Hermit Crabs of the Family Diogenidae Ortmann, 1892 (Crustacea: Decapoda: Anomura) in Indonesia: Diversity, Distribution and Habitat

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ABSTRACT

Hermit crabs of the family Diogenidae are ubiquitous organisms along the coasts of the Indonesian archipelago. This study aims to contribute additional data to enhance the current understanding of the geographical distribution patterns, bathymetric distribution, and habitat preferences of diogenid hermit crab species within the framework of Indonesia's marine ecoregions. Distributional data of Diogenidae in Indonesian waters were obtained from scientific literature, dissertations, and unpublished Museum Zoologicum Bogoriense (MZB) specimen data. The diversity analysis of the family Diogenidae in Indonesia identified 116 species in 13 genera. These hermit crabs are widely distributed throughout the country, occurring in all 12 previously defined marine ecoregions. They are found across a broad depth range, and most species are found in more than one substrate such as rocky shores, sand flats, and muddy bottoms, as well as ecosystems including seagrass beds, mangroves, and coral reefs. Seventy percent of species inhabit the littoral zone, which extends from 0 to a depth of 50 m. Among the species studied, *Paguropsis andersoni* exhibited the broadest vertical distribution, ranging from the littoral zone down to the bathyal zone, with recorded depths between 30 and 548 m. The genera *Diogenes* and *Clibanarius* comprise the highest number of species, with 27 and 26 respectively. Among the ecoregions analyzed, the Banda Sea shows the greatest species richness, with a total of 66 identified species of Diogenidae. The most commonly found species in Indonesian waters is *Clibanarius striolatus*.

Keywords: Bathymetric, *Clibanarius*, *Diogenes*, Ecoregion, Geographical

INTRODUCTION

Hermit crabs are a group of crustaceans from the order Decapoda, classified into six families: *Coenobitidae, Diogenidae, Paguridae, Parapaguridae, Pylochelidae* and *Pylojacquesidae* (McLaughlin *et al*., 2007, WoRMS, 2025). These species inhabit tropical, subtropical, and cold waters, ranging from terrestrial environments to deep seas. Generally, hermit crabs exhibit an asymmetric body structure, with a soft abdomen that requires protective housing. Ecologically, hermit crabs play a significant role as predator, scavengers, detritovores and filter feeders (Schembri, 1982). They are considered vital ecosystem engineers in marine habitats, primarily due to their role in utilizing and recycling gastropods shells (Williams and McDermott, 2004) and the availability of gastropod shells can act as a limiting factor for hermit crab presence (Kellogg, 1976).

The study of hermit crabs in Indonesian waters began in 19th century and to date, around 210 different species have been discovered and

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Received 19 June 2025 / Accepted 8 February 2026

described, with the Diogenidae family being the richest (Buitendijk, 1937; Forest, 1987; Haig and Ball, 1988; McLaughlin, 1997; Rahayu and Forest, 1992; 1995; 1999; Rahayu, 2003; 2005; 2006; Rahayu and Wahyudi, 2008; McLaughlin and Lemaitre, 2009; Lemaitre, 2014; Rahayu and Pratiwi, 2022; Rahayu, 2024; Fitrian *et al*., 2024; Shih *et al*., 2025). However, detailed studies on biodiversity, ecology, and geographic distribution of this family in Indonesian waters have not been comprehensively documented.

This study aims to provide current data on the biodiversity of the family Diogenidae in Indonesia, mapping the geographical distribution across the different ecoregions as defined by Spalding *et al*. (2007) and Huffard *et al*. (2012), and describing their ecological patterns. Furthermore, the findings are expected to serve as a valuable scientific resource for future research, conservation planning, and sustainable management of marine biodiversity in tropical ecosystems.

MATERIALS AND METHODS

Distributional data for each species of the family Diogenidae in Indonesian waters were compiled through a comprehensive review of scientific literature published between 1937 and 2024, and academic dissertations that document taxonomic records, along with unpublished data from specimens stored at the Museum Zoologicum Bogoriense (MZB), Bogor, Indonesia. Sixty-three species in the collection of the Museum were examined. Representative specimens of Diogenidae collected from various Indonesian waters were photographed to show the colour in life. Photos were taken from fresh specimens using a Canon DSLR. The literatures sources consist of 35 scientific publications that document taxonomic records, species descriptions, and distributional data. The references include the works of Buitendijk, 1937; Haig and Ball, 1988; Forest, 1984; 1992; 1995; Rahayu and Forest, 1992; 1995; 1999; Rahayu, 1996; 1999; 2002; 2003; 2004; 2005; 2006; 2007; 2012; 2021; 2022; 2024; Rahayu and Hortle, 2002; Rahayu and Wahyudi, 2008; Rahayu and Setyadi, 2009; Rahayu and Pratiwi, 2022; Nugroho, 2011; Nirwantono *et al*., 2011; Handayani *et al*., 2014; Lemaitre *et al*., 2018; Malay *et al*., 2018; Permana *et al*., 2018; Asakura, 2020; Fitrian *et al*., 2022; 2024; Fitriani *et al*., 2024; Nugroho *et al*., 2024.

Distribution analyses

Indonesia, with its unique status as an archipelagic country, has been classified into 12 marine ecoregions: Western Sumatra (WS), Malacca Strait (MS), Southern Java (SJ), Java Sea (JS), North Borneo (NB), Lesser Sunda (LS), Sulawesi Sea (SS), Tomini Bay (TB), Banda Sea (BS), Halmahera (HA), Papua (PA), and Arafura Sea (AS) (Spalding *et al*., 2007; Huffard *et al*., 2012). The composition of all species of hermit crabs in the family Diogenidae in Indonesia was visualized, while the composition of genera was based on the number of species in each genus across the Indonesian marine ecoregions. The distribution patterns of hermit crabs in Indonesia were classified according to these marine ecoregions using a Bray-Curtis similarity-based clustering analysis, and the resulting dendrograms were visualized using the "*ggdendro*" package in R version 4.5.0 software (de Vries and Ripley, 2024). Bathymetric analysis was undertaken to characterize depth variations across the study area, with the results presented as depth categories. Data on *Diogenidae* hermit crabs were analyzed to assess patterns of species occurrence across ecological settings. The number of species was quantified according to ecosystem type to identify habitat-specific richness. In addition, a heatmap was generated to visualize the distribution of *Diogenidae* species across ecosystems, highlighting spatial variation in occurence. Substrate preferences were further examined by associating species records with documented substrate categories, thereby providing insights into habitat utilization and ecological adaptation.

RESULTS

Species richness

The results identified a total of 116 species of hermit crabs belonging to the Diogenidae family and classified into 13 different genera. The

presence of species of this family is confirmed in all the previously defined marine ecoregions (Table 1). The genus Diogenes has the largest number of species, with 27 species representing 23% of the total. It is closely followed by the genus *Clibanarius*, which includes 26 species, representing 22% of the total. Conversely, the genera *Bathynarius* and *Strigopagurus* exhibited low species richness, with only one species (1%) recorded (Figure 1).

Geographic distribution

The 116 hermit crab species belonging to the family Diogenidae are widely distributed across the 12 marine ecoregions in Indonesia (Figure 2, Table 1), and occupying a wide variety of habitats. The species of the genus *Clibanarius* show the widest geographical coverage, occurring in all 12 marine ecoregions in Indonesia, while species of the genus *Diogenes* are found in 10 marine ecoregions (Figure 2). Two genera, *Bathynarius* and *Strigopagurus* are species-poor genera, with only a single species documented in the ecoregions of the Banda Sea (BS) and Arafura Sea (AS), respectively.

The composition of Diogenidae based on the number of species in each genus across the Indonesian marine ecoregions is presented in Figure 3. Among these, the ecoregion of the Banda Sea (BS) showed the highest species richness, comprising 12 of the 13 total genera of Diogenidae, with a total of 66 species. Following the Banda Sea ecoregion, the second and third highest species richness were documented in the Lesser Sundas (LS), with 55 species (8 genera), and the Sulawesi Sea (SS), accounting for 52 species (10 genera). In the Western Sumatra (WS) was characterized by the presence of two genera, *Aniculus* and *Clibanarius*. The genus *Aniculus* was represented by two species, *A. retipes* and *A. ursus*. Meanwhile, the genus *Clibanarius* comprised five species: *Clibanarius humilis, C. longitarsus, C. merguiensis,* and *C. striolatus*, which are widely distributed across Indonesia and were recorded in 8, 9, 9, and 10 ecoregions, respectively. In contrast, *C. infraspinatus* was documented in only four ecoregions. In the Malacca Strait (MS) ecoregion, only 2 species were reported, *Clibanarius ransoni* and *Diogenes avarus*; these species were also recorded in a total of 7 and 9 ecoregions across Indonesia, respectively.

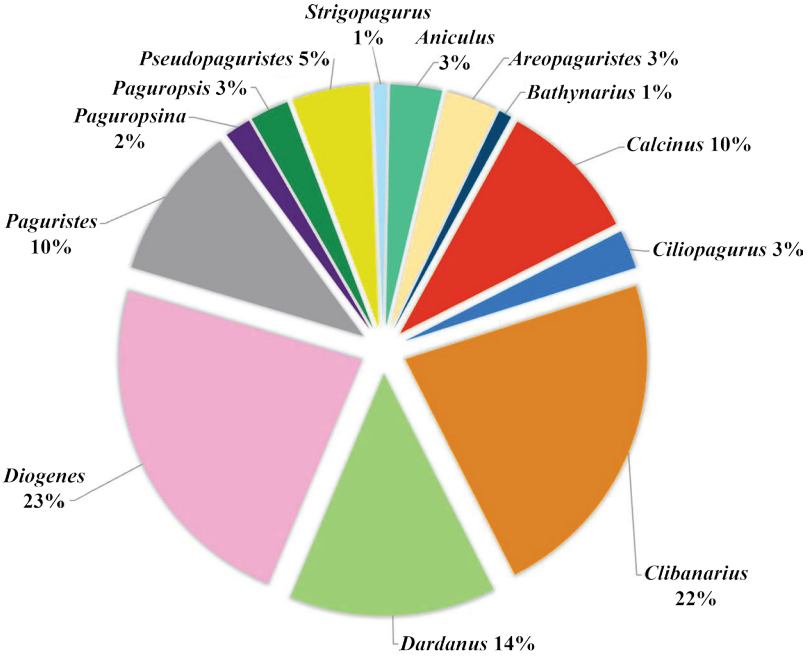


Figure 1. Proportion of species in each of the genera belonging to the family Diogenidae recorded in Indonesian waters.

Table 1. Species of the family Diogenidae occurring in each marine ecoregion.

Species	Marine ecoregion of Indonesia												Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS		
Aniculus erythraeus									✓				Haig and Ball, 1988	
			✓										Permana *et al*., 2018	
Aniculus retipes									✓				Haig and Ball, 1988	
	✓												Forest, 1984	
Aniculus sibogae											✓		Forest, 1984	
Aniculus ursus	✓		✓			✓					✓		Forest, 1984	
Areopaguristes breviantennatus								✓					Rahayu, 2005	
Areopaguristes micheleae						✓			✓			✓	Rahayu, 2005	
			✓										Rahayu, 2021	
			✓										Examined by the authors	Sunda Strait, 25 March 2018, collected by trawl from SJADES Expedition (Figure 14g)
Areopaguristes ngochoae						✓							Rahayu, 2005	
Areopaguristes tuberculatus									✓				Rahayu, 2005	
Bathynarius wolffi									✓				Forest, 1992	
Calcinus anani											✓		Rahayu and Wahyudi, 2008	
Calcinus elegans									✓				Haig and Ball, 1988	
			✓					✓					Handayani *et al*., 2014	
						✓		✓	✓				Rahayu and Wahyudi, 2008	
Calcinus gaimardii									✓				Haig and Ball, 1988	
								✓					Rahayu and Forest, 1999	
						✓		✓	✓				Rahayu and Wahyudi, 2008	
				✓									Nugroho, 2011	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Sira-Lombok Island, collected by hand, 15 February 2018 (Figure 9a)
Calcinus guamensis									✓				Haig and Ball, 1988	
						✓			✓				Rahayu and Wahyudi, 2008	
Calcinus laevimanus					✓	✓					✓	✓	Buitendijk, 1937	
									✓				Haig and Ball, 1988	
						✓							Rahayu, 1992 (dissertation)	
				✓									Rahayu, 2004	
						✓		✓	✓				Rahayu and Wahyudi, 2008	
				✓									Nugroho, 2011	
			✓										Permana *et al*., 2018	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Teluk Boro, Lombok Island, 4 August 2020, intertidal collection, collected by hand (Figure 9b)

Table 1. Conted.

Species	Marine ecoregion of Indonesia												Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS		
Calcinus latens						✓			✓				Buitendijk, 1937	
									✓				Haig and Ball, 1988	
						✓							Rahayu, 1992 (dissertation)	
						✓		✓	✓				Rahayu and Wahyudi, 2008	
				✓									Nugroho, 2011	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Teluk Boro, Lombok Island, 4 August 2020, intertidal collection, collected by hand,
Calcinus lineapropodus				✓									Rahayu, 2004	
				✓					✓				Rahayu and Wahyudi, 2008	
								✓					Examined by the authors	Pandanan, Lombok Island, 12 October 2021, dive collection, collected by hand
Calcinus minutus						✓		✓		✓			Buitendijk, 1937	
									✓				Haig and Ball, 1988	
							✓						Rahayu, 1992 (dissertation)	
				✓									Rahayu, 2004	
						✓		✓	✓				Rahayu and Wahyudi, 2008	
								✓					Examined by the authors	Pandanan, Lombok Island, 12 October 2021, dive collection, collected by hand (Figure 9d)
Calcinus morgani						✓							Rahayu and Forest, 1999	
			✓										Permana *et al*., 2018	
						✓		✓	✓				Rahayu and Wahyudi, 2008	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Pandanan, Lombok Island, 12 October 2021, dive collection, collected by hand (Figure 9e)
Calcinus pulcher									✓				Haig and Ball, 1988	
				✓									Rahayu, 2004	
								✓	✓				Rahayu and Wahyudi, 2008	
								✓					Examined by the authors	Pandanan, Lombok Island, 12 October 2021, dive collection, collected by hand (Figure 9g)
Calcinus vachoni								✓					Examined by the authors	Teluk Boro, Lombok Island, 24 January 2023, intertidal collection, collected by hand (Figure 9f)

Table 1. Conted.

Species	Marine ecoregion of Indonesia												Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS		
Ciliopagurus krempfi						✓							Forest, 1995	
Ciliopagurus macrolepis				✓					✓			✓	Forest, 1995	
Ciliopagurus strigatus									✓				Haig and Ball, 1988	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Sira, Lombok Island, 17 January 2020, dive collection, collected by hand (Figure 9h)
Clibanarius ambonensis									✓				Rahayu and Forest, 1992	
												✓	Rahayu, 2003	
												✓	Rahayu and Setyadi, 2009	
										✓			Nugroho *et al*., 2024	
Clibanarius antennatus									✓				Rahayu and Forest, 1992	
						✓							Rahayu, 1992 (dissertation)	
												✓	Rahayu, 2003	
												✓	Rahayu and Setyadi, 2009	
Clibanarius bistriatus									✓				Rahayu and Forest, 1992	
								✓					Nugroho *et al*., 2024	
								✓					Examined by the authors	Teluk Kombal, Lombok Island, 5 June 2023, collected by hand (Figure 10a)
Clibanarius boschmai						✓	✓		✓				Buitendijk, 1937	
									✓				Haig&Ball,1988	
								✓					Rahayu and Wahyudi, 2008	
Clibanarius corallinus									✓				Haig and Ball, 1988	
						✓			✓	✓			Rahayu and Forest, 1992	
			✓										Permana *et al*., 2018	
								✓					Examined by the authors	Teluk Kombal, Lombok Island, 23 January 2023, collected by hand
Clibanarius cruentatus						✓		✓	✓	✓			Buitendijk, 1937	
						✓			✓	✓	✓		Rahayu and Forest, 1992	
				✓									Nugroho, 2011	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Teluk Kombal, Lombok, 8 September 2023, collected by hand (Figure 10b)

Table 1. Conted.

Species	Marine ecoregion of Indonesia											Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS	
Clibanarius danai						✓							Rahayu and Forest, 1992	
Clibanarius demani								✓	✓				Buitendijk, 1937	
									✓				Rahayu and Forest, 1992	
				✓									Rahayu, 2004	
								✓			✓		Examined by the authors	Ujung Betok, Lombok Island, 25 February 2020 (Figure 10c) and Ekas, Lombok Island February 2024, collected by hand
Clibanarius englaucus									✓				Haig and Ball, 1988	
						✓			✓	✓	✓		Rahayu and Forest, 1992	
				✓									Nugroho, 2011	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Kuta, Lombok Island, 5 July 2023, collected by hand (Figure 10d)
Clibanarius eurysternus					✓	✓		✓	✓	✓	✓		Buitendijk, 1937	
									✓				Haig and Ball, 1988	
						✓		✓	✓	✓	✓		Rahayu and Forest, 1992	
				✓									Nugroho, 2011	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Kuta, Lombok Island, 5 July 2023, collected by hand (Figure 10e)
Clibanarius harisi												✓	Rahayu, 2003	
												✓	Rahayu and Setyadi, 2009	
											✓		Examined by the authors	Minajerwi, Papua, 23 June 2023, dredge (Figure 10i)
Clibanarius humilis					✓				✓	✓			Buitendijk, 1937	
	✓					✓			✓	✓			Rahayu and Forest, 1992	
				✓									Nugroho, 2011	
			✓										Permana *et al*., 2018	
								✓					Examined by the authors	Kuta, Lombok Island, 18 June 2023, collected by hand (Figure 10f)
Clibanarius infraspinatus						✓							Buitendijk, 1937	
				✓		✓			✓				Rahayu and Forest, 1992	
	✓												Fitriani *et al*., 2024	
									✓				Examined by the authors	Selayar Island, 26 November 2024, collected by hand (Figure 11a)

Table 1. Conted.

Species	Marine ecoregion of Indonesia												Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS		
Clibanarius laevimanus					✓			✓				✓	Buitendijk, 1937	
									✓			✓	Rahayu and Forest, 1992	
Clibanarius longitarsus					✓	✓		✓	✓		✓	✓	Buitendijk, 1937	
									✓				Haig and Ball, 1988	
				✓		✓			✓	✓	✓		Rahayu and Forest, 1992	
												✓	Rahayu, 2003	
				✓									Rahayu, 2004	
												✓	Rahayu and Setyadi, 2009	
	✓												Fitriani *et al*., 2024	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Ekas, Lombok Island February 2024 and Medana Lombok Island, collected by hand (Figure11b)
Clibanarius merguiensis					✓	✓		✓	✓	✓			Buitendijk, 1937	
	✓					✓			✓	✓	✓		Rahayu and Forest, 1992	
				✓									Nugroho, 2011	
			✓										Permana *et al*., 2018	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Teluk Nara, Lombok Island, 4 August 2020, collected by hand (Figure 11c)
Clibanarius padavensis					✓			✓				✓	Buitendijk, 1937	
								✓				✓	Rahayu and Forest, 1992	
Clibanarius ransoni						✓		✓	✓	✓	✓		Rahayu and Forest,1992	
		✓											Rahayu, 1996	
				✓									Rahayu, 2004	
		✓											Rahayu, 2022	
Clibanarius rhabdodactylus												✓	Rahayu and Forest, 1992	
Clibanarius rubroviria								✓					Rahayu, 1999	
Clibanarius rutilus						✓	✓						Rahayu, 1999	
Clibanarius serenei				✓		✓			✓				Rahayu and Forest, 1992	
Clibanarius similis						✓							Rahayu and Forest, 1992	
Clibanarius snelliusi							✓	✓					Buitendijk, 1937	
						✓			✓	✓			Rahayu and Forest, 1992	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Teluk Kombal Lombok Island, 16 July 2023, collected by hand (Figure 11d)

Table 1. Conted.

Species	Marine ecoregion of Indonesia												Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS		
Clibanarius striolatus					✓	✓		✓	✓			✓	Buitendijk, 1937	
	✓					✓			✓	✓	✓		Rahayu and Forest, 1992	
				✓									Rahayu, 2004	
				✓									Nugroho, 2011	
			✓										Permana *et al*., 2018	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Medana, Lombok Island, 11 September 2023, collected by hand (Figure 11e)
Clibanarius virescens					✓	✓		✓	✓	✓	✓		Buitendijk, 1937	
									✓				Haig and Ball, 1988	
						✓			✓	✓	✓		Rahayu and Forest, 1992	
				✓									Nugroho, 2011	
			✓										Permana *et al*., 2018	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Kuta, Lombok Island, 18 June 2023, collected by hand (Figure 11f)
Dardanus arrosor									✓			✓	Examined by the authors	Arafura Sea, October 1991, collected by trawl
Dardanus callichela												✓	Examined by the authors	Arafura sea, September 1994, collected by trawl
Dardanus dearmatus									✓				Rahayu and Wahyudi, 2008	
									✓	✓			Examined by the authors	Halmahera Island, 17 October 1993; Ambon Island, 25 May 1995, collected by dredge
Dardanus deformis						✓		✓	✓	✓	✓		Buitendijk, 1937	
						✓		✓	✓				Rahayu and Wahyudi, 2008	
										✓			Nugroho *et al*., 2024	
					✓		✓	✓	✓				Examined by the authors	Kalimantan, 1994; Maluku, 16 June 1989; Lombok Island, May 1995, Medana, Lombok Island, 10 July 2022, collected by hand (Figure 12d)
								✓					Examined by the authors	

Table 1. Conted.

Species	Marine ecoregion of Indonesia												Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS		
Dardanus gemmatus									✓				Haig and Ball, 1988	
						✓			✓				Rahayu and Wahyudi, 2008	
								✓					Examined by the authors	Medana, Lombok Island, 10 July 2022, dive collection (Figure 12e)
						✓			✓				Examined by the authors	Binongko Islands, Marsegu Island, 30 June 1993, collected by trap net
Dardanus guttatus									✓				Haig and Ball, 1988	
						✓			✓				Rahayu and Wahyudi, 2008	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Teluk Kodek, 10 July 2022, dive collection (Figure 12g)
Dardanus hessii												✓	Haig and Ball, 1988	
			✓	✓		✓			✓				Examined by the authors	Collected by trawl and collected by hand during the year 1971 - 1991 from Seribu island, Karimata strait and Maluku,
Dardanus imbricatus												✓	Haig and Ball, 1988	
												✓	Examined by the authors	Arafura Sea, September 1994, collected by trawl
Dardanus lagopodes									✓				Haig and Ball, 1988	
				✓									Rahayu, 2004	
						✓		✓	✓				Rahayu and Wahyudi, 2008	
				✓									Nirwantono *et al*., 2011	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Teluk Boro, Lombok Island, 23 January 2023, collected by hand (Figure 12c)
					✓	✓		✓	✓	✓	✓		Examined by the authors	Kalimantan, 22 October 1994; Maluku, June 1993, collected by hand
Dardanus megistos					✓	✓		✓	✓	✓			Buitendijk, 1937	
									✓				Haig and Ball, 1988	
						✓		✓	✓				Rahayu and Wahyudi, 2008	
			✓										Permana *et al*., 2018	
										✓			Nugroho *et al*., 2024	
					✓	✓		✓	✓	✓	✓		Examined by the authors	collected during the year 1989 - 2022 in Indonesian waters by hand or trawl (Figure 12f)

Table 1. Conted.

Species	Marine ecoregion of Indonesia												Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS		
Dardanus pedunculatus								✓	✓	✓			Buitendijk, 1937	
									✓				Haig and Ball, 1988	
						✓			✓				Rahayu and Wahyudi, 2008	
								✓					Examined by the authors	Medana, Lombok Island, 10 July 2022, collected by hand
									✓				Examined by the authors	Maluku, July 1989, collected by hand
Dardanus rufus				✓									Buitendijk, 1937	
Dardanus sanguinolentus							✓	✓	✓				Malay *et al*., 2018	
								✓					Examined by the authors	Lombok Island (Figure 12a)
Dardanus scutellatus								✓		✓			Buitendijk, 1937	
					✓	✓		✓	✓	✓	✓		Rahayu, 1992 (dissertation)	
									✓				Rahayu and Wahyudi, 2008	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Medana, Lombok Island, 16 December 2023, collected by hand (Figure 12b)
Dardanus setifer												✓	Haig and Ball, 1988	
								✓					Examined by the authors	Ekas, Lombok Island, collected by hand
												✓	Examined by the authors	Arafura sea, September 1994, collected by trawl
Dardanus woodmasoni									✓				Haig and Ball, 1988	
									✓				Rahayu, 1992 (dissertation)	Ambon Bay, July 1989
								✓					Examined by the authors	Ekas, Lombok Island, July 2007, collected by hand
Diogenes avarus									✓				Haig and Ball, 1988	
				✓		✓			✓	✓	✓		Rahayu and Forest, 1995	
		✓											Rahayu, 1996	
												✓	Rahayu and Hortle, 2002	
												✓	Rahayu and Setyadi, 2009	
												✓	Fitrian *et al*, 2022	
										✓			Nugroho *et al*., 2024	
							✓	✓					Examined by the authors	Teluk Kombal, Lombok Island, 5 June 2023, collected by hand (Figure 13a)
Diogenes berduri			✓										Rahayu, 2021	
			✓										Examined by the authors	Sunda Strait, 26 March 2018, dredge from SJADES Expedition (Figure 13c)

Table 1. Conted.

Species	Marine ecoregion of Indonesia												Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS		
Diogenes biramus						✓			✓				Rahayu and Forest, 1995	
								✓					Rahayu and Pratiwi, 2022	
								✓					Examined by the authors	Medana, 21 September 2022 (Figure 13b)
Diogenes crassus			✓										Asakura, 2020	
Diogenes custos				✓									Rahayu and Forest, 1995	
								✓				✓	Examined by the authors	Teluk Kombal, Lombok Island, 5 June 2023 collected by hand, Timika-Papua 29 Mei 2019
Diogenes dorotheae												✓	Rahayu and Hortle, 2002	
												✓	Rahayu and Setyadi, 2009	
Diogenes dubius												✓	Rahayu and Hortle, 2002	
												✓	Rahayu and Setyadi, 2009	
												✓	Examined by the authors	Minajerwi, Papua, 23 June 2023, dredge (Figure 13d)
Diogenes fasciatus				✓		✓							Rahayu and Forest, 1995	
				✓		✓							Asakura, 2020	
Diogenes foresti												✓	Rahayu and Hortle, 2002	
												✓	Rahayu and Setyadi, 2009	
												✓	Fitrian *et al*., 2022	
										✓			Nugroho *et al*., 2024	
												✓	Examined by the authors	Minajerwi, Papua, 23 June 2023, dredge (Figure 13e)
Diogenes goniochirus						✓							Rahayu and Forest, 1995	
Diogenes haigae												✓	Asakura, 2020	
Diogenes hawisi												✓	Fitrian *et al*., 2024	
												✓	Examined by the authors	Timika-Papua, Oktober 2021 (Figure 13f)
Diogenes jousseaumei												✓	Haig and Ball, 1988	
												✓	Rahayu and Forest, 1995	
												✓	Rahayu and Setyadi, 2009	
												✓	Examined by the authors	Tipoeka estuary, Timika-Papua 28 June 2000
Diogenes klaasi						✓							Rahayu and Forest, 1995	
Diogenes kombalensis								✓					Rahayu, 2024	
								✓					Examined by the authors	Kombal Bay-Lombok Island, 20 May 2023 (Figure 13g)

Table 1. Conted.

Species	Marine ecoregion of Indonesia												Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS		
Diogenes leptocerus						✓			✓				Rahayu and Forest, 1995	
												✓	Rahayu and Hortle, 2002	
												✓	Rahayu and Setyadi, 2009	
Diogenes luteus								✓					Rahayu, 2024	
								✓					Examined by the authors	Kombal Bay-Lombok Island, 4 June 2023 (Figure 13h)
Diogenes matabiru								✓					Rahayu and Pratiwi, 2022	
								✓					Examined by the authors	Jerowaru-Lombok Island 29 September 2014 (Figure 13i)
Diogenes mixtus						✓							Rahayu and Forest, 1995	
Diogenes moosai				✓									Rahayu and Forest, 1995	
Diogenes pallescens									✓				Haig and Ball, 1988	
							✓		✓				Rahayu and Forest, 1995	
				✓									Nugroho, 2011	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Medana, Lombok Island, 16 December 2023, collected by hand (Figure 14a)
Diogenes platyops				✓									Rahayu and Forest, 1995	
												✓	Examined by the authors	Arafura sea, 26 November 1998
Diogenes rectimanus												✓	Haig and Ball, 1988	
Diogenes spinicarpus				✓									Rahayu, 2004	
									✓	✓	✓		Asakura, 2020	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Kuta, Lombok Island, 23 June 2023, collected by hand (Figure 14d)
Diogenes takedai								✓					Rahayu, 2012	
								✓					Examined by the authors	Lombok Island, 25 October 2009, collected by hand (Figure 14b)
Diogenes tumidus						✓			✓	✓	✓		Rahayu and Forest, 1995	
												✓	Rahayu and Hortle, 2002	
												✓	Rahayu and Setyadi, 2009	
				✓									Nugroho, 2011	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Kuta, Lombok Island, 23 June 2023, collected by hand (Figure 14c)

Table 1. Conted.

Species	Marine ecoregion of Indonesia												Sources	Methods (locations, collection dates, sampling methods)
	WS	MS	SJ	JS	NB	SS	TB	LS	BS	HA	PA	AS		
Diogenes viridis									✓				Haig and Ball, 1988	
Paguristes aciculus								✓	✓				Rahayu, 2006	
Paguristes antennarius								✓	✓			✓	Rahayu, 2006	
Paguristes arostratus						✓			✓				Rahayu, 2006	
Paguristes brachyrostris						✓		✓					Rahayu, 2006	
Paguristes calvus			✓										Rahayu, 2021	
Paguristes miyakei			✓										Rahayu, 2021	
Paguristes palythophilus						✓	✓	✓	✓			✓	Rahayu 2006	
			✓			✓							Rahayu 2021	
Paguristes puniceus						✓			✓			✓	Rahayu 2006	
			✓										Rahayu 2021	
Paguristes pusillus						✓						✓	Rahayu, 2006	
Paguristes rectus			✓										Rahayu, 2021	
			✓										Examined by the authors	Sunda Strait, 25 March 2018 collected by trawl from SJADES Expedition (Figure 14h)
Paguristes runyanae									✓				Haig and Ball, 1988	
									✓				Rahayu, 2006	
Paguristes triton			✓										Rahayu, 2021	
Paguropsina inermis									✓				Lemaitre *et al*., 2018	
Paguropsina pistillata									✓				Lemaitre *et al*., 2018	
Paguropsis andersoni												✓	Lemaitre *et al*., 2018	
Paguropsis confus						✓							Lemaitre *et al*., 2018	
Paguropsis typica				✓					✓			✓	Lemaitre *et al*., 2018	
Pseudopaguristes asper								✓					Rahayu, 2005	
Pseudopaguristes bicolor			✓										Rahayu, 2021	
			✓										Examined by the authors	Sunda Strait, Sunda Strait, 26 March 2018, collected by dredge from SJADES Expedition (Figure14f)
Pseudopaguristes hians						✓		✓					Rahayu, 2005	
Pseudopaguristes kuekenthali									✓				Haig and Ball, 1988	
									✓				Rahayu, 2005	
Pseudopaguristes laurentae				✓					✓			✓	Rahayu, 2005	
									✓				Rahayu, 2007	
			✓										Rahayu, 2021	
Pseudopaguristes monoporus									✓				Haig and Ball, 1988	
									✓	✓			Rahayu, 2005	
										✓			Nugroho *et al*., 2024	
								✓					Examined by the authors	Teluk Kombal, Lombok Island, 1 Desember 2021, collected by hand (Figure 14e)
Strigopagurus boreonotus												✓	Forest,1995	

Note: WS = Western Sumatra; MS = Malacca Strait; SJ = Southern Java; JS = Java Sea; NB = North Borneo; LS = Lesser Sunda; SS = Sulawesi Sea; TB = Tomini Bay; BS = Banda Sea; HA = Halmahera; PA = Papua; AS = Arafura Sea

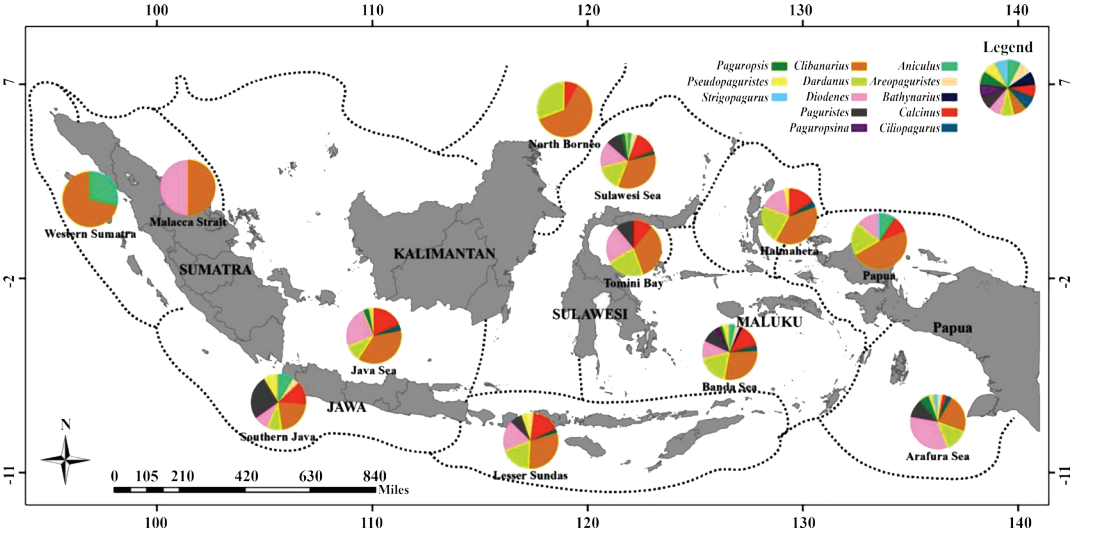


Figure 2. Map showing distribution of the Family Diogenidae across the 12 marine ecoregions of Indonesia.

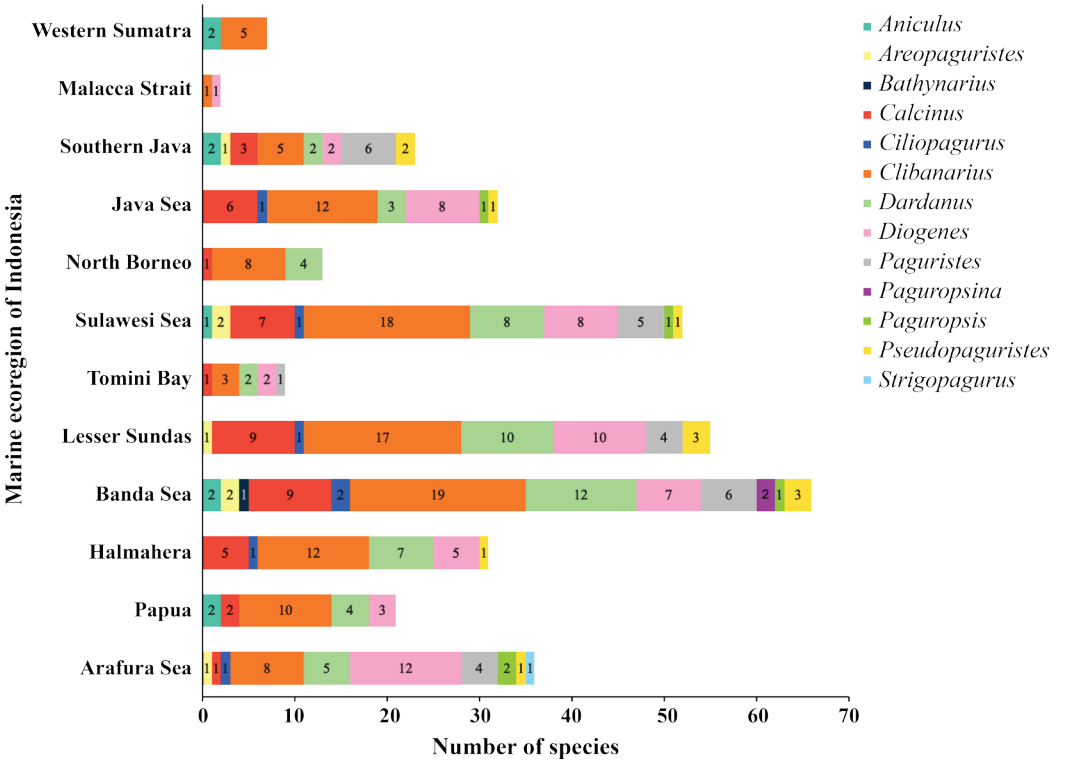


Figure 3. Distribution and composition of the family Diogenidae across the marine ecoregion of Indonesia, based on the number of species of each genus.

The distributional relationships among Indonesian marine ecoregions, based on the species composition of the family Diogenidae, are illustrated by a hierarchical dendrogram constructed using Bray–Curtis similarity (Figure 4). The clustering reveals distinct ecoregional groups with varying degrees of similarity in species assemblages, indicating shared ecological conditions and biogeographical affinities. A close association is observed among the Java Sea (JS), Sulawesi Sea (SS), Halmahera (HA), Lesser Sunda (LS), and Banda Sea (BS) ecoregions, with North Borneo (NB), and Papua (PA) also exhibiting strong affinities with this group. Although Western Sumatra (WS), Arafura Sea (AS), and Southern Java (SJ) are positioned within the same major cluster, the dendrogram indicates that they are separated at higher dissimilarity levels, suggesting comparatively distinct assemblages likely adapted to specific habitat conditions. In contrast, the Malacca Strait (MS) and Tomini Bay (TB) form a separate cluster, indicating a comparatively distinct species composition. This separation may be related to localized environmental factors. While some ecoregions with distinct species compositions may reflect differences in ecological drivers and historical connectivity, others demonstrate stronger biogeographical affinities. The observed clustering pattern highlights pronounced spatial variability in the distribution of Diogenidae species across Indonesian marine ecoregions.

Bathymetric distribution

An analysis of the bathymetric distribution of 116 diogenid species reveals that most of the species, 70% (81 species), are concentrated in the littoral zone, which ranges from the 0 to a depth of 50 m. In contrast, 16% (18 species) were recorded from the bathyal zone (200–1,000 m), while the remaining 9% (11 species) were found in the sublittoral zone, between 50 and 200 m depth (Figure 5).

The graph depicting the bathymetric distribution of Diogenidae species (Figure 6) illustrates the depth range of each species recorded in Indonesian waters. Species belonging to

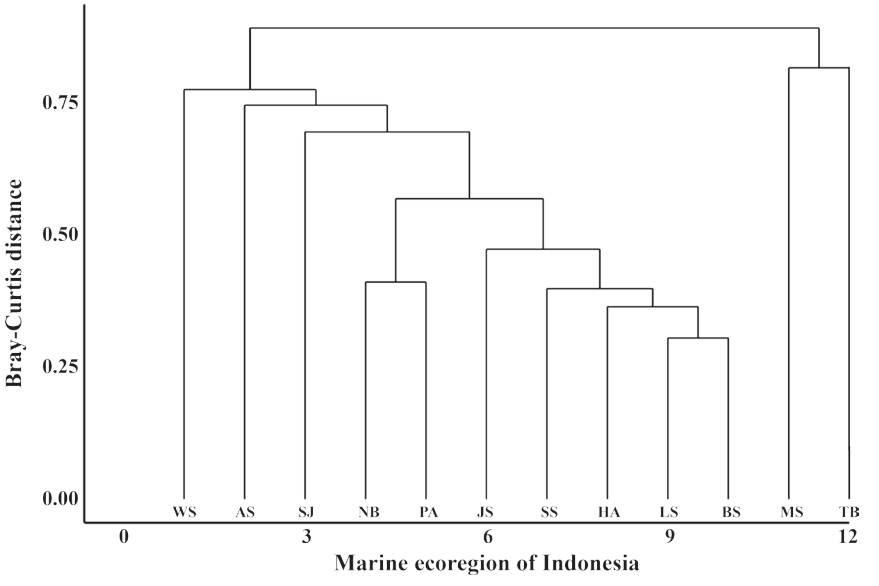


Figure 4. Hierarchical clustering of Indonesian marine ecoregions based on Bray-Curtis similarity of Diogenidae species composition

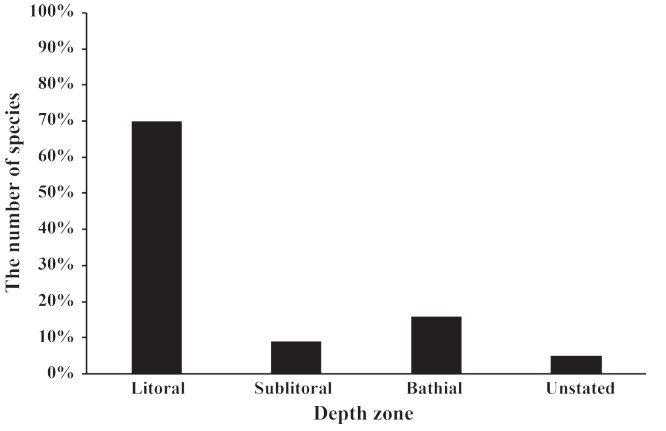


Figure 5. Percentage of Diogenidae species in Indonesian waters classified into depth categories.

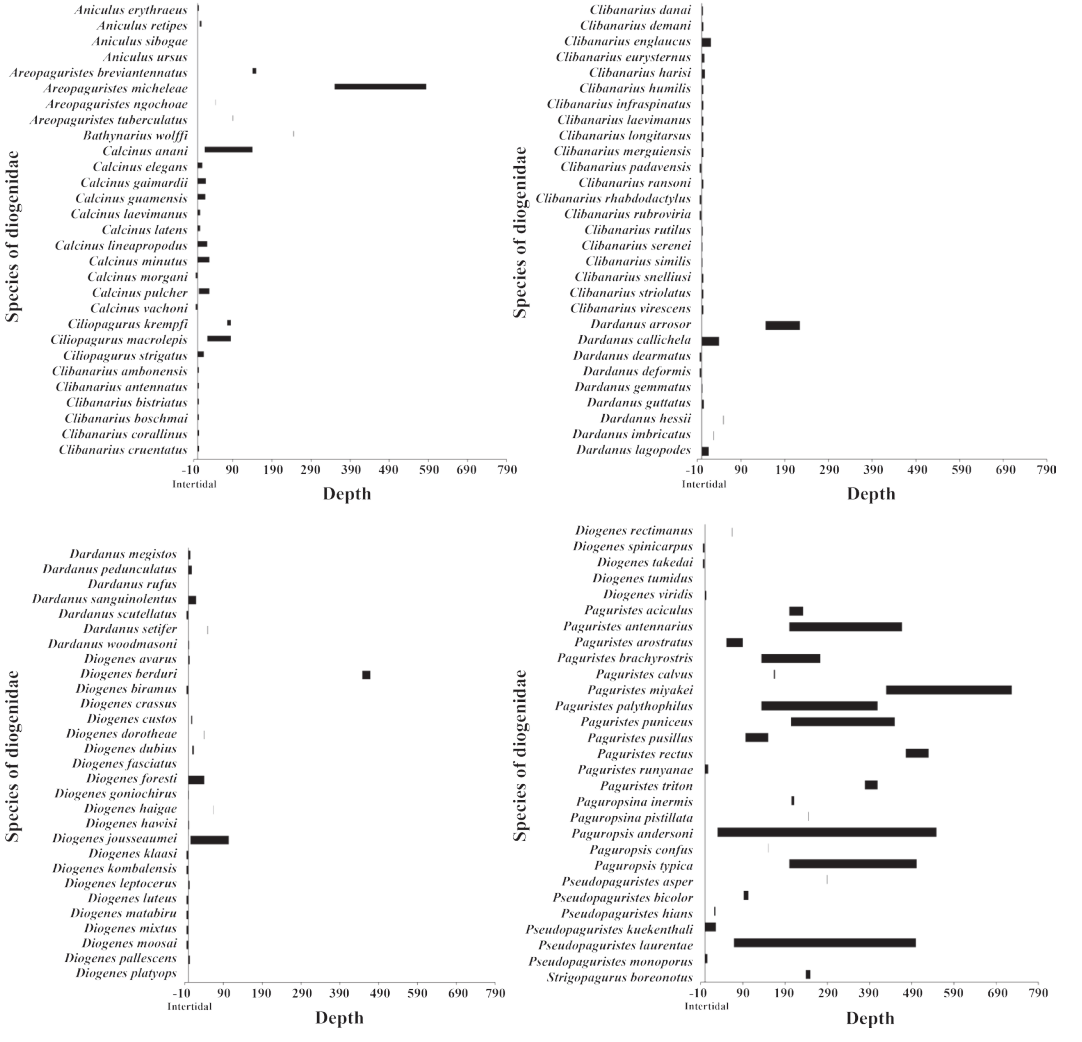


Figure 6. Bathymetric distribution of Diogenidae species recorded in Indonesian waters.

the genera *Aniculus, Aeropaguristes, Calcinus, Ciliopagurus, Clibanarius, Dardanus, Diogenes,* and *Pseudopaguristes* are predominantly distributed from the depth 0 to 50 m. The 26 recorded species of the genus *Clibanarius* were exclusively observed within this zone. Similarly, 26 out of the 27 species of *Diogenes* were confined to the littoral zone, with the exception of *Diogenes berduri*, which was collected from the bathyal zone at depths between 448 and 469 m. The bathyal zone also supports the presence of *Paguristes* and *Areopaguristes* species, both of which are typically classified as deep-sea species. The genus *Paguristes* comprises seven species: *Paguristes aciculus, P. antennarius, P. miyakei, P. palythophilus, P. puniceus, P. rectus,* and *P. triton*. In particular, *Paguristes miyakei* was recorded from the greatest depths among all species, ranging from 429 to 727 m, while *P. runyanae* is the only *Paguristes* species recorded in the littoral region. *Paguropsis andersoni* exhibited the broadest bathymetric distribution, occurring from the littoral to the bathyal zone, at depths between 30 and 548 m.

Ecosystems, habitats and substrates

The results of the analysis of ecosystem, habitats and substrate usage show that *Diogenidae* species inhabit a wide variety of habitats in Indonesia, including coral reefs, seagrass beds, mangroves, algae-dominated habitats, estuaries, rocky shores, sandy flats, and muddy substrates. Most of these species are distributed from the immediate littoral zone to the littoral sand flat zone. The rocky shores host the highest number of species, while those associated with algae have the fewest. However, many taxonomic studies lack information on associated ecosystems, resulting in numerous entries marked as unstated (Figure 7).

The heatmap (Table 2) shows the distribution of Diogenidae genera across the eight coastal and marine ecosystem types defined above. The genus *Clibanarius* exhibits the broadest ecological range, with high species richness recorded across all habitat types, particularly in mangrove and muddy areas, where 18 species were documented in each of them. Other broadly distributed genera include *Calcinus, Dardanus*, and *Diogenes*, which were commonly found in coral reefs, rocky shores, sand flats, and seagrass beds. In contrast, some genera showed more limited ecological plasticity, with species of *Diogenes* strongly associated with soft-bottom habitats like sand flats (15 species) and muddy substrates (13 species), and species of *Aniculus* with coral reefs and rocky shores. The species of the genera *Paguropsina, Paguropsis,*

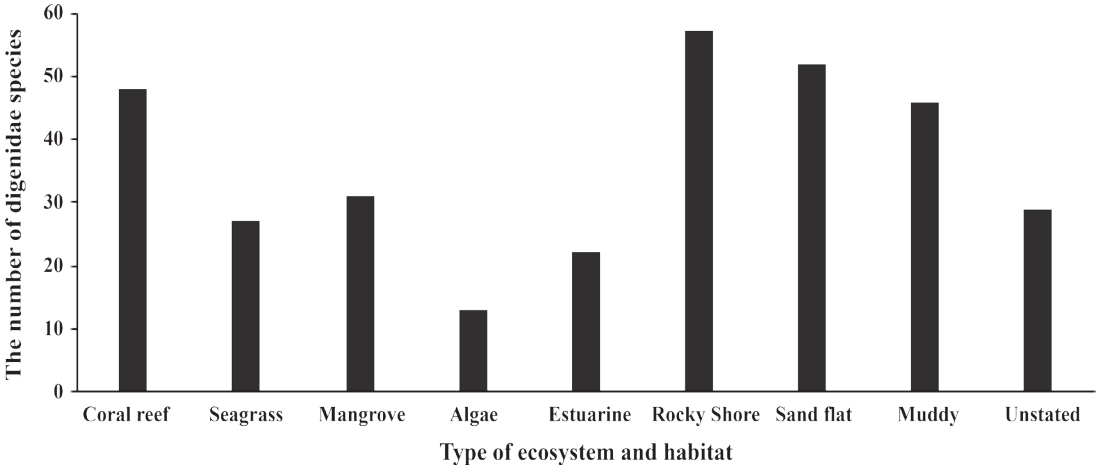


Figure 7. Number of Diogenidae species by ecosystem and habitat type.

Table 2. Heatmap of Diogenidae distribution by ecosystem and habitat type.

Genus	Ecosystem and habitat							
	Coral reef	Seagrass	Mangrove	Algae	Estuarine	Rocky shore	Sand flat	Muddy
Aniculus	4	1	0	1	0	1	0	0
Areopaguristes	2	0	0	0	0	2	3	0
Bathynarius	1	0	0	0	0	0	0	0
Calcinus	9	3	1	2	0	10	6	0
Ciliopagurus	1	0	1	0	0	0	0	0
Clibanarius	15	13	18	8	15	15	14	18
Dardanus	7	6	2	2	0	8	8	6
Diogenes	4	3	8	0	7	12	15	13
Paguristes	2	0	0	0	0	5	4	5
Paguropsina	0	0	0	0	0	0	0	0
Paguropsis	0	0	0	0	0	0	0	0
Pseudopaguristes	3	1	1	0	0	4	2	4
Strigopagurus	0	0	0	0	0	0	0	0

Strigopagurus, Areopaguristes, and *Paguristes* mostly inhabit the deep sea. The habitat is generally described in the literature as consisting of shell and coral debris, coarse sand, and bryozoan sand such as shell and coral debris, coarse sand, bryozoan sand. Overall, the mangrove ecosystem emerges as a critical habitat, particularly for species of *Clibanarius* and *Diogenes*, underscoring the ecological importance of vegetated coastal habitats in supporting Diogenidae diversity in Indonesia. The genus *Clibanarius* shows the widest distribution, with species found in all major ecosystems. Within this genus, *Clibanarius englaucus, C. humilis, C. ransoni, C. striolatus,* and C. virescens are the most widely distributed species, occurring in coral reefs, seagrass beds, mangroves, algae, estuaries, rocky shores, sand flats, and muddy substrates.

The distribution of Diogenidae species across various substrate types is depicted in the bar chart (Figure 8). The four substrate categories shown include hard substrate, fine substrate, both (species associated with both hard and fine substrates), and unstated (species without specific substrate information). The results show greater species richness in the hard and fine substrate categories, with almost 70 different species, highlighting the ecological importance of these habitat types for the family. Due to gaps in data on habitat association, the "Both" category exhibits a moderate species count, while the "Unstated" category shows the lowest number of species.

The consistent dominance of genera such as *Diogenes, Clibanarius, Calcinus* and *Paguristes* across all substrate categories underscores their broad ecological adaptability. Other genera, such as *Bathynarius* and *Cilipopagurus*, exhibit more substrate-specific distributions, which may indicate habitat specialization. Interestingly, *Diogenes* is a dominant genus in every category, suggesting that it is widely distributed across a range of substrate conditions. Some specimens of Diogenidae obtained from Indonesian waters are illustrated in Figures 9–14.

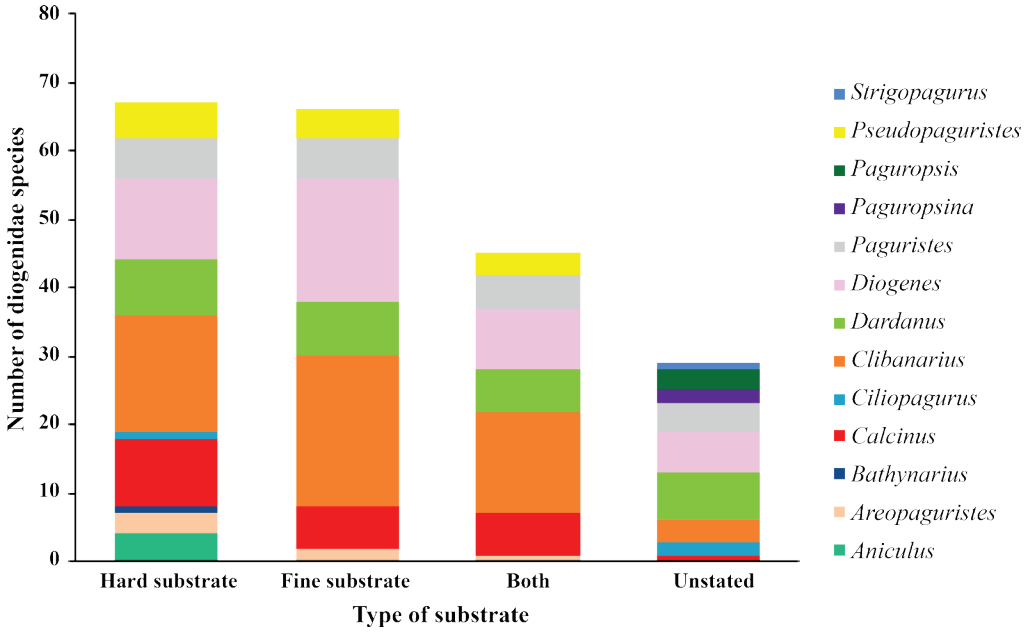


Figure 8. Substrate preferences of Diogenidae hermit crabs in Indonesia.

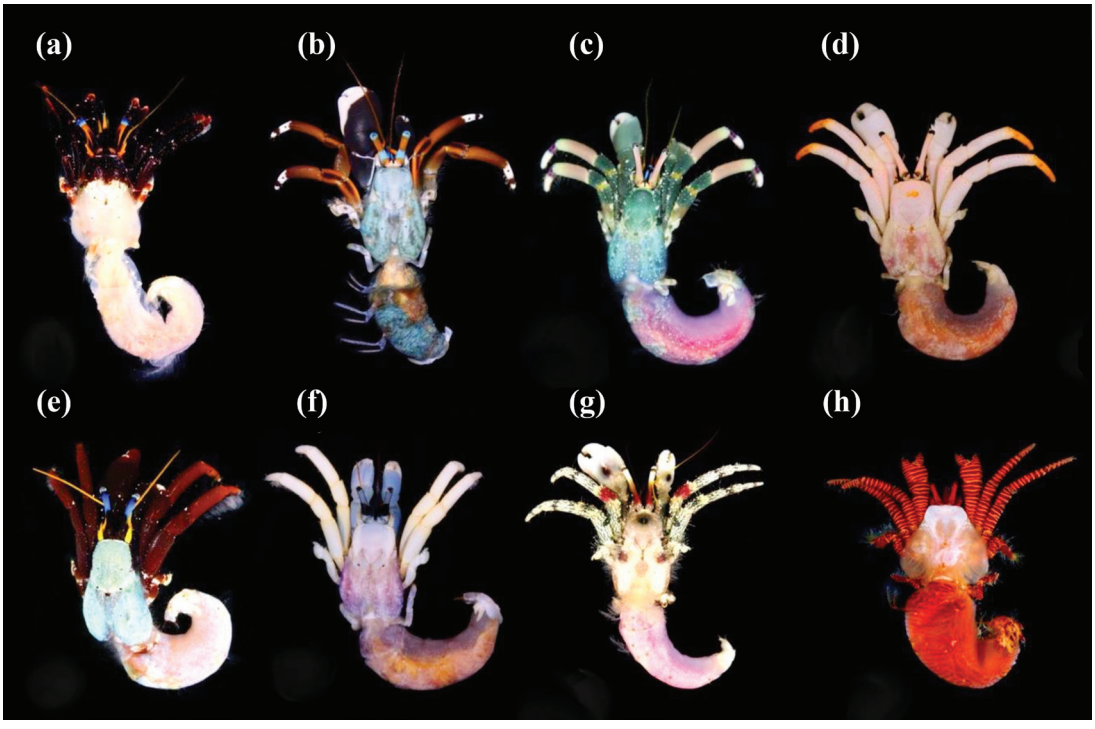


Figure 9. Representative specimens of Diogenidae from Lombok Island, Indonesia: (a) *Calcinus gaimardi*; (b) *Calcinus laevimanus*; (c) *Calcinus latens*; (d) *Calcinus minutus*; (e) *Calcinus morgani*; (f) *Calcinus vachoni*; (g) *Calcinus pulcher*; (h) *Ciliopagurus strigatus*.

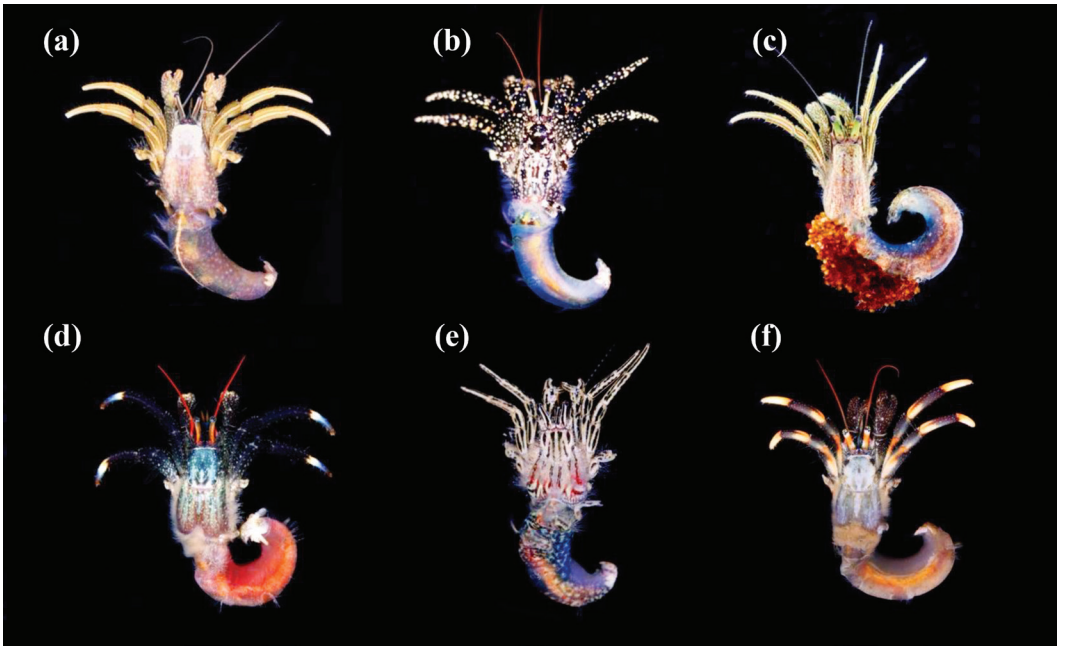


Figure 10. Representative specimens of *Clibanarius* from Indonesian waters: (a) *Clibanarius bistriatus*; (b) *Clibanarius cruentatus*; (c) *Clibanarius demani*; (d) *Clibanarius englaucus* (e) *Clibanarius eurysternus*; (f) *Clibanarius humilis*; panels (a–f) are specimens from Lombok Island, Indonesia.

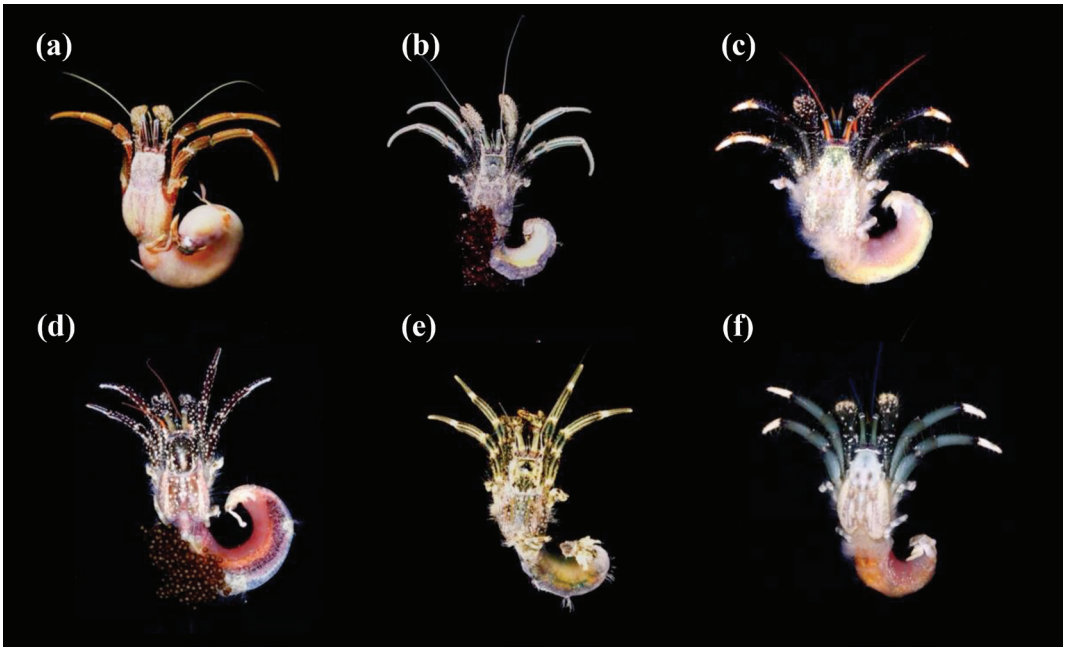


Figure 11. Representative specimens of *Clibanarius* from Indonesian waters: (a) *Clibanarius infraspinatus*; (b) *Clibanarius longitarsus*; (c) *Clibanarius merguiensis*; (d) *Clibanarius snelliusi*; (e) *Clibanarius striolatus*; (f) *Clibanarius virescens*. Panels (b–f) are specimens from Lombok Island, Indonesia, (a) is a specimen from Selayar Island, South Sulawesi, Indonesia.

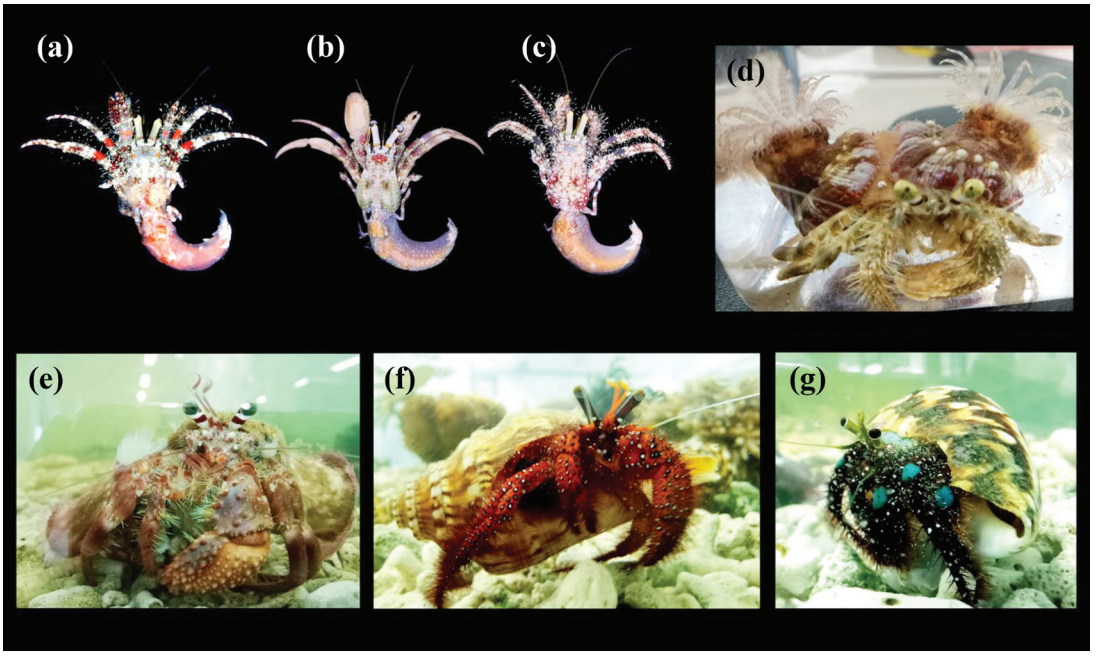


Figure 12. Representative specimens of *Dardanus* from Lombok Island, Indonesia: (a) *Dardanus sanguinolentus*; (b) *Dardanus scutellatus*; (c) *Dardanus lagopodes*; (d) *Dardanus deformis*; (e) *Dardanus gemmatus*; (f) *Dardanus megistos*; (g) *Dardanus guttatus*.

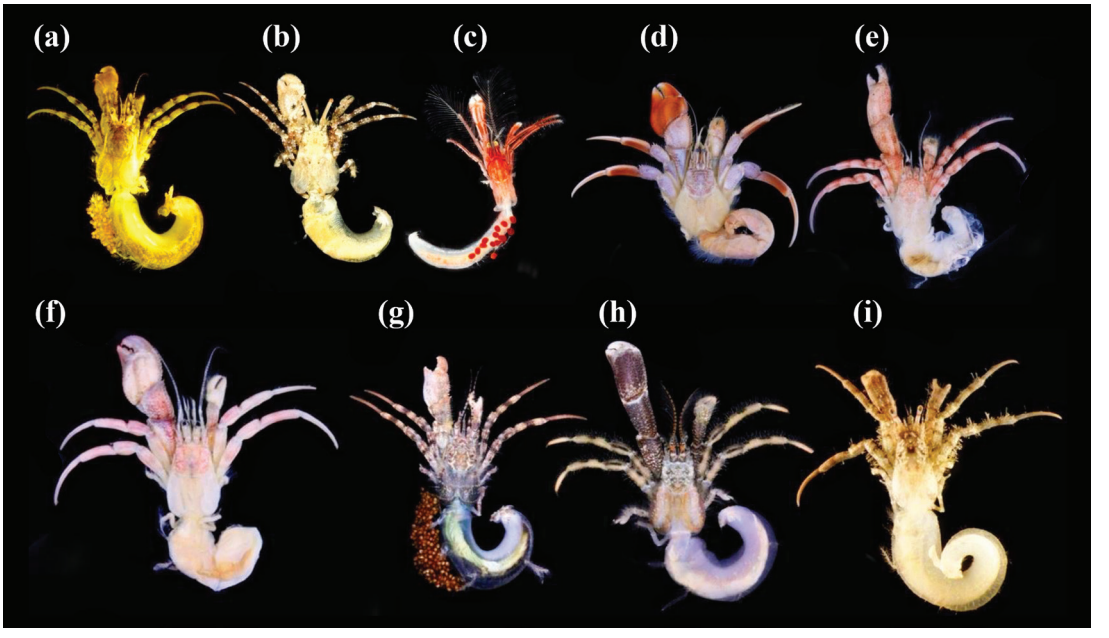


Figure 13. Representative specimens of *Diogenes* from Indonesian waters: (a) *Diogenes avarus*; (b) *Diogenes biramus*; (c) *Diogenes berduri*, Sunda Strait; (d) *Diogenes dubius*; (e) *Diogenes foresti*; (f) *Diogenes hawisi*; (g) *Diogenes kombalensis*; (h) *Diogenes luteus*; (i) *Diogenes matabiru*. Panels (a–c) and (g–i) are specimens from Lombok Island, Indonesia; panels (d–f) are specimens from Papua, Indonesia.

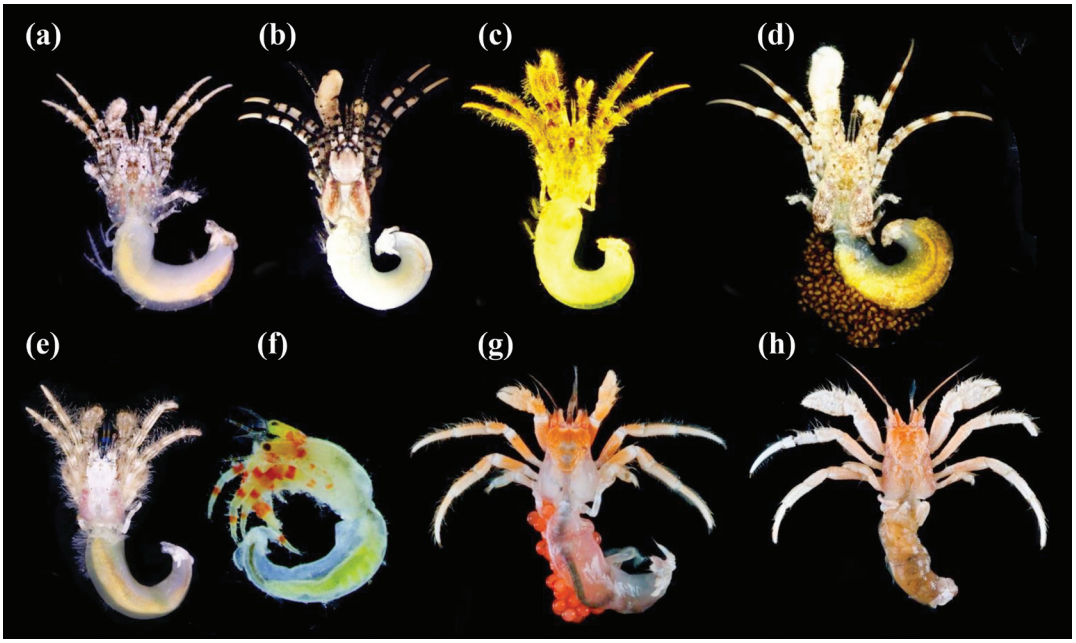


Figure 14. Representative specimens of Diogenidae from Indonesian waters: (a) *Diogenes pallescens*; (b) *Diogenes takedai*; (c) *Diogenes tumidus*; (d) *Diogenes spinicarpus*; (e) *Pseudopaguristes monoporus*; (f) *Pseudopaguristes bicolor*; (g) *Areopaguristes micheleae*; (h) *Paguristes rectus*. Panels (a–e) are specimens from Lombok Island, Indonesia; panels (f–h) are specimens from south of Jawa Island, Indonesia.

DISCUSSION

Overall, a total of 116 species belonging to 13 genera of the Diogenidae family have been recorded across the 12 defined ecoregions in Indonesian waters. They cover the littoral, sublittoral, and bathyal zones, with depths ranging from 0 to a maximum of 727 m, and occupy virtually all habitats, with a high percentage of species associated with hard and fine substrates.

Insights derived from the analyses have allowed the extraction of new information that can be of particular value for the assessment of the diogenid fauna across the whole area. The species *Paguropsis andersoni* showed the widest vertical distribution range, spanning from littoral to bathyal zones, with recorded depths ranging from 30 to 548 m. According to Lemaitre *et al*. (2018), the genus *Paguropsis* exhibits a broad bathymetric distribution, ranging from 30 to as deep as 1,125 m, indicating its adaptability to both continental shelf and upper bathyal environments. This genus is primarily found in subtropical to tropical waters across the Indo-West Pacific region, reflecting a wide ecological amplitude in both temperature and depth regimes. Such extensive vertical and geographical distribution suggests that *Paguropsis* may play a significant ecological role across various marine habitats, from reef-associated zones to deeper continental slope environments. Pretterebner *et al*. (2012) further substantiated this view by showing that hermit crabs in the Northern Adriatic Sea are capable of tolerating sublittoral depths and reduced oxygen availability, playing a significant role in structuring benthic communities and maintaining symbiotic interactions under environmentally stressful conditions. Its occurrence across a broad depth range also emphasizes the importance of including both shallow and deep-sea sampling in biodiversity assessments to capture the full extent of species distributions within the Diogenidae family. The congeneric species *Paguropsis typica* is frequently cited as an example of the extraordinary adaptive specialization and diversity within the Anomura (McLaughlin, 2015). This species is

recognized for its remarkable symbiotic relationship with a colonial sea anemone, which it can extend over its cephalic shield and part of its cephalothoracic appendages, resembling a blanket. This unique behaviour has led to its common name, the blanket crab (Lemaitre *et al*., 2018).

The greatest diversity of diogenid hermit crabs has been found in the marine ecoregion of the Banda Sea, with 12 genera and a total of 66 species recorded. Cluster analyses revealed that species recorded in the Java Sea, Sulawesi Sea, Banda Sea, and Lesser Sundas ecoregions made substantial contributions to the delineation of distinct marine ecoregional groupings in Indonesia. These regions not only demonstrated high species richness but also supported species that are biogeographically distinctive, thereby reinforcing their ecological uniqueness. The presence of region-specific taxa suggests that these areas may serve as biodiversity hotspots for the family Diogenidae and play a critical role in shaping regional faunal assemblages. As such, the clustering patterns observed underscore the significance of these marine zones in contributing to Indonesia's overall hermit crab diversity and highlight the importance of incorporating ecoregional perspectives in marine biodiversity assessments and conservation planning.

The genus *Diogenes* comprises 84 species and is reported from the Indo-Pacific and East Atlantic regions (Almon *et al*., 2022; Rahayu, 2022; 2024; Fitrian *et al*., 2024; WoRMS, 2025), with about 32.14% of these species recorded in Indonesian waters. This genus has a broad distribution in Indonesia, as evidenced by ecoregion clustering analyses, with species documented in 11 regions and predominantly found in the littoral, sublittoral, and bathyal zones, ranging from 0 to depths of up to 469 m.

The genus *Clibanarius* comprises 57 species and is commonly recorded throughout the Indo-Pacific region (Rahayu and Forest, 1992; Rahayu, 2003; McLaughlin *et al*., 2007; Marin, 2016; WoRMS, 2025), with about 45.61% of these species recorded in Indonesian waters. Based on the analyses conducted, the genus *Clibanarius* exhibits the most extensive distribution in Indonesia, with species documented in 12 different ecoregions, and predominantly found in shallow coastal habitats, especially within the littoral zone, ranging from 0 to depths of less than 20 m. This wide ecological range suggests a high level of adaptability to diverse environmental conditions, from coral reefs and rocky shores to mangrove forests and muddy substrates. According to McLaughlin *et al*. (2007), due to their efficient osmoregulatory mechanisms, they are better adapted than other paguroid genera to survive and reproduce in low-salinity environments, such as estuaries and river mouths. Their widespread presence across geographically and ecologically distinct regions underscores the genus's potential role as an indicator of environmental gradients in tropical marine systems.

Nearly half of Indonesian Diogenidae species occur in coral reef ecosystems. Almost all species of the genus *Calcinus* studied are closely associated with live coral habitats, particularly favoring the complex structures provided by branching corals. These hermit crabs are frequently observed inhabiting coral rubble as well, although their presence is most prominent within healthy, living coral colonies. This habitat preference suggests a strong ecological association between *Calcinus* species and coral reef environments, where they likely benefit from the structural complexity, protection from predators, and access to food resources that such habitats offer. The occurrence of *Calcinus* among branching corals also indicates their potential sensitivity to reef degradation, making them valuable indicators of coral reef health and stability in tropical marine ecosystems. This is likely due to their reliance on gastropod shells for protection. Since hermit crabs do not kill gastropod to obtain shells, they must compete for the best available ones. The diversity of habitats directly affects shell availability, as more complex systems such as coral reefs, which are recognized for their high biodiversity and soft coral dominance, sustain diverse gastropod communities that in turn support higher hermit crab diversity (Teoh *et al*., 2014; Cox *et al*., 2021; Reverter *et al*., 2021).

Dardanus deformis is a hermit crab species that exhibits notable ecological behaviour by frequently carrying sea anemones on its shell, forming a mutualistic relationship that provides both protection and camouflage. The presence

of anemones may deter potential predators and enhance the crab's survival, while the anemones benefit from increased mobility and access to food particles (Ross, 1971; McLean and Mariscal, 1973; Jonsson *et al*., 2001). The preference of *D. deformis* for structurally complex environments, such as seagrass meadows and rocky coastal zones, highlights its reliance on benthic habitats that offer both shelter and foraging opportunities. This species' distribution and behavior underscore its ecological significance within shallow marine ecosystems in the Indo-Pacific region. Even in less diverse habitats, hermit crabs can thrive if suitable shells are present.

Several Diogenidae species are associated with specific substrates and gastropod shells across different habitats, including intertidal pools, seagrass beds, and sandy or muddy bottoms (Rahayu and Forest, 1995; Asakura, 2020; Rahayu, 2005; 2006; 2012). For instance, *Diogenes goniochirus* is commonly found in association with Cerithidea shells (Forest, 1956), while *Diogenes klaasi* utilizes shells from various genera such as *Cantharus, Cerithium, Clypeomorus, Engina, Morula,* and *Pyrene* (Rahayu and Forest, 1995). Along the Sabah coast in Malaysia, *Diogenes klaasi* exhibits even greater specialization, exclusively occupying shells of *Clypeomorus batillariaeformis* (Family Cerithiidae) (Teoh *et al*., 2014). The distribution of Diogenidae species may be significantly influenced by the availability of suitable habitats and empty gastropod shells, which are essential for their survival and dispersal (Mantelatto *et al*., 2004). The occurrence of hermit crabs in a given area can thus be considered an ecological indicator of gastropod availability, as the presence of unoccupied shells often constitutes a key limiting resource for these crustaceans.

CONCLUSIONS

The Diogenidae family is widely distributed across Indonesian waters, from shallow coastal regions to deep-sea environments, inhabiting various substrate types. This variety in habitat adaptation highlights the ecological importance of this group within marine ecosystems. Analyzing distribution patterns based on Indonesia's marine ecoregions provides insights into species diversity, habitat associations, and biogeographic trends, while also supporting conservation prioritization and sustainable coastal management. Given the length of the Indonesian coastline and its habitat variability, further studies are needed to comprehensively document the region's rich diversity of hermit crab species.

ACKNOWLEDGEMENTS

We thank to the staff of the Museum Zoologicum Bogoriense (MZB), Bogor, Indonesia, for their support during examination of the Museum specimens. The photographs from Lombok were taken by DL Rahayu from Research Centre for Biosystematics and Evolution- National Research and Innovation Agency (BRIN), and from South Jawa Island were taken by Tim-Yam Chan from National Taiwan Ocean University and Rene Ong from National University of Singapore. We are especially grateful to Hadiyanto from Research Centre for Biota Systems- National Research and Innovation Agency (BRIN) for the valuable discussions and insights that greatly contributed to this work. Moreover, we sincerely appreciate the reviewers' insightful comments and suggestions, which have contributed significantly to improving this manuscript.

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