Size structure and DNA barcoding of mangrove clams collected in Tolongano, Donggala District, Central Sulawesi, Indonesia

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Abstract. Mangrove clams of the Cyrenidae family are widely collected for human consumption. Despite reports of declining populations, data are limited, while taxonomic revisions highlight the need for correct species identification to support effective management. Mangrove clam collection contributes to food security and income in Tolongano Village, Donggala District, Central Sulawesi Province, Indonesia. This study conducted from September to October 2020 aimed to identify the mangrove clams collected in Tolongano using molecular biology methods (DNA barcoding - Cytochrome Oxidase I Mitochondrial DNA, Sanger sequencing) and to evaluate the clam population status and characteristics based on size-frequency, morphometric and weight data. Clams purchased from collectors were measured, weighed, and sorted into size classes. The NCBI BLAST-n routine and phylogenetic tree constructed in MEGA 11 gave the closest sequence matches (99.47-99.61% identity) with *Geloina expansa*, a species with many (non-valid) synonyms including *Polymesoda erosa*, consonant with identification based on morphological traits. However, phylogenetic analysis revealed multiple clades within the *G. expansa*/*G. erosa* complex and precluded definitive species-level identification. Clam shell length and weight ranges were 24.38-65.03 mm and 6-127 g, respectively. Clam size distribution was strongly left-skewed with very few individuals over 44 mm. The common and maximum sizes were small compared to SeaLifeBase data (70 mm, 100 mm). The results indicate high levels of clam harvesting and a need for appropriate regulation.

Key Words: Cytochrome Oxidase I Mitochondrial DNA*, Geloina,* gleaning fisheries management, length-frequency distribution*, Polymesoda*.

Introduction. Bivalves have been widely collected for human consumption around the world since prehistoric times (Szabó & Amesbury 2011; Carter 2014; Albert et al 2022). In the mangrove ecosystems of southeast Asia, at least 175 bivalve species belonging to 34 families are collected, with at least 99 species reported from Indonesia (Yahya et al 2020). In particular, mangrove-dwelling clams of the family Cyrenidae are still widely collected across the Indo-Pacific (Carter 2014; Aswani et al 2015; Lokuge & Hilhorst 2017; Yahya et al 2020; Argente & Ilano 2021; Idris et al 2021) and can still be found in areas converted from mangrove forests to brackish-water aquaculture ponds (Anunciado et al 2021). These clams are still typically collected using simple gleaning methods, which have changed little over thousands of years (Albert & Bujang 2021), and often predominantly by women (Quimby 2015; Burgos 2016; Lokuge & Hilhorst 2017). In addition to their nutritional and economic value, some clams such as *Geloina expansa* (Mousson, 1849) have also been used in traditional ethnomedicine (Hamdan et al 2020), and have been proposed as bioindicators for monitoring pollution and environmental change (Burgos 2016; Bernales et al 2022).

The Cyrenidae is one family within the subclass Pteriomorphia (Bivalvia), a taxonomic grouping that has undergone considerable revisions in recent years at multiple levels, including super-family, family, genus and species (Matsumoto 2003; Graf 2013). These revisions have been based on a combination of genetic, morphological and other traits, and are further complicated by successive freshwater radiations, as in the case of the genus *Corbicula* (Graf 2013). Challenges associated with suspected cryptic species and, conversely, morphological variation within accepted species, as well as the variety of past and present nomenclature and putative diagnostic traits, all contribute to greatly complicate the identification of mangrove clams of the Cyrenidae, especially the nominal genera *Polymesoda* and *Geloina* (Carter 2014). However, correct species identification is vital in many fields (Carter 2014), including in the effective management of exploited taxa (Chang et al 2017; Abdullah et al 2020; Razi et al 2021).

Molecular methods such as DNA barcoding (Hebert & Gregory 2005) are increasingly used in many fields related to biodiversity conservation and natural resource management, *inter alia* to help resolve taxonomic ambiguities in the identification of cryptic taxa (Lara et al 2010; Moore et al 2019; Liu et al 2020; Ndobe et al 2022; Gostel & Kress 2022). Arguably, the cytochrome oxidase I mitochondrial DNA (COI mtDNA) is the most commonly used molecular marker for the DNA barcoding of many taxa including molluscs (Hebert et al 2003; Bucklin et al 2011; Barco et al 2016; Habib et al 2021). However, one limiting factor is the limited coverage of reference sequences in global databases such as the NCBI GenBank and BOLD, especially in global biodiversity hotspots such as Indonesia (Mugnai et al 2021).

Gleaning fisheries have tended to be overlooked in modern fisheries and resource management systems, despite their economic, cultural and food security importance (Aswani et al 2015; Furkon et al 2019; Alati et al 2020). While data on the status of mangrove clam populations are limited, as in other mollusc gleaning fisheries (Alati et al 2020), there are reports of declines in mangrove clam population abundance and/or size (Primavera et al 2002; Carter 2014; Aswani et al 2015; Barclay et al 2017; Nasution et al 2021), as well as other indications of unsustainably high levels of exploitation (Argente & Ilano 2021). These and other reported mangrove clam population declines are mostly associated with anthropogenic activities, especially overexploitation and habitat degradation. This situation calls for holistic and locally adapted resource management based on sound science.

In Indonesia, cyrenid mangrove clams of the genus known as *Geloina* or *Polymesoda* are widely collected across the archipelago, including in Aceh (Sarong et al 2015, 2019a; Quimby 2015), Mentawai Archipelago (Burgos 2016), Riau (Nasution et al 2021), Segara Anakan, Java (Suryono 2012, 2016), South Sulawesi (Samawi et al 2020; Risa et al 2021), Southeast Sulawesi (Sanda et al 2021), North Sulawesi (Baderan et al 2019), East Nusa Tenggara (Haru et al 2018), and Papua (Setyadi et al 2021). In particular, mangrove clams locally known as "kerang kalatue" are collected by the coastal community of Tolongano Village, Banawa Selatan Subdistrict, Donggala District, Central Sulawesi Province. The clams are collected in the still-standing mangrove forests and in areas that have been converted to brackish-water ponds and contribute to villager food security and income. This study aimed to identify the mangrove clam species collected in Tolongano Village using molecular biology methods, as well as to evaluate the status and characteristics of the clam population based on length-frequency, morphometric and weight data.

Material and Method

Description of the study site. This study was conducted in Tolongano Village, Banawa Selatan Subdistrict, Donggala District, Central Sulawesi Province, Indonesia (Figure 1). This site comprises a lagoon with a narrow inlet surrounded by still extensive mangrove forests, despite the conversion of a large proportion to brackish-water aquaculture ponds or other land-uses such as agriculture, dwellings and strip development along the coastal road. The hinterland is mountainous, with considerable deforestation. The research took place from September to October 2020.

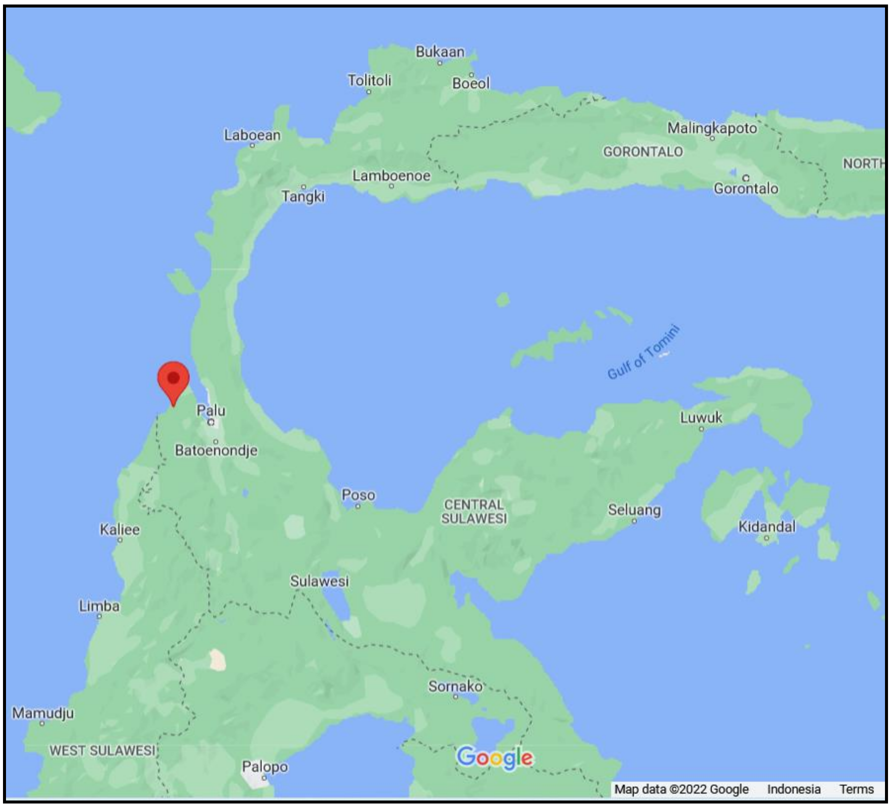

Figure 1. Map of the study site in Tolongano Village, Banawa Selatan Subdistrict, Donggala District, Central Sulawesi Province, Indonesia (https://www.google.com/maps).

Sample collection, measurement and morphological identification. Mangrove clam samples (N=95) were purchased from local collectors (gleaning fishers). The shell length of each specimen was measured (electronic callipers, precision 0.01 mm). The specimens were weighed using electronic scales (Camry LPK 112, precision 1 g) and labelled. The body weight of a representative sub-sample (n=78) was determined. The living tissue was removed from the shell and weighed using electronic scales (precision 0.01 g). Tentative taxonomic identification was based on morphological traits and followed published literature (Morton 1976; Compagno 1998; Carter 2014; Santhanam 2018) and on-line databases: SeaLifeBase (https://www.sealifebase.ca/), Molluscabase (https://www.molluscabase.org/) and World Register of Marine Species (WoRMS) (https://www.marinespecies.org/).

DNA Barcoding and BLAST-n. Tissue from the muscular foot of one specimen (15% of body weight excluding the shell) was placed in a 1.5 mL Eppendorf tube filled with 96% absolute ethanol and sent to the Bionesia Laboratory in Denpasar, Bali, Indonesia for DNA barcoding using the Cytochrome Oxidase I Mitochondrial DNA (COI mtDNA) molecular marker. Polymerase chain reaction (PCR) was conducted using a universal COI mtDNA primer pair. The PCR product was sent to FirstBase Laboratories in Singapore for Sanger sequencing. The forward and reverse nucleotide trace files (.abi files) were trimmed and combined in MEGA 11 to produce a consensus sequence. The NCBI BLAST-n online tool was used to search the GenBank accession repository to find similar sequences.

The top 24 accessions output by the BLAST-n algorithm were listed under the genus *Geloina* or synonym *Polymesoda*, while the remainder of the top 100 matches were listed under the genus *Corbicula*, indicating that these two genera are sister taxa. All *Geloina*/*Polymesoda* BLAST-n output sequences with over 90% coverage and more than 85% identity were selected for phylogenetic analysis, and two *Corbicula* sequences were selected as an outgroup. The majority of these 19 GenBank accessions (Table 1) were recent direct submissions not linked to any published reference.

Table 1
GenBank accessions (genus *Geloina* and outgroup genus *Corbicula*) obtained through the BLAST-n routine and used in the phylogenetic analysis

Accession Number	*Country/Region of origin*	*Submitted taxon*	*Currently assigned taxon*	*Cover %*	*Identity %*	*Reference*
AB498812	Japan/Okinawa	*G. expansa*	*G. expansa*	95.00	86.92	Iida et al (2012)
AB722088	Japan/Okinawa	*G. expansa*	*G. expansa*	95.00	98.90	
AB722089	Japan/Okinawa	*G. expansa*	*G. expansa*	95.00	86.53	
AB722090	Japan/Okinawa	*G. expansa*	*G. expansa*	95.00	87.08	
MK481951	India	*Geloina* sp.	*Geloina* sp.	99.00	87.23	Unpublished (2019)
MK481952	India	*Geloina* sp.	*Geloina* sp.	99.00	87.94	
MN608338	China/Hainan Is.	*G. expansa*	*G. expansa*	95.00	87.73	Unpublished (2019)
MW311111	Indonesia/Sumatra	*Polymesoda expansa*	*G. expansa*	99.00	90.76	Unpublished (2020)
MW311112	Indonesia/Sumatra	*P. expansa*	*G. expansa*	99.00	90.41	
OM791690	Malaysia/Terengganu	*G. erosa*	*G. erosa*	99.00	86.95	Unpublished (2022)
OM791691	Malaysia/Terengganu	*G. erosa*	*G. erosa*	99.00	86.77	
OM791692	Malaysia/Terengganu	*G. erosa*	*G. erosa*	99.00	86.95	
OM791693	Malaysia/Terengganu	*G. erosa*	*G. erosa*	99.00	86.77	
OM791694	Malaysia/Terengganu	*G. erosa*	*G. erosa*	99.00	86.95	
OM791697	Malaysia/Terengganu	*G. expansa*	*G. expansa*	100.00	99.47	Unpublished (2022)
OM791698	Malaysia/Terengganu	*G. expansa*	*G. expansa*	100.00	99.47	
OM791699	Malaysia/Terengganu	*G. expansa*	*G. expansa*	100.00	99.47	
KC211287*	Japan	*Corbicula leana*	*C. leana*	99.00	81.66	Pigneur et al (2014)
MF401395*	Spain	*C. fluminea*	*C. fluminea*	99.00	81.53	Clusa et al (2017)

Note: * - outgroup.

Phylogenetic analysis. The 19 GenBank accessions (Table 1) and the mangrove clam sequence were aligned (ClustalW, default parameters) and trimmed in MEGA 11 (Tamura et al 2021), giving a dataset with 518 nucleotides. A phylogenetic tree was constructed in MEGA 11; the evolutionary history was inferred using the Maximum Likelihood method and the Tamura-Nei model (Tamura & Nei 1993) with 100 bootstrap replications.

Size structure analysis. The data on clam size and weight were tabulated and analysed in Microsoft Excel 365. The data were sorted into ten length classes and a length-frequency histogram was constructed. The ratios between length, width and height were calculated (mean ± standard deviation). The length-weight relationship ($W=aL^b$) was calculated through linear regression of log-transformed data (Froese 2006) to determine the growth pattern based on the value of b ($b<3$ allometric negative; $b=3$ isometric; $b>3$ allometric positive). The relationship between the weight of the soft body and total weight (soft body and shell) was determined though linear regression. The data were evaluated with respect to data on other populations of the genus *Geloina*/*Polymesoda* obtained from the scientific literature and on-line databases.

Results

Taxonomic identification and phylogenetic analysis. Based on morphological traits, the clams were identified as belonging to the genus *Geloina* (formerly *Polymesoda*). The conflicting information in references regarding the species within this genus precluded a definitive identification to species level. Based on DNA barcoding, the closest BLAST-n matches for the mangrove clam from Tolongano were recently deposited (and as yet unpublished) barcode sequences for *Geloina expansa* from Terengganu in Malaysia (99.61% identity, accessions OM791695 and OM791696). However, due to the % cover below 90%, these were not included in the phylogenetic analysis. The nearest matches (99.47% identity) with 100% query cover were three *G. expansa* accessions from the same source (OM791697-OM791699). With an E-value of 0, this identification has a very high level of confidence. This result is also consonant with identification of the clams as belonging to the genus *Geloina* based on morphological traits. The maximum likelihood phylogenetic tree (Figure 2) shows high confidence (100% or close to 100% bootstrap values) in delineating several major clades within the genus *Geloina*.

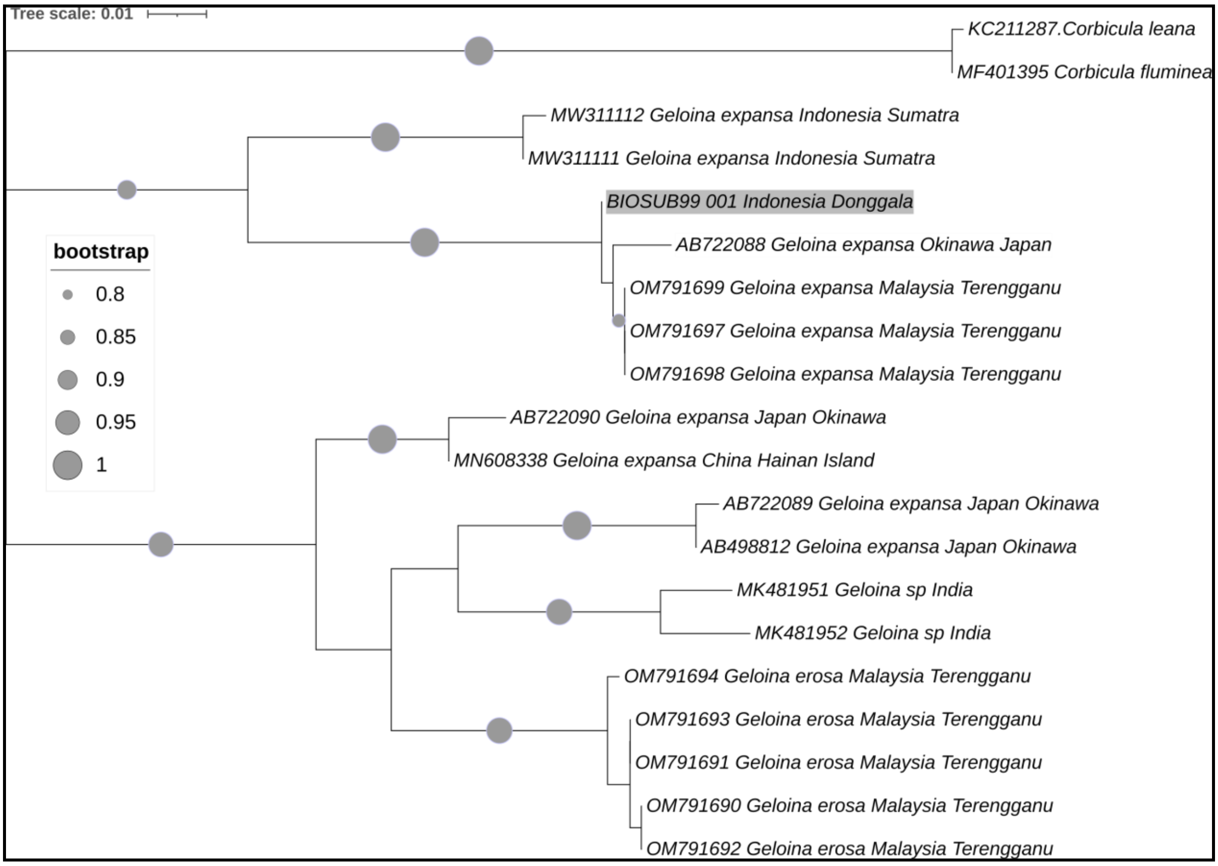

Figure 2. Maximum likelihood phylogenetic tree of the Tolongano mangrove clam with GenBank accessions of the genus *Geloina* and outgroup genus *Corbicula*.

Size-frequency and morphology. The clams sold ranged from 29.2 to 65.03 mm shell length, with a mean of 36.39±8.47 mm. The size distribution was strongly left-skewed with very few individuals over 44 mm (Figure 3).

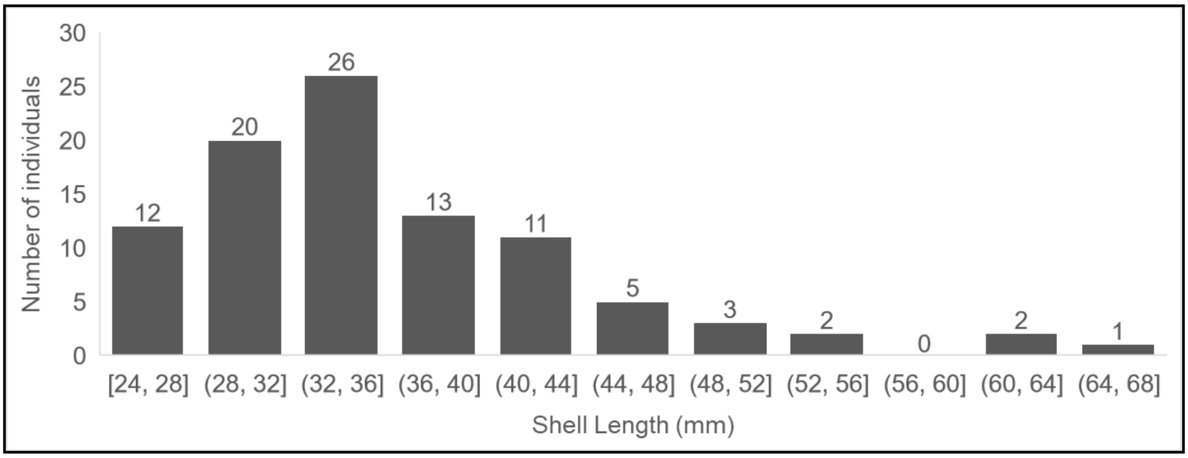

Figure 3. Length-frequency distribution of mangrove clams (*Geloina* sp.) from Tolongano.

The most abundant size class (27.4%) was class III (32 to 35 mm). Width range was 30.80-72.48 mm and height range was 13.15-42.93 mm. The ratios between length, width and height (mean ± standard deviation) were as follows: length/width 85.96±8.13%; height/length 59.68±9.1%. Data on common and maximum sizes as well as some life history data reported for this species in SeaLifeBase and in studies on other populations are presented in Table 2.

Table 2
Size and life history data on clams of the genus *Geloina* (formerly *Polymesoda*) in regions of Indonesia and other countries

Country/Location	*Published taxon*	*Length range (cm)*	*Common length (cm)*	*Remarks*	*Reference*
SeaLifeBase	*P. erosa* *P. expansa*	7 7	10.5 10	These species are considered synonymous by several sources	[c]
Indonesia					
Donggala, Central Sulawesi	*Geloina* sp.	2.9-6.5	3.1-4	Common length = interquartile range (Q1-Q3); median = 3.45 cm	Present study
ParePare, South Sulawesi	*Polymesoda* sp.	2.3-7.7	4.2-5.9	100 clams in 3 size groups (sampled for heavy metal content study)	Samawi et al (2020)
Kendari Bay, Southeast Sulawesi	*P. erosa*	3.4-11.8	≈5-7.5	Random sampling; weight 1.2–36.8 g Adult size: >5 cm	Sanda et al (2021)
Segera Anakan Java	*P. erosa*	2.3-7.8	No data	Sampling method not stated	Widowati et al (2005)
	Geloina sp.	<3->8	6-7	Sampling stratified by salinity; Values inferred from graph	Irwani & Suryono (2006); Suryono (2016)
	P. expansa	≈3-5.5	≈3.2-4.6	Size ranges inferred from graphs	Widianingsih et al (2020b)
	P. erosa *P. expansa*	No data	4.3-5.5	Based on mean size data at three sites	Widianingsih et al (2020a)
Aceh, Sumatra	*G. erosa*	2.9-6.7	3.5-5.5	Some mature oocytes at 3.5 cm; % mature oocytes increased with clam size	Sarong et al (2015)
Siberut Island, Aceh, Sumatra	*G. erosa*, *G. expansa*, *P. bengalensis*	No data	5-10	Common weight 150-300 g, one basket typically up to 80 clams/16 kg, typical daily catch 80-120 clams/gleaner	Burgos (2016)
Padang, Sumatra	*P. erosa*	1.5->4.7	3.1-4.3	Stratified sampling across 3 zones	Wulandari et al (2022)
Jayapura, Papua	*P. erosa*	2.9-9.2	4.4-7.8	Adult size: above 5.5-5.7 cm	Wanimbo & Kalor (2019)
Other Countries					
Solomon Islands	*Polymesoda* spp.	Small->10 cm	6-7.9	Larger and more abundant in permanently protected and temporal closure areas	Aswani et al (2015)
	P. erosa *P. expansa*	5.9-10.9 6.4-9.3	Median 8.3 Median 7.9	Species based on local knowledge and substrate type [a]	Carter (2014)
Philippines	*P. erosa*	1.4-7.9	Mean 3-4.9	Stratified sampling	Ordonio et al (2018)

Country/Location	*Published taxon*	*Length range (cm)*	*Common length (cm)*	*Remarks*	*Reference*
	G. expansa	≈2.4-8.9	≈4.4-6.2	Time series – 28 points from 2012-2015 Lengths inferred from graphs	Argente & Ilano (2021)
Malaysia	*P. erosa* *P. expansa*	8.8 maximum 8.8 maximum	3.4-6.2 3.4-6.3	Size was related to age	Ransangan et al (2019)
Malaysia (Sabah)	*Polymesoda* (*Geloina*) *erosa*	5.5-9.5	6.5-8.5	Clams >5.5. cm mature (adult); Overall sex ratio 1:1 [b]	Duisan et al (2021)
Japan (Okinawa)	*Polymesoda* (*Geloina*) spp.	4.2-11.7	Mean 8.1-9.2	All clams considered as one taxon (genus level identification)	Washitani et al (2017)

Notes: [a] - *P. erosa* in harder mud closer to the seaward edge, typically dominated by *Rhizophora* mangroves and *P. expansa* in softer mud closer to the landward edge where *Bruguiera* is typically the dominant mangrove genus; [b] - clams <6.5 cm mostly male (3:1; M:F), clams >8.5 cm mostly female (1:4; M:F); [c] - https://www.sealifebase.ca/summary/Polymesoda-erosa.html and https://www.sealifebase.ca/summary/Polymesoda-expansa.html

Length-weight and body to total weight relationships. The weight of the clams ranged from 6.28 to 127 g, while the body weight (without the shell) ranged from 0.94 to 28 g. The length weight relationship based on the log-transformed data gives b=2.752 (Figure 4a). As b is less than 3, the growth pattern for this population is allometric negative. The regression of body weight against total weight (body and shell) shows high correlation ($R^2=0.903$; $p<0.0001$; F=705.5), despite the increasing spread of the data for larger individuals (Figure 4b). The body to total weight ratio ranged from 8.33% to 28.13%, with a mean of 15.39±4.4%.

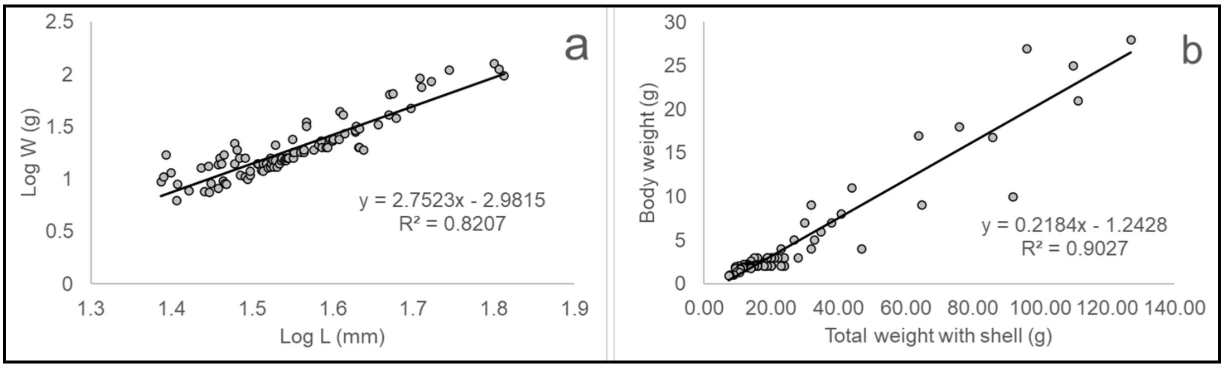

Figure 4. Log-transformed regression of weight against length (n=95) (a) and regression of body weight against total weight (n=78) (b) for *Geloina* sp. mangrove calms from Tolongano.

Discussion. The taxonomy of the nominal genera *Geloina* and *Polymesoda* is an ongoing subject of study and debate. In SeaLifeBase (Palomares & Pauly 2022), the genus name *Polymerosa* is still in usage, with *P. erosa* and *P. expansa* listed as separate taxa, each with several (non-valid) synonyms. According to the World Register of Marine Species (WoRMS 2022), the currently accepted name *Geloina expansa* Mousson 1849 (original name *Cyrena expansa* Mousson, 1849) is a species-level taxon with many (now non-valid) synonyms including the still widely used *Polymesoda erosa* (Lightfoot, 1786) and *Polymesoda expansa* (Mousson, 1849), as well as *Cyrena (Corneocyclas) galatheae* (Mörch, 1850), *Cyrena compta* (Deshayes, 1855), *Cyrena fallax* (Deshayes, 1854), *Cyrena moluccensis* (E. von Martens, 1897), *Cyrena oblonga* (Deshayes, 1855), *Cyrena similis* (Deshayes, 1854), *Cyrena wilkinsii* (R. I. Johnson, 1959), *Cyrena yaeyamensis* (Pilsbry, 1894), and *Polymesoda (Geloina) galatheae* (Mörch, 1850). A recent review on mangrove-associated bivalves in Southeast Asia (Yahya et al 2020) lists three *Geloina* species from Indonesia: *G. bengalensis* Lamarck, 1818, *G. coaxans* Gmelin, 1791, and *G. expansa*, along with two other Cyrenidae (*Corbicula* sp. and *C. fluminea* O. F. Müller, 1774), with a fourth undetermined taxon *Geloina* sp. listed in the neighbouring country of Malaysia. A study in Aceh Besar, Sumatra, Indonesia (Sarong et al 2019b) using a nuclear DNA marker (16S rDNA) found that samples identified as three species based on morphological identification (*G. erosa*, *G. expansa*, and *G. coaxans*) had more than 99% identity with each other and with an accession submitted as *Polymesoda caroliniana* (Bosc, 1801), a Caribbean and Western Atlantic species. As the authors pointed out, this is a level of similarity generally found within, rather than between species. While the World Register of Marine Species (WoRMS) database and the world checklist of freshwater Bivalvia species (Bogan 2013) consider *G. coaxans* (originally *Venus coaxans* Gmelin, 1791) a valid taxon, separate from the supposedly synonymous *G. erosa* and *G. expansa*, SeaLifeBase (Palomares & Pauly 2022) considers *G. coaxans* as a synonym of *Polymesoda* (*Geloina*) *erosa*, but not *G. expansa*, while Sarong et al (2019b) considered specimens identified as three species (*G. coaxans, G. erosa* and *G. expansa*) based on their morphology as one species based on the 16S rDNA molecular marker.

The clades within *Geloina* in Figure 2 are similar to the structure reported for the sister genus *Corbicula*, specifically the taxon *Corbicula japonica* (Prime, 1864), which appears to be a species complex, comprised of several clades with an unresolved taxonomic status (species, sub-species, stocks/strains etc.) as of yet in east Asian seas (Iida et al 2012). An analysis of the bivalve subclass Pteriomorphia (Matsumoto 2003) placed *G. erosa* in Heterodonta, along with representatives of five other bivalve genera including *Tridacna*, but no representatives of the genus *Corbicula* were included. The COI mtDNA sequence used in Matsumoto (2003) and deposited in the GenBank (accession AB076927) only had an overlap of 371 nucleotides with the sequences used to construct the phylogenetic tree in Figure 2. However, a maximum likelihood tree constructed for this overlapping region placed the accession in the same clade as the sample from Tolongano, as well as *G. expansa* accessions from Japan (AB702288) and Malaysia (OM791697-OM791699) with 100% bootstrap value. This clade was clearly separated from the clade containing accessions submitted as *G. erosa*.

Overall, the phylogenetic analysis strongly supports the identification of the mangrove clam from Tolongano in Donggala, Central Sulawesi, as belonging to the genus *Geloina*. The most likely species is *G. expansa*, with the caveat that the Malaysian (accession OM791697-OM791699) and Japanese (accession AB722088, (Iida et al 2012)) clams in the same clade were accurately identified. However, the phylogenetic analysis also indicates considerable structure within the genus *Geloina*. Figure 2 shows two first-order clades with, respectively, two and four (total of six) second-order clades, all with high bootstrap support. This structure is further supported by neighbour-join trees with essentially the same topography (also constructed using the routine in MEGA 11, but not presented here). The first major clade in Figure 2 contains the Tolongano specimen and accessions listed as *G. expansa* from Indonesia (Sumatra), Malaysia (Terengganu) and Japan (Okinawa), with a deep divide between the Sumatran accessions and the remainder of the clade (100% bootstrap), indicating two distinct populations that likely represent distinct sub-species or species. The second major clade contains three nominal species with *G. erosa* from Malaysia (Terengganu) and *Geloina* sp. from India each forming a well-separated sub-clade. The accessions submitted as *G. expansa* formed two deeply separated sub-clades, one of which contains an accession from China (Hainan Island), while accessions from Japan (Okinawa) are found in both sub-clades. This structure indicates that *G. erosa* and *G. expansa* may not be one species (synonyms) as stated in the World Register of Marine Species (WoRMS 2022), but rather two of the names used for a species complex requiring further research to clarify the number and level of taxa (species and/or subspecies) within this complex.

Morton (1976) gave a detailed description of *G. erosa*, while the FAO guide to fisheries species (Compagno 1998) provides diagnostic traits to distinguish *G. erosa* from *G. expansa*. A study in Segera Anakan found differences in two morphometric characters (ratios) between *P. erosa* and *P. expansa* (Widianingsih et al 2020a). Although the differences were quite small and the statistical confidence level was not stated, the differences were consistent across three sites. Another study (Carter 2014) in the Solomon Islands found within-site zonation of these two putative species, each having a distinct local name and body of traditional ecological knowledge (TEK). Carter (2014) found differences in the relationship between shell dimensions and weight, with a "slightly more elongated, considerably less inflated shape" in *P. expansa*, hypothesizing that the thicker, heavier shell of *P. erosa* may be related to a need to retain water for longer periods at low tide. Carter (2014) also mentioned considerable individual variation in some morphometric characters and considered that the observed differences between the populations (putative species based on TEK and scientific literature) might be due to environmental factors rather than representing different species, a concern also raised by a study in Malaysia (Hamli et al 2015). Another study in Malaysia (Idris et al 2021) found no significant difference in the 14 morphometric ratios calculated between these two putative species, although both differed significantly from *G. bengalensis* in the length of the cardinal tooth. A study in Okinawa, Japan, stated that *G. erosa* and *G. expansa* are indistinguishable based on external morphology (Washitani et al 2017). None of these studies used molecular methods to verify the classical taxonomic methods used to discriminate between *Geloina*/*Polymerosa* species.

Even though a few large individuals were found, Table 2 shows that the maximum length of the *Geloina* sp. samples from Tolongano was below the "common" length in SeaLifeBase as well as below the maximum sizes reported by all seven studies from other countries and 7 out of 11 studies at nine sites across Indonesia from 2005 to 2021. With respect to the common sizes, the clams from Tolongano were generally smaller than those from both Indonesian (8 out of 10) and overseas (6 out of 7) studies. The Indonesian exceptions, with a size range around the common and maximum lengths in SeaLifeBase (Palomares & Pauly 2022), were in Kendari Bay (Sanda et al 2021) and in Siberut Island in the Mentawai Archipelago, Aceh, Sumatra, where the weight range (150-300 g) reported for the three putative *Geloina* species collected at this site under the same local name of "meggu" (Burgos 2016) was also considerably larger compared to that of the *Geloina* clams from Tolongano (6-127 g). The overseas exception was a study in the Philippines (Ordonio et al 2018). The size distributions for a heavily exploited population in the Philippines at 28 points in time over the period 2012-2015 (Argente & Ilano 2021) shows that the size structure can fluctuate considerably between seasons as well as years, with most individuals attaining a length of around 5 cm in one year, indicating most individuals attain sexual maturity at around 1 year of age. Even though the maximum and common sizes were larger than in our study, the exploitation at this site in the Philippines was considered unsustainable based on the population dynamics parameters. Five studies from Segara Anakan in Java (Widowati et al 2005; Irwani & Suryono 2006; Suryono 2016; Widianingsih et al 2020a,b) indicate a decline in size from 2005-2012 to 2020. Although the size range is similar, the length-frequency data from Tolongano show a higher predominance of smaller sized clams compared to recent data from Segara Anakan. These comparisons indicate that the current pattern and/or levels of exploitation in the Tolongano mangrove clam gleaning fishery are highly unlikely to be sustainable.

The collection methods in Tolongano are similar to some of those described for Malaysia and the Solomon Islands in both historic and prehistoric times (Carter 2014; Albert & Bujang 2021; Albert et al 2022), involving manual collection by digging in the muddy substrate at low tide. These methods are intrinsically unselective at the digging stage, but could become selective if clams outside certain agreed criteria are released rather than collected. Therefore, management measures such as size limits are feasible from a technical point of view. However, the greater challenge is the social aspect in this effectively open access gleaning fishery. Therefore, there will be little incentive to agree or implement size limits if undersized clams returned to their habitat are most likely to be collected by someone else. Other possible approaches include temporary closures (Cohen & Foale 2013). These have proven effective in increasing and maintaining clam abundance and size as well as socially acceptable in the Solomon Islands (Aswani et al 2015). In the future, aquaculture may also be an option as part of sustainable management, according to preliminary studies on the aquaculture potential of *G. expansa* in the Philippines (Argente & Ilano 2021; Argente et al 2021).

Conclusions. This study identified the mangrove clams collected at Tolongano in Central Sulawesi, Indonesia, as belonging to the genus *Geloina*, formerly *Polymesoda*. Phylogenetic analysis indicates that the nominal genus *Geloina* likely comprises several cryptic (and probably frequently misidentified) species, or that it could be a species complex in the process of sympatric (as indicated by the two clades in Terengganu, Malaysia and three clades in Okinawa, Japan) and/or allopatric speciation. Therefore, the species identity of the Tolongano clams could not be determined. Studies using multiple molecular markers, specimens from across a wide geographic area, and breeding trials could probably help to clarify the evolutionary history and current relationships within the genus *Geloina*, as well as the biogeography and taxonomy of this taxonomic group. Meanwhile, the length-frequency data indicate heavy and most likely unsustainable levels of harvesting and a need for appropriate regulation of the *Geloina* sp. gleaning fishery in Tolongano.

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