *C. cavipes* or *C. violascens*. These two species share the following characters: a brush of stiff setae on the upper margin of the palms of both chelipeds, the dactylus of P3 is laterally broad and flattened, and the coxae of male P5 has a calcified sexual tube which forms a short projection. As discussed by Fize & Serène (1955), the morphological characters of *Coenobita* species show substantial individual variation and colour is unreliable as a specific character by itself. Nakasone (1988) used the following criteria to distinguish the species in *Coenobita*: (a) position of antennal acicle to the second segment of antennal peduncle; (b) the presence or absence of a stridulatory apparatus on the upper outer face of the left cheliped; (c) the presence or absence of a brush of setae on the upper margin of the palm of both chelipeds; (d) the strength and shape of the lobe-like proximal projection on the lower margin of the palm; (e) the presence of a dark patch on the outer face of the palm; (f) the concavity of the inner surface of the P3 propodus; (g) the presence of short projection on the coxae of male P5 which forms a short sexual tube; and (h) the size of the sternal protuberance between the coxae of male P5.

Examination of numerous specimens of *Coenobita* showed that the live colour, the strength and shape of the lobe-like proximal projection on the lower margin of palm, and the presence or absence of a dark patch on the outer face of palm, are not reliable characters at the species level, as they

Table 3. Morphological differences between *Coenobita lila* n. sp., *C. cavipes* and *C. violascens*.

| Morphology | *Coenobita lila* | *Coenobita cavipes* | *Coenobita violascens* |
|---|---|---|---|
| Shield | 1.6 times as long as broad, covered by tubercles and stiff setae | 1.7 times as long as broad, punctate | 1.4 times as long as broad, punctate |
| Antennular peduncles | Basal segment 0.7 as long as penultimate segment; penultimate segment as long as ultimate segment | Basal segment 0.9 as long as penultimate segment; penultimate segment 1.1 times as long as ultimate segment | Basal segment 0.7 as long as penultimate segment; penultimate segment as long as ultimate segment |
| Left cheliped | Brush of setae on upper margin of palm; no stridulating mechanism; lower outer surface of palm covered with tubercles | Brush of setae on upper margin of palm; no stridulating mechanism; lower outer surface of palm with few scattered tubercles | Brush of setae on upper margin of palm; no stridulating mechanism; lower outer surface of palm smooth |
| Right cheliped | Brush of setae on upper margin of palm; no setae on lower margin of merus; palm covered with corneous-tipped tubercles bearing tufts of setae | Brush of setae on upper margin of palm; no setae on lower margin of merus; palm with few tubercles bearing tufts of setae | Brush of setae on upper margin of palm; no setae on lower margin of merus; palm with few flattened tubercles bearing tufts of setae |
| Left P2 | Longitudinal ridge of tiny corneous teeth present on ventral surface of dactylus; lateral face of propodus densely tuberculated | Longitudinal ridge of tiny corneous teeth present on ventral surface of dactylus; lateral face of propodus with few scattered tubercles | Longitudinal ridge of tiny corneous teeth present on ventral surface of dactylus; lateral face of propodus with few scattered tubercles |
| Left P3 | Longitudinal ridge of tiny corneous teeth present on ventral surface of dactylus; lateral face of propodus densely tuberculated; dorsolateral margin of propodus delimited only on fourth-fifth by weak tubercles, dorsal surface broad | Longitudinal ridge of tiny corneous teeth present on ventral surface of dactylus; lateral face of propodus only with few scattered tubercles; dorsolateral surface delimited by row of corneous-tipped tubercles, dorsal surface narrowing proximally | Longitudinal ridge of tiny corneous teeth present on ventral surface of dactylus; lateral surface of propodus punctuate; dorsolateral margin of propodus strongly delimited by longitudinal ridge, dorsal surface relatively broad |
| Right P2 | Longitudinal ridge of tiny corneous teeth on ventral surface of dactylus absent; dactylus and propodus covered entirely with tubercles | Longitudinal ridge of tiny corneous teeth present on ventral surface of dactylus; dactylus and propodus with few scattered tubercles | Longitudinal ridge of tiny corneous teeth present on ventral surface of dactylus; dactylus with few corneous-tipped tubercles, propodus punctate |
| Right P3 | Longitudinal ridge of tiny corneous teeth on ventral surface of dactylus absent; lateral surface of dactylus and propodus densely tuberculated | Longitudinal ridge of tiny corneous teeth present on ventral surface of dactylus; lateral surface of propodus only with few scattered tubercles | Longitudinal ridge of tiny corneous teeth on ventral surface of dactylus absent; lateral surface of propodus punctate |
| Coxae of P5 | Produced as sexual tube; sternal protuberance subpentagonal, large | Produced as sexual tube; sternal protuberance ovate, moderately large | Produced as sexual tube; sternal protuberance elongated, small |
| Sexual tube | Moderately long, elongated, subtriangular, papillae small, triangular | Moderately short, subquadrate, papillae broad with pointed tip | Short, broad, papillae broad, triangular |
| Telson | broad, with shallow lateral indentation; anterior lobe shorter than posterior lobe; left and right posterior lobe subequal | narrow, with deep lateral indentation; anterior lobe as long as posterior lobe; left and right posterior lobe subequal | narrow, with deep lateral indentation; anterior lobe as long as posterior lobe; posterior lobe with left distinctly longer than right |

vary with the size of individual. In this study, we have added three characters to distinguish the species in *Coenobita*: (1) the degree of tuberculation on the palm of the chelipeds; (2) the outer face of the propodus of the left P3, and (3) the shape of the telson.

The chela of the left cheliped of *C. violascens* is smooth on the outer lower surface of palm and on the fixed finger, with only a few small tubercles present on the outer upper surface of the palm. The lateral surface of the propodus of the left P3 is nearly smooth and the longitudinal ridge on the ventral surface is indistinct. The posterior lobes of telson are asymmetrical, with the left lobe broader and longer, and separated from the right by a deep median cleft. The male sexual tube is broadly quadrate, with the papillae broadly triangular; and the sternal protuberance between the coxae of male P5 is small. These characters clearly separate *C. violascens* from *C. cavipes* s. l. (Table 3).

However, available specimens initially identified with *C. cavipes* can be separated into two morphological groups, and this is supported by molecular data (Table 2). One of the two forms is described here as a new species, *C. lila*. *Coenobita lila* can be separated from *C. cavipes* by the basal segment of the antennular peduncles being 0.7 times as long as the penultimate segment and the penultimate segment as long as ultimate segment (Fig. 1B) (as opposed to the basal segment 0.9 times length of penultimate segment and the ultimate segment 1.1 times as long as penultimate segment in *C. cavipes*; Fig. 7B); the chelipeds and the propodus of the left P3 are densely tuberculated (Figs. 2A, C, 4A–C, 5A–C) (as compared to the presence of only a few scattered tubercles in *C. cavipes*, Figs. 4D–F, 5D–F, 8A, C); the longitudinal ridge consisting of small corneous teeth is present only on the ventral surface of the dactylus of the left P2 and P3 (Fig. 3A, B) (present on the ventral surface of the dactylus of the right and left of P2 and P3 in *C. cavipes*, Fig. 9); the sexual tube on the coxae of male P5 is elongated, subtriangular, with the papillae small and triangular (Figs. 1D, 2G) (subquadrate in the shape, papillae broad with a pointed tip in *C. cavipes*, Figs. 7D. 8G); and the sternal protuberance between the coxae of male P5 is subpentagonal in the shape (Figs. 1D, 2G) (cylindrical in *C. cavipes*, Figs. 7D, 8G). In addition, the dorsolateral margin of the propodus of the left P3 in *C. lila* is weakly delimited and with a broad dorsal surface (Figs. 2E, 6A–C) while in *C. cavipes*, this area is strongly defined by a ridge and the dorsal surface is narrow (Figs. 6D–F, 8E). The shield of *C. lila* is also proportionately slightly narrower (1.6 times as long as broad) with the surface covered by small and large tubercles and short, stiff setae (Fig. 1A) (1.7 times as long as broad and the surface is more punctate rather than tuberculated in *C. cavipes*, Fig. 7A).

*Coenobita lila* differs from *C. violascens* in the absence of prominent longitudinal ridge separated the dorsal and lateral surface of P3 propodus (Fig. 6A–C) (with a prominent longitudinal ridge separated dorsal and lateral surfaces of propodus of P3 in *C. violascens*, cf. Nakasone, 1988: 173, fig. 7C); in the slightly elongated, subtriangular shape of the male sexual tube produced from the coxae of P5 (Figs. 1D, 2G) (short, squarish shape of male sexual tube produced from coxae of P5 in *C. violascens*, cf. Nakasone, 1988: fig. 7F); and the large, subpentagonal sternal protuberance between the coxae of the male P5 (Figs. 1D, 2G) (small, elongated sternal protuberance in *C. violascens*, cf. Nakasone, 1988: fig. 7F). In addition, the telson of *C. lila* is relatively broad, with shallow lateral indentations, with the anterior lobe clearly shorter than the posterior lobe, and the posterior lobe is divided by an indistinct median clef with the left lobe slightly longer or as long as the right (Fig. 1E). In *C. violascens*, the telson is only moderately narrow, with deep lateral indentations, the anterior and posterior lobes are almost the same size, and the posterior lobe is separated by deep median cleft with the left lobe distinctly longer than the right (Table 3).

The coloration of the adult *C. lila* in general is violet or dark purple, purplish blue or brownish purple (Figs. 10, 11A–C). In the young male and adult female of *C. lila*, the colour is pale or light purple, with some specimens possessing a greenish white shield; a large brown patch on the outer lower surface of the palm; and greenish white P2 and P3 with light brown streaks on the lateral faces of the propodus and merus (Fig. 10D–F). Adult *C. purpureus* Stimpson, 1858, and *C. brevimanus* Dana 1852, are also purple in life. *Coenobita purpureus* is easily separated from *C. lila* and *C. cavipes* by the presence of an oblique series of stridulatory mechanism on the upper outer surface of the palm of the left cheliped, and an asymmetrical sexual tube, with the right one being more slender and longer than the left; while *C. brevimanus* differs by having the ocular peduncles not compressed, the antennal acicle is not fused with the second segment of its peduncle and the absence of a brush of setae on the upper margin of the palm of the left cheliped.

Compared to the intraspecific and interspecific K2P divergence of COI of *Calcinus*, 0–6% and 4–25%, respectively (Malay et al., 2009), the interspecific divergence is at least 7 or 8 times more than intraspecific values (i.e., the ratio of the smallest interspecific distance to the largest intraspecific distance) for the three species of *Coenobita* examined this study (Table 2). The barcoding gap (Hebert et al., 2003; Meyer & Paulay, 2005) is large enough to support *C. lila* n. sp. as a distinct species.

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