

ONTOGENETIC COLOR CHANGE AND SIZE VARIATION OF THE LAND HERMIT CRAB *COENOBITA VIOLASCENS* HELLER, 1862 (ANOMURA, COENOBITIDAE)

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ABSTRACT

Ontogenetic color change and size variation between two color morphs as well as between sexes and among reproductive stages of the land hermit crab *Coenobita violascens* Heller, 1862 were investigated. Hermit crabs were collected from the supralittoral zone at low tide in the area of Cape Panwa on Phuket Island in the Andaman coast of Thailand during January 2011 and March 2012. Two color morphs of *C. violascens* were observed in both sexes and described in detail. A brownish-red morph was observed in small to medium-sized individuals (2.99–7.22 mm CSL [cephalothoracic shield length]), whereas a violet-colored morph was found in medium to large individuals (7.54–15.73 mm CSL). Violescent individuals had a mean CSL size of 11.15 ± 1.85 mm ($n = 29$) while brownish-red individuals had a mean CSL of 5.04 ± 1.36 mm ($n = 18$). The fact that coloration differences between individuals are related to developmental stage, and do not represent genetic variability, indicates that color “phase”, rather than “morph” is a more appropriate descriptive term. The beginning of color change on the body and appendages between two morphs of *C. violascens* is discussed. The results suggest that color change from brownish-red to violet (7.22–7.54 mm CSL) appears before sexual maturation, based on the size of the smallest ovigerous female (9.64 mm CSL). The results of the current study provide fundamental knowledge for the conservation of *C. violascens*.

Keywords: Coenobitidae, *Coenobita violascens*, Terrestrial hermit crab, Color pattern, Ontogeny, Size difference, Juvenile, Adult

INTRODUCTION

Land hermit crabs in the genus *Coenobita*, Family Coenobitidae, are distributed in particular tropical and subtropical coastal and insular areas (HARTNOLL, 1988a). Adult land hermit crabs inhabit supralittoral areas and farther inland habitats, including beaches, mangroves, beach forest and rainforest (WILDE, 1973; NAKASONE, 1988; WOLCOTT, 1988; DOI ET AL., 2016). These crabs occupy discarded empty shells as mobile shelters to protect their soft abdomen from environmental stresses (SALLAM ET AL., 2008; LAIDRE & VERMEIJ, 2012). The occupied shells of land hermit crabs also offer protection from desiccation and predators (GREENAWAY, 2003). Their feeding habit is as a generalist scavenger, accelerating the recycling of nutrients and energy in food webs (LAIDRE, 2013). Consequently, land hermit crabs are an important component in the marine–land interface of supralittoral zones (MORRISON & SPILLER, 2006).

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Seventeen valid species of the genus *Coenobita* have been named from tropical and subtropical areas throughout the world (DE GRAVE *ET AL.*, 2009; McLAUGHLIN *ET AL.*, 2010; RAHAYU *ET AL.*, 2016). *Coenobita violascens* Heller, 1862 is widely distributed in the Indo-Pacific region from the east coast of Africa, Madagascar to Thailand, Taiwan, the Philippines, and Japan (NAKASONE, 1988; McLAUGHLIN, 2002; McLAUGHLIN *ET AL.*, 2007 [in part]; RAHAYU *ET AL.*, 2016). In Thailand, *C. violascens* has been reported from both coasts of Andaman Sea and Gulf of Thailand (McLAUGHLIN, 2002). This species occurs in mangrove-associated habitats and on beaches (NAKASONE, 1988; McLAUGHLIN *ET AL.*, 2007; DOI *ET AL.*, 2016). Studies on the life history of *C. violascens* have reported on many aspects, including distribution in natural habitats (FUJIKAWA *ET AL.*, 2017; HAMASAKI *ET AL.*, 2017a); functional morphology related to water uptake (BECCHI *ET AL.*, 2015); shell occupation (BUNDHITWONGRUT, 2018a); larval release and tree-climbing behavior (DOI *ET AL.*, 2016); larval survival, growth, development and duration under laboratory condition (HAMASAKI *ET AL.*, 2015b, 2016, 2017b, 2018a, 2020; KATO *ET AL.*, 2015); settlement behavior of early glaucothoes (or postlarvae) (FUJIKAWA *ET AL.*, 2018b); emigration behavior, molting and survival during the sea-to-land transition (HAMASAKI *ET AL.*, 2015a; FUJIKAWA *ET AL.*, 2018a); thermal tolerance of early juveniles (SANDA *ET AL.*, 2019; KASUYA *ET AL.*, 2020); and recruitment to adult habitat (HAMASAKI *ET AL.*, 2018b). Additionally, information on trade of *C. violascens* as pets has been recently reported (BUNDHITWONGRUT, 2018b, 2020).

Color change in animals can be categorized as morphological (chromogenic) and physiological (chromomotor) (SWIERK, 2022). In crustaceans, morphological color change is relatively fixed and species-specific and this adaptive pattern is associated with ontogenetic change, probably related to specific developmental stages or ages (McNAMARA & MILOGRANA, 2015). Ontogenetic color change between juvenile and adult stages of land hermit crabs has been reported in *Coenobita brevip manus*, *C. cavipes*, *C. perlatus*, *C. purpureus*, *C. rugosus* and *C. violascens* (NAKASONE, 1988; FUJITA & NARUSE, 2016; HAMASAKI *ET AL.*, 2017a, 2017b). Moreover, ontogenetic changes of body coloration in laboratory-raised juveniles of six coenobitid species (i.e., *Birgus latro*, *C. brevip manus*, *C. cavipes*, *C. purpureus*, *C. rugosus* and *C. violascens*) have recently been reported (HAMASAKI *ET AL.*, 2017b). As for *C. violascens*, different color morphs between developmental stages have been briefly described as brownish-red juveniles and vioulescent adults (NAKASONE, 1988). The size variation between these color morphs of *C. violascens* has not been recorded, nor has size been compared between sexes and among reproductive groups. The hypothesis of the present study is that size transitions between the color morphs and between developmental stages should be congruent or nearly co-occurring based on puberty molt as the beginning of sexual maturation, because morphological changes (e.g., condition of female pleopods in *C. perlatus* and *C. rugosus* [PAGE & WILLASON, 1982]) are usually associated with this significant molt (HARTNOLL, 1988b). Therefore, the objectives of the present study are to describe ontogenetic change in coloration and to determine the size variation between color morphs, between sexes and among reproductive groups, as well as to investigate the relationship between color morphs and the environment of *C. violascens* sampled in its natural habitat at Cape Panwa, Phuket Island, Andaman coast of Thailand.

MATERIALS AND METHODS

The study was carried out from January 2011 to March 2012. *Coenobita violascens* were collected monthly using multiple quadrat sampling (BARNES, 1999; BUNDHITWONGRUT *ET AL.*, 2014, 2015) from the area behind the Phuket Marine Biological Center (PMBC) at Cape Panwa, Phuket Island (7°48'26"N 98°24'35"E; see map and details of environmental conditions in BUNDHITWONGRUT *ET AL.* [2014]). Crabs were collected by hand at low tide from the supralittoral zone in the early morning. Four temporary line transects were placed at 15-m intervals perpendicular to the shoreline. In addition, 16 temporary quadrats (1×1 m with walls 10 cm high to prevent the agile crabs from escaping during collection) were also placed at 5-m intervals on transects from 5 m to 45 m horizontally from the tidemark at the time. The number of quadrats on each transect was unequal due to the different distances between the starting quadrat and the cliffs on each transect. After sampling, each crab was carefully pulled out of its shell in order to investigate its characters. After the investigation, all crabs were allowed to reinhabit their previously occupied shells and released unharmed into the natural habitat at the point where they were collected.

Each crab sampled was measured for cephalothoracic shield length (CSL = from the tip of the rostrum to the midpoint of the posterior edge of the cervical groove) to the nearest 0.01 mm using digital vernier calipers. All crabs were also weighed (BW) to the nearest 0.1 g on a digital scale. Sex was determined by gonopore position (FOREST *ET AL.*, 2000; McLAUGHLIN *ET AL.*, 2007; TUDGE *ET AL.*, 2012). Crab reproductive groups comprised males, all females, non-ovigerous females, and ovigerous (egg-carrying) females. Juveniles were defined as crabs of either sex smaller than the smallest ovigerous female, and adults as crabs of either sex equal to or larger than the smallest ovigerous female (SALLAM & MANTELATTO, 2010; BUNDHITWONGRUT *ET AL.*, 2014, 2015). Categories of coloration of *C. violascens* were "brownish red" and "violescent" (= "violascens"), as previously reported by NAKASONE (1988). Color descriptions of live crabs of both morphs were also recorded in detail. Additionally, crabs were categorized into 0.5-mm CSL size classes according to NAKASONE (2001) and SALLAM *ET AL.* (2008) to determine and compare the size frequency distributions of the two color morphs (i.e., brownish red and violescent) and developmental stages (i.e., juvenile and adult). As for size variation, the mean and standard deviation of CSL and BW of *C. violascens* were calculated for each category of color morph, sex, and developmental stage. The relative numbers and densities of the two color morphs were measured within each 5-m interval of distance from the tidemark to determine if color was related to the environment of the crabs.

RESULTS

Color Description

Brownish-red morph (2.99–7.22 mm CSL; Fig. 1A–C, Fig. 2A–C)

Overall body color ranging from reddish orange or bright red to brownish red as they grow. Small individuals possessing brighter color than larger ones. Ocular peduncles each with a longitudinal light orange stripe on dorsal surface and reddish orange, red to brownish red on lateral surface (Fig. 2A, B). Cornea black. Ocular acicles uniformly reddish orange or bright red to brownish red (Fig. 2B). Shield creamy or light orange dorsally with two irregular longitudinal brownish bands, nearly parallel to each lateral side of dorsal surface

(Fig. 2B). These bands enlarge and cover nearly all the area in larger individuals. Lateral surface of shield brownish red or brownish. Posterior carapace creamy or light orange with irregular longitudinal brownish-red or brownish streaks on dorsal surface. Antennular peduncles and flagella crimson. Antennal acicles light orange in small individuals or light lavender in larger ones. Antennal peduncles reddish orange in small individuals to red or brownish red in larger ones. Antennal flagella dark brown. Overall color of outer surface of chelipeds varying from reddish orange or red to brownish red. Cutting edge and ventral margin of left cheliped light orange (Fig. 2C). Most of mesial surface of chelipeds light orange in small individuals or light lavender in larger ones. Larger individuals usually with a prominent longitudinal brownish stripe on dorsolateral surface of carpus of left cheliped. Outer surfaces of second and third pereiopods generally reddish orange, red to brownish red. Mesial surfaces of second and third pereiopods light orange or light lavender. Proximal and distal margins of carpus, propodus and dactylus of second and third pereiopods of some larger individuals white or light orange.

Violescent morph (7.54–15.73 mm CSL; Fig. 1D, E)

Overall body color ranging from light lavender to violet or dark violet. Ocular peduncles grayish violet, dark violet or dark gray dorsally and dark gray laterally. Lateral surface of each ocular peduncle of some light-lavender individuals with an irregular longitudinal light-lavender patch. Cornea black. Ocular acicles uniformly light lavender to violet or dark violet. Shield light lavender to grayish violet dorsally and light lavender to violet laterally. Posterior carapace light lavender or light violet. Antennular peduncles red to reddish brown. Antennular flagella red to red brownish. Antennal acicles light lavender to violet or grayish violet. Antennal peduncles light lavender to violet. Antennal flagella dark brown. Overall chelipeds, second and third pereiopods light lavender to violet or dark violet with dark brown tubercles. Dorsolateral and distal ends of chelipeds, second and third pereiopods with lighter color. Some individuals with a large dark-brown, brown or brownish-yellow patch on the outer lower surface of palm of left cheliped.

Size Variation between Color Morphs

Coloration of both sexes of *Coenobita violascens* comprised two morphs: brownish-red and violescent. Violescent individuals had the mean CSL size of 11.15 ± 1.85 mm ($n = 29$), whereas the mean CSL size of brownish-red individuals was 5.04 ± 1.36 mm ($n = 18$) (Table 1, Fig. 3). Crabs of the brownish-red morph were small to medium-sized ranging from 2.99 to 7.22 mm CSL ($n = 18$), whereas crabs of the violescent morph were medium-sized to large, between 7.54 and 15.73 mm CSL ($n = 29$) (Fig. 4A). Violescent individuals were found in both sexes and in all reproductive groups, but the brownish-red morph was not found in the ovigerous female category (Table 1). Sizes at color transition from the brownish-red to the violescent morphs of males were 6.48 to 7.54 mm CSL while those of females were 7.22 to 8.44 mm CSL.

Relationship between Color Morphs and the Environment

During 15 months of the study period, the number of individuals of *C. violascens* found in each sampling month was between 0 and 6. The crab number in each sample quadrat ranged from 0 to 4 ($n = 240$ quad.) with a relative density of *C. violascens* equal to 0.20 ± 0.53 crabs/m². In the sample quadrats, the density of brownish-red individuals was between 1 ($n = 16$

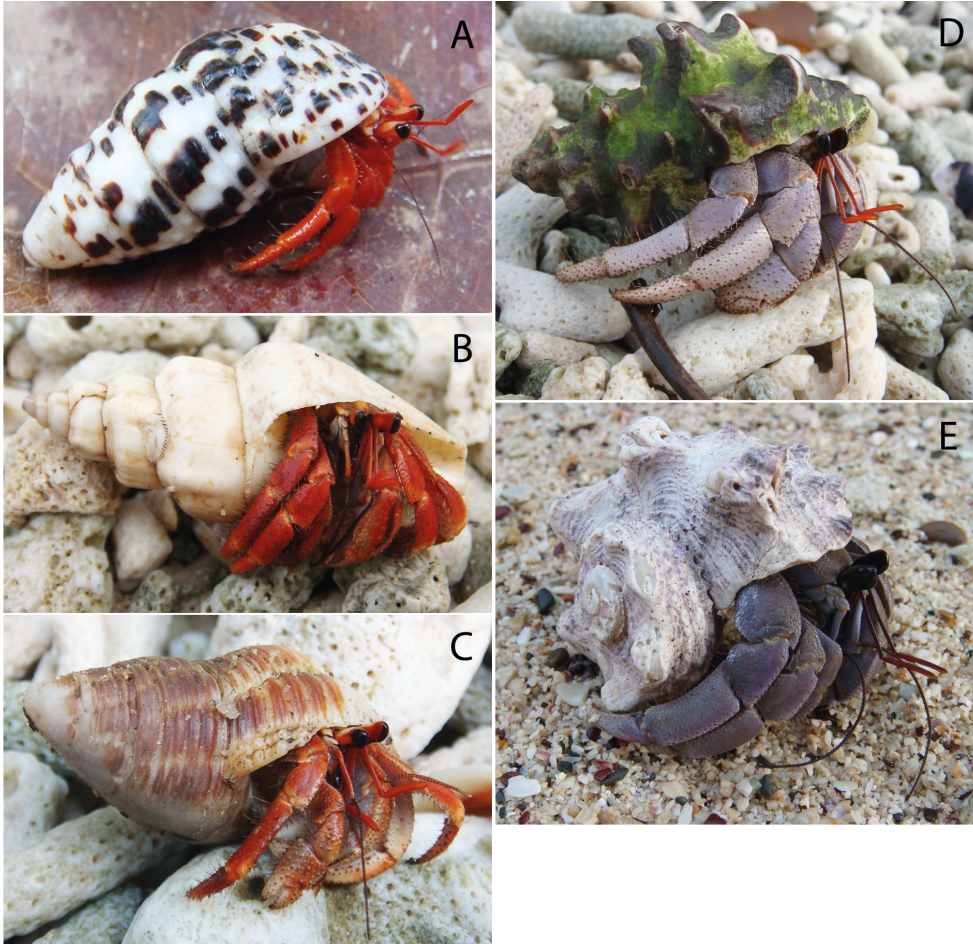


Figure 1. Color morphs of *Coenobita violascens*. Brownish red: A, female (2.99 mm CSL, 28 November 2011); B, female (6.28 mm CSL, 13 January 2012); C, male (6.48 mm CSL, 11 March 2012). Violescent: D, female (11.77 mm CSL, 10 March 2012); E, male (13.80 mm CSL, 1 October 2011). Photographs by Thanakhom Bundhitwongrut.

quad.) and 2 ($n = 1$ quad.), whereas the density of violescent individuals was slightly higher, ranging from 1 to 3 (ave. = 1.56) crabs. Moreover, brownish-red individuals of *C. violascens* were found at 5 m ($n = 4$ ind.) and 25–45 m ($n = 14$ ind.) from the tidemark while violescent individuals were encountered from 5 to 45 m ($n = 29$ ind.), except at 30 and 40 m, from the tidemark (Fig. 5).

Size Variation between Sexes and among Reproductive Groups

A total of 47 individuals of *C. violascens* were collected, including 26 males (55%) and 21 females (45%) (19 non-ovigerous females [40%] and 2 ovigerous females [4%]). The mean CSL size \pm SD and size range (minimum–maximum) of all individuals, males, all females,

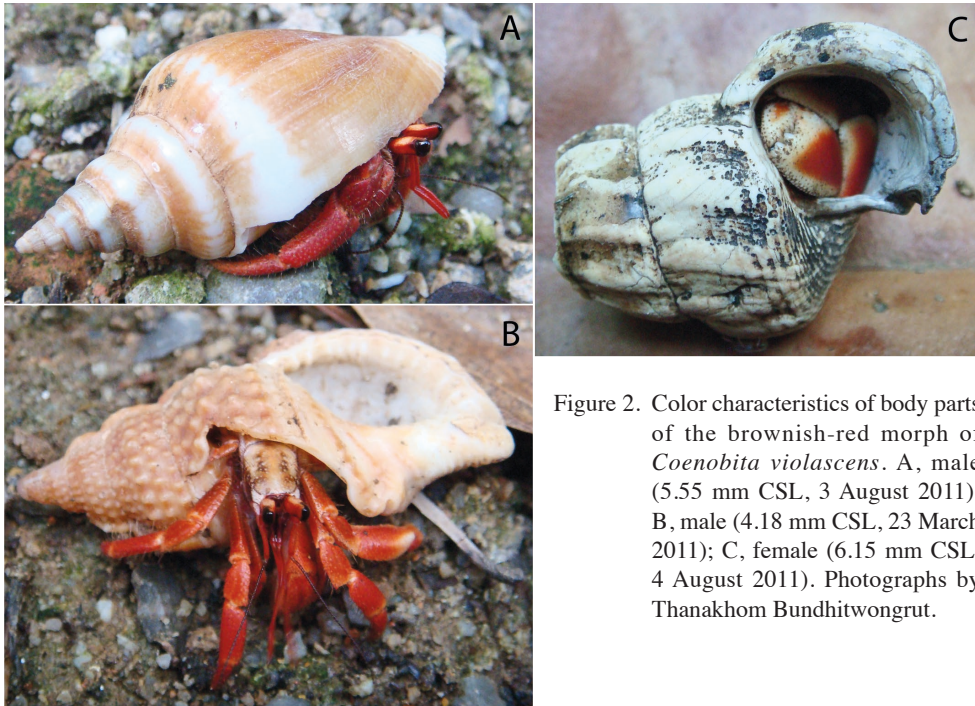


Figure 2. Color characteristics of body parts of the brownish-red morph of *Coenobita violascens*. A, male (5.55 mm CSL, 3 August 2011); B, male (4.18 mm CSL, 23 March 2011); C, female (6.15 mm CSL, 4 August 2011). Photographs by Thanakhom Bundhitwongrut.

and ovigerous females of *C. violascens* are shown in Table 1. Based on the smallest ovigerous female of *C. violascens* in this study, 9.64 mm CSL was the beginning of sexual maturity, or the transitional size between juvenile and adult (Fig. 4B).

The mean CSL size \pm SD and size range of all male *C. violascens* were 9.69 ± 3.74 (range 3.39–15.73) mm ($n = 26$) whereas those of all females were 7.72 ± 2.71 (range 2.99–11.77) mm ($n = 21$). The mean BW \pm SD and range of all male *C. violascens* were 8.1 ± 6.7 (range 0.3–24.7) g while those of all females were 4.0 ± 3.1 (range 0.2–10.3) g.

DISCUSSION

The present study contributes to our knowledge about ontogenetic change in coloration of *Coenobita violascens* by providing comprehensive descriptions of the two color morphs previously reported by NAKASONE (1988), as well as a comparison with individual size. NAKASONE (1988) provides abbreviated detail of the coloration of adult and juvenile *C. violascens* without any indication of the size disparity between these developmental stages. HAMASAKI *ET AL.* (2017b) recently describes ontogenetic change of body coloration in small juveniles of *C. violascens* (1.06–2.83 mm CSL) raised in the laboratory. The present study reveals ontogenetic changes in coloration of larger juveniles and adults of *C. violascens* (2.99–15.73 mm CSL) sampled from their natural habitat. Additionally, size variation between sexes and among reproductive groups of this species was also investigated.

Table 1. The mean CSL size \pm SD, size range (minimum–maximum) and the number of crabs sampled of both color morphs of *Coenobita violascens* at Cape Panwa, Phuket Island, Thailand from January 2011 to March 2012.

Reproductive group		Color morph	
		Brownish red	Violescent
Males	mean \pm SD (mm)	4.80 \pm 1.21	11.86 \pm 1.92
	range (mm)	3.39–6.48	7.54–15.73
	<i>n</i>	8	18
All females	mean \pm SD (mm)	5.23 \pm 1.50	9.97 \pm 0.93
	range (mm)	2.99–7.22	8.44–11.77
	<i>n</i>	10	11
Ovigerous females	mean \pm SD (mm)	-	9.70 \pm 0.08
	range (mm)	-	9.64–9.76
	<i>n</i>	-	2
All individuals	mean \pm SD (mm)	5.04 \pm 1.36	11.15 \pm 1.85
	range (mm)	2.99–7.22	7.54–15.73
	<i>n</i>	18	29

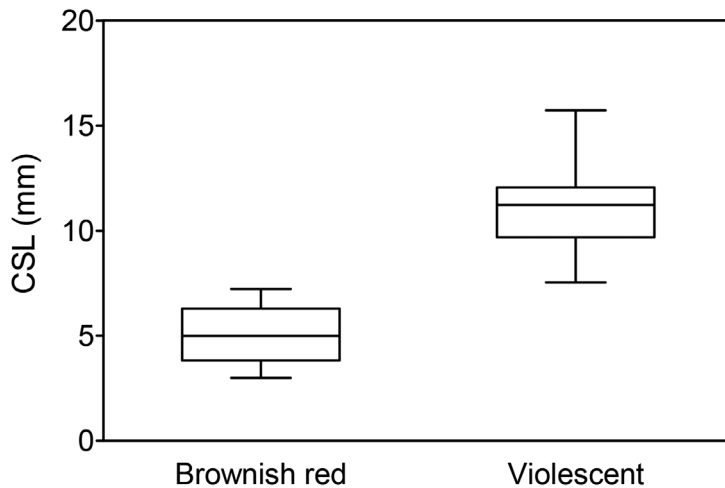


Figure 3. Boxplots of the cephalothoracic shield length (CSL) of the two color morphs of *Coenobita violascens* sampled at Cape Panwa, Phuket Island between January 2011 and March 2012.

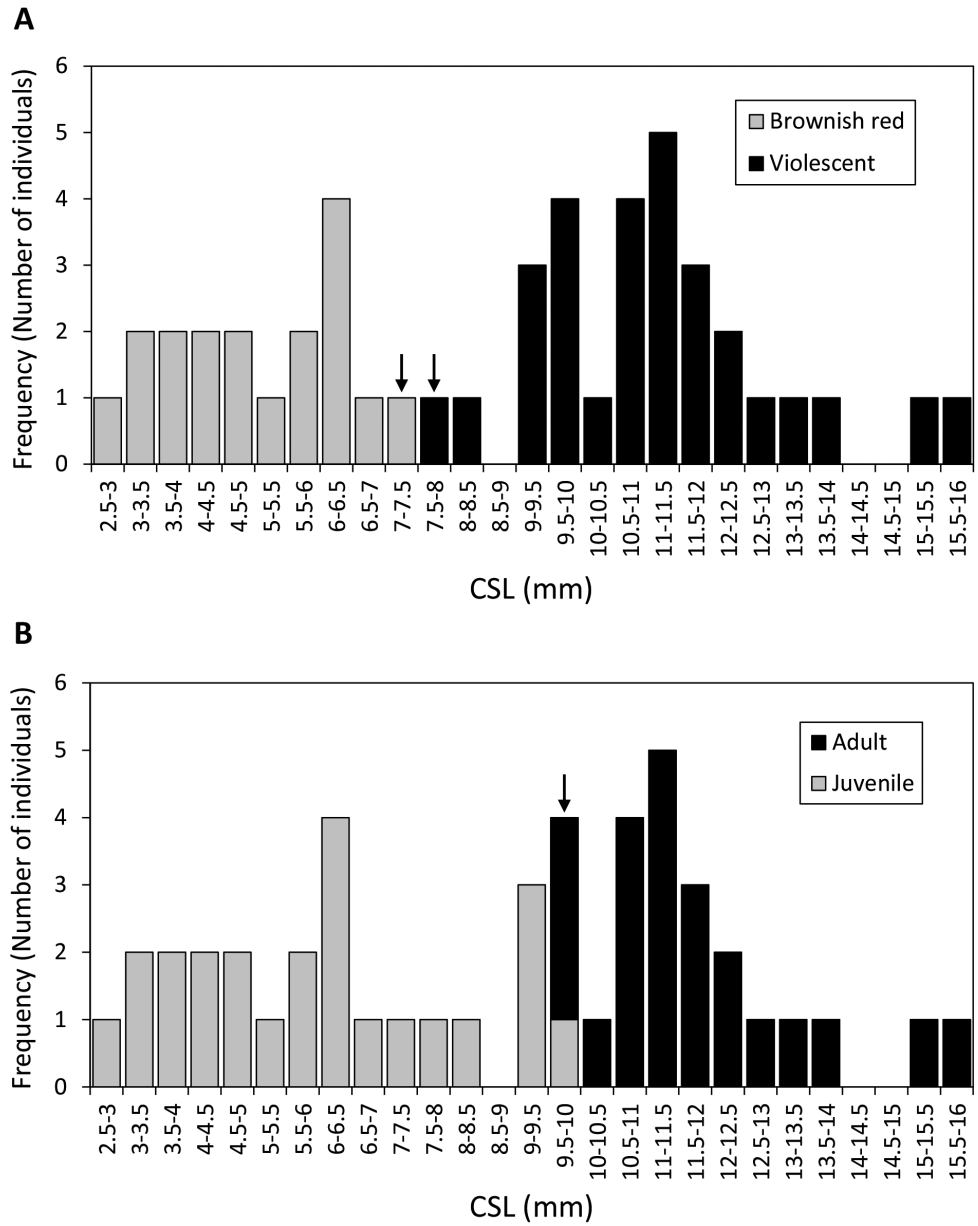


Figure 4. Size frequency distribution based on the cephalothoracic shield length (CSL) of *Coenobita violascens*. A, between color morphs; B, between developmental stages. Arrows indicate size classes containing transitional sizes.

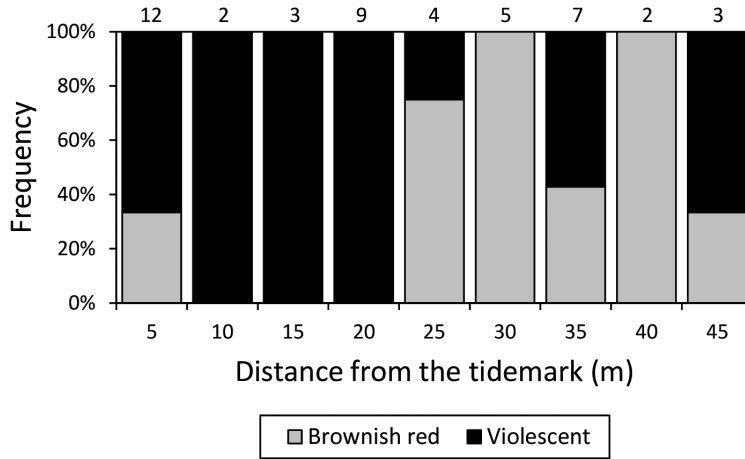


Figure 5. Proportion of the brownish-red and the violescent morphs of *Coenobita violascens* in function of the distance from 5 m to 45 m horizontally from the tidemark at the time. Value above each column is the total number of individuals sampled at each 5-m interval.

Ontogenetic color change of different color morphs of *Coenobita violascens* is morphological (chromogenic) (McNAMARA & MILOGRANA, 2015) because it is associated with gradual changes related to developmental stage (i.e., juvenile and adult). NAKASONE (1988) mentioned brownish-red individuals as juvenile and violescent individuals as adult *C. violascens*. Nevertheless, in the present study, all brownish red ($n = 18$) and some small violescent individuals ($n = 6$) were juvenile, whereas most larger violescent individuals ($n = 23$) were adult, assuming that the smallest ovigerous female (9.64 mm CSL) was at the beginning of maturity, or transitional in size between juvenile and adult. Some brownish-red individuals had variable coloration in the study area. Overall body color of this morph ranged from reddish orange or bright red to brownish red as they grew. The results also suggest that the transitional size between the two color morphs (7.22–7.54 mm CSL) is not congruent with and does not match the transitional size between the developmental stages (9.64 mm CSL) (Fig. 4). According to the present hypothesis, however, the puberty molt marks the beginning of sexual maturation and is usually marked by morphological changes (HARTNOLL, 1988b). The color change of *C. violascens* from brownish red to violescent in this study appeared before sexual maturation. Additionally, sizes at the transition from brownish-red to violescent morphs between sexes of *C. violascens* are seemingly different, as the males undergo color change before females. However, the sample sizes of *C. violascens* in this study are relatively small. More specimens from further investigations using different sampling techniques or by surveys in different study sites, particularly in its main habitat in estuarine areas, will confirm this hypothesis of ontogenetic color change between sexes.

The present study provides details of ontogenetic coloration of large juveniles and adult *Coenobita violascens* (2.99–15.73 mm CSL) that extend the observations by HAMASAKI ET AL. (2017b) on first stage crabs to small juveniles of *C. violascens* (1.06–2.83 mm CSL). The ontogenetic color changes from small to large juveniles are as follows. The white dorsal surface of the ocular peduncles changes to a longitudinal light orange stripe on the dorsal

surface of each ocular peduncle. Shield color changes from whitish/creamy to creamy/light orange. Two longitudinal dark reddish brown bands on the middle part of the shield expand as two irregular longitudinal brownish bands, and enlarge to cover almost the whole area of the shield in some large brownish-red individuals. A dark reddish-brown band at the anterior lower part of each side wall of the shield enlarges and covers all areas of the lateral surface of the shield. Longitudinal white stripes on the middle and ventral parts of the left cheliped palm become light orange in most large brownish-red individuals, as the whitish rings between the proximal and distal parts of each segment of the chelipeds and the second and third pereopods disappear.

The finding that the color “morphs” represent ontogenetic stages rather than genetic morphotypes suggests that the color “phase” is a more appropriate term than “morph”. However, I will continue following tradition and use the term morph, with the understanding that an apparent morphotype may in many instances represent an ontogenetic phase, as in the present case.

The transitional color changes between the two morphs of *Coenobita violascens* are indicated in the current investigation. The change from brownish-red to violet in *C. violascens* seems to start with a light lavender color appearing on the antennal acicles and mesial surfaces of the chelipeds and pereopods in the large brownish-red morph. However, more samples of *C. violascens* are needed to allow us to study variations in the ontogenetic color change from brownish-red to violet morphs. We need further observations of larger juvenile *C. violascens* raised in captivity until they become adults to provide more detailed knowledge of the ontogenetic color change.

The bright coloration of juvenile *Coenobita violascens* contrasts with the coloration of its habitat of sparse vegetation on sand alternating with dense vegetation at the current study site (BUNDHITWONGRUT *ET AL.*, 2014). Camouflage by background color matching is often seen in juvenile crabs, potentially reducing predation risk (PALMA & STENECK, 2001; STEVENS & MARILAITA, 2009; LAVALLI & SPANIER, 2015; HAMASAKI *ET AL.*, 2017b; CARO, 2018). Although bright coloration may serve as warning coloration or aposematism (COTT, 1940; BOOTH, 1990; QUICKE, 2017), there is no harmful model for juvenile *C. violascens* to mimic at this study site (personal observation). Although there is no proven example of aposematism in decapod crustaceans (CARO, 2018), some information on warning coloration of potential toxins in brachyuran crabs has been recorded (LAVALLI & SPANIER, 2015). Nevertheless, there is no record of toxin or distastefulness in *C. violascens*. Interestingly, HAMASAKI *ET AL.* (2022) recently reported that, in the laboratory, the fiddler crab *Paraleptuca crassipes*, with its bright red and black body color patterns, encounters lower predation risk by the mudskipper *Periophthalmus argentilineatus* than the fiddler crab *Austruca perplexa* which has brownish-white coloration. This suggests that the bright coloration of *P. crassipes* may represent incidental mimicry of the unpalatable red/orange-colored polychaete worms that mudskippers might have learned to avoid. However, that the brightly colored polychaete worms are unpalatable to the crabs living in the same habitat needs further confirmation if this is to be taken as an example of aposematism (HAMASAKI *ET AL.*, 2022). Therefore, whether the bright coloration of *C. violascens* is adaptive warning coloration is unknown.

It is also possible that the variation in coloration functions in intraspecific communication. Differing coloration between juveniles and adults probably assists prereproductive recognition to prevent adults from trying to mate with juveniles, or decreases conspecific aggression towards juveniles by adults (BOOTH, 1990). The obvious evidence is that ovigerous females

of *Coenobita violascens* sampled in this study were all violescent morphs. Another important aspect that needs study is how *C. violascens* perceives color, which is presently unknown. Currently, we have limited information related to the visual abilities of only a few coenobitid crab species: *C. clypeatus* (PING ET AL., 2015; SHRAGAI ET AL., 2017), *C. compressus* (MOPAN-CHILITO ET AL., 2021), *C. brevimanus* and *C. rugosus* (HOW ET AL., 2023). Further investigations of mating behavior and color perception of *C. violascens* are needed to test this hypothesis.

The relative density of *Coenobita violascens* at the site (0.20 ± 0.53 crabs/m²) is much smaller than that of *C. rugosus* (6.98 ± 0.36 crabs/m², BUNDHITWONGRUT ET AL. [2014]). The habitat of the present study area, primarily supralittoral sandy beach (BUNDHITWONGRUT ET AL., 2014; BUNDHITWONGRUT, 2018), is not the most preferred habitat type for this coenobitid species which has been more often recorded in more productive habitats such as mangroves and terrestrial areas near estuaries (NAKASONE, 1988; McLAUGHLIN ET AL., 2007; DOI ET AL., 2016). Furthermore, the number of *C. violascens* in the sample quadrats was relatively very low (0–4 ind./quad. for all individuals, in comparison with the number of *C. rugosus* (1–28 ind./quad., BUNDHITWONGRUT ET AL. [2014])). This may indicate that *C. violascens* at the present study site lives solitarily or forages at different times than other coenobitid species in the area to reduce competition. Brownish-red individuals of *C. violascens* were encountered mainly between 25 and 45 m from the tidemark at the present study site, areas which are mostly covered by vegetation (personal observation). This possibly means that juvenile *C. violascens* (all brownish-red and small violescent individuals) depend on the vegetation for shelter and predator protection, as do *C. rugosus* in the same study area (BUNDHITWONGRUT ET AL., 2014). Violescent individuals were found at nearly all distances from 5 to 45 m from the tidemark. Most violescent crabs were adults, from which we may infer that their larger size protected them from predation and allowed them to forage throughout the habitat with less dependence on vegetation shelter.

From the *Coenobita violascens* collected, males attained larger CSL and BW than females, which demonstrates sexual dimorphism in size as previously reported in *C. clypeatus* by WILDE (1973), *C. scaevola* by SALLAM & MANTELATTO (2010) and *C. rugosus* by BUNDHITWONGRUT ET AL. (2014). The sexual size dimorphism is probably due to difference in energy allocation, as males grow to larger size while females allocate more energy to reproduction (ABRAMS, 1988). Furthermore, the smallest ovigerous female of *C. violascens* at Cape Panwa, Phuket, Thailand in the present study (9.64 mm CSL) was larger than those from Ishigakijima Island, Ryukyu Archipelago, Japan (7–8 mm CSL size class, FUJIKAWA ET AL., 2017). Discrepancies between these two geographically separated populations of *C. violascens* could be attributed to dissimilar environments and habitats, different life histories, or differing sampling methods and periods (GARCIA & MANTELATTO, 2000; MANTELATTO & GARCIA, 2000; BUNDHITWONGRUT ET AL., 2014). Reproductive system dissection of both sexes of *C. violascens* was not carried out in this study. Further anatomical investigations should be conducted to confirm and compare maturity between sexes of *C. violascens*. The smallest ovigerous female may not be a reliable indicator of maturity, as used as the traditional criterion of sexual maturity (BUNDHITWONGRUT ET AL., 2014), because males and females probably differ in size at maturity (e.g., NAKASONE, 2001).

In conclusion, the present study provides a comprehensive description of two color morphs of *Coenobita violascens* as well as the transitional characters involved in ontogenetic color change. From *C. violascens* sampled in this investigation, the change from brownish red to violescent body coloration occurs before sexual maturation. *C. violascens* is sexually dimorphic in size, as males achieve larger CSL and BW than females. Therefore, the results

of this study will contribute to a better understanding of the life history of *C. violascens* and aid conservation efforts for this land hermit crab species.

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