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An Indo-West Pacific Distribution for the Coral-Dwelling Gall Crab *Lithoscaptus doughnut* (Decapoda: Cryptochiridae)

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Abstract: Coral-dwelling gall crabs (Cryptochiridae) are common inhabitants of scleractinian corals. Several species have been described as new in recent years, including *Lithoscaptus doughnut*, which was described from Hong Kong based on a single female retrieved from the coral *Plesiastrea peroni*. Here we extend the distribution range of *L. doughnut* with nine additional localities throughout the Indo-West Pacific, from the Red Sea to the Coral Triangle and Japan. We describe a male specimen of *L. doughnut* for the first time, based on a specimen from Malaysia, and provide photographs of life and preserved material. Haplotype networks based on COI mtDNA (n = 12) and 16 rRNA sequences (n = 12) were created. We retrieved eleven COI haplotypes and six 16S haplotypes, however no clear geographic distribution pattern was discerned. Intraspecific variation in *L. doughnut* was 1.4% for COI and 0.2% for 16S. Lastly, the first colour photos and records of associated parasites of this species are provided.

Keywords: haplotype network; reef-associated fauna; Scleractinia; symbiosis

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1. Introduction

Tropical coral reefs are among the most biodiverse ecosystems on the planet. A large part of the biodiversity on coral reefs is composed of invertebrates that live in close association with sessile organisms. Reef-building stony corals (Scleractinia) provide habitat to a wide range of species, and their associated fauna has been reviewed in several papers [1–3]. Although the exact nature of these associations is not always well understood, with species exhibiting dependencies ranging from facultative to obligate symbiosis, this small majority is an important component of the biodiversity on coral reefs.

Decapod crustaceans form a major part of the coral-associated fauna [3]. The small, coral-dwelling gall crabs of the family Cryptochiridae Paulson, 1875 are obligately symbiotic with scleractinian corals and have been the subject of various recent studies on, for example, their reproductive morphology, occurrence patterns, biogeography, and even fluorescence [4–7]. Their association with host corals is strong and not affected by intraspecific coral competition [8]. Gall crabs are found on coral reefs worldwide. They are most abundant on shallow-water tropical reefs, but are known to also occur in the deep sea at >500 m depth [9]. There are currently 54 described species across 21 genera [10], however, recent studies highlighted the presence of large (cryptic) diversity in the genera *Hapalocarcinus* Stimpson, 1859 and *Opecarcinus* Kropp & Manning, 1987 [7,11]. Cryptochirids show varying degrees of host specificity; most species inhabit a single coral genus or several closely related species [12–14]. The Atlantic species *Troglocarcinus corallicola* Verrill, 1908 is the only host generalist in the family [9,15]. Besides this variation in host-specificity, cryptochirids differ in their geographic distribution. Some species are very widespread, whereas others are only known from a smaller geographic area [7,15]. The Coral Triangle is the biodiversity hotspot for scleractinian corals [16,17], with the Red Sea as a secondary centre of biodiversity [17]. Geographic range shifts are thought to play a critical role in generating the observed species diversity gradients on coral reefs [16], however for many invertebrates, including gall crabs, these distribution ranges need to be studied in more detail [7,18].

Gall crabs of the genus *Lithoscaptus* A. Milne-Edwards, 1862 inhabit corals of the family Merulinidae H. Milne Edwards & Haime, 1857 [13]. The genus is composite in nature and in need of revision [19,20]. It currently comprises 13 described species; however, more diversity is expected, based on preliminary data [20]. The recently described species *L. semperi* Van der Meij, 2015, *L. tuerkayi* Van der Meij, 2017, and *L. aquarius* Van der Meij, 2023 strictly associate with *Trachyphyllia geoffroyi* (Audouin, 1826), *Caulastrea* spp. Dana, 1846, and *Catalaphyllia jardinei* (Saville-Kent, 1893), respectively, whereas other species have been recorded from multiple host genera [13,21]. Like many other gall crab genera, *Lithoscaptus* has been recorded throughout most of the Indo-West Pacific (IWP), albeit with patchily known distribution records [13].

Recently, the species *Lithoscaptus doughnut* Wong, Tsao, Qui & Chan, 2023 was described based on a single female specimen collected from *Plesiastrea peroni* H. Milne Ewards & Haime, 1857 near Basalt Island (Hong Kong), limiting the species' known distribution to the type locality. Here, we extend the distribution range of *L. doughnut* throughout the IWP, based on material collected from the Red Sea to the Coral Triangle and Japan. We illustrate and describe the male of *L. doughnut*, based on a specimen from Malaysia, provide haplotype networks based on sequence data of the cytochrome c oxidase subunit I gene (COI) and 16S mtDNA and the first colour photographs of the species. Lastly, we comment on the identity of *L.* cf. *doughnut* based on 16S data.

2. Material and Methods

2.1. Sampling

Gall crabs were sampled from *Plesiastrea peroni* during fieldwork between 2007 and 2016 in the Red Sea, Maldives, Malaysia, Indonesia, and Japan (Table 1, Figure 1), and provisionally identified as a new species by the senior author under the placeholder name *Lithoscaptus "Plesi"*. One sample was collected from a free-living colony (corallith) of *Cyphastrea chalcidicum* (Forskål, 1775). Most samples were collected from deeper parts of the reef, between 8 and 24 m depth. Based on morphology, COI barcoding, and host data, these samples are now identified as *Lithoscaptus doughnut*. All specimens are deposited in the scientific collections of Naturalis Biodiversity Center in Leiden (The Netherlands), with the collections coded as RMNH.CRUS.D. All corals were photographed in situ in the field, whereas the crabs were photographed in field laboratories using a digital SLR camera equipped with a macro lens. Abbreviations used: CL: carapace length; P: pereiopod; MXP-3: maxilliped 3; G1: gonopod 1; G2: gonopod 2.

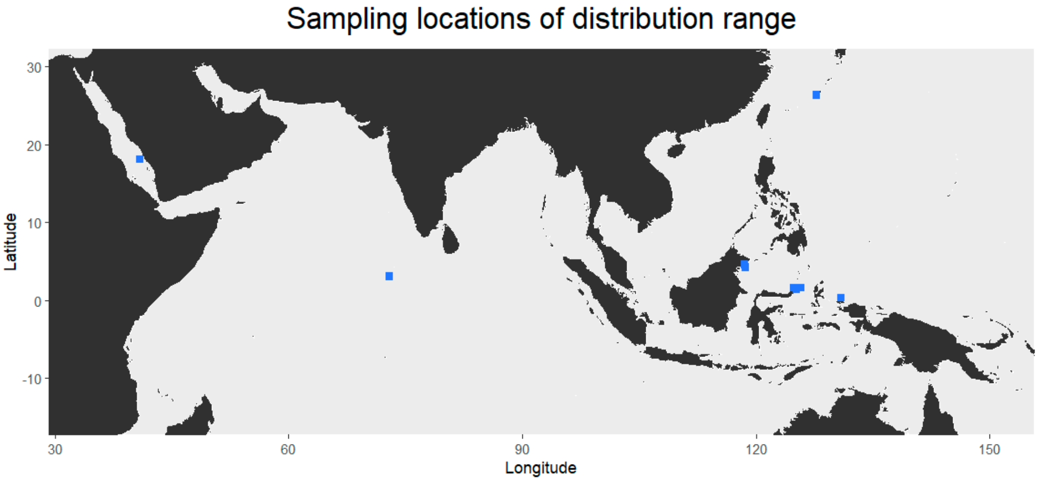

Figure 1. Map showing sampling locations (in blue) of *Lithoscaptus doughnut* other than the type locality.

Table 1. Overview of material used for genetic analyses.

Voucher Code	COI	16S	Host Coral	Country	Locality
CEL-Hapa-040/ASIZCR	OP103644	n/a	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Hong Kong	Basalt Island, Sai Kung
CEL-Hapa-006	OP103613	OP114856	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Hong Kong	Long Ke Tsai, Sai Kung
RMNH.CRUS.D.54169	OR710957	OR711069	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Indonesia	Tanjung Nanas II, Lembeh Isl., N Sulawesi
RMNH.CRUS.D.54172	OR710956	OR711070	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Indonesia	Pulau Abadi, Lembeh Isl., N Sulawesi
RMNH.CRUS.D.54106	OR710954	OR711068	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Indonesia	Lekuan III, Bunaken Isl., N Sulawesi
RMNH.CRUS.D.54063	OR710953	OR711067	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Indonesia	Tiwoho, Bunaken Isl., N Sulawesi
RMNH.CRUS.D.53890	OR710955	OR711066	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Indonesia	Mayalibit Bay, E Manil Isl., Raja Ampat, W Papua
RMNH.CRUS.D.57236	NA	OR711074	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Japan	Mizugama, Okinawa
RMNH.CRUS.D.53725	OR710951	OR711064	*Cyphastrea chalcidicum* (Forskål, 1775)	Malaysia	Mabul Isl., Eel Garden, Semporna
RMNH.CRUS.D.53740	OR710952	OR711065	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Malaysia	Mata Pahi Isl., Semporna
RMNH.CRUS.D.58330	OR710958	OR711072	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Maldives	Free Climbing, Faafu Atoll
RMNH.CRUS.D.58331	OR710959	OR711073	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Maldives	Route 66, Faafu Atoll
RMNH.CRUS.D.54404	OR710960	OR711071	*Plesiastrea peroni*, Milne Edwards & Haime, 1857	Saudi Arabia	Shib Radib, offshore of Farasan Banks

2.2. Haplotype Networks

Sequences of COI mtDNA (COI [22]) and 16S rRNA (16L2 and 16H10 [23]) were obtained following the protocol in Van der Meij [14]. Sequences were assembled in Sequencher 4.10.1 [24] and aligned using ClustalW Multiple Alignment in BioEdit v7.0.5.3 [25], together with the sequences from Wong et al. [26]. Sequences were trimmed to have the same maximum length, 620 bp for COI and 585 bp for 16S. Median-joining haplotype networks were constructed with PopArt 1–7 [27] for both sets of sequences. All samples were assigned to their sampling localities; both networks span 9 locations throughout the IWP (Table 1).

2.3. Intraspecific Divergence

MEGA11 [28] was used to determine the intraspecific divergence of *L. doughnut.* The best-fitting model of nucleotide substitution was calculated using MEGA11, resulting in the Tamura 3-parameter model for both datasets [29], which was subsequently used to calculate the within-group intraspecific divergence.

3. Results and Discussion

3.1. Distribution and Haplotype Networks

Lithoscaptus doughnut is now recorded from nine localities ranging from the Red Sea to the Coral Triangle and Japan, extending the distribution range of the species from Hong Kong to all throughout the IWP (Figure 1). The distribution is roughly in line with the distribution of its host *P. peroni* [30]. The Pacific Ocean, where *P. peroni* also occurs, has not yet been sampled for *L. doughnut*. The haplotype network based on COI sequences data shows eleven different haplotypes; however, no clear geographical pattern was observed (Figure 2). The 16S haplotype network yields six haplotypes, providing less diversity in comparison to the COI haplotype network (Figure 3). Here, all sequences from the Coral Triangle are included in the main haplotype or differ one or two base pairs from this most common haplotype.

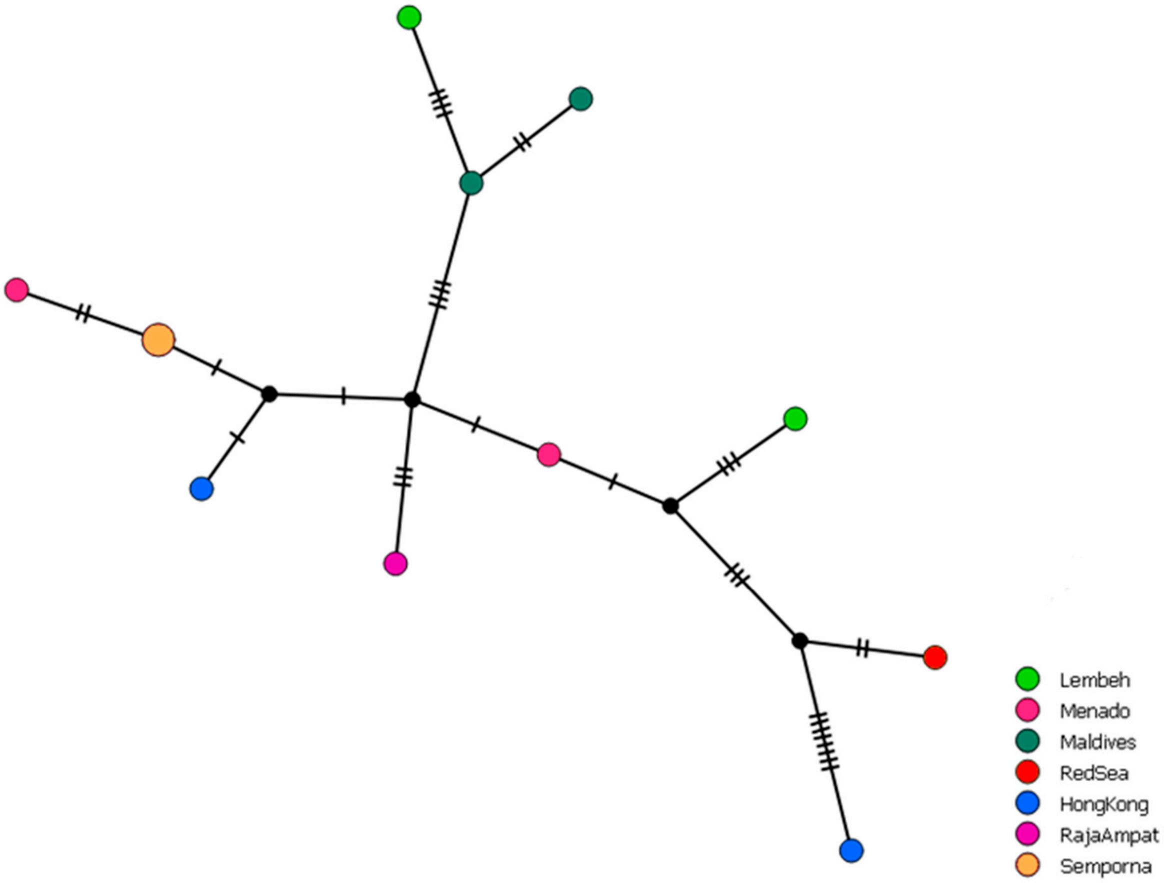

Figure 2. Haplotype network of *Lithoscaptus doughnut* based on COI sequences (n = 12). Marks across the branches indicate the amount of different nucleotides between haplotypes. The small coloured circles correspond to a single sequence, circle size increases when sequences are identical.

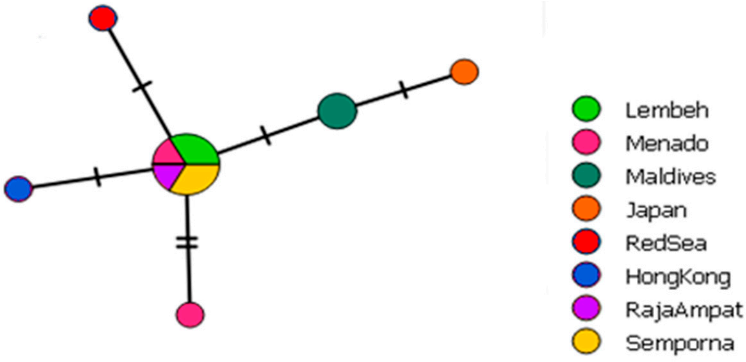

Figure 3. Haplotype network of *Lithoscaptus doughnut* based on 16S mtDNA (n = 12). Marks across branches indicate the amount of different nucleotides between haplotypes. The small circles correspond to a single sequence, circle size increases when sequences are identical.

The difference in the number of haplotypes between the COI and 16S networks is supported by the different evolutionary divergence estimates. The intraspecific difference within the sequences is 1.4% for COI and 0.2% for 16S.

3.2. Coral Host

Plesiastrea peroni was identified as the host of *L. doughnut* by Wong et al. [26]. This is in agreement with our samples, which were retrieved from the same coral host. Earlier studies recorded *Plesiastrea versipora* (Lamarck, 1816) as the host of this species [31,32]; however, *Plesiastrea* corals in (sub)tropical waters should be referred to as *P. peroni* instead [30]. *Plesiastrea versipora* is restricted to temperate waters, and, so far, no gall crabs have been recorded from this species. One of our samples (from Semporna, Malaysia) was collected from a *Cyphastrea chalcidicum* corallith. It is not uncommon for host-specific species to occasionally end up in the 'wrong' host [33], perhaps caused by the crab needing to settle after reaching the megalopa stage.

Plesiastrea peroni belongs to the Plesiastreidae Dai & Horng, 2009, a family with just two species. Plesiastreidae cluster basal to Montastraeidae Yabe & Sugiyama, 1941 and Diploastraeidae Chevalier & Beauvais, 1987, as well as the species-rich coral families Lobophylliidae Dai & Horn, 2009 and Merulinidae [34]. All other *Lithoscaptus* species are associated with Merulinidae corals; hence, *L. doughnut* is currently the only *Lithoscaptus* species associated with a non-Merulinidae coral. *Cyphastrea*, the host genus of one of our specimens, does belong to the Merulinidae.

3.3. Phylogenetic Position

Wong et al. [26] retrieved *L. doughnut* as a sister to *L. paradoxus* A. Milne-Edwards, 1862 and *L. scottae* Wong, Tsao, Qiu & Chan, 2022 based on COI phylogeny, albeit without support. *Lithoscaptus doughnut* was already included in the phylogenetic reconstruction of Van der Meij and Klaus [35] under the placeholder name *Lithoscaptus "Plesi"*. Based on their three-marker phylogeny, the species was retrieved in a fully supported clade containing *Lithoscaptus paradoxus*, *Lithoscaptus semperi*, *Lithoscaptus prionotus* Kropp, 1994, and *Xynomaia sheni* (Fize & Serène, 1956). *Lithoscaptus aquarius* Van der Meij, 2023, associated with *Catalaphyllia jardinei*, also belongs to this clade [36]. Here, we confidently place *L. doughnut* as a sister to the above-mentioned taxa.

3.4. Lithoscaptus cf. doughnut

A second specimen from *P. peroni* obtained by Wong et al. [26] was identified as *Lithoscaptus* cf. *doughnut*. The COI sequence obtained from this specimen was shorter in length (567 bp) and had a Kimura 2-parameter (K2P) distance of 2.73%. The authors chose to stay conservative and not fully assign this specimen to *L. doughnut*, also because this second specimen was damaged and a few morphological differences were observed. The intraspecific divergence falls within the range of our COI sequence data. Based on 16S data, *Lithoscaptus* cf. *doughnut* differs by just one base pair from the most common 16S haplotype found in the Coral Triangle (Figure 3). Based on the COI and 16S data presented here, there appears to be enough support to simply regard *L.* cf. *doughnut* as *L. doughnut.* The observed morphological differences could potentially be regarded as intraspecific diversity.

3.5. Colour in Life

The colour of *L. doughnut* is overall beige. The deflected anterior one-third of the dorsal surface is a dark brown, whereas the posterior two-thirds are light beige. Granules are a lighter shade (Figure 4A). Chelipeds are dark beige with brown chelae (Figure 4A,B), and another specimen shows clear white markings on the chelae (Figure 4C,D). Pereiopod two is beige with reddish-brown propodus and dactylus, whereas pereiopods three to five are translucent with few off-white markings (Figure 4A–D). The telson from a specimen from the Red Sea is largely translucent (Figure 4C,D), whereas the first and second segments of a specimen from Indonesia have dark brown speckles (Figure 4A,B). The third maxilliped is dark brown, with translucent antennule with white bands, and reddish-brown cornea.

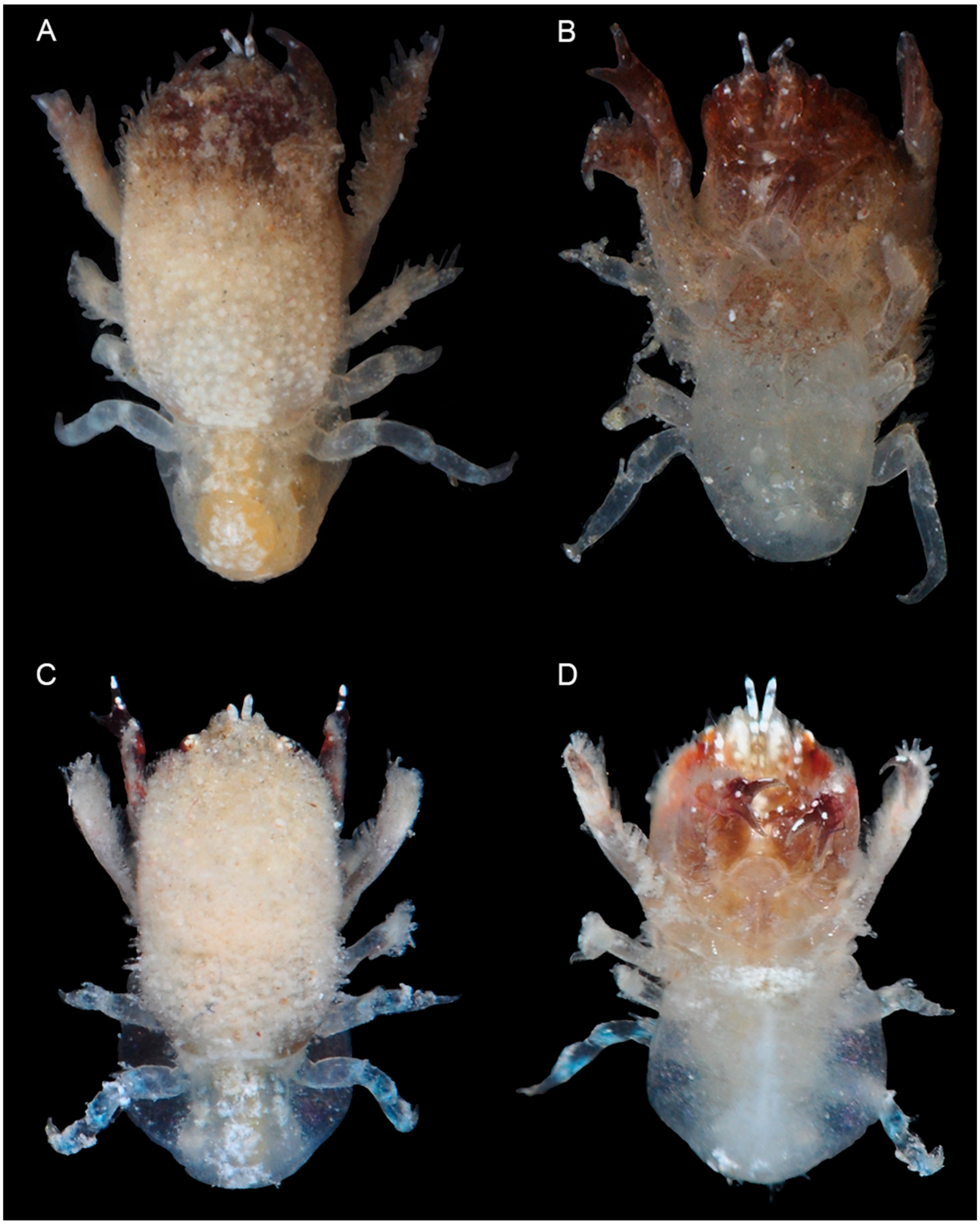

Figure 4. Colour in life of *Lithoscaptus doughnut*. Non-ovigerous females. (**A**,**B**) RMNH.Crus.D.54172; dorsal view and ventral view. (**C**,**D**) RMNH.Crus.D.54404; dorsal view and ventral view. Photos not to scale. Photos (**A**,**B**) by SET van der Meij; photos (**C**,**D**) by A Anker.

3.6. Description of Male L. doughnut

Material examined: ♂(1.6 mm × 1.3 mm, RMNH.CRUS.D.53725, Genbank; COI: OR710951; 16S: OR711064), collected from *Cyphastraea chalcidium* (Figure 5).

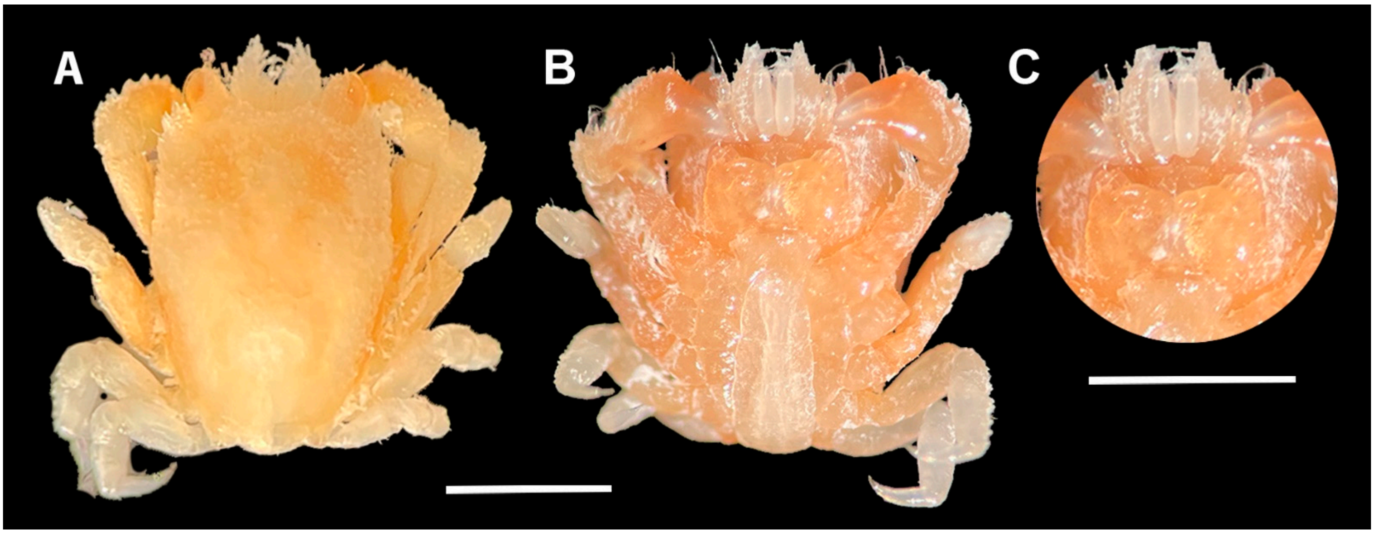

Figure 5. Male *Lithoscaptus doughnut* (RMNH.CRUS.D.53725): (**A**) dorsal view (**B**) ventral view. (**C**) close-up view of MXP-3. Photos by Tao Xu.

Description: Carapace 1.2 times as long as broad, mildly convex, less so than female. Anterior half squaroid, posterior half trapezoid with the shorter base at the posterior end. Anterior half of carapace strongly deflected, with two depressions antero-laterally of mesogastric region. Mesogastric region inflated; lacks distinct longitudinal grooves observed in females. Carapace mildly granulated, well isolated from each other, distribution of granules sparse at posterior half giving a smooth appearance. Antero-lateral edge with spines at outer corners, small spines at inner orbital angle. Lateral edge finely serrated anteriorly, smooth towards posterior end. External orbital angles similar height to internal orbital angle. Orbit broadly V-shaped. Female specimen from the same lot (RMNH.CRUS.D.53725) has an inner orbital angle protruding further than described of the holotype of L. doughnut (see description [26]: Figure 10a). Eye-stalks stout, 1.2 times as long as broad, and more straight than eye-stalks of female. Cornea anterolateral. Pterygostomial region similar to that of female, but lacking granules.

Cheliped stout, merus strongly compressed, half as long as carpus, propodus and merus strongly granulated dorsally, dactylus as long as palms, straight dorsal margin but rounded and open on palmar side, distal tips of fingers touching. Tip of left movable finger is damaged. Several rows of rounded tubercles on dorsal margin of propodus. Carpus armed with small spines, more so than female. Pereiopods decreasing in size: P2 1.3 times longer than P5. Propodus of P2–4 serrated along dorsal margin, dorsal margin of P5 smooth. Proportions of segments similar to female's. P2-left missing.

Antennulae smooth and tubular. Distal projection of antennular peduncles triangular, strongly toothed and extending beyond eye-stalks, congruent with antennular peduncles of female. Epistome does not show longitudinal crests, unlike female. MXP-3 squaroid with rounded margins, mesial margin of ischium lacking clear granules. Merus with distal external angle. Carpus and propodus grape-like in shape. Propodus with small tuft of setae. Exopod identical to female. Clearly accentuated pleural ridge. Abdomen elongated and straight, approximately three times longer than broad. Abdomen only covers middle of thoracic region, whereas female's abdomen forms a brood pouch covering the entire thoracic region. Telson rounded. Middle thoracic segments broader than anterior and posterior segments. Anterior plate of thoracic sternites broad, devoid of granules. G1 slightly curved laterally, broad at shoulder, apex pointed. G2 approximately one-third length of G1, inserted into base of G1.

Remarks: colour in life was not recorded.

3.7. Parasites

In a review paper of all known parasites of Cryptochiridae, the bopyrid parasite Carcinione platypleura Bourdon, 1983 was recorded from two Lithoscaptus sp. B specimens from N Sulawesi, Indonesia (RMNH.CRUS.D.54106, RMNH.CRUS.D.54172) [32]. Carcinione platypleura appears to be the most common parasite of gall crabs, with a wide distribution in the Indo-West Pacific. Furthermore, the parasitic epicaridean isopod Cabirnalia nausicaa Boyko & Van der Meij, 2018 was described from material obtained from various hosts, including Lithoscaptus sp. B (RMNH.CRUS.D.57236). Lithoscaptus sp. B was undescribed at the time but is now known as Lithoscaptus doughnut; hence, L. doughnut is an involuntarily host to C. platypleura and C. nausicaa parasites.

3.8. Concluding Remarks

Cryptochiridae show a mix of more widely distributed species and species seemingly confined to smaller geographic areas [7,18]. Here we showed that *Lithoscaptus doughnut* is a widely distributed species associated with *P. peroni* across its range. Parts of the range of *P. peroni*, from the the Red Sea to the Polynesian archipelago in the Pacific Ocean [30], still need to be sampled for the presence of this crab species. One *L. doughnut* sample was collected from a *Cyphastrea chalcidicum* corallith. We confidently showed that *L. doughnut* belongs to a clade with the type species *L. paradoxus*. The genus remains in urgent need of revision, and the diversity, host associations, and distribution patterns of many *Lithoscaptus* species are poorly understood. Further research is needed to solve the composite nature of *Lithoscaptus* and study its divergence across hosts and basins.

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Conflicts of Interest: The authors declare no conflicts of interest.

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