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To cite this article: D C Murniati *et al* 2023 *IOP Conf. Ser.: Earth Environ. Sci.* **1271** 012005

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Genetic structure of *Ilyoplax delsmanni* (Crustacea: Decapoda: Brachyura: Dotillidae) on the western Indonesian waters

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Abstract. Estuarine crab disperses passively to different areas during their larval stage through sea currents. *Ilyoplax delsmanni*, one of the estuarine crabs, is widely distributed in the Indo-Malaysia Archipelago. The present study aims to discern the genetic structure of *Ilyoplax delsmanni* in the western part of Indonesia. Specimens were collected from three sites, i.e. one site in Kalimantan and two sites in Java Island. We analyzed the genetic structure of *I. delsmanni* with COI gene using MEGA-X, DNASP v6.12.03, Arlequin v3.5.2.2., and Network v10.2. The constructed phylogenetic tree with MEGA-X with maximum likelihood (ML) using Kimura 2 parameter based on the COI gene revealed two distinct clades, i.e., Kalimantan_5133-Java_5135 as Clade 1 and Java_5136 as Clade 2. The genetic distance within the clade range from 0.2% to 2.2%, meanwhile the distance between the clades is approximately 19.3%–20.7%. Moreover, the haplotype network and F_{ST} values calculated between pairs of localities generate a congruent result with the phylogenetic tree. Through calculation using MEGA-X, we estimate that the divergence time between both clades is approximately 42.49 mya, aligning with the middle Eocene period. Hence, we deduce that both clades represent distinct species.

Key words: distinct species, divergence time, estuarine crab, genetic distance, phylogeny, sea currents

1. Introduction

It is commonly known that estuarine crab disperses to other areas during their larval stage, with the planktonic larva being passively transported by the sea currents. These facts are in line with some findings that certain species exhibit to have a wide distribution range. However, molecular analysis has revealed that species previously reported widely distributed also exhibit high genetic diversity, constitute a species complex, a set of cryptic species or have undergone diversification [1–4].

The Indonesian Archipelago, comprising 70% of sea areas, exhibit distinct currents in its eastern and western parts due to geomorphologic and oceanographic changes during the Tertiary and Quaternary. Different directions of the sea currents not only facilitate the dispersal of marine organisms but also



serve as barriers to their colonization [5]. As a result, certain marine and estuarine crustaceans are distributed throughout Indonesian waters, whilst others are confined to specific areas. *Ocypode ceratophthalma* and *Austruca annulipes* are among of the estuarine crab that are widely distributed in Indonesia. In contrast, species such as *Tubuca jocelynae* and *T. seismella* have been reported exclusively in the eastern part of Indonesia and other Pacific Islands [2, 6].

Estuarine dotillid crabs, belonging to the genus *Ilyoplax*, are an ecologically important group of crab that is widely distributed in the Indo-West Pacific (IWP) [7]. The genus comprises a total of 28 species [8]. Among them, *Ilyoplax delsmanni* is one of the most widespread in the Indo-Malaysia Archipelago [4, 9, 10]. The species was firstly described by De Man in 1926 with type locality is Java Island. This species was also recorded in Halmahera [11, 12]. However, genetic structure of this species in Indonesia remains unexplored.

Regarding the type locality, we intend to focus on analyzing the species of *I. delsmanni* found in the western region of Indonesia. This particular area had the Java Sea positioned centrally, bordered by Makassar Strait to the east, the South China Sea to the north, and the Indian Ocean to the south. We hypothesize that there is gene flow among different populations. Therefore, the aim of the present study is to elucidate the genetic structure of *I. delsmanni* within the western part of Indonesia.

2. Materials and methods

2.1. Examined materials

In the present study, we use 29 samples of *I. delsmanni* collected from three localities (figure 1, table 1). Collection recommendation from Secretariat of Scientific Authority for Biodiversity, Indonesian institute of sciences with letter nomor B-142/SKIKH/KS.02.04/IX/2020. These samples were collected from September until November 2020 and have been deposited in Museum Zoologicum Bogoriense (MZB), Directorate of Scientific Collection Management-BRIN, Indonesia. The fixation using gradual concentration of ethanol from 50% until 70% and the preservation using ethanol 90% following the previous study [13]. The morphology of these specimens is confirmed similar with the holotype specimens deposited in Naturalis Biodiversity Center (figure 2).

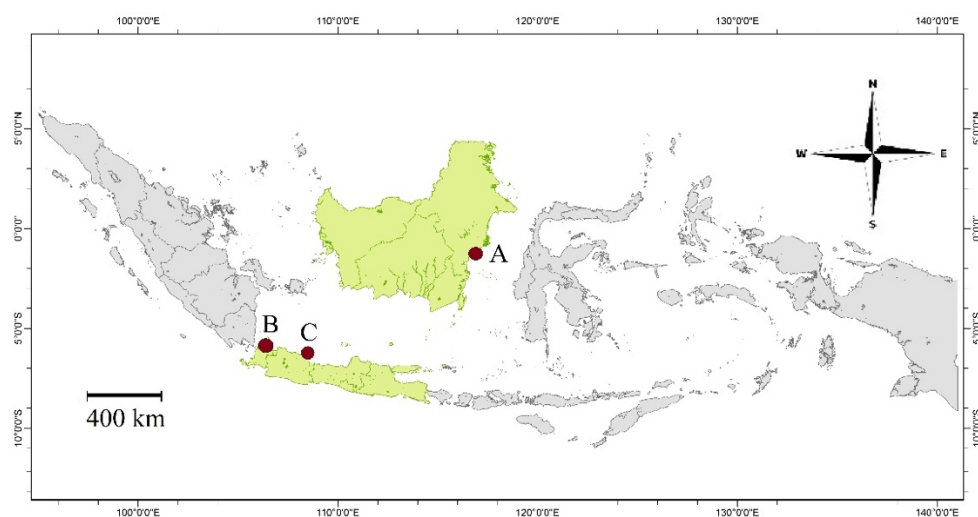


Figure 1. Map of the sampling sites. The colored islands are the designated sampling localities. A, Penajam, East Kalimantan; B, Serang, Banten; C, Indramayu, West Java.

2.2. DNA Extraction, amplification, and sequencing

One ambulatory pereopod of *I. delsmanni* from Kalimantan and Java was removed from each individual with small surgery scissors and prepared for DNA extraction. The collected tissue was then put in a 1.5 ml tube. Total DNA from muscle tissue was isolated using Roche High Pure PCR template preparation

kit following the manufacturer's protocol. A region of ~550 base pairs (= bp) of the 5'-end of the COI gene was amplified by PCR with the specific and universal primers meanwhile a portion of the COI gene was amplified by PCR with universal primers (table 2). The PCR conditions for the above primers were denaturation for 50 s at 94°C, annealing for 70 s at 45–47°C, and extension for 60 s at 72°C (40 cycles), followed by extension for 10 min at 72°C. PCR products were visualized on ca. 1.5% agarose gel. The PCR products were sent to a commercial service provider, Genetika Science, for DNA sequencing. Sequences were obtained by automated sequencing (Applied Biosystems 3730).

Table 1. Examined materials of *I. delsmanni* deposited in Museum Zoologicum Bogoriense (MZB), Indonesia (MZB.Cru.) and Naturalis Biodiversity Center, The Netherland (RMNH.CRUS.)

	Catalog number	Locality	Date	Samples
<i>I. delsmanni</i> 1	MZB.Cru.5133	Penajam, East Kalimantan	24-10-2020	14
<i>I. delsmanni</i> 2	MZB.Cru.5135	Pancer Mangrove Forest, Serang, Banten	20-09-2020	12
<i>I. delsmanni</i> 3	MZB.Cru.5136	Menir River, Indramayu, West Java	11-11-2020	5
<i>I. delsmanni</i> (Holotype)	RMNH.Crus.241884	Batavia (Jakarta), Java Island.	unknown	1

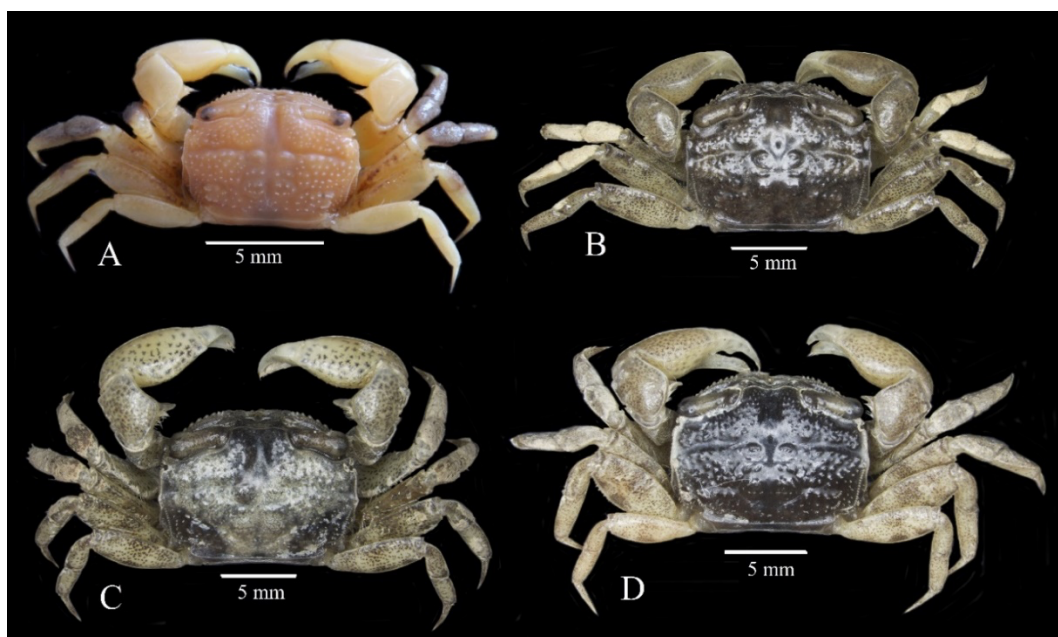


Figure 2. Habitus dorsal of male *I. delsmanni*. A, holotype RMNH.CRUS.241884; B, MZB.Cru.5133; C, MZB.Cru.5135; D, MZB.Cru.5136.

Table 2. Primers used for amplification of cytochrome C oxidase subunit I (COI)

Primer	Sequence	Reference
LCOI490	5'-GGTCAACAAATCATAAAGATATTGG-3'	14
HCO2198	5'-TAAACTTCAGGGTGACCAAAAAATCA-3'	14

2.3. Sequence alignment and inter- and intraspecific genetic distance

In total, 31 COI sequences of the *I. delsmanni* specimens were used for inferring the genetic structure. These sequences were edited and aligned with MUSCLE function in MEGA-X, after verification with the complimentary strand.

Genetic distances on COI gene of *I. delsmanni* populations were calculated using MEGA-X with Kimura 2 parameter model based. The pairwise genetic distance is presented in a graphic following the calculation.

2.4. Phylogenetic analysis and divergence time

The analysis of the COI gene was conducted on sequences alignment of 603bp, with *I. orientalis* as the outgroup. MEGA-X, Maximum likelihood (ML) using Kimura 2 parameter model with Nearest Neighbour Interchange (NNI). The 10.000 bootstrap method was used to assess the internal consistency of the branches. Divergence time was measured with MEGA-X and calibrated with the divergence time of *Austruca annulipes*, *A. perplexa*, *Mictyris brevidactylus*, and *Ocypode ceratophthalma*. The divergence time of those closely related taxa is collected from the database of the Time tree of life with time unit million years ago (mya) [15, 16].

2.5. Analysis of the genetic structure

Genetic structure analysis with a mitochondrial marker, the COI gene, was conducted with DNASP v6.12.03 and Arlequin v3.5.2.2. to calculate haplotypes (*h*), haplotype diversity (*Hd*), nucleotide diversity (π), Polymorphic sites (*S*), mean pairwise nucleotide differences (*K*), neutrality (Tajima's *D* and Fu's *FS*), AMOVA, and pairwise difference (*Fst*). The haplotype network was drawn using Network 10.2.

3. Results

3.1. Phylogenetic analysis and divergence time

Figure 3 displays the phylogenetic tree with an estimation of divergence time, incorporating calibration using the divergence time of other closely related taxa. The tree comprising two clades formed by three populations. Clade 1 encompasses the population of Kalimantan_5133 and Java_5135, meanwhile, Clade 2 independently consists of population of Java_5136. Based on the database of the Timetree of life, the estimated divergence time between *M. brevidactylus* and *O. ceratophthalmus* is estimated to be 90 mya, and the divergence time between *O. ceratophthalmus* and *A. annulipes* is estimated to be 62 mya. Employing these calibrations, the phylogenetic tree reveals that Clade 1 and Clade 2 of *I. delsmanni* diverge approximately 42.49 mya.

3.2. Genetic distance

It is postulated that Clade 1 and Clade 2 represent distinct species, giving rise to both intraspecific and interspecific genetic distances. The intraspecific genetic distance ranges from approximately 0.2% to 2.2%, meanwhile the interspecific genetic distance falls within the range of 19.3% to 20.7%. Consequently, a notable disparity existed between the intraspecific and interspecific genetic distance, as illustrated in figure 4.

3.3. Genetic structure

Table 3 provides an overview of the genetic structure of *I. delsmanni* from three populations. Among them, Kalimantan population exhibit the highest genetic diversity (*hd* and π). Conversely, for the Java (5136) population, the calculation of the haplotype and nucleotide diversity were unsuccessful, resulting the values of zero (0). Table 4 presents the genetic variation that occurs among three populations and within a population. The percentage values clearly show that variation among population is distinctly higher compared to within population. Table 5 displays the *Fst* value between the two populations. The analysis reveals that the lowest value is calculated between the population of Kalimantan_5133 and Java_5135, meanwhile the highest value is between the population of Java_5135 and Java_5136.

Table 3. Values of polymorphic sites (S), number of haplotypes (h), haplotype diversity (Hd), nucleotide diversity (π), and mean pairwise nucleotide differences (K) for each sampled locality along *I. delsmanni* distribution based on sequences of COI

MZB.Cru.	Population	N	S	h	hd	π	K
5133	Kalimantan	14	20	11	0.956	0.011	6.63
5135	Java_1	12	9	5	0.576	0.002	1.5
5136	Java_2	5	0	1	0	0	0
5133 & 5135	Kalimantan–Java_1	26	28	16	0.902	0.009	5.474

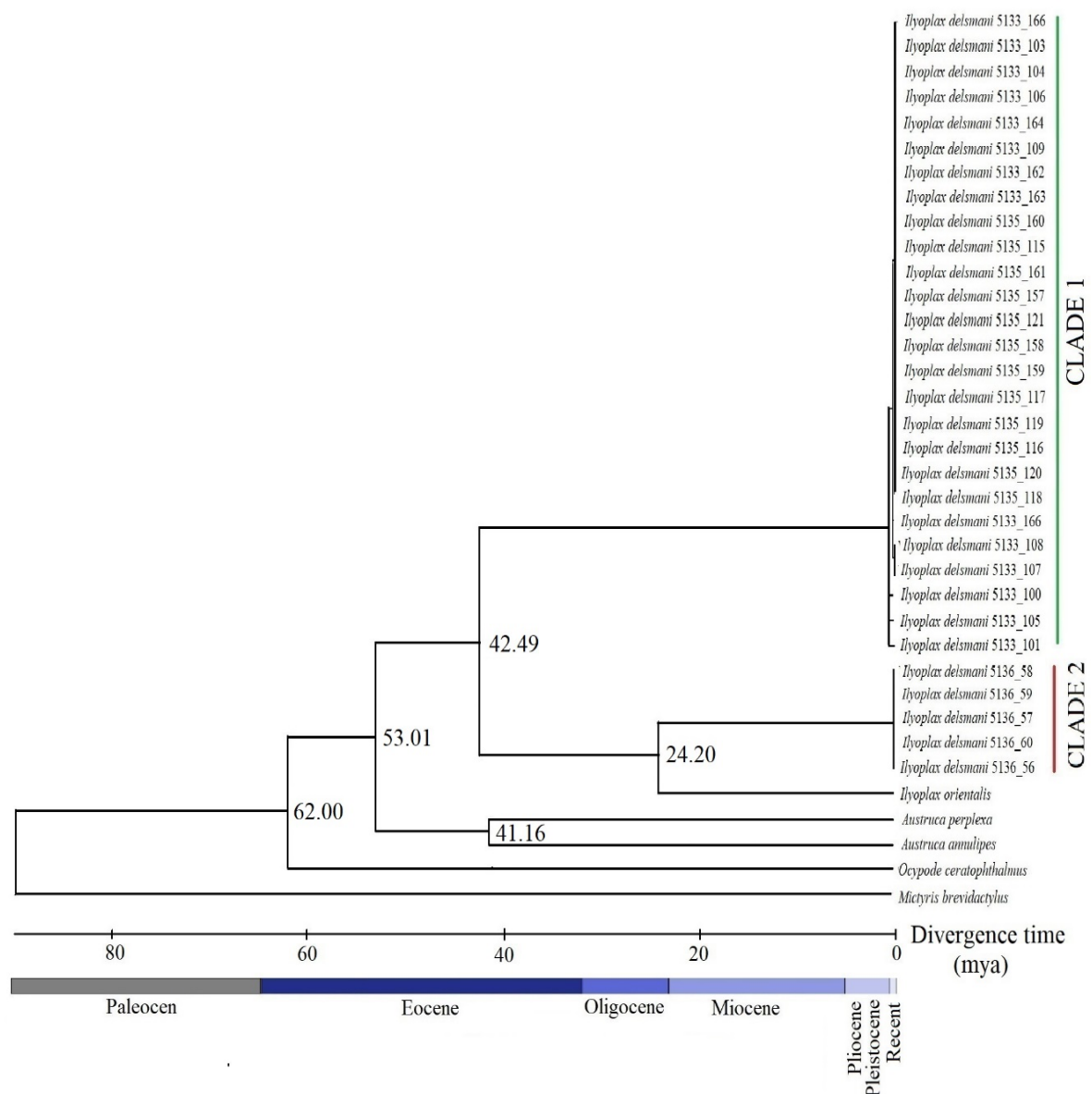


Figure 3. Phylogenetic tree of *I. delsmanni* with divergence time constructed from 31 sequences 603 bp of COI gene.

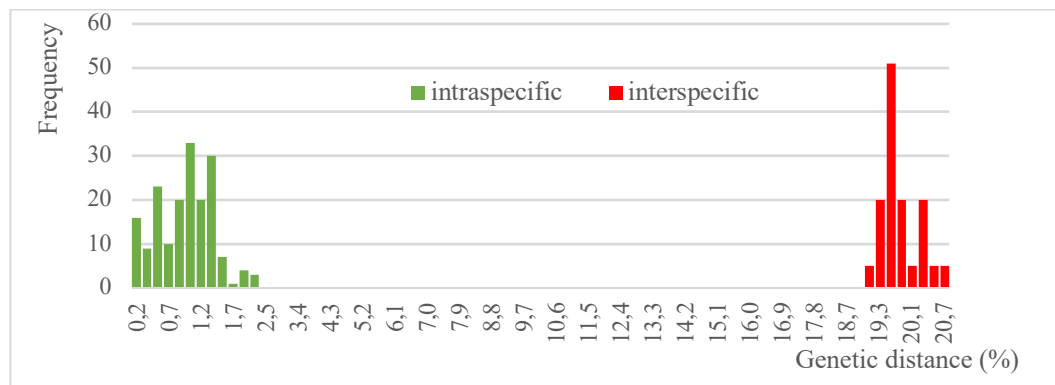


Figure 4. Graphic of the genetic distance of *I. delsmanni* from Clade 1 and Clade 2.

Table 4. Analysis of Molecular Variance (AMOVA) on two clades (Clade 1 and Clade 2) based on sequences of COI of *I. delsmanni*.

Source of variation	d.f.	sum of squares	Variance components	Percentage of variation	Fixation index
Among population	3	471.87	12.01 Va	84.15	$\Phi_{st} = 0.84$
Within population	53	119.82	2.26 Vb	15.85	

Table 5. Pairwise F_{ST} calculated between pairs of localities from the Indonesian Archipelago based on sequences of COI of *I. delsmanni*.

Population_ (MZB.Cru.)	Kalimantan_(5133)	Java_(5135)	Java_(5136)
Kalimantan_(5133)	–		
Java_(5135)	0.35	–	
Java_(5136)	0.95	0.99	–

Table 6 presents the result of neutrality test for each population. Of the three populations, calculation was successfully performed for two populations, i.e., Kalimantan_5133 and Java_5135. The values of Tajima's D and Fu's FS for between these two populations are distinctly different. Tajima's D and Fu's FS of Kalimantan_5133 population show non-significant positive and negative values, respectively. Meanwhile, Java_5135 population shows significant negative values for both tests. However, the test for the population of Java_5136 is failed to be calculated hence the value is zero (0).

Table 6. Neutrality tests based on sequences of COI of *I. delsmanni*

Population	Tajima's D	Fu's FS
Kalimantan_5133	0.23; $P > 0.10$, not significant	–2.76; $P > 0.10$, not significant
Java_5135	–2.02; $P < 0.05$, significant	–0.9; $P < 0.02$, significant
Java_5136	0	0

The haplotype network reveals the presence of two distinct populations, i.e., Kalimantan_5133–Java_5135 (H₂–H₁₇) and Java_5136 (H₁) (figure 5). This network is congruent with the phylogenetic tree (figure 3). Within this network, no shared haplotype is identified. However, there are two dominant haplotypes that represent the central haplotypes, H₃ for population of Clade 1 and H₁ for the population of Clade 2. The high-frequency of central haplotype belongs to Java_5135, with small closely related low-frequency haplotypes. Kalimantan_5133 has evenly low-frequency haplotypes.

Notably, the population of Clade 2 demonstrate a more complex evolutionary trajectory compared to the first clade, involving multiple steps of genetic divergence.

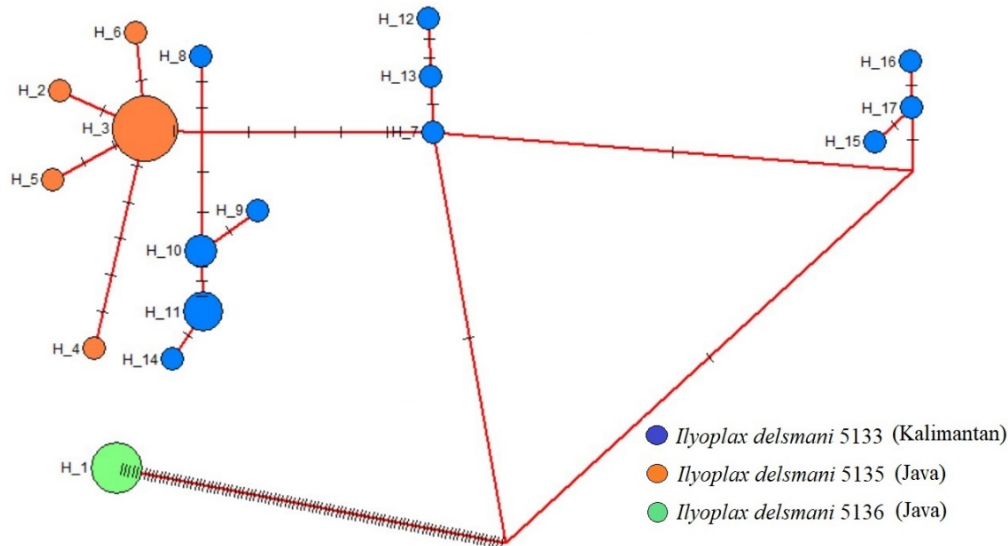


Figure 5. Haplotype network of *I. delsmanni* from 2 Islands. Number after species name indicates the catalog number of MZB.Cru. Black lines show occurrence of mutation.

4. Discussion

4.1. Phylogenetic analysis and divergence time

Ilyoplax delsmanni from Kalimantan_5133 and Java_5135, both belonging to Clade 1, are classified as the same species, meanwhile *I. delsmanni* from Java_5136 in Clade 2 is classified as distinct species that is different from Clade 1. This taxonomic assignment is supported by robust statistical calculation, as evidenced by the high overall probability (generally 100%) of the phylogenetic tree. An analysis using only COI gene to recognize cryptic species has been conducted with a number of specimens used for amplification is less than five for each locality [3].

The divergence time between Clade 1 and Clade 2, calculated at 42.49 mya, implies a separation event during the middle Eocene (figure 3). Major changes in sea level and land movement began during Eocene [17]. During the early Eocene, the sea level declined around 15–30 m. Concurrently, in the Indonesian Archipelago, Sunda Arc stretched from Sumatra through Java. The stretching of the Sundaland margin resulted in creation of the Makassar Strait, a deep-sea channel separating Kalimantan and Sulawesi [18]. At the middle Eocene, 43.6, 42.9, and 40.8 Mya, the sea level continues to fall to -20 m, followed by a rise to 40 m at 40.1 mya, and the dropping again to -20 m at 39.5 mya. By the Late Eocene the sea levels experienced a decline of -40 m [18]. Those dynamic changes have significantly contributed to the present pattern of the sea current [20, 21].

4.2. Genetic distance

The present study reveals the first genetic distance between two species of *Ilyoplax*. The minimum genetic distance of interspecific is 19.3%. This value is distinctly high compared to the other related taxa. For example, in fiddler crabs, the genetic distance for pseudocryptic species *T. alcocki* and *T. urvillei* is 3.78% [22]. Genetic distance between *O. stimpsoni* and *O. mortoni* is 6.25%; between *Scopimera globosa* and *S. ryukyuensis* is 4.43% [2, 22–25]. Regarding these results and references, the specimen from Java_5136 is conceivable categorized as the sister taxa of specimens from

Kalimantan_5133 and Java_5135. Therefore, further morphological observation is necessary for the recognition of new species.

4.3. Genetic structure

The haplotype network reveals the presence of gene flow between the Kalimantan_5133 and Java_5135 populations (figure 5). Between these populations, Kalimantan_5133 has higher genetic diversity compared to Java_5135 (table 3). The origin of dispersal tends to possess the highest genetic diversity [26]. Therefore, it can be inferred that the population of Kalimantan_5133 represents the source population, while the population of Java_5135 has undergone expansion. Additionally, the population of Java_5135 exhibit low-frequency haplotypes connected to a central haplotype. This result aligned with the previous study which suggested that low π values indicate a low mutation rate and the presence of several low-frequency haplotypes associated with a common central haplotype is evidence of population expansion [27]. In addition, the observed low genetic diversity is likely attributed to a founder effect [26].

Fst values are used to infer the population genetic processes that have caused patterns of genetic differentiation [28]. In the present study, a low *Fst* value is observed between Kalimantan_5133 and Java_5135 (table 5). The low values of *Fst* indicate that there is an effective migration rate between these two populations. At this stage, all individuals from both populations are nearly homozygous. This finding is supported by the AMOVA analysis, which reveals with a low value of variation within population (table 4).

Neutrality tests with Tajima's D and Fu's were conducted to analyze population demographic expansion. Overall, both tests yielded negative values. However, it is noteworthy that only the population of Java_5135 exhibited statistically significant negative values. These results align with the the previous findings where a negative value indicates population expansion in the absence of selection [26].

Estuarine crabs are known to have a planktonic larval stage. The larval disperse to other areas following to the direction of sea currents [26, 29]. Larval dispersal of *I. deltsmani* from the east coast of Kalimantan and the north coast of Java to other areas is likely controlled by two currents. Firstly, the seawater originating from the Pacific Ocean flows into the Sulawesi Sea, subsequently passing through the Makassar Strait, before bifurcating into the Lombok Strait and the Banda Sea [30]. These currents facilitate the transportation of crab larva from the east coast of Kalimantan to various islands around the Lombok Straits and the Banda Sea, including Bali, Lombok, Sumbawa, and Sumba. The second is the seawater originates from the South China Sea enter the Karimata Strait, subsequently flowing into the Java Sea. This particular current contributed in the dispersal of larva along the northern coast of Java as well as northern coast of Sumatra and the southern coast of Kalimantan. Both currents present a limited opportunity for gene flow to occur between the crab populations from the east coast of Kalimantan and north coast of Java. However, it is important to acknowledge that anthropogenic mechanisms may also contribute to this larval dispersal. The larvae have a chance to be passively transported by the sea currents during ballast water discharge or by the movement of ships [1].

5. Conclusion

Ilyoplax deltsmani recorded from the western part of Indonesia exhibit two closely related taxa with high genetic distance. The phylogenetic tree delineates two distinct species, i.e., Clade 1 as species 1, encompassing populations from Kalimantan and Java, whilst Clade 2 is indicated as species 2 comprising the Java population. The divergence between these two species occurred during the middle Eocene. Analysis of the genetic structure reveals the presence of gene flow within Clade 1, specifically occurred from Kalimantan to Java.

Acknowledgements

I would like to thank my colleagues from BRIN for their assistances in the Laboratory i.e., Rini Nuraeni former technician of Laboratory of Genetics, Research Center for Biosystematics and Evolution, and

Julianto from Research Center of Experimental Zoology. The present study was funded by the Indonesia Endowment Fund for Education (LPDP), Ministry of Finance of the Republic of Indonesia and supported by Seto Marine Biological Laboratory, Kyoto University, Japan.

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