

DNA barcoding of museum-voucherized samples collected from fish markets reveals an unexpected diversity of consumed gastropods in Vietnam

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ARTICLE INFO

Keywords:
 Edible marine gastropods
 Museomics
 Traceability
 Food safety
 Alternative protein source
 Biodiversity
 Monitoring
 Reference sequence data
 Food security
 Resilience
 Food diversification
 Marine snails

ABSTRACT

Despite the rich diversity of marine gastropods, limited taxonomic investigations on edible species raise concerns regarding fisheries management and food safety in Vietnam. In this study, we employed iterative taxonomy by combining morphological identification and DNA barcoding using the COI, 12S-rRNA, 18S-rRNA, 28S-rRNA, and histone H3 gene markers, to confirm the taxonomy of 126 marine gastropod museum specimens collected from various fish markets in Vietnam. Morphological identification assigned 113 of the 126 specimens to 53 species. Sequences were obtained for all samples, although not all genes were successfully sequenced for every specimen. When all gene markers were used, 58 % in 2023 and 79 % in 2025 of the 113 samples were identified at the species level (excluding the morphologically unidentified individuals), compared to only 51 % in 2023 and 62 % in 2025 when only COI was used. The higher match rates in 2025 likely reflect ongoing improvements in public reference databases. Phylogenetic and genetic distance analyses supported these results, revealing monophyletic species and genera. This study revealed that >50 species are part of local diets, emphasizing the importance of fundamental biodiversity studies, including alpha taxonomic surveys, for managing marine gastropod fisheries and highlighting marine gastropods' potential as novel food resources. By utilizing voucherized museum specimens, this study also contributes to developing a reliable reference database for identification and monitoring edible marine gastropods in Vietnam and Southeast Asia.

1. Introduction

Animal meat is an important source of proteins and essential nutrients in human diets (Klurfeld, 2018). Conventional animal protein sources, such as cattle (20 %), poultry (34 %), pork (34 %), and other meats (12 %), account for the majority of global protein consumption (FAO, 2023). Their protein efficiency ranges from 3.8 to 25 %, with feed requirements of 1.7 kg (chicken) to 10 kg (beef) per kilogram of meat produced (Ritchie et al., 2017; Fry et al., 2018). This inefficiency

significantly raises the carbon footprint of animal-based food production (Steinfeld et al., 2006; Kevany, 2023), underscoring the urgent need to explore underutilized resources, including culturally significant species (Hunter et al., 2019), that might offer a solution for ensuring sustainable and resilient animal protein supplies (van Huis et al., 2013; Hertel et al., 2023; Figaredo et al., 2024; Figaredo and Chatsawan, 2024). With lower carbon footprints than terrestrial livestock, marine fisheries and aquaculture offer a sustainable way to diversify protein sources and address environmental pressures, including through the exploration of

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underutilized marine species in food systems (Poore and Nemecek, 2018; Gephart et al., 2021; Nuñez, 2021). This approach holds promise for meeting rising protein demands while relying on sustainable fisheries to preserve ecosystems (Golden et al., 2021; Melnychuk et al., 2021; Nuñez, 2021). However, successfully incorporating these novel protein sources into mainstream food systems also requires robust traceability measures to ensure safety and security while preventing overexploitation, thereby maintaining sustainability and resilience (Fishwise, 2018; Future of Fish, 2020; Traynor et al., 2024; Gleadall et al., 2024).

Marine gastropods could be used as a resilient protein source potentially capable of mitigating the challenges posed by climate change and thus might contribute to long-term food security (Khan and Liu, 2019; Pissia et al., 2021; Gupta and Khanal, 2024). In addition to their nutritional benefits (Felici et al., 2020; Chakraborty and Joy, 2020), marine gastropods hold significant cultural and culinary value in many regions, offering a unique opportunity to align sustainable food practices with traditional diets and local heritage (Kikutani and Yamakawa, 1999; Penner, 2022). This is particularly evident in biodiversity-rich countries like Vietnam, where marine gastropods have been integral to local traditional diets (Imam et al., 2019; Lien, 2016). These animals not only represent an important food source but also highlight the potential for sustainable fisheries to meet the growing demand for animal proteins

while preserving cultural traditions. Vietnam serves as a case study, showcasing both the extensive consumption of marine gastropods and the challenges related to their sustainable management and safety.

Vietnam is estimated to host approximately 10 % of the world's species, distributed across its mountains, rivers, forests, coastal areas, and seas, making it a biodiversity hotspot (CITES, 2008; World Bank, 2016; Thuaire et al., 2021), including ca. 11,000 marine species (Appeltans et al., 2012; Nguyen, 2018). Of the approximately 35,000 described species of gastropods worldwide, approximately 1500 species can be found in Vietnam (Do et al., 2019, 2021). Many species of marine gastropods are consumed in Vietnam as a major source of animal protein (Imam et al., 2019; Vietnam Coracle Team, 2016). These gastropods are regularly sold in traditional markets and served at meals and banquets (Fig. 1). Archaeological evidence indicates that gastropods have been consumed in Vietnam for over 10,000 years (Lien, 2016). However, despite the extensive consumption of gastropods through fisheries catches in Vietnam, there is a dearth of systematic records of the species caught and consumed, complicating reliable identification and cataloguing of biodiversity. This gap in data raises concerns about food safety and traceability, particularly given Vietnam's heavy reliance on the extensive, unregulated consumption of marine gastropods as a protein source. An accurate species identification system of edible gastropods using a less invasive but highly accurate, simple, and economical

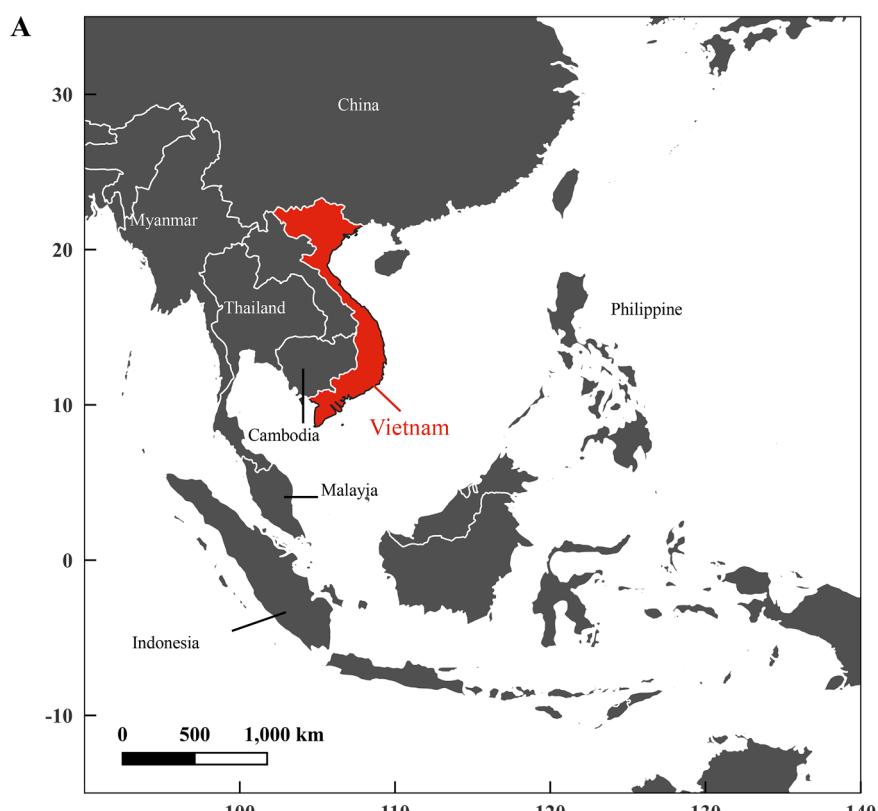


Fig. 1. (A) Map of Vietnam. (B) Pictures of a fish market in Vietnam and Vietnamese gastropod cuisine. Some of the samples of edible shelled gastropods analyzed in this study were collected here. The map was created with Natural Earth (<https://www.naturalearthdata.com/about/terms-of-use/>).

method is an urgent issue that needs to be addressed to improve local Vietnamese fisheries and fish market management, safety, controls, and traceability.

Species identification has traditionally relied on morphological methods, which require specialized knowledge and years of practice but can be challenging, especially when species or individuals at certain developmental stages appear similar and difficult to differentiate (Hebert et al., 2003b; Meier et al., 2006). Additionally, accurate identification of species often requires sacrificing samples, which might result in a decrease or loss of yield and/or the commercial value of the samples. Furthermore, it is not practical to sample and identify all caught individuals, which could lead to only a small subset of individuals being randomly chosen for identification. This can be problematic, especially when rapid and accurate identification related to food safety is required.

DNA barcoding has emerged as a practical solution for quick and accurate species identification using short DNA fragments from specific gene markers (Hebert et al., 2003b). This method is less invasive than morphological inspections and allows the rapid analysis of a much larger number of samples, making it particularly useful for species identification in food safety contexts and thus ensuring proper traceability (Collins et al., 2012; Ferrito and Pappalardo, 2017; Stern et al., 2017; Minoudi et al., 2020; Keskin and Atar, 2013; Ghouri et al., 2020). In addition, DNA barcoding has been shown to work on cooked and processed foodstuffs (Ferrito and Pappalardo, 2017; Pollack et al., 2018). DNA barcoding is particularly effective due to recent developments in DNA sequencing methods and the establishment of reference sequence databases (Nakazato and Jinbo, 2022).

The mitochondrial gene *cytochrome c oxidase subunit I* (COI) is a widely used marker for DNA barcoding of metazoans, including fisheries species and marine gastropods (Hebert et al., 2003a; Borges et al., 2016). However, the use of multiple gene markers can further improve the accuracy and reliability of barcoding results (e.g., Buhay, 2009; Setiamarga et al., 2019; De Mattia et al., 2012; Talavera et al., 2022; Vitecek et al., 2017). Markers such as the mitochondrial gene 12S-rRNA (12S) and the nuclear genes 18S-rRNA (18S), 28S-rRNA (28S), and *histone H3* (H3) are widely used for molecular phylogenetics and species delimitation of metazoans (Fukunaga et al., 2021; Oliverio and Mario-ttini, 2001; Bandyopadhyay et al., 2008; Koufopanou et al., 1999; Zhan et al., 2013; Whiting et al., 1997; Colgan et al., 1998). Although genetic distance analysis can confirm species delimitation, especially for closely related sister species that are morphologically similar (Bandyopadhyay et al., 2008; Teruya et al., 2022; Puillandre et al., 2010; Ekimova et al., 2022), the threshold for delimitation varies widely among species and genetic markers (Petit and Excoffier, 2009; Yang and Rannala, 2010; Luo et al., 2018; Hillis, 2019), requiring additional threshold data from various gastropod species to improve accuracy. Nevertheless, DNA barcoding remains a powerful tool for species identification, particularly when rapid and accurate results are required, such as for food security or safety issues (Keskin and Atar, 2013; Ghouri et al., 2020; Tinacci et al., 2018).

Tying DNA barcoding data to morphological identifications can improve the accuracy and reliability of species identification (Hebert et al., 2003b). Accordingly, molecular approaches are often applied within an iterative taxonomy framework, which treats species boundaries as testable hypotheses evaluated using multiple independent lines of evidence (Will et al., 2005; Yeates et al., 2011). In this approach, species boundaries are first hypothesized using one dataset, such as morphology, and then evaluated using another dataset, such as DNA barcoding (Padial et al., 2010; Will et al., 2005; Schlick-Steiner et al., 2010). This increases the reliability of species delimitation, especially in applications that require high accuracy such as biodiversity assessments and food safety monitoring.

When applied to voucherized museum specimens, iterative taxonomy that includes DNA barcoding forms the basis of museomics, an innovative approach that integrates molecular data with museum collections

(Lalueza-Fox, 2022). The use of voucherized specimens (museum-preserved samples), particularly those documenting traditional and cultural items (e.g., Hartnup et al., 2011), ensures accuracy and reliability due to their detailed cataloguing and documentation (Raxworthy and Smith, 2021). Integrating molecular data with voucherized specimens and museum records enhances species identification and enables researchers to track changes in species distributions and genetic variations (Nakahama et al., 2018), thereby supporting biodiversity monitoring and sustainable resource management (Nakahama, 2021). This is particularly relevant for food systems, where reliable reference databases enable accurate identification, critical for traceability, resilience, and sustainable marine resource utilization.

In this study, by using the iterative taxonomy framework, we investigated the taxonomic placement of gastropods sold at Vietnamese fish markets (Fig. 2; Supp. Table 1) using a DNA barcoding-based museomics approach. The samples were collected, morphologically identified, and voucherized at The University Museum of The University of Tokyo (UMUT). We utilized partial sequences from multiple gene markers (COI, 12S-rRNA, 18S-rRNA, 28S-rRNA, and histone H3) to improve species identification accuracy and phylogenetic resolution at both species and higher taxonomic levels (Fukunaga et al., 2021; Setiamarga et al., 2019) by providing a subset of independent lines of molecular evidence, alongside morphology, for iterative taxonomy (Gatesy et al., 1999; Yeates et al., 2011). Our analyses also provided insights into the current state of gastropod reference data in GenBank and produced reliable data for future biodiversity assessments. In addition to contributing taxonomic information on edible Vietnamese gastropods, this study supports the development of a reference database for biodiversity monitoring and food safety research. Overall, our findings demonstrate the utility of DNA barcoding for improving food safety and sustainability in Vietnam's seafood markets.

2. Materials and methods

2.1. Taxon sampling

Samples of shelled gastropods were collected from various fish markets in Vietnam in February and March 2015, March 2016, February 2017, and March 2018 (Fig. 1; Fig. 2; Fig. 3; Supplementary Table S1). Interviews with fishermen and sellers conducted by one of the authors (DVT) confirmed that the gastropod samples used in this study were locally caught from the surrounding coastal area near the markets where they were sold. Collected specimens were first morphologically identified (= "morphospecies"), fixed in 99.5 % EtOH, and then divided into two sets. One primary set of specimens was deposited at the Institute of Ecology and Biological Resources (IEBR) in Vietnam, and another set was deposited at The University Museum, The University of Tokyo (UMUT), under an official access and benefit sharing (ABS) agreement between IEBR and UMUT. For genetic analysis, we subsampled 126 of the voucherized specimens from the UMUT collection to roughly represent the morphospecies (Supplementary Table S1; Supplementary Table S2). Whenever possible, we obtained multiple individuals from one morphospecies. Morphological identification indicated that our samples included 109 Caenogastropoda, three Heterobranchia, five Patellogastropoda, and nine Vetigastropoda. Of these, 113 samples were morphologically identified to the species level (53 species), while 13 samples were identifiable only to the genus level. These morphospecies have also been reported as native Vietnamese species (Do et al., 2019, 2021).

2.2. DNA extraction and sequence acquisition

Approximately 25–30 mg of mantle tissue was excised from each sample. Genomic DNA was extracted from the tissue samples using the standard CTAB-phenol-chloroform method. Partial sequences of the COI, 12S-rRNA, 18S-rRNA, 28S-rRNA, and histone H3 genes were

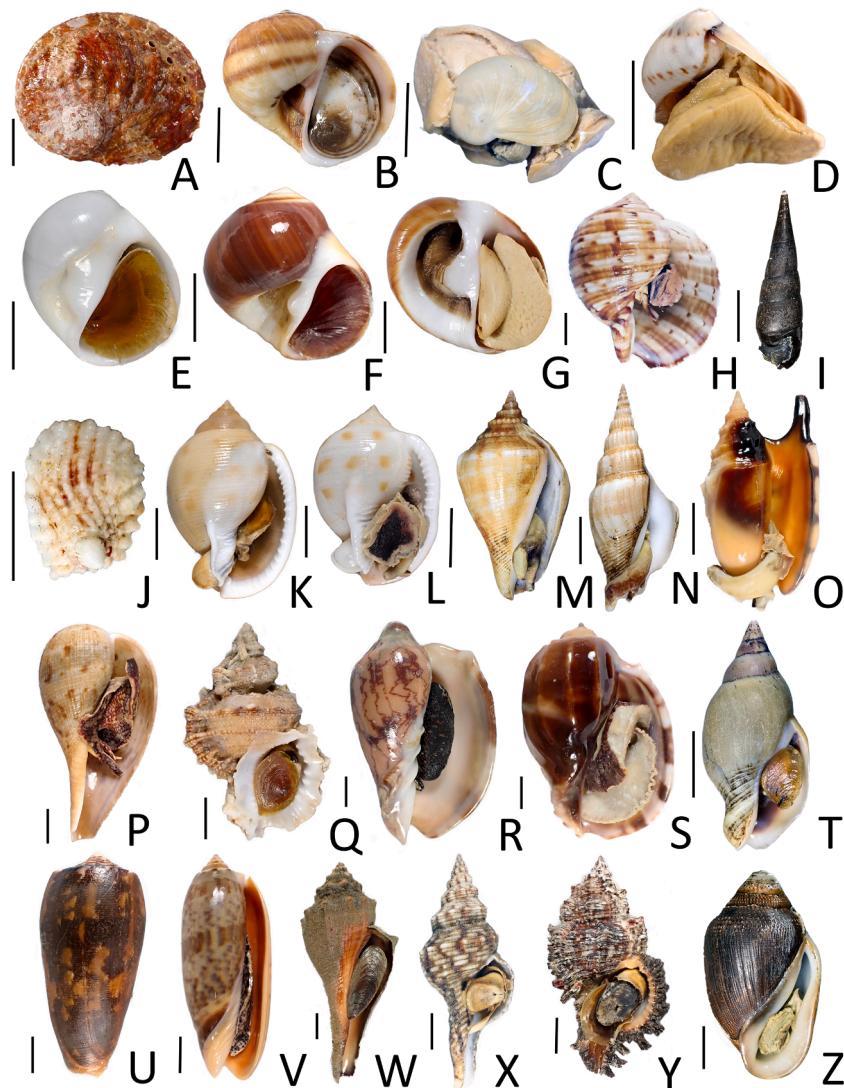


Fig. 2. Pictures of some of the newly sequenced species in this study. (A). *Haliotis ovina* (Vt023). (B). *Natica spadicea* (Vt001). (C). *Sinum planulatum* (Vt112). (D). *Mammilla melanostomoides* (Vt054). (E). *Polinices mammilla* (Vt021). (F). *Polinices powisianus* (Vt036). (G). *Polinices albumen* (Vt048). (H). *Tonna chinensis* (Vt182). (I). *Faunus ater* (Vt149). (J). *Sabia conica* (Vt003). (K). *Semicassis bisulcata* (Vt004). (L). *Semicassis bisulcata pila* (Vt035). (M). *Neodilatilabrum robustum* (Vt105). (N). *Doxander vittatus* (Vt039). (O). *Euprotomus aratrum* (Vt058). (P). *ficus* (Vt028). (Q). *Tutufa oyamai* (Vt019). (R). *Cymbiola nobilis* (Vt136). (S). *Harpa major* (Vt033). (T). *Tomlinia frausseri* (Vt204). (U). *Conus striatus* (Vt022). (V). *Oliva miniacea* (Vt005). (W). *Brunneifusus ternatanus* (Vt219). (X). *Marmorofusus nicobaricus* (Vt188). (Y). *Chicoreus miquellus* (Vt100). (Z). *Ellobium aurismidae* (Vt208). Scales = 1 cm.

amplified using standard PCR protocols with modified annealing temperatures and previously reported primers. PCR was performed using one annealing temperature in one set of cycles (one step) and two sets of cycles with different annealing temperatures (two steps). PCR and primer are details provided in Supplementary Table S3. Successfully amplified samples were Sanger sequenced in both directions using respective forward and reverse primers (outsourced to FASMAC Ltd., Kanagawa, Japan). Sequence assemblies of the successfully sequenced forward and reverse sequences were conducted either manually using the online version of MAFFT ver. 7 (<https://mafft.cbrc.jp/alignment/server/>; accessed between February 2019 and June 2022) (Katoh et al., 2019) or automatically using the online version of CAP3 (<https://doua.prabi.fr/software/cap3>; accessed in February 2019) (Huang and Madan, 1999).

2.3. DNA barcoding through BLASTn searches

To confirm the identity of the obtained sequences, BLASTn searches on the NCBI nucleotide database were conducted using assembled

contigs as queries in May 2022 and July 2023 for initial screenings, and in March 2025 for the final confirmation (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>). Taxonomic confirmation of accepted species names follows the information provided in WoRMS (World Register of Marine Species; www.marinespecies.org) and MolluscaBase (<https://www.molluscabase.org/>), both accessed in December 2021 and June 2023 for initial screenings (Supplementary Table S4), and in March 2025 for the final confirmation (Supplementary Table S5).

To improve the accuracy of evaluating congruence between morphological identifications and BLASTn-based species assignments, we established a set of rules for determining homology level based on taxonomic synonymy and accepted species names. We applied the following criteria: (1) when both the morphological identification and the BLASTn hit referred to a single taxonomic name, whether accepted or a synonym, we treated them as matching at the species or genus level; (2) when the two names were different but both were unaccepted synonyms of the same accepted name, we treated them as matching; (3) when the two names were both accepted names but had a shared unaccepted synonym, we did not consider them as matching; (4) when

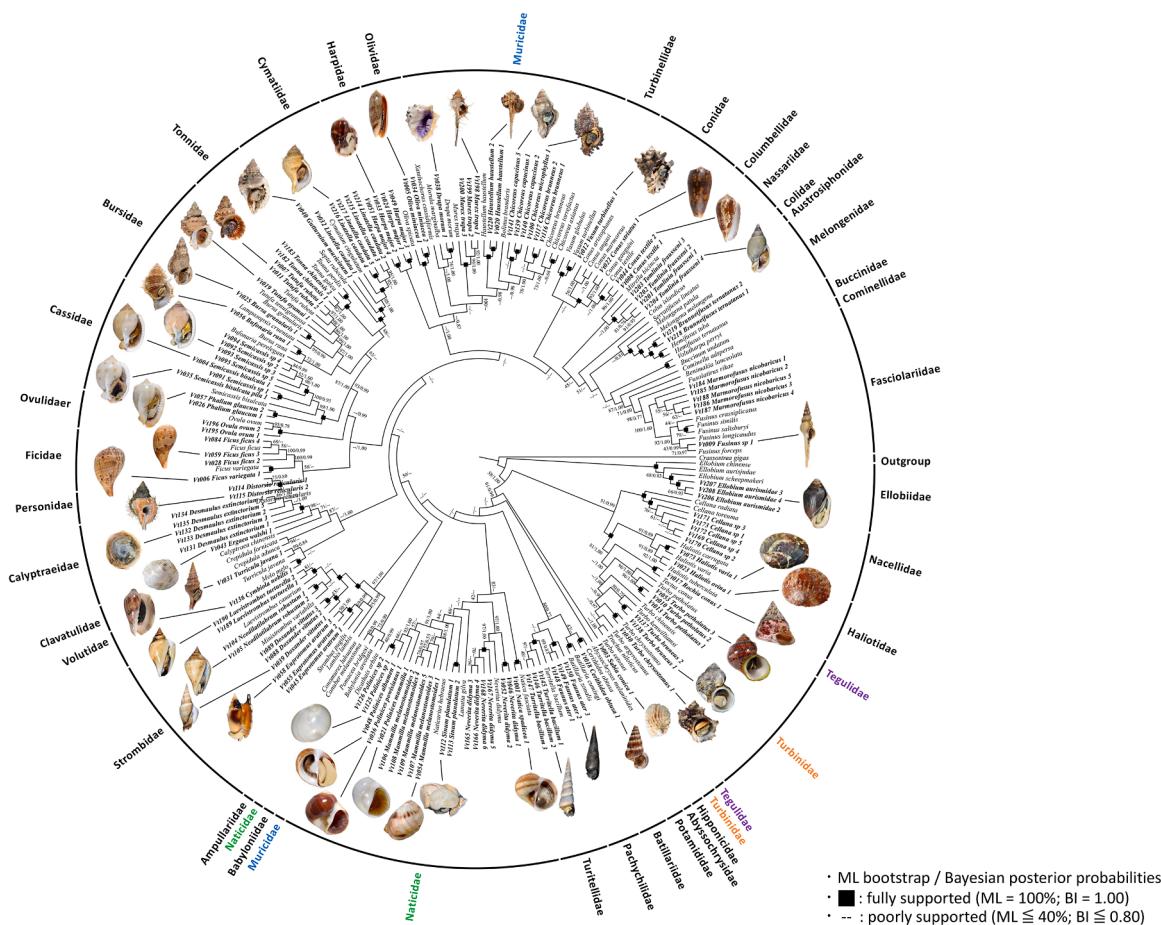


Fig. 3. Maximum Likelihood and Bayesian trees inferred from Dataset 1. Monophlyies of most families (with the exceptions of Muricidae, Naticidae, Tegulidae, and Turbinidae; shown in blue, green, purple, and orange, respectively), genera, and species were recovered. A detailed explanation is provided in the manuscript. Fully supported nodes (BS = 100 %, PP = 1.00) are denoted by black squares on the nodes, while bootstrap support values lower than BS = 40 % and PP = 0.80 are denoted with “–”. Branch lengths are not shown. Versions with the branch lengths shown are given in Supplementary Fig. S1 for the Maximum Likelihood tree, and Supplementary Fig. S2 for the Bayesian Inference tree.

both names were unaccepted synonyms of each other and their respective accepted names differed, we also treated them as non-matching; (5) when one name was a synonym of the other, and the accepted name was either one of the two, we treated them as matching; and (6) when two names had previously been treated as synonyms of each other but are now both accepted as distinct species, we treated them as non-matching. These rules were applied uniformly across all five gene markers. This framework allowed us to minimize false matches due to outdated or inconsistent nomenclature in GenBank and provided a more taxonomically robust assessment of homology-level identification.

Our stepwise evaluation of agreement between different taxonomic data (morphological vs. molecular) reflects the logic of iterative taxonomy, in which species hypotheses are tested and refined using independent datasets (Will et al., 2005; Yeates et al., 2011).

2.4. Dataset building

Assembled sequence contigs were aligned using the online version of MAFFT ver. 7 (accessed in June 2023) (Katoh et al., 2019), with G-INS-I for protein-coding genes (COI and histone H3) to allow for global alignments and Q-INS-I for ribosomal RNA-coding genes (12S-rRNA, 18S-rRNA, 28S-rRNA) to allow for the consideration of the secondary structure of RNA. Ambiguously aligned sequences were removed using trimAL (Capella-Gutiérrez et al., 2009) with the gappyout setting and used in subsequent analyses. Eight datasets were built and analyzed (Supplementary Table S6). Homologues of the five markers of

Crassostrea gigas were obtained from GenBank to be used as outgroups in subsequent analyses (accessed and obtained in August 2022). The sequences were added to our sequences using the -add function in MAFFT. Sequences with BLASTn hits were also acquired and added using the -add function to Datasets 1 and 3.

2.5. Species delimitation analysis

To assess species delimitation, genetic distances were calculated for all five genes using the Kimura 2-parameter (K2P) model (Pmin: 0.001; Pmax: 0.1; Step: 10; X (relative gap width: 1.0)) in the Automatic Barcode Gap Discovery (ABGD) program (Puillandre et al., 2012) on post-alignment Datasets 4–8 (single-gene datasets) prior to the addition of the outgroup. A total of 126 samples, including 53 morphologically identified and 13 unidentified species, were used for this analysis, and only those for which sequence data were obtained in this study were analysed by ABGD (53 morphologically identified + 13 unidentified species = 126 samples for COI; 48 morphologically identified + 11 unidentified species = 111 samples for 12S-rRNA; 52 morphologically identified + 13 unidentified species = 125 samples for 18S-rRNA; 48 morphologically identified + 13 unidentified species = 106 samples for 28S-rRNA; 47 morphologically identified + six unidentified species = 100 samples for histone H3) (Table 1).

This analysis is intended to provide a general overview of genetic distance patterns across markers to support barcoding evaluation and not intended for formal species delimitation. The complete pairwise

Table 1

Number of specimens and morphospecies with successful sequence acquisition.

gene	Mitochondrial		Nuclear		
	COI	12S	18S	28S	H3
samples	126–13=113	111–11=100	125–13=112	106–13=93	100–6 = 94
morphospecies	53	48	52	48	47

Sample counts indicate individuals for which sequences were successfully obtained (detailed in Supplementary Table S1). Subtracted numbers denote specimens unidentifiable to species level. For example, COI sequences were obtained for all 126 specimens used in this study, including 13 that were morphologically unidentifiable.

distance datasets used for this analysis are provided in Supplementary Dataset in xlsx format, allowing researchers to explore intraspecific and interspecific distances at different taxonomic levels as needed.

2.6. Phylogenetic analysis

Phylogenetic inferences were conducted across Gastropoda because our samples included morphospecies from multiple major lineages. This was necessary to assess whether morphologically identified taxa formed monophyletic clades, as well as to evaluate the resolution of each gene marker at species and higher taxonomic levels. A relatively resolved tree also provides an intuitive visual representation of taxonomic congruence, particularly for assessing the monophyly of focal taxa. Moreover, given the poor representation of tropical gastropods in public databases, phylogenetic support was essential for validating species identification.

Heuristic Maximum Likelihood (ML) phylogenetic inferences were conducted for all eight datasets with RAxML-GUI 2.0 beta (Edler et al., 2021), using the GTRGAMMAI model with 1000X bootstrap iterations. Model selection was conducted in MEGA X (Kumar et al., 2018) with default settings. GTRGAMMAI was selected as the best model under both BIC (Schwarz, 1978) and AIC (Hurvich and Tsai, 1989) for all partitions. For Datasets 1 and 2, in which all gene sequences were concatenated, datasets were partitioned per gene.

To confirm the robustness of the datasets and resulting phylogenies despite the use of different inference methods, Bayesian inference was conducted on Datasets 1, 2, and 4 in MrBayes 3.2.7a (Ronquist and Hulsenbeck, 2003) with nst = 6, rate = invgamma, and mcmc ngen = 5000,000. Trees were sampled every 1000 generations. The first 40 % (for Dataset 1) and 10 % (for Datasets 2 and 4) of the trees were discarded as burn-in. Burn-in for each dataset was decided based on log-likelihood trace plots and effective sample size values, visualized in Tracer v.1.7.2 (Rambaut et al., 2018), to ensure that only post-convergence samples were used for the final consensus tree construction.

3. Results

3.1. Sequence data acquisition

In this study, from a total of 126 samples, 113 samples were morphologically identified into 53 species (Table 1). We successfully obtained sequences for all samples, although not all genes were available for every sample (Table 1, Supplementary Table S1). Specifically, we obtained sequences for 100 % (126/126) of the samples for COI, 88 % (111/126) for 12S-rRNA, 99 % (125/126) for 18S-rRNA, 84 % (106/126) for 28S-rRNA, and 79 % (100/126) for histone H3. COI sequences were available for all samples, and we obtained sequence data for at least three genes (COI and two others) for every sample, with histone H3 having the lowest coverage (79 %). The total sequence lengths before alignment and editing were approximately 560 bp for COI, 560 bp for 12S-rRNA, 480 bp for 18S-rRNA, 770 bp for 28S-rRNA, and 370 bp for histone H3. After alignment and removal of ambiguously aligned regions, the retained sequence lengths were 555 bp for COI, 606 bp for 12S-rRNA, 375 bp for 18S-rRNA, 609 bp for 28S-rRNA, and 354 bp for histone H3. These results thus demonstrate that the primers used in this

study are suitable for DNA barcoding of shelled gastropods.

3.2. Results of DNA barcoding based on BLASTn searches

Of the 126 gastropod samples used in this study, 113 individuals were morphologically identified as 53 species (“morphospecies”), while 13 samples remained unidentifiable at the species level (Supplementary Table S1). GenBank searches using the 53 morphospecies names as queries indicated an increase in the number of morphospecies registered on GenBank, with the number of morphospecies lacking registered sequences decreasing from 13 (49 individuals) in July 2023 to eight (17 individuals) by March 2025, with the proportion of morphospecies represented in GenBank increased for each marker, rising from 66 % to 83 % of the 53 species for COI, 46 % to 69 % of the 48 species for 12S-rRNA, 29 % to 37 % of the 52 species for 18S-rRNA, 40 % to 58 % of the 48 species for 28S-rRNA, and 30 % to 34 % of the 47 species for histone H3 (Table 2). The differing species count for each gene reflects that only COI sequences were obtained for all samples (Table 1; Supplementary Table S1). Species-level hit rates based on BLASTn searches improved from 2023 to 2025 across all gene markers (Table 3; Supplementary Table S4; Supplementary Table S5; Supplementary Table S7). For the 113 morphologically identified individuals (Species a), hit rates increased from 51 % to 65 % for COI, 29 % to 52 % for 12S-rRNA, 4 % to 13 % for 18S-rRNA, 15 % to 19 % for 28S-rRNA, and 22 % to 25 % for histone H3. For all 126 samples (Species b), hit rates increased from 54 % to 67 % for COI, 35 % to 65 % for 12S-rRNA, 8 % to 15 % for 18S-rRNA, 14 % to 24 % for 28S-rRNA, and 21 % to 23 % for histone H3. At the family level, the mismatches between morphology-based identities and BLASTn hits in 2025 for all 126 individuals were 4 % for 12S-rRNA, 18 % for 18S-rRNA, 5 % for 28S-rRNA, and 15 % for histone H3, while all COI sequences matched morphology at the family level. This is a significant increase from the result of 2023 (6 % for COI, 5 % for 12S-rRNA, 29 % for 18S-rRNA, 5 % for 28S-rRNA, and 19 % for histone H3).

We successfully identified 10 of the 13 individuals for which we were unable to assign a species-level identification based on morphology into two species, *Semicassis bisulcata* and *Cellana toreuma* (Supplementary Table S4; Supplementary Table S5). Five individuals (Vt091–095), which were identified only at the genus level (*Semicassis* sp.) by morphology, were confirmed as *Semicassis bisulcata* (GenBank Accession no. MH581369.1 and JF693409.1; e-value 0.00, identity 91.71–99.68 % (COI), MH571301.1; e-value 9.00E-179–2.00E-175, identity 95.00–95.50 % (12S-rRNA)). Our phylogenetic trees (e.g., Figs. 3 and 4; reported in 3.3) also supported this identification: The four individuals form a monophyletic clade with Vt004 and Vt035, both were morphologically identified as *S. bisulcata*. However, species- and genus-level data were not available in public databases for the remaining markers, reflecting the continued lack of species-level reference data for this species in public databases. Similarly, another five individuals (Vt169–173), which were identified only as *Cellana* sp. by morphology, matched the sequence of *Cellana toreuma* (GenBank Accession no. KR132887.1; e-value 0.00, identity 99.84–100 % (COI), GQ455887.1; e-value 0.00–1E-159, identity 97.66–97.97 % (12S-rRNA), AF308646.1; e-value 0.00, identity 99.59–99.62 % (18S-rRNA)). While only three markers yielded matches in 2023, the 2025 BLASTn update additionally

Table 2

Species-level GenBank availability of target genes for 53 morphologically identified species.

gene	Mitochondrial				Nuclear				All			
	COI	12S	18S	28S	H3	2025	2023	2025	2023	2025	2023	2025
Year	2023	2025	2023	2025	2023	2025	2023	2025	2023	2025	2023	2025
Number of species	53	53	48	48	52	52	48	48	47	47	53	53
Genbank	35	44	22	33	15	19	19	28	14	16	40	45
(%)	66 %	83 %	46 %	69 %	29 %	37 %	40 %	58 %	30 %	34 %	75 %	85 %

Table 3

Hit rate of BLASTn searches at each taxonomic level for each gene.

Gene	Mitochondrial				Nuclear				All genes			
	COI	12S	18S	28S	H3	2025	2023	2025	2023	2025	2023	2025
Year	2023	2025	2023	2025	2023	2025	2023	2025	2023	2025	2023	2025
Class	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %
Subclass	98 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %	100 %
Order	95 %	100 %	98 %	100 %	90 %	100 %	100 %	100 %	94 %	100 %	100 %	100 %
Superfamily	95 %	100 %	98 %	100 %	83 %	85 %	95 %	95 %	86 %	86 %	100 %	100 %
Family	94 %	100 %	95 %	96 %	71 %	82 %	95 %	95 %	81 %	85 %	99 %	100 %
Subfamily	85 %	93 %	81 %	93 %	53 %	53 %	68 %	69 %	51 %	54 %	98 %	98 %
Genus	81 %	89 %	73 %	86 %	29 %	34 %	47 %	49 %	44 %	49 %	94 %	94 %
Species ^a	56 %	65 %	29 %	52 %	4 %	13 %	15 %	19 %	22 %	25 %	65 %	79 %
Species ^b	50 %	59 %	26 %	47 %	4 %	11 %	14 %	18 %	21 %	23 %	58 %	71 %
Species ^c	58 %	67 %	35 %	57 %	8 %	15 %	14 %	24 %	21 %	23 %	66 %	79 %

Species a: Samples morphologically unidentifiable at the species level were excluded from the analysis.

Species b: Samples morphologically unidentifiable at the species level were treated as genus-level matches.

Species c: Samples morphologically unidentifiable at the species level but treated as species-level matches when the same species was consistently inferred by BLAST results across multiple genetic markers, were included in the analyses as species-level matches.

recovered a 28S-rRNA match. All five individuals matched *Cellana torreuma* (LC535312.1; e-value 0.00, identity 99 %), which further confirms our previous result.

3.3. Molecular phylogenetics and taxonomic insights

We obtained well-resolved phylogenetic trees across multiple datasets, allowing us to evaluate taxonomic congruence at species, genus, and higher levels. To assess phylogenetic resolution and topological consistency, we conducted analyses based on eight datasets that differed in gene composition and the inclusion of GenBank sequences. In this section, we focus on three representative datasets: Dataset 1, which includes concatenated sequences of five genes (COI, 12S-rRNA, 18S-rRNA, 28S-rRNA, and histone H3) from our samples together with corresponding sequences retrieved from GenBank; Dataset 2, which includes only our newly obtained sequences of the same five genes, also concatenated; and Dataset 3, which includes only our newly obtained COI sequences combined with COI sequences retrieved from GenBank. Fig. 3 shows the maximum likelihood (ML) tree inferred from Dataset 1, Fig. 4 the ML tree inferred from Dataset 2, and Fig. 5 the ML tree from Dataset 3. In all trees, bootstrap support values and posterior probabilities from Bayesian inference are plotted on the corresponding nodes. Maximum likelihood trees with branch lengths depicted are presented in Supplementary Fig. S1, Supplementary Fig. S3, and Supplementary Fig. S5. Meanwhile, Bayesian trees are presented in Supplementary Fig. S2, Supplementary Fig. S4, and Supplementary Fig. S6.

The overall topologies were relatively congruent across datasets, particularly at the species and genus levels, with all species and genera recovered as monophyletic, except for some inconsistencies involving GenBank-retrieved sequences. However, differences became more apparent at higher taxonomic levels, especially among subfamilies and families. The COI-only tree (Fig. 5; Dataset 3) generally resembled those based on multi-gene datasets but exhibited lower or no support for some clades. Datasets 1 and 2 both yielded well-resolved trees, although their resolution varied depending on taxonomic level and the inclusion of GenBank sequences. Dataset 2 (Fig. 4), which excluded GenBank data,

showed clearer monophyly at the subfamily and family levels, whereas Dataset 1 (Fig. 3), which incorporated GenBank sequences, showed slightly reduced resolution in some higher-level clades. These differences may reflect variability in the annotation or taxonomic consistency of publicly available sequences. Across Datasets 1 and 2, monophyly was consistently recovered at the species and genus levels, while some subfamilies and families were not monophyletic (e.g., subfamilies: Naticinae and Polinicinae; families: Muricidae, Naticidae, Tegulidae, and Turbinidae, in Fig. 3; subfamilies: Polinicinae, families: Muricidae in Fig. 4).

3.4. Species delimitation and genetic distance analysis

Species delimitation was carried out for each gene, for which the result showed that species boundaries differed for each genetic marker. Species delimitation based on the COI and 12S-rRNA genes resulted in different identification results between morphospecies and “molecular” species, with more species being identified molecularly. For example, species delimitation using COI sequences classified the 113 morphologically identifiable samples (of the total of 126 individuals as 53 morphospecies) as 60 molecular species, with 24 individual samples not overlapping between the morpho- and molecular species (Table 4; Table 5; Supplementary Table S8). For example, although Vt024, Vt033, Vt049, and Vt051 were all identified as one morphospecies, *Harpa major*, ABGD assigned Vt024 and Vt049 to molecular species Group 46 (genetic distance: 0.0 %), while Vt033 and Vt051 were assigned to Group 47 (genetic distance: 0.4 %). The genetic distance between the two groups is 7.2 % (± 0.0000), while the average genetic distance of the four individuals is 4.9 % (± 0.0332). Although both Vt004 and Vt035 were morphologically identified as *Semicassis bisulcata*, their genetic distance is relatively high at 8.7 %. ABGD assigned Vt004 to distinct molecular species Group 26 and Vt035 to Group 27. BLASTn search of Vt035, however, returned a hit to the subspecies *S. bisulcata pilosa*. In another example, Vt131–Vt135 were morphologically identified as *Desmaulus extlectorium*. However, ABGD split them into three molecular species: Vt131 was assigned to Group 5, Vt132, Vt134, and

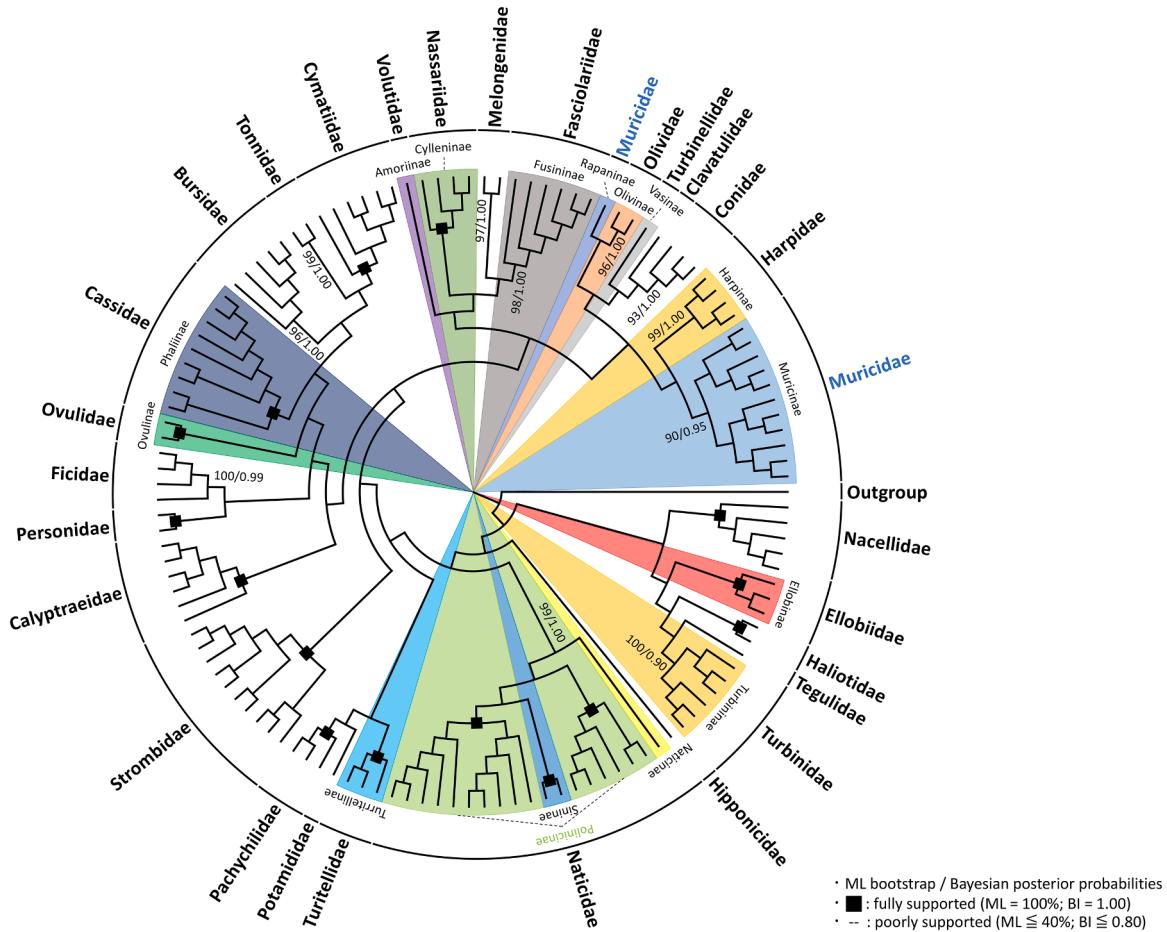


Fig. 4. Maximum likelihood and Bayesian trees inferred from Dataset 2. Monophlyies of most families (with the exceptions of only Muricidae; depicted in blue), genera, and species were recovered. A detailed explanation is provided in the manuscript. Only the bootstrap supports of families are shown. Fully supported nodes (BS = 100 %, PP = 1.00) are denoted by black squares on the nodes, while bootstrap support values lower than BS = 40 % and PP = 0.80 are denoted with “–”. Branch lengths are not shown. Versions with the branch lengths shown are given in Supplementary Fig. S3 for the Maximum Likelihood tree, and Supplementary Fig. S4 for the Bayesian Inference tree.

Vt135 to Group 58, and Vt133 to Group 59. The genetic distance between Group 5 and Group 58 is 0.0018 (± 0.0982), while that between Group 5 and Group 59 is 0.0036. Group 58 and Group 59 differ by 0.0018 (± 0.000). The average genetic distance among the five individuals is 0.0018 (± 0.0011). BLASTn searches in 2023 and 2025 of these sequences returned hits to *Bicatillus extictorum* (AF546061.1), an unaccepted synonym of *D. extictorum*, and can thus be considered as a species-level concordant. The summary of COI genetic distance comparisons for morphospecies split into multiple molecular species is shown in Supplementary Table S9.

The average genetic distance for COI at the intraspecies level was 1.2 % (\pm 0.0034), while the average genetic distance at the interspecies level (excluding unidentified species designated as "sp.") was 13.7 % (\pm 0.0094). The intraspecific distance of Caenogastropoda is 1.3 % (\pm 0.0038), and the interspecific distance is 11.7 % (\pm 0.0069). Meanwhile for Vetigastropoda, the intraspecific distance is 0.7 % (\pm 0.0025) and the interspecific distance is 18.6 % (\pm 0.0170). A summary of the average genetic distances for each marker, including COI, is provided in Table 5.

Species delimitation using 12S-rRNA also resulted in 56 molecular species because the same morphospecies were classified into different molecular species as with COI. 18S-rRNA and 28S-rRNA yielded fewer molecular species than morphospecies because some different morphospecies were classified as the same molecular species. Meanwhile, for species delimitations based on histone H3, some different morphospecies were classified as the same molecular species, while some

individuals belonging to the same morphospecies were classified as different molecular species. The result is summarized in [Table 4](#) and [Supplementary Table S8](#).

4. DISCUSSION

4.1. The diversity of marine gastropods being consumed in Vietnam

Our study reveals a fascinating diversity of at least 55 marine gastropod species consumed in Vietnam, all identified from museum-voucherized specimens collected from wet fish markets. Among them, 53 species were identified through morphology and corroborated molecularly through DNA barcoding, while an additional two species were identified solely through molecular data. This finding helps fill existing gaps in species-level records for edible marine gastropods in Vietnam. The confirmed consumption of >50 species of marine gastropods in Vietnam suggests their potential as a sustainable and resilient protein source, while also offering insights into how culturally significant food sources could be developed for future food systems. However, we also would like to emphasize that realizing this potential requires ecological safeguards, including improved traceability, responsible management of wild harvest, and prioritization of sustainable aquaculture. Such development can be assisted by the methods and data presented here, which contribute to the development of reference sequence databases and provide a foundation for future biodiversity assessments and monitoring.

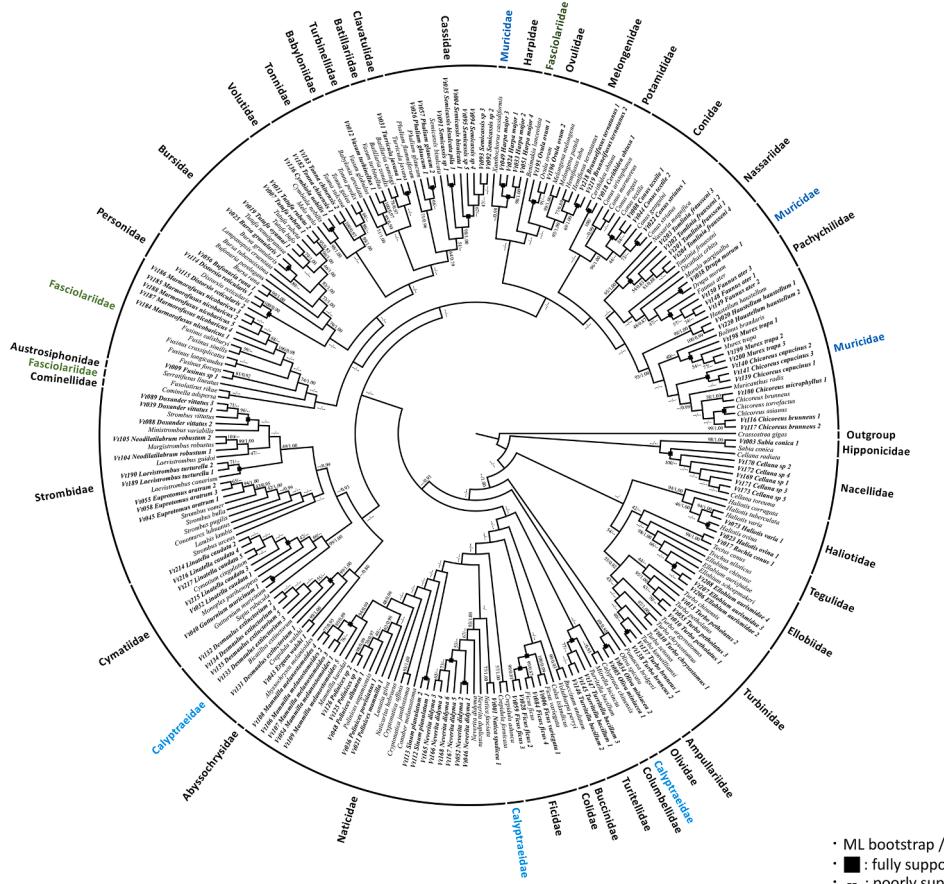


Fig. 5. Maximum likelihood and Bayesian trees inferred from Dataset 3 (single gene: COI). Monophlyies of most families (with the exceptions of Calyptraeidae, Fascioliidae, and Muricidae; shown in light blue, dark green and blue, respectively). A detailed explanation is provided in the manuscript. Fully supported nodes ($BS = 100\%$, $PP = 1.00$) are denoted by black squares on the nodes, while bootstrap support values lower than $BS = 40\%$ and $PP = 0.80$ are denoted with “–”. Branch lengths are not shown. Versions with the branch lengths shown are given in Supplementary Fig. S5 for the Maximum Likelihood tree, and Supplementary Fig. S6 for the Bayesian Inference tree.

Table 4
Number of morphospecies vs. delimited molecular species for each gene marker

gene	Mitochondrial		Nuclear		
	COI	12S	18S	28S	H3
Morphospecies	53	48	52	48	47
Molecular Species	60	56	36	38	45

The identified species spanned four major lineages within Gastropoda (Caenogastropoda, Vetigastropoda, Patellogastropoda, and Heterobranchia), with 85 % of the consumed species morphologically classified as Caenogastropoda (82 % when including the successfully barcoded samples). None of the species identified in this study belonged to groups rarely or never reported as edible, such as opisthobranchs. This suggests that the species diversity documented here remains within the culturally or ecologically feasible scope of marine food consumption and thus supports the relevance of our sampling to actual market availability and dietary practices in Vietnam. Furthermore, out of the 55 species (53 morphospecies and 2 species identified through DNA barcoding), 24 % (in July 2023) and 14 % (in March 2025) had limited or no representation in public genetic databases, particularly for the 18S-rRNA (although slightly increasing from 29 % in 2023 to 37 % in 2025) (Table 2), highlighting the scarcity of curated molecular data for edible marine gastropods in the region. The combined use of morphological identification and multi-marker barcoding applied to voucherized specimens provides a consistent and verifiable approach that supports

future biodiversity monitoring, food traceability studies, and the continued refinement of reference databases. These findings underscore the value of integrating museum-based sampling with molecular methods to enhance documentation of marine invertebrate diversity, particularly in documenting underrepresented and underexplored biodiversity in the tropical regions such as Vietnam in particular, and Southeast Asia in general.

4.2. Molecular insights into Vietnamese marine gastropod identification

The integration of molecular data into marine gastropod identification revealed valuable insights into the genetic diversity and taxonomic resolution afforded by DNA barcoding. COI, widely recognized as a universal marker for DNA barcoding of metazoans (Hebert et al., 2003a), provided the highest resolution for species-level identification among the markers analyzed (Hajibabaei et al., 2007; Bucklin et al., 2011; Trivedi et al., 2016; Folmer et al., 1994; Kano, 2008). We successfully obtained COI sequences for all samples, with genetic distance analyses demonstrating an average inter-species (congeneric) distance of 13.7 % (± 0.0094) and an intra-species distance of 1.2 % (± 0.0034), making it an effective benchmark for species delimitation (Table 5). The robustness of COI is further reflected in phylogenetic analyses, where its topology largely mirrored the results obtained from concatenated datasets (Figs. 3 and 4), albeit with reduced support in some clades (Fig. 5).

Interestingly, however, a discrepancy between the number of molecular species and morphospecies was detected in all genes, including

Table 5

Average pairwise genetic distances for each gene across taxonomic levels.

	COI	12S-rRNA	18S-rRNA	28Sr-RNA	Histone H3
All Gastropoda					
Inter-genus (confamilial)	13.7 % (±0.0175)	10.5 % (±0.0207)	0.6 % (±0.0043)	5.3 % (±0.0109)	3.7 % (±0.0070)
Inter-species (congeneric) ^a	10.9 % (±0.0136)	6.9 % (±0.0128)	0.1 % (±0.0001)	2.1 % (±0.0063)	1.9 % (±0.0052)
Inter-species (congeneric) ^b	13.7 % (±0.0094)	8.8 % (±0.0147)	0.1 % (±0.0002)	2.4 % (±0.0244)	2.3 % (±0.0058)
Intra-species	1.2 % (±0.0034)	1.3 % (±0.0047)	0.0 % (±0.0000)	0.5 % (±0.0026)	0.1 % (±0.0003)
Caenogastropoda					
Inter-genus (confamilial)	13.7 % (±0.0175)	10.5 % (±0.0207)	0.6 % (±0.0043)	5.3 % (±0.0109)	3.7 % (±0.0070)
Inter-species (congeneric) ^a	10.1 % (±0.0136)	6.9 % (±0.0120)	0.1 % (±0.0003)	1.5 % (±0.0037)	1.9 % (±0.0052)
Inter-species (congeneric) ^b	11.7 % (±0.0069)	8.0 % (±0.0126)	0.1 % (±0.0005)	1.5 % (±0.0227)	2.5 % (±0.0058)
Intra-species	1.3 % (±0.0038)	1.5 % (±0.0054)	0.0 % (±0.0000)	0.3 % (±0.0015)	0.1 % (±0.0003)
Vetigastropoda					
Inter-genus (confamilial)	—	—	—	—	—
Inter-species (congeneric) ^a	18.6 % (±0.0136)	6.9 % (±0.0252)	0.1 % (±0.0000)	7.1 % (±0.0245)	2.6 % (±0.0110)
Inter-species (congeneric) ^b	18.6 % (±0.0170)	12.9 % (±0.0252)	0.1 % (±0.0000)	7.1 % (±0.0710)	2.6 % (±0.0110)
Intra-species	0.7 % (±0.0025)	0.3 % (±0.0012)	0.0 % (±0.0000)	2.5 % (±0.0175)	0.0 % (±0.0007)

Inter-species (congeneric)^a: Including morphologically unidentifiable samples.Inter-species (congeneric)^b: Excluding morphologically unidentifiable samples.

COI, where the 113 individuals identified as 53 morphospecies were delimited into 60 species (Table 4; Table 5; Supplementary Table S8). When looked at more closely, it seems that ABGD split individuals from the same morphospecies into different molecular species when the genetic distance exceeded 3 %. This “3 % threshold” is commonly accepted as a ballpark for intraspecific variation (Meyer and Paulay, 2005; Buršić et al., 2021; Menabit et al., 2022). Such a difference might indicate demographical, population-level, geographical, or subspecies-level divergence. Therefore, further population genetic studies incorporating taxonomy will still be needed to clarify this. However, other studies have indicated that interspecific genetic distances in gastropods are typically between 2 % and 38 %, and intraspecific distances between 0 % and 7 % (Meyer and Paulay, 2005; Borges et al., 2016; Ran et al., 2020; Buršić et al., 2021; Menabit et al., 2022). Our results presented above are consistent with these ranges, and thus we believe are reasonable and robust, at least given the present availability of data.

Meanwhile, markers such as 12S-rRNA, 18S-rRNA, and histone H3 showed varying levels of effectiveness based on their substitution rates and evolutionary constraints. For example, 12S-rRNA achieved an inter-species resolution of 8.8 %, while 18S-rRNA and histone H3 had much lower inter-species distances (0.1 % and 2.3 %, respectively), which probably limit their ability to distinguish closely related species. These differences are due to variations in substitution rates, influenced by lineage sorting and selective pressures related to the functional roles of these genes (Dickerson, 1971; Yang and Rannala, 2010; Luo et al., 2018; Hillis, 2019; Alvarez-Ponce, 2021). Therefore, the multi-marker approach offers distinct advantages (Fukunaga et al., 2021; Quicke et al. 2012; Setiamarga et al., 2019; Alex Smith et al., 2013; Whitfield et al. 2002). Slower-evolving markers such as the nuclear gene markers can provide better resolution at broader taxonomic levels, while concatenating multiple gene sequences improves phylogenetic robustness (Figs. 3 and 4). Because each marker has its own limitations in coverage and performance, even COI (e.g. Meier et al., 2006), using multiple markers improves the reliability of identification, especially when reference data are incomplete. Our BLASTn searches also showed that species-level matches for the 113 morphologically identified samples were 58 % in 2023 and 79 % in 2025 when using all markers

combined, compared to 51 % in 2023 and 58 % in 2025 when using only COI (Table 3; Supplementary Table S7). These findings highlight the advantage of using multiple markers for species identification, particularly in field settings where traceability must be achieved quickly but accurately.

We provided the summary of genetic distances from this study as a quick and practical ballpark for field-based practitioners to assess the likelihood of species-level differences among edible marine gastropods (Supplementary Dataset).

4.3. Taxonomic nomenclature inconsistencies and their implications for identification and traceability

During this study, we encountered another important issue, where multiple inconsistencies between morphological identification and BLASTn hits were not due to genetic divergence but to discrepancies in taxonomic nomenclature across GenBank entries (Supplementary Table S4; Supplementary Table S5). These were identified through detailed synonym checks using WoRMS and MolluscaBase and corrected by aligning all names to their current accepted nomenclature.

For example, Vt003 was identified morphologically as *Sabia conica*, but in both our 2023 and 2025 BLASTn searches, its H3 sequence matched *Hipponix australis* (JF750988.1). Although the genus names differ, *Hipponix australis* is now regarded as a synonym of *Sabia australis*, and both names are currently placed in the genus *Sabia*. The result was therefore treated as genus-level concordant. Meanwhile, Vt003's 18S-rRNA sequence matched *Abyssochrysos melanioides* (AB930376.1), and was thus considered a subclass-level hit. The sample's 28S-rRNA matched conspecifically (AB930364.1) to *S. conica* in both 2023 and 2025 BLASTn searches. Although its COI matched *Hipponix* sp. (AF546073.1) in our 2023 search, it matched conspecifically to *S. conica* (MZ559574.1) in our 2025 search. Although *Hipponix australis* (Lamarck, 1819) is presently an unaccepted species, *Hipponix* is an accepted genus (*Hipponix* Blainville, 1819) (WoRMS, accessed in June 2025). However, since our 2023 COI BLASTn result matched only *Hipponix* sp., without species-level resolution, we interpreted this as subfamily-level concordant despite the accepted genus placement.

Another example is of Vt039, identified morphologically as *Doxander vittatus*. In our 2023 and 2025 BLASTn searches, the sample's COI matched *Strombus vittatus* (JF693433.1), a synonym of *D. vittatus*, and we thus treated this as a species-level match. However, Vt039's 12S-rRNA matched *Laevistrombus guidoi* (HQ401625.1) in 2023, and the full mitochondrial genome of *Dolomena robusta* (OR978594.1) in 2025. Although these names are currently accepted and each is linked historically to *Strombus*, at present, they do not share a common accepted name (WoRMS, accessed in May 2025; Maxwell et al., 2019; Irwin et al., 2024). Therefore, we treated this case as both genus- and species-level non-concordant. Vt039's 18S-rRNA hit *lambis* (HQ833996.1) in 2023, an unaccepted species. Since the species is now placed under the genus *Strombus*, and *Lambis* itself is an accepted genus, we also treated this as genus- and species-level non-concordant. Our 2025 result matched Vt039's 18S-rRNA with *Ministrobus variabilis* (MZ920131.1), an accepted species but historically also linked with *Strombus* and *Dolomena* (WoRMS, accessed in June 2025). However, we treated this match as a family-level hit. Vt039's Histone H3 matched *Laevistrombus turturella* (MH106430.1) in 2023, and *Dolomena turturella* (MH106428.1) in 2025. For similar reasons mentioned above, these hits were considered family-level concordant.

The COI and 12S-rRNA sequences of Vt020, identified morphologically as *haustellum*, matched its conspecific sequences (GU575380.1 and FN651860.1, respectively) in our 2023 and 2025 searches. However, its 18S-rRNA and Histone H3 matched *Chicoreus asianus* (HQ834013.1 and HQ834147.1, respectively). Both names are currently accepted but belong to different genera: *Haustellum* and *Chicoreus*. Although both genera have historically been classified under *Murex*, since the presently accepted genera are not the same, the matches were not considered genus- and species-level concordant.

A separate issue involved *Ficus variegata*, which exists under both zoological and botanical nomenclature. The gastropod *Ficus variegata* Röding, 1798 (Ficidae) and a tropical fig tree species *Ficus variegata* Blume, 1825 (Moraceae) are both valid under their respective codes. This can cause ambiguity in cross-kingdom database searches.

These cases show that unstable taxonomy can interfere with the interpretation of molecular identification results. Moreover, the fact that in many cases, both 2023 and 2025 BLASTn searches still hit the same unaccepted names or synonyms indicates that GenBank data probably have not caught up with taxonomic name revisions. For field workers involved in seafood traceability, unresolved name mismatches can lead to incorrect species labeling, which in turn might compromise traceability and eventually food safety.

4.4. Mitigating challenges in biodiversity monitoring for traceability and safety of marine gastropods as a food source

We understand that, as with many survey-based studies, our present study is not without limitations. For example, it is possible that different species were caught and sold during months when sampling was not conducted. Additionally, since only a few individuals were collected for each species from the market, we may have overlooked some cryptic species. The random selection of 126 individuals from the UMUT collection could have further limited our ability to capture the full extent of the biodiversity of consumed gastropods in Vietnam. Furthermore, the lack of reference data for gastropods registered in GenBank (Table 3) is an obvious concern that highlights the dangers of relying solely on BLASTn searches for species identification (Bagheri et al., 2020).

In this study, several sequences for which species data were unavailable had hits with confamilial or congeneric sequences. For example, although Vt137 was morphologically identified as *Turbo brunneus*, BLAST searches performed on sequences obtained from the individual hit *Gastropoda sp.* for COI (KJ168057.1), *T. kenwilliamsi* for 12S-rRNA (FR695555.1), *T. chinensis* for 18S-rRNA (KX267149.1), *T. chrysostomus* for 28S-rRNA (AM403989.1), and *T. setosus* for histone H3 (AY923981.1), with very low e-values and high percentages of

identity (Supplementary Table S4; Supplementary Table S5). This suggests that no reference sequence for any of the markers was available for this species, leading to sequences of congeners yielding hits in BLAST searches. Moreover, our BLAST searches sometimes matched registered sequences with no taxonomic information. For example, both COI sequences of Vt137 and Vt138 matched "Gastropoda sp." (KJ168057.1) as the first hit and "Turbo sp." (MN388988.1) as the second. The first "sp." is likely to originate from monitoring studies where no organismic samples were collected, such as eDNA or DNA barcoding studies based only on partial tissue samples, or from morphologically unidentifiable sources, while the second one probably came from an organismic specimen that was collected but unidentifiable.

To complicate matters, a hit in a BLAST search might not always provide a reliable identification since the taxonomic information associated with a sequence in the database may not be correct (Hofstetter et al., 2019; Crocetta et al., 2015; Bagheri et al., 2020). This possibility was also suggested by our phylogenetic trees (Figs. 3 and 5), which indicated that some of the registered sequences on GenBank (Supplementary Table S10) might derive from improperly identified samples, causing spurious phylogenetic placements. This might affect species identification by introducing misleading topologies or incorrect reference points, especially when relying solely on BLASTn-based taxonomic assignments. Such limitation affected our ability to confidently identify some species, highlighting the urgent need to improve reference databases of gastropods to support biodiversity monitoring and food safety efforts.

The lack of systematic lists of consumed gastropods, especially those sold freely in Vietnamese markets, could lead to undesirable consequences, such as food safety concerns stemming from a lack of proper traceability and misidentification of products. For example, although there have been no reports of zoonotic diseases caused by marine gastropod parasites in humans, hosted parasites could still adversely affect other mollusks, including fisheries species (e.g., Kristmundsson and Freeman, 2018). Certain gastropod species act as intermediate hosts for dangerous parasites (Lu et al., 2018). In addition, marine gastropods could act as intermediate hosts in the life cycles of fish parasites causing human diseases (Lu et al., 2018; Nguyen et al., 2013; Marcogliese, 2007; Pérez-del-Olmo et al., 2011). Only a handful of gastropod species are known as suspension feeders, including mucous, ciliate, and filter feeders (Declerck, 1995). This feeding behavior might lead to the accumulation of harmful chemicals, such as heavy metals and toxic substances, accidentally taken in from the surrounding environment (Nguyen et al., 2014). Marine gastropods can also host an array of dangerous microbes that might directly affect human health (Errani et al., 2022) or contain toxins harmful to humans when consumed (Jen et al., 2014; Dao et al., 2020; Biessy et al., 2019). Seafood poisoning has also been reported in Vietnam, further underscoring the need for improved safety measures in gastropod consumption (FAO, 2012; Ha and Sato, 2010).

Nevertheless, despite these limitations, our study demonstrates the value of a multi-marker museomics approach for addressing the challenges in species identification and biodiversity monitoring. By integrating molecular data with voucherized museum specimens, this study has contributed to the creation of a robust reference database that bridges critical gaps in existing resources for edible marine gastropods in Southeast Asia, a region rich in biodiversity and cultural food practices yet remains underexplored.

4.5. Cultural and traditional food, resilience, and sustainable development through marine gastropod consumption

As global demand for animal protein rises, sustainable food systems with minimal environmental impacts are increasingly critical (Herrero et al., 2020). The growing global interest in edible insects, such as crickets and mealworms, demonstrates how unconventional protein sources can transition into mainstream food systems (van Huis, 2013;

European Commission, 2023a; 2023b; if3-Moonshot, 2021; all accessed in December 2024). These species are recognized for their high nutritional value, low environmental impact, and versatility in food products (Oonincx and Boer, 2012; Smetana et al., 2015; Huis et al., 2013). Policies, education initiatives, and innovative processing techniques have also helped address challenges such as consumer acceptance, safety, and traceability (Roccatello et al., 2024). Marine gastropods, rich in protein, omega-3 fatty acids, and essential micronutrients, share similar advantages and offer a promising alternative protein source (Felici et al., 2020; Chakraborty and Joy, 2020). These animals have a smaller environmental footprint compared to livestock, requiring less water and land while emitting significantly lower greenhouse gases (Khan and Liu, 2019; Pissia et al., 2021; Gupta and Khanal, 2024). However, like edible insects, marine gastropods face challenges related to consumer acceptance, safety, traceability, and scalability. By applying lessons from the successful development of edible insects to address these challenges, marine gastropods can be developed to contribute to sustainable food systems that meet growing global protein demands while minimizing environmental impact.

Marine gastropods have historically been vital in the diets of many coastal communities. Coastal cultures across North America, such as the Coast Salish, Nootka, Micmac, and Wampanoag, have traditionally consumed various marine gastropods such as *Calyptaea fastigiata* (Pacific Chinese hat snails), *Polinices lewisi* (moon snails), and *Crepidula fornicate* (Atlantic slippersnails) as delicacies. In Indonesia, coastal communities have traditionally consumed marine gastropods (Isroni et al., 2023; Merly et al., 2022; Prasetyawan et al., 2023; Sujarta et al., 2022), including the culturally significant “*siput gonggong*” (“dog snails”; possibly *Multiple species of Laevistrombus* and *Strombus*) consumed in Malay communities in Riau and Sumatra (Muzahar et al., 2018; Viruly et al., 2019). In Mediterranean regions, marine gastropods are also used as ingredients in culinary traditions (Pérez-Lloréns et al., 2021). In Japan, archaeological evidence from shell middens provides insights into the historical significance of marine gastropods (Setiamarga et al., 2025). Species such as *Lunella coreensis* (“*sugai*”), traditionally prepared with vinegar, were commonly consumed, alongside *Japeuthria ferrea* (“*isonina*”), *Tegula rustica* (“*gangara*”), and *Cellana* spp. (“*kasagai*” or “*matsubagai*”). These gastropods used to be an integral part of diets in ancient coastal communities across Japan, but their consumption has declined significantly due to urbanization and changing dietary preferences. Today, species like these, collectively referred to as “isomon” (meaning “intertidal critters” in the Wakayama dialect), are largely consumed in specific rural coastal areas and regarded as less desirable. Conversely, commercially farmed species such as *Haliotis* (abalone; “*awabi*”) and *Turbo* (turban shell; “*sazae*”) dominate modern markets due to their controlled production systems, which ensure consistent supply while reducing pressure on wild populations.

Expanding aquaculture to include a broader range of marine gastropod species is critical for balancing biodiversity conservation with economic viability (Fraga-Corral et al., 2022; Leiva and Castilla, 2002). While species like *Haliotis* (abalone) (Campbell, 2000; Cook, 2016; 2023) and *Turbo* (turban shell) (Hayakawa et al., 2008; Yamauchi, 1991) are successfully farmed, aquaculture must diversify to include additional species to reduce reliance on wild populations and broaden market offerings (Cai et al., 2023; Froehlich et al., 2023), and thus enhancing aquaculture’s resilience against climate change, disease outbreaks, and market fluctuations, thereby supporting the sector’s long-term sustainability (Balmer, 2024; Hanson, 2020). Ideal candidates for aquaculture should exhibit resilience to environmental changes, fast growth rates, high reproductive potential, and adaptability to controlled environments with minimal ecological impact (Torrella, 2024).

However, in many coastal regions, including Vietnam, wild capture remains a key component of seafood protein supply, including gastropods, making its responsible management a critical issue (Mora et al., 2009). Effective fisheries management remains essential to prevent overexploitation of wild populations, requiring measures such as catch

limits, seasonal closures, and habitat protection (Clayton and Galland, 2024). Preserving critical habitats, including mangroves and coral reefs that support gastropod reproduction and survival, is equally important (Jones, 2024; McSherry et al., 2023). A combined approach integrating sustainable aquaculture with carefully managed wild capture provides a balanced pathway to meet global protein needs while safeguarding marine ecosystems (Ahmed et al., 2019; Diana, 2009; Mossler, 2021; Ogollo et al., 2024).

4.6. Policy and technological frameworks toward a sustainable integration of marine gastropods as novel food

To fully realize the potential of marine gastropods as sustainable food sources, robust technological frameworks are essential. These frameworks must address challenges in regions like Vietnam and Southeast Asia, where gastropods are culturally significant but under-regulated. Enhancing traceability mechanisms is key, with technologies like DNA barcoding (Hebert et al., 2003b; Nakazato and Jinbo, 2022), museomics (Lalueza-Fox, 2022), and environmental DNA (eDNA) (Murakami et al., 2019; Suzuki et al., 2024; Thomsen and Willerslev, 2015) playing critical roles in accurate species identification, taxonomic validation, and non-invasive, real-time monitoring of gastropod populations and habitats. These tools, combined with curated museum specimens (Nakahama, 2021; Nakazato and Jinbo, 2022; Raxworthy and Smith, 2021), can establish comprehensive reference systems and databases that underpin sustainable resource management. Integrating big-data repositories for data-driven systems into these frameworks would enable advanced analytics, such as predictive modeling of population dynamics, habitat suitability, and environmental impacts, which is critical for transparency, traceability, and informed decision-making (Bradley et al., 2019; Diaz, 2020; Dietze, 2017; Grémillet et al., 2022; Kearney and Porter, 2009; Kelly et al., 2022; Pandey, 2024; United Nations, 2024; Zhao et al., 2024). These systems can process large datasets from molecular, ecological, and morphological sources to identify patterns and guide strategic decisions for sustainable fisheries and aquaculture management. Public health regulations must also mitigate risks such as parasite transmission (Lu et al., 2018), toxin bioaccumulation (Nguyen et al., 2014; Errani et al., 2022), and food-borne illnesses (Dao et al., 2020; Biessy et al., 2019). Community-driven monitoring programs (e.g., House et al., 2023; Kauer et al., 2024; Secretariat of the Pacific Community, 2010), supported by advanced tools such as eDNA, machine learning/AI-based recognition tools (e.g., Hasegawa et al., 2024; Kim et al., 2024; Yoshida et al., 2024; Welch et al., 2024) and blockchain technology (Alwi et al., 2024; Ellahi et al., 2023), can empower local stakeholders to actively contribute to conservation and sustainable management.

In conjunction with the adoption of advanced molecular and analytical tools for traceability, policies must prioritize the development of integrated databases that link molecular, ecological, and morphological data from museum collections and field samples (Nakazato and Jinbo, 2022; Lalueza-Fox, 2022). These databases should adhere to international standards, ensuring that data collection, dataset building, curation, analysis, and publication activities fully comply with the Nagoya Protocol on Access and Benefit-Sharing (ABS) while fostering ethical data sharing through standardized Material Transfer Agreements (MTAs) (ABS Information Forum, 2016; CETAf, 2014; Convention on Biological Diversity, 2024; Secretariat of the Convention on Biological Diversity, 2011; WHO, 2024; Le, 2024). Regional collaboration through platforms like the ASEAN Working Group on Coastal and Marine Environment (AWGCME) (ASEAN, 2017) could harmonize data management, research protocols, and trade standards, promoting joint conservation and aquaculture initiatives.

It is to be noted that through this study, we do not intend to promote increased harvesting of wild marine gastropods without appropriate management. On the contrary, we believe our data presented here can aid in identifying which species are currently being consumed and

inform future strategies for traceability and monitoring to support sustainable food systems through improved management of both local capture fisheries and aquaculture development. Such systems align with the Sustainable Development Goals (SDGs), supporting efforts to achieve sustainable production and consumption (Ritchie et al., 2017; Fry et al., 2018; van Huis, 2013), biodiversity conservation (Golden et al., 2021; Poore and Nemecek, 2018; Gephart et al., 2021; Melnychuk et al., 2021; Nuñez, 2021; Hunter et al., 2019), and climate resilience (Hertel et al., 2023; Future of Fish, 2020; Gleadall et al., 2024).

Language editing during manuscript writing

During manuscript preparation, AI tools (ChatGPT and QuillBot) were used, but only to assist minor linguistic edits, such as grammar, syntax, and stylistic adjustments and not for content creation. Before using these tools, the manuscript was entirely prepared and written by the authors, mainly the first author, and further edited by all co-authors. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication. In addition, we also had the English of our much earlier manuscript proofread and edited by a professional scientific English editing service (Springer Nature Research Editing Service).

Ethics declarations

The target animals of this research are not vertebrates or higher invertebrates. We also followed the guidelines for animal experiments of The University of Tokyo.

Ethical declaration - studies in humans and animals

This study did not involve any human participants. All animal specimens were sourced from market vendors and subsequently cataloged at the University Museum of the University of Tokyo. In the preparation of these specimens, the researchers meticulously adhered to the established protocols and ethical guidelines governing the use of lower invertebrate animals in experimental research.

CRediT authorship contribution statement

Davin H.E. Setiamarga: Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Moe Shimizu:** Writing – review & editing, Visualization, Validation, Methodology, Formal analysis, Data curation. **Satoko Nakashima:** Methodology, Formal analysis, Data curation. **Chihiro Osaki:** Formal analysis, Methodology. **Kazuki Hirata:** Writing – review & editing, Validation, Data curation. **Lukytwati Anggraeni:** Writing – review & editing, Methodology, Investigation. **Do Van Tu:** Writing – review & editing, Validation, Resources, Methodology, Investigation, Conceptualization. **Takenori Sasaki:** Writing – review & editing, Supervision, Resources, Project administration, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Nagisa Nakaji and Masaki Yamamoto (Natl. Inst. Tech. (KOSEN), Wakayama College (NITW) and The University of Tokyo) for assistance with research and sampling and for providing invaluable

technical advice. DHES and MS also thank Dr. Makoto Nishimoto (NITW) for her support as the co-assessor of MS graduation thesis from NITW. This research was partially supported by the National Institute of Technology (KOSEN), Wakayama College Competitive Internal Research Grant for Education and Research no. B-2017, Nakatsuji Foresight Foundation Research Grant 2019, Grants-in-aid for Scientific Research C no. 19K12424, The Sasakawa Peace Foundation: Oceanshot (all awarded to DHES), and Grants-in-aid for Exploratory Research no. 19K21646 (awarded to TS and DHES). DHES and KH were also partially supported by KOSEN GEAR 5.0 of the National Institute of Technology (KOSEN): Agriculture and Fisheries Project.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.fufo.2025.100689.

Data availability

All animal specimens are vouchered at The University Museum of The University of Tokyo. Sequence data were registered in GenBank (accession numbers are provided in Supp. Table 1). Genetic distance data of all samples are also provided in the Supplementary Material.

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