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Research Article

Mollusc Diversity from the Prehistory Context of Kompleks Ceruk Pajangan Archaeological Site (Java, Indonesia)

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ABSTRACT
Mollusc shells from prehistoric sites in a karst region offer insights into past biodiversity, human survival strategies, and the environments where they lived. This article covers mollusc study results from Kompleks Ceruk Pajangan that have not been studied before. In this study, we determine which species were exploited by the human inhabitants, and assess their palaeoenvironmental conditions. The study identified 3378 mollusc specimens across 16 families and 25 species, including 8 species from 5 families of bivalves, and 17 species from 11 families of gastropods. Kompleks Ceruk Pajangan exhibited low mollusc diversity and evenness, indicating human preference on how these molluscs were collected and discarded in the past. Rather than randomly, they were collected as food sources and these low indices reflect the site inhabitants' preferences towards freshwater molluscs. Additionally, a significant presence of molluscs from marine/estuarine habitats suggests that this site, 6000-8000 years ago, was much closer to the coastal area than at present.

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INTRODUCTION

Mollusc shells are particularly significant data in the archaeology of Southeast Asia, where coastal and riverine environments have been central to human settlement and subsistence. Shell middens (an archaeological term for extensive deposits of discarded mollusc shells in cave sites) are abundant in the region and provide valuable evidence of dietary practices and resource exploitation by prehistoric communities (Szabó & Amesbury 2011). Furthermore, mollusc shells have been used in archaeological contexts to create tools, ornaments, and trade items, highlighting technological innovations and social interactions within and beyond the region (Campbell 2017; Ridout-Sharpe 2017; Bailey & Hardy 2021). Radiocarbon dating of mollusc shells has been crucial for archaeologists in establishing chronological frameworks for understanding the timing and development of human activities, including the transition from foraging to agriculture (Bellwood 2017).

Recent efforts have focused on analysing mollusc ecofacts from archaeological sites in the Rembang Zone, a karst area on the north coast of Java and Madura which stretches from Pati/Grobogan (Java) in the westernmost part to the Kangean Islands (Madura) in the easternmost part (van Bemmelen 1949; Wibowo & Alifah 2022; Wibowo et al. 2022a). In the Rembang Zone of Java, numerous mollusc shells were recovered from archaeological excavations at Gua (Cave) Kidang, Gua Bedug, and Kompleks Ceruk Pajangan (Pajangan Rockshelter Complex) (Figure 1). Of these three excavated sites, the mollusc shells from Kompleks Ceruk Pajangan are the only ones that have not been studied previously.

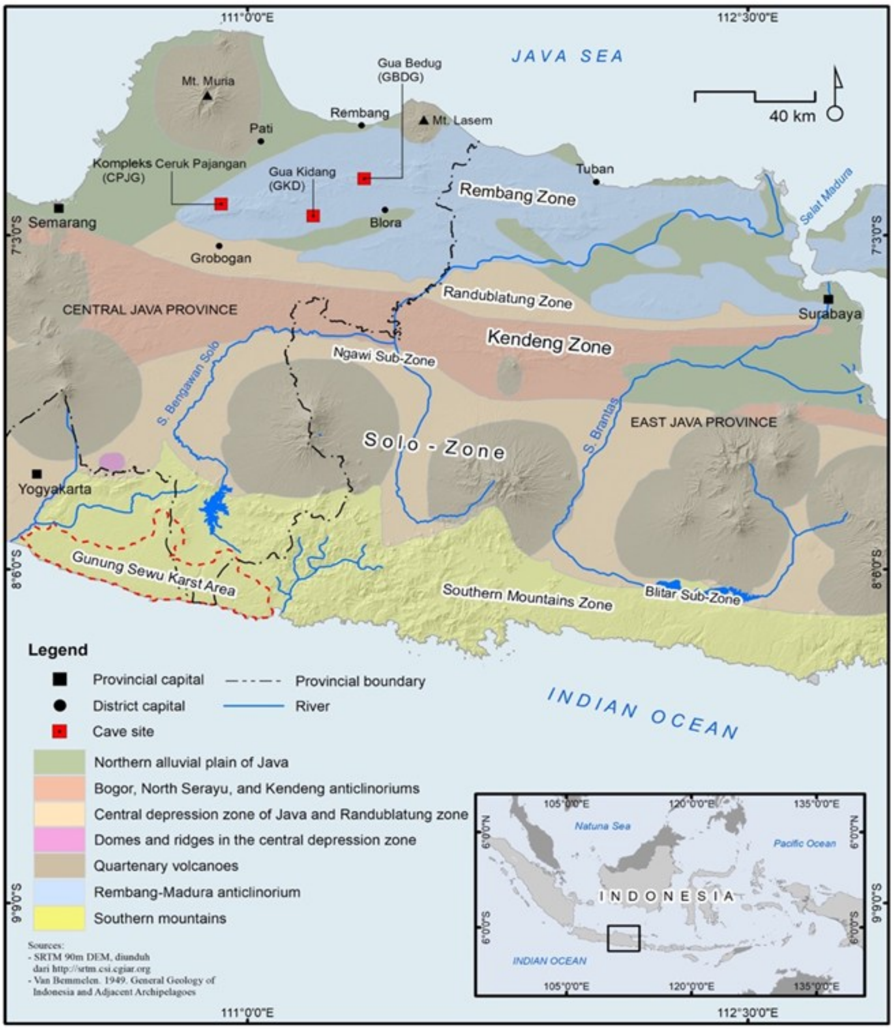

Figure 1. The location of Kompleks Ceruk Pajangan among other sites within the same karst area (Credits: Ahmad Surya Ramadhan and Hari Wibowo 2024).

This article provides a taxonomic identification of the mollusc shells from Kompleks Ceruk Pajangan along with their palaeoenvironmental contexts. This prehistoric occupation site was discovered in 2021 during a survey in Pati, Central Java, Indonesia (Wibowo et al. 2021, 2022a). An archaeological excavation at this site in 2022 yielded a total of 4787 mollusc ecofacts and artefacts (Tanudirjo et al. 2022). AMS Radiocarbon dating from this site was carried out using Unionidae freshwater molluscs, indicating human occupation from at least 6743-6302 cal BP to 8286 - 7869 cal BP (Wibowo & Fajari 2023).

The study of mollusc shells from Kompleks Ceruk Pajangan will complement studies of two other sites in the same karst area that have been previously analysed, Gua Kidang (Blora Regency) and Gua Bedug (Rembang Regency). These two sites were inhabited during a period relatively similar to that of Kompleks Ceruk Pajangan. The upper human occupation layer of Gua Kidang was dated to 5719-5578 BP cal BP (Wibowo et al. 2022b), while the lower layer date of 9440 ± 220 BP (11.275-10.188 cal BP) is considered as less reliable because using conventional dating methods (Nurani & Hascaryo 2012; Nurani et al. 2019). AMS radiocarbon dating for Gua Bedug are indicating that this site was inhabited from 6012 - 5895 cal BP to 8777 - 8542 cal. BP (Wibowo et al. 2022b, 2024, 2025). Current results of mollusc shell studies from these two sites show not only similarities but also differences, even though they are in the same karst area and are only 14-20 km apart.

A total of 1751 mollusc shells from Gua Kidang were analysed, most of which were identified only to the family level, consisting of 8 families (Kirana 2013). For Gua Bedug, the identification of 5845 mollusc ecofacts successfully classified them into 13 families, comprising 19 species (Sulistiyo & Wibowo 2023). Combined with previous studies from Gua Kidang and Gua Bedug, this article, which covers mollusc shells from Kompleks Ceruk Pajangan, aims to provide a clearer picture of the prehistory of the north coast of Java, 6000-8000 years ago. In particular, the mollusc diversity at these sites can offer insights into past environments and the subsistence strategies of the humans who inhabited them.

MATERIALS AND METHODS

Materials

The mollusc shell specimens studied in this research were collected during the 2022 archaeological excavation of Kompleks Ceruk Pajangan. All specimens were physically transported to the laboratory for analysis. The collection procedure adhered to standard archaeological excavation methods, using basic tools such as trowels and bamboo spatulas. Archaeological excavation is an irreversible process, as the same area of the ground cannot be excavated twice (Barker 1993). Due to this irreversible nature, detailed field recordings were taken to document the findings within each excavation unit.

Basic field recording methods were employed during the collection process. Mollusc shells recovered from excavation units were documented through field notes, drawings, and photographs. Within each excavation unit, shells were sorted and categorised by class (bivalves or gastropods), depth interval, and soil stratigraphy layer. Each category was stored and labelled separately in zip plastic bags, which were then placed in plastic containers for transportation to the laboratory. While packaging precautions were taken to ensure the physical integrity of the specimens, no additional measures were implemented to control storage temperature or humidity during transportation.

Ten excavation units were excavated across three sectors: Sector Pajangan (U14 T18, U18 T15, U18 T20, U18 T21, U16 T20), Sector Pajangan A (TP 1), and Sector Pajangan B (U6 T2, U6 T3, U5 T2, U5 T3) (see Figure 2). A total of 4787 mollusc shell specimens, both intact and fragmentary, were collected from depths ranging from 0 cm to 270 cm relative to the secondary datum point (SDP = 198 m asl).

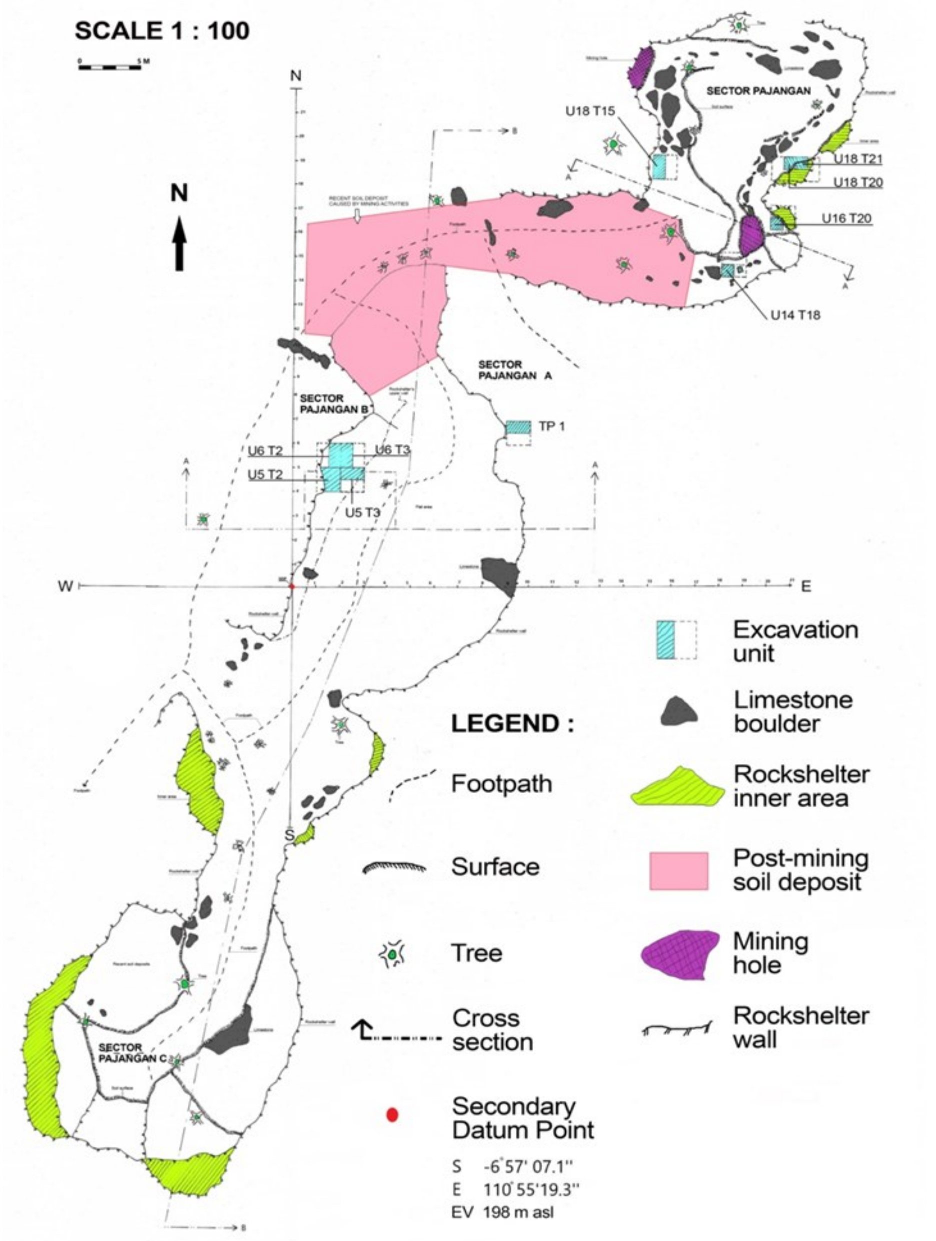

Figure 2. Site plan of Kompleks Ceruk Pajangan, excavation units are marked with light blue and Secondary Datum Point marked with red (Credits: Fadly Ginanjar and Hari Wibowo 2023).

To focus on the mollusc shells from the prehistoric context, not all collected specimens are presented in this study. Specimens from excavation units TP 1, U5 T3, and U6 T3 were excluded due to indications of stratigraphic disturbance caused by modern or contemporary activities. From the remaining seven units, specimens were further filtered by soil stratigraphy layers. Specimens collected from the surface or disturbed layers were also excluded. Consequently, of the original 4787 mollusc shells, only 3378 are included in this article.

Methods

The management and analysis of mollusc specimens followed the methods outlined by Sulistiyo and Wibowo (2023). The results of these analyses were then compared with literature on gastropods and bivalves from Indonesia, particularly Java, including works by Dharma (1992), Marwoto et al. (2020), and van Benthem Jutting (1950, 1952, 1953, 1956). Specimen identifications were validated using mollusc databases such as the World Register of Marine Species (WoRMS Editorial Board 2024) and MolluscaBase (MolluscaBase eds. 2024) to ensure compliance with current nomenclature.

Morphometric measurement of the mollusc shells followed guidelines from Carpenter and Niem (1998) and Raup and Stanley (1971). Specimens were quantified using common zooarchaeological methods, including NISP (Number of Identified Specimens) and MNI (Minimum Number of Individuals), as described by Lyman (2018) and Harris et al. (2015). Taxonomic richness, diversity, and evenness were then assessed using the number of taxa (NTAXA), Simpson's diversity index (1-D), Shannon-Wiener diversity index (H'), and Shannon's evenness index (E) (Shannon & Weaver 1964). Diversity in this study adopts the category based on Irsyad et al. (2015): $H' < 1.5$ indicates low diversity, $1.5 \leq H' \leq 3$ indicates moderate diversity, and $H' > 3$ indicates high diversity.

Mollusc shell ecofacts were identified to the species level when possible to determine their habitats and reconstruct past environmental conditions. Four main habitat categories were defined in this study: freshwater, marine/estuary, forest litter, and arboreal. The freshwater habitat includes rivers, ponds, and lakes, while the marine/estuary habitat encompasses seas, coastal areas, and mangroves. Forest litter habitats refer to terrestrial environments where molluscs live on the forest floor, often among leaf litter, deadwood, or decomposing organic material. Arboreal habitats are for molluscs primarily living in trees or forested areas.

Mollusc shell presence at the site was classified as either anthropic or native. The anthropic category includes molluscs brought to the site through human activities in prehistoric times. Indicators for this category include habitat context and taphonomic observations. Molluscs transported from their natural habitats and accumulated at the site-either by humans or animals-were considered anthropic if taphonomic evidence, such as cut marks or purposeful breakage, suggested human involvement (Allen 2017). For instance, gastropod shells may display purposeful breakage near the apex or lip to extract the soft body (Hunt & Hill 2017), while bivalves may show prying marks along the hinge (Pickard et al. 2017). Gastropod opercula found detached from the aperture may also indicate efforts to extract the soft body for consumption (Allen 2017). The native category includes molluscs naturally inhabiting the site vicinity, with no evidence of human interference. These molluscs exhibit no taphonomic traces suggesting human activity.

RESULTS AND DISCUSSION

Initial investigations of land molluscs in the Sukolilo karst revealed that 17 % of the total known land snail species in Java are present in the area (Nurinsiyah 2014). From the Kompleks Ceruk Pajangan archaeological site, 3378 mollusc specimens with prehistoric contexts were analysed. These mollusc shells were identified as belonging to 16 families and 25 species. The bivalve class comprises 5 families and 8 species, while the gastropod class comprises 11 families and 17 species (see Table 1, Figures 3 and 4).

Mollusc Diversity at Kompleks Ceruk Pajangan

Of the 3378 mollusc shell specimens, 97.63 % (n = 3298) were successfully identified (NISP). Among these, the Minimum Number of Individuals (MNI) was determined to be 47.20 % (n = 1557). Observations show that the bivalve class is more often recovered in fragmented conditions due to the fragile nature of their shells. Bivalve mollusc shells are prone to breaking, either intentionally or naturally, after being discarded and buried in the soil (Glover & Kidwell 1993). Similarly, large terrestrial gastropod shells are also fragile and prone to breakage (Sulistiyo & Fakhri 2023). Shells that tend to remain intact

Table 1. Identification results of Kompleks Ceruk Pajangan mollusc specimens.

	Family/ Species	Habitat	Presence
BIVALVE	**Cyrenidae**		
	Geloina expansa (Mousson, 1849)	MR/ ES	A
	Batissa violacea (Lamarck, 1818)	MR/ ES	A
	Arcidae		
	Tegillarca granosa (Linnaeus, 1758)	MR/ ES	A
	Pectinidae		
	Chlamys sp. (Röding, 1798)	MR/ ES	A
	Placunidae		
	Placuna sp. (Lightfoot, 1758)	MR/ ES	A
	Unionidae		
	Pilsbryoconcha exilis (I. Lea, 1838)	FW	A
	Rectidens sumatrensis (Dunker, 1852)	FW	A
	Lens contradens (I. Lea, 1838)	FW	A
GASTROPOD	**Potamididae**		
	Telescopium telescopium (Linnaeus, 1758)	MR/ ES	A
	Terebralia palustris (Linnaeus, 1758)	MR/ES	A
	Viviparidae		
	Filopaludina javanica (von dem Busch, 1844)	FW	A
	Ampullariidae		
	Pila ampullacea (Linnaeus, 1758)	FW	A
	Pachychilidae		
	Sulcospira testudinaria (von dem Busch, 1842)	FW	A
	Thiaridae		
	Melanoides tuberculata (O. F. Müller, 1774)	FW	A
	Camaenidae		
	Amphidromus sp. (Albers, 1850)	AR	N
	Tricheulota zodiacus (A. Férussac, 1821)	AR	N
	Landouria sp. (Godwin-Austen, 1918)	AR	N
	Ariophantidae		
	Hemiplecta sp. (Albers, 1850)	AR	N
	Achatinidae		
	Paropeas achatinaceum (L. Pfeiffer, 1846)	FL	N
	Cyclophoridae		
	Opisthoporus corniculus (Mousson, 1849)	FL	N
	Cyclophorus perdix (Broderip & G. B. Sowerby I, 1830)	FL	N
	Cyclophorus sp. (Montfort, 1810)	FL	N
	Dyakiidae		
	Elaphroconcha javacensis (Férussac, 1821)	FL	N
	Elaphroconcha sp. (Gude, 1911)	FL	N
	Trochomorphidae		
	Trochomorpha sp. (Albers, 1850)	FL	N

Note:
Habitat : (MR/ ES) Marine/ Estuary, (FW) Freshwater, (FL) Forest Litter, (AR) Arboreal
Presence : (A) Anthropic, (N) Native

exhibit a high NISP-to-MNI ratio, such as small terrestrial and aquatic gastropods (Table 2).

Based on species MNI, diversity and evenness were measured using the Shannon-Wiener diversity and evenness indices (Table 3). Overall, the site falls into the category of low diversity, with a diversity index of less than 1.5. Additionally, the bivalve class is observed to be more diverse than the gastropod class. Examining diversity by sectors, Sector Pajangan is more diverse than Sector Pajangan B. However, for the gastropod class, Sector Pajangan B is slightly more diverse than Sector Pajangan. The most diverse mollusc shells at this site were recovered from Sector Pajangan, specifically from unit U16 T20 for the bivalve class and unit U18 T15 for the gastropod class. All

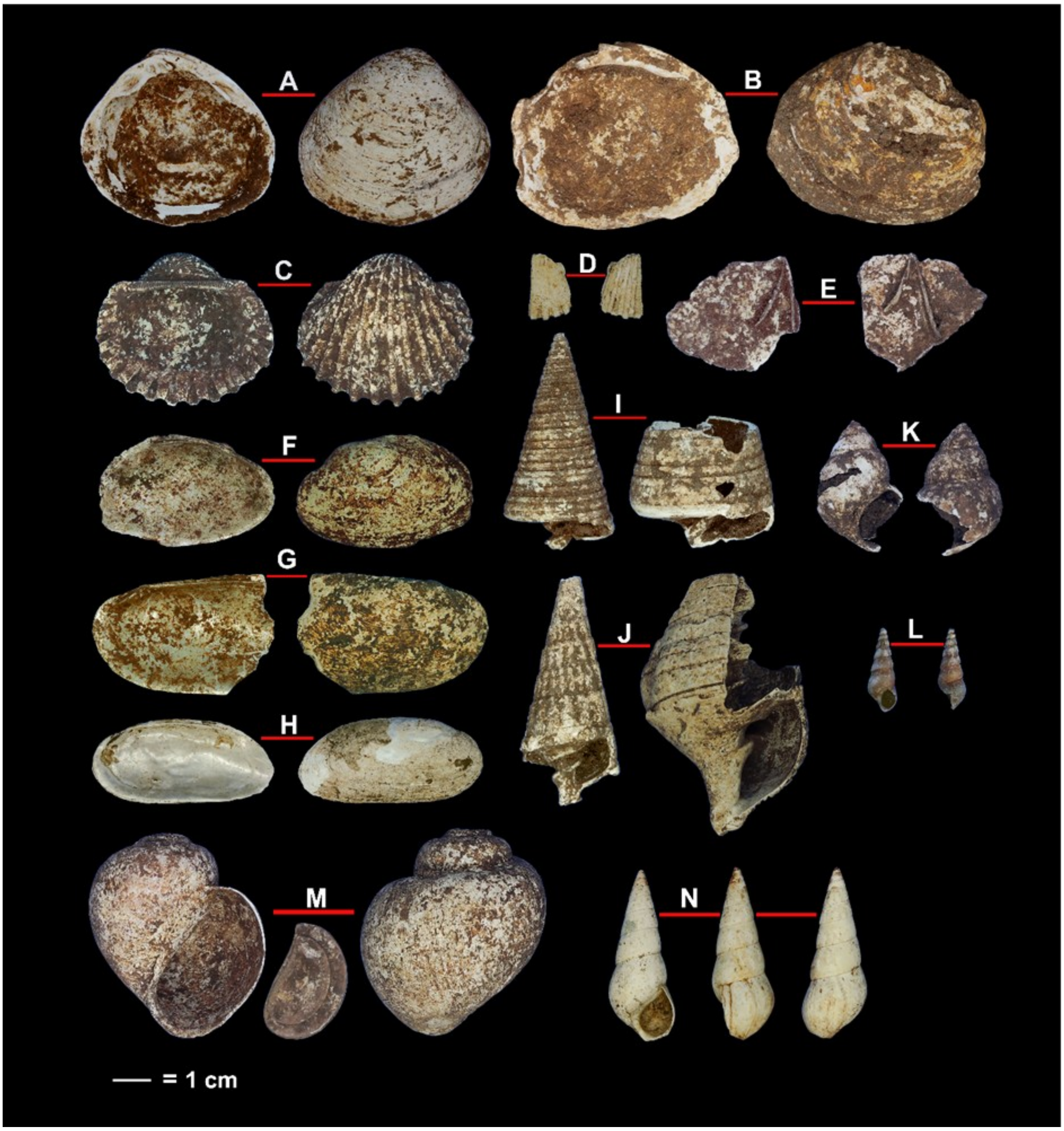

Figure 3. Aquatic bivalves and gastropods: A. *Geloina expansa*; B. *Batissa violacea*; C. *Tegillarca granosa*; D. *Chlamys* sp.; E. *Placuna* sp.; F. *Lens contradens*; G. *Pilsbryoconcha exilis*; H. *Rectidens sumatrensis*; I. *Telescopium telescopium*; J. *Terebralia palustris*; K. *Filopaludina javanica*; L. *Melanoides tuberculata*; M. *Pila ampullacea*; N *Sulcospira testudinaria* (Photo: Restu Budi Sulistiyo 2023).

excavation units in both sectors fall into the low diversity category for both mollusc classes, except for the gastropod diversity index of unit U18 T15, which marginally exceeds the minimum value for the moderate diversity category.

Regarding the evenness index, the bivalve class is overall more evenly distributed than the gastropod class. When divided by sectors, the evenness indices of gastropod and bivalve classes are relatively similar in Sector Pajangan B. In contrast, in Sector Pajangan, the difference between the two classes is more pronounced. The more balanced evenness results in Sector Pajangan B are influenced by the lower number of gastropods recovered in that sector, whereas in Sector Pajangan, the bivalve class was recovered in much smaller numbers compared to gastropods. This is further supported by the results of the Simpson diversity index (1-D). A value closer to 1 indicates higher diversity and a more even distribution of species. The values for both mollusc classes are similar in Sector Pajangan B, whereas a larger gap is observed in Sec-

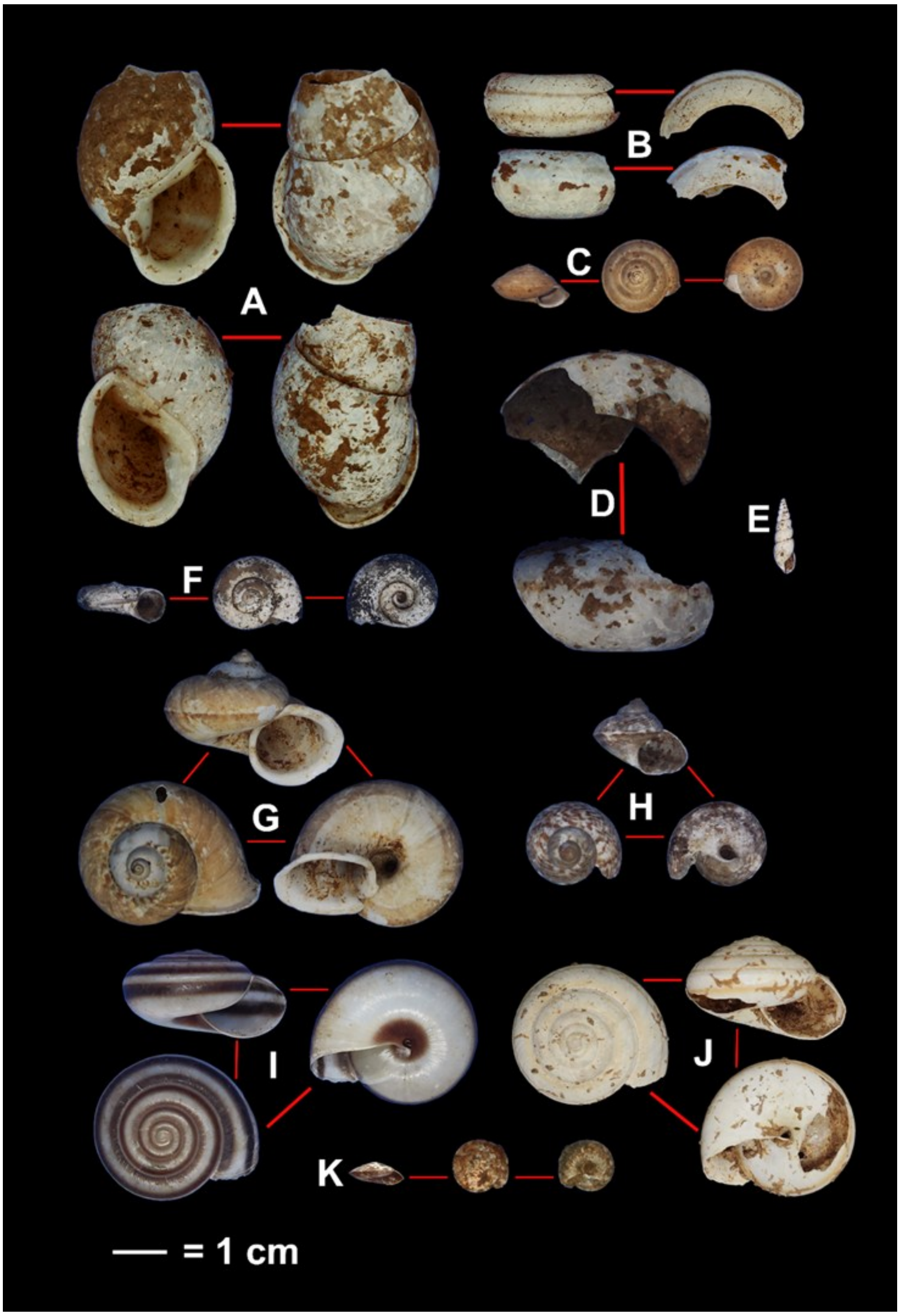

Figure 4.Terrestrial gastropods: A. *Amphidromus* sp.; B. *Tricheulota zodiacus*; C. *Landouria* sp.; D. *Hemiplecta* sp.; E. *Paropeas achatinaceum*; F. *Opisthoporus corniculus*; G. *Cyclophorus perdix*; H. *Cyclophorus* sp.; I. *Elaphroconcha javacensis*; J. *Elaphroconcha* sp.; K. *Trochomorpha* sp. (Photo: Restu Budi Sulistiyo 2023).

tor Pajangan.

The low diversity and evenness indices may reflect the fact that these mollusc shells were products of human activity in prehistoric times. Rather than being randomly collected, they were likely gathered by the site's past inhabitants for specific purposes. These indices may also indicate a preference for certain types of molluscs by the site's inhabitants, leading to both low diversity and low evenness, particularly in the gastropod class.

The presence of molluscs at Kompleks Ceruk Pajangan and subsistence efforts

Of the 25 identified species, 14–or more than half– are associated with anthropic activities, meaning they were brought by humans to the vicinity of the rockshelter site (see Table 1 and 4). Previous studies have revealed that

Table 2. Number of Identified Specimens and Minimum Number of Individuals quantification result.

Family/ Species	NISP	%	MNI	%	Ratio
Cyrenidae	22	0.7	1	0.1	
Geloina expansa (Mousson, 1849)	422	12.5	123	7.9	29.1
Batissa violacea (Lamarck, 1818)	80	2.4	23	1.5	28.8
Arcidae	1	0.0	1	0.1	
Tegillarca granosa (Linnaeus, 1758)	1	0.0	1	0.1	100.0
Pectinidae					
Chlamys sp. (Röding, 1798)	1	0.0	1	0.1	100.0
Placunidae					
Placuna sp. (Lightfoot, 1758)	84	2.5	24	1.5	28.6
Unionidae	158	4.7	16	1.0	10.1
Pilsbryoconcha exilis (I. Lea, 1838)	202	6.0	103	6.6	51.0
Rectidens sumatrensis (Dunker, 1852)	8	0.2	8	0.5	100.0
Lens contradens (I. Lea, 1838)	10	0.3	10	0,6	100,0
Potamididae					
Telescopium telescopium (Linnaeus, 1758)	56	1.7	30	1.9	53.6
Terebralia palustris (Linnaeus, 1758)	50	1.5	33	2.1	66.0
Viviparidae					
Filopaludina javanica (von dem Busch, 1844)	5	0.1	4	0.3	80.0
Ampulariidae		0,0		0,0	
Pila ampullacea (Linnaeus, 1758)	1716	50.8	786	50.5	45.8
Pachychilidae					
Sulcospira testudinaria (von dem Busch, 1842)	292	8.6	292	18.8	100.0
Thiaridae					
Melanoides tuberculata (O. F. Müller, 1774)	1	0.0	1	0.1	100.0
Camaenidae	23	0.7	15	1.0	65.2
Amphidromus sp. (Albers, 1850)	17	0.5	12	0.8	70.6
Tricheulota zodiacus (A. Férussac, 1821)	55	1.6	20	1.3	36.4
Landouria sp. (Godwin-Austen, 1918)	1	0.0	1	0.1	100.0
Ariophantidae					
Hemiplecta sp. (Albers, 1850)	48	1.4	22	1.4	45.8
Achatinidae					
Paropeas achatinaceum (L. Pfeiffer, 1846)	5	0.1	5	0.3	100.0
Cyclophoridae	1	0.0	1	0.1	
Opisthoporus corniculus (Mousson, 1849)	2	0.1	2	0.1	100.0
Cyclophorus perdix (Broderip & G. B. Sowerby I, 1830)	19	0.6	9	0.6	47.4
Cyclophorus sp. *(Montfort, 1810)*	9	0.3	4	0.3	44.4
Dyakiidae					
Elaphroconcha javacensis (Férussac, 1821)	1	0.0	1	0.1	100.0
Elaphroconcha sp. (Gude, 1911)	1	0.0	1	0.1	100.0
Trochomorphidae					
Trochomorpha sp. (Albers, 1850)	7	0.2	7	0.4	100.0
Unidentified bivalve fragments	30	0.9			
Unidentified gastropod fragments	50	1.5			
NISP - MNI	3298	97.6	1557	47.2	
Total Number of Fragments	3378	100.0			

mollusc consumption was common among prehistoric populations (Stephens et al. 2008; García-Escárzaga & Gutiérrez-Zugasti 2021; Sulistiyo & Fakhri 2023; Sulistiyo & Wibowo 2023). This indicates that the inhabitants of this site collected molluscs from their original habitats, transported them to the site, consumed them, and discarded the shells, which were subsequently deposited in the soil.

Almost all freshwater aquatic molluscs in the anthropic category represent subsistence efforts by the prehistoric inhabitants, as they were transported to the site specifically for consumption. Several freshwater mollusc specimens also exhibit breakage patterns indicative of efforts to extract the soft

Table 3. Molluscs diversity and evenness measurements.

Unit	Bivalve				Gastropod			
	N-TAXA	1-D	H'	E	N-TAXA	1-D	H'	E
U18 T15	4	0.39	0.754	0.544	10	0.69	1.53	0.664
U18 T20	1	0	0	0	3	0.04	0.118	0.107
U18 T21	2	1	0.693	1	5	0.28	0.604	0.375
U16 T20	6	0.63	1.31	0.733	12	0.5	0.898	0.362
U14 T18	4	0.61	1.13	0.814	9	0.68	1.39	0.632
Sector Pajangan	**7**	**0.7**	**1.4**	**0.722**	**16**	**0.53**	**1.14**	**0.412**
U5 T2	5	0.67	1.23	0.763	4	0.59	1	0.721
U6 T2	3	0.37	0.661	0.601	3	0.41	0.687	0.625
Sector Pajangan B	**5**	**0.55**	**1.03**	**0.641**	**6**	**0.58**	**1.1**	**0.613**
Site Overall	**8**	**0.69**	**1.39**	**0.668**	**17**	**0.53**	**1.16**	**0.409**

Note: (N-TAXA) Number of Taxa, (1-D) Simpson's index, (H') Shannon-Wiener's index, (E) Shannon's evenness

Table 4. Species distribution in each excavation unit.

Species	U18 T15	U18 T20	U18 T21	U16 T20	U14 T18	U6 T2	U5 T2
*Geloina expansa**	++	-	++	++	++	++	++
*Batissa violacea**	-	-	++	++	++	-	++
*Tegillarca granosa**	-	-	-	-	-	-	+
Chlamys sp.*	+	-	-	-	-	-	-
Placuna sp.*	-	-	-	++	++	++	++
*Lens contradens**	-	-	-	++	-	-	-
*Pilsbryoconcha exilis**	++	++	++	++	++	++	++
*Rectidens sumatrensis**	++	-	-	++	-	-	-
*Telescopium telescopium**	++	-	++	++	++	++	-
*Terebralia palustris**	-	-	++	++	++	-	-
*Turritella terebra**	-	-	-	-	-	-	-
*Filopaludina javanica**	-	-	-	+	+	-	-
*Pila ampullacea**	++	++	++	++	++	++	++
*Sulcospira testudinaria**	++	++	-	++	++	-	++
Hemiplecta sp.	+	+	-	+	-	-	-
*Melanoides tuberculata**	-	-	-	+	-	-	-
Amphidromus sp.	-	-	-	+	+	-	+
Tricheulota zodiacus	+	-	-	+	+	-	-
Landouria sp.	+	-	-	-	-	-	-
Lissachatina fulica	-	-	-	-	-	-	-
Paropeas achatinaceum	-	-	-	-	-	-	+
Opisthoporus corniculus	+	-	-	+	-	-	-
Cyclophorus perdix	+	-	+	+	-	-	+
Cyclophorus sp.	-	-	+	-	+	+	-
Lagocheilus obliquistriatus	-	-	-	-	-	-	-
Elaphroconcha javacensis	+	-	-	-	-	-	-
Elaphroconcha sp.	+	-	-	+	+	-	-
Trochomorpha sp.	+	-	-	+	-	-	+
Apoecus sp.	-	-	-	-	-	-	-

Note: (+) Present, (-) Absence, (*) Anthropic, (++) Abundant (as food).

body parts, likely for food (Hunt & Hill 2017). Furthermore, the mollusc shells at this site are relatively intact. If the accumulation and consumption of molluscs had been carried out by animals such as rodents or otters, the shells would typically be more heavily damaged or fragmented (Hunt & Hill 2017; Sulistiyo & Fakhri 2023).

The primary dietary molluscs include freshwater species from families such as Ampullariidae, Pachychilidae, and Unionidae. The gastropod *Pila ampullacea* is likely the main food source for the prehistoric inhabitants of Kompleks Ceruk Pajangan, as its shells and opercula were recovered in abundance across all excavation units. Similarly, the gastropod species *Sulcospira testudinaria* was also found in large quantities and appears in nearly all units, except U18T21 and U6T2. From the bivalve class, the Unionidae family includes species such as *Pilsbryoconcha exilis*, *Rectidens sumatrensis*, and *Lens contradens*, with *P. exilis* being commonly found across all excavation units. Previous studies suggest that Unionidae bivalves were commonly consumed as food by prehistoric people (Corr 2000; Thomas 2002; Stephens et al. 2008; Faulkner 2011; Pickard et al. 2017; Sulistiyo & Wibowo 2023).

Within the same karst area, mollusc records are similar at the family level across different sites, but dietary preferences vary. At Gua Bedug and Gua Kidang, located within the same karst region, Unionidae bivalves and *Sulcospira testudinaria* gastropods were also identified as food sources (Kirana 2013; Sulistiyo & Wibowo 2023). However, dietary emphasis differs between sites. At Gua Kidang, Unionidae bivalves were the primary food source, followed by Camaenidae gastropods (Kirana 2013). At Gua Bedug, *Sulcospira testudinaria*, a species of Pachychilidae family was the most exploited food source, followed by Unionidae (Sulistiyo & Wibowo 2023). These differences may reflect local variations in mollusc availability between sites. However, as part of the broader karst region, the inhabitants of Kompleks Ceruk Pajangan, Gua Bedug, and Gua Kidang shared a similar subsistence practice of prioritising the exploitation of freshwater molluscs over other types.

The morphometric measurement of *Pila ampullacea* opercula provides valuable insights into the dietary habits of the Kompleks Ceruk Pajangan inhabitants. The operculum of *Pila ampullacea* is calcareous, making it harder and more likely to be preserved compared to the softer, corneous operculum of Sulcospira testudinaria, which decomposes easily. Corneous opercula are primarily composed of organic materials like keratin or similar proteinaceous substances. These materials are biodegradable and susceptible to enzymatic breakdown by microorganisms, fungi, and other decomposers in the environment. In contrast, calcareous opercula consist largely of calcium carbonate ($CaCO_3$), an inorganic mineral. This mineral structure is highly resistant to biological decay and can persist in the environment for extended periods under favourable conditions (Glover & Kidwell 1993; Kidwell & LaBarbera 1993).

Due to its composition and hardness, *Pila ampullacea* operculum is not edible, whereas the softer operculum of *Sulcospira testudinaria* may still be consumable. No *Sulcospira testudinaria* opercula were recovered from any excavation units at this site. However, this absence does not necessarily confirm their consumption, as they may have decomposed naturally. In contrast, *Pila ampullacea* opercula were found in abundance, suggesting that the prehistoric inhabitants consumed only the soft body parts of this species and discarded the opercula.

Interestingly, *Pila ampullacea* opercula were recovered from all seven excavation units, while their shells were found in only five. A particularly noteworthy observation, as reflected in Figure 5, is the abundance of *Pila ampullacea* opercula in units U18 T20 and U18 T21, where their shells were absent. This may indicate a food preparation process: the soft bodies of *Pila ampullacea* were likely extracted in a different area of the site and subsequently brought to units U18 T20 and U18 T21 for consumption, leaving only the opercula deposited in these units.

Both the shells and opercula of *Pila ampullacea* were most frequently found in unit U16 T20 in terms of both quantity and preservation. In this unit, the highest quantities and best-preserved *Sulcospira testudinaria* remains were also discovered. The vertical distribution of these two species suggests that *Pila ampullacea* was consumed alongside *Sulcospira testudinaria* (Figure 6).

Originating from the same freshwater habitat, *Sulcospira testudinaria* likely served as a complementary food source to *Pila ampullacea*.

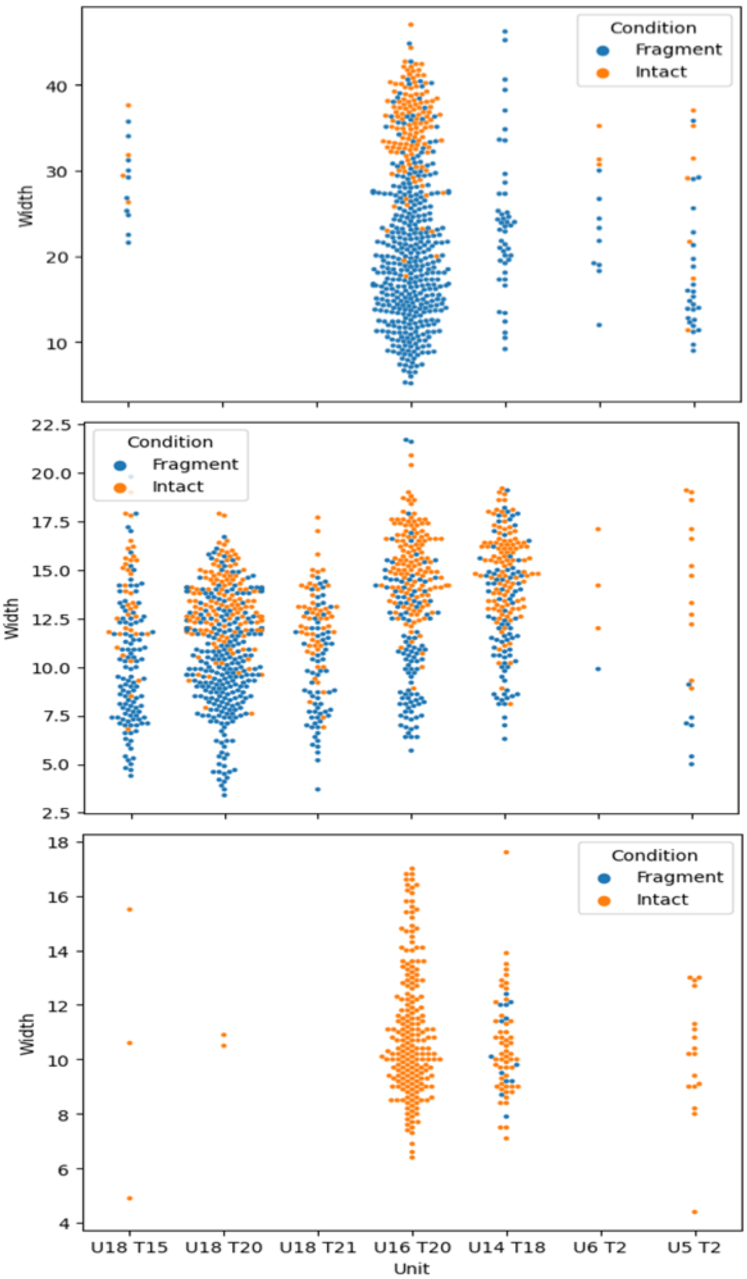

Figure 5. Swarmplot showing distribution of *Pila ampullacea* shells (above, n=611) and opercula (middle, n=1105), and *S. testudinaria* shells (below, n=292) across all units.

Besides freshwater molluscs, the inhabitants of Kompleks Ceruk Pajangan also consumed molluscs from marine and estuarine habitats. Common families in this habitat category include Cyrenidae, Placunidae, and Potamididae. Bivalves from the Cyrenidae family include the species *Geloina expansa* and *Batissa violacea*. *Geloina expansa* shells are prevalent in nearly all excavation units except U18T20, whereas *Batissa violacea* is less common. *Geloina expansa* was also found at Gua Bedug in fewer quantities (Sulistiyo & Wibowo 2023), and absent as a ecofacts at Gua Kidang (Kirana 2013). Another bivalve, *Placuna sp*., was identified, though its thin shells were highly fragmented. Gastropods from the Potamididae family, including *Telescopium telescopium* and *Terebralia palustris*, were recovered in edible size. *Telescopium telescopium* shells are abundant, while *Terebralia palustris* appears to be limited to only a few excavation units. All the molluscs mentioned above remain commonly consumed today (Carpenter & Niem 1998). A unique pattern was observed in the Pajangan Sector, particularly in unit U14 T18, where marine and estuarine molluscs appeared to have been consumed more frequently than freshwater bivalves during a specific period (Figure 6).

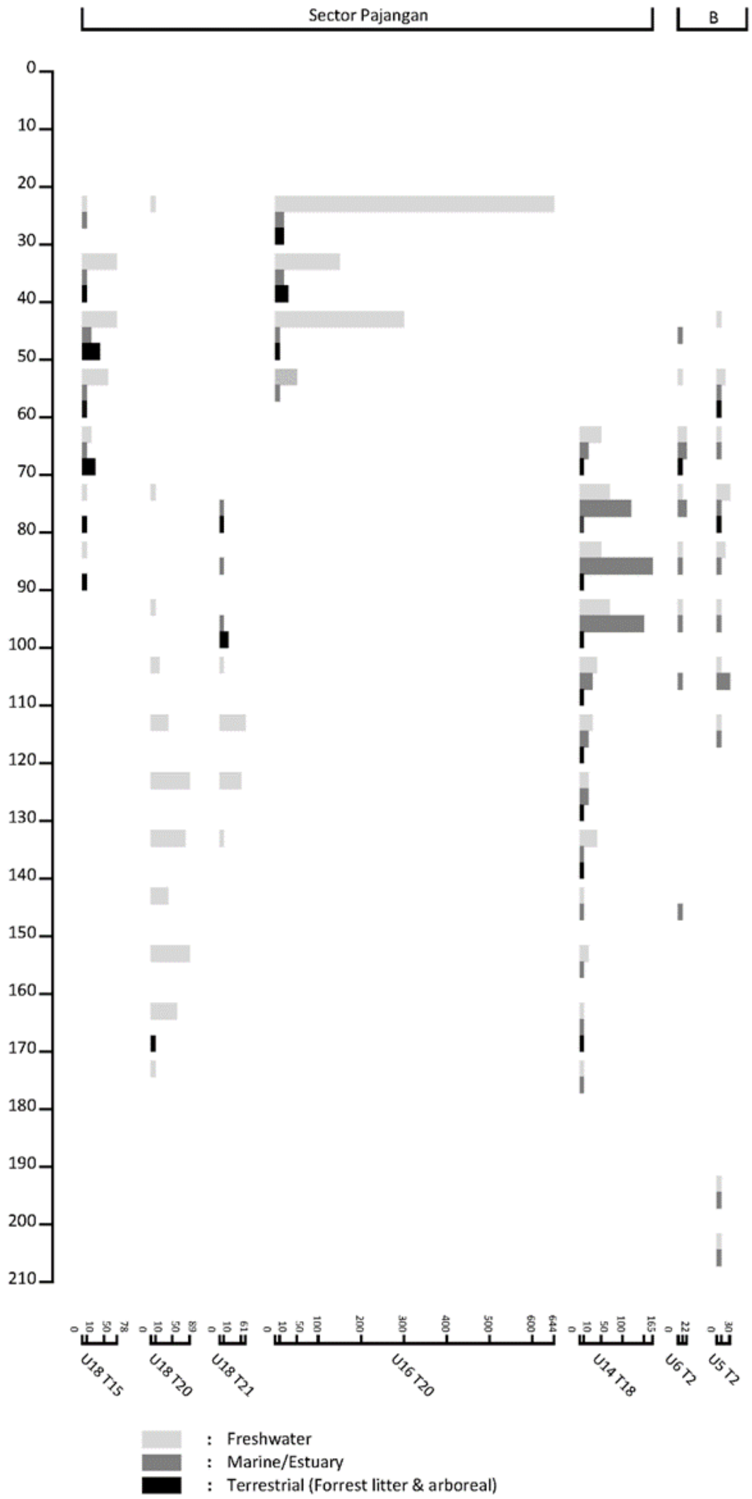

Figure 6. Barplot showing vertical distribution of mollusc shells based on habitat, excluding shells that are unidentified across units (in cm, n=3298).

In addition to aquatic molluscs, terrestrial gastropods such as *Amphidromus* sp. and *Hemiplecta* sp. are known from other studies to have been exploited by prehistoric peoples (van Benthem Jutting 1952; Kirana 2013; Sulistiyo & Fakhri 2023; Sulistiyo & Wibowo 2023). These land snails, although low in fat, are high in protein, making them better suited as supplementary rather than primary food sources. Land snails are often utilised when preferred food sources are scarce or unavailable (Hunt & Hill 2017). At Kompleks Ceruk Pajangan, the shells of *Amphidromus* sp. can still be observed as food from the cut apices, as seen in Gua Kidang (Kirana 2013) and Gua Bedug (Sulistiyo & Wibowo 2023). *Hemiplecta* sp. were found in highly fragmented conditions. This fragmentation prevents the identification of taphonomic markers that could confirm their consumption. While such fragmentation could result from human efforts to extract soft body parts as observed in other studies (Sulistiyo & Fakhri 2023), it may also have occurred naturally.

Certain other mollusc species appear to have been transported from aquatic environments by human activity but do not show evidence of consumption. Marine and estuarine species such as *Chlamys* sp. and *Tegillarca granosa* might have been accidentally collected by the inhabitants of Kompleks Ceruk Pajangan while gathering other molluscs. A similar explanation may apply to the freshwater species *Filopaludina javanica* and *Melanoides tuberculata*. Their presence at the site is minimal, and in their natural habitats, they are often found alongside other frequently gathered freshwater molluscs (Sulistiyo & Fakhri 2023; Sulistiyo & Wibowo 2023).

The Paleoenvironment surrounding Kompleks Ceruk Pajangan

Four main habitats are identified from the mollusc record, providing a clearer understanding of the surrounding environment at Kompleks Ceruk Pajangan 6000–8000 years ago. During this time, the mollusc evidence suggests that the area was characterised by forested landscapes, abundant freshwater resources, and close proximity to marine/estuarine environments. This is supported by the presence of 33 specimens from the forest litter habitat, 96 from arboreal habitats, 714 from marine/estuary habitats, and 2391 specimens from freshwater habitats (Figure 7).

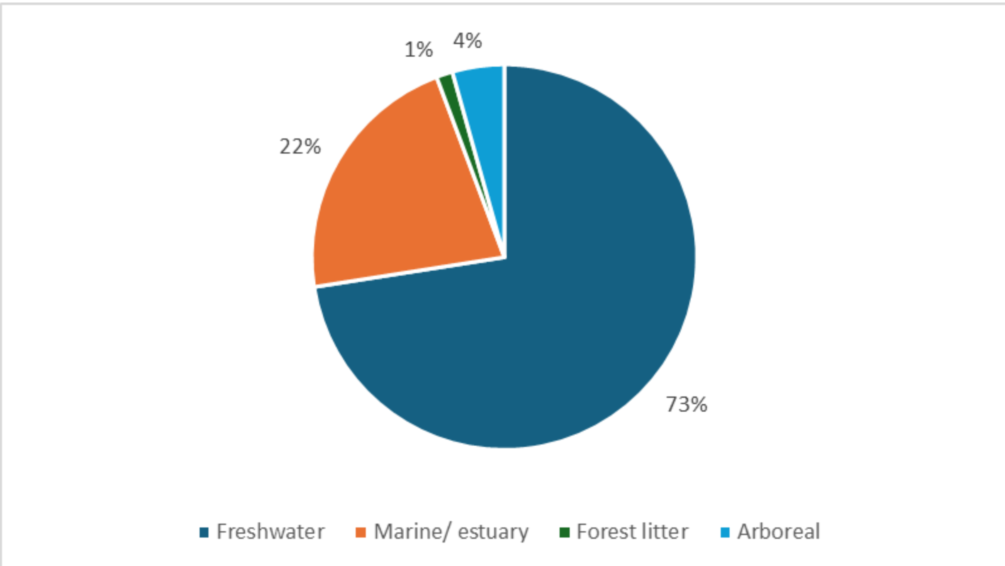

Figure 7. Habitat distribution of mollusc ecofacts in Kompleks Ceruk Pajangan (n=3298).

Given that this site is currently located 43 km from the modern coastline of northern Java, the abundance of marine/estuarine specimens is remarkable. This habitat is represented archaeologically by five species. The bivalve of *Geloina expansa* and gastropods of *Telescopium telescopium* and *Terebralia palustris* are commonly found in muddy substrates within mangroves or coastal mudflats. *Placuna* sp. and *Tegillarca granosa* also inhabit coastal environments such as lagoons, sheltered bays, and estuaries, while *Batissa violacea* resides in riverbanks and riverbeds, favouring fresh and brackish, often flowing water. Rather than indicating a broad foraging range for the prehistoric inhabitants, the abundance of marine/estuarine specimens likely reflects significant changes in the coastline over at least 5000 years. Furthermore, the high degree of coastline changes on the north coast of Java was also been well documented in the historical records.

Historical records document dramatic shifts along the northern coast of Java. For example, areas such as Pati, Demak, and Kudus were once part of a strait that separated Mount Muria from Java. Large ships navigated this strait in 800 CE, and small boats could still traverse it until the 18th century, despite sedimentation-induced shallowing (De Graaf & Pigeaud 1986). It has been proposed that the ancient coastline followed the 25-metre contour line on modern topographic maps (Soekmono 1967), suggesting that low-lying areas between Semarang and Rembang were once submerged (Figure 8).

Considering the ancient coastline, during the occupation of Kompleks Ceruk Pajangan (6000-8000 years ago), this site was approximately 2,5 km from the shoreline. This close proximity explains the abundance of marine/estuarine molluscs compared to other sites in the same karst area. For instance, Gua Kidang yielded only three ecofact specimens of marine/estuarine molluscs (two from Marginellidae and one from Donacidae) (Kirana 2013). The other marine/estuarine molluscs of Cyrenidae (8) and Arcidae (1) at Gua Kidang were used as artefacts. Gua Bedug in total yielded 63 specimens, more than Gua Kidang and less than Kompleks Ceruk Pajangan. Gua Bedug is estimated to have been 14 km from the ancient coastline, and Gua Kidang 19 km. This trend suggests that the quantity of marine/estuarine molluscs diminishes with increasing distance from the coast.

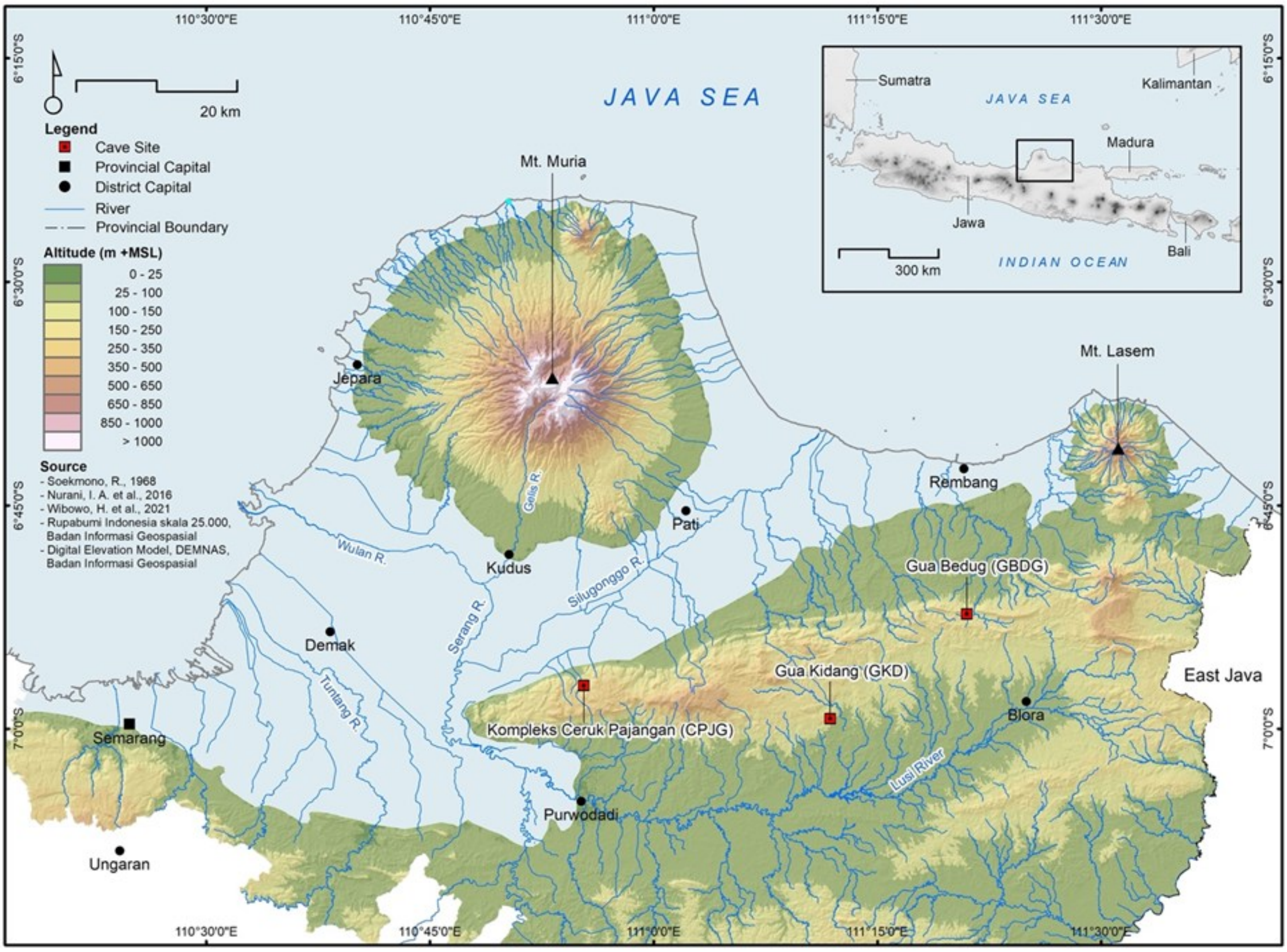

Figure 8. Ancient coastline along the Muria Strait, reconstructed based on Soekmono (1967) and overlaid with present-day river networks (Credits: Ahmad Surya Ramadhan and Hari Wibowo 2024).

Further mollusc data indicate that the ancient coastal area near Kompleks Ceruk Pajangan was surrounded by forested environments with plentiful freshwater resources. Forest environments are represented by molluscs from arboreal and forest litter habitats (Figure 9). Tree snail species such as *Amphidromus* sp., *Tricheulota zodiacus*, and *Hemiplecta* sp. depend on vegetation cover and forest canopy, while *Landouria* sp. relies on herbaceous plants but not heavily on forest litter (Heryanto 2017).

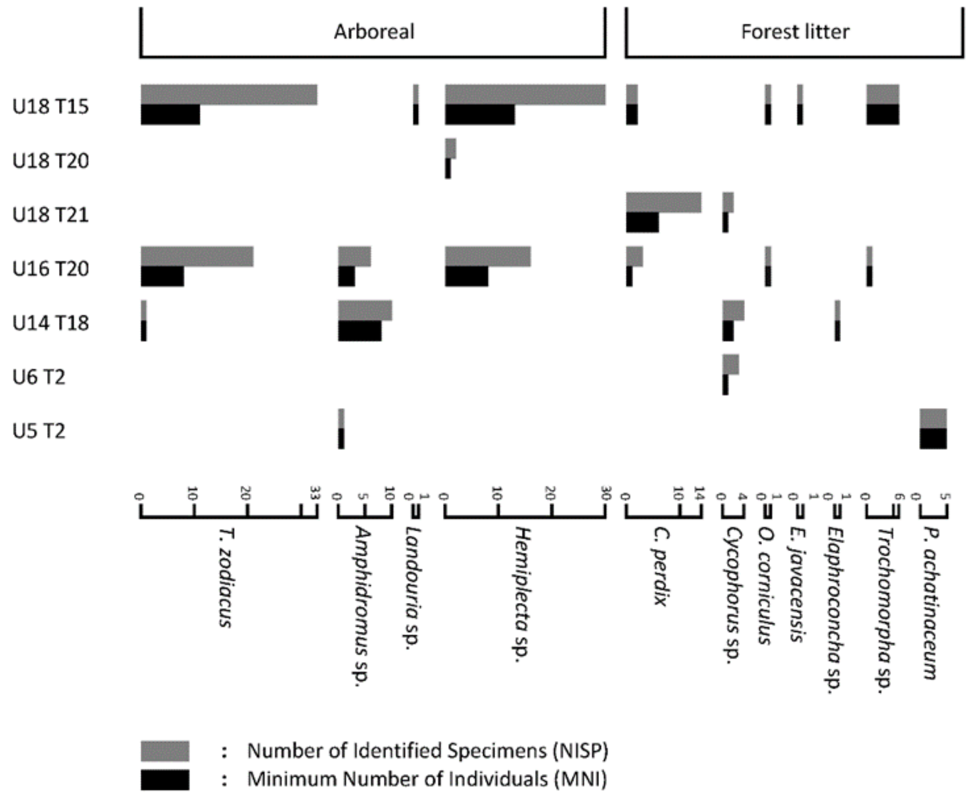

Figure 9. Barplot showing distribution of mollusc ecofacts based on arboreal and forest litter habitats across all units (n=165).

Species from Achatinidae, Cyclophoridae, Dyakiidae, Trochomorphidae, and Enidae families further indicate forest environments. These species prefer leaf litter and organic material on the forest floor, hiding in moist locations such as rocks or deadwood to maintain humidity (Hunt & Hill 2017; Sulistiyo & Fakhri 2023). The presence of these species at Kompleks Ceruk Pajangan likely reflects their attraction to organic waste left by human inhabitants. Notably, species like *Paropeas achatinaceum* and *Trochomorpha* sp. were found inside aquatic mollusc shells, indicating their entry into the site after these shells were discarded (Figure 10).

The palaeoenvironment around Kompleks Ceruk Pajangan included several streams that flowed into the ancient strait, which are now tributaries of the Silugonggo River (Figure 8). The abundance of freshwater resources is evidenced by the dominance of freshwater molluscs, which were a primary food source for the site's inhabitants (Figure 11). Species such as *Pila ampullacea* and *Sulcospira testudinaria* are epifaunal molluscs living on substrates in calm waters like ponds, swamps, and lakes (Isnaningsih & Listiawan 2010; Marwoto et al. 2020). Infaunal bivalves from the Unionidae family thrive in mixed mud and sand substrates in low-current waters, where they filter feed. Resilient species like *Melanoides tuberculata* and *Filopaludina javanica* are species that are currently commonly found. These species are more resistant to polluted water conditions (Marwoto et al. 2020).

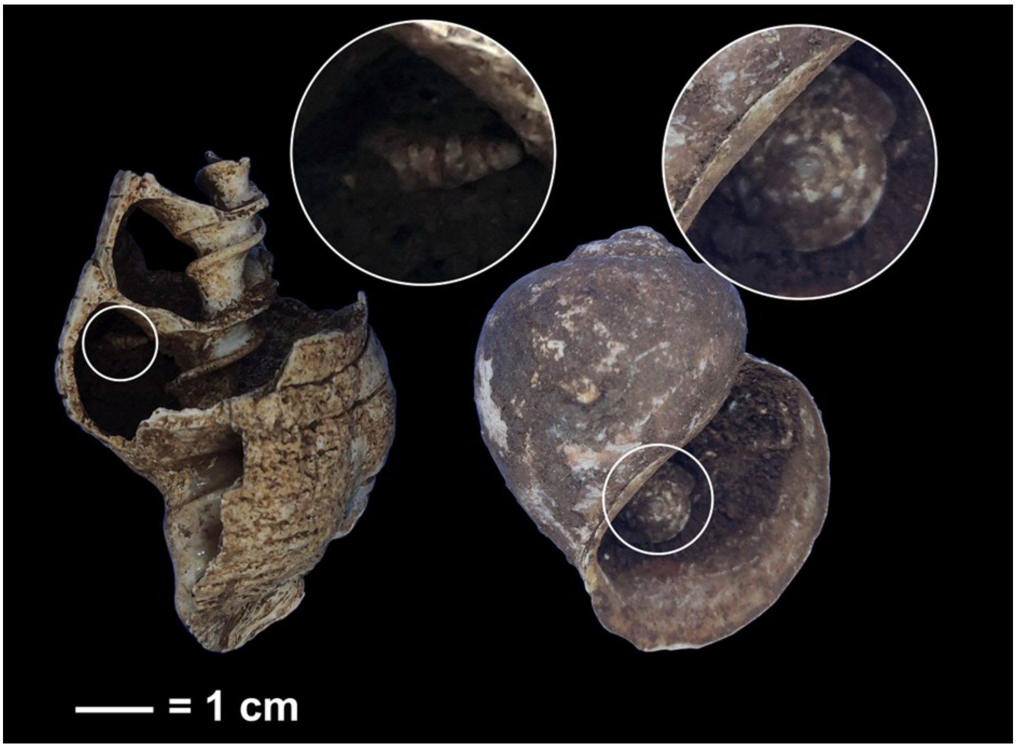

Figure 10. *Paropeas achatinaceum* inside *Terebralia palustris* shell (left) and *Trocomorpha* sp. inside *Pila ampullacea* shell (right) (Photo: Restu Budi Sulistiyo).

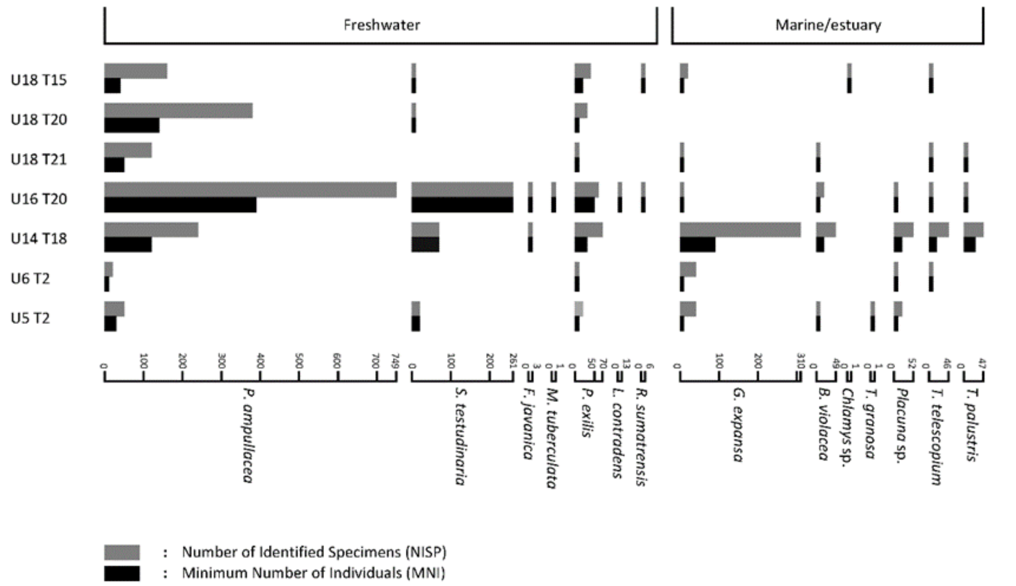

Figure 11. Barplot showing distribution of mollusc ecofacts based on their aquatic habitat across all units (n=2928).

CONCLUSIONS

Human activity significantly influenced the diversity of molluscs found in the archaeological record of Kompleks Ceruk Pajangan. Prehistoric preferences for gathering specific molluscs as food resulted in a low diversity and evenness index, as freshwater molluscs were favoured over other types. The abundance of marine/estuarine specimens supports previous hypotheses and historical data that suggest the presence of an ancient strait. Compared to other sites in the same karst area, these marine/estuarine specimens also highlight the role of proximity to natural resources in shaping past subsistence strategies. While freshwater molluscs were the primary food source, the proportion of consumed marine/estuarine molluscs increased in sites closer to the ancient coastline.

AUTHOR CONTRIBUTION

D.A.T., H.W., and S.N. designed the research and collected the data. H.W. supervised the entire process, contributed to the map, and wrote the initial manuscript. R.B.S. contributed to species identification, documentation, validation, analysed the data, and wrote the initial manuscript. D.A.T., C.R., and S.N. supervised, reviewed, and edited the initial manuscript. All authors have reviewed, revised, and proofread the final manuscript.

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CONFLICT OF INTEREST

The authors declare that there is no conflict of interest in any part of this research.

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