

No geographical variation but strong microhabitat partitioning: integrative taxonomy and infestation ecology of *Octolasmis* barnacles on *Scylla serrata* across three Indonesian ecoregions

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ABSTRACT. Species identification of *Octolasmis* barnacles on mud crabs based solely on morphology can be challenging, and whether infestation parameters vary geographically across the vast Indonesian archipelago remains unknown. This study integrated morphological taxonomy and DNA barcoding using the cytochrome c oxidase subunit I (COI) gene to identify species and compare the infestation ecology of *Octolasmis* on *Scylla serrata* across four locations representing three Indonesian ecoregions: Singkawang and Tanah Laut (Sunda Shelf), Donggala (Wallacea), and Teminabuan (Papua). A total of 240 crabs (60 per location) were examined. Phylogenetic analysis confirmed the presence of two morphospecies, *Octolasmis cor* and *O. angulata*. However, Bayesian Poisson Tree Processes (bPTP) species delimitation analysis revealed potential cryptic diversity, partitioning *O. cor* into four distinct lineages and *O. angulata* into three lineages (support values 0.951–1.000). Generalized linear models with Bonferroni correction showed no significant differences among locations for prevalence, intensity, or abundance ($P > 0.05$). *O. cor* exhibited higher prevalence (85%) and intensity (40.2 ± 8.7) than *O. angulata* (72%; 15.1 ± 4.3). Co-infestation recorded the highest intensity (62.0 ± 12.1). Paired t-tests demonstrated that both species had a significant preference for the hyperbranchia over the hypobranchia ($P < 0.001$). These findings confirm that *Octolasmis* infestation parameters on *S. serrata* are homogeneous across the ecoregions studied, suggesting that control strategies could potentially be implemented nationally. However, the cryptic lineages detected by bPTP warrant further investigation with additional genetic markers and broader geographic sampling.

Keywords: *Octolasmis*, *Scylla serrata*, cryptic diversity, Indonesian Throughflow, microhabitat partitioning, species delimitation

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1. Introduction

The ectoparasite *Octolasmis* spp. (Cirripedia: Poecilasmatidae) infestation of the gills causes mechanical tissue damage, oxidative stress responses, and a decrease in hyaline cells as nonspecific immune markers (Lerssuthichawal and Penprapai, 2013; Sarjito et al., 2025). *Octolasmis* infestation of gills causes mechanical tissue damage, oxidative stress responses, and a decrease in hyaline cells as nonspecific immune markers, with heavy infestation leading to mortality of up to

30% (Hudson and Lester, 1994; Saravanan et al., 2025). Although these findings derive from mixed *Octolasmis* spp. infestations, it remains unknown whether the two species, *O. cor* and *O. angulata*, exert significantly different immunosuppressive effects. In Indonesia, *S. serrata* is intensively exploited from mangrove ecosystems across various regions, including Kalimantan, Sulawesi, and Papua (Indarjo et al., 2020; Manalu and Bengen, 2021; Riyanto et al., 2025). However, high parasitic pressure on crabs without accurate species-specific management risks reducing fishery productivity and

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threatening the sustainability of aquaculture and wild stock availability.

Most previous studies on *Octolasmis* in Indonesia have relied on morphological identification (Yusgita et al., 2019; Hamid et al., 2019; Albar et al., 2026). This approach can introduce bias and is suboptimal for distinguishing cryptic species within the genus. This limitation leads to prevalence, intensity, and ecological impact data often being reported at the genus level, obscuring differences in pathogenicity and infestation strategies among species. Morphological differences between *O. cor* and *O. angulata* are very subtle. It was found that the percentage coverage of the capitular disc reached 28.3% in *O. cor* and 10.5% in *O. angulata*, indicating that the morphometric ratio of the capitulum region can serve as an interspecific differentiator (Albar et al., 2026). Consequently, reliance on conventional morphological identification is a major obstacle to understanding host–parasite interactions precisely, especially when interspecific differences are minimal and not easily measured consistently.

Although *Octolasmis* is the dominant ectoparasite on mud crab gills in Indonesia, its spatial distribution and inter-regional variation remain poorly understood. Specifically, three questions remain unanswered by previous studies: (1) Do the same *Octolasmis* species infest *S. serrata* in Kalimantan, Sulawesi, and Papua? (2) Do prevalence, intensity, and spatial preference on gills vary systematically among ecoregions? (3) Do the Wallace and Weber Lines act as biogeographic barriers for planktonic *Octolasmis* larvae, or does the widely distributed *S. serrata* facilitate genetic homogenization of the parasite? This geographic gap is striking because existing research is generally limited to a single location (Yusgita et al., 2019; Hamid et al., 2019; Albar et al., 2026). Consequently, our understanding of the parasite's spatial distribution remains fragmentary, and regionally based quarantine and control strategies cannot be optimally designed.

To address both methodological and geographical gaps, an integrative taxonomic approach combining morphology and mitochondrial COI molecular marker has been recognized as the international standard for barnacle identification (Simon-Blecher et al., 2021; Nigro et al., 2016). Although Albar et al. (2026) reported a COI phylogenetic tree confirming genetic differences between *O. cor* and *O. angulata*, this study did not report these differences across Indonesian regions. Based on the more widely available corpus, no study has directly reported these COI genetic distances. However, evidence from various crustacean and cirripedia groups consistently shows clear barcoding gap patterns. In the barnacle *Conchoderma*, interspecific distances reach 9.7% (Chan and Chen, 2022). In cephalopods, the intraspecific distance is 0.89% (Xu et al., 2020). Referring to these cross-taxon patterns, a threshold of <2% is generally used to indicate populations of the same species, whereas >8% indicates different species, a pattern that is highly likely to apply to the genus *Octolasmis* given its taxonomic position within Cirripedia. However, in Indonesia, no integrative study covering more than two locations simultaneously has been conducted. In fact, the regions of Kalimantan,

Sulawesi, and Papua are within different marine ecoregions (Sunda Shelf, Wallacea, and Papua ecoregions), separated by the Wallace and Weber Lines, potentially leading to population differentiation or even cryptic speciation in parasites with planktonic larval stages (Hidayani et al., 2020; Reid et al., 2006). These ecological differences allow for a correlational evaluation of the influence of ecoregion on infestation parameters (without simultaneous measurement of physico-chemical parameters, which is a limitation of this study). Theoretically, this study will test whether the Wallace and Weber Lines act as biogeographic barriers for *Octolasmis* or whether the widely distributed host *S. serrata* facilitates the genetic homogenization of the parasite.

Using an integrative taxonomic approach (morphology and COI gene sequencing on *S. serrata* individuals), this study aims to: confirm the *Octolasmis* species present based on morphology and COI genetic distance, compare infestation prevalence, intensity, and abundance among four locations, analyze spatial preference on the gill surface (hyperbranchia vs. hypobranchia), and evaluate whether there is geographic variation in species composition or infestation parameters.

2. Materials and Methods

2.1. Crab Samples

The sampling was conducted from May to December 2025. A total of 240 individual mud crabs *S. serrata* were used in this study, obtained from four locations in Indonesia representing three ecoregions: the Sunda Shelf, Wallacea, and Papua. Of the total samples, 60 individuals each were collected from Singkawang (West Kalimantan) and Tanah Laut (South Kalimantan) located in the Sunda Shelf ecoregion, 60 individuals from Donggala (Central Sulawesi) in the Wallacea transition zone, and 60 individuals from Teminabuan (Southwest Papua) in the Papua ecoregion. The crab carapace width range for all locations was 12–15 cm with a weight of 258–421 g. (Fig. 1)

2.2. Ethical Procedures and Anesthesia

This study used mud crabs (*Scylla* spp.) in accordance with the provisions of Article 5 Paragraph (2) of the Minister of Marine Affairs and Fisheries of the Republic of Indonesia Regulation Number 7 of 2024. The research method involved non-invasive observation of gills using ice-chilling as anesthesia, thus not involving live challenge tests or causing suffering to the crabs. This study was formally approved by the Health Research Ethics Committee of Tanjungpura University in accordance with the relevant protocol for the use of experimental animals.

2.3. Identification and Characterization of *Octolasmis* spp. Parasites

Mud crabs were first anesthetized by placing them in a container filled with brackish water at 12°C. After the carapace width and weight of each crab

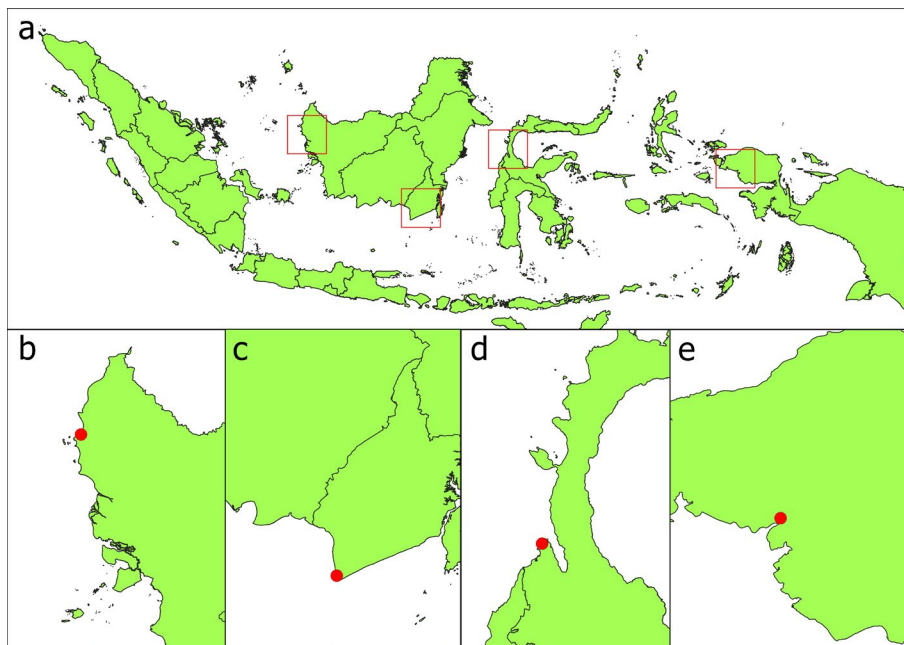


Fig.1. Sampling locations and *S. serrata* at four locations representing Indonesian mangrove ecosystems. a. Sampling distribution in Indonesia, b. Singkawang, c. Tanah Laut, d. Donggala, e. Teminabuan.

were measured and recorded, the crab gills were visually examined to isolate *Octolasmis* spp. ectoparasites. Parasite specimens were collected using a preparation needle and stored in microtubes containing different fixative solutions: 95% ethanol for molecular analysis and 10% formalin for morphological analysis (Baskin, 2014; Chew et al., 2024). All *Octolasmis* spp. parasites found were counted and identified directly under a stereo microscope (Olympus SZX7, Tokyo, Japan) equipped with a Dinolite eyepiece camera connected to a computer monitor.

Octolasmis spp. parasites were prepared for morphological identification to the genus or species level based on identification keys developed by Rasheed and Mustaqim (2017). Parasite specimens fixed in 10% formalin were then placed on a glass slide pre-dotted with mounting fluid (alcohol and glycerin mounting fluid) and covered with a coverslip. Specific morphological characteristics observed included the tergum, scutum, carina, cirri, peduncle, and capitulum. Observations were made using an Olympus SZX7 stereo microscope at 40 $\times$ –100 $\times$ magnification. Additionally, the shape and size of the capitulum and the presence or absence of calcareous plates along with their variations were observed. The identification of *Octolasmis* spp. was based on previous studies (Rasheed and Mustaqim, 2017; Ihwan et al., 2015; Adday et al., 2019; Khattab, 2018).

2.4. Extraction of *Octolasmis* spp. DNA and Polymerase Chain Reaction (PCR) Amplification

Molecular identification was performed on eight *Octolasmis* specimens identified as *O. cor* and *O. angulata*. DNA extraction was performed using a gSYNC DNA Extraction Kit (GeneAid Biotech Ltd., Taipei, Taiwan), according to the manufacturer's instructions.

Octolasmis spp. specimens were placed in sterile 1.5 mL tubes and homogenized using a micropestle. The process began by mixing 200 μ L GST buffer, 20 μ L proteinase K, and 10 mg of tissue sample. The mixture was incubated overnight at 60 $^{\circ}$ C. After incubation, 200 μ L of 100% ethanol and 200 μ L of GSB buffer were added to the sample. The mixture was then transferred to a GS column placed in a 2 mL collection tube. Subsequently, 400 μ L of W1 buffer was added to the column. The GS column was then washed with 600 μ L of wash buffer and centrifuged. The filtrate was discarded, and an additional centrifugation step was performed to dry the column matrix. The spin column was transferred to a new microtube, and 100 μ L of pre-heated elution buffer was added to the center of the column matrix. After standing for three minutes, a final centrifugation step was performed. The purity and quality of the extracted DNA were determined using a Nanodrop spectrophotometer, and the DNA was stored at –20 $^{\circ}$ C for preservation and subsequent procedures.

DNA amplification was performed using the polymerase chain reaction (PCR) technique on a Peqlab PeqSTAR 96X (Standard) thermal cycler. The PCR reaction was carried out in a total volume of 50 μ L containing the following components at the specified concentrations: 2 μ L of DNA template with a concentration of 25 ng/ μ L, 5 μ L of 10X Ex Taq buffer, 2 μ L of each primer (10 μ M), 0.25 μ L of GoTaq DNA polymerase enzyme (Promega, Madison, WI, USA), 2.5 μ L of dNTP mix (10 mM), and 36.25 μ L of distilled water. Universal primers LCO1490 (5'-GGTCAAACAAATCATAAAGATATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3'), which target the COI gene, were used (Folmer et al., 1994). The PCR mixture was run under the following conditions: initial denaturation at 94 $^{\circ}$ C for 3 min, followed by 35 cycles at 94 $^{\circ}$ C for 45 s, annealing at 42 $^{\circ}$ C for 45 s, and extension at 72 $^{\circ}$ C for 45 s. A final extension was then performed at 72 $^{\circ}$ C for 7

min before the samples were cooled to 4°C. All amplified PCR products were visualized on a 2% agarose gel stained with GelRed DNA dye and documented using a mobile phone camera.

2.5. Sequencing and Phylogenetic Analysis

PCR product purification and DNA sequencing were performed by 1st Base Company in Malaysia through PT Genetika Science, Indonesia. Nucleotide sequences of the DNA barcodes were obtained as chromatogram files (.ab1). Chromatogram files were checked for quality, and forward and reverse nucleotide sequences for each specimen were cleaned, trimmed, and assembled using the MEGA 11 software to generate consensus DNA barcode sequences for each specimen (Tamura et al., 2021). The NCBI GenBank BLASTn tool was used to obtain homologous sequences from related taxa. Phylogenetic trees were constructed in MEGA 11 (Tamura et al., 2021) using ML and NJ methods with 1000 bootstrap replicates. The best-fit substitution model was selected using BIC in MEGA 11. Genetic distances were calculated using the same model. GenBank sequences (PV961088.1, PX823314.1, KC138499.1, PV701129.1, KU204351.1) were added to the dataset, with *Lepas anatifera* (KU204351.1) as the outgroup. Species delimitation was performed using the Bayesian Poisson Tree Processes (bPTP) web server (<https://species.h-its.org>) following Zhang et al. (2013), with 100,000 MCMC generations and a burn-in of 0.1.

2.6. Parameters of *Octolasmis* spp Infestation

The gills of each crab were thoroughly examined, with particular attention paid to the hyperbranchial and hypobranchial regions, to isolate and enumerate all attached *Octolasmis* spp. individuals. The left and right gills were dissected and placed in Petri dishes containing 70% ethanol for fixation and ease of handling. Each gill was subsequently observed under an Olympus SZX7 stereo microscope at magnifications ranging from 8× to 56× to ensure accurate identification and counting. All attached *Octolasmis* spp. individuals, including *O. cor* and *O. angulata*, found on the hyperbranchial or hypobranchial surfaces were recorded using a handheld digital counter. The infestation patterns of *Octolasmis* spp. on mud crab gills were analyzed by calculating prevalence, intensity, and abundance, following the methodology recommended by Nur et al. (2021).

$$\text{Prevalence(\%)} = \left(\frac{\text{Number of infested crabs}}{\text{Total number of crabs examined}} \right) \times 100$$

$$\text{Intensity} = \frac{\text{Total number of } Octolasmis \text{ spp. counted}}{\text{Number of infested crabs}}$$

$$\text{Abundance} = \frac{\text{Total number of } Octolasmis \text{ spp. counted}}{\text{Total number of crabs examined}}$$

2.7. Statistical Analysis

All statistical analyses were performed at a significance level of $\alpha = 0.05$. Before parametric tests, the Shapiro–Wilk normality test and Levene’s homogeneity of variance test were conducted, and all assumptions were met. A comparison of intensity between *O. cor* and *O. angulata* on the same individual crabs (co-infestation) was analyzed using a paired t-test. For comparisons among locations (Singkawang, Tanah Laut, Donggala, and Teminabuan), a generalized linear model (GLM) was used with appropriate distributions: binomial for prevalence data and Poisson (or negative binomial if overdispersed) for intensity and abundance data. Location was the fixed factor, followed by Tukey’s post-hoc test for pairwise comparisons among locations. Because multiple comparisons were made, the Bonferroni correction was applied with $\alpha' = 0.05 / n$, where n is the number of tests performed. The reported p-values are adjusted p-values. Spatial preference between the hyperbranchia and hypobranchia for each species was analyzed using a paired t-test.

3. Results

3.1. Morphology

This study was conducted at four geographically separated locations: Teminabuan (Southwest Papua), Tanah Laut (South Kalimantan), Singkawang (West Kalimantan), and Donggala (Central Sulawesi). At each location, morphological identification based on capitulum, scutum, carina, and peduncle characteristics consistently revealed the presence of the same two *Octolasmis* species, *O. cor* and *O. angulata* (Fig. 2). Morphometric analysis showed homogeneous results among locations. The mean capitulum length of *O. cor* ranged from 2.60 to 2.65 mm across the four locations (combined value 2.62 ± 0.23 mm), while that of *O. angulata* ranged from 2.49 to 2.53 mm (combined value 2.51 ± 0.21 mm). The patterns of key morphological differences were also identical across all locations: *O. cor* consistently exhibited a complete capitular disc with a mean plate coverage of $28.3 \pm 0.20\%$ and a broad, robust scutum, whereas *O. angulata* consistently showed a reduced capitular disc with a plate coverage of only $10.5 \pm 0.17\%$ and a tapered scutum tip. Differences in carina shape and peduncle length were also consistently observed across the four locations.

3.2. Phylogeny

Phylogenetic analysis revealed distinct clustering patterns, which unequivocally identified *O. cor* specimens from various locations (Singkawang, Tanah Laut, Teminabuan, Donggala, and Papua) forming a strongly supported monophyletic group with reference sequences KC138499.1 (*O. cor* from Taiwan) and PV961088.1 (*O. cor* from India). Meanwhile, *O. angulata* specimens from Singkawang, Donggala, and the Philippines (PV701129.1) formed a separate monophyletic group clearly distinct from *O. cor*. The overall

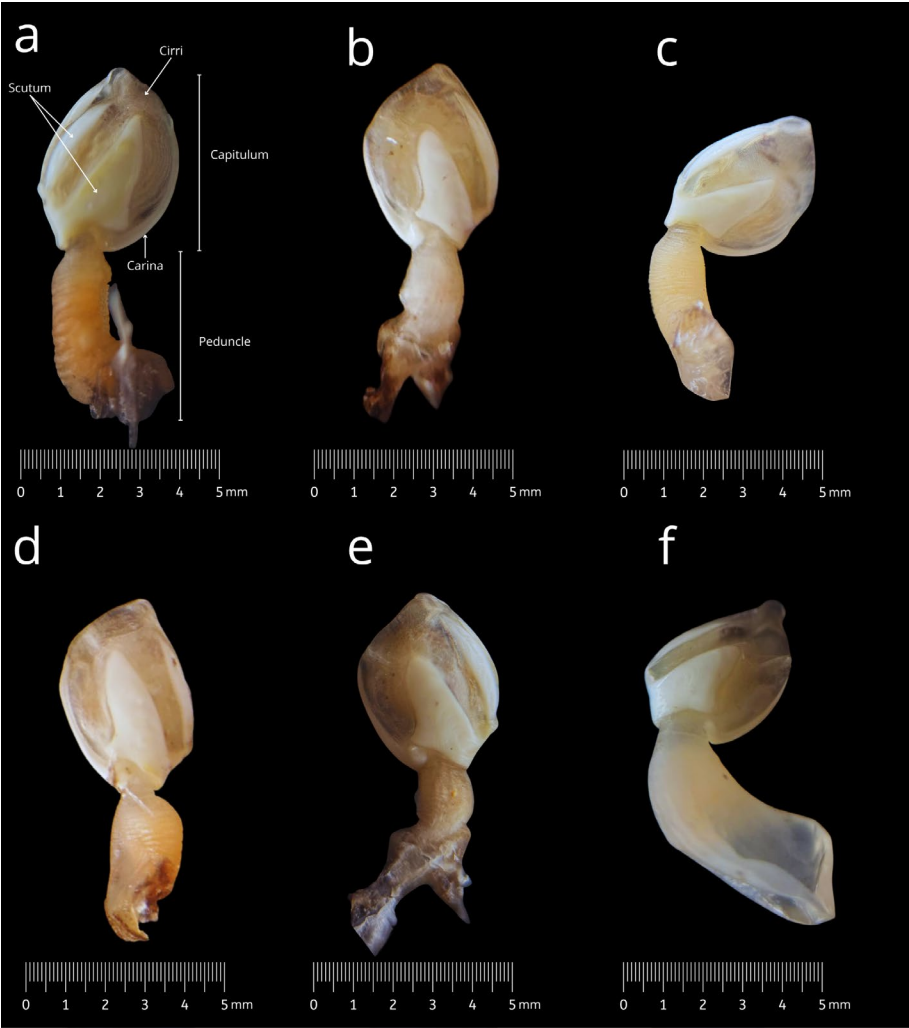


Fig.2. Morphology of *Octolasmis* sp. on crabs found at the study locations. (A) Morphology of *O. cor* from b. Singkawang, c. Tanah Laut, d. Donggala, e. Teminabuan. f. Morphology of *O. angulata* from Teminabuan.

tree topology illustrates the evolutionary relationships among species within the genus *Octolasmis* and shows substantial genetic divergence (scale bar=0.02 substitutions per site). These results confirm the taxonomic validity of the two *Octolasmis* species found and support the previous morphological identification.

The bPTP species delimitation analysis revealed potential cryptic diversity within both *Octolasmis* species. Eight putative species were delimited, with support values ranging from 0.951 to 1.000 (Table 1). Notably, *O. cor* was partitioned into four distinct lineages, and *O. angulata* into three lineages. These support values represent Bayesian posterior probabilities, with values > 0.95 considered statistically significant

Pairwise Kimura 2-parameter (K2P) distances (Table 2) showed intraspecific divergences of 3.18% (1.64–3.81%) for *O. cor* (n=4) and 2.37% (1.18–3.56%) for *O. angulata* (n=4), whereas interspecific distances between the two species ranged from 20.95% to 23.42% (mean: 22.17%). A clear barcode gap was observed (intra < 4% vs. inter > 20%), which substantially exceeded the typical crustacean COI species delimitation threshold (6–10%). Distances to the out-group *L. anatifera* (26.23–26.45%) confirmed appropriate taxonomic placement. These results strongly support *O. cor* and *O. angulata* as two distinct species, consistent with the phylogenetic tree topology (Fig. 3) and morphological identification.

Table 1. Results of the bPTP species delimitation analysis based on COI sequences.

Specimen	Support
<i>Lepas anatifera</i> (KU204351.1)	1.000
<i>O. cor</i> India + <i>O. cor</i> Tanah Laut	0.967
<i>O. cor</i> Singkawang	1.000
<i>O. cor</i> Papua + <i>O. cor</i> Teminabuan	0.968
<i>O. cor</i> Taiwan + <i>O. cor</i> Donggala	0.951
<i>O. angulata</i> Teminabuan	1.000
<i>O. angulata</i> Filipina + <i>O. angulata</i> Donggala	0.968
<i>O. angulata</i> Singkawang + <i>O. angulata</i> Tanah Laut	0.996

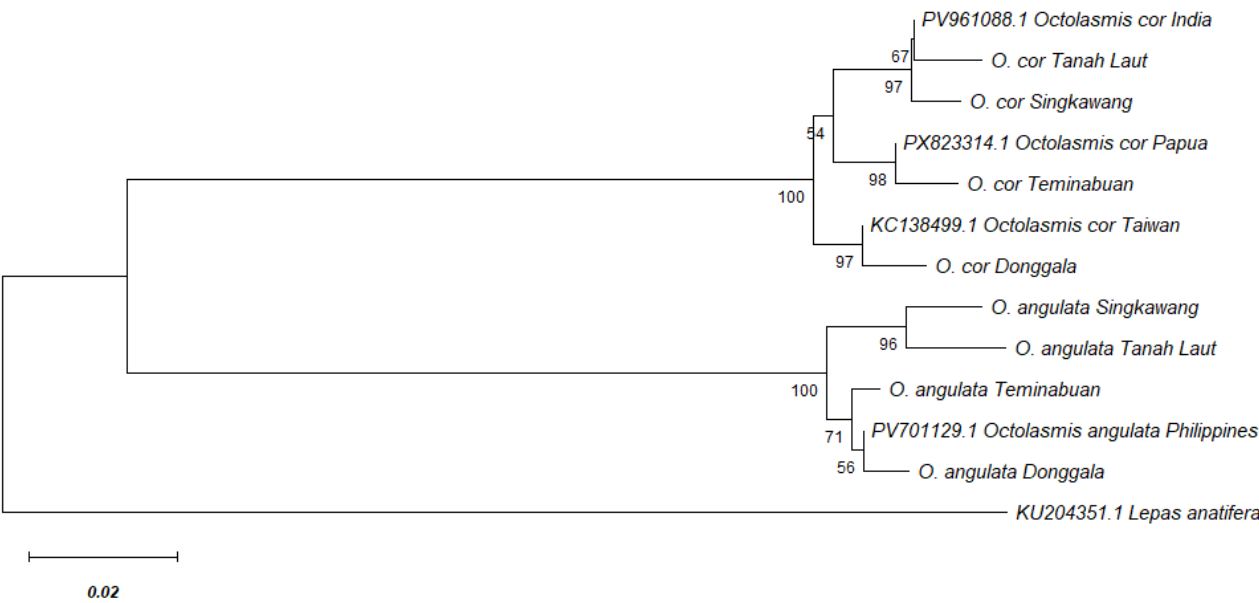


Fig.3. Phylogenetic tree of *Octolasmis* species based on genetic analysis. *L. anatifera* (KU204351.1) was used as the outgroup.

3.3. Infestation of *Octolasmis* spp.

Ecological infestation parameters are presented in Table 3. Overall, *O. cor* showed the highest prevalence (85%), followed by *O. angulata* (72%) and co-infestation (72%). However, co-infestation had the highest intensity (62 individuals/infested crab) and abundance (45 individuals/crab). The intensity of *O. cor* (40 individuals/infested crab) was significantly higher than that of *O. angulata* (15 individuals/infested crab) ($t=14.05$, $P<0.001$). This pattern was consistent across all locations (Singkawang, Tanah Laut, Donggala, Teminabuan), with co-infestation always showing the highest total parasite load.

Paired t-tests showed that both *Octolasmis* species were significantly more abundant on the inner gill surface (hyperbranchia) than on the outer surface (*O. cor*: $t=-12.53$, $P<0.001$; *O. angulata*: $t=-13.03$, $P<0.001$) (Table 4). The mean intensity of *O. cor* on the inner surface (53.8 ± 29.6) was nearly four times higher than that on the outer surface (14.2 ± 9.5). Independent t-tests (based on Table 4 data) confirmed that *O. cor* consistently had higher intensity than *O. angulata* on both the outer surface (14.2 ± 9.6 vs. 4.1 ± 3.6 ; $t=14.05$, $P<0.001$) and the inner surface (53.8 ± 29.6 vs. 16.2 ± 10.5 ; $t=11.63$, $P<0.001$). These results indicate clear microhabitat partitioning between the two parasite species on the gill system of the mud crab (*S. serrata*).

4. Discussion

This study confirms that *S. serrata* infestation at four separate locations in Indonesia (Singkawang, Tanah Laut, Donggala, and Teminabuan) is caused by two taxonomically distinct *Octolasmis* species, *O. cor* and *O. angulata*. This validation is based on the integration of quantitative morphological characters and molecular phylogenetic analysis. Morphologically, *O. cor* has a mean capitular plate coverage of $28.3 \pm 0.20\%$ and a broad, robust scutum, whereas *O. angulata* shows highly reduced plate coverage ($10.5 \pm 0.17\%$) with a tapered scutum. These differences were consistent across all locations, indicating that these characters are diagnostic and not influenced by geographic variation. Phylogenetically, COI sequences from all *O. cor* specimens in Indonesia formed a monophyletic clade with reference sequences from Taiwan (KC138499.1) and India (PV961088.1), whereas *O. angulata* grouped with a sequence from the Philippines (PV701129.1), however broader geographic sampling is required to reliably infer biogeographic patterns.

Interestingly, a bPTP species delimitation analysis (Zhang et al., 2013) revealed potential cryptic diversity within both *Octolasmis* species, partitioning *O. cor* into four distinct lineages and *O. angulata* into three lineages (support values 0.951–1.000; Table 1). These results suggest that the genetic structure of *Octolasmis* barnacles on *S. serrata* may be more complex than ini-

Table 2. Kimura 2-parameter (K2P) genetic distances (%; based on COI gene sequences) of *Octolasmis* specimens from four Indonesian locations.

Species	Intra-specific (%)	Inter-specific (vs <i>O. angulata</i>)
<i>O. cor</i> (n = 4)	3.18 (1.64–3.81)	22.17 (20.95–23.42)
<i>O. angulata</i> (n = 4)	2.37 (1.18–3.56)	-
Outgroup (<i>L. anatifera</i>)	-	26.23–26.45

Table 3. Ecological infestation parameters of *Octolasmis* spp. on mud crabs (*S. serrata*). Co-infestation refers to the mixed *O. cor* and *O. angulata* infestations on the same host.

Location	Infestation Type	Prevalence (%)	Intensity (<i>Octolasmis</i> /mud crab)	Abundance (<i>Octolasmis</i> /mud crab)
Singkawang	<i>O. cor</i>	82%	38.20 ± 9.55 ^a	31.30 ± 7.83 ^a
	<i>O. angulata</i>	70%	14.50 ± 3.63 ^a	10.15 ± 2.54 ^a
	Co-infestation	68%	60.10 ± 15.03 ^a	40.90 ± 10.23 ^a
Tanah Laut	<i>O. cor</i>	87%	41.50 ± 10.38 ^a	36.10 ± 9.03 ^a
	<i>O. angulata</i>	74%	16.20 ± 4.05 ^a	12.00 ± 3.00 ^a
	Co-infestation	75%	65.30 ± 16.33 ^a	49.00 ± 12.25 ^a
Donggala	<i>O. cor</i>	80%	37.40 ± 9.35 ^a	29.90 ± 7.48 ^a
	<i>O. angulata</i>	68%	13.80 ± 3.45 ^a	9.40 ± 2.35 ^a
	Co-infestation	66%	58.90 ± 14.73 ^a	38.90 ± 9.73 ^a
Teminabuan	<i>O. cor</i>	84%	40.20 ± 10.05 ^a	33.80 ± 8.45 ^a
	<i>O. angulata</i>	71%	15.30 ± 3.83 ^a	10.90 ± 2.73 ^a
	Co-infestation	70%	63.50 ± 15.88 ^a	44.50 ± 11.13 ^a

tially recognized. However, several caveats must be considered. First, the bPTP analysis was based solely on a single mitochondrial marker (COI), which may overestimate species diversity due to maternal inheritance, incomplete lineage sorting, and the presence of intraspecific geographic structure (Maroni et al., 2026; Esquerré et al., 2019; Eyer et al., 2016). Second, although the geographic sampling covered three Indonesian ecoregions, it remained limited to only two specimens per location. Therefore, the lineages detected by bPTP should be interpreted as potential cryptic species or strong population structure rather than confirmed species. Formal species delimitation using additional nuclear markers (e.g., ITS, 28S) and broader geographic sampling is required to test whether these lineages represent distinct species.

The genetic distributions of the two species exhibited different patterns. Based on phylogenetic analysis, *O. cor* appears to have a wide transoceanic distribution, from India to Papua, whereas *O. angulata* appears to be more restricted to the western Pacific region (Philippines, Singkawang, Donggala). However, the bPTP species delimitation analysis (Zhang et al., 2013) suggested that *O. cor* may consist of multiple distinct lineages rather than a single panmictic population. Therefore, the apparent wide distribution of *O. cor* might reflect the presence of multiple cryptic species or strongly structured populations. Although the maximum intraspecific distance for *O. cor* (3.81%) slightly

exceeds the conventional 3% threshold for some crustaceans, this value remains comparable to documented intraspecific variation in other barnacle species across wide geographic ranges (Chan and Chen, 2022). Meanwhile, interspecific distances between the two species ranged from 20.95% to 23.42% (mean: 22.17%), substantially exceeding the standard 6–10% species delimitation threshold for crustacean COI (Daniels et al., 2025; Lopes-Lima et al., 2024). A clear barcode gap was observed (intra < 4% vs. inter > 20%), which is also consistent with barcode gap patterns in barnacles in general (Hosie et al., 2021). Distances to the out-group *L. anatifera* (26.23–26.45%) confirmed appropriate taxonomic placement. These results strongly support *O. cor* and *O. angulata* as two distinct species, consistent with the phylogenetic tree topology (Fig. 3) and morphological identification.

This pattern may be related to the Indonesian Throughflow (ITF) system, which functions as a dispersal corridor for the passive larvae of epibionts (Zamroni et al., 2025; Hood et al., 2024). The ITF transports Pacific water masses into the Indian Ocean through the Indonesian archipelago (Sprintall et al., 2014; Gordon et al., 2008; Sprintall, 2019), creating a major trans-archipelagic corridor that could facilitate the broad dispersal of *O. cor* from India to Papua. Conversely, population fragmentation in *O. angulata* across the western Pacific may reflect the influence of regional current systems that generate asymmetric gene flow, as asymmet-

Table 4. Distribution and infestation levels of *O. cor* and *O. angulata* in mud crabs (*S. serrata*). Data show the total number, mean, and standard deviation of parasites found on the outer and inner surfaces of the host's hyperbranchia. Mean values represent the number of parasites per crab, indicating the infestation intensity of the hyperbranchia.

Parameter	<i>O. cor</i>	<i>O. angulata</i>	Statistic (paired t-test)	p-value
On Outer Surface	14.2 ± 9.5	4.1 ± 3.6	16.58	< 0.001
On Inner Surface	53.8 ± 29.6	16.2 ± 10.5	19.68	< 0.001
Paired t-Test (Inside vs. Outside)				
t-value	-12.53	-13.03	-	-
p-value	< 0.001	< 0.001	-	-

ric current-driven dispersal and current-aligned genetic breaks are widely documented for marine taxa in the Pacific (Xuereb et al., 2018; Snead et al., 2023; Ravago-Gotanco et al., 2007; Li et al., 2017; Wares et al., 2001). The heterogeneity of ocean currents in Indonesia might play a dual role, acting both as dispersal routes and as agents of population vicariance, driving phylogeographic divergence in *Octolasmis* spp., with *S. serrata* having limited mobility relative to currents. However, it should be acknowledged that the interpretation of biogeographic patterns of these two *Octolasmis* species is limited by the restricted geographic scope of the dataset. Broader sampling is needed to validate these findings.

Ecological infestation parameters (Table 3) showed that *O. cor* was consistently more dominant than *O. angulata*, both in terms of prevalence (85% vs. 72%) and intensity (40 vs. 15 individuals/infested crab). An independent t-test confirmed that this difference was highly significant ($t = 14.05$; $P < 0.001$). The competitive advantage of *O. cor* can be explained by its more robust attachment morphology: the complete capitular disc and broad scutum allow *O. cor* to attach securely to relatively flat and extensive gill surfaces, even at high densities (Yap et al., 2015; Blomsterberg et al., 2004; Ihwan et al., 2015; Albar et al., 2026). Conversely, *O. angulata*, with its reduced calcification and tapered scutum, is more suited to occupying narrow crevices but has a lower carrying capacity (Yap et al., 2015; Blomsterberg et al., 2004; Ihwan et al., 2015; Albar et al., 2026). Interestingly, co-infestation resulted in the highest parasite load (intensity 62 individuals/infested crab; abundance 45 individuals/crab). This phenomenon is hypothesized to result from ecological facilitation, in which *O. angulata*, as a pioneer species, may modify the gill microhabitat, for example, by creating surface irregularities or triggering host responses that ultimately favor more massive *O. cor* colonization (Albar et al., 2026). This pattern was identical across the four distant locations, indicating that the regulating factors are general and not location-specific.

A key finding of this study is the existence of clear microhabitat partitioning between *O. cor* and *O. angulata* on the mud crab gill system. Based on paired t-tests (Table 4), both species showed a significant preference for the inner gill surface (hyperbranchia) over the outer surface (hypobranchia) ($P < 0.001$). The intensity of *O. cor* on the hyperbranchia was nearly four times higher than that on the hypobranchia. The preference for hyperbranchia is hypothesized to be related to more favorable microhabitat conditions, such as a stable respiratory water flow, higher dissolved oxygen levels, and lower risk of mechanical abrasion during gill movement. *O. cor* had significantly higher infestation intensity than *O. angulata* on both gill surfaces (Table 3; $P < 0.001$). Interestingly, the abundance ratio of *O. cor*/*O. angulata* was slightly higher on the outer surface compared to the inner surface. This suggests that *O. angulata* is proportionally more tolerant of relatively more extreme hypobranchial conditions (more turbulent flow and lower oxygen). This tolerance is potentially supported by the smaller body size of

O. angulata and its tapered scutum, which allows it to penetrate narrow crevices between gill lamellae. This study provides the first quantitative evidence of microhabitat partitioning in crustacean epibionts of the gill system, a phenomenon rarely documented statistically.

The infestation type of *Octolasmis* on *S. serrata* gills did not differ significantly among ecoregions. The GLM results (Table 3) confirmed that parasite prevalence, intensity, and abundance did not differ significantly among the four study locations. This spatial homogeneity may be due to the widespread distribution and high population connectivity of the host *S. serrata* in Indo-Pacific waters (Fratini and Vannini, 2002; Waiho et al., 2018). The implications of this finding are very important for mud crab health management in Indonesia. Because infestation parameters did not vary spatially, *Octolasmis* control strategies proven effective in one location (e.g., quarantine, freshwater dipping, or stocking density management) could potentially be adopted nationally without the need for location-specific modifications. However, further research covering a wider range of locations (including eastern Indonesia, such as Maluku and Lombok) and more detailed micro-environmental analysis (temperature, salinity, dissolved oxygen, and pH around the gills) is necessary to confirm this generalization. Although these locations represent different ecoregions, we did not measure in situ water parameters; therefore, causal relationships between environmental variation and infestation parameters cannot be established.

5. Conclusions

Using an integrative approach, this study confirms that only two species, *O. cor* and *O. angulata*, infest *S. serrata* at four locations representing three Indonesian ecoregions (Sunda Shelf, Wallacea, and Papua). *O. cor* was more dominant than *O. angulata*, and co-infestation of both species resulted in the highest parasite load. Both species showed a strong preference for the inner gill surface (hyperbranchia) over the outer surface (hypobranchia), indicating microhabitat partitioning of the mud crab gill system. Most importantly, no significant geographic variation in infestation parameters was found among locations, suggesting that the Wallace and Weber Lines do not act as dispersal barriers for *Octolasmis* in the Indonesian regions studied. However, the bPTP species delimitation analysis revealed potential cryptic diversity within both species, partitioning *O. cor* into four distinct lineages and *O. angulata* into three lineages. These preliminary findings require confirmation with additional genetic markers and broader geographic sampling before any formal taxonomic revision can be proposed.

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Conflict of Interests

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